United States
Department
of Agriculture

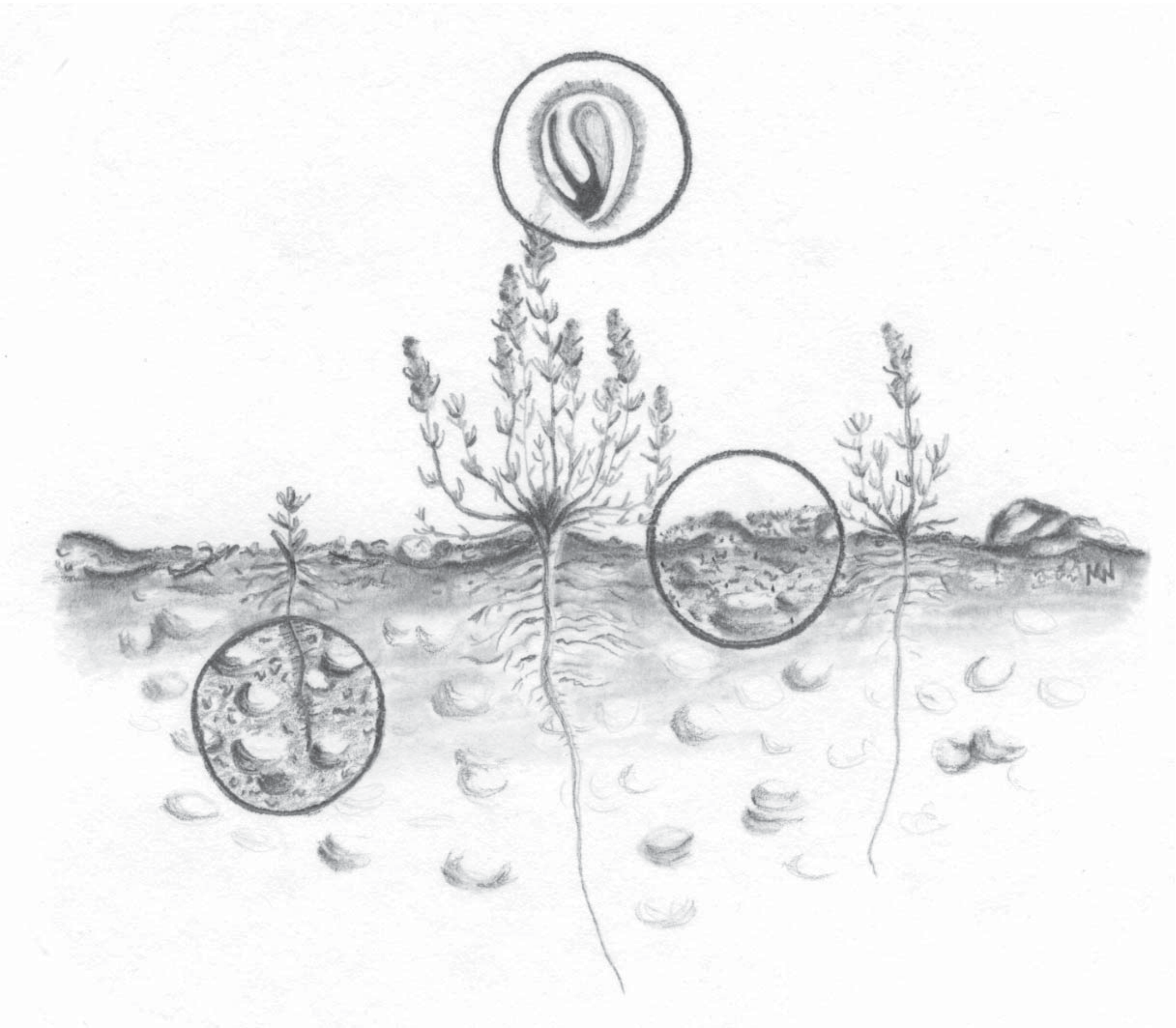
Forest Service

Rocky Mountain
Research Station

Proceedings
RMRS-P-31

February 2004

Seed and Soil Dynamics in Shrubland Ecosystems: Proceedings



Abstract

Hild, Ann L.; Shaw, Nancy L.; Meyer, Susan E.; Booth, D. Terrance; McArthur, E. Durant, comps. 2004. **Seed and soil dynamics in shrubland ecosystems: proceedings**; 2002 August 12–16; Laramie, WY. Proc. RMRS-P-31. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 216 p.

The 38 papers in this proceedings are divided into six sections; the first includes an overview paper and documentation of the first Shrub Research Consortium Distinguished Service Award. The next four sections cluster papers on restoration and revegetation, soil and microsite requirements, germination and establishment of desired species, and community ecology of shrubland systems. The final section contains descriptions of the field trips to the High Plains Grassland Research Station and to the Snowy Range and Medicine Bow Peak. The proceedings unites many papers on germination of native seed with vegetation ecology, soil physio-chemical properties, and soil biology to create a volume describing the interactions of seeds and soils in arid and semiarid shrubland ecosystems.

Keywords: wildland shrubs, seed, soil, restoration, rehabilitation, seed bank, seed germination, biological soil crusts

Acknowledgments

The symposium, field trips, and subsequent publication of this volume were made possible through the hard work of many people. We wish to thank everyone who took a part in ensuring the success of the meetings, trade show, and paper submissions. We thank the University of Wyoming Office of Academic Affairs, the Graduate School, and its Dean, Dr. Steve Williams, for their assistance. We recognize the Student Union Staff and the University of Wyoming Conferences and Institute Staff for logistic support. Especially helpful in coordinating the meetings were Kimm Malody, Kelli Belden, and Cindy Wood. Jennifer Muscha (Boyle), Leah Burgess, Courtney Ladenburger, Brian Mealor, and Sonja Parson of the Department of Renewable Resources provided excellent help during the sessions. We also thank all of the trade show contributors, especially Truax, Inc., for their generous support. Technical sessions were chaired by D. Terrance Booth, Leah Burgess, Kathleen Dwire, C. Lynn Kinter, Susan Meyer, Brian Mealor, Steve Monsen, Jean D. Reeder, Bruce Roundy, and Steve Williams. Mary I. Williams provided original artwork for the cover. We thank the Rocky Mountain Research Station Publishing Services and Louise Kingsbury for preparing the final publication.

Ann L. Hild
Nancy L. Shaw
Susan E. Meyer
D. Terrance Booth
E. Durant McArthur
Compilers

Publisher's note: Papers in this report were reviewed by the compilers. Rocky Mountain Research Station Publishing Services reviewed papers for format and style. Authors are responsible for content.

Illustration on the cover is by Mary I. Williams. 2002. Drawing of winterfat. Used with permission.

Seed and Soil Dynamics in Shrubland Ecosystems: Proceedings

Laramie, WY, August 12–16, 2002

Compilers

Ann L. Hild, Department of Renewable Resources, University of Wyoming, Laramie, WY.
Nancy L. Shaw, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Boise, ID.
Susan E. Meyer, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Shrub Sciences Laboratory, Provo, UT.
D. Terrance Booth, U.S. Department of Agriculture, Agricultural Research Service, High Plains Grassland Research Station, Cheyenne, WY.
E. Durant McArthur, Project Leader, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Shrub Sciences Laboratory, Provo, UT.

Shrub Research Consortium

USDA Forest Service, Rocky Mountain Research Station, Shrub Sciences Laboratory*, Provo, Utah, E. Durant McArthur (chair)
Brigham Young University*, Provo, Utah, Daniel J. Fairbanks
USDA Agricultural Research Service, Renewable Resource Center*, Reno, Nevada, James A. Young
Utah State University*, Logan, Eugene W. Schupp
State of Utah, Department of Natural Resources, Division of Wildlife Resources*, Ephraim, Scott C. Walker
University of California, Los Angeles, Philip W. Rundel
Colorado State University, Fort Collins, William K. Lauenroth
University of Idaho, Moscow, Steven J. Brunsfeld
University of Montana, Missoula, Donald J. Bedunah
Montana State University, Bozeman, Carl L. Wambolt
University of Nevada, Reno, Paul T. Tueller
University of Nevada, Las Vegas, Stanley D. Smith
Oregon State University, Corvallis, Lee E. Eddleman
New Mexico State University, Las Cruces, Kelly W. Allred
Texas A & M System, Texas Agricultural Experiment Station, San Angelo, Darrell N. Ueckert
Texas Tech University, Lubbock, Ronald E. Sosebee
USDA Agricultural Research Service, High Plains Grassland Research Station, Cheyenne, Wyoming, D. Terrance Booth
USDA Agricultural Research Service, Jornada Experimental Range, Las Cruces, New Mexico, Jerry R. Barrow
USDA Forest Service, Rocky Mountain Research Station, Great Basin Ecology Laboratory, Reno, Nevada, Robin J. Tausch
Universtiy of Utah, Salt Lake City, James R. Ehleringer
Weber State University, Ogden, Utah, Barbara A. Wachocki
Battelle Pacific Northwest Laboratories, Richland, Washington, Janelle L. Downs
Bechtel Nevada, Las Vegas, W. Kent Ostler
University of Wyoming, Laramie, Ann L. Hild

---

*Charter members

The Shrub Research Consortium (SRC) was formed in 1983 with five charter members (see list). Over time SRC has grown to its present size of 25 institutional members. The SRC had three principal objectives in its charter: (1) developing plant materials for shrubland rehabilitation; (2) developing methods of establishing, renewing, and managing shrublands in natural settings; and (3) assisting with publication and dissemination of research results. These objectives have been met by a series of symposia sponsored by the Consortium and partners. This publication is the 12th in the series; the previous 11 are listed on the next page. The U.S. Department of Agriculture, Forest Service, Intermountain Research Station and Rocky Mountain Research Station have published proceedings of all symposia to date. The executive committee has plans for another symposium in 2004 in Lubbock, Texas, with the theme of Shrublands Under Fire. Each symposium has had a theme, but the executive committee has encouraged attendance and participation by shrubland ecosystem biologists and managers with wider interests than any particular symposium theme—the heart of the Consortium’s programs are wildland shrub ecosystem biology, research, and management.

Availability of Previous Wildland Shrub Symposia Proceedings

First: Tiedemann, A. R.; Johnson, K. L., compilers. 1983. Proceedings—research and management of bitterbrush and cliffrose in Western North America; 1982 April 13–15; Salt Lake City, UT. General Technical Report INT-152. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 279 p. Out of print—available from National Technical Information Service as document PB83-261537 A13.

Second: Tiedemann, A. R.; McArthur, E. D.; Stutz, H. C.; Stevens, R.; Johnson, K. L., compilers. 1984. Proceedings— symposium on the biology of *Atriplex* and related chenopods; 1983 May 2–6; Provo, UT. General Technical Report INT-172. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 309 p. Out of print—available from National Technical Information Service as document PB85-116358 A14.

Third: McArthur, E. D.; Welch, B. L., compilers. 1986. Proceedings—symposium on the biology and management of *Artemisia* and *Chrysothamnus*; 1984 July 9–13; Provo, UT. General Technical Report INT-200. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 398 p. Out of print—available from National Technical Information Service as document PB86-182318 A18.

Fourth: Provenza, F. D.; Flinders, J. T.; McArthur, E. D., compilers. 1987. Proceedings—symposium on plant herbivore interactions; 1985 August 7–9; Snowbird, UT. General Technical Report INT-222. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 179 p. A few copies are available from the Rocky Mountain Research Station; otherwise available from National Technical Information Service as document PB 90-228578 A09.

Fifth: Wallace, A.; McArthur, E. D.; Haferkamp, M. R., compilers. 1989. Proceedings—symposium on shrub ecophysiology and biotechnology; 1987 June 30–July 2; Logan, UT. General Technical Report INT-256. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 183 p. Out of print—available from National Technical Information Service as document PB89-156442 A09

Sixth: McArthur, E. D.; Romney, E. M.; Smith, S. D.; Tueller, P. T., compilers. 1990. Proceedings—symposium on cheatgrass invasion, shrub die-off, and other aspects of shrub biology and management; 1989 April 5–7; Las Vegas, NV. General Technical Report INT-276. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 351 p. Out of print—available from National Technical Information Service as document PB91-117275 A16.

Seventh: Clary, W. P.; McArthur, E. D.; Bedunah, D.; Wambolt, C. L., compilers. 1992. Proceedings—symposium on ecology and management of riparian shrub communities; 1991 May 29–31; Sun Valley, ID. General Technical Report INT-289. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 232 p. Out of print—available from National Technical Information Service as document PB92-227784 A11.

Eighth: Roundy, B. A.; McArthur, E. D.; Haley, J. S.; Mann, D. K., compilers. 1995. Proceedings: wildland shrub and arid land restoration symposium; 1993 October 19–21; Las Vegas, NV. General Technical Report INT-GTR-315. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 384 p. Available from Rocky Mountain Research Station.

Ninth: Barrow, J. R.; McArthur, E. D.; Sosebee, R. E.; Tausch, R. J., compilers. 1996. Proceedings: shrubland ecosystem dynamics in a changing environment; 1995 May 23–25; Las Cruces, NM. General Technical Report INT-GTR-338. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 275 p. A few copies are available from the Rocky Mountain Research Station; otherwise available from National Technical Information Service as document PB 96-178637 A09.

Tenth: McArthur, E. D.; Ostler, W. K.; Wambolt, C. L. compilers. 1999. Proceedings: shrubland ecosystem ecotones; 1998 August 12–14; Ephraim, UT. Proceedings RMRS-P-11. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 299 p. Available from Rocky Mountain Research Station.

Eleventh: McArthur, E. D.; Fairbanks, D. J., compilers. 2001. Shrubland ecosystem genetics and biodiversity: proceedings; 2000 June 13–15; Provo, UT. Proc. RMRS-P-21. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 365 p. Available from Rocky Mountain Research Station.

Contents

		Page
Introduction and Overview		1
Nancy L. Shaw Ann L. Hild	Seed and Soil Dynamics in Shrubland Ecosystems: Introduction	3
Ann L. Hild Nancy L. Shaw	Shrub Research Consortium: Distinguished Service Award Honoring E. Durant McArthur	4
Restoration and Revegetation		7
Edith B. Allen	Restoration of *Artemisia* Shrublands Invaded by Exotic Annual *Bromus*: A Comparison Between Southern California and the Intermountain Region	9
C. Lynn Kinter Richard N. Mack	Comparing Phenotype and Fitness of Native, Naturalized, and Invasive Populations of Downy Brome (Cheatgrass, *Bromus tectorum*)	18
Mary I. Williams Mohammed Tahboub John T. Harrington David R. Dreesen April Ulery	Root Growth of Apache Plume and Serviceberry on Molybdenum Mine Overburden in Northern New Mexico	24
Kathleen J. Miglia D. Carl Freeman E. Durant McArthur Bruce N. Smith	Importance of Genotype, Soil Type, and Location on the Performance of Parental and Hybrid Big Sagebrush Reciprocal Transplants in the Gardens of Salt Creek Canyon	30
Robert R. Blank James A. Young	Revegetation of Saline Playa Margins	37
Laurel E. Vicklund Gerald E. Schuman Ann L. Hild	Influence of Sagebrush and Grass Seeding Rates on Sagebrush Density and Plant Size	40
Soil Components and Microsites		45
Thomas A. Monaco Jay B. Norton Douglas A. Johnson Thomas A. Jones Jeanette M. Norton	Soil Nitrogen Controls on Grass Seedling Tiller Recruitment	47
Robert R. Blank	Enzyme Activity in Temperate Desert Soils: Influence of Microsite, Depth, and Grazing	51
Jerry R. Barrow	Unique Characteristics of a Systemic Fungal Endophyte of Native Grasses in Arid Southwestern Rangelands	54
Jay B. Norton Thomas A. Monaco Jeanette M. Norton Douglas A. Johnson Thomas A. Jones	Cheatgrass Invasion Alters Soil Morphology and Organic Matter Dynamics in Big Sagebrush-Steppe Rangelands	57
R. L. Pendleton B. K. Pendleton G. L. Howard S. D. Warren	Response of Lewis Flax Seedlings to Inoculation With Arbuscular Mycorrhizal Fungi and Cyanobacteria	64

J. D. Reeder D. W. Grant G. G. Jezile R. D. Child	Heterogeneity in Soil C and N in Late- and Mid-seral Sagebrush-Grass Rangeland	69
Roger Rosentreter David J. Eldridge	Monitoring Rangeland Health: Using a Biological Soil Crust Stability Index	74
David J. Eldridge Roger Rosentreter	Shrub Mounds Enhance Water Flow in a Shrub-Steppe Community in Southwestern Idaho, U.S.A.	77
Stephen E. Williams Joe D. Johnson Larry C. Munn Terry Nieder	Edaphic Characteristics of Nitrogen Fixing Nodulation (*Actinorhizae*) by *Cercocarpus montanus* Raf. and *Purshia tridentata* (Pursh) DC.	84
Germination and Seedling Establishment		93
D. T. Booth Y. Bai E. E. Roos	Cultural Methods for Enhancing Wyoming Big Sagebrush Seed Production	95
Ann DeBolt Carol S. Spurrier	Seeds of Success and the Millennium Seed Bank Project	100
Susan C. Garvin Susan E. Meyer David L. Nelson	Recruitment Failure of Chenopod Shrub Populations in the Great Basin	109
M. R. Haferkamp M. D. MacNeil	Annual Brome Seed Germination in the Northern Great Plains: An Update	115
Robert Hammon Gary Noller	Fate of Fall-Sown Bitterbrush Seed at Maybell, Colorado	120
Susan E. Meyer Stephanie L. Carlson	Comparative Seed Germination Biology and Seed Propagation of Eight Intermountain Species of Indian Paintbrush	125
R. L. Pendleton B. K. Pendleton G. L. Howard S. D. Warren	Effects of Biological Soil Crusts on Seedling Growth and Mineral Content of Four Semiarid Herbaceous Plant Species	131
Michael P. Schellenberg	Seeding Time and Method for Winterfat in the Semiarid Region of the Canadian Prairies	134
L. St. John P. Blaker	New Native Plant Releases from the USDA-NRCS, Aberdeen, ID, Plant Materials Center	138
Jeffrey R. Taylor Bruce A. Roundy Phil S. Allen Susan E. Meyer	Predicting Seedling Emergence Using Soil Moisture and Temperature Sensors	140
Community Ecology		147
Donald J. Bedunah Kristi D. Pflug Thad E. Jones	Antelope Bitterbrush Flowering, Survival, and Regeneration Following Ponderosa Pine Forest Restoration Treatments	149
Justin D. Derner Charles R. Tischler H. Wayne Polley Hyrum B. Johnson	Effects of Elevated CO_2 on Growth Responses of Honey Mesquite Seedlings From Sites Along a Precipitation Gradient	156

Charles R. Tischler Justin D. Derner H. Wayne Polley Hyrum B. Johnson	Responses of Seedlings of Five Woody Species to Carbon Dioxide Enrichment	161
Simon A. Lei	Soil Moisture Attributes of Three Inland Sand Dunes in the Mojave Desert	164
Simon A. Lei	Leaf Temperatures of Blackbrush: Relationships With Air and Soil Surface Temperatures	170
Jennifer M. Muscha Ann L. Hild Larry C. Munn Pete D. Stahl	Impacts of Livestock Exclusion From Wyoming Big Sagebrush Communities	176
W. A. Laycock D. L. Bartos K. D. Klement	Species Richness Inside and Outside Long-Term Exclosures	183
J. Kent McAdoo Sherman R. Swanson Brad W. Schultz Peter F. Brussard	Vegetation Management for Sagebrush-Associated Wildlife Species	189
Carl L. Wambolt Trista Hoffman	Browsing Effects on Wyoming Big Sagebrush Plants and Communities	194
Kristene A. Partlow Richard A. Olson Gerald E. Schuman Scott E. Belden	Effects of Wildlife Utilization and Grass Seeding Rates on Big Sagebrush Growth and Survival on Reclaimed Mined Lands	198
Field Trips		207
D. T. Booth J. D. Derner	Research at the High Plains Grassland Research Station	209
Larry Munn C. Lynn Kinter	Soils and Vegetation of the Snowy Range, Southeastern Wyoming Wildland Shrub Symposium Field Trip: Laramie to Woods Landing, Riverside, Libby Flats, and Centennial, Wednesday, August 14, 2002	212

SHRUB RESEARCH CONSORTIUM

Introduction and Overview

Restoration and Revegetation

Soil Components and Microsites

Germination and Seedling Establishment

Community Ecology

Field Trips

SHRUB RESEARCH CONSORTIUM

Introduction and Overview

Illustration on the reverse side is by Eva Teseo and Meggan Laxalt. In: Engwistle, P. G.; DeBolt, A. M.; Kaltenecker, J. H.; Steenhof, K., comps. 2000. Proceedings: sagebrush steppe ecosystems symposium. Pub. BLM/ID/PT-001001+1150. Boise, ID: U.S. Department of the Interior, Bureau of Land Management. 145 p.

Seed and Soil Dynamics in Shrubland Ecosystems: Introduction

Nancy L. Shaw
Ann L. Hild

This proceedings is the twelfth in a series on the biology and management of wildland shrub ecosystems, sponsored by the Shrub Research Consortium and published by the Rocky Mountain Research Station. Other cosponsors of the symposium on Seed and Soil Dynamics in Shrubland Ecosystems included the University of Wyoming Department of Renewable Resources and the USDA-ARS High Plains Grassland Research Station.

The twelfth wildland shrub symposium united above- and below-ground research on shrublands to more clearly delineate the dynamic nature of shrubland ecosystems. The keynote address (Allen, this proceedings) characterized differences in exotic brome invasions and impacts depending on geographic locations and poses some interesting questions relative to the common trends of invasion of annual grasses. The meeting also provided the venue for presentation of the first Shrub Research Consortium Distinguished Service Award to Dr. E. Durant McArthur, Project Leader, Shrub Sciences Laboratory, USDA Forest Service, in Provo, UT (Hild and Shaw, this proceedings).

Our symposium intended to unite plant ecology academics, managers, and soil scientists into a dialogue to consider below-ground dynamics and their ties to shrubland ecosystem restoration and management. The 38 papers in this volume report research on below-ground biology, seedbanks, biological soil crusts, microsite and soil surface ecology, invasive species competition, restoration and revegetation in sagebrush steppe, blackbrush, salt desert shrub, annual grasslands, Chihuahuan and Sonoran Desert shrublands, and mountain shrub communities. Field trips included travel from Laramie west through the Snowy Mountains near Riverside and Encampment to examine vegetative ecology, soils, and geomorphology of the Snowy Range. Travel to the east from Laramie included the USDA-Agricultural Research Service High Plains Grassland Research Station in Cheyenne, WY, where participants examined long-term research on grazing and carbon sequestration. The poster session included 42 academic poster presentations and numerous trade exhibitors.

The thirteenth Wildland Shrub Symposium will be held in Lubbock, TX, in summer 2004, and will consider the theme "Shrublands Under Fire." Previous symposia cover a wide variety of topics relevant to shrubland ecosystems (see front pages of this proceedings for their availability).

In: Hild, Ann L.; Shaw, Nancy L.; Meyer, Susan E.; Booth, D. Terrance; McArthur, E. Durant, comps. 2004. Seed and soil dynamics in shrubland ecosystems: proceedings; 2002 August 12–16; Laramie, WY. Proceedings RMRS-P-31. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Nancy L. Shaw is a Research Botanist, USDA Forest Service, Rocky Mountain Research Station, Boise, ID 83702, U.S.A. Ann L. Hild is an Associate Professor, Department of Renewable Resources, Box 3354, University of Wyoming, Laramie, WY 82071, U.S.A.; e-mail: annhild@uwyo.edu.

Shrub Research Consortium: Distinguished Service Award Honoring E. Durant McArthur

Ann L. Hild
Nancy L. Shaw

In August 2002, at the Twelfth Wildland Shrub Symposium held in Laramie, WY, the Shrub Research Consortium presented its first Distinguished Service Award to Dr. E. Durant McArthur, Project Leader at the Shrub Sciences Laboratory in Provo, UT, for his phenomenal contributions to our understanding of shrubland ecology and biology. The award honors the long and productive career of this great shrubland scientist. We include this award paper in the proceedings to recognize some of the many contributions made by Durant over his more than 30 years of service with the USDA Forest Service as a Research Geneticist and Shrubland Ecologist.

Professional Background

Durant graduated from Dixie College in St. George, UT, with an A.S. degree in 1963. He received a B.S. degree in molecular and genetic biology (cum laude) in 1965, an M.S. degree in molecular and genetic biology with a minor in botany, and a Ph.D. degree in plant genetics in 1970 from the University of Utah. His doctoral work examined the cytogenic and evolutionary development of aneuploid-tetraploid *Mimulus glabratus* (*Scrophulariaceae*). In 1971 he completed post-doctoral research on the cytogentetics of domesticated and wild Brassicaceae at the University of Leeds, England.

In 1972 Durant began his career with the USDA Forest Service, Intermountain Forest and Range Experiment Station, as a Research Geneticist assigned to the Great Basin Experimental Range in Ephraim, UT. In 1975 he was assigned to the Shrub Sciences Laboratory in Provo, UT, where, since 1983, he has served as Project Leader of the Shrubland Biology and Restoration Research Work Unit of what is now the Rocky Mountain Research Station. Durant has also served as an Adjunct Faculty member with the Department of Botany and Range Science at Brigham Young University since 1976.

Formation of the Shrub Research Consortium

Dr. McArthur was instrumental in organizing the Shrub Research Consortium in 1983 and has served as Chair of the Consortium for the last 20 years. Under his guidance the Shrub Research Consortium has sponsored 12 symposia to date, providing a forum for shrubland researchers and managers from around the globe to present research, discuss management techniques, and ultimately advance our knowledge of shrubland ecosystems. Proceedings of these meetings have been and continue to be valuable references for shrubland ecologists and land managers, irrespective of their training or agency affiliation.

Professional Honors and Research Contributions

Durant's contributions have provided the foundation papers on genetic differentiation in Subgenus *Tridentatae* of *Artemisia* and numerous other shrub genera and species. His recent work on hybridization of subspecies of *Artemisia tridentata* amplifies our understanding of evolutionary change in shrub populations distributed across variable environmental gradients. His work involves the collaboration of scientists from around the globe. He has published more than 350 research papers including numerous journal articles and several book chapters. Durant has been a key compiler for the Wildland Shrub Symposia Proceedings (10 of 12 proceedings to date). His research expertise includes selection and breeding of shrubland species for rangeland rehabilitation, chromosome studies of *Artemisia* subgenus *Tridentatae*, adaptation, breeding system, and seed production of *Atriplex canescens*, habitat requirements of desert tortise, and genetic structure of wildland restoration plantings. He has been directly involved in development of cultivar and germplasm releases in cooperation with the USDA-NRCS Plant Materials Program, the Utah Division of Wildlife Resources, and State Agricultural Experiment Stations. Species he has assisted with include "Rincon" fourwing saltbush, "Immigrant" forage kochia, "Hobble Creek" mountain big sagebrush and "Timp" Utah sweetvetch. His enthusiasm and guidance have united innovative research in ecology with genetic variation within wildland populations to form practical applications that have improved shrubland restoration efforts throughout the Intermountain West.

In: Hild, Ann L.; Shaw, Nancy L.; Meyer, Susan E.; Booth, D. Terrance; McArthur, E. Durant, comps. 2004. Seed and soil dynamics in shrubland ecosystems: proceedings; 2002 August 12–16; Laramie, WY. Proceedings RMRS-P-31. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Ann L. Hild is an Associate Professor Department of Renewable Resources, Box 3354, University of Wyoming, Laramie, WY 82071, U.S.A.; e-mail: annhild@uwyo.edu. Nancy L. Shaw is a Research Botanist, USDA Forest Service, Rocky Mountain Research Station, Boise, ID 83702, U.S.A.

Durant has been honored with numerous awards over the years, including the USDA Forest Service Superior Scientist Award (1990) and Distinguished Scientist Award (1996), the USDA Forest Service Rocky Mountain Research Station Eminent Scientist Publication Award (2001), and the Society for Range Management Outstanding Achievement Award (1992). He has served as Chairman of the Shrub Research Consortium since 1983, President of the Utah Section of the Society for Range Management (1987), and President of the Intermountain Consortium for Arid Lands Research (1991 to present). In 2002, just prior to receiving the Shrub Research Consortium Award, Durant received the USDA Forest Service New Century of Service Award for the Rocky Mountain Research Station. We are pleased that the Shrub Research Consortium is led by such a nationally honored public servant and distinguished scientist.

Mentorship Legacy

Durant has been a guiding force and has served an inspirational role for many young scientists (fig. 1). His genuine encouragement of new scholars has been demonstrated repeatedly in meetings, on field excursions, and in his role on many M.S. and Ph.D. graduate committees. He is commonly involved in field trips for student groups (fig. 2) and visiting scientists (for which the authors are especially grateful). Durant has devoted endless hours to interagency cooperation and is always willing to consult with managers on specific shrubland management issues.

In his role as research leader, he has directed the work of a long series of talented scientists at the Shrub Sciences Laboratory. His model scientific abilities and genuine love for people has allowed Durant to serve as an inspirational and energetic leader of some of the premier shrubland researchers in the world.

Personal Accomplishments

Durant married Virginia in December 20, 1963, and became the proud father of two sons, Ted and Curt, and two daughters, Monica and Denise. He is now a proud grandfather of 11 grandchildren (thus far). He has remained active in many community groups and activities in Provo.

Conclusion

The Shrub Research Consortium is proud to have the association and leadership of such a well-respected leader and well-recognized scientific mind as that of Dr. E. Durant McArthur. It is with great pride that we presented Durant with the first Shrub Research Consortium Distinguished Service Award in gratitude for his tireless efforts in promoting the recognition and understanding of global shrubland ecosystems.

SHRUB RESEARCH CONSORTIUM

Distinguished Service Award

Presented to

E. DURANT MCARTHUR

For his sustained leadership of the Shrub Research Consortium, his exemplary research career, and his dedication to enhancing our understanding of the biology and management of shrublands in North America and around the globe.

University of Wyoming
Laramie, Wyoming
August 13, 2002

Figure 1—USDA Forest Service Intermountain Forest and Range Experiment Station personnel gathered at the Desert Range Experiment Station on the occassion of a range science retreat, June 8, 1983. Front row (left to right): Mike Stanley, Susan Koniak, Bruce Welch, Renee O'Brien, Ralph Holmgren, John Kinney. Row 2: Jeanne Chambers, Dale Bartos, Walt Mueggler, Warren Clary. Row 3: Bob Ferguson, Fred Wagstaff, Sherel Goodrich, Duane Lloyd. Row 4: Art Tiedemann, Durant McArthur, Keith Evans, Roy Harniss, Rich Everett.

Figure 2—An enthusiastic Durant sharing his research on the University of Wyoming shrubland ecology graduate class field trip to central Utah in May 2002.

Restoration and Revegetation

Aquilegia laramiensis

Illustration on the reverse side is by Isobel Nichols. In: Fertig, W.; Refsdal, C.; Whipple, J. 1994. Wyoming rare plant field guide. Cheyenne: Wyoming Rare Plant Technical Committee. Available at: http://www.npwrc.usgs.gov/resource/distr/others/wyplant/species.htm (Accessed 12/18/03).

Restoration of *Artemisia* Shrublands Invaded by Exotic Annual *Bromus*: A Comparison Between Southern California and the Intermountain Region

Edith B. Allen

Abstract: Sagebrush shrublands of southern California and the Great Basin are both undergoing massive vegetation-type conversion to exotic annual grasslands dominated by brome species. In southern California the main players are California sagebrush and red brome, while the Intermountain Region has big sagebrush and cheatgrass. Exotic annuals tend to be more dominant in soils with moderate to high levels of soil P and N. The type conversion of California sagebrush shrublands has been occurring during the last 25 to 30 years, compared to the last 100 years in the Great Basin. One reason for this might be the recent increase in anthropogenic N deposition caused by automobile emissions, up to 30 kg N per ha year. Field fertilization experiments in southern California also showed the exotic annual grasses have increased biomass with elevated N. The increased grass biomass has likely fueled more frequent fires in California. Even though California shrublands are adapted to fire compared to the big sagebrush-grasslands, frequent fire inhibits the re-establishment of shrubs when brome and other annual grasses are abundant. Restoration attempts have included timed fire to deplete the annual seedbank, herbicides, mowing, grazing, and reseeding and replanting. A comparison of some of these restoration efforts will be done for the two regions.

Introduction

The invasion of exotic annual grasses into native vegetation has been proceeding in some areas of the world for the last 100 years (D'Antonio and Vitousek 1992), and is currently affecting two major regions of the United States. The invasion of cheatgrass (*Bromus tectorum*) into big sagebrush (*Artemisia tridentata*) shrub-grasslands of the Intermountain Region is by now well documented (Mack 1981; McArthur and others 1990; Monsen and Kitchen 1994), although few large-scale solutions to restore native species have been implemented (Pellant 1994). A parallel but more recent invasion is occurring with the invasion of red brome (*Bromus madritensis* ssp. *rubens*) and other species of brome grasses, wild oats (*Avena*), barley (*Hordeum*), and annual fescues (*Vulpia*) into California sagebrush (*Artemisia californica*) shrublands of the coastal sage scrub vegetation of California. The latter invasion is so recent, an event that has been occurring over the past 25 to 30 years, that there is still little awareness that it is even occurring, or that it represents a permanent shift in vegetation type from perennial shrubland to annual grassland (Allen and others 1998; Minnich and Dezzani 1998). Yet this invasion has such similarities with the better-studied cheatgrass invasion that the parallel cannot be missed. Through a comparative examination we can learn lessons from cheatgrass invasion that may be applied to California sagebrush invaded by annual brome and other grasses, both what to expect and what control and restoration measures may be implemented. The objective of this review is to examine the similarities and differences of the two invasions by examining the ecology of the species, the climates, soils and disturbance regimes of the two regions. I will discuss potential reasons for the recent invasion and vegetation-type conversion of California sagebrush, and the potential for restoration of this vegetation as compared to big sagebrush.

Land Area Affected and Site Descriptions

California sagebrush is one of several dominant shrubs of the coastal sage scrub (CSS) vegetation that extends along the coast from the San Francisco Bay area southward into Baja California. The vegetation has its greatest extent and inland distribution in southern California in Riverside County and adjacent counties, where it is called inland sage scrub or Riversidean sage scrub (Westman 1981). The more inclusive term CSS will be used to include those areas codominated by such species as California buckwheat (*Eriogonum fasciculatum*) and brittlebush (*Encelia farinosa*) that are also undergoing conversion to exotic annual grasslands.

The CSS of southern California is among the most intensively human-impacted vegetation types in the United States. For this reason it has become a focus for mitigation and restoration (Bowler 1990), driven by the legal requirements

---

In: Hild, Ann L.; Shaw, Nancy L.; Meyer, Susan E.; Booth, D. Terrance; McArthur, E. Durant, comps. 2004. Seed and soil dynamics in shrubland ecosystems: proceedings; 2002 August 12–16; Laramie, WY. Proceedings RMRS-P-31. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Edith B. Allen is Professor, Department of Botany and Plant Sciences, University of California Riverside, Riverside, CA 92521-0124, U.S.A., e-mail: eallan@citrus.ucr.edu

of the Endangered Species Act (ESA). Currently, Habitat Conservation Plans under the ESA are underway in a number of counties of southern California that have large components of potential CSS, some with up to 160 threatened, endangered, and sensitive species (http://www.ecoregion.ucr.edu). CSS has been subject to urbanization, agriculture, and invasion by exotic annuals to such a large extent that one estimate gives only 10 percent of the original vegetation in good condition (Westman 1981). A more recent estimate puts CSS loss at 66 percent (O'Leary and others 1992), but in either case it is a significant loss because CSS covers only about 1.2 million ha of land area. The difference between the estimates may lie in the inability to estimate accurately how much of the natural potential vegetation is CSS, and it may lie in the condition of the remaining vegetation, which is often very weedy. Large expanses of CSS have been invaded by Mediterranean annual grasses and forbs (Freudenberger and others 1987), and in many areas the shrub understory is dominated by exotic rather than native annuals (Minnich and Dezzani 1998; Stylinski and Allen 1999). The conversion of shrubland to Mediterranean annual grassland has occurred primarily in the last 25 to 30 years, with 90 percent loss in shrub cover close to urban areas in western Riverside County and permanent replacement by annual grasses (Minnich and Dezzani 1998). Exotic annual grasses invaded California native grasslands over the past 200 years (Heady 1977), but the vegetation type-conversion of CSS to exotic annual grassland is a recent phenomenon.

The big sagebrush-grasslands of the Great Basin, the Columbia Plateau, and the Colorado Plateau have been undergoing invasion of cheatgrass and other species for more than 100 years (Billings 1990; Mack 1981; Young and others 1972). I will rely on literature citations and use less detail in explaining the cheatgrass conversion, as it is better documented than the California situation, and was the subject of two earlier Shrub Symposium volumes (McArthur and others 1990; Monsen and Kitchen 1994). Some 18 million acres of Intermountain rangeland have been invaded by cheatgrass plus medusahead (Pellant and Hall 1994). In fact, cheatgrass is still invading new areas where it has been sparse or absent, as in shrub-grasslands of the Colorado Plateau in Utah (Gelbard and Belnap 2003).

The big sagebrush type-conversion does not have the extensive conservation implications for endangered species as does the CSS. There are, however, several notable restoration projects for endangered animals such as the black-footed ferret and the sage grouse (Wrobleski and Kauffmann 2003; Wirth and Pyke 2003) in the big sagebrush-grasslands, as well as some endangered plant species such as *Silene spaldingii* in Montana (Lesica 1997) and *Gaura neomexicana* subsp. *coloradensis* in Wyoming (Munk and others 2002). However, huge land areas of big sagebrush are involved relative to the California CSS, and although certain species are of concern, the area does not have the hundreds of sensitive species that California has. This fact has implications for policy on restoration, which is driven by mitigation coupled with development in California, while restoration is more often driven by land productivity needs in the big sagebrush-grassland regions.

Climate and Phenology

Cheatgrass and the Mediterranean grasses occur in semi-arid, winter-wet, and summer-dry climates, but cheatgrass occurs in areas with winter frost, while the Mediterranean grasses are frost intolerant. Their precipitation regimes are broadly overlapping, although red brome also occurs in cool and/or less dry desert areas. Cheatgrass typically germinates in the fall in areas where few or no native species are adapted as winter annuals, as it has frost-tolerant seedlings. Cheatgrass is not persistent in the eastern edge of big sagebrush-grassland where summer rains are more frequent than in the Great Basin. Warm season grasses make their appearance in regions with summer rain, and winter annuals cannot compete. In addition, the high basins and high plains of regions to the east of the Great Basin have cold winters that are not conducive to the survival of winter annuals. In the sagebrush-grassland (1,500 m) of eastern Wyoming, cheatgrass is a spring annual in most years that senesces by early summer (Allen and Knight 1984).

The Mediterranean annual grasses also germinate with the onset of fall rains, and are often phenologically earlier than California native annuals and perennials (Chiariello 1989). The earlier phenology makes the exotic grasses highly competitive with native species. Plant growth occurs during the mild and rainy winter growing season in California, as summers are dry. The following spring the grasses produce seeds and senesce at the same time or earlier than native annuals. In the Mediterranean, rainfall typically continues later into the spring and early summer, giving an advantage to native perennial species that persist into the dry summer. Annual grasslands are considered early successional in the Mediterranean, and the extent of annual grasslands is less than in California (Jackson and Roy 1989). The annual grass phenology coupled with the shorter rainfall season is cited as the reason for persistence of the annual grasslands in California (Jackson and Roy 1989). Another argument is made below that soils may also contribute to the dominance of Mediterranean grasses in California.

Soil Nitrogen and Phosphorus

Soil nutrients may also contribute to the abundance of exotic annual grasslands in the Western United States. The Mediterranean has primarily calcareous soils originating from marine limestone deposits (Blondel and Aronson 1999), while much of southern California has granitic soils (Norris and Webb 1976). Both regions have volcanic outcroppings, more extensive in northern California. The calcareous soils of the Mediterranean are phosphorus fixing, with low extractable levels of P (Rabinovitch-Vin 1983). Grasslands dominate in volcanic outcroppings that have higher levels of soil P, but not in calcareous soils. For instance, the region around the Sea of Galilee in Northern Israel is volcanic with an annual grassland, while nearby calcareous soils are dominated by Mediterranean shrublands (Rabinovitch-Vin 1983). The soils of southern California tend to have moderate to high P levels. Measured amounts in sites in San Diego and Riverside Counties were 20 to 40 mg per kg bicarbonate extractable P, and 700 to 1,000 mg per kg total P (Cannon and others 1995; Nelson and Allen 1993; Padgett and others 1999).

Not only soils of southern California, but also much of the Great Basin are relatively high in extractable P. A survey of soil P from 90 locations across the Western United States where big sagebrush (*A. tridentata* ssp. *tridentata*) occurs, showed that most of the sites had levels of P from 11 to 20 mg per kg, with a mean of 15.3 (S.E. = 0.9). The exceptions were sites on the edges of its distribution, such as North Dakota and Baja California, that had under 10 mg per kg (fig. 1). This indicates that big sagebrush is a species of moderate to high P soils, but may also explain why it is so invasible by exotic species that have their greatest extent in soils rich in P in their home environment. Many invasive species have agricultural origins, either from cropland or pasture, and may be well adapted to soils naturally rich in nutrients.

Some Great Basin soils are also relatively high in N, and cheatgrass is highly responsive to N fertilizer (for example, Yoder and Caldwell 2002). The soils of southwest Wyoming sagebrush-grassland had 6 percent organic matter and 0.5 percent total Kjeldahl N, a surprisingly high amount for a semiarid soil (Waaland and Allen 1985). The richness of these soils may be explained by their geologic history. Some are relicts of more mesic vegetation from the last glaciation, while others are in sedimentary basins that in some cases were Pleistocene lake bottoms (Fiero 1986). Exotic plant invasion was highly correlated to soils high in P and N in southern Utah (Bashkin and others 2003).

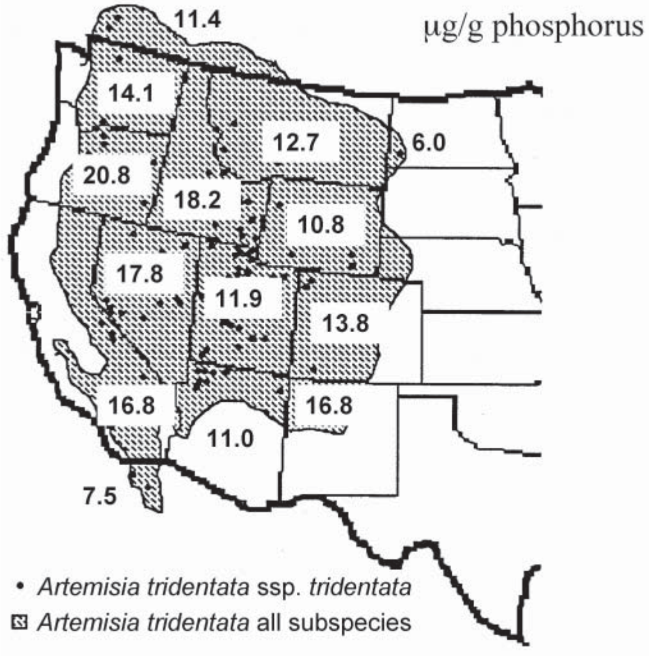


Figure 1—Concentrations of bicarbonate extractable soil P in sites dominated by *Artemisia tridentata* ssp. *tridentata* (data from E. Allen and M. Allen).

Nitrogen Deposition as a Cause of Invasion

The relatively high soil nutrient levels may explain in part why annual brome grasses have invaded big sagebrush-dominated lands of the Intermountain Region in the past, but not why the CSS of California has been recently invaded. The urbanizing areas of southern California are also subject to anthropogenic nitrogen deposition, which has been occurring for the past 40 years primarily as NOx from automobile emissions (fig. 2). The adoption of the catalytic converter in the mid-1980s caused a general decline in emissions, but NOx is still high enough to cause elevated soil N (Padgett and others 1999). NOx is converted to the plant-available forms of HNO_3 per NO_3^- in the atmosphere. In agricultural regions, NH_3 per NH_4^+ is the more abundant form of deposited N, but it forms only about 10 percent of the total deposited N in urban southern California, depending on the proximity to agricultural sources (Fenn and others 2003; Padgett and others 1999). Some of the fixed N is deposited as wetfall, but up to 90 percent may be deposited as particulate or ionic forms to plant and soil surfaces in the dry Mediterranean summers. The dryfall N accumulates on surfaces until the following rainy season when it is leached into the soil and taken up by plants. Levels of N deposition are high in southern California, with 30 kg per ha per year of N in shrublands (Bytnerowicz and others 1987) and up to 50 kg per ha per year in higher elevation pine forest (Fenn and others 2003). Only the Netherlands has higher levels, up to 90 kg per ha per year, mainly in the form of NH_3 per NH_4^+. These high levels have been experimentally shown to cause loss of shrub cover in heathlands, with a concomitant increase in perennial native grasses (Bobbink and Willems 1987).

Soils in southern California CSS have up to 87 kg per ha per year extractable N measured near urban areas with the greatest atmospheric NO_3^- concentrations (Padgett and others 1999). These high levels of N may also be the cause of the recent exotic grass invasion (Allen and others 1998,

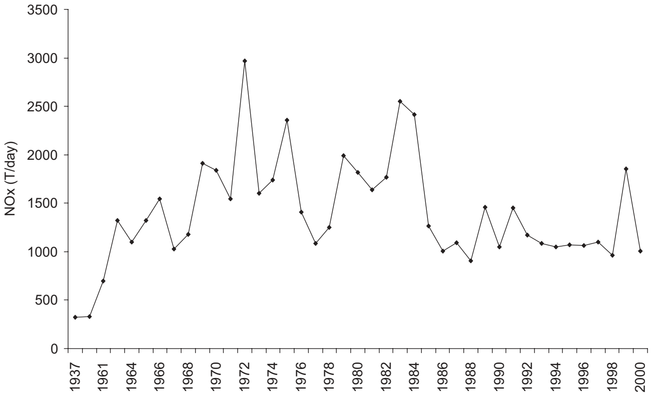


Figure 2—Emissions of NOx in the South Coast Air Basin of southern California, 1937 to 2000 (Alexis and others 2000).

2000). Like cheatgrass in the Great Basin, the Mediterranean brome grasses were introduced to California more than 100 years ago, and some species arrived in the mid-1700s with the first Spanish missions (Heady 1977). Species such as wild oats were abundant in the Central Valley by the mid-1800s where extensive farming and grazing was already underway. But the CSS was also grazed until the early 1900s, and was burned by ranchers to increase annual grass cover (Burcham 1957). However, it appears to have been resilient to permanent vegetation type conversion until the 1960s (Minnich and Dezzani 1998). The Forest Service Vegetation Type Map survey was done throughout California during the 1930s, including some 100 sites in CSS of western Riverside County. Minnich resurveyed these areas in the early 1990s and found that some had lost up to 90 percent of their shrub cover, especially those near urban areas (Minnich and Dezzani 1998). Local botanists have also noted that the diverse native shrubland, with its colorful understory of spring flowers, has converted to monotypic exotic annual grassland in the past 25 to 30 years (for example, Oscar Clark, retired herbarium curator, and Andrew Sanders, herbarium curator, University of California-Riverside).

The simplest explanation for type conversion under N deposition would be that the exotic grasses are responsive to elevated soil N to a greater extent than the native shrubs, as occurred in the Netherlands (Bobbink and Willems 1987), but the situation is more complex in this semiarid climate. Three invasive species, *Bromus rubens*, *A. fatua*, and *Brassica geniculata*, were all highly responsive to N fertilization, but three native shrub species were also responsive, including California sagebrush (Padgett and Allen 1999). Plant response to N in the greenhouse alone did not explain the observed shifts from shrubland to annual grassland, so field studies were initiated. A long-term fertilization experiment was initiated in CSS 40 km south of Riverside, CA, in an area with low N deposition. The site was burned by a wildfire in fall of 1993, and was fertilized yearly thereafter with 60 kg per ha per year of NH_4NO_3 (Allen and others 1998). Annual grasses responded to N fertilizer with an increase in biomass during the wet years, but there were no long-term changes in shrub cover (fig. 3). If there are direct effects of N on shrubs they may be even longer term than this experiment. For instance, species shifts in shortgrass prairie fertilized with 100 kg N annually for 4 years did not materialize until about 5 years after the cessation of fertilization (Milchunas and Lauenroth 1995), so further observations of these plots will continue. However, elevated grass biomass has another impact, which is to increase the fire cycle, and N fertilization may have more immediate effects than species shifts in this vegetation type by altering the fire cycle, as discussed next.

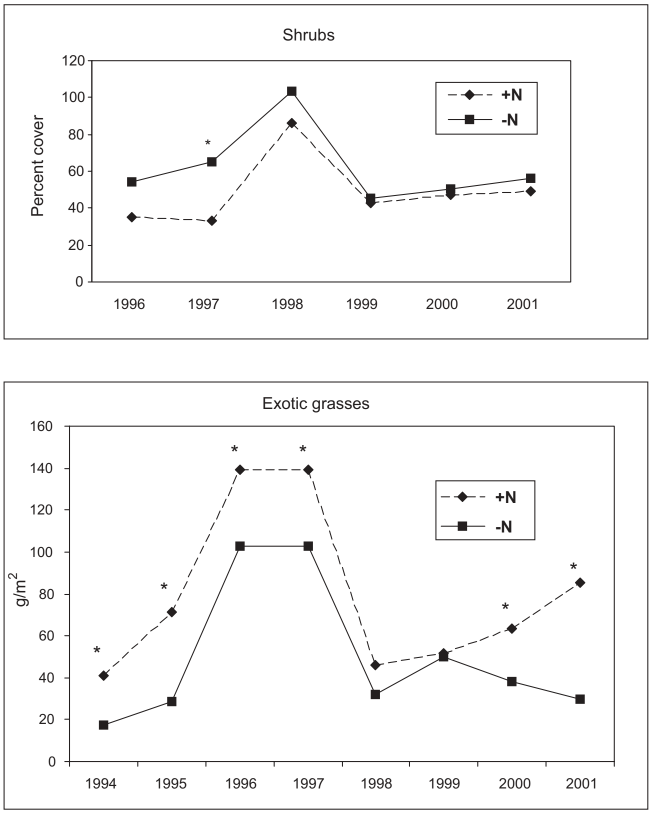


Figure 3—Responses of exotic annual grasses and native shrubs to N fertilization, which was begun in spring 1994 following a November fire in 1993 (data from Allen and others, in press).

Nitrogen and the Fire Cycle

The fire frequency has been reduced from 60- to 100-year to 5-year intervals in big sagebrush-grassland invaded by cheatgrass (Billings 1990; Whisenant 1990). This is largely because cheatgrass forms a fine, continuous fuel that carries fire from shrub to shrub, or from one bunchgrass to the next. Bunchgrasses, like shrubs, are not as efficient at carrying fire long distances (Whisenant 1990). The increase in fine fuel frequency with an increase in the fire cycle has occurred in cheatgrass-invaded lands over the past 100 years, but has only been anecdotally recognized in the past 20 years in CSS. Short fire intervals cause conversion of shrubland to grassland (Calloway and Davis 1993), but short fire intervals can only occur when there is sufficient fuel to carry a fire in subsequent years, for example, following annual grass invasion. The normal fire interval in CSS is about 30 years (Westman and O'Leary 1986). Urban parks in western Riverside County, such as Box Springs Mountain and Mt. Rubidoux, that were dominated by CSS only 20 years ago are now largely annual grasslands because of fires that burn at 2- to 5-year intervals (Cione and others 2002; Minnich 1988). Based on observations from aerial photos, fire frequency probably increased in urban Riverside County in the mid-1960s when persistent patches of annual grasses appeared (Minnich, personal communication). However, even sites that have not burned in 30 years have lost shrub cover, and grass-dominated sites that burned or were disturbed several decades ago have not recovered to their former diversity of native shrubs and understory herbs (Freudenberger and others 1987; Stylinski and Allen 1999). We can learn from cheatgrass-dominated big sagebrush, where initial small incursions of grass promoted fire, which produced a positive feedback loop of grass and fire until an annual grassland stabilized under a frequent fire cycle. Nitrogen deposition will exacerbate the positive feedback by increasing the fine fuel.

Restoration

Restoration is driven by different needs in southern California CSS and in Intermountain sagebrush-grasslands. Fire hazards and large-scale loss of productive grazing lands are primary drivers for restoration in the Intermountain Region, with enhancement of endangered species a secondary or regional issue, depending upon local species occurrence. Conversely, the large number of endangered species coupled with rapid urban development in southern California has created enormous species conservation issues that are in part addressed through mitigation restoration. The fire hazard of CSS located adjacent to urban areas has also increased as fine grass fuels invade, and control of grasses to reduce flammability is a goal in these areas. Rangeland productivity is rarely considered a revegetation goal in CSS any more, because most of the remaining rangelands have been or are being converted to conservation reserves. Where rangeland productivity and fire control of big sagebrush is the goal, revegetation plantings tend to focus on exotic species, while revegetation in CSS nowadays is always done with native plants because of the sensitive species issues. Whether the objective is restoration for rare species or to reduce the fire hazard, the first step is to control annual grasses. A few of the techniques to control the grasses, and their relative success in California and the Intermountain Region, are compared below. These are primarily fire, grazing, herbicides, and mechanical control.

Controlled spring burning of exotic grasses has been used successfully to restore perennial purple needlegrass (*Nassella* [= *Stipa*] *pulchra)* grassland at the Santa Rosa Plateau, a former ranch that is managed by The Nature Conservancy as part of the Riverside County Multispecies Habitat Conservation Plan. While results of fire management from this site are not in the published literature, the managers have demonstrated that late summer or fall burning maintains the annual grass cover, most likely because the seed density is not reduced by fire. By contrast, spring burns before the seeds have shattered enable a complete burn of the potential seedbank. The seedbank of these species is not persistent for many years, with 1 percent or less remaining in the soil after fall germination, so that seedbank control is readily achieved with spring fire (Young and others 1981).

Fire has not been used as a tool to restore weedy CSS because the dynamics of plant response to fire are different in CSS than in grassland. Perennial bunchgrasses resprout immediately after a spring fire, but reseeding shrubs (most species in CSS are reseeders following fire) must compete with residual weed seeds in the seedbank. Prescribed fire has also seldom been used as a tool for restoration of weedy big sagebrush-grassland because native seed banks are often depleted, and cheatgrass will become more abundant with the removal of the shrub cover (Rasmussen 1994). Fire was successfully used to restore native forbs, either seeded or from the seedbank (Wirth and Pyke 2003; Wrobleski and Kauffmann 2003), but these studies were done in areas with low cheatgrass cover. Fires in weedy big sagebrush must typically be seeded because of the lack of a native seedbank (Rasmussen 1994), and similar measures would need to be undertaken in weedy CSS.

Mechanical or herbicide removal of grasses followed by shrub planting is frequently used in CSS restoration mitigation. For instance, grasses (red brome, ripgut brome [*Bromus diandrus*], wild oats) were experimentally thinned by hand to densities varying between 0 and 500 grasses per m^2. Growth of planted California sagebrush was reduced even at the lowest density, 25 grasses per m^2 compared to the control (Eliason and Allen 1997). In another study, control of grasses by mowing or grass-specific herbicide enabled establishment of seeded shrub species, including California sagebrush, but weedy control plots had no shrub establishment at all (Cione and others 2002). Similarly, native plants establish poorly in dense stands of cheatgrass. However, several studies have shown that exotic perennials originating from Asia may readily be seeded into cheatgrass, sometimes even if it has received little treatment to control the annual grasses (Davis and Harper 1990; McArthur and others 1990; Monsen and Turnipseed 1990).

Because of the reluctance to use fire in CSS, studies are underway to control annual grasses and increase shrub and native understory herbs. The study reported here took advantage of the native seedbank, and did not include seeding. The study site is at Lopez Canyon in the Western Riverside County Multispecies Reserve, 55 km south of Riverside, CA, in an area with relatively low N deposition. The area was grazed by cattle until the mid-1980s when it was transferred to Riverside County as mitigation habitat for development of CSS vegetation in other parts of the County. The site was burned by a wildfire in 1993, but has a relatively high proportion of grasses in the understory. The grass invasion may be related to the grazing history of the site. Two treatments, plus an untreated control, were applied in each of three replicate, 1-ha plots: (1) sheep grazing in March per April 1999, 2000, and 2001, and (2) Fusilade (grass-specific) herbicide application in February/March 1999 and 2000. Sheep grazing was done by fencing each of the 1-ha plots, and allowing 200 sheep to remain in each plot for 48 hours. Grazing was done for 3 consecutive years because grasses had already gone to seed the first 2 years, and sheep did not consume the grasses until the third year when more forage was available. Plots were arranged in a randomized block design with the three treatments plus a control in each of the three blocks. Percent cover data of vegetation were collected in 0.5- by 1.0-m plots, 20 plots per ha, in late April/early May of each year. No additional treatments were applied in 2002, but percent cover data were collected.

The exotic grass cover (mainly red brome, with some ripgut brome, wild oats, and annual fescue) decreased with the herbicide treatment in 1999 compared to control plots, and decreased more in 2000 (fig. 4). No additional herbicide was applied in 2001, but exotic grass cover was still significantly lower than in control plots. By 2002 there were no significant differences among the treatments, but this was the driest year on record in this region since recordkeeping began in the State, only about 10 cm in an area that receives 28 cm.

The grazing treatment was not effective in controlling grasses until 2001 (fig. 4). The grazing was done in March, before the data were collected in each year, and showed that the sheep did not consume grasses until 2001. This was the

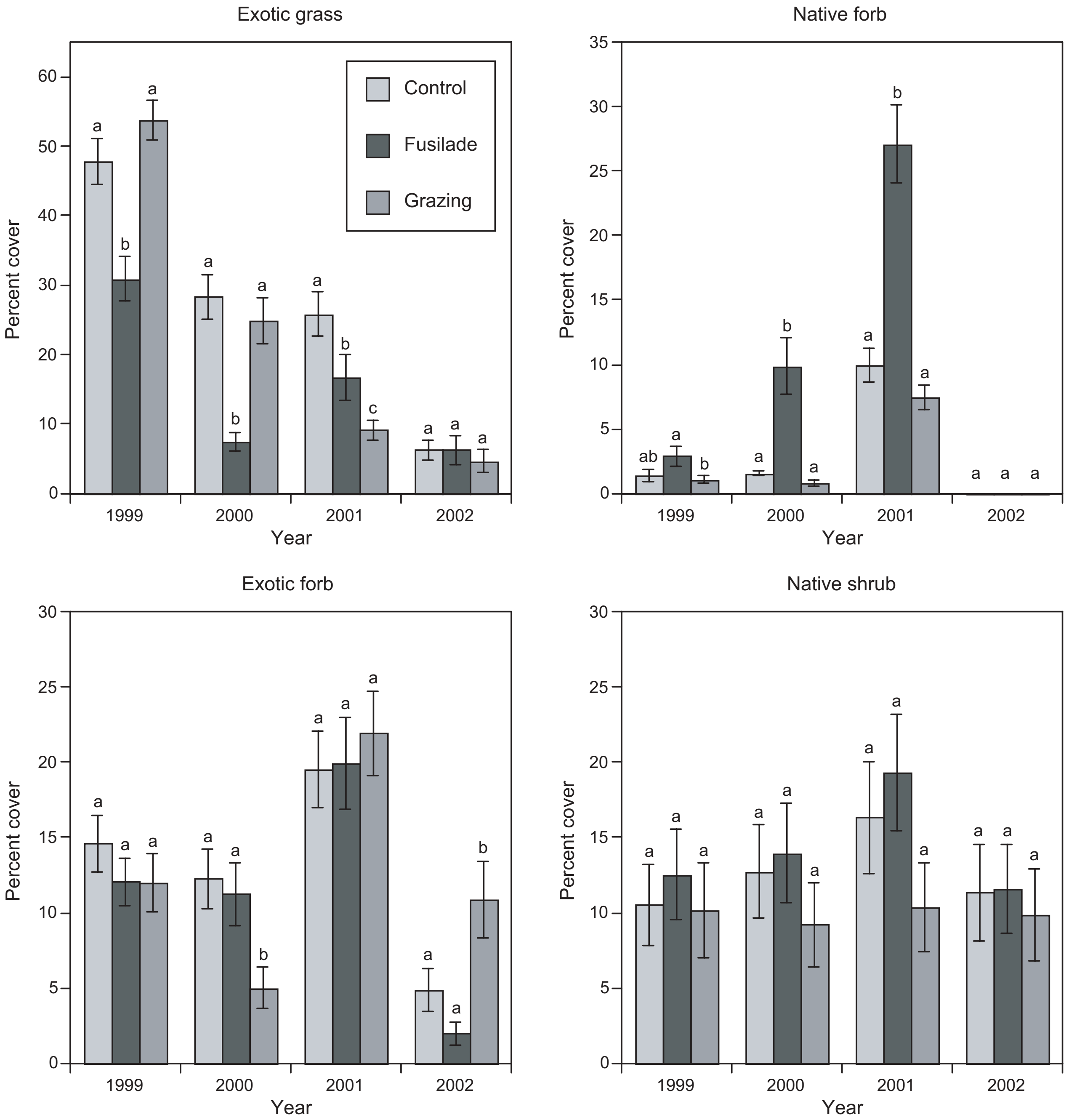


Figure 4—Effects of sheep grazing, grass specific herbicide, and herbicide plus dethatching on percent cover of native forbs, exotic forbs, and shrubs in a coastal sage scrub site in southern California over 4 years. The 2002 growing season was extremely dry, with virtually no germination of native forbs.

only year when the grasses had not produced seed by the time the sheep were placed in the plots. This was not due to poor management, but rather to timing of rains. The rains came late in 1999 and 2000, and by the time grasses had produced forage for sheep to graze, they had also produced seeds. Timing of precipitation was more conducive to annual grass grazing in 2002.

The native forbs consisted of some 20 to 30 annual and perennial species each year, none of which was very abundant individually. Their combined cover increased significantly in the 2000 and 2001 growing seasons in response to the herbicide treatment, but decreased with grazing. In 2002 there was virtually no forb growth at all due to the drought. The sheep consumed the forbs preferentially, but to determine whether the sheep had positive or negative long-term effects on the native forbs the plots will need to be observed for additional years. Whether the native forbs can recover from sheep grazing will depend on the longevity of their seedbanks. This is likely quite long, as the annuals are largely fire-following species that rest in the soil between the 30-year fire intervals in CSS.

The exotic forbs consisted mainly of storksbill (*Erodium cicutarium* and *E. brachythecium*) with less than 2 percent wild mustard (*Brassica geniculata*), but there were no significant differences among the treatments in any year. Similarly, the native shrubs did not respond in cover to the treatments. We examined the sample quadrats for germinating shrub seedlings, but did not observe any in response to any of the treatments.

Overall, the study showed that native forbs increase in cover following grass-specific herbicide, but there was no improvement of shrub cover. Whether this requires seeding or longer term treatment is unknown. Some of the shrubs have improved germination with smoke or fire (Keeley 1991), so a fire treatment may be needed, but controlled fire is currently unlikely because managers fear further loss of the shrub canopy, as described above.

Restoration at Lopez Canyon will be difficult even without the added grass productivity that comes from elevated soil N. A more difficult case of CSS restoration with high soil N was done in Riverside under high N deposition in a pure stand of exotic grasses. Mowing and herbicide treatments were used to control the grasses so seeded shrubs could establish. There was no native seed in the seedbank, as shown by absence of native plant emergence in weeded but unseeded plots (Cione and others 2002). The addition of mulch is a technique that can help reduce soil N and improve grass establishment. A restoration study on a pipeline disturbance with elevated soil N showed that bark mulch was more effective than straw mulch at immobilizing soil N, and bark also promoted growth of larger California sagebrush plants (Zink and Allen 1998). However, mulching will probably not be a large-scale method of restoration because transporting mulch to large areas is not cost effective. Where grass biomass is high because of ambient or elevated soil N levels, grass control methods are likely more cost effective over large areas than mulch for re-establishment of native vegetation. Cheatgrass-invaded lands may in fact become reduced in N over time due to increased N turnover and leaching (Evans and others 2001), although no change in N dynamics was observed in another study (Svejcar and Sheley 2001).

Conclusions: Vegetation Stability and the Limits to Restoration

The stability of restored vegetation on lands invaded by exotic annual grasses is still in question. California sagebrush and big sagebrush-dominated lands are invasible, at least in part, because the soils are moderate to high in P and N, and subject to N deposition in urbanized California. Annual brome grasses tend to be highly responsive to nutrients, and thus preadapted to these high soil nutrient levels. If the natural vegetation is ecologically unstable and subject to grass invasion, restored vegetation will likely also be unstable. In contrast, some of the most stable revegetated lands once dominated by cheatgrass are those planted to exotic perennials such as forage kochia or crested wheatgrass (*Agropyron cristatum*) in the Intermountain region. Recent hopeful studies show that one native species, squirreltail (*Elymus elymoides*), colonizes cheatgrass naturally, and preferentially allows establishment of sagebrush but not cheatgrass (Booth and others 2003). This may open the door for restoration of big sagebrush, but a similar solution for restoration of CSS is not at hand. Bowler (1990) has stated that the real test of the success of CSS restoration will come after a restored site has burned, and then re-established again. One incident occurred in replanted CSS in Riverside, where a late spring fire burned annual grasses, but adjacent stands of planted shrubs did not burn (Cione and others 2002). The fire did not burn shrubs because of differences in fuel moisture, as grasses were senescent and dry while the deeper rooted shrubs stayed green later into the summer. The goals of a reduced fire cycle and improved forage for grazing can likely be met readily by use of suitable exotic species in cheatgrass-invaded lands, but the more difficult goal of restoration of native plant species and animal habitat will not only require more initial effort, but also long-term maintenance to control invasion of annual grasses.

References

Allen, E. B.; Knight, D. H. 1984. The effects of introduced annuals on secondary succession in sagebrush grassland, Wyoming. The Southwestern Naturalist. 29: 407–421.

Allen, E. B.; Padgett, P. E.; Bytnerowicz, A.; Minnich, R. 1998. Nitrogen deposition effects on coastal sage vegetation of southern California. In: Arbaugh, M., ed. Proceedings of the international symposium on air pollution and climate change effects on forest ecosystems; 1996 February 5–9; Riverside, CA. Gen. Tech. Rep. PSW-GTR-166. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station: 131–140. http://www.rfl.psw.fs.fed.us/pubs/psw-gtr-164/fulltext/allen/allen/allen.html#anchor1473574.

Allen, E. B.; Sirulnik, A. G.; Egerton-Warburton, L.; Kee, S. N.; Bytnerowicz, A.; Padgett, P. E.; Temple, P. J.; Fenn, M. E.; Poth, M. A.; Meixner, T. [In press]. Air pollution and vegetation change in southern California shrublands. In: Kus, B. E.; Beyers, J. L., eds. Planning for biodiversity in southern California: bringing research and management together: proceedings of the symposium; 2000 February 29–March 3; Pomona, CA. Riverside, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station.

Bashkin, M.; Stohlgren, T. J.; Otsuki, Y.; Lee, M.; Evangelista, P.; Belnap, J. 2003. Soil characteristics and plant exotic species invasions in the Grand Staircase-Escalante National Monument, Utah, USA. Applied Soil Ecology. 22: 67–77.

Bobbink, R.; Willems, J. H. 1987. Increasing dominance of *Brachypodium pinnatum* (L.) Beauv. in chalk grasslands: a threat to a species-rich ecosystem. Biological Conservation. 40: 301–314.

Bowler, P. A. 1990. Coastal sage scrub restoration. I. The challenge of mitigation. Restoration and Management Notes. 8: 78–82.

Burcham, L. T. 1957. California range land: an historico-ecological study of the range resource of California. Sacramento, CA: Division of Forestry, Department of Natural Resources.

Bytnerowicz, A.; Miller, P. R.; Olszyk, D. M.; Dawson, P. J.; Fox, C. A. 1987. Gaseous and particulate air pollution in the San Gabriel Mountains of southern California. Atmospheric Environment. 21: 1805–1814.

Billings, W. D. 1990. *Bromus tectorum*, a biotic cause of ecosystem impoverishment in the Great Basin. In: Woodwell, G. M., ed. The earth in transition: patterns and processes of biotic impoverishment. New York: Cambridge University Press: 301–322.

Blondel, J.; Aronson, J. 1999. Biology and wildlife of the Mediterranean region. Oxford University Press.

Booth, M. S.; Caldwell M. M.; Stark, J. M. 2003. Overlapping resource use in three Great Basin species: implications for community invasibility and vegetation dynamics. Journal of Ecology. 91: 36–48.

Bowler, P. A. 1990. Coastal sage scrub restoration. I. The challenge of mitigation. Restoration and Management Notes. 8: 78–82.

Callaway, R. M.; Davis, F. W. 1993. Vegetation dynamics, fire, and the physical environment in coastal central California. Ecology. 74: 1567–1578.

Cannon, J. P.; Allen, E. B.; Allen, M. F.; Dudley, L. M.; Jurinak, J. J. 1995. The effects of oxalates produced by *Salsola tragus* on the phosphorus nutrition of *Stipa pulchra.* Oecologia. 102: 265–272.

Chiariello, N. R. 1989. Phenology of California grasslands. In: Huenneke, L. F.; Mooney, H. A., eds. Grassland structure and function: California annual grassland. Dordrecht: Kluwer Academic Publishers: 47–58.

Cione, N. C.; Padgett, P. E.; Allen, E. B. 2002. Restoration of a native shrubland impacted by exotic grasses, frequent fire and nitrogen deposition in southern California. Restoration Ecology. 10: 376–384.

D'Antonio, C. M.; Vitousek, P. M. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annual Review of Ecology and Systematics. 3: 3–87.

Davis, J. N.; Harper, K. T. 1990. Weedy annuals and establishment of seeded species on a chained juniper-pinion woodland in central Utah. In: McArthur, E. D.; Romney, E. M.; Smith, S. D.; Tueller, P. T., eds. Proceedings—symposium on cheatgrass invasion, shrub die-off, and other aspects of shrub biology and management. Gen. Tech. Rep. INT-GTR-313. Ogden, UT: U.S. Department of Agriculture, Forest Service. Intermountain Research Station: 71–79.

Eliason, S. A.; Allen, E. B.. 1997. Competition as a mechanism for exotic grass persistence following conversion from native shrubland. Restoration Ecology. 5: 245–255.

Evans, R. D.; Rimer, R.; Sperry, L.; Belnap, J. 2001. Exotic plant invasion alters nitrogen dynamics in an arid grassland. Ecological Applications. 11: 1301–1310.

Fenn, M. E.; Baron, J. S.; Allen, E. B.; Rueth, H. M.; Nydick, K. R.; Geiser, L.; Bowman, W. D.; Sickman, J. O.; Meixner, T.; Johnson, D. W. 2003. Ecological effects of nitrogen deposition in the Western United States. Bioscience.

Fiero, B. 1986. Geology of the Great Basin. Reno: University of Nevada Press.

Freudenberger, D. O.; Fish, B. E.; Keeley, J. E. 1987. Distribution and stability of grasslands in the Los Angeles basin. Bulletin of the Southern California Academy of Sciences. 86**:** 13–26.

Gelbard J. L.; Belnap J. 2003. Roads as conduits for exotic plant invasions in a semiarid landscape. Conservation Biology. 17: 420–432.

Heady, H. F. 1977. Valley grasslands. In: Barbour, G.; Majors, J., eds. Terrestrial vegetation of California. New York: Wiley & Sons: 491–514.

Huenneke, L. F.; Mooney, H. A., eds. 1989. Grassland structure and function: California annual grassland. Dordrecht: Kluwer Academic Publishers.

Jackson, L. E.; Roy, J. 1989. Comparative ecology of annual grasses: native versus Californian habitats. In: Huenneke, L. F.; Mooney, H. A., eds. Grassland structure and function: California annual grassland. Dordrecht: Kluwer Academic Publishers: 81–92.

Keeley, J. E. 1991. Seed germination and life history syndromes in the California chaparral. The Botanical Review. 57: 81–116.

Lesica, P. 1997. Demography of the endangered plant, *Silene spaldingii* (Caryophyllaceae) in northwest Montana. Madroño. 44: 347–358.

Mack, R. N. 1981. Invasion of *Bromus tectorum* into Western North America: an ecological chronicle. Agro-Ecosystems. 7: 145–165.

McArthur, E. D.; Blauer, A. C.; Stevens, R. 1990. Forage kochia competition with cheatgrass in Central Utah. In: McArthur, E. D.; Romney, E. M.; Smith, S. D.; Tueller, P. T., eds. Proceedings—symposium on cheatgrass invasion, shrub die-off, and other aspects of shrub biology and management. Gen. Tech. Rep. INT-GTR-313. Ogden, UT: U.S. Department of Agriculture, Forest Service Intermountain Research Station: 56–66.

McArthur, E. D.; Romney, E. M.; Smith, S. D.; Tueller, P. T., eds. 1990. Proceedings—symposium on cheatgrass invasion, shrub die-off, and other aspects of shrub biology and management. Gen. Tech. Rep. INT-GTR-313. Ogden, UT: U.S. Department of Agriculture, Forest Service Intermountain Research Station.

Milchunas, D. G.; Lauenroth, W, K. 1995. Inertia in plant community structure—state changes after cessation of nutrient-enrichment stress. Ecological Applications. 5: 452–458.

Minnich, R. A. 1988. The biogeography of fire in the San Bernardino Mountains of California. University of California Publications, Geography. 28: 36–40.

Minnich, R. A.; Dezzani, R. J. 1998. Historical decline of coastal sage scrub in the Riverside-Perris Plain, California. Western Birds. 29: 366–391.

Monsen, S. B.; Kitchen, S. G. 1994. Proceedings—ecology and management of annual rangelands. Gen. Tech. Rep. INT-276. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station.

Monsen, S. B.; Turnipseed, D.; 1990. Seeding forage kochia onto cheatgrass-infested rangelands. In. McArthur, E. D.; Romney, E. M.; Smith, S. D.; Tueller, P. T., eds. Proceedings—symposium on cheatgrass invasion, shrub die-off, and other aspects of shrub biology and management. Gen. Tech. Rep. INT-GTR-313. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 66–71.

Munk, L. M.; Hild, A. L.; Whitson, T. D. 2002. Rosette recruitment of a rare endemic forb (*Gaura neomexicana* subsp *coloradensis*) with canopy removal of associated species. Restoration Ecology. 10: 122–128.

Nelson, L. L.; Allen, E. B. 1993. Restoration of *Stipa pulchra* grasslands: effects of mycorrhizae and competition from *Avena barbata*. Restoration Ecology. 1: 40–50.

Norris, R. M.; Webb, R. W. 1976. Geology of California. New York: John Wiley & Sons.

Padgett, P. E.; Allen, E. B. 1999. Differential responses to nitrogen fertilization in native shrubs and exotic annuals common to Mediterranean coastal sage scrub of California. Plant Ecology. 144: 93–101.

Padgett, P. E.; Allen, E. B.; Bytnerowicz, A.; Minnich, R. A. 1999. Changes in soil inorganic nitrogen as related to atmospheric nitrogenous pollutants in Southern California. Atmospheric Environment. 33: 769–781.

Pellant, M. 1994. History and applications of the Intermountain greenstripping program. In: Monsen, S. B.; Kitchen, S. G. Proceedings—ecology and management of annual rangelands. Gen. Tech. Rep. INT-276. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 63–68.

Pellant, M.; Hall, C. 1994. Distribution of two exotic grasses on Intermountain rangelands: status in 1992. In: Monsen, S. B.; Kitchen, S. G. Proceedings—ecology and management of annual rangelands. Gen. Tech. Rep. INT-276. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 109–112.

Rabinovitch-Vin, A. 1983. Influence of nutrients on the composition and distribution of plant communities in Mediterranean-type ecosystems of Israel. In: Kruger, F. J.; Mitchell, D. T.; Jarvis, J. U. M., eds. Mediterranean-type ecosystems: the role of nutrients. Berlin: Springer-Verlag: 74–85.

Rasmussen, 1994. Prescribed burning considerations in sagebrush annual grass communities. In: Monsen, S. B.; Kitchen, S. G. 1994. Proceedings—ecology and management of annual rangelands. Gen. Tech. Rep. INT-276. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 69–74.

Stylinski, C. D.; Allen, E. B. 1999. Lack of native species recovery following severe exotic disturbance in southern California shrublands. Journal of Applied Ecology. 36: 544–554.

Svejcar, T.; Sheley, R. 2001. Nitrogen dynamics in perennial- and annual-dominated arid rangeland. Journal of Arid Environments. 47: 33–46.

Young, J. A.; Evans, R. A.; Raguse, C. A.; Larson, J. R. 1981. Germinable seeds and periodicity of germination in annual grasslands. Hilgarida. 49: 1–37.

Waaland, M. E.; Allen, E. B. 1987. Relationships between VA mycorrhizal fungi and plant cover following surface mining in Wyoming. Journal of Range Management. 40: 271–276.

Westman, W. E.; O'Leary, J. F. 1986. Measures of resilience: the response of coastal sage scrub to fire. Vegetatio. 65: 179–189.

Whisenant, S. 1990. Changing fire frequencies on Idaho's Snake River Plains: ecological and management implications. In: McArthur, E. D.; Romney, E. M.; Smith, S. D.; Tueller, P. T., eds. 1990. Proceedings—symposium on cheatgrass invasion, shrub die-off, and other aspects of shrub biology and management. Gen. Tech. Rep. INT-GTR-313. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 4–10.

Wirth, T. A.; Pyke, D. A. 2003. Restoring forbs for sage grouse habitat: fire, microsites, and establishment methods. Restoration Ecology. 11: 370-377.

Wrobleski, D. W.; Kauffmann, J. B. 2003. Initial effects of prescribed fire on morphology, abundance, and phenology of forbs in big sagebrush communities in southeastern Oregon. Restoration Ecology. 11: 82–90.

Yoder, C.; Caldwell, M. M. 2002. Effects of perennial neighbors and nitrogen pulses on growth and nitrogen uptake by *Bromus tectorum*. Plant Ecology. 158: 77–84.

Young, J. A.; Evans, R. A.; Rageuse, C. A.; Larson, J. R. 1981. Germinable seeds and periodicity of germination in annual grasslands. Hilgardia. 49: 1–37.

Zink, T. A.; Allen, M. F. 1998. The effects of organic amendment on the restoration of a disturbed coastal sage scrub habitat. Restoration Ecology. 6: 52–58.

Comparing Phenotype and Fitness of Native, Naturalized, and Invasive Populations of Downy Brome (Cheatgrass, *Bromus tectorum*)

C. Lynn Kinter
Richard N. Mack

Abstract: The Eurasian grass downy brome (cheatgrass, *Bromus tectorum* L.) was introduced into arid and semiarid bunchgrass and shrub communities in New Zealand and North America over 100 years ago, but has strikingly different histories in these ranges. On New Zealand's South Island, it persists at low levels, while in Western North America, it dominates vast areas. Inherent high fitness in founder populations may have contributed to the invasive character of North American populations, while low fitness may have precluded a New Zealand invasion. In four common greenhouse environments, 62 populations from Western North America, New Zealand, and the native range in Western Europe were compared for 15 phenotypic and fitness traits (including height, days to flowering, vegetative biomass). Significant differences among source locations were evident for most traits. North American populations were typically most vigorous, followed by European, and lastly New Zealand populations. North American plants flowered earlier, and New Zealand plants later, than those from the native range. Differences in levels of fitness between the sources of founder populations have likely contributed to radically different histories of downy brome in two of its new ranges. Our research has important implications for screening and predicting invaders and controlling invasive species.

Downy brome, or cheatgrass (*Bromus tectorum*), is a cleistogamous, annual C_3 grass native to Eurasia and northern Africa. It was introduced from Europe (Novak and Mack 2001) into both North America and New Zealand over 100 years ago (Kirk 1869; Mack 1981), but has radically different histories in the new ranges. In Western North America, it dominates vast areas formerly dominated by shrubs and bunchgrasses (Mack 1981). On these rangelands, it changes the structure of the community, often comprising over 90 percent of the vegetative cover. It decreases forage values, causes loss of native biodiversity, and increases fire frequency, erosion, and siltation. In contrast, in the central part of New Zealand's South Island, downy brome is naturalized at low levels in shrub and bunchgrass communities (Connor 1964; Williams 1980). There, it persists primarily on disturbed sites, such as roadsides or trampled areas, but does not become dominant over large acreages.

These performance differences might typically be attributed to environmental differences between the two introduced ranges. However, in the region of New Zealand where downy brome has persisted for decades, the physiognomies of the native plant communities, climate, and recent fire and grazing history are similar to those features in Western North America where downy brome has invaded heavily (Mack 1986; Wardle 1991). Even two species that commonly attack downy brome in its native range—head smut fungus (*Ustilago bullata*) and bird cherry-oak aphid (*Rhopalosiphum padi*)—have been known for at least a century in both introduced ranges (Lowe 1961; Pergande 1904). Consequently, we hypothesized that differences in performance of downy brome in these new ranges may be explained by differences in the founder genotypes, rather than differences in the environments in the new ranges.

We assessed the potential for different performance among downy brome from three ranges: the portion of its native range in Western Europe that served as the donor region for both North America and New Zealand (Novak and Mack 2001), and the new ranges in Western North America and the South Island of New Zealand. By growing all populations in common greenhouse environments, we investigated genetically based differences in phenotype, vigor, and fitness among these three ranges.

Methods

Sample Collection

In the native range, we based our collecting efforts on Novak and Mack's (2001) allozyme research. They found that the widespread genotypes in Western North America were most closely related to those in Europe, and less closely related to genotypes in Eastern North America, Asia, and Northern Africa. They deduced that the cheatgrass genotypes, which were the early founders that spread widely

---

In: Hild, Ann L.; Shaw, Nancy L.; Meyer, Susan E.; Booth, D. Terrance; McArthur, E. Durant, comps. 2004. Seed and soil dynamics in shrubland ecosystems: proceedings; 2002 August 12–16; Laramie, WY. Proceedings RMRS-P-31. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

C. Lynn Kinter is a Botanist and Ph.D. Candidate, and Richard N. Mack is a Professor of Botany, School of Biological Sciences, Washington State University, Pullman, WA 99164-4236. FAX: (509) 335-3184; phone: (208) 373-4381; e-mail: lkinter@fs.fed.us

across Western North America, were from Central and Western Europe, probably around Slovakia, Czech Republic, or the eastern part of Germany. For this study, we sampled heavily in that region, as well as north into Sweden and west across The Netherlands, where Novak and Mack did not sample but where many immigrants and shipments left for the New World. We also included samples from Spain and Italy. In the native range, downy brome is found at low levels in native plant communities, such as stabilized dunes, and on disturbed sites, such as railroad beds, farmsteads, and cereal grain fields.

In Western North America, we sampled three populations each in the vicinity of six founder locations identified by Novak and Mack (2001)—from Nevada and Utah north to British Columbia. In New Zealand, founder information is not known, so we sampled three populations in the region around Lake Pukaki and Bendigo (Canterbury and Otago Counties) where herbarium specimens have been collected since the 1930s. In total, we sampled 62 populations: 41 in Europe, 18 in Western North America, and three in New Zealand. From each population, we randomly collected 30 individuals, and ultimately chose six of those at random for use in experiments.

Common Greenhouse Experiments

In December 2000, we planted seeds from six individuals from each of 62 populations in four common greenhouse environments: control, low water, low nutrients, and low temperature. These seeds were one generation grown out from the wild to minimize maternal effects (Roach and Wulff 1987; Schaal 1984). No mortality occurred during the grow-out phase, and all parent plants produced numerous seeds for experiments. In the experimental phase, seeds were sown in standard potting medium (60 percent peat, 20 percent pumice, 20 percent sand; pH 6.9–7.0) in individual 15-cm fiber pots on greenhouse benches under ambient light. Temperatures were 24/16 °C (12h/12h) for 6 weeks after sowing, followed by a 9-week cold period at 4/2 °C (10h/14h) to ensure vernalization. Plants in the control environment were watered daily to container capacity, and fertilized weekly with Peters 20:20:20 delivered in line during watering. Each of the remaining experimental environments differed from the control in only one factor. Plants in the low-water environment were watered to container capacity when the soil moisture content of 10 randomly chosen pots had fallen 50 percent. Plants in the low-nutrients environment received only the nutrients initially in the potting medium and trace minerals in tap water. Three weeks after the seeds were sown, plants in the low-temperature environment were placed in an adjacent greenhouse room for a cold period of 4/2 °C (10h/14h) that was 3 weeks longer than in the other environments. With the exception of plants in the low-temperature environment during these 3 weeks, plants were arranged in a completely randomized design, and rotated and re-randomized weekly to minimize block and bench effects. Water and fertilizer treatments continued until all plants had senesced. Each plant's aboveground biomass was harvested when chlorophyll pigmentation in the panicles was no longer visible—167 to 259 days after emergence—then dried at room temperature for 16 weeks. Throughout the study, any extraneous plant material or collection bags were autoclaved before disposal to prevent escape of genetic material.

While the plants were actively growing, we recorded days to emergence, height of the tallest leaf every 30 days following emergence, width of the tallest leaf at 60 and 120 days after emergence, tiller number at 60 days after emergence, and days from emergence to flowering. At senescence, we recorded days from flowering to senescence, number of panicles, and first internode length of the tallest panicle. After harvest and drying, first internode diameter of the tallest panicle, aboveground vegetative biomass, panicle biomass, and presence of glume hairs were recorded. Three traits were also recorded before seeds were sown: weight of 50 seeds, seed length, and awn length.

Statistical Analyses

To assess trait differences among ranges, we compared responses using Multivariate Analysis of Variance (MANOVA) and Analysis of Variance (ANOVA) in Proc GLM (SAS 2000) with a two-stage nested design: population nested within range, and six replicates nested within population. Both population and range were fixed effects. Data from each environment were analyzed separately due to small but significant range by environment interactions. We conducted a multivariate analysis of seven of the response variables (height, leaf width, and tiller number at 60 days; culm diameter, vegetative biomass, panicle biomass, days from emergence to flowering) using Canonical Discriminant Function Analysis (SAS 2000). All European and New Zealand populations were included, but only the geographically central population from each of the six North American founder sites was included to facilitate interpretation of the scatterplot by reducing the amount of overlap in symbols. In all comparisons, differences were determined to be significant when $P < 0.05$.

Results and Discussion

We found significant differences among ranges for nearly every trait assessed in each of the four environments. For example, in all but the early cold treatments, plants from North America were significantly taller, those from New Zealand were shorter, and those from Europe were intermediate (fig. 1). Similarly, North American plants had wider leaves, New Zealand plants had narrower leaves, and European plants were intermediate (fig. 2). For aboveground vegetative biomass at senescence, North American plants had higher values and New Zealand plants had lower values than did the European plants in each treatment; however, differences were not significant in every comparison (fig. 3). The small number of populations from New Zealand ($n = 3$) reduced test power and significant differences in some cases.

For most of the remaining phenotypic traits we found significant differences among ranges in each experimental environment. In each of the four environments, North American plants flowered earliest and New Zealand plants latest (fig. 4)—147 days for North America, 151 for Europe, and

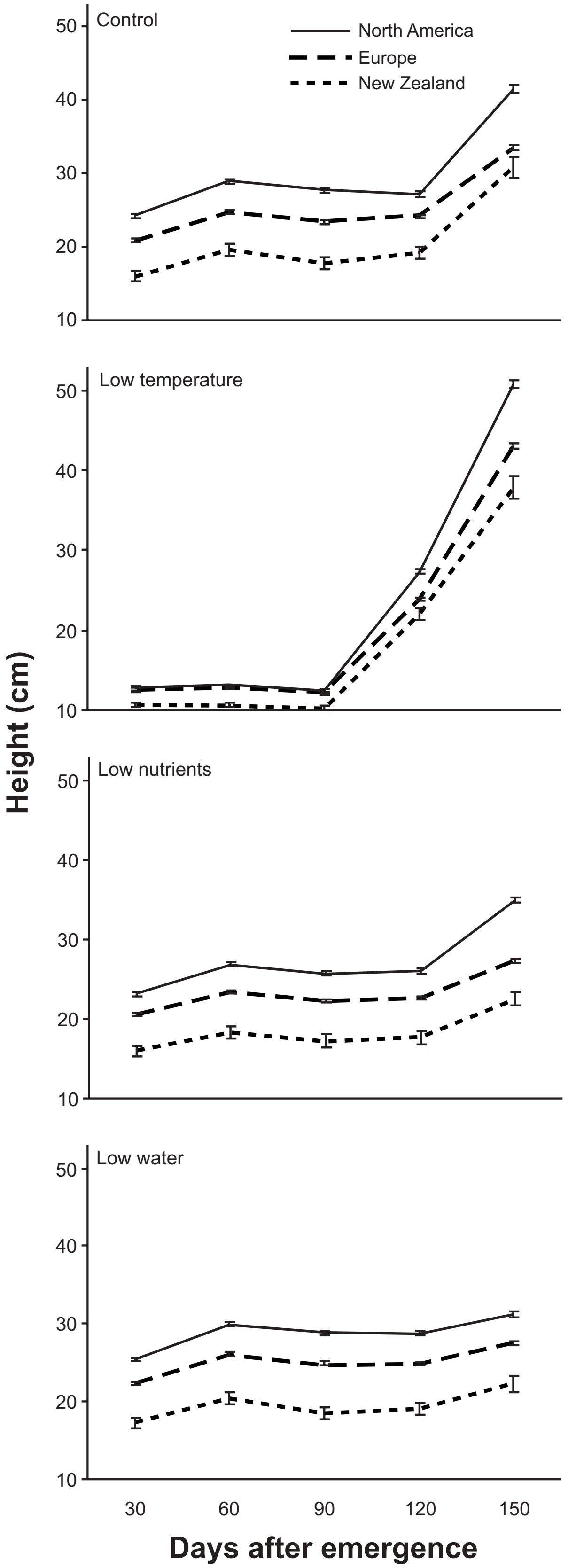


Figure 1—Mean height (cm) of downy brome populations from North America, Europe, and New Zealand at 30-day intervals after emergence in each of four test environments. Error bars indicate standard error.

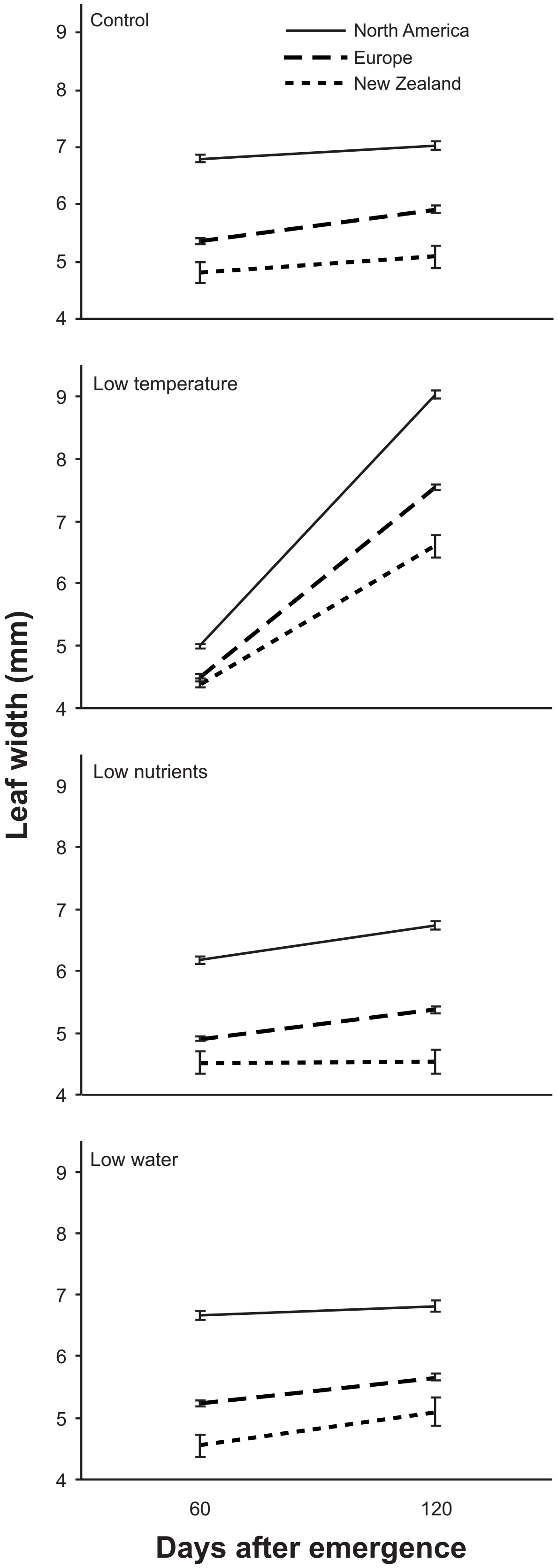


Figure 2—Mean leaf width (mm) of downy brome populations from North America, Europe, and New Zealand at 60-day intervals after emergence in each of four test environments. Error bars indicate standard error.

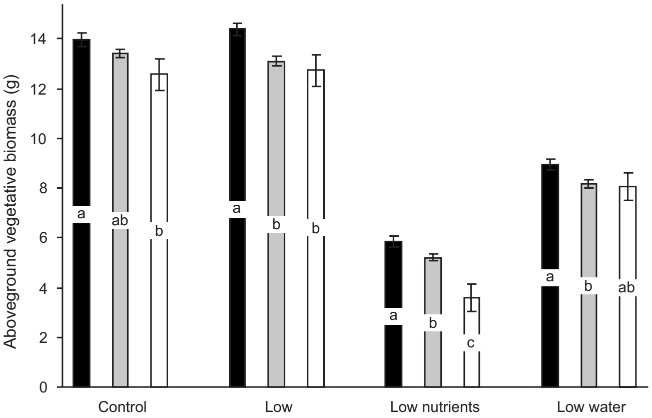


Figure 3—Aboveground vegetative biomass for downy brome populations from North America (black), Europe (gray), and New Zealand (white) in each of four environments. Error bars indicate standard error. Within environments, differing letters indicate significant differences (P < 0.05) among ranges.

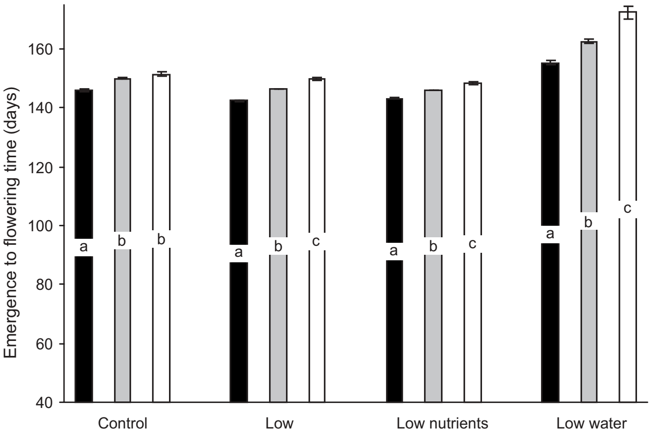


Figure 4—Time from emergence to flowering for downy brome populations from North America (black), Europe (gray), and New Zealand (white) in each of four environments. Error bars indicate standard error. Within environments, differing letters indicate significant differences (P < 0.05) among ranges.

156 days for New Zealand—when averaged across the four environments. Not only are these differences statistically significant, they are likely to be ecologically significant, because previous work (Mack and Pyke 1983, 1984; Rice and others 1992) has shown that a few days difference in flowering time can allow seed filling in arid environments.

Though population-level variability is not the key focus of this study, we note that for nearly every trait assessed, we found significant differences among populations within a single range. This parallels findings by other researchers working on Western North American populations and measuring traits such as biomass and seed dormancy (Meyer and Allen 1999; Rice and Mack 1991a,b). Additionally, we found less phenotypic variability among North American and New Zealand populations than European populations, as would be expected with the restricted genetic variability following founder events based on a small number of introduced genotypes (Barrett and Husband 1990).

In analyzing all phenotypic traits simultaneously using Canonical Discriminant Function Analysis in SAS, we found that the centroids for each range were significantly different from each other at $P < 0.0001$ (fig. 5). In each of the four environments, the introduced phenotypes are essentially a subset of the native phenotypes. North American phenotypes most closely match those from Austria, Slovakia, and Southeastern Germany, while New Zealand phenotypes mostly closely match those from Northwestern Germany and The Netherlands—areas that lie geographically to the northwest of the North American matches.

While plants from the three ranges clearly differ in phenotype and vigor, fitness differences may occur as well. We found differences in mortality during a single time period when plants in the low water treatment became extra dry in a sudden spell of very hot days. North American plants had a significantly lower death rate, 8.33 ± 2.66 percent, compared to European and New Zealand plants at 22.95 ± 2.69 percent and 27.78 ± 10.60 percent, respectively. A set of experimental stress tests under different environments may show that North American plants typically have higher survival. They may also be more water use efficient, and we plan to compare water use efficiency among the ranges using carbon isotope analysis.

To further assess fitness, we are conducting seed germination trials and cleaning seeds from panicles to get a measure of seed biomass produced in the four treatments. We will use these two measures to calculate relative fitness values for each population. Although these data are still being collected, some insight may be found in a previous analysis we conducted in a single environment with one North American population from Smoot Hill, WA, and 10 populations from Central and Western Europe. In this pilot study, the North American plants ranked second for relative fitness between populations from first-ranked Bratislava, Slovakia, and third-ranked Vienna, Austria. Plants from these two European populations were among those that displayed phenotypes most similar to those from North America in the four greenhouse environments, and which were most genetically similar based on allozyme data (Novak and Mack 2001). If the pattern found in the pilot study corresponds to the larger test in four environments, we expect plants from Western North America to rank among those with highest fitness from the native range.

Conclusions

To summarize our findings, plants from the invasive range in North America were typically largest and most vigorous, followed by those from the native European range, and lastly those from the naturalized New Zealand range. These and other phenotypic differences we have documented among ranges indicate that genetic differences, rather than environment alone, explain many performance differences between native and introduced populations. Our findings highlight the importance of studying representative genotypes

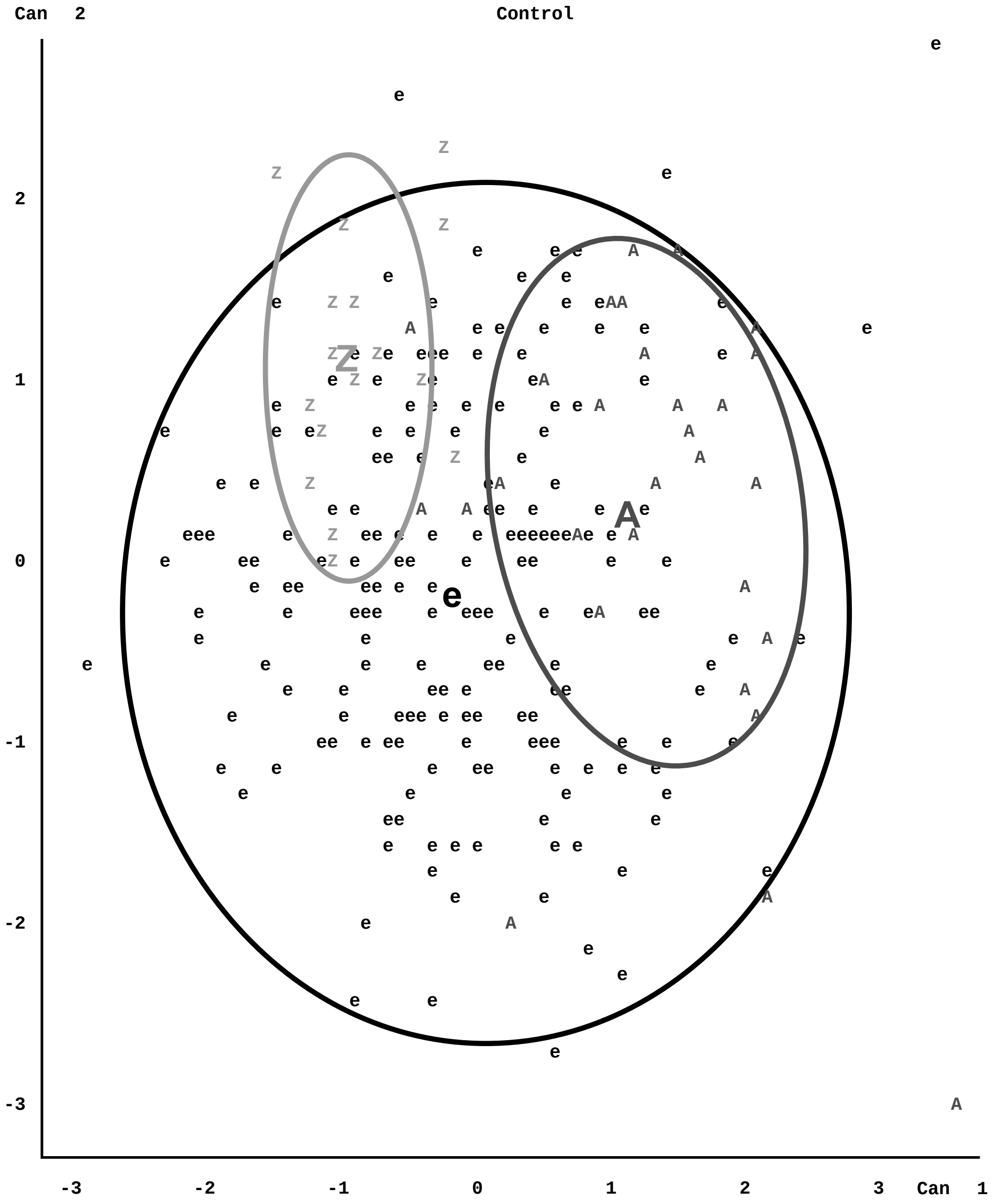


Figure 5—Canonical Discriminant Function Analyses of seven phenotypic measurements of downy brome in the control environment. Centroids of each range are indicated by large letters: New Zealand (Z), Europe (e), and North America (A).

from across a species' range in screening for invasive potential, testing for effectiveness of herbicides and biocontrol agents, or similar studies. These results have ramifications for quarantine regulations because, at present, an introduced species is often not considered to be a threat if it has not been a problem in the past. Our study illustrates that the outcome of an introduction can be very different based on random genetic sampling in the native range. Serious ecological consequences may have occurred in New Zealand if favorable habitats on the South Island had gained plants from the populations that we unfortunately gained in Western North America.

Acknowledgments

We thank J. R. Alldredge, M. A. Evans, and M. S. Minton for statistical assistance; R. S. Bussa, C. A. Cody, M. A. Darbous, M. Erneberg, S. K. Foster, G. K. Radamaker, B. D. Veley, and K. D. Walker for technical assistance; and J. Baar, L. Barkan, C. E. Hellquist, A. Klaudisova, N. L. Mack, H. C. Prentice, R. R. Pattison, K. D. Rode, T. Sebastia-Alvarez, A. Tudela, and L. J. van der Ent for seed collection assistance. We acknowledge helpful discussions with R. A. Black, L. D. Hufford, M. Morgan, S. J. Novak, P. S. Soltis, and M. S. Webster. Funding sources include Betty W. Higinbotham and Noe Higinbotham Research Awards, Hardman Foundation Award, Sigma Xi—Scientific Research Society Grant-in-Aid-of-Research, and Washington State University College of Sciences and School of Biological Sciences.

References

Barrett, S. C. H.; Husband, B. C. 1990. The genetics of plant migration and colonization. In: Brown, A. H. D.; Clegg, M. T.; Kahler, A. L.; Weir, B. S., eds. Plant population genetics, breeding, and genetic resources. Sunderland: Sinauer Associates.

Connor, H. E. 1964. Tussock grassland communities in the Mackenzie Country, South Canterbury, New Zealand. New Zealand Journal of Botany. 2: 325–351.

Kirk, T. 1869. On the naturalized plants of New Zealand, especially with regard to those occurring in the Province of Auckland. Transactions Proceedings of New Zealand Institute. 2: 131–146.

Lowe, A. D. 1961. The cereal aphid in wheat. New Zealand Wheat Review. 8: 21–26.

Mack, R. N. 1981. Invasion of *Bromus tectorum* L. into Western North America: an ecological chronicle. Agro-Ecosystems. 7.

Mack, R. N. 1986. Alien plant invasion in the Intermountain West: a case history. In: Mooney, H. A.; Drake, J. A., eds. Ecology of biological invasions of North America and Hawaii. New York: Springer-Verlag: 192–213.

Mack, R. N.; Pyke, D. A. 1983. The demography of *Bromus tectorum* L.: variation in time and space. Journal of Ecology. 71: 69–93.

Mack, R. N.; Pyke, D. A. 1984. The demography of *Bromus tectorum*: the role of microclimate, predation and disease. Journal of Ecology. 72: 731–748.

Meyer, S. E.; Allen, P. S. 1999. Ecological genetics of seed germination regulation in *Bromus tectorum* L. I. Phenotypic variance among and within populations. Oecologia. 120: 27–34.

Novak, S. J.; Mack, R. N. 2001. Tracing plant introduction and spread: genetic evidence from *Bromus tectorum* (cheatgrass). Bioscience. 51: 114–122.

Pergande, T. 1904. On some of the aphides affecting grains and grasses of the United States. USDA Division of Entomology Bulletin. 44: 5–23.

Rice, K. J.; Black, R. A.; Radamaker, G.; Evans, R. D. 1992. Photosynthesis, growth, and biomass allocation in habitat ecotypes of cheatgrass (*Bromus tectorum*). Functional Ecology. 6: 32–40.

Rice, K. J.; Mack, R. N. 1991a. Ecological genetics of *Bromus tectorum*. 1. A hierarchical analysis of phenotypic variation. Oecologia. 88: 77–83.

Rice, K. J.; Mack, R. N. 1991b. Ecological genetics of *Bromus tectorum*. 3. The demography of reciprocally sown populations. Oecologia. 88: 91–101.

Roach, D. A.; Wulff, R. D. 1987. Maternal effects in plants. Annual Review of Ecology and Systematics. 18: 209–235.

SAS. 2000. Version 8.1. Cary, NC: SAS Institute, Inc.

Schaal, B. A. 1984. Life-history variation, natural selection, and maternal effects in plant populations. In: Dirzo, R.; Sarukhan, J., eds. Perspectives on plant population ecology. Sunderland: Sinauer Associates: 188–207.

Wardle, P. 1991. Vegetation of New Zealand. Cambridge University Press.

Williams, P. A. 1980. *Vittadinia triloba* and *Rumex acetosella* communities in the semi-arid regions of the South Island. New Zealand Journal of Ecology. 3: 13–22.

Root Growth of Apache Plume and Serviceberry on Molybdenum Mine Overburden in Northern New Mexico

Mary I. Williams
Mohammed Tahboub
John T. Harrington
David R. Dreesen
April Ulery

Abstract: This study evaluated root growth of Apache plume (*Fallugia paradoxa*) and Saskatoon serviceberry (*Amelanchier alnifolia*) on overburden at the Molycorp mine near Questa, NM. Container grown, 1-year-old seedlings were transplanted, and either fertilized or not fertilized at the time of planting in August 1995. Survival and shoot growth were monitored in 1996 and 2000. Root density was determined at three distances (planes) from the base of the plant at six depths in 2000. Fertilization effects on serviceberry root densities were depth dependent. Total root density of unfertilized plants was greater than fertilized plants. Serviceberry total root density differed among planes (distances from base of plant) between fertilization treatments. Fertilized plants had fewer roots in the 10-cm plane relative to the 20- and 30-cm planes. Fertilized plants of Apache plume had higher total root densities at depths >20 cm within the 20-cm plane than plants not fertilized at time of planting. Although overall performance in terms of shoot growth was positive for both species, survival was generally low and root density varied when fertilized at time of planting. Factors including fertilizer characteristics, planting date, and site conditions may have influenced species performance.

Introduction

New Mexico State and Federal laws require that mined lands be reclaimed to support a designated postmining land use (State of New Mexico 1999). Forestry as a postmining land use has been encouraged by regulatory agencies since the mid to late 1990s (Boyce 1999). Metal mines within the mountainous Western United States including the Molycorp molybdenum mine near Questa, NM, are selecting forestry as a postmine land use to re-establish a plant community comparable to adjacent native vegetation.

Open-pit mining at the molybdenum mine generated over 300 million metric tons of overburden from 1965 until 1983. The overburden exists in piles that range in altitude from 2,400 to 3,000 m and are composed of mixed igneous rocks (rhyolite and andesite) and black andesite and aplite materials (referred to as neutral rock). Mine overburden can be low in organic matter, soil microorganisms, and plant nutrients such as nitrogen and phosphorus and can lack soil structure and texture that are important to soil fertility and water holding capacity (Allen 1989; Feagley 1985). These properties make it challenging for plants to establish, thus overburden or plant amendments are often recommended (Brown and others 1996; Gardiner 1993).

Research studies on the survival of directly transplanted trees and shrubs on the overburden began in the early 1990s (Harrington and others 2001a,b,c). These studies indicated that the overburden was suitable to support plant life, in terms of transplant survival. In most instances, however, shoot growth was limited. Other research has shown that shoot growth of newly transplanted tree and shrub seedlings can benefit from supplemental fertilization in both minimally disturbed (Fan and others 2002; Houle and Babeux 1994; Walker 1999a) and drastically disturbed ecosystems (Fisher and others 1983; Voeller and others 1998; Walker 1999b). Growth response to fertilizer application, however, can be both species specific (Voeller and others 1998; Houle and Babeux 1994) and site specific (Gleason and others 1990).

The ability of transplanted seedlings to establish new roots into a planting medium is essential to their survival and subsequent growth. Plants with a well-established root system add to the success of postmine revegetation, control erosion, and improve overall postmine conditions. Most fertilization studies, however, focus primarily on shoot growth characteristics and disregard belowground growth. Early plantings of ponderosa pine (*Pinus ponderosa*) at the Molycorp mine were evaluated for root growth after 6 years of growth. Rooting depth of some plants extended beyond 2 m in the

---

In: Hild, Ann L.; Shaw, Nancy L.; Meyer, Susan E.; Booth, D. Terrance; McArthur, E. Durant, comps. 2004. Seed and soil dynamics in shrubland ecosystems: proceedings; 2002 August 12–16; Laramie, WY. Proceedings RMRS-P-31. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Mary I. Williams and John T. Harrington are Senior Research Assistant and Associate Professor and Superintendent, Mora Research Center, New Mexico State University, P.O. Box 359, Mora, NM 87732, U.S.A., e-mail: maiwill@nmsu.edu. Mohammed Tahboub and April Ulery are Graduate Research Assistant and Assistant Professor, Department of Agronomy and Horticulture, New Mexico State University, Las Cruces, NM, U.S.A. David R. Dreesen is an Agronomist, U.S. Department of Agriculture, Natural Resources and Conservation Service, Plant Materials Center, Los Lunas, NM 87031, U.S.A. FAX: (505) 387-9012.

overburden (Harrington, unpublished data). This observation led to questions regarding growth allocation of directly transplanted trees and shrubs at the Molycorp mine with fertilization treatments.

This study evaluated the influence of fertilization at time of planting on root distribution and growth of two native woody shrubs, Saskatoon serviceberry (*Amelanchier alnifolia*) (hereafter referred to as serviceberry) and Apache plume (*Fallugia paradoxa*), transplanted into overburden at the Molycorp Questa Mine. Root densities and distributions were described at six depths and three distances from the base of each plant to examine the effects of fertilizer applications at the time of planting.

Materials and Methods

Site Description

Molycorp, Inc., molybdenum mine is located near Questa, NM, in the Red River Canyon and produces the largest amount of molybdenum in the State (Schilling 1965; State of New Mexico 1999). Overburden from open-pit mining was deposited on the steep mountainsides of Red River Canyon. The overburden piles are highly heterogeneous, consisting of parent materials with a range of acidic and soluble salt levels (Steffan and Kirsten 1995).

Vegetative communities surrounding the mine consist of coniferous forests dominated by ponderosa pine, mixed conifer (Douglas fir [*Pseudotsuga menziesii*] and limber pine [*P. flexilis*]), and spruce-fir (Engelmann spruce [*Picea engelmannii*] and white fir [*Abies concolor*]) stands (Harrington and Wagner 1994). Naturally formed alteration scars occurring in acidic (pH = 1.8 to 3.5) materials, occur at the mine and throughout the Red River Canyon (Meyer and Leonardson 1990; Steffan and Kirsten 1995). Plants from adjacent communities have established in the periphery of these scars (Wagner and Harrington 1994).

Two planting sites (Blind Gulch and Spring Gulch) were located on terraced portions of overburden piles at the molybdenum mine. Spring Gulch (2,780 m) is composed primarily of neutral rock with an average pH of 7.7, electrical conductivity (EC) of 0.5 dS/m, and coarse fragment fraction (content) of 69 percent. Blind Gulch (2,860 m) consists of both acidic and neutral overburden materials. Chemical composition of the overburden across the planting area at Blind Gulch was varied. Average values for pH, EC, and coarse fragment fraction (content) in planting blocks one and two were 4.4 and 7.3, 1.2 and 1.3 dS/m, and 60 and 59 percent, respectively.

Planting Stock

Seedlings of Apache plume (Questa, NM, seed source) and serviceberry (Utah seed source) were propagated at the Natural Resources Conservation Service Plant Materials Center in Los Lunas, NM. Seedlings were grown in 164-cm^3 containers (Ray Leach Super Cells) in a peat:perlite growing media (two parts peat moss and one part perlite by volume). Plants were fertilized with a water soluble 20-10-20 fertilizer (Peter's Peat Lite Special).

Fertilization Treatments

Prior to transplanting, sites were ripped to a depth of 45 cm and irrigated. Ripping was accomplished using three 65-cm ripping bars attached to the back of a crawler tractor. In August 1995, seedlings (approximately 10 to 20 cm tall) were transplanted into the two sites in a randomized complete block design and irrigated the day after planting. Three blocks per site were established and each block had two parallel rows, 50 cm apart. Within each row, plant spacing was 30 cm. One row of each replicate block received fertilization treatment at the time of planting and the other row did not receive fertilizer (control plots). Six grams of Sierra, Inc., 17-6-12 plus micronutrients slow-release fertilizer (Scotts Company, Marysville, OH) were placed into each planting hole prior to transplanting the seedlings. Release duration of this fertilizer is 3 to 4 months at 21 °C. From 1996 through 2000 all plants received supplemental fertilization once each year.

Survival and Shoot Growth

In September 1996 and August 2000 survival of both species was documented. In Spring 2001, shoot growth (height and crown width) was measured to the nearest centimeter for each plant. An average crown width was calculated for each plant using two perpendicular measurements of crown width oriented at 45 degrees to the direction of the planting row.

Root Measurements

In blocks one and two from each site, two plants per species per fertilization treatment were measured for root growth and distribution. Roots were evaluated using techniques described by Parsons and others (1998). Initial excavation in November 2000 was performed using a backhoe to create a trench 1.5 m deep and 2 m long, 45 cm from the base of each shrub row. A 30 by 30 cm vertical plane was hand excavated 30 cm from the base of each plant where a 30 by 30 cm sampling frame was placed for root evaluation. The frame was constructed out of clear Plexiglas and divided by lines into 36, 5 by 5 cm grid cells. In each grid cell, roots were counted and divided into three diameter classes: <0.5, 0.5 to 2.0, and >2.0 mm. Root measurements were repeated at 20 and 10 cm from the base of each plant within the same vertical sampling frame.

Data Analysis

The experimental design was a completely randomized design set in a split-split plot. Whole plot treatment was site and block within site was the whole plot error term. The split factor was fertilization treatment and the split-split factors were plane and depth. "Plane" refers to the horizontal distance away from the plant perpendicular to the row (10, 20, or 30 cm).

Survival of each species in 1996 and 2000 was analyzed through Chi-square tests in SAS using PROC FREQ (SAS Institute 1997). Shoot growth (height and crown width) was analyzed for each species using analysis of variance in SAS

(PROC GLM) to indicate simple and interaction effects of site and treatment.

Root counts were analyzed separately for each species using analysis of variance in a 2 (site) x 2 (fertilization treatment) x 3 (plane) x 6 (depth) factorial (PROC MIXED, SAS Institute 1997). Roots from three categories were combined for a weighted total to obtain a total root density (number of roots per 150 cm^2). Roots 0 to 0.05 mm were assigned a midpoint value of 0.025, roots 0.05 to 2.00 mm were assigned a midpoint value of 1.25, and roots greater than 2.00 mm were assigned a midpoint value of 2.25.

For root response, PROC MIXED calculated F statistics, means, and standard errors of both main effects and interaction combinations. Main effects of plane and depth and their interactions with fertilization treatments were evaluated, and least significant differences (LSD) were carried out for pairwise comparisons of main effects of plane and depth on root growth. All treatment effects for survival, and shoot and root growth were evaluated for significance at the 0.05 alpha level.

Results

Saskatoon Serviceberry

Fertilization at time of planting increased serviceberry crown width relative to unfertilized control plants ($p = 0.0015$). Crown widths of fertilized and control plants were 31.2 and 19.0 cm, respectively. However, fertilization at time of planting reduced survival of serviceberry, compared to controls, at both planting sites in 1996 ($P = 0.0006$) and 2000 ($p = 0.0002$). Survival of nonfertilized control plants was highest at the Spring Gulch site (table 1).

Fertilization at time of planting influenced total root density of serviceberry depending on sampling depth ($P < 0.0001$; fig. 1). Fertilized plants had lower total root densities at 5- to 10- and 10- to 15-cm depths than control plants. Across horizontal planes, fertilization treatments influenced total root density of serviceberry ($P < 0.010$, fig. 2). Serviceberry plants not fertilized at time of planting had greater total root density in the 10-cm plane than fertilized plants.

Apache Plume

Shoot growth of Apache plume plants fertilized at time of planting was greater than unfertilized plants (height, $P < 0.0001$; crown width, $P = 0.0022$). Average height and crown width of fertilized plants were 42.4 and 43.2 cm, while average height and crown width of control plants were 21.3 and 29.0 cm, respectively. Survival of Apache plume was influenced by site and fertilization treatments in 1996 ($p = 0.0035$) and 2000 ($p = 0.0018$). Nonfertilized plants at Spring Gulch had the highest survival in both years out of all site by treatment combinations, while fertilized plants at Blind Gulch had the lowest survival in 1996 and 2000 (table 2).

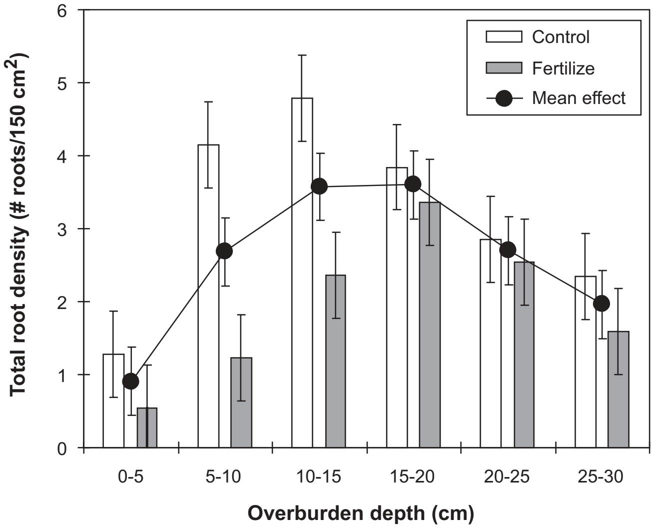


Figure 1—Total root density of serviceberry for control and fertilization treatments across overburden depths. Mean represents the effect of overburden depth averaged across fertilization treatments. Bars represent ± one standard error, n = 4.

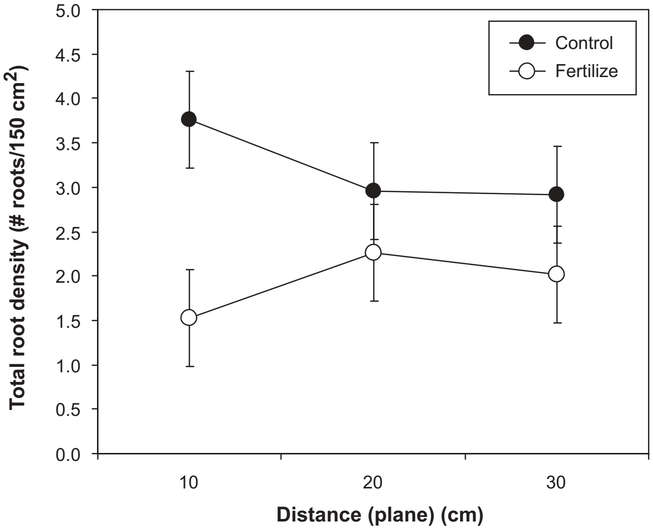


Figure 2—Total root density of serviceberry for control and fertilization treatments at three distances (planes). Bars represent ± one standard error, n = 4.

Table 1—One- and 5-year survival of serviceberry by site and fertilization at time of planting.

Site	Treatment	Survival[a] 1996	Survival[a] 2000	Percent[b]
Spring Gulch	Control	15	14	93
Blind Gulch	Control	10	10	67
Spring Gulch	Fertilize	6	4	27
Blind Gulch	Fertilize	5	4	27

[a] Survival as in number of individual plants, n = 15.
[b] Percent survival in 2000.

Fertilization at time of planting influenced Apache plume total root density depending on depth and plane ($P = 0.0012$;

Table 2 —One- and five-year survival of Apache plume by site and fertilization at time of planting.

Site	Treatment	Survival[a] 1996	Survival[a] 2000	Percent[b]
Spring Gulch	Control	21	20	95
Blind Gulch	Control	13	12	57
Spring Gulch	Fertilize	16	16	76
Blind Gulch	Fertilize	11	9	43

[a] Survival as in number of individual plants, n = 21.
[b] Percent survival in 2000.

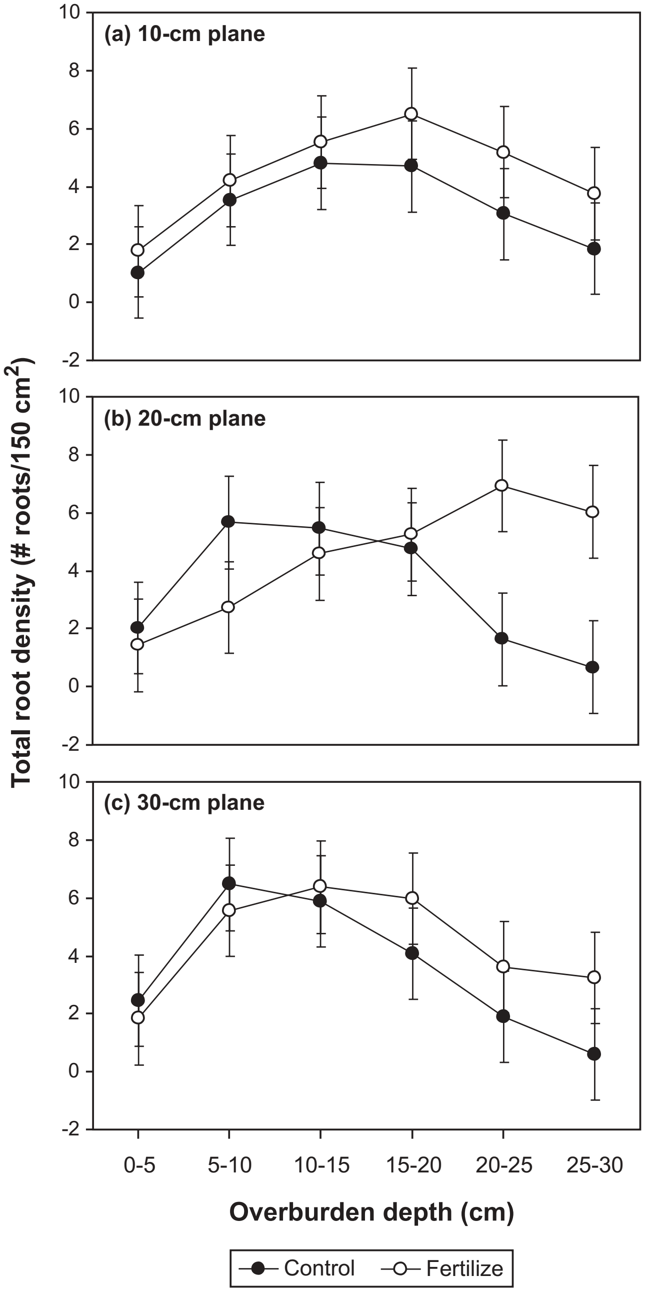


Figure 3—Total root density of Apache plume for control and fertilization treatments across overburden depths at three distances (planes). Bars represent ± one standard error, n = 4.

fig. 3). In the 20-cm plane, total root density of fertilized plants was greater at depths below 20 cm than all other treatments.

Discussion

Survival and Shoot Growth

Survival of fertilized serviceberry and Apache plume plants was low the first year after planting, although fertilized plants that survived were larger than control plants. Increased shoot growth with fertilizer applications is concurrent with other literature. Burgess and others (1995) found NPK fertilization treatments improved shoot growth of white pine (*Pinus strobiformis*). Fertilizer applications on a reclamation site in Idaho increased growth of both native and introduced plant species (Williams and others 1990). Nitrogen and phosphorus applications greatly increased pine seedling height on mine overburden in Alabama (Zarger and others 1973).

Low survival has been associated with the use of slow-release fertilizers in other studies. Fisher and others (1983) observed slow-release fertilizer caused high mortality in juniper seedlings (*Juniperus monosperma*). At an eastern Sierra Nevada surface mine, slow-release fertilizers applied at doses of 30 g increased mortality of containerized, transplanted Jeffrey pine (*Pinus jeffreyi*), whereas doses of 10 and 20 g did not affect mortality (Walker 1999b). Transplanting date and release time of the fertilizer used in the study may have caused the observed mortality during the first year for serviceberry. Fisher and others (1983) suggest transplanting and fertilizing containerized tree seedlings during the summer rainfall period (July) in the Southwest rather than in late summer and fall. Slow-release fertilizer applications in August were more detrimental to juniper seedling growth and survival than May and July applications. It was speculated that low night temperatures following recent nutrient additions resulted in frost damage in August (Fisher and others 1983). Mortality of ponderosa pine seedlings in northern Idaho was influenced by dose and rate of slow-release fertilizer, with high doses and 9- and 12-month release times increasing mortality (Fan and others 2002).

Survival and shoot growth of transplanted and fertilized woody seedlings appear to be influenced by many abiotic factors including planting date and the amount, formulation, and rate of release of slow-release fertilizer. Based on published reports and our findings, transplanting Apache plume and serviceberry earlier in the growing season, early to midsummer, with a concurrent application of a slow-release fertilizer that releases nutrients when plants are actively growing, may reduce mortality and promote shoot growth for both species.

Root Growth

Fertilization treatment effects on plant root density and distribution vary in the literature. In this study, there was no main effect of fertilization on overall root density for either species, but fertilization at time of planting did affect root distribution. Studies have shown alteration in plant root distribution in relation to fertilizer applications. For example, grasses increased their root growth in response to increased soil nutrients (Eissenstat and Caldwell 1988). Friend and others (1990) found that Douglas-fir plants produced more roots in nitrogen-rich than in nitrogen-poor microenvironments. In nitrogen stressed environments, Douglas-fir plants had a greater frequency of roots within nitrogen rich microenvironments than in nonstressed environments (Friend and others 1990). Similarly, Ringwall and others (2000) observed that fertilized leafy spurge plants allocated a greater portion of root biomass within the first 10 cm of soil and distributed a larger portion of roots in fertilized areas of the planting medium. It appears that root system distribution can be manipulated by fertilization at time of planting, but responses may be species dependent, as seen in our study.

Fertilization at time of planting had a negative effect on total root density of serviceberry at the base of the plant relative to the nonfertilized control. The rapid release of nutrients coupled with transplanting in late summer when plants were still actively growing may have promoted shoot development at the expense of root development into the overburden. As a consequence, plants receiving fertilizer at time of planting may have had insufficient root systems to support their growth and survival during the first year following plantings. Fertilization had an overall positive effect on total root density of Apache plume deeper in the profile at 20 cm from the base of the plant. Although fertilization decreased survival of Apache plume, its effect on shoot growth and root density suggests that the treatments were not as detrimental to the plant's performance as it was in serviceberry. Species were analyzed separately in this study; however, comparisons as to their response to fertilization at time of planting are important for future decisions about species selection and revegetation designs.

Fertilizer applications at time of planting may increase the establishment of herbaceous species (annuals, grasses, and forbs), which can negatively impact (for example, nutrient and water competition) survival and shoot and root growth of transplanted shrubs and trees (Cook and others 1974). Although not measured, plots fertilized at time of planting did have an observable increase of volunteer herbaceous plants (grasses and annual forbs) compared to control plots in 2000. It is not known when these plants became established, but favorable conditions did exist for them to establish within these plots. Favorable conditions may include fertilizer applications and lack of root competition near the soil surface (<20 cm), since both species fertilized at time of planting allocated a greater portion of roots deeper in the soil than at the surface. However, further evaluations are needed to determine whether the observed root response in both species was due directly to fertilizer applications or indirectly from competition from volunteer plants, or both.

Conclusions

Although overall performance in terms of shoot growth was positive for both species when fertilized at time of planting, other fertilizer-related factors will need to be investigated to enhance establishment, growth, and long-term survival of plants planted directly into mine overburden at high elevations. Slow-release fertilizer formulation, release rate and total amount applied should be investigated more closely. While these factors have been investigated in other systems (Fan and others 2002; Walker 1999a,b), the impact of these treatments on plants at high elevations (>2,500 m) remains largely unknown.

Additional factors, which need further investigation, are related to fertilizer treatments for high elevation planting and include time of planting relative to the end of the growing season. Previous studies at this mine indicate two periods suitable, in terms of available moisture, for transplanting. These are during the midsummer rain period and in early fall. Incorporation of fertilizer, in particular nitrogen fertilizer, on fall plantings is not recommended; however, further work is warranted to look at planting and fertilizing earlier in the growing season than was performed in this study. The effects of incorporating slow-release fertilizer at this time will impact plant response. Too slow a release rate or too short a timeframe to the end of the growing season may increase mortality rates. Transplanting in midsummer, as recommended by Fisher and others (1983), may have prevented mortality in both species when fertilized. Timed properly this treatment can result in larger, more vigorous plants.

References

Allen, M. F. 1989. Mycorrhizae and rehabilitation of disturbed arid soils: processes and practices. Arid Soil Research and Rehabilitation. 3: 229–241.

Boyce, Richard L.; Lucero, Scott A. 1999. Role of roots in winter water relations of Engelmann spruce saplings. Tree Physiology. 19: 893–898.

Brown, R. W.; Amacher, M. C.; Williams, B. D.; Mueggler, W. F.; Kotuby-Amacher, J. 1996. Revegetation of acidic mine spoils at high elevations: restoration of native plant communities. Association of Abandoned Mine Land Programs Conference; 1996 September 15–18; Kalispell, MT.

Burgess, D.; Baldock, J. A.; Wetzell, S.; Brand, D. G. 1995. Scarification, fertilization and herbicide treatment effects on planted conifers and soil fertility. Plant and Soil. 169: 513–522.

Cook, C. W.; Hyde, R. M.; Sims, P. L. 1974. Revegetation guidelines for surface mined areas. Science Series No 16. Fort Collins, CO: Colorado State University, Range Science Department.

Eissenstat, D. M.; Caldwell, M. M. 1988. Seasonal timing of root growth in favorable microsites. Ecology. 69: 870–873.

Fan, Zhaofei; Moore, James A.; Shafii, Bahman; Osborne, Harold L. 2002. Three-year response of ponderosa pine seedlings to controlled-release fertilizer applied at planting. Western Journal of Applied Forestry. 17: 154–164.

Feagley, S. E. 1985. Chemical, physical and mineralogical characteristics of the overburden. Southern Coop Series Bull. 294. Fayetteville: Arkansas Agricultural Experimental Station.

Fisher, James T.; McRae, John B.; Aldon, Earl F. 1983. Methods for establishing containerized native juniper on surface disturbed sites in the Southwest. In: Pope, P. E., ed. Better reclamation with trees conference: proceedings; 1983 June 2–3; Terre Haute, IN. Purdue University: 76–88.

Friend, Alexander L.; Eide, Marvin R.; Hinckley, Thomas M. 1990. Nitrogen stress alter root proliferation in Douglas-fir seedlings. Canadian Journal of Forest Research. 20: 1524–1529.

Gardiner, D. T. 1993. Revegetation status of reclaimed abandoned mined land in western North Dakota. Arid Soil Research and Rehabilitation. 7: 79–84.

Gleason, J. F.; Duryea, M.; Rose, R.; Atkinson, M. 1990. Nursery and fertilization of 2+0 ponderosa pine seedlings: the effect on morphology, physiology, and field performance. Canadian Journal of Forest Research. 20: 1766–1772.

Harrington, J. T.; Dreesen, D. R.; Wagner, A. M.; Murray, L.; Sun, P. 2001a. Results of species trials on low pH overburden materials for mine land reclamation. In: Barnhisel, R. I.; Buchanan, B. A.; Peterson, D.; Pfeil, J. J., comps. Land reclamation: a different approach: proceedings; 2001 June 3–7; Albuquerque, NM. Lexington, KY: American Society of Surface Mining and Reclamation.

Harrington, J. T.; Dreesen, D. R.; Wagner, A. M.; Murray, L.; Sun, P. 2001b. The influence of seed source and stock size on first-year performance of direct transplanted conifer seedlings. In: Barnhisel, R. I.; Buchanan, B. A.; Peterson, D.; Pfeil, J. J., comps. Land reclamation: a different approach: proceedings; 2001 June 3–7; Albuquerque, NM. Lexington, KY: American Society of Surface Mining and Reclamation.

Harrington, J. T.; Wagner, A. M.; Dreesen, D. R. 2001c. Influence of *pisolithus tinctorius* inoculation on greenhouse growth and first-year transplant survival of conifer seedlings. In: Barnhisel, R. I.; Buchanan, B. A.; Peterson, D.; Pfeil, J. J., comps. Land reclamation: a different approach: proceedings; 2001 June 3–7; Albuquerque, NM. Lexington, KY: American Society of Surface Mining and Reclamation.

Houle, G.; Babeux, P. 1994. Fertilizing and mulching influence on the performance of four native woody species suitable for revegetation in subarctic Quebec. Canadian Journal of Forest Research. 24: 2342–2349.

Meyer, J.; Leonardson, R. 1990. Tectonic, hydrothermal and geomorphic controls on alteration scar formation near Questa, New Mexico. In: New Mexico Geologic Society guidebook 41st field conference; Southern Sangre de Cristo Mountains, New Mexico: 417–422.

Parsons, W. F.; Ehrenfeld, J. G.; Handel, S. N. 1998. Vertical growth and mycorrhizal infection of woody plant roots as potential limits to the restoration of woodlands on landfills. Restoration Ecology. 6(3): 280–289.

Ringwall, Kirstin; Biondini, Mario E.; Grygiel, Carolyn E. 2000. Effects of nitrogen fertilization in leafy spurge root architecture. Journal of Range Management. 53: 228–232.

SAS Institute Inc. 1997. SAS/STAT® software: changes and enhancements through release 6.12. Cary, NC: SAS Institute Inc. 1167 p.

Schilling, J. H. 1965. Molybdenum resources of New Mexico. Socorro, NM: State Bureau of Mines and Minerals Resources, New Mexico Institute of Mining and Technology Campus Station. 76 p.

State of New Mexico. 1999. New Mexico Natural Resources: data and statistics for 1998. New Mexico Energy, Minerals and Natural Resources Department. Santa Fe: New Mexico Printing Office. 65 p.

Steffen, Robertson; Kirsten (SRK Inc.) 1995. Questa molybdenum mine geochemical assessment: Molycorp Inc. Lakewood, CO.

Voeller, P. J.; Zamora, B. A.; Harsh, J. 1998. Growth response of native shrubs to acid mine spoil and to proposed soil amendments. Plant and Soil. 198: 209–217.

Wagner, A. M.; Harrington, J. T. 1994. Revegetation report for Molycorp, Inc. New Mexico Mine Permit TA001RE. Questa, NM.

Walker, R. F. 1999a. Artificial regeneration of Jeffrey pine in the Sierra Nevada: growth, nutrition, and water relations as influenced by controlled release fertilization and solar protection. Journal of Sustainable Forestry. 9: 23–39.

Walker, R. F. 1999b. Reforestation of an eastern Sierra Nevada surface mine with containerized Jeffrey pine: seedling growth and nutritional responses to controlled release fertilization and ectomycorrhizal inoculation. Journal of Sustainable Forestry. 9: 127–147.

Williams, B. D.; Brown, R. W.; Sidle, R. C.; Mueggler, W. F. 1990. Greenhouse evaluation of reclamation treatments for perlite-pumice mine spoils. Res. Pap. INT-426. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 7 p.

Zarger, T. G.; Bengston, G. W.; Allen, J. C.; Mays, D. A. 1973. Use of fertilizers to speed pine establishment on reclaimed coal-mine spoil in northeastern Alabama: II. Field experiments. In: Hutnik, R. J.; Davis, R., ed. Ecology and reclamation of devastated land: volume II. New York: Gorden and Breach.

Importance of Genotype, Soil Type, and Location on the Performance of Parental and Hybrid Big Sagebrush Reciprocal Transplants in the Gardens of Salt Creek Canyon

Kathleen J. Miglia
D. Carl Freeman
E. Durant McArthur
Bruce N. Smith

Abstract: The majority of flowering plant species are descendent from hybridization events; therefore, understanding hybridization in nature is essential to understanding plant speciation. Hybrid zones, common and often stable, provide one source of hybridization. Stable hybrid zones are particularly important in evolutionary theory because they violate adaptive speciation theory and call into question the universality of reproductive isolation in speciation. Under this model, hybrids are assumed to be unfit regardless of environment, due to endogenous selection, thereby contributing to reproductive isolation. However, a number of stable hybrid zones show hybrids to be most fit within the hybrid zone due to ecological selection. Regardless of the type of selection occurring, stability of the hybrid zone results from a balance between gene flow and selection. What is not known is how hybridization allows hybrids to become adapted to the habitat of the hybrid zone. An understanding of the interactions between novel hybrid plant genotypes and their ecological habitats is important to understanding plant speciation. Results from a reciprocal transplant experiment involving the big sagebrush hybrid zone (*Artemisia tridentata* ssp. *tridentata* x *A. t.* ssp. *vaseyana*) in Salt Creek Canyon, UT, show that the parental and hybrid genotypes are not adapted to either the soils or location. Rather, it appears that the microorganisms in the soils are adapted to their location. It is possible that the plants are adapted to the microorganisms in their native soils. Our data also do not support the common assumption of hybrid unfitness.

Introduction

Hybridization plays a key role in adaptive speciation theory (Dobzhansky 1940; Grant 1963; Mayr 1942; Stebbins 1950) because it is necessary for reinforcement of premating isolating barriers. Accordingly, the parental taxa are believed to diverge genetically due to some period of isolation, and subsequently come into contact again forming hybrids. If these hybrids are unfit they will be selected against, and genes that cause the parental species not to mate with each other will spread, generating or reinforcing premating isolating barriers, with the hybrids and hybridization eliminated over time. However, if hybrids are more fit than the parental taxa, then introgression will occur with the replacement of the parental taxa by introgressed populations. Either way the hybrid zone should be ephemeral. Stable hybrid zones violate adaptive speciation theory because hybrids can persist indefinitely (for example, the cottonwood hybrid zone studied by Eckenwalder [1984] is believed to be 2 million years old).

Three models (reviewed by Arnold 1997) seek to explain stable hybrid zones, with each postulating that selection balances gene flow. The models differ in the nature of that selection and the importance of the environment. Stable plant hybrid zones are particularly useful for studying these models because plants can be easily used in reciprocal transplant experiments (Emms and Arnold 1997; Wang and others 1997) and are often well adapted to local environmental conditions (reviewed in Linhart and Grant 1997), which is a key feature in adaptive speciation.

The *Dynamic Equilibrium Model* (Barton 1979a,b; Barton and Hewitt 1985, 1989; Hewitt 1988) posits that endogenous selection against hybrids balances gene flow into the hybrid zone, thereby accounting for hybrid zone stability. It is predicted that the hybrid zone will become trapped in areas of low population density, fixing it in space, but otherwise the model is environmentally neutral. Data from the big sagebrush hybrid zone (the subject of this report) does not support this model for two main reasons: big sagebrush

---

In: Hild, Ann L.; Shaw, Nancy L.; Meyer, Susan E.; Booth, D. Terrance; McArthur, E. Durant, comps. 2004. Seed and soil dynamics in shrubland ecosystems: proceedings; 2002 August 12–16; Laramie, WY. Proceedings RMRS-P-31. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Kathleen J. Miglia is Research Associate and D. Carl Freeman is Professor, Department of Biological Sciences, Wayne State University, Detroit, MI 48202, U.S.A.; e-mail: kmiglia@sun.science.wayne.edu. E. Durant McArthur is Project Leader, Shrub Sciences Laboratory, Rocky Mountain Research Station, USDA Forest Service, Provo, UT 84606, U.S.A. Bruce N. Smith is Professor, Department of Plant and Animal Sciences, Brigham Young University, Provo, UT 84602, U.S.A.

hybrids are more fit than the parental taxa within the boundaries of the hybrid zone, but less fit outside it (Wang and others 1997), and the hybrid zone does not occur in a population density trough (Freeman and others 1999a,b).

The *Mosaic Hybrid Zone Model* (Britch and others 2001; Harrison 1990; Harrison and Rand 1989; Howard and others 1993; Rand and Harrison 1989; Rieseberg and others 1998; Ross and Harrison 2002) also posits endogenous selection against hybrids, but assumes that the hybrid zone is a mosaic of parental habitats. Exogenous selection acts against the nonindigenous parental genotype, and while hybrids are always produced, their formation is balanced by endogenous selection against them. Again, data from the parental and hybrid big sagebrush at Salt Creek Canyon do not support this model because hybrids are the most fit genotype within the hybrid zone (that is, there is no endogenous selection against hybrids in the hybrid zone) and the hybrid zone is not a patchwork of the two parental habitat types (Freeman and others 1999a; Wang and others 1997, 1998).

The *Bounded Hybrid Superiority Model* (Moore 1977) assumes hybrid superiority in the hybrid zone, with selection against nonindigenous genotypes in both the parental and hybrid zone habitats. Hybrids are thus believed to be adapted within, but not outside, the hybrid zone, with the parental genotypes likewise superiorly adapted to their indigenous habitats. Prior results of our reciprocal transplant experiments are entirely consistent with this model (Freeman and others 1999a; Wang and others 1997, 1998, 1999). Implicit in this theory is that the parental and hybrid habitats differ from one another, as do the niches of the parental taxa and their hybrids. Wang and others (1998, 1999) found such niche separation when they analyzed the elemental composition of soils and leaves from plants in the reciprocal transplant gardens at Salt Creek Canyon. For example, basin habitat soils are deeper, and have a higher pH and lower concentrations of K, Mg, and Ba than soils from the mountain habitat. The soils in the hybrid zone have some elements in greater (Ca, K, Na) or lesser (Cu) concentrations than the soils of either parental habitat; therefore, they cannot be simply considered intermediate between the parental populations (Wang and others 1998). Similarly, the concentration of B in the leaves of basin parental plants was three times higher in the basin garden than in either the middle hybrid or mountain gardens, while the concentration of B in leaves of middle hybrid plants was nearly three times greater in the middle hybrid zone garden than in either the basin or mountain gardens. Mountain plants exhibited equal concentrations of B in their leaves in the two parental gardens, but markedly lower concentrations in the middle hybrid zone garden, and the concentration of B in their leaves was markedly lower overall compared to the other genotypes. In conclusion, the genotype by environment interactions for leaf elemental concentrations of plants all grown in the same three gardens strongly indicated niche separation.

Whittam (1989) proposed that herbivorous insects are more abundant in plant hybrid zones because hybridization disrupts defensive coadapted gene complexes, rendering hybrids more palatable than parental populations. We examined phytophagous insects in the Salt Creek reciprocal transplant gardens (Graham and others 2001a,b). The hybrid zone and each parental habitat have unique insect communities, but the hybrids did not suffer higher insect densities. This again illustrates the different niches occupied by the different genotypes.

Plant community structure was not examined across the hybrid zone at Salt Creek Canyon because the area was reseeded; consequently, we examined the plant communities in a big sagebrush hybrid zone at Clear Creek Canyon in South Central Utah. We found that less than one-third of the species occur in both parental habitats; one-fourth of the species are unique to the basin habitat, and over half are unique to the mountain habitat. Fifteen species occur only within the hybrid zone (Freeman and others 1999a).

Together our prior data show that (1) basin and mountain big sagebrush and their hybrids are components of different biotic communities, (2) the hybrid zone occurs at an ecotone, and (3) hybrids are not universally unfit as the Dynamic Equilibrium and Mosaic Hybrid Zone models predict. Instead, genotype by environment interactions appear to be stabilizing the big sagebrush hybrid zone, in keeping with the predictions of the Bounded Hybrid Superiority model.

Methods

Our previous reciprocal transplant experiments involved growing parental and hybrid seedlings in the basin, mountain, and middle hybrid zone habitats. Because the taxa are parapatrically distributed along an elevational gradient, these earlier transplant experiments confounded both location and soils; consequently, we were unable to sort out the nature of the adaptation of the parental taxa and hybrids to their respective indigenous habitats. This confounding is especially true between the soils and temperature. Here, we report on a reciprocal transplant experiment in which both the soils and big sagebrush plants were transplanted into the gardens at Salt Creek Canyon.

Big Sagebrush

The big sagebrush (*Artemisia tridentata*) complex is a group of long-lived perennial, evergreen shrubs that dominates the landscape in the Western United States, providing forage for livestock and wildlife (Beetle 1960; McArthur 1994; Trimble 1989; Wambolt 1996; Welch and McArthur 1986). The species is composed of five subspecies: *A. t.* ssp. *tridentata* (basin big sagebrush), *A. t.* ssp. *vaseyana* (mountain big sagebrush), *A. t.* ssp. *wyomingensis* (Wyoming big sagebrush), *A. t.* ssp. *spiciformis* (snowbank big sagebrush), and *A. t.* ssp. *xericensis* (xeric big sagebrush). We examined one hybrid zone between basin and mountain big sagebrush. These subspecies differ genetically, morphologically, and ecologically from each other (table 1) and are sympatrically or parapatrically distributed, forming narrow hybrid zones along the sides of mountains or other points of contact.

Study Site

The study site is located in Salt Creek Canyon, near Nephi, in Juab County, UT, where basin and mountain big sagebrush are parapatrically distributed, with the basin subspecies occurring below 1,790 m in elevation and the

Table 1—Some characteristics that differ between basin and mountain big sagebrush.

Characteristic	Mountain	Basin	Reference
Habitat	Shallow, well-drained soils on foothills and mountains	Dry, deep, well-drained alluvial soils on plains, valleys, and foothills	McArthur 1994
Height	0.7 to 1.2 m	1.0 to 4.0 m	McArthur and Plummer 1978
Root system	Shallow	Deep	Welch and Jacobson 1988
Shoot morphology	• Spreading branches with an even-topped crown • Main stem is usually divided • Branches are layered	• Erect, heavily branched shrub with an uneven-topped crown • Main stem is undivided (trunk-like) • Branches are not layered	McArthur and others 1979
Leaf morphology	Broadly cuneate	Narrowly lanceolate	Beetle and Young 1965
Inflorescence	Spikate with many heads	Paniculate with few heads	Beetle and Young 1965
Palatability to mule deer	More palatable	Less palatable	Welch and McArthur 1986

mountain subspecies at elevations ranging from 1,850 m to timberline on neighboring Mt. Nebo (Graham and others 1995). The hybrid zone is a narrow band, approximately 380 m wide (per measurements by EDM and KJM in 2001), situated between the parental populations at elevations ranging from 1,790 to 1,830 m. Three fenced common gardens (8 by 15 m) were established across the hybrid zone in October 1994: one in each of the parental populations and one in the middle of the hybrid zone (Wang 1996).

Experimental Procedure

Battery operated HOBO™ Weather Station Data Loggers (Onset Computer Corp., Bourne, MA) were installed at each garden. This type of weather station can store up to 500,000 measurements, even if the batteries fail. Hourly temperatures were measured from September 12, 2000, until July 10, 2001. Hourly and daily average temperatures were analyzed using a mixed model ANOVA with site crossed with month and day nested within month. Daily, maximum, and minimum recorded temperatures were analyzed using a factorial design.

Putative reciprocal F_1, parental and indigenous hybrid seeds (B x M, M x B, B x B, M x M, and H x H, respectively, where B = basin big sagebrush, M = mountain big sagebrush, and H = hybrid between basin and mountain big sagebrush) were made in the field following the procedures of McArthur and others (1988). The first letter denotes the maternal parent and the second the paternal parent. While pollinations were highly controlled, some self-pollination may have occurred. In May 1999, seeds were germinated and subsequent seedlings raised in randomly arranged pots in the USDA Forest Service Shrub Sciences Laboratory greenhouse in Provo, UT. Seedlings were given equal amounts of water (table 2) when needed and pots rotated approximately every 6 weeks to balance any effects due to uneven greenhouse conditions. Greenhouse temperatures were controlled for favorable growth conditions (table 3). A 15:30:15 (available, water-soluble nitrogen:phosphate: potash) fertilizer solution was applied twice to the pots on January 25, 2000, and March 13, 2000. Five replicates of each genotype were planted in each of three soil types (basin, mountain, and middle-hybrid zone) collected at sites immediately adjacent to the three common gardens. Three trenches (approximately 60 cm wide, 90 cm deep, and 12 m long) were excavated with a backhoe in each garden in May 2000, lined with 4 ml polyethylene sheeting,

Table 2—The watering schedule of seedlings during their stay in the greenhouse. The amounts listed are approximate averages.

Date	Amount	Date	Amount	Date	Amount
	mL		*mL*		*mL*
6/24/99	104.9	9/20/99	136.3	1/28/00	93.1
6/26/99	61.8	9/24/99	86.5	2/01/00	129.7
6/28/99	193.1	9/28/99	91	2/04/00	101.3
7/01/99	84.5	10/01/99	111.7	2/07/00	115.8
7/06/99	118.5	10/05/99	82.2	2/11/00	88.0
7/08/99	106.5	10/09/99	124.4	2/15/00	109.8
7/12/99	87.7	10/13/99	104.7	2/18/00	74.8
7/14/99	117.6	10/15/99	97.9	2/22/00	86.4
7/16/99	77.9	10/21/99	72.8	2/25/00	79.4
7/19/99	122.8	10/27/99	111.1	2/28/00	87.5
7/21/99	53.8	11/01/99	90.0	3/03/00	106.7
7/23/99	120.9	11/04/99	111.4	3/06/00	93.7
7/26/99	94.7	11/08/99	98.8	3/10/00	117.2
7/28/99	118.8	11/12/99	100.0	3/13/00	157.4
7/30/99	83.6	11/16/99	136.5	3/17/00	160.7
8/01/99	115.3	11/22/99	85.5	3/20/00	164.2
8/04/99	102.4	11/27/99	160.7	3/24/00	137.5
8/07/99	74.2	12/01/99	78.4	3/27/00	152.9
8/09/99	128.7	12/06/99	125.1	3/31/00	166.1
8/12/99	123.4	12/13/99	87.5	4/03/00	137.9
8/14/99	99.8	12/16/99	186.6	4/06/00	160.5
8/17/99	102.6	12/20/99	116.0	4/09/00	135.5
8/20/99	121.0	12/23/99	70.8	4/12/00	187.9
8/23/99	101.0	12/26/99	60.1	4/14/00	207.8
8/26/99	70.6	12/29/99	80.6	4/17/00	187.6
8/29/99	57.8	1/02/00	108.6	4/19/00	190.8
9/01/99	103.9	1/06/00	75.3	4/21/00	69.0
9/07/99	120.1	1/10/00	66.8	4/24/00	170.0
9/09/99	100.5	1/14/00	115.7	4/28/00	174.0
9/11/99	96.4	1/17/00	75.3	5/01/00	125.0
9/14/99	114	1/21/00	87.3		
9/17/99	150.1	1/25/00	86.0		

Table 3—The average minimum and maximum temperatures in the greenhouse during the first year of seedling growth.

Month/year	Minimum temperature	Maximum temperature	N
	- - - - - - - - - - - - -°C -	- - - - - - - - - -	
6/99	13	41	21
7/99	15	40	31
8/99	16	38	31
9/99	9	35	30
10/99	8	39	31
11/99	8	35	30
12/99	9	34	31
1/00	9	31	31
2/00	9	34	29
3/00	10	37	31
4/00	10	39	30
5/00	11	36	8

and then filled with one of the same three soil types used in the greenhouse (that is, each of the three soil types was represented in each garden, including the indigenous soil type for each garden). One-year-old seedlings were then planted at random in the soil-filled trenches, with the choice of trench corresponding to the soil type to which a seedling was exposed during its stay in the greenhouse. There were 25 transplants per trench, giving a total of 75 transplants per garden. Each plant was marked with a labeled rebar. Plants were watered in the gardens weekly until watering was tapered to once every other week in mid-August 2000 and then stopped completely in mid-September 2000.

Data Collection and Statistical Analyses

Measurements were taken in August 2001 and August 2002 for the following growth and reproductive parameters: crown diameters 1 and 2 (crown 1 = greatest diameter of plant; crown 2 = diameter directly perpendicular to crown 1), tallest vegetative branch, tallest branch (tallest vegetative branch plus tallest inflorescence branch, when present), and length of three representative inflorescences

All temperature and morphological data were analyzed using the SPSS version 10.0 statistical software (SPSS Inc. 2001). All morphological data were analyzed using a MANOVA (SPSS Inc. 2001). Cases involving equal variances were followed by Bonferroni *post hoc* tests (SPSS). Data violating the assumption of equal variances were square-root transformed. In those cases where data transformation did not yield equal variances, Dunnett's T3 *post hoc* tests were performed (SPSS Inc. 2001).

Results

Temperature

The average daily minimum temperature differed significantly among the sites ($F_{2,873} = 19.20$, $P < 0.001$), with the basin garden site having the lowest average daily minimum temperature and the mountain garden site having higher daily minimum temperatures than either the basin or middle hybrid zone garden sites (table 4). The average daily and maximum temperatures did not differ significantly among the gardens; however, the middle hybrid zone garden site had both the lowest average daily temperature and highest average maximum temperature (table 4).

Height

We measured height two ways. First, we measured the height of the tallest vegetative branch and second, the height of the tallest branch that included an inflorescence. Both measures of height differed significantly among the gardens ($F_{2,152} = 8.117$, and 2.54, $P < 0.001$ and 0.08, respectively). Plants in the middle hybrid zone garden were significantly taller than those in the parental gardens; the average height of plants in the parental gardens did not differ from each other (table 5). Vegetative height also differed significantly among the genotypes ($F_{2,152} = 5.39$, $P < 0.001$). Both types of F_1 hybrids were significantly shorter than either the basin or indigenous hybrid plants. The F_1 plants did not differ in size from the mountain plants nor did mountain plants differ from either the basin or indigenous hybrid plants.

Vegetative height was independent of soil type; however, when the inflorescences were included, the middle hybrid zone soils produced significantly shorter plants than the other two soil types, which did not differ from each other. There was a highly significant garden by soil type interaction for both the vegetative and vegetative plus inflorescence measures of height ($F_{4,152} = 3.035$, and 7.574, respectively; $P < 0.02$ and 0.001, respectively). The trend was most dramatic for the inflorescence measure. In the basin garden, plants grew best in the basin soils. However, in the middle hybrid zone garden, middle hybrid zone soils yielded the greatest height. There was no trend observed for this measure in the mountain garden (figs. 1b and 1c).

Crown Diameter

Average crown diameter differed significantly among the genotypes ($F_{4,\ 152} = 4.23$, $P < 0.003$), but not among the gardens or soil types (table 6). Basin plants produced significantly smaller crown diameters than the other four genotypes, which did not differ among themselves. The garden by soil interaction was also significant ($F_{4,152} = 3.45$, $P < 0.01$) (fig. 1d). Indigenous hybrids produced their greatest crown diameter in the middle hybrid zone garden in the middle hybrid zone soils, whereas both of the parental genotypes

Table 4—Temperature profiles in each of the three gardens[a].

Site	Average daily temperature	Average daily minimum temperature	Average Daily maximum temperature
Basin	8.10a	–2.01a	18.66a
Hybrid	7.78a	–1.64a	19.68a
Mountain	8.14a	–0.10b	18.79a

[a] Different letters in columns indicate significant ($P < 0.05$) differences among values.

Table 5—Averages for vegetative height, vegetative plus inflorescence height, average inflorescence length and crown diameter for plants in each of the three gardens[a].

Garden	Vegetative height	Height including inflorescence	Average inflorescence length	Average crown diameter
	cm			
Basin	45.50a	48.62a	16.35a	43.56a
Hybrid	51.17b	54.22b	19.75b	48.37a
Mountain	43.09a	44.94a	16.58a	43.99a

[a]Different letters in columns indicate significant ($P < 0.05$) differences among values.

Table 6—Averages for vegetative height, vegetative plus inflorescence height, average inflorescence length and crown diameter for each of the five genotypes[a].

Genotype	Vegetative height	Height including inflorescence	Average inflorescence length	Average crown diameter
	cm			
B x B	51.02a	46.37a	15.42a	38.54a
B x M	40.38b	41.41a	15.43a	48.02b
M x B	43.50b	52.80a	19.49a	45.39b
M x M	50.42a	54.02a	19.46a	46.68b
H x H	45.81ab	49.79a	17.52a	49.04b

[a]Different letters in columns indicate significant ($P < 0.05$) differences among values.

produced their greatest crown diameters in the basin garden in the basin soils.

Inflorescence Length

The average inflorescence length differed significantly among the gardens $F_{2,152} = 2.87$, $P < 0.06$) and soils ($F_{2,152} = 5.74$, $P < 0.005$), but not among the genotypes. Plants in the middle hybrid zone garden produced significantly longer inflorescences than in the other two gardens, which did not differ from each other. Plants in the basin soils produced longer inflorescences than did plants in the middle hybrid zone soils. Inflorescence length of plants in the mountain soils was intermediate between those in the middle hybrid zone and basin soils and did not differ significantly from either. There was a highly significant garden by soil interaction ($F_{4,152} = 9.85$, $P < 0.001$). Plants in the middle hybrid zone soils performed very poorly in the basin garden, while in the middle hybrid zone garden, plants in the middle hybrid zone soils performed better than in the other two soil types (fig. 1a).

Discussion

Our findings indicate that the minimum temperature differed greatly across the hybrid zone. This finding coupled with those examining soils (Wang and others 1998), elemental leaf concentrations (Wang and others 1999), and the insect (Graham and others 2001a,b) and plant communities (Freeman and others 1999b) strongly indicate that the habitats occupied by the parental taxa and their hybrids are distinct from one another. Thus, the big sagebrush hybrid zone occurs at an ecotone. Our results also confirm earlier studies showing that the different subspecies of big sagebrush exhibit different morphologies and that these differences are preserved in common gardens—indicating a genetic basis for both the growth habits and niche separation (McArthur 1994; McArthur and others 1979; McArthur and Welch 1982). However, our most important result from this study is somewhat disconcerting. Earlier work (Wang and others 1997) had shown that basin and mountain big sagebrush are each adapted to their indigenous habitat and that indigenous hybrids were the most fit genotype within the hybrid zone. The transplant experiments involved in that study confounded the physical location with the soils. In the present study, we reciprocally transplanted both the soils and seedlings into the gardens to sort out these effects, if any. We anticipated that the seedlings might be adapted to their indigenous soils and perhaps their indigenous physical location, as well. This is not what we observed. Neither the genotype-by-garden nor garden-by-soil interactions were significant for any variable. However, the garden-by-soil interaction was significant for every variable, which was indicative of adaptation in two cases: basin soils in the basin garden and middle hybrid zone soils in the middle hybrid zone garden. This leads us to conclude that the indigenous *soils* are adapted at each of these locations, implying that it is the soil microorganisms that have become adapted to a particular location and not the plants themselves. The results of this study coupled with our earlier results (Wang and others 1997) imply that the different genotypes must be adapted to the indigenous microorganisms and that these microorganisms are adapted to the soils and physical location in the garden of their indigenous habitat. We have yet to determine whether or not this is case, and also if the microorganisms in the middle of the hybrid zone are distinct from those in either parental habitat. If our conclusions are correct, then hybrid zone theory needs to be expanded to include symbiotic interactions as well as the physical and chemical aspects of the environment.

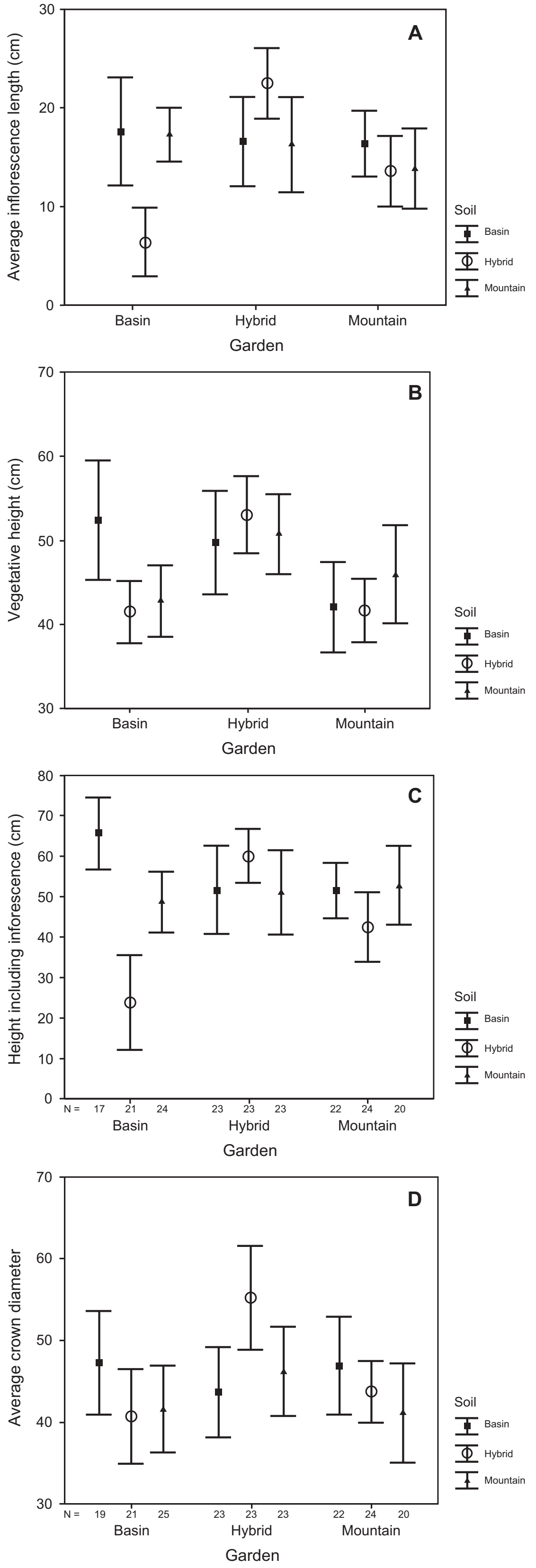


Figure 1—Mean (A) average inflorescence length of plants, (B) vegetative height, (C) vegetative height including inflorescence, and (D) average crown diameter in each of the three soils in each of the three gardens.

Acknowledgments

We express appreciation to Gary Jorgensen, Stewart Sanderson, and Jeffrey Ott for assistance in data collection and maintenance of the hybrid zone gardens.

References

Arnold, M. L. 1997. Natural hybridization and evolution. New York: Oxford University Press.

Barton, N. H. 1979a. Gene flow past a cline. Heredity. 44: 277–278.

Barton, N. H. 1979b. The dynamics of hybrid zones. Heredity. 43: 341–359.

Barton, N. H.; Hewitt, G. M. 1985. Analysis of hybrid zones. Annual Review of Ecology and Systematics. 16: 113–148.

Barton, N. H.; Hewitt, G. M. 1989. Adaptation, speciation and hybrid zones. Nature. 341: 497–503.

Beetle, A. A. 1960. A study of sagebrush, the section *Tridentatae* of *Artemisia*. Bull. 368. Laramie: University of Wyoming, Agriculture Experiment Station. 83 p.

Beetle, A. A.; Young, A. 1965. A third subspecies in the *Artemisia tridentata* complex. Rhodora. 67: 405–406.

Britch, S. C.; Cain, M. L.; Howard, D. J. 2001. Spatio-temporal dynamics of the *Allonemobius fasciatus-A. socius* mosaic hybrid zone: a 14-year perspective. Molecular Ecology. 10: 627–638.

Dobzhansky, T. 1940. Speciation as a stage in evolutionary divergence. American Naturalist. 74: 312–321.

Eckenwalder, J. E. 1984. Natural intersectional hybridization between North American species of *Populus* (Salicaceae) in sections Aigeiros and Tacamhaca. III. Paleobotany and evolution. Canadian Journal of Botany. 62: 336–342.

Emms S. K.; Arnold, M. L. 1997. The effect of habitat on parental and hybrid fitness: reciprocal transplant experiments with Louisiana irises. Evolution. 51: 1112–1119.

Freeman, D. C.; Miglia, K. J.; McArthur, E. D.; Graham, J. H.; Wang, H. 1999a. Narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*: Asteraceae): X. Performance in reciprocal transplant gardens. In: McArthur, E. Durant; Ostler, W. Kent, Wambolt, L. Carl, comps. Proceedings: shrubland ecotones; 1998 August 12–14; Ephraim, UT. Proc. RMRS-P-11. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 15–24.

Freeman, D. C.; Wang, H.; Sanderson, S. C.; McArthur, E. D. 1999b. Characterization of a narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*: Asteraceae). VII. Community and demographic analyses. Evolutionary Ecology Research. 1: 487–502.

Graham, J. H.; Freeman, D. C.; McArthur, E. D. 1995. Narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*: Asteraceae). II. Selection and dispersal. American Journal of Botany. 82: 709–716.

Graham, J. H.; McArthur, E. D.; Freeman, D. C. 2001a. Narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*: Asteraceae). XI. Plant-insect interactions in reciprocal transplant gardens. In: McArthur, E. Durant; Fairbanks, Daniel J., comps. Shrubland ecosystem genetics and biodiversity: proceedings; 2000 June 13–15; Provo, UT. Proc. RMRS-P-21. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 118–126.

Graham, J. H.; McArthur, E. D.; Freeman, D. C. 2001b. Narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*: Asteraceae). XII. Galls on sagebrush in a reciprocal transplant garden. Oecologia. 126: 239–246.

Grant, V. 1963. The origins of adaptations. New York: Columbia University Press.

Harrison, R. G. 1990. Hybrid zones: windows on evolutionary process. Oxford Surveys in Evolutionary Biology. 7: 69–128.

Harrison, R. G.; Rand, D. M. 1989. Mosaic hybrid zones and the nature of species boundaries. In: Otte, D.; Endler, J., eds. Speciation and its consequences. Sunderland, MA: Sinauer Associates: 111–113.

Hewitt, G. M. 1988. Hybrid zones—natural laboratories for evolutionary studies. Trends in Ecology and Evolution. 3: 158–167.

Howard, D. J.; Waring, G. L.; Tibbets, C. A.; Gregory, P. G. 1993. Survival of hybrids in a mosaic hybrid zone. Evolution. 47: 789–800.

Linhart, Y. A.; Grant, M. C. 1997. Evolutionary significance of local genetic differentiation in plants. Annual Review of Ecology and Systematics. 27: 237–277.

Mayr, E. 1942. Systematics and the origin of species. New York: Columbia University Press.

McArthur, E. D. 1994. Ecology, distribution, and values of sagebrush within the Intermountain region. In: Monsen, S. B.; Kitchen, S. G., comps. Proceedings—ecology and management of annual rangelands; 1992 May 18–21; Boise, ID. Gen. Tech. Rep. INT-GTR-313. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 347–351.

McArthur, E. D.; Blauer, A. C.; Plummer, A. P.; Stevens, R. 1979. Characteristics and hybridization of important Intermountain shrubs. III. Sunflower family. Res. Pap. INT-220. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 82 p.

McArthur, E. D.; Plummer, A. P. 1978. Biogeography and management of native western shrubs: a case study, section *Tridentatae* of *Artemisia*. Great Basin Naturalist Memoirs. 2: 229–243.

McArthur, E. D.; Welch, B. L. 1982. Growth rate differences among big sagebrush (*Artemisia tridentata*) accessions and subspecies. Journal of Range Management. 35: 396–401.

McArthur, E. D.; Welch, B. L.; Sanderson, S. C. 1988. Natural and artificial hybridization between big sagebrush (*Artemisia tridentata*) subspecies. Journal of Heredity. 79: 268–276.

Moore, W. S. 1977. An evaluation of narrow hybrid zones in vertebrates. Quarterly Review of Biology. 52: 263–277.

Rand, D. M.; Harrison, R. G. 1989. Ecological genetics of a mosaic hybrid zone: mitochondrial, nuclear, and reproductive differentiation of crickets by soil type. Evolution. 43: 432–449.

Rieseberg, L. H.; Baird, S. J. E.; Desrochers, A. M. 1998. Patterns of mating in wild sunflower hybrid zones. Evolution. 52: 713–726.

Ross, C. L.; Harrison, R. G. 2002. A fine-scale spatial analysis of the mosaic hybrid zone between *Gryllus firmus* and *Gryllus pennsylvanicus*. Evolution. 56: 2296–2312.

Stebbins, G. L. 1950. Variation and evolution in plants. New York: Columbia University Press.

SPSS Inc. 2001. Version 10.0 statistical software. Chicago, IL.

Trimble, S. 1989. The sagebrush ocean, a natural history of the Great Basin. Reno: University of Nevada Press. 248 p.

Wambolt, C. L. 1996. Mule deer and elk foraging preference for 4 sagebrush taxa. Journal of Range Management. 49: 499–503.

Wang, H. 1996. Ecological analysis of a stable hybrid zone between two big sagebrush subspecies (*Artemisia tridentata* ssp. *tridentata* and *A. t.* ssp. *vaseyana*). Detroit, MI: Wayne State University. 132 p. Dissertation.

Wang, H.; Byrd, D. W.; Howard, D. L.; McArthur, E. D.; Graham, J. H.; Freeman, D. C. 1998. Narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*: Asteraceae). V. Soil properties. International Journal of Plant Sciences. 159: 139–147.

Wang, H.; McArthur, E. D.; Freeman, D. C. 1999. Characterization of a narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*: Asteraceae). IX. Elemental uptake and niche separation. American Journal of Botany. 86: 1099–1107.

Wang, H.; McArthur, E. D.; Sanderson, S. C.; Graham, J. H.; Freeman; D. C. 1997. Narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*: Asteraceae). IV. Reciprocal transplant experiments. Evolution. 51: 95–102.

Welch, B. L.; McArthur, E. D. 1986. Wintering mule deer preference for 21 accessions of big sagebrush. Great Basin Naturalist. 46: 113–115.

Welch, B. L.; Jacobson, T. L. C. 1988. Root growth of *Artemisia tridentata*. Journal of Range Management. 41: 332–334.

Whittam, T. G. 1989. Plant hybrid zones as sinks for pests. Science. 244: 1490–1493.

Revegetation of Saline Playa Margins

Robert R. Blank
James A. Young

Abstract: New shrub recruitment in saline playa margins is limited by extremely high osmotic potentials of the seedbed. In the Eagle Valley playa near Fernley, NV, recruitment is rare and occurs mostly in recently deposited eolian and flood-deposited sediments of low osmotic potential. In most instances, however, sediment is of insufficient thickness to support long-term growth. In 1990, as part of a plant/soil relationship study in the eastern end of Eagle Valley playa, soil pits were excavated by backhoe in an environment consisting of mounds occupied by *Sarcobatus vermiculatus*, *Atriplex lentiformis* ssp. *torreyi*, and *Allenrolfea occidentalis* amid unvegetated interspaces. Soil pits were refilled, but depressions about 2 by 0.5 m in area to a depth of between 20 and 60 cm remained. Within 5 years, a thick veneer of eolian dust had accumulated in all the pits and supported robust recruitment of *S. vermiculatus*, *A. torreyi*, and *A. occidentalis*. By the year 2002, some shrubs were over 0.5 m in stature. Excavating small depressions in saline playa environments appears to be an effective revegetation technology provided the area has a source of low osmotic potential eolian material.

Introduction

Creation of small depressions in the soil surface is a useful seedbed preparation technique to facilitate seedling establishment in dry environments. The technology, alternately named land imprinting, gouging, and pitting, has been shown to enhance water availability to plants in the critical early establishment phase (Munshower 1994; Whisenant 1999). Our purpose here is to report on the recruitment of salt desert shrubs in depressions left from research activities on an extremely saline playa margin environment. We hypothesize that the reason these depressions facilitated shrub recruitment is a combination of enhanced water availability and capture of seeds and eolian dust, which serves as a low osmotic potential media for seed germination and early establishment.

Methods

The study area is the Eagle Valley playa (39˚44' N, 119˚2' W) just southeast of Fernley, NV. The western boundary was the terminus of the Truckee River during pluvial periods and consists of coarse-textured deltaic and reworked eolian sands. Elevation is 1,234 m. The site is a gradient from barren, flat, fine-textured, salt-encrusted sediments to a higher coarser textured and less saline complex of reworked beach material, eolian sands, and alluvial colluvial material. Based on monitor wells, the water table is less than 3 m in most years. Vegetation occurs on mounds and is dominated by *Allenrolfea occidentalis* ([S. Watson] Kuntze), *Atriplex lentiformis* ssp. *torreyi* ([S. Watson] H.M. Hall & Clements), *Sarcobatus vermiculatus* ([Hook.] Torrey), and by the grass *Distichlis spicata* ([L.] Greene). In the less saline and coarse-textured beach and colluvial deposits, vegetation is dominated by *Atriplex confertifolia* ([Torrey and Frémont] S. Watson) and *Sarcobatus baileyi* ([Cov.] Jepson). In 1990, we described a sequence of seven soils along a transect encompassing the width of the mounded area from the barren playa surface southeast to the less saline upland interface (transect distance about 1.2 km). A backhoe was used to excavate to a depth of approximately 3 m. After description of soils, pits were refilled with stockpiled soil, but settling created depressions averaging over 0.5 m in depth and 2 by 0.5 m in area. The site was ignored for several years, and when we returned in 1995, we were surprised at the robust recruitment of salt desert shrubs from the depressions. Photos presented here were taken in May of 2002.

Results and Discussion

The playa margin community of which this study focuses is an inhospitable environment for plant growth with extreme aridity and high salt content (fig. 1; Blank and others 1998). The surface soil seedbed is far too saline to allow seed germination; total soil water potentials measured monthly throughout a 2-year period average between –35 and –111 MPa for mounds microsite and between –25 and –86 MPa for interspace site (Blank and others 1994). Recruitment does occur along flood washes and impediments where eolian dust accumulates. Our data suggest that these microsites accumulate sediment of low enough osmotic potential to support germination (table 1). However, the low osmotic strength substrate is generally too thin to support plant

---

In: Hild, Ann L.; Shaw, Nancy L.; Meyer, Susan E.; Booth, D. Terrance; McArthur, E. Durant, comps. 2004. Seed and soil dynamics in shrubland ecosystems: proceedings; 2002 August 12–16; Laramie, WY. Proceedings RMRS-P-31. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Robert R. Blank is Soil Scientist and James A. Young is Range Scientist, USDA Agricultural Research Service, Exotic and Invasive Weed Research Unit, 920 Valley Road, Reno, NV 89512, U.S.A., e-mail: blank@unr.nevada.edu

Figure 1—General view of Eagle Valley playa looking northeast from the study area. In the middle background is barren, nearly level, lacustrine sediments. Surrounding this central core is a complex mound-intermound community extending outward and merging into alluvial fans. The mounds are occupied by halophytic shrubs. *Distichlis spicata* often occupies intermound areas. Extensive measurements indicate that the total soil water potential (mostly osmotic) is far too negative to allow seed germination. New recruitment requires microsites where low osmotic potential substrates can accumulate.

growth until the roots can reach the water table and sustain growth (Trent and others 1997).

Our soil excavations have allowed eolian dust to accumulate along with seeds and thereby facilitate plant recruitment (figs. 1 through 5). Other factors that may come into play include (1) micro-meteorological benefits from increased shading and (2) a greater chance of roots reaching the water table. We suggest that creating small depressions in similar landscapes may be a cost effective way to recruit new plants into similar saline environments provided there is a source of low osmotic potential wind-driven substrate and a source of seeds.

Table 1—Electrical conductivity and theoretical osmotic potentials for recent eolian sediment and underlying material.

Sample	Electrical conductivity (dS m^{-1})	Theoretical osmotic potential (MPa)[a]
Recent eolian	1.93 sd = 1.10	0.046
Underlying material	29.3 sd = 11.7	.81

[a] Based on 298 °K assuming osmoticum is NaCl.

Figure 2—Partially filled soil description pit in a very saline portion of the study area. There is almost no recruitment of new plants in this community. Most of the established shrubs are nearly dead in this area, which is difficult to judge in this black and white photograph. Even in this inhospitable environment, recruitment of *Sarcobatus vermiculatus* has occurred, fostered by the accumulation of eolian sediments in the soil pit.

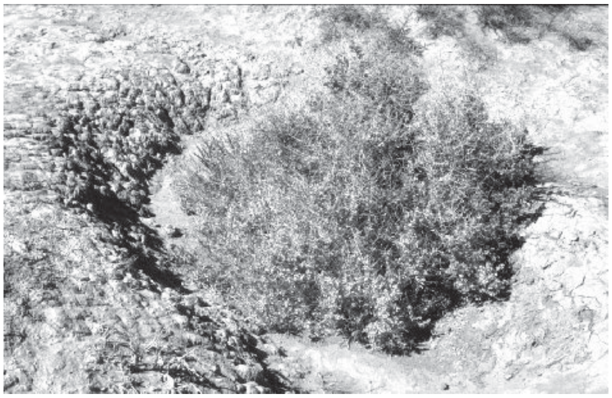


Figure 3—Robust plant of *Atriplex lentiformis* ssp. *torreyi* that recruited into one of our soil description pits. This is the largest shrub in any of our soil pits and attests to how conditions in the soil pits facilitate rapid plant growth.

Figure 4—A soil description pit now nearly completely filled in by eolian sediments. Notice the spoil pile in the background. In this soil pit there was recruitment of *Sarcobatus vermiculatus*, *Allenrolfea occidentalis*, *Atriplex lentiformis* ssp. *torreyi*, and *A. confertifolia*.

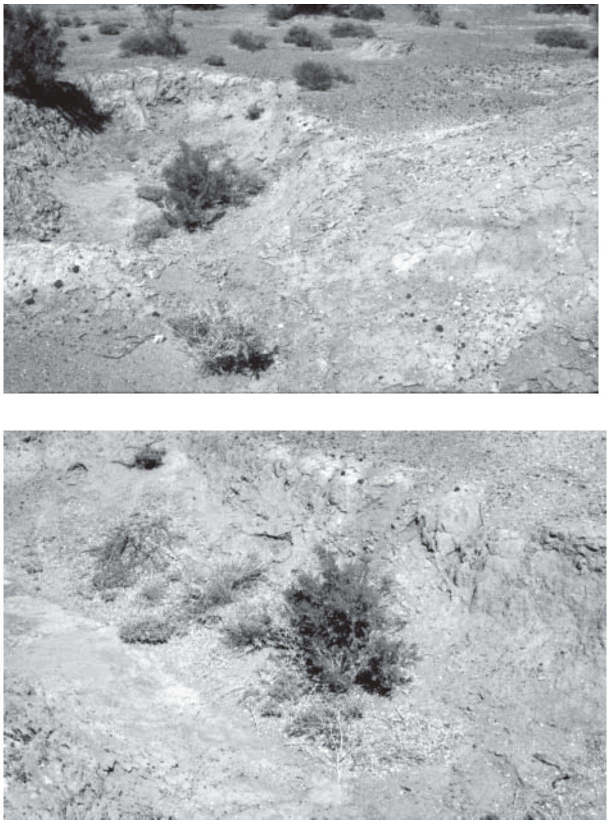


Figure 5—Soil description pit showing recruitment of *Sarcobatus vermiculatus* and *Atriplex confertifolia*. The more general top view shows very minor recruitment in the surrounding area. Photo is taken facing south and shows how eolian sediments accumulate mainly on the west side of pits. Bottom closeup photo shows that the depressions collect seeds.

References

Blank, R. R.; Young, J. A. ; Martens, E.; Palmquist, D. E. 1994. Influence of temperature and osmotic potential on germination of *Allenrolfea occidentalis*. Journal of Arid Environments. 26: 339–347.

Blank, R. R.; Young, J. A.; Trent, J. D.; Palmquist, D. E. 1998. Natural history of a saline mound ecosystem. Great Basin Naturalist. 58: 217–230.

Munshower, F. F. 1994. Practical handbook of disturbed land revegetation. Boca Raton, FL: Lewis Publishers, Inc. 265 p.

Trent, J. D.; Blank, R. R.; Young, J. A. 1997. Ecophysiology of the temperate desert halophytes: *Allenrolfea occidentalis* and *Sarcobatus vermiculatus*. Great Basin Naturalist. 57: 57–65.

Whisenant S. G. 1999. Repairing damaged wildlands: a process-oriented, landscape-scale approach. Cambridge, UK: Cambridge University Press. 312 p.

Influence of Sagebrush and Grass Seeding Rates on Sagebrush Density and Plant Size

Laurel E. Vicklund
Gerald E. Schuman
Ann L. Hild

Abstract: Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) establishment on mined lands in Wyoming is a critical element of reclamation success. Because of its importance to wildlife, shrub density is used to assess reclamation success for wildlife habitat in Wyoming. Research was initiated at the Belle Ayr Mine near Gillette in 1999 to evaluate the effects of Wyoming big sagebrush seeding rates and grass competition on sagebrush establishment. Sagebrush seedling densities demonstrated consistent increases with increased sagebrush seeding rates. The 4 kg PLS per ha sagebrush seeding rate resulted in significantly greater density than either the 2 or 1 kg PLS per ha seeding rate in 1999 to 2001. Grass competition (grass seeding rates of 0, 2, 4, 6, 8, 10, and 14 kg PLS per ha of a mixture of C_3 native species) did not significantly affect sagebrush seedling density. However, 1999 and 2000 precipitation was above or near normal, resulting in adequate moisture for seedling emergence and growth of all seeded species. Sagebrush seedling density declined at the higher grass seeding rates in 2001, but seedling density was not significantly affected by grass seeding rates ($P = 0.12$). Precipitation in 2001 was well below normal, and grass competition significantly affected sagebrush seedling canopy volume. Sagebrush seedling canopies were significantly smaller at grass seeding rates greater than or equal to 4 kg PLS per ha. Continued evaluation of these treatments on sagebrush seedling performance will enable development of a seeding strategy that enhances establishment of Wyoming big sagebrush on reclaimed mine lands.

Introduction

Mined land reclamationists in the Western United States must meet many requirements to achieve successful reclamation. In August 1996, specific shrub density requirements were imposed on mine reclamation in Wyoming (Wyoming DEQ 1996). This standard required that the dominant postmining shrub on lands identified as wildlife habitat be reestablished at a density of 1 shrub per m^2 on 20 percent of the disturbed landscape. Herbaceous species can create significant competition for shrub seedlings (Eissentat and Caldwell 1988; Schuman and others 1998; Williams and others 2002). However, reclamation guidelines and regulations require topsoil stabilization immediately after the topsoil is replaced using a permanent vegetation cover that is at least as productive as premine conditions. Establishment of a perennial vegetative cover that protects the topsoil resource from erosion can prevent the establishment of shrubs and other difficult-to-establish native plants. However, establishment of both herbaceous and shrub species is necessary to provide the desired plant community diversity and appropriate species for wildlife habitat. This study was conducted to further evaluate the establishment of Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) when sown at three rates with a mixture of cool-season native grasses sown at seven seeding rates (competition levels).

Methods

The study site was located at the RAG Coal West, Inc., Belle Ayr Mine, 29 km southeast of Gillette, WY. Climate at the site is continental, elevation is 1,460 m, mean air temperature is 6.7 °C and the average annual precipitation is 376 mm (Belle Ayr Coal Mine 2001). The premine vegetation of the area is a northern mixed-grass prairie primarily comprised of cool- and warm-season grasses and Wyoming big sagebrush. Soils are derived from Tertiary and Upper Cretaceous shale, limestone, and sandstone. The topsoil was a sandy clay loam, with a pH of 7.6, EC of 2.0 dS per m, total nitrogen concentration of 700 mg per kg, and a soil organic carbon content of 1.0 percent.

Topsoil replacement (56 cm) was completed in December 1997 to January 1998, and the area was seeded to barley (*Hordeum valgare* var. “Steptoe”) in April 1998 to establish a stubble mulch. In December 1998, seven grass seeding rate treatments (0, 2, 4, 6, 8, 10, and 14 kg PLS [pure live seed] per ha) were randomly drilled into 6.5 by 27 m main plots within each of four replicate blocks. The grass mixture (approximately equal seed numbers of each species) was

---

In: Hild, Ann L.; Shaw, Nancy L.; Meyer, Susan E.; Booth, D. Terrance; McArthur, E. Durant, comps. 2004. Seed and soil dynamics in shrubland ecosystems: proceedings; 2002 August 12–16; Laramie, WY. Proceedings RMRS-P-31. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Laurel E. Vicklund is Senior Environmental Engineer, RAG Coal West, Inc., Belle Ayr Mine, Gillette, WY 82717, U.S.A. Gerald E. Schuman is Soil Scientist, High Plains Grasslands Research Station, USDA-ARS, Cheyenne, WY 82009, U.S.A. FAX: (307) 637-6124; e-mail: gschuman@lamar.colostate.edu. Ann L. Hild is Associate Professor, Department of Renewable Resources, University of Wyoming, Laramie, WY 82071, U.S.A.

composed of three cool-season native perennials: western wheatgrass (*Pascopyrum smithii* [Rydb.] A. Love), thickspike wheatgrass (*Elymus lanceolatus* [Scribner & J.G. Smith] Gould), and slender wheatgrass (*Elymus trachycaulus* [Link] Gould ex Shinners). Each grass seeding treatment plot was subdivided into three, 6- by 9-m plots, which were randomly seeded to one of three Wyoming big sagebrush seeding rates (1, 2, or 4 kg PLS per ha) in March 1999.

Six 1-m^2 quadrats were permanently marked in each sagebrush seeding rate subplot in early 1999 before seedling emergence. Sagebrush seedlings were counted within each of these quadrats on June 30, August 3, August 31, and October 25, 1999; June 5 and September 18, 2000; and June 20 and September 27, 2001. In 1999, a high density of colonizing forb species (*Kochia scoparia, Melilotus officinalis, Salsola kali*) were present on the site. To mimic reclamation practices and to aid in the counting of sagebrush seedlings the plots were mowed at about 15 to 18 cm in height and the material removed from the plots. In July 2000 and 2001 herbaceous plant biomass at peak standing crop was determined by clipping four 0.18-m^2 quadrats within each of the 84 sagebrush by grass seeding rate subplots. Aboveground biomass was separated into planted grasses, exotic grasses (*Bromus japonicus, B. tectorum, E. junceus*), and forbs. Volunteer barley from the stubble mulch was included with the exotic grasses but comprised a very small portion of the total biomass.

In 2001, sagebrush seedling volume was estimated on all of the seedlings counted within the permanent quadrats. This parameter was included because of the visual perception of differences in sagebrush seedling size among grass seeding rates. Sagebrush seedling volume was determined by using a caliper to measure the plant canopy diameter at its widest point, crown diameter perpendicular to the first measurement, and the plant height. Plant volume was calculated with the assumption that plant shape most closely resembled an ellipse cone.

Analysis of variance was conducted on plant biomass, sagebrush seedling density, and sagebrush seedling volume using a split-split plot randomized block design (SAS Institute 1999). Mean separation was accomplished using Fisher's protected least significant difference procedures. All statistical analyses were evaluated at $P \leq 0.05$.

Results and Discussion

Sagebrush seedling density data (1999 and 2000) and aboveground plant biomass data (2000) were reported earlier by Williams and others (2002) but will be included in this paper to demonstrate longer term trends and responses over a wider range of climatic conditions. Precipitation in 2001 was considerably less than in 1999 and 2000, which were near-normal or above-normal precipitation years (fig. 1).

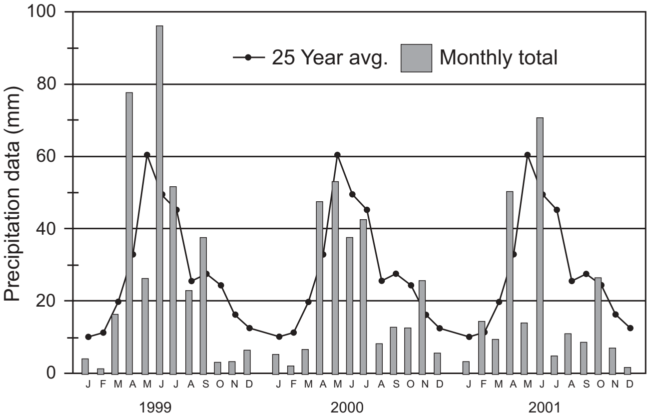


Figure 1—Monthly precipitation for 1999 to 2001 and long-term average annual precipitation, Belle Ayr Mine, RAG Coal West, Inc., Gillette, WY (Belle Ayr Coal Mine 2001).

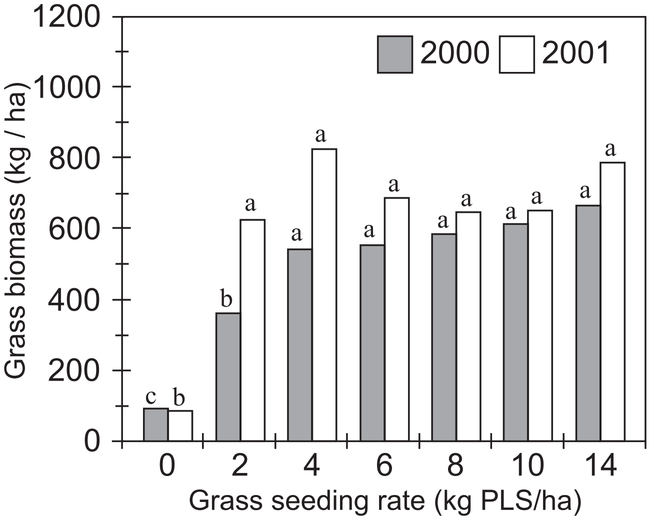


Figure 2—Aboveground grass biomass for 2000 and 2001 at seven grass seeding rates. Belle Ayr Mine, RAG Coal West, Inc., Gillete, WY (means within a year across grass seeding rates with the same lower case letter are not significantly different, $P \leq 9,95$).

Grass Seeding Rate Responses

Biomass of planted grasses in 2000 and 2001 showed similar trends (fig. 2). In 2000, aboveground biomass of planted grasses was significantly lower for grass seeding rates of 0 and 2 kg PLS per ha and did not differ among grass seeding rates of greater than or equal to 4 kg PLS per ha. In 2001, planted grass aboveground biomass did not differ among grass seeding rates greater than or equal to 2 kg PLS per ha. These data indicate that grass seeding rates of 2 to 14 kg PLS per ha can produce similar aboveground production in the second and third year after establishment. Therefore, grass seeding rates could be lowered considerably from rates typically used by mine reclamation specialists and still achieve the mandated production standards (equal to or greater than premine). Reducing grass seeding rates could aid natural recruitment of native grass, forb, and shrub species that are less competitive (Fortier 2000; Stevenson and others 1995). Because the grass species planted in this study were a mixture of bunchgrass and rhizomatous species, soil protection was adequate to ensure soil stability.

Sagebrush seedling density after three growing seasons was not significantly different among grass seeding rates (fig. 3), although, sagebrush seedling density within the 14 kg PLS per ha grass seeding rate was less than half that observed at the lower grass seeding rates. Grass seeding rate did not affect sagebrush seedling density even though precipitation (221 mm) in 2001 was below the long-term average (336 mm) for the site. Therefore, it appears that sagebrush seedling density did not respond to grass competition in the first 3 years of the study.

Aboveground sagebrush seedling size (canopy volume) differed among the grass seeding rates (fig. 4). Canopy volume of sagebrush seedlings was significantly smaller at grass seeding rates of greater than or equal to 4 kg PLS per ha than at the 0 and 2 kg PLS per ha grass seeding rate. No differences in sagebrush seedling volume were observed for grass seeding rates of 4 to 14 kg PLS per ha.

Sagebrush Seeding Rate Responses

Sagebrush seedling densities differed among the three sagebrush seeding rates within each sampling date. Sagebrush seedling density for all three seeding rates was greatest on the June 2000 count and generally declined throughout the growing season due to seedling mortality (fig. 5). In both years (2000 and 2001) sagebrush seedling density was greater with increased sagebrush seeding rate. Highest densities occurred at the 4 kg PLS per ha seeding rate. Even the 1 kg PLS per ha seeding rate resulted in sagebrush seedling densities greater than the 1 seedling per m^2 shrub standard. However, considering the long-term survival for big sagebrush reported by Kiger and others (1987) and Schuman and Belden (2002), seedling densities observed at the 1 kg PLS per ha seeding rate in our study would not meet the shrub standard after years 9 and 10, when the standard is assessed. Kiger and others (1987) reported survival rates of 28 to 32 percent after 11 years on a volunteer stand at a coal mine in northwestern Colorado (believed to be mountain big sagebrush, *Artemisia tridentata* ssp. *vaseyana*). However, Schuman and Belden (2002) reported a 59 percent average survival rate across several cultural treatments after 8 years in the Powder River Basin of Wyoming in a Wyoming big sagebrush stand seeded at 2.2 kg PLS per ha.

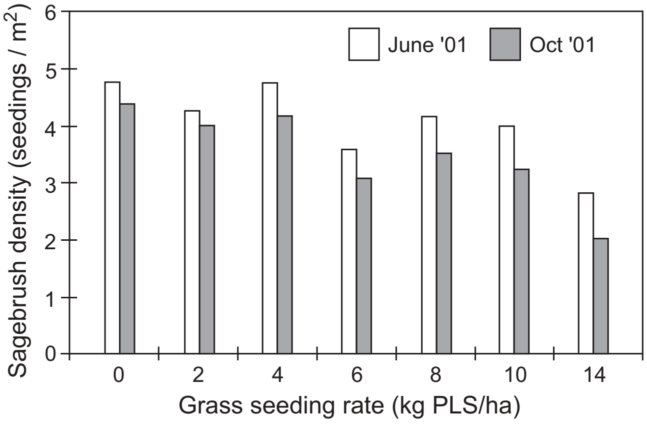


Figure 3—Influence of seven grass seeding rates on Wyoming big sagebrush seedling density in 2001, Belle Ayr Mine, RAG Coal West, Inc., Gillette, WY (sagebrush seedling density did not differ among grass seeding rates, P > 0.05).

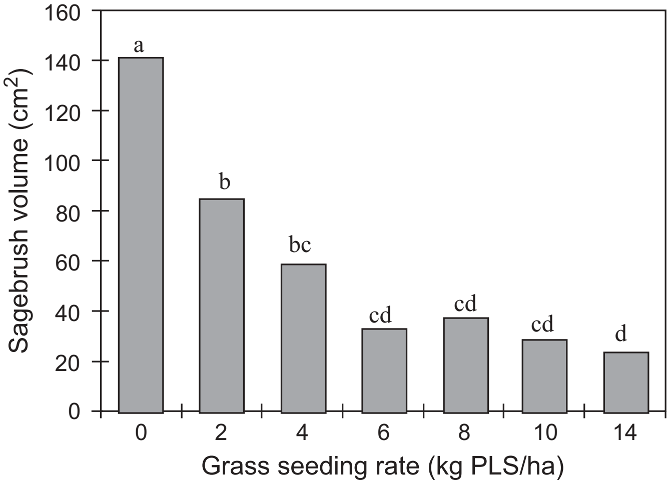


Figure 4—Influence of grass seeding rate on Wyoming big sagebrush canopy volume in 2001, Belle Ayr Mine, RAG Coal West, Inc., Gillette, WY (means with the same lower case letters are not significantly different, P > 0.05).

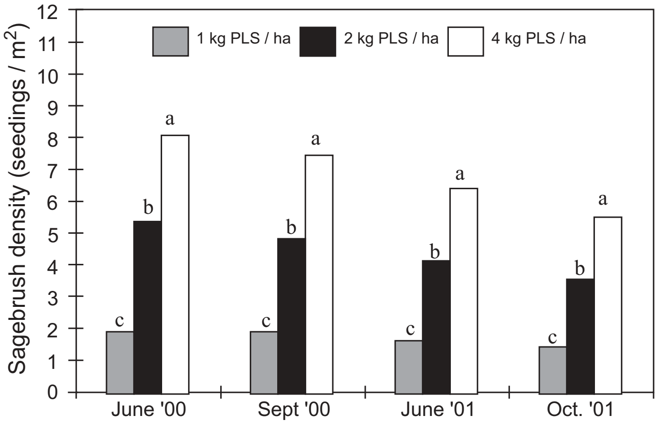


Figure 5—Wyoming big sagebrush seedling density at three sagebrush seeding rates averaged across grass seeding rates, 2000 to 2001, Bellel Ayr Mine, RAG Coal West, Inc., Gillette, WY (means within a sampling date with the same lower case letter are not significantly different, P > 0.05).

Summary and Conclusions

Based on the observed sagebrush seedling densities as affected by grass seeding rate it would be difficult to make foolproof recommendations for a grass seeding rate that would provide a sagebrush density that meets the shrub standard after 10 years. However, if one assesses the effect of the grass seeding rate on sagebrush seedling density and canopy growth in the context of the sagebrush seeding rates and planted grass aboveground biomass, we suggest that sagebrush seeding rate of 2 kg PLS per ha and a grass seeding rate of 4 kg PLS per ha will likely meet management goals on comparable sites. This recommendation is based on the lack of differences in planted grass aboveground biomass in the 6 to 14 kg PLS per ha grass seeding rates, while grass seeding rates greater than or equal to 4 kg PLS per ha greatly reduced canopy size of the sagebrush seedlings. Early results indicate a trend (nonsignificant) of fewer sagebrush seedlings above the 6 kg PLS per ha grass seeding rate in 2001. We know that as grass seeding rates increase, natural recruitment and establishment of difficult-to-establish native species are significantly reduced, particularly desired forbs and shrubs (Bergelson and Perry 1989; Eissenstat and Caldwell 1988; Richardson and others 1986). We believe this recommendation should result in adequate cover, provide adequate forage production, reduce vegetative competition, and enable establishment of Wyoming big sagebrush to meet the shrub density standard required for successful mine reclamation.

Acknowledgments

We would like to thank Mary (Fortier) Williams, Rich Vincent, and Darrell Ueckert for their review of this paper. We also acknowledge the assistance of Mary Williams, Matt Mortenson, Cliff Bowen, Kristene Partlow, Jennifer (Boyle) Muscha, Leah Burgess, Krissie Peterson, Larry Griffith, Pam Freeman, Ernie Taylor, Doug Miyamoto, Kelli Sutphin, and Wes Brown and other technical support staff for help in collecting the field data. We acknowledge support of RAG Coal West, Inc., Belle Ayr Mine, Gillette, WY; the USDA ARS High Plains Grasslands Research Station, Cheyenne, WY; and the Department of Renewable Resources, University of Wyoming. This research was supported in part by the Wyoming Abandoned Coal Mine Land Research Program, administered by the Office of Research, University of Wyoming, and the Abandoned Mine Land Division, Wyoming Department of Environmental Quality, Cheyenne.

References

Belle Ayr Coal Mine. 2001. Belle Ayr mine annual report. RAG Coal West, Inc., Gillette, WY.

Bergelson, J.; Perry, R. 1989. Interspecific competition between seeds: relative planting date and density affect seedling emergence. Ecology. 70: 1639–1644.

Eissenstat, D. M.; Caldwell, M. M. 1988. Competitive ability is linked to rates of water extraction: a field study of two aridland tusssock grasses. Oecologia. 75: 1–7.

Fortier, M. I. 2000. Wyoming big sagebrush establishment on mined lands: seeding rates and competition. Laramie: University of Wyoming. Thesis.

Kiger, J. A.; Berg, W. A.; Herron, J. T.; Phillips, C. M.; Atkinson, R. G. 1987. Shrub establishment in the mountain shrub zone. In: Proceedings, 4th biennial symposium on surface mining and reclamation of the Great Plains and 4th annual meeting of the American Society for Surface Mining and Reclamation; 1987 March 16–20; Billings, MT. Montana Reclamation Research Unit Report 8704. Bozeman: Montana State University: L-3-1 to L-3-6.

Richardson, B. Z.; Monsen, S. B.; Bowers, D. M. 1986. Interseeding selected shrubs and herbs on mine disturbance in southeastern Idaho. In: McArthur, E. D.; Welch, B. L., comps. Proceedings: symposium on the biology of *Artemisia* and *Chrysothamnus*. Gen. Tech. Rep. INT-200. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 134–139.

SAS Institute. 1999. SAS/STAT user's guide, release 8.0. Cary, NC.

Schuman, G. E.; Belden, S. E. 2002. Long-term survival of direct seeded Wyoming big sagebrush seedlings on a reclaimed mine site. Arid Land Research and Management. 16: 309–317.

Schuman, G. E.; Booth, D. T.; Cockrell, J. R. 1998. Cultural methods for establishing Wyoming big sagebrush on mined lands. Journal of Range Management. 51: 223–230.

Stevenson, M. J.; Bullock, J. M.; Ward, L. K. 1995. Re-creating semi-natural communities: effect of sowing rate on establishment of calcareous grassland. Restoration Ecology. 3: 279–289.

Williams, M. I.; Schuman, G. E.; Hild, A. L.; Vicklund, L. E. 2002. Wyoming big sagebrush density: effects of seeding rates and grass competition. Restoration Ecology. 10: 385–391.

Wyoming Department of Environmental Quality, Land Quality Division. 1996. Coal rules and regulations. Chapter 4, appendix A. State of Wyoming, Cheyenne.

Soil Components and Microsites

Eriogonum exilfiolium

Illustration on the reverse side is by Walt Fertig. In: Wyoming Natural Diversity Database. 2000. Available at: http://uwadmnweb.uwyo.edu/wyndd (Accessed 12/18/03).

Soil Nitrogen Controls on Grass Seedling Tiller Recruitment

Thomas A. Monaco
Jay B. Norton
Douglas A. Johnson
Thomas A. Jones
Jeanette M. Norton

Abstract: Establishment of perennial grass seedlings is critical for repairing rangeland ecosystems in the Western United States. Mineral N in the soil may be one of the controlling factors for seedling establishment and may improve the competitive ability of perennial grasses compared to the annual grass, cheatgrass (*Bromus tectorum* L.). A greenhouse experiment was conducted to investigate the effects of immobilizing mineral soil N on tiller recruitment in grass seedlings. The perennial grasses big squirreltail (*Elymus multisetus* [J.G. Smith] M.E. Jones), "Goldar" bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] A. Löve), and "CD II" crested wheatgrass (*Agropyron cristatum* [L.] Gaertner x *A. desertorum* [Fisch. ex Link] Schultes) were grown alone or with cheatgrass in pots for 7 weeks. Plants were grown in soil amended with ground barley straw to produce the following four treatments designed to immobilize mineral N: (1) no straw added (control), (2) 0.25 mg straw kg^{-1} soil, (3) 0.50 mg straw kg^{-1} soil, and (4) 1.00 mg straw kg^{-1} soil. Number of tillers for perennial grasses grown alone was not significantly different than perennial grasses grown with cheatgrass. Cheatgrass and crested wheatgrass plants grown alone produced significantly fewer (36 to 39 percent) new tillers per plant in the 1.00 mg kg^{-1} treatment compared to the control. Squirreltail had significantly fewer tillers per plant in the highest straw treatment compared to the control when grown with cheatgrass. Cheatgrass produced more than twice as many tillers as the perennial grasses both in the control (high mineral N) and in the high straw treatment (low mineral N). Soil in pots containing cheatgrass had 94 percent less mineral N than soil in pots containing bluebunch wheatgrass. These results suggest that cheatgrass will likely be an effective competitor with perennial grasses even if mineral soil N is drastically reduced by microbial immobilization.

Introduction

Establishing perennial grasses in rangelands degraded by invasive annual grasses continues to be one of the greatest challenges to repairing ecosystems in the Intermountain West. Many characteristics of the invasive annual cheatgrass (*Bromus tectorum* L.) allow it to be a superior competitor for belowground soil resources (Harris 1967). A better understanding of how changes in mineral N availability alters species competitive interactions between cheatgrass and perennial grasses (Grime and others 1987; Tilman 1984) may lead to new weed management strategies for enhancing perennial grass establishment.

Annual plants such as cheatgrass generally have a higher growth rate than longer lived perennial grasses (Arredondo and others 1998). In addition, annual grasses have higher NO_3^- uptake and greater N productivity (Garnier and Vancaeyzeele 1994; Poorter and others 1990), which may reduce the success of seeded perennial grasses on semiarid rangelands (Hironaka 1961). High growth rate and mineral N uptake allow cheatgrass seedlings to emerge earlier (for example, Pyke 1990) and exhibit greater early spring root growth and root proliferation in fertilized soil microsites (Caldwell and others 1991; Eissenstat and Caldwell 1988) than native perennial grasses. Recent evidence suggests that low concentrations of mineral N hinder potential shoot and root growth of both cheatgrass and native perennial grasses (Monaco and others 2003). However, it is uncertain whether reducing mineral N will improve the establishment of perennial grasses under competition with cheatgrass.

We conducted a greenhouse experiment with potted plants to evaluate the hypothesis that low mineral N would improve the competitive ability of perennial grasses when grown with cheatgrass. Specifically, we anticipated that treatments designed to reduce soil mineral N would hinder juvenile tiller recruitment of cheatgrass relatively more than that of perennial grasses. Number of tillers were evaluated because tiller numbers directly affect numerous demographic and ecological processes including plant size, competitive ability, productivity, grazing resistance, and population persistence (Briske 1991). In seedlings of perennial and annual grasses, tiller number provides an effective measure of a plant's potential growth and establishment.

Materials and Methods

The effects of low mineral N on tiller recruitment in cheatgrass, squirreltail, bluebunch wheatgrass, and crested wheatgrass were evaluated in a greenhouse experiment in Logan, UT. A coarse-loamy soil characterized as a Xeric

---

In: Hild, Ann L.; Shaw, Nancy L.; Meyer, Susan E.; Booth, D. Terrance; McArthur, E. Durant, comps. 2004. Seed and soil dynamics in shrubland ecosystems: proceedings; 2002 August 12–16; Laramie, WY. Proceedings RMRS-P-31. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Thomas A. Monaco, Douglas A. Johnson, and Thomas A. Jones, USDA-ARS Forage and Range Research Laboratory, Utah State University, Logan, UT 84322-6300, U.S.A. Jay B. Norton and Jeanette M. Norton, Utah State University, Plants, Soils, and Biometeorology Department, Logan, UT 84322-4820, U.S.A.

Torriorhent was excavated from Dugway Proving Grounds (40° 14' 23" N, 112° 50' 47" W) in Tooele County, UT, to a maximum depth of 60 cm. The top 2 cm of soil and litter were discarded to remove existing seeds in the upper soil layer. Total soil carbon (C) (13 g kg^{-1}) and total soil N (1.0 g kg^{-1}) were determined by direct combustion. The soil was passed through a 6-mm sieve to remove rocks and organic debris, and then thoroughly mixed.

Four soil treatments were established by mixing 7 kg of soil with 0, 0.25, 0.50, and 1.00 mg kg^{-1} of ground barley straw in a 5-gallon bucket and then placing the individual soils into 8-L plastic pots. The 0 mg kg^{-1} straw treatment served as a control. The straw treatment was designed to decrease overall mineral N (NH_4^+, NO_2^-, and NO_3^-) availability by promoting microbial immobilization of mineral N with a high C:N ratio organic material. The C:N ratio of the straw was 98 as measured by direct combustion. Preliminary experiments indicated nearly all (>95 percent) extractable soil mineral N was immobilized by the 1.00 mg kg^{-1} level within 5 days when soils were maintained at field capacity (6.9 percent soil water content). Mineral N concentrations (mg kg^{-1}) were 0.75 ± 0.01 (n = 8) in the control and 0.07 (n = 8) in the 1.00-mg-kg^{-1} straw treatment. All pots were watered and weighed to reach field capacity for 5 consecutive days before seedlings were transplanted into pots.

Soil mineral N concentrations were analyzed according to the methods described by Hart and others (1994). A 10-g soil sample was taken, homogenized, and extracted with 2 M KCl within 4 hours. Extracts were filtered through filter paper preleached with 2 M KCl and frozen until analyzed. Concentrations of $NO_2^- + NO_3^-$ and NH_4^+ were analyzed colorimetrically with a flow injection autoanalyzer using standard procedures (Lachat 1989, 1990).

Seeds of each grass were germinated on blotter paper, and four seedlings were transplanted into each pot. Grasses were planted alone or in a 2:2 mixture with cheatgrass. Each grass x mixture x treatment combination was replicated four times. Pots were randomly arranged on greenhouse benches and grown for 7 weeks under 50-percent ambient solar radiation to help maintain air temperature at 70 °C during the experiment in late spring and summer (May to June 2001). Plants were watered each day with the amount of water required to reach field capacity. After 7 weeks, the number of tillers produced was counted on all plants. Many plants of each grass appeared to be N deficient in the straw treatments. As a result, all pots were fertilized at 7 weeks with 500 ml of NPK (20-20-20) fertilizer to revive active vegetative growth. After an additional 6 weeks of growth, soil mineral N was analyzed for the control pots of grasses grown without cheatgrass competition (n = 4).

Tiller numbers were analyzed individually for each species with analysis of variance to determine the effects of straw treatment and species mixture. A Tukey's test was performed on treatment means when a significant main effect was observed. All statistical tests were performed with $\alpha = 0.05$.

Results and Discussion

No significant differences in tiller numbers were observed between perennial grass plants grown alone and those grown in competition with cheatgrass (table 1). In contrast, the high straw treatment significantly reduced the number of tillers compared to the control for squirreltail when grown with cheatgrass and for crested wheatgrass when grown alone. Immobilizing mineral N with straw also significantly reduced tiller numbers of cheatgrass plants grown alone (table 2). Of the four grasses we evaluated, bluebunch wheatgrass was the only grass that did not show a significant decrease in tiller numbers under low mineral N. Our results do not support our initial hypothesis that reducing mineral N would improve the establishment of perennial grasses with cheatgrass competition.

Two alternative hypotheses may account for our results that tiller numbers of cheatgrass, squirreltail, and crested wheatgrass were negatively impacted by low soil concentrations of mineral N, while tiller numbers for bluebunch wheatgrass were not. One possible hypothesis is that high growth rates in the three responsive grasses could not be supported when mineral N was limiting (Berendse and others 1992; van der Werf and others 1993a,b). Bluebunch wheatgrass, which is known to have a lower growth rate than the other three grasses (Arredondo and others 1998), may have been the least responsive grass to the straw treatments because it is likely functioning closer to its "optimal growth and metabolic rate" when soil N is limiting (for example, Chapin and others 1987).

A second hypothesis that may partially explain the tiller number responses we observed is that fast-growing invasive annual grasses and slow-growing perennial grasses may allocate available soil N differently to shoots and roots. For

Table 1—Mean (± 1 SE, n = 4) number of tillers per plant for squirreltail, bluebunch wheatgrass, and crested wheatgrass when grown alone and in equal mixture with cheatgrass. Means within a row followed by the same letters are not significantly different.

		Treatment			
Species		Control	0.25	0.50	1.00
		mg barley straw kg^{-1} soil			
Squirreltail	Alone	3.8 ± 0.4	4.4 ± 0.7	3.6 ± 0.6	2.8 ± 0.6
	with cheatgrass	5.0 ± 1.0a	3.1 ± 0.3ab	2.8 ± 0.4ab	2.1 ± 0.4b
Bluebunch wheatgrass	Alone	3.8 ± 0.7	2.3 ± 0.3	2.3 ± 0.4	2.0 ± 0.6
	with cheatgrass	2.8 ± 0.6	2.8 ± 0.3	3.3 ± 0.8	3.8 ± 1.0
Crested wheatgrass	Alone	6.3 ± 0.3a	4.9 ± 0.1ab	4.3 ± 0.3b	4.0 ± 0.5b
	with cheatgrass	6.6 ± 0.6	3.9 ± 0.6	5.0 ± 0.5	4.9 ± 0.1

Table 2—Mean (± 1 SE) number of tillers for cheatgrass plants when grown alone and in equal mixture with squirreltail, bluebunch wheatgrass, and crested wheatgrass for 6 weeks. Means within a row followed by the same letters are not significantly different.

		Treatment			
Cheatgrass	**n**	**Control**	**0.25**	**0.50**	**1.00**
		- - - - - - - - - - - *mg barley straw kg^{-1} soil* - - - - - - - - - - -			
Alone	12	11.2 ± 0.8a	9.2 ± 0.6ab	7.5 0.6b	6.8 ± 0.6b
With squirreltail	4	14.5 ± 1.9	8.3 ± 2.1	9.0 ± 1.8	5.9 ± 1.3
With bluebunch wheatgrass	4	12.5 ± 1.7	11.6 ± 2.2	7.3 ± 0.8	9.1 ± 1.0
With crested wheatgrass	4	12.1 ± 2.3	8.4 ± 0.8	9.6 ± 1.1	7.0 ± 0.7

example, Monaco and others (2003) found that invasive annual grasses primarily allocate N and biomass to shoots, whereas allocation was primarily to roots in the native perennial bluebunch wheatgrass. Thus, cheatgrass, squirreltail, and crested wheatgrass may have responded to reductions in soil N by altering aboveground structures (tillers), while low N conditions may have had greater impacts on root growth in bluebunch wheatgrass.

High growth rates and different shoot and root allocation patterns may have collectively enabled cheatgrass, squirreltail, and crested wheatgrass to better exploit the limiting N supply in pots and perform relatively better than or equal to bluebunch wheatgrass (fig. 1). The amount of soil N remaining in pots occupied by these grasses indicated that cheatgrass pots had the least amount of mineral N followed by crested wheatgrass, squirreltail, and bluebunch wheatgrass. Pots containing cheatgrass had 94 percent less mineral N than bluebunch wheatgrass. High consumption of mineral N by cheatgrass likely facilitated its production of more than twice as many tillers as the perennial grasses, both in the control (high mineral N) and in the high straw treatment (low mineral N). However, it remains unclear why tiller numbers for perennial grasses grown alone were not significantly different than when grown with cheatgrass, given the ability of cheatgrass to modify mineral N availability. Additional insight into the question of whether competitive ability of perennial grasses increases relative to cheatgrass under low mineral N may become apparent with more detailed experiments (Gibson and others 1999). Our results suggest that cheatgrass will likely be an effective competitor with perennial grasses even if mineral soil N is drastically reduced by microbial immobilization.

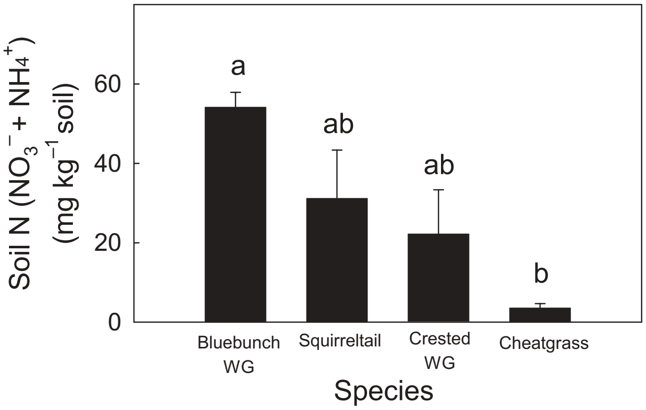


Figure 1—Mean (± 1 SE, n = 4) mineral N (NO_3^- and NH_4^+) of soils containing bluebunch wheatgrass (WG), squirreltail, crested wheatgrass (WG), and cheatgrass. Vertical bars labeled with different lowercase letters are significantly ($P < 0.05$) different.

Acknowledgments

Research was funded by USDA-ARS and USDA-CSREES Grant No. 97-38300-4892. We thank Justin Williams, Brandon Gordon, Kevin Connors, and Jacqueline Adams for assisting with plant maintenance and data collection.

References

Arredondo, J. T.; Jones, T. A.; Johnson, D. A. 1998. Seedling growth of Intermountain perennial and weedy annual grasses. Journal of Range Management. 51: 584–589.

Berendse, F.; Elberse, W. Th.; Geerts, R. H. M. E. 1992. Competition and nitrogen loss from plants in grassland ecosystems. Ecology. 73: 46–53.

Briske, D. D. 1991. Developmental morphology and physiology of grasses. In: Heitschmidt, R. K.; Stuth, J. W., eds. Grazing management: an ecological perspective. Portland, OR: Timber Press: 85–108.

Caldwell, M. M.; Manwaring, J. H.; Durham, S. L. 1991. The microscale distribution of neighbouring plant roots in fertile soil microsites. Functional Ecology. 5: 765–772.

Chapin, F. S., III; Bloom, A. J.; Field, C. B.; Waring, R. H. 1987. Plant responses to multiple environmental factors. Bioscience. 37: 49–57.

Eissenstat, D. M.; Caldwell, M. M. 1988. Seasonal timing of root growth in favorable microsites. Ecology. 69: 870–873.

Garnier E.; Vancaeyzeele, S. 1994. Carbon and nitrogen content of congeneric annual and perennial grass species: relationships with growth. Plant, Cell and Environment. 17: 399–407.

Gibson, D. J.; Connolly, J.; Hartnett, D. C.; Weidenhamer, J. D. 1999. Designs for greenhouse studies of interactions between plants. Journal of Ecology. 87: 1–16.

Grime J. P.; Mackey, J. M. L.; Hillier, S. H.; Read, D. J. 1987. Floristic diversity in a model system using experimental microcosms. Nature. 328: 420–422.

Harris, G. A. 1967. Some competitive relationships between *Agropyron spicatum* and *Bromus tectorum*. Ecological Monographs. 37: 89–111.

Hart, S. C.; Stark, J. M. E.; Davidson, A.; Firestone, M. K. 1994. Nitrogen mineralization, immobilization and nitrification. In: Weaver, R. W.; Angle, S.; Bottomley, P.; Bezdicek, D.; Smith, S.;

Tabatabai, A.; Wollum, A., eds. Methods of soil analysis microbiological and biochemical properties. 3d ed. Madison, WI: Soil Science Society of America: 985–1018.

Hironaka, M. 1961. The relative rate of root development of cheatgrass and medusahead. Journal of Range Management. 14: 263–267.

Lachat. 1989. Operations manual for the QuikChem automated ion analyzer. Quikchem 12-107-04-1-B (nitrate). Milwaukee, WI: Lachat.

Lachat. 1990. Operations manual for the QuikChem automated ion analyzer. Quikchem 12-107-06-2-A (ammonium). Milwaukee, WI: Lachat.

Monaco, T. A.; Johnson, D. A.; Norton, J. M.; Jones, T. A.; Connors, K. J.; Norton, J. B.; Redinbaugh, M. B. 2003. Contrasting responses of Intermountain West grasses to soil nitrogen. Journal of Range Management. 56: 282–290.

Poorter, H.; Remkes, C.; Lambers, H. 1990. Carbon and nitrogen ecology of 24 wild species differing in relative growth rate. Plant Physiology. 94: 621–627.

Pyke, D. A. 1990. Comparative demography of co-occurring introduced and native tussock grasses: persistence and potential expansion. Oecologia. 82: 537–543.

Tilman, D. 1984. Plant dominance along an experimental nutrient gradient. Ecology. 65: 1445–1453.

van der Werf, A.; van Nuenen, M.; Visser, A. J.; Lambers, H. 1993a. Contribution of physiological and morphological plant traits to a species' competitive ability at high and low nitrogen supply. Oecologia. 94: 434–440.

van der Werf, A.; Visser, A. J.; Schieving, F.; Lambers, H. 1993b. Evidence for optimal partitioning of biomass and nitrogen at a range of nitrogen availabilities for fast and slow-growing species. Functional Ecology. 7: 63–74.

Enzyme Activity in Temperate Desert Soils: Influence of Microsite, Depth, and Grazing

Robert R. Blank

Abstract: The enzyme status of soil influences mineralization kinetics, and thus, the supply of nutrients to plants. We quantified urease, asparaginase, glutaminase, phosphatase, and arylsulfatase activity in a sagebrush/grass ecosystem northeast of Reno, NV. Enzyme activity was evaluated by depth (0 to 5 cm, 5 to 10 cm, 10 to 20 cm), microsite (sagebrush, crested wheatgrass, cheatgrass, cryptogamic crust in shrub interspace, noncryptogamic crust in shrub interspace), and treatment (grazed and ungrazed). For most enzymes evaluated, there was a significant depth x microsite interaction. In general, enzyme activity declined with depth. Moreover, the noncryptogamic interspace microsite often had the lowest enzyme activity among the other microsites. Depending on soil depth and microsite, the grazing treatment significantly reduced urease, asparaginase, and alkaline phosphatase activity compared to the ungrazed treatment. Enzyme activity is an important soil attribute and may serve as a robust measure of soil health.

Introduction

Soil is a critical component of the Earth's biosphere. From food production, degradation of toxic compounds, and as a medium for the geochemical recycling of many elements, proper management of soil is crucial for the continued prosperity of humans. Yet, given that most soils of the world have only been intensively cultivated and grazed for a relatively short period of time, there are concerns whether our soil resources are sustainable (Hillel 1991). Scientists have recently attempted to quantify soil health or quality as an index of sustainability (Doran and others 1994). One potentially important soil attribute that may be a good proxy for soil health is enzyme activity (Dick 1994; Saviozzi and others 2001) because it is an integration of life processes occurring within the soil. The study was conducted to ascertain how several common soil enzymes vary by soil depth, soil microsite, and grazing in a sagebrush/grass plant community.

Methods

Field

The study area is in the Bedell Flat area, 30 km north of Reno, NV (119^o 50' E 39^o 51' N). The slope is less than 4 percent with a northeastern aspect. Elevation is 1,548 m. The soil is mapped as the Bedell series, a coarse-loamy, mixed, mesic, Aridic Argixeroll developed in mixed colluvium dominantly from granite. Present vegetation consists of crested wheatgrass (*Agropyron desertorum* [Fischer] Schultes), cheatgrass (*Bromus tectorum* L.), big sagebrush (*Artemisia tridentata* ssp. *tridentata* Nutt.), needle-and-thread (*Hesperostipa comata* Trin. & Rupr.), Thurber's needlegrass (*Achnatherum thurberianum* [Piper] Barkworth), squirreltail (*Elymus elymoides* [Raf.] Swezey), and green rabbitbrush (*Chrysothamnus viscidiflorus* [Hook.] Nutt.). On July 19, 1995, soil (four replicates) was collected from grazed and ungrazed treatment plots. The plots are on either side of an exclosure constructed in 1958. Three depths were sampled (0 to 5 cm, 5 to 10 cm, and 10 to 20 cm). Microsites sampled on the grazed plot included sagebrush, (ARTR), cheatgrass, (BRTE), and noncryptogamic barren shrub interspaces (INTER). Microsites sampled in the ungrazed plot included crested wheatgrass, (AGDE), cryptogamic crust covered shrub interspaces (CRPTO), cheatgrass (BRTE), and sagebrush (ARTR).

Laboratory

The soils were returned to the laboratory where they were air dried and sieved to remove material greater than 2 mm in size. The soils were then stored in paper bags in the refrigerator prior to the particular enzyme assays. Assays were completed within 2 weeks. Enzyme activity procedures are as outline in Tabatabai (1994). Three enzymes that cleave amine groups (amidohyrolases) were evaluated: asparaginase, urease, and glutaminase. These assays are based on the determination of ammonium released when buffered soil (5 g) is incubated individually with known amounts of the substrates, L-glutamine, L-asparagine, or urea at 37 °C for 2 hours. After incubation, cleaved ammonium is extracted with 2 M KCl containing $AgSO_4$ to stop enzyme activity. Ammonium present in the original soil and ammonium cleaved due to non-enzymatic processes are subtracted out via running a blank. Ammonium is quantified using a flow injection membrane-diffusion method. Quantification of arylsulfatase, and acid and alkaline phosphatase activity is based on the cleaving of the sulfate or phosphate group attached to *p*-nitrophenyl. One g of THAM-buffered soil is incubated with the appropriate

---

In: Hild, Ann L.; Shaw, Nancy L.; Meyer, Susan E.; Booth, D. Terrance; McArthur, E. Durant, comps. 2004. Seed and soil dynamics in shrubland ecosystems: proceedings; 2002 August 12–16; Laramie, WY. Proceedings RMRS-P-31. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Robert R. Blank is Soil Scientist, USDA Agricultural Research Service, Exotic and Invasive Weed Research Unit, 920 Valley Road, Reno, NV 89512 U.S.A., e-mail: blank@unr.nevada.edu

substrate at 37 °C for 1 hour. The *p*-nitrophenyl remaining is extracted with KCl and quantified colorimetrically.

Statistics

For each individual enzyme, data were analyzed using a fixed effect, two-way analysis of variance with unequal replication for depth and microsite. A separate two-way analysis of variance was performed on depth and treatment for microsites CRPTO/INTER, BRTE, and ARTR. If the analysis showed a significant F-value, mean separation was accomplished using Duncan's new multiple range test. For the prepared graphs, variance of data is shown by standard error about the mean.

Results

There was a significant (P = 0.05) depth x microsite interaction for enzyme activities of urease, asparaginase, arylsulfatase, and glutaminase (fig. 1). Urease and arylsulfatase activities were more variable than asparaginase or glutaminase activity. Moreover, the INTER microsite generally has the lowest enzyme activities among the microsites and the most inconsistent trend in enzyme activities with depth. Urease activity displayed a declining trend with depth for the CRPTO, ARTR, and BRTE microsites, but activity for the INTER site significantly increased with depth. Asparaginase was the only enzyme whose activity consistently declined with depth. Arylsulfatase activity was inconsistent with depth. The ARTR microsite had the highest enzyme activities, but only statistically higher in the 0- to 5-cm depth increment for urease and asparaginase.

Alkaline phosphatase had significant main effects for depth and microsite (fig. 2). Enzyme activity declined significantly with depth. The CRPTO microsite had the most activity followed by ARTR, AGDE, BRTE, and finally INTER with the least enzyme activity.

Asparaginase and urease activities were influenced by a significant microsite x treatment interaction (fig. 3). In the 0- to 5-cm depth increment, the grazed plot had significantly less enzyme activities of asparaginase and urease in the INTER microsite compared to the ungrazed CRPTO microsite. In addition, for the BRTE microsite, urease activity was significantly less in 10- to 20-cm depth increments of the grazed plot compared to the corresponding ungrazed plot. Finally, alkaline phosphatase activity was significantly less on the grazed INTER microsite than on the ungrazed CRPTO sites.

Discussion

Plant microsite did significantly affect enzyme bioassays, which has been reported in the literature (Neal 1973; Saviozzi and others 2001). In general, enzyme activity was highest in

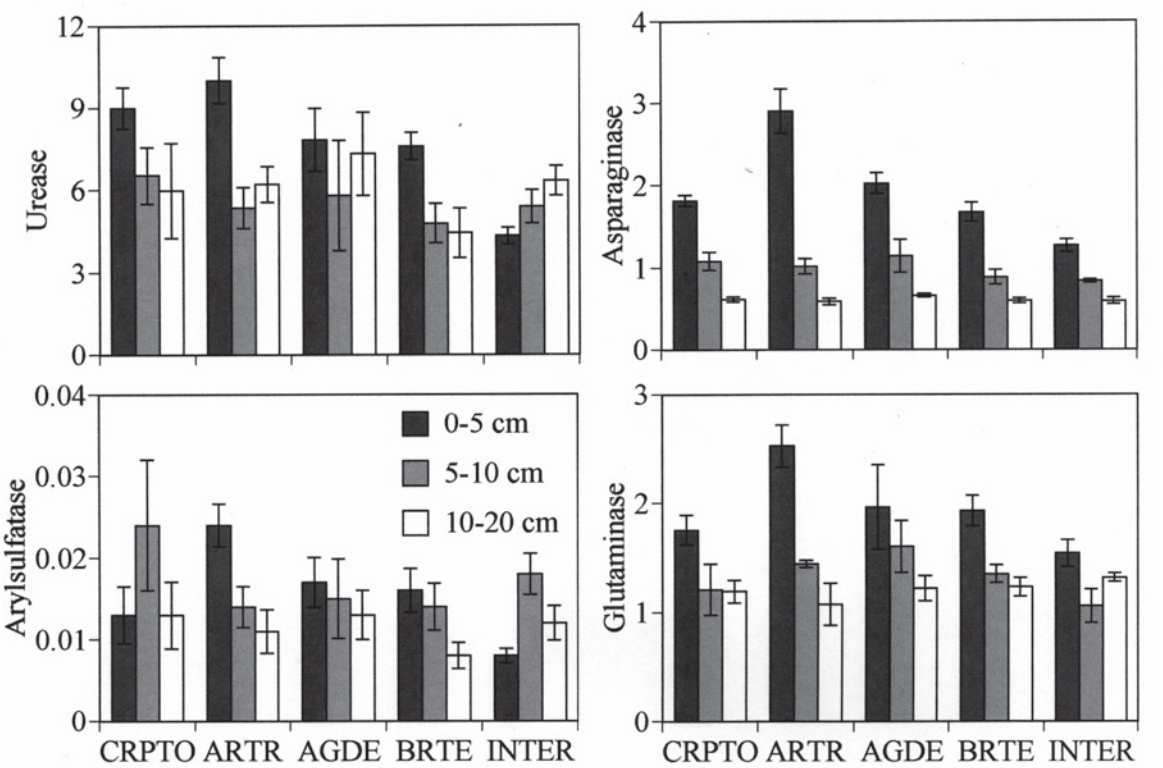


Figure 1—Soil enzyme activities that were influenced by a significant soil depth by microsite interaction. Units are µmol of substrate cleaved g^{-1} hr^{-1}.

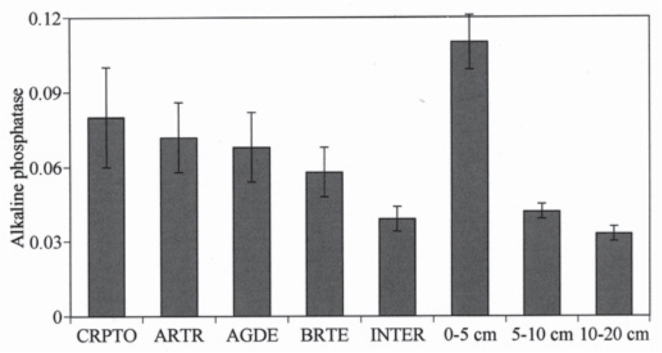


Figure 2—Phosphatase activity main effects of microsite and soil depth. Units are µmol of substrate cleaved g^{-1} hr^{-1}.

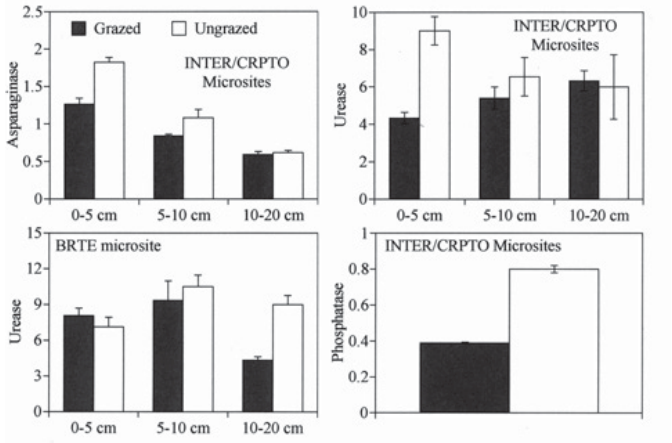


Figure 3—Soil enzyme activities that were influenced by a significant main effect or interaction with treatment. Units are µmol of substrate cleaved g^{-1} dry soil hr^{-1}.

the surface soil (0 to 5 cm). Burke and others (1989) and Bolton and others (1993), whose experiments were also conducted in a sagebrush ecosystem, found similar results. For the cryptogamic crust and sagebrush interspace sites, however, enzyme activity was least in the 0- to 5-cm depth increment. The lack of higher plant life, which would afford some moderation of the intense desert sun and engender greater microbial numbers, may explain these findings. Grazing-induced reduction of enzyme activities has been reported in the literature (Holt 1996). Given that enzyme activity of soil is both a microbial (largely) and a plant mediated process (Tate 1995), one would suspect that grazing has reduced those microbes and higher plants that produce urease, asparaginase, and alkaline phosphatase. This conclusion is of course complicated by the fact that, in the shrub interspaces where the grazing effect is most pronounced, the soil lacks well-expressed cryptogamic organisms. The large reduction in urease activity on grazed BRTE microsites is perplexing; however, it seems reasonable to speculate that grazing of cheatgrass may have reduced root elongation into the 10- to 20-cm depth increment. It seems plausible that the grazing reduction of the amidohydrolases urease and asparaginase could potentially reduce N mineralization kinetics (Holt 1997). Likewise grazing-induced reduction of phosphatase could reduce P availability. We are planning future experiments to clarify these unknowns.

References

Bolton, H., Jr.; Smith, J. L.; Link, S. O. 1993. Soil microbial biomass and activity of a disturbed and undisturbed shrub-steppe ecosystem. Soil Biology and Biochemistry. 25: 545–552.

Burke, I. C. 1989. Control of nitrogen mineralization in a sagebrush steppe landscape. Ecology. 70: 1115–1126.

Dick, R. P. 1994. Soil enzyme activities as indicators of soil quality. In: Defining soil quality for a sustainable environment. SSSA Spec. Publ. 35. Madison, WI: Soil Science Society of America: 107–124

Doran, J. W.; and others, eds. 1994. Defining soil quality for a sustainable environment. SSSA Spec. Publ. 35. Madison, WI: Soil Science Society of America. 244 p.

Hillel, D. J. 1991. Out of the Earth, civilization and the life of the soil. New York: The Free Press. 321 p.

Holt, J. A. 1997. Grazing pressure and soil carbon, microbial biomass and enzyme activities in semi-arid Northeastern Australia. Applied Soil Ecology. 5: 143–149.

Neal, J. L., Jr. 1973. Influence of selected grasses and forbs on soil phosphatase activity. Canadian Journal of Soil Science. 53: 119–121.

Saviozzi, A.; Levi-Minzi, R.; Cardelli, R.; Riffaldi, R. 2001. A comparison of soil quality in adjacent cultivated, forested, and native grassland soils. Plant and Soil. 233: 251–259.

Tabatabai, M. A. 1994. Soil enzymes. In: Methods of soil analysis, part 2, microbiological and biochemical properties. Madison, WI: Soil Science Society of America: 775–833.

Tate, R. L. 1995. Soil microbiology. New York: John Wiley & Sons. 398 p.

Unique Characteristics of a Systemic Fungal Endophyte of Native Grasses in Arid Southwestern Rangelands

Jerry R. Barrow

Abstract: Native grasses and shrubs in arid Southwestern rangelands are more extensively colonized by dark septate endophytic fungi than by traditional mycorrhizal fungi. A histochemical method was developed that revealed active internal structures that have not been observed using conventional protocol for fungal analysis. These fungi nonpathogenically and totally colonize all sieve elements, cortical and epidermal cells. They grow intercellularly and intracellularly, forming an intimate, integrated association with all root and leaf cells. Their internal morphology is often atypical of commonly recognized symbiotic or pathogenic fungal colonization. These endophytes accumulate and disperse large quantities of lipids through the root. They form a saturated mucilage layer on both the root and leaf surface, which protects them and maintains hydraulic continuity with dry soil. Our results suggest that these fungi function as carbon managers and enhance nutrient and water uptake in arid ecosystems.

Mycorrhizal fungi profoundly influence plant communities in all ecosystems. The most extensively studied are the arbuscular mycorrhiza (AM) that are associated with at least 85 percent of all vascular plants. These fungi colonize the root cortex, extend into the soil, and transport P to arbuscules within the root cortex where it is released to the plant. The term "mycorrhizae" means fungus root (Smith and Read 1997). These fungi are harmonious components of and are an extension of the root system. Fungi are well adapted for nutrient acquisition; their small size allows exploration of microscopic soil pores, and they are able to function at lower water potentials than other organisms (Griffin 1979). They function as microscopic pipelines where carbon and minerals are actively transported simultaneously to and away from the plant.

Little is known of the mycorrhizal status of desert plants, and studies have focused primarily on the presence of arbuscules in plant roots. Plant roots are also colonized by many other kinds of fungi, including saprophytic or weakly pathogenic fungi that may have symptomless endophytic or biotrophic phases in their life cycles that are not apparent to causal observers (Parbery 1996). Factors that distinguish between beneficial and detrimental plant-fungus relationships are relative to the quantitative reciprocal exchange of photosynthetic carbon for mineral nutrients, water, or protection (Smith and Smith 1996). Nonmycorrhizal plants are frequently colonized by septate fungi that may function like mycorrhizal fungi, but their study and importance have been minimized because they do not conform to established mycorrhizal morphology (Trappe 1981). Barrow and others (1997) have found that dominant shrubs and grasses are more extensively colonized by dark septate fungal endophytes (DSE) than by traditional mycorrhizae. DSE are characterized by stained and melanized septate fungal structures (Jumpponen 2001). In a review by Jumpponen and Trappe (1998), DSE fungi colonize a wide range of plant species in stressed ecosystems. Barrow and Aaltonen (2001) developed dual-staining methodology and high magnification differential interference microscopy that revealed substantially greater incidence of unique, active fungal structures that are not detected using conventional fungus-staining methods and casual low-magnification observations.

Materials and Methods

Material Collection

Roots and leaves were sampled weekly during 2001 from a native population of black grama, *Bouteloua eriopoda* (Torr.) Torr. (BOER), located on the USDA Agricultural Research Service's Jornada Experimental Range in southern New Mexico. Soil was chronically dry, and soil moisture was generally less than 3 percent at most sampling times, except for brief periods following precipitation events when the soil was nearly saturated. Blue grama, *Bouteloua gracilis* (Kunth) Lag. Ex Steud. (BOGR), from various northern and high elevations was also collected periodically. BOGR is adapted to more mesic, higher elevations than BOER on the Jornada Experimental Range. Some samples were taken from actively growing sites that received normal and above precipitation during the growing season. Fungal colonization was determined to be consistent, and expression was uniform in this and previous studies within the population at each sampling period. For this study, roots from two to five plants of each species were collected, bulked, and sealed in a plastic bag and taken to the laboratory for preparation and analysis.

In: Hild, Ann L.; Shaw, Nancy L.; Meyer, Susan E.; Booth, D. Terrance; McArthur, E. Durant, comps. 2004. Seed and soil dynamics in shrubland ecosystems: proceedings; 2002 August 12–16; Laramie, WY. Proceedings RMRS-P-31. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Jerry R. Barrow is a Research Scientist at the USDA-ARS Jornada Experimental Range, Las Cruces, NM 88003, U.S.A. FAX: (505) 646-5889, e-mail: jbarrow@nmsu.edu

Tissue Preparation and Clearing

Methods developed by Bevege (1968), Brundrett and others (1983), Kormanik et al. (1980), and Phillips and Hayman (1970) were modified for optimal visualization of fungi in native grass roots. Roots were washed in tap water to remove soil. From each bulked sample, healthy feeder roots of uniform maturity and appearance (approximately 0.250 mm in diameter) were randomly selected and cleared by placing in an autoclave in 2.5 percent KOH. Temperature was increased to 121 °C over 5 minutes, maintained for 3 minutes, and after 8 minutes, samples were removed from the autoclave. Roots were rinsed in tap water, bleached in 10 percent alkaline H_2O_2 for 10 to 45 minutes to remove pigmentation, and placed in 1 percent HCL for 3 minutes. Decolorized roots were rinsed for 3 minutes in dH_2O before staining with either trypan blue (TB) or sudan IV (SIV), or they were dual stained with TB and SIV. To stain with TB, roots were placed in prepared TB stain (0.5 g trypan blue in 500 ml glycerol, 450 ml dH_2O and 50 ml HCL), autoclaved at 121 °C for 3 minutes, and stored in acidic glycerol (500 ml glycerol, 450 ml H_20, and 50 ml HCL). For SIV staining, roots were placed in prepared SIV (3.0 g Sudan IV in 740 ml of 95 percent ETOH plus 240 ml dH_2O), autoclaved at 121 °C for 3 minutes, and stored in acidic glycerol. For dual staining, roots were stained first in TB, autoclaved as above, and destained 24 hours in the acidic glycerol. Roots were then transferred to the SIV stain and autoclaved as above. Dual stained roots were destained in dH_2O for 3 minutes, and roots were stored in acidic glycerol until mounting.

Ten to twelve 2-cm root segments were placed on a microscope slide in several drops of permanent mounting medium. A cover slip was placed over the root sections and pressed firmly to facilitate analysis at high magnification. Analysis was done with a Zeiss Axiophot microscope using both conventional and DIC optics at 1000x. Leaves were prepared similar to the roots.

Results

This method revealed a number of unexpected associations of DSE fungi with the native grama grasses that differ from known pathogenic and symbiotic fungal associations (Barrow 2003). Active fungal structures were dynamic and morphologically different from typical fungal morphology and were influenced by external environmental conditions. The most prevalent structures in physiologically active roots were fungal protoplasts that had no distinguishable walls. As root activity decreased, structures with hyaline, stained, or pigmented walls characteristic of DSE fungi became increasingly evident and were connected with fungal protoplasts. A distinguishing feature of fungal structures was a virtually constant association with lipid bodies of varied size and shape. The fungus was systemic and formed an intimate, integrated interface with all root and leaf cells. The nondestructive colonization of sieve elements of healthy roots was unexpected. Colonization of cortical cells was less evident in physiologically active roots, but as roots became dormant, DSE fungi were observed in all cortical cells. Another unique observation was the colonization of all root meristematic cells. The fungus was observed extending from the root cortex and formed a loosely configured network within a mucilaginous layer on the root surface. Fungi were also observed extending from the root surface into the soil. The same fungal morphology was observed associated with sieve elements and bundle sheath and mesophyll cells of the leaves. Colonization of epidermal cells and the stomatal complex was likewise unique. Lipid bodies within fungal structures that ranged from very small to occupying the entire internal volume of the subsidiary cells were also observed. Lipid-filled fungal protoplasts were also observed extruding from the stomatal apertures.

Disscussion

The novel method used in this study revealed a substantially greater colonization of native grasses by DSE fungi and atypical fungal structures that escape detection by conventional methodology. Systemic colonization is assured because of colonization of meristem cells and distribution of the fungus at cell division to developing roots and shoots. The nature and extent of fungal colonization indicate several potential ecological roles. The colonization of sieve elements is presently relegated to pathogenic fungi and is unique for beneficial or endophytic fungi. This also distinguishes DSE fungi from traditional mycorrhizal fungi that are restricted to the root cortex and surface.

Staining with sudan IV, specific for lipids, revealed many internal fungal structures that are not observed using conventional microscopy. The quantity and size of fungal lipid bodies indicate substantial assimilation of host photosynthate. This would generally be viewed as a parasitic association; however, there is no detrimental affects to the host plants. Therefore, it is concluded that DSE fungi are carbon managers and utilize host carbon for the protection and benefit of the host plant. Evidence for this is the protective mucilaginous layer observed on both root and leaf surfaces. Mucilage is an important organic carbon component of plants and soil that affects water infiltration, retention, and soil stability. This matrix is viewed as a protective, saturated microenvionment that would maintain hydraulic continuity between the root and dry soil (Read and others 1999). Equally important is the colonization of cells of the stomatal complex. Accumulation of lipids in the subsidiary cells could physically influence stomatal closure. Lipid-filled fungal protoplasts occupying stomatal apertures could potentially trap and retain transpired water. Such mechanisms would enhance water use efficiency and regulation and plant survival in drought-stressed arid ecosystems.

References

Barrow, J. R. 2003. Atypical morphology of dark septate fungal root endophytes of *Bouteloua* in arid Southwestern USA rangelands. Mycorrhiza. 13: 239–247.

Barrow, J. R.; Aaltonen, R. E. 2001. A method of evaluating internal colonization of *Atriplex canescens* (Pursh) Nutt. roots by dark septate fungi and how they are influenced by host physiological activity. Mycorrhiza. 11: 199–205.

Barrow, J. R.; Havstad, K. M.; McCaslin B. D. 1997. Fungal root endophytes in fourwing saltbush, *Atriplex canescens*, on arid rangelands of Southwestern USA. Arid Soil Research Rehabilitation. 11: 177–185.

Bevege, D. I . 1968. A rapid technique for clearing tannins and staining intact roots for detection of mycorrhizas caused by *Endogone* spp., and some records of infection in Australian plants. Transactions of the British Mycological Society. 51: 808–810.

Brundrett, M. C.; Piche, Y.; Peterson, R. L. 1983. A new method for observing the morphology of vesicular-arbuscular mycorrhizae. Canadian Journal Botany. 62: 2128–2134.

Griffin, D. M. 1979. Water potential as a selective factor in the microbial ecology of soils. In: Parr, J. F.; Gardner, W. R.; Elliot, L. F., eds. Water potential relations in soil microbiology. SSSA reprinted 1985, Special Publ. 9. Madison, WI: Soil Science Society of America: 141–151.

Jumpponen, A. 2001. Dark septate endophytes: are they mycorrhizal? Mycorrhiza. 11: 207–211.

Jumpponen, A.; Trappe, J. M. 1998. Dark septate endophytes: a review of facultative biotrophic root-colonizing fungi. New Phytologist. 140: 295–310.

Kormanik, P. P.; Bryan, W. C.; Schultz, R. C. 1980. Procedures and equipment for staining large numbers of plant root samples for endomycorrhizal assay. Canadian Journal of Microbiology. 26: 536–538 .

Parbery, D. G. 1996. Trophism and the ecology of fungi associated with plants. Biological Review. 71: 473–527.

Phillips, J. M.; Hayman, D. S. 1970. Improved procedures for clearing roots and staining parasitic and vesicular-arbuscular mycorrhizal fungi for rapid assessment of infection. Transactions British Mycological Society. 55: 158–161.

Read, D. B.; Gregory, P.; Bell, A. E. 1999. Physical properties of axenic maize root mucilage. Plant Soil. 211: 87–91.

Smith, S. E.; Read, D. J., eds. 1997. Mycorrhizal symbiosis. 2d ed. San Diego and London: Academic Press: 59–60.

Smith, F. A.; Smith, S. E. 1996. Mutualism and parasitism: diversity in function and structure in the "arbuscular" (VA) mycorrhizal symbioses. Advances in Botanical Research: 22: 1–43.

Trappe, J. M. 1981. Mycorrhizae and productivity of arid and semiarid rangelands. In: Manassah, J. T.; Briskey, E. J., eds. Advances in food-producing systems for arid and semiarid lands. Part A. New York: Academic Press: 581–593.

Cheatgrass Invasion Alters Soil Morphology and Organic Matter Dynamics in Big Sagebrush-Steppe Rangelands

Jay B. Norton
Thomas A. Monaco
Jeanette M. Norton
Douglas A. Johnson
Thomas A. Jones

Abstract: Cheatgrass (*Bromus tectorum* L.) is an invasive annual grass that increases wildfire frequency, degrades native ecosystems, and threatens agriculture across vast areas of the Western United States. This research examines how cheatgrass invasion may alter physical and biological properties of soils. Proliferation of very fine roots and high production of low-quality litter by cheatgrass increases porosity and near-surface microbial activity, which may enhance decomposition of soil organic matter (SOM) similar to cultivated systems. This may enlarge active SOM pools (mineral and microbial biomass C and N) at the expense of slow pools and humus. To test this hypothesis, soil properties beneath long-term cheatgrass-invaded areas were compared with carefully matched soils under shrub canopies and grass-covered interspaces at seven undisturbed Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) plant communities in northern Utah and southeastern Idaho. Soils under cheatgrass had (1) higher porosity in surface horizons, (2) higher concentrations of mineral N throughout the soil profiles at the time of sampling, and (3) a larger proportion of mineralizable C and N in total SOM of surface horizons than soil under native shrub-steppe plant communities. These results support our hypothesis and suggest that long-term cheatgrass invasion may alter ecological stability and resilience by depleting slow and passive SOM pools. This research will contribute to improved understanding of fundamental ecosystem processes required for successful ecological restoration.

Introduction

The exotic annual grass cheatgrass (*Bromus tectorum* L.) has invaded large areas of shrub-steppe ecosystems in the Western United States, and is now dominant on much of the Great Basin, Snake River Plain, and Columbia Plain physiographic provinces (Knapp 1996; Knick 1999; Mack 1981). The area covered by cheatgrass and its ecological impact on shrub-steppe plant communities rivals ecosystem conversion from grasslands to annual crops that took place in Central North American (Samson and Knopf 1994). Numerous investigations of native ecosystem conversion to croplands provide an understanding of agriculture-related environmental change, particularly of nutrient cycling and soil organic matter (SOM) dynamics in both natural and disturbed ecosystems (Parton and others 1987; Schimel 1986). As impacts of invasive plants on ecosystem processes begin to be understood (D'Antonio and Vitousek 1992; Ehrenfeld and Scott 2001), application of concepts from cropland conversion may further this understanding. In this paper, we describe research that compared soils under cheatgrass to those under native shrub-steppe grasslands. We discuss ecological parallels between annual crops and cheatgrass invasion and their implications for restoration of diverse native plant communities.

On a worldwide basis, conversion of native ecosystems to cropland results in about a 30-percent long-term decrease in soil organic carbon (SOC). Annually, such conversion accounts for nearly one-fifth of the net carbon (C) transfer from terrestrial ecosystems to the atmosphere from changing land uses (Davidson and Ackerman 1993). In general, cropland conversion is thought to change native ecosystems from net C sinks to important sources of atmospheric CO_2 (Schlesinger 1999). In semiarid shortgrass-steppe grasslands, the long-term decrease in SOC from conversion to cropland is often more than 60 percent (Aguilar and others 1988; Schimel 1986), most of which is lost in the first few years of cultivation (Bowman and others 1990). Cultivation also reduces labile C in soils as well as labile C as a proportion of SOC (Bowman and others 1990). Cropland soils typically have less total nitrogen (N), less labile N, and lower labile N:total N than their uncultivated counterparts. However, these N decreases with cultivation are proportionally less than that for SOC, resulting in narrowing C:N ratios in both total and labile fractions after cultivation of grassland soils (Bowman and others 1990). Inorganic N

In: Hild, Ann L.; Shaw, Nancy L.; Meyer, Susan E.; Booth, D. Terrance; McArthur, E. Durant, comps. 2004. Seed and soil dynamics in shrubland ecosystems: proceedings; 2002 August 12–16; Laramie, WY. Proceedings RMRS-P-31. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Jay B. Norton is County Director, University of California, Cooperative Extension, Tuolumne County, Sonora, CA 95370; e-mail: jbnorton@ucdavis.edu. Jeanette M. Norton is an Associate Professor, Department of Plants, Soils, and Biometeorology, Utah State University, Logan, UT 84322-4820, U.S.A. Thomas A. Monaco, Douglas A. Johnson, and Thomas A. Jones are Research Scientists, USDA Forage and Range Research Laboratory, 695 N 1100 E, Logan, UT 84322-6300, U.S.A. FAX: (435) 797-3075.

concentrations are often reported to be higher in cropland than grassland soils, even without the effects of inorganic fertilizers (DeLuca and Keeney 1993a). Native grasslands are often described in terms of "tight," conservative SOM cycling, wherein diverse and growing microbial communities immobilize limited amounts of N as fast as it mineralizes from decomposing SOM (DeLuca and Keeney 1993a; Schimel 1986). In contrast, cropland soils are thought to have decaying microbial communities that "leak" inorganic nutrients as SOM mineralization exceeds uptake of inorganic nutrients (Schimel 1986; Smith and others 1994). Previous studies of cheatgrass invasion found greater concentrations of inorganic N in soils beneath cheatgrass than native shrub-steppe vegetation (Evans and others 2001; Svejcar and Sheley 2001). Other studies reported changes in the amount of labile C as a proportion of TOC (Bolton and others 1990; Gill and Burke 1999; Smith and others 1994).

Conversion from grassland to cropland changes SOM dynamics in three ways: (1) reduced SOM inputs because of crop harvest, (2) lower root:shoot ratios in annual crops than perennial herbaceous and woody vegetation, and (3) increased decomposition rates from aeration and more labile organic substrates (Schimel 1986). Conversion of native shrub-steppe to dominance by cheatgrass impacts SOM dynamics in five similar ways: (1) reduced SOM inputs from frequent fires that volatilize litter almost annually in many areas (Knick and Rotenberry 1997; Whisenant 1990), (2) reduced root:shoot ratios compared to native grasses and shrubs (Monaco and others 2003), (3) higher litter decomposition rates from more labile litter compared to native plants, (4) altered soil structural properties (Gill and Burke 1999) due to differences in root architecture between cheatgrass and native species (Arredondo and Johnson 1999), and (5) different assemblages of soil microbes (Kuske and others 2002) and fauna (Belnap and Phillips 2001) associated with cheatgrass and native soils. Conversion from perennial vegetation to annual vegetation may lead to larger active (inorganic and labile) SOM pools and smaller slow and passive (protected SOM and humus) pools (Parton and others 1987) (fig. 1). With cheatgrass invasion, these changes may result in feedback processes that progressively alter soil structure (Angers and Caron 1998), soil hydrology, and decomposition rates. Degradative feedbacks could ultimately lead to impoverished soils that may limit restoration alternatives.

Similarities between the impacts of annual crops and cheatgrass on SOM dynamics notwithstanding, clear differences in SOM content, composition, and cycling between soils underneath cheatgrass-dominated and shrub-steppe vegetation are difficult to detect (Bolton and others 1990; Svejcar and Sheley 2001). The objective of our study was to evaluate changes in soil morphology and the distribution and composition of SOM associated with cheatgrass invasion of sagebrush-steppe communities. Our underlying hypothesis is that soils under cheatgrass-dominated vegetation exhibit morphological characteristics and organic matter dynamics that facilitate depletion of slow and passive SOM that turns over in the timeframe of decades to centuries and enrich active SOM that turns over every 2 years or less (fig. 1).

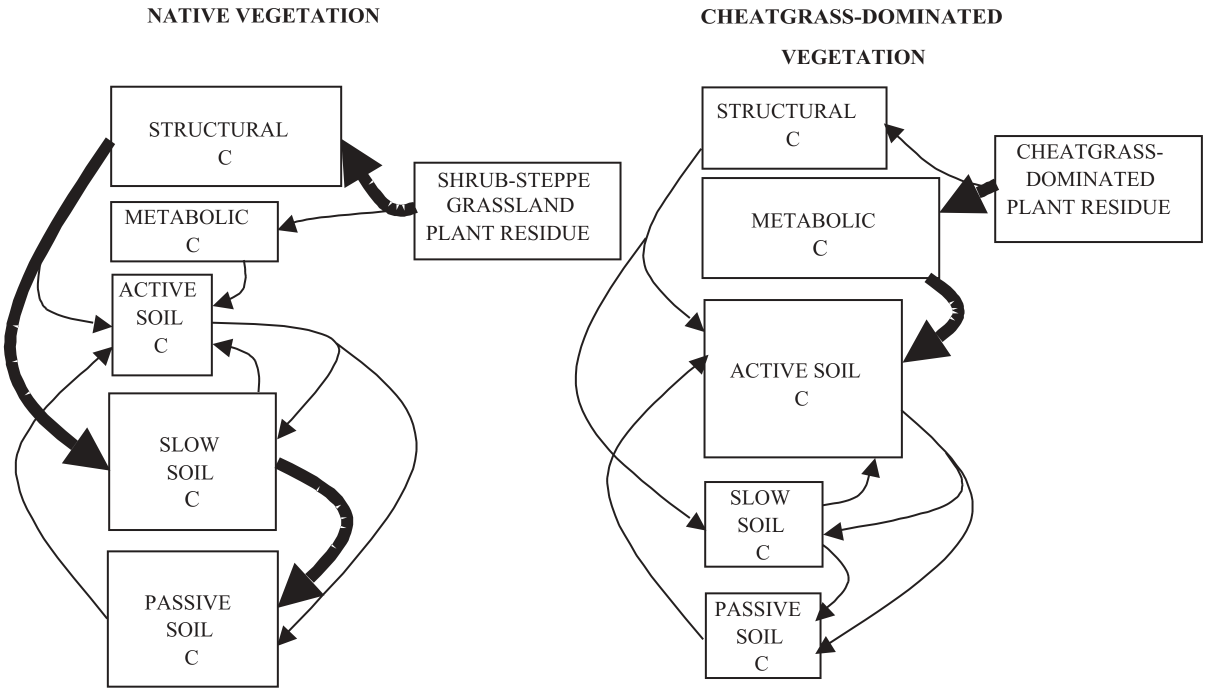


Figure 1—Conceptual diagram of relative C flows in native shrub-steppe and cheatgrass-dominated vegetation (based on Parton and others 1987). Structural and metabolic C in plant residues have residence times of approximately 3 and 0.5 years, respectively. Active, slow, and passive soil C pools have approximate turnover rates of 1.5, 25, and 1,000 years.

Materials and Methods

Soil morphology and SOM dynamics were compared in soils beneath cheatgrass-dominated and diverse Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis* Beetle & A.W. Young)-associated vegetation using a series of seven paired sites in Utah and Idaho. Soil samples and data were collected during summer and fall 2001 from soil profiles and replicated points randomly distributed within adjacent cheatgrass-dominated and Wyoming big sagebrush-associated vegetation (fig. 2). Soil-forming factors (such as, parent material, topography, climate, land use) at each paired site were similar between cheatgrass-dominated and adjacent sagebrush-steppe vegetation. Cheatgrass-dominated areas were nearly monocultures with documented dates of conversion from native vegetation. Cheatgrass invasion was not a result of livestock corrals, cultivation, excavation, or similar forms of severe disturbance.

Soil profiles were described and sampled following soil survey procedures (NRCS 1993). Soil profile descriptions are reported in Norton and others (in press). Soil pits in native vegetation were located with pit walls beneath grass and shrubs representative for the area within each site. One bulk soil sample was collected from three of the pit walls for each soil horizon and placed on ice for transport to the laboratory. Slope steepness, aspect, vegetation cover, description of landform and parent material, and likely cause of cheatgrass invasion were recorded at each soil pit. Replicated samples were collected from two depths (0 to 5 cm and 5 to 20 cm) at five random bearings (0 to 360 degrees) and distances (1 to 25 m) from each soil pit. Two distinct locations were sampled in the native half of each pair, including an area adjacent to the nearest perennial grass plants and an area beneath the nearest shrub canopy (fig. 2). Soil samples were homogenized shortly after collection, and about 10 g of each sample was placed in a preweighed sample cup that contained 100 ml of 2*M* KCl for field extraction of nitrate-N (NO_3^-–N) and ammonium-N (NH_4^+–N). Cups were immediately capped and stored on ice for transport to the laboratory. Vegetation at each site was evaluated for areal cover (Daubenmire 1968) and frequency by species (Smith and others 1987) along three transects, each with a total of 20 quadrats 0.25-m x 0.25-m square (fig. 2).

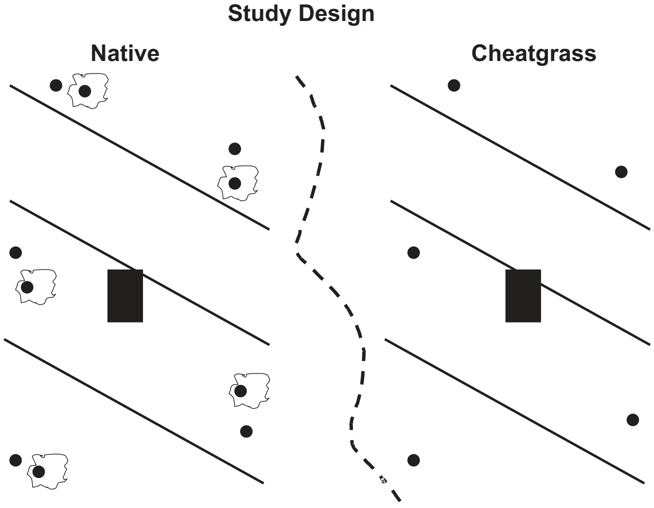


Figure 2—Schematic diagram of study design. Polygons represent shrubs, black dots represent two-depth replicated soil samples, black rectangles represent soil pits, and diagonal lines represent vegetation transects. See text for further description.

Immediately upon returning to the laboratory, field extractions were reweighed to determine exact amount of soil sample, placed horizontally on a rotating shaker at 200 rpm for 30 minutes, and then allowed to settle overnight in a 4 °C refrigerator. Samples were filtered with Whatman no. 4 filters (Whatman International, Ltd., Maidstone, England) and wet-sieved through 2-mm screens to remove gravel. Gravel was dried, weighed, and the weight was subtracted from the field-moist weight of the extracted sample. KCl field extracts were frozen for further inorganic N analyses.

All soil samples were stored overnight in sealed sample bags maintained at 4 °C in a refrigerator, sieved through 2-mm screens (reserving at least three aggregates from each soil profile sample for bulk density analysis), and partitioned for determination of gravimetric moisture and mineralizable C and N. Mineralizable C was determined by aerobic incubation of ~20-g samples brought to 23 percent soil water content and incubated for 12 days in a 20 °C incubator in 0.95-L canning jars fitted with rubber septa. Gas in the headspace was sampled on days 1, 6, and 12 during the incubation (Zibilske 1994) and injected into a LI-COR 6400 infrared gas analyzer (LI-COR Corp., Lincoln, NE) for determination of CO_2 concentration. Each jar was vacuum vented and returned to the incubator after CO_2 measurements on day 1 and day 6. Inorganic N in the incubated ~20-g samples was determined by 2M KCl extraction after the 12-day incubation (Hart and others 1994). Concentration of NO_3^-–N and NH_4^+–N were determined with a Lachat flow injection autoanalyzer (Lachat Instruments, Milwaukee, WI) for field samples and postincubation samples. Postincubation inorganic N concentration (the amount of inorganic N after the 12-day incubation) represents the active N pool and is reported as "active N." Bulk density was determined by the clod method (Blake and Hartge 1986). Total C and N were determined by dry combustion with a Leco CHN 2000 Autoanalyzer (Leco Corp., St. Joseph, MI). Inorganic-C concentration was determined gravimetrically (Loeppert and Suarez 1996) and subtracted from total-C concentration to determine organic-C concentration. Data from upper soil horizons were analyzed by paired difference t-test and correlation procedures using the Microsoft Excel Data Analysis Toolpak (Microsoft Corp., Redmond, WA). Cheatgrass-native comparisons for the native half of the replicated samples were based on weighted means derived from percent shrub cover and soil properties beneath grasses and shrubs.

Results and Discussion

Our results suggest that conversion of native shrub-steppe vegetation to cheatgrass dominance affects both the soil environment and SOM dynamics in ways that are analogous to grassland conversion to cropland. However, absolute, whole-solum SOM loss is not as distinct with cheatgrass conversion as observed under cropland conversion (Bowman and others 1990; Davidson and Ackerman 1993).

Our analysis of vegetation cover shows that the native shrub-steppe areas were diverse, with up to 29 species in all three life forms (grass, shrub, and forb) well represented at the seven sites. Shrub cover ranged from 0 to 21 percent for the native areas. In contrast, cheatgrass areas had a maximum of 18 species, many of which were exotic annual weeds. Cheatgrass-dominated areas had very few shrubs, and most sites had nearly 100 percent cheatgrass, although sandberg bluegrass (*Poa secunda* J. Presl.) was well represented at some sites (maximum of 13 percent cover). Thus, vegetation at our sites was representative of cheatgrass-invaded areas (Mack 1981).

Soil porosity (the inverse of bulk density) was significantly higher in surface soil horizons under cheatgrass than native shrub-steppe vegetation, but this difference diminished in the subsurface (fig. 3). Higher porosity under cheatgrass is likely the result of the dense, very fine, and shallow root mass observed in *A* horizons under cheatgrass, which had 83 percent more very fine roots (<1 mm diameter) than *A* horizons under shrub-steppe vegetation. Fine-root density was the same beneath the two vegetation types below the *A* horizons. Cheatgrass soils had no roots coarser than 1 mm diameter, while size classes of very fine through coarse were well represented in shrub-steppe soils. Because cheatgrass dies each summer, decaying roots leave behind a high density of very fine tubular pores, which we observed in *A* horizons under cheatgrass. This combination of greater porosity and greater inputs of very fine roots accelerates decomposition by enhancing air and water movement in surface soils, and contributes to a relatively large and labile substrate each year. These changes induced by cheatgrass may facilitate pulses of microbial activity when moisture becomes available. These conditions may also enhance germination and establishment of cheatgrass seedlings. However, this relatively high porosity and labile SOM content is dependent on annual production by cheatgrass and may disintegrate rapidly if cheatgrass germination is prevented, as with preemergent herbicides that often precede planting of perennial species.

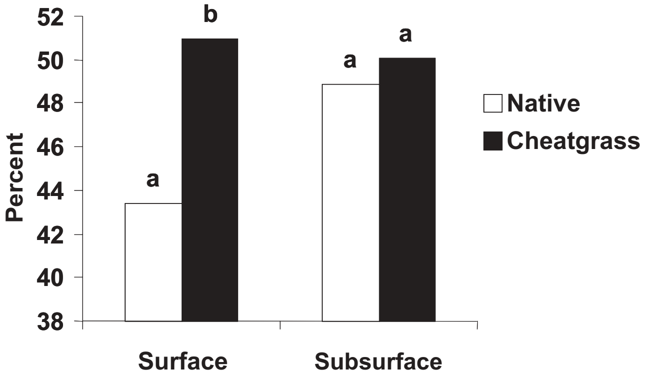


Figure 3—Percent porosity of soils beneath cheatgrass-dominated and native shrub-steppe vegetation based on means of seven cheatgrass sites and seven native sites. Different letters above columns indicate significant differences (P < 0.05) resulting from paired-difference analysis.

Differences in SOM distribution and composition beneath cheatgrass-dominated and shrub-steppe vegetation were analogous to differences beneath grasslands and croplands, but losses of SOM appeared to be less pronounced in shrub-steppe vegetation. The most significant differences occurred in soil N fractions with higher concentrations of total N, inorganic N, and active-pool N beneath cheatgrass than shrub-steppe vegetation, and lower CO_2–C:active-pool N ratios beneath cheatgrass than shrub-steppe soils.

On a whole-solum basis, soils beneath cheatgrass had less SOC and more total N than soils beneath shrub-steppe vegetation at five of the seven sites (table 1). Although the differences among averages for all sites were not significant ($P > 0.05$), cheatgrass solums had 30 percent less SOC ($P = 0.14$) and 4 percent more N ($P = 0.40$) than shrub-steppe solums. SOC concentrations in surface soils beneath cheatgrass were equal to those under native shrub-steppe vegetation (figs. 4 and 5), while total N concentrations were higher in cheatgrass than shrub-steppe *A* horizons. This is opposite to observed changes in grassland soils following conversion to cropland (Bowman and others 1990). In our study, SOC levels declined more with soil depth under cheatgrass than under shrub-steppe vegetation at each of the sites (fig. 4). Average SOC concentration in the upper subsoil under cheatgrass averaged about half that of upper subsoils under shrub-steppe vegetation. The magnitude of the difference between SOC in *A* horizons and upper subsoils under cheatgrass correlates with the approximate age of cheatgrass invasion (fig. 6). Total N concentrations in the subsoil were equal for the two vegetation types. Subsoils of semiarid grasslands have higher decomposition rates than surface horizons because they hold more moisture for more of the year (Gill and others 1999). Higher soil water content, along with lower root inputs to subsoils and the possibility of a mineralization priming effect caused by large precipitation-induced pulses of microbial activity, may lead to depletion of subsoil SOC under cheatgrass-dominated vegetation. A mineralization priming effect is often observed in agricultural soils when a labile C source is combined with aeration caused by cultivation, which creates a large pulse of microbial activity. The C source is rapidly consumed, but enzymes remain capable of mineralizing SOM stored in slow and passive pools (DeLuca and Keeney 1993b). The result is uptake of more SOM mineralization products than in the original C source and depletion of SOM stored as slowly decomposing materials and humus. Gill and Burke (1999) found lower concentrations of slow-pool SOC beneath cheatgrass than under adjacent shrub-steppe vegetation.

Field-extracted inorganic N differed significantly between vegetation type and soil depth (table 2). Cheatgrass-dominated areas had 75 percent more ($P = 0.02$) NO_3^-–N in the 0- to 5-cm soil depth and 66 percent more ($P = 0.03$) in the 5- to 20-cm soil depth than shrub-steppe vegetation areas at the time of sampling (table 2). Ammonium N concentrations (not presented) followed similar trends, but were highly variable. Nitrate N also made up a higher proportion of total N at both soil depths (table 2). Higher inorganic N concentrations are often observed following conversion of grassland to cropland

Table 1—Whole-solum organic C and total N under Wyoming big sagebrush steppe (native) and cheatgrass vegetation (CG).

	Organic C				Total N			
Site	**Native**	**CG**	**Diff.**[a]	***P***	**Native**	**CG**	**Diff.**	***P***
	------ *g m*$^{-2b}$ -----		*percent*		----- *g m*$^{-2}$ ---		*percent*	
Cedar Creek	10,894	13,689	26		931	1,418	52	
Cedar Knoll	6,933	6,179	–11		1,196	1,666	39	
Five Mile Junction	36,625	15,135	–59		3422	2,328	–32	
Horse Butte	4,821	3,517	–27		847	700	–17	
Hogup Mountains	11,187	6,282	–44		1,076	1,230	14	
Johnson Canyon	4,961	6,125	23		502	627	25	
Mickel-Watson	10,672	9,547	–11		1,079	1,480	37	
Mean	12,299	8,639	–30	0.14	1,293	1,350	4	0.40

[a] Percent differences based on "native" values.

[b] Calculated from bulk density of soil samples from each horizon.

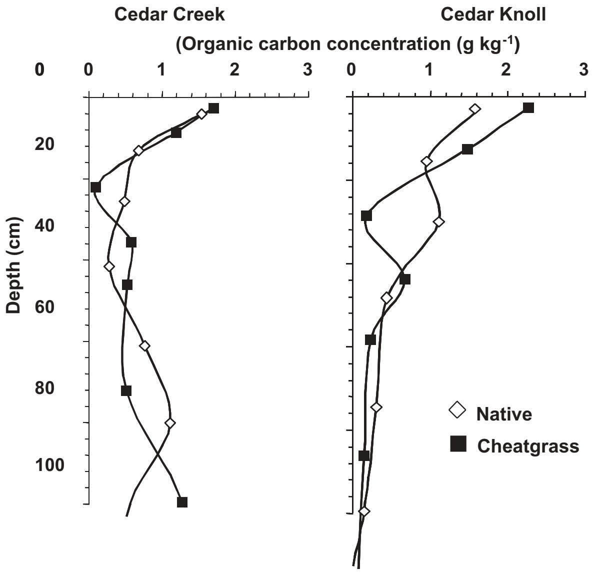


Figure 4—Soil organic carbon concentration in paired soil profiles under cheatgrass-dominated and Wyoming big sagebrush-steppe vegetation at two of the seven study sites. SOC concentrations followed similar trends at each of the seven study sites.

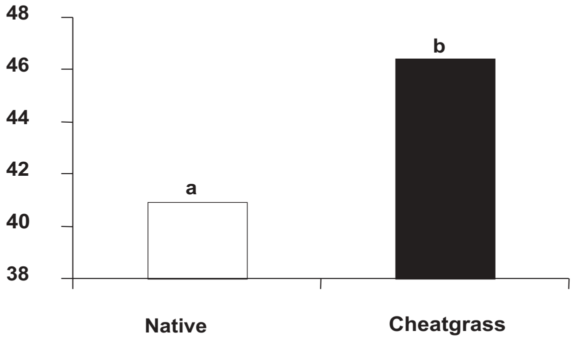


Figure 5—Percent difference in SOC concentrations between the 0- to 5-cm soil depth and the 5- to 20-cm soil depth based on means from all replicated points. Different letters above columns indicate significant differences (P <0.05) resulting from paired-difference analysis.

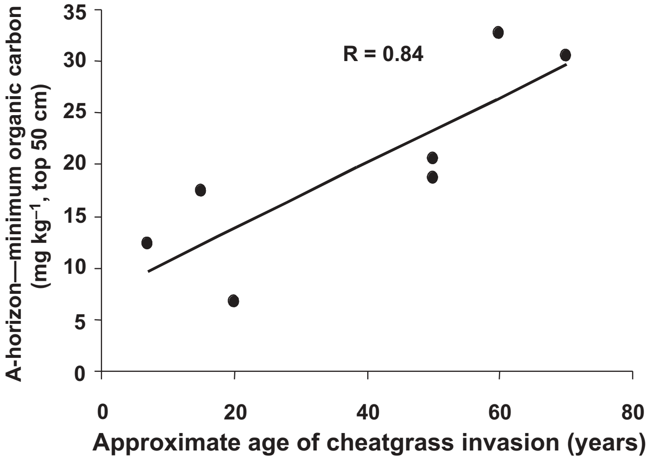


Figure 6—Difference in SOC concentration between A-horizons (maximum in upper 50 cm) and minimums within the top 50 cm in each of seven cheatgrass soil profiles as a function of approximate time since cheatgrass became the dominant vegetation.

and are considered indicative of decaying, C-limited SOM systems that "leak" mineralized nutrients after short-lived pulses of microbial activity drive mineralization of stored SOM (Schimel 1986). A similar explanation may apply to higher inorganic-N concentrations beneath cheatgrass than native shrub-steppe vegetation.

Active-pool C (C mineralized during 12-day incubations) was nearly the same under the two vegetation types. Active-pool N (postincubation inorganic N) concentrations, however, were 39 percent higher ($P = 0.04$) in the 0- to 5-cm soil depth and 34 percent higher ($P = 0.12$) in the 5- to 20-cm soil depth in cheatgrass-dominated areas than shrub-steppe areas (table 2). Mineralized C accounted for about the same proportion of total SOC in both vegetation types, but active N accounted for a higher proportion of total N in cheatgrass-dominated than shrub-steppe soils at both depth increments (table 2). These proportions suggest that cheatgrass-dominated vegetation creates a mineralizing environment

Table 2—Paired difference analysis[a] of selected soil properties under Wyoming sagebrush-teppe (native) and cheatgrass-dominated vegetation (CG).

	Organic C			Total N			Field NO_3^-–N			Active-pool C		
Depth	**Native[b]**	**CG**	**Diff.[c]**	**Native**	**CG**	**Diff.**	**Native**	**CG**	**Diff.**	**Native**	**CG**	**Diff.**
cm	- - - *g kg^{-1}*	- - -	*percent*	- - - *g kg^{-1}*	- -	*percent*	- - *mg kg^{-1}*	- -	*percent*	- - - *mg kg^{-1}*	- -	*percent*
0 to 5	20.53	21.85	6.5	2.14	2.34	9.6	5.33	9.31	74.8[d]	190.48	210.31	10.4
5 to 20	12.13	11.71	–3.5	1.44	1.36	–6.0	2.17	3.61	65.9[d]	64.33	60.50	–6.0

	Active-pool N			NO_3^-–N/Total N			Active-pool N/Total N			Active-pool C:N		
	Native	**CG**	**Diff.**	**Native**	**CG**	**Diff.**	**Native**	**CG**	**Diff.**	**Native**	**CG**	**Diff.**
	- - *mg kg^{-1}*	- -	*percent*	*mg NO_3^-–N g^{-1}TN*		*percent*	*mg NO_3^-–N g^{-1}TN*		*percent*			*percent*
0 to 5	23.71	33.05	39[d]	2.54	4.07	60[d]	12.05	15.59	29[e]	9.29	10.19	10
5 to 20	5.60	7.52	34	1.53	2.92	91[d]	4.04	6.36	57[d]	17.33	8.39	–52[d]

[a] Means from seven study sites, each with 10 native samples (five grass and five shrub) and five cheatgrass samples at each depth.
[b] Weighted means based on proportion of grass and shrub cover on sites.
[c] Percent difference based on "native" value.
[d] Significant at the $P < 0.05$ level.
[e] Significant at the $P < 0.10$ level.

where uptake is limited by shortage of labile C caused by rapid decomposition and relatively low root:shoot ratios.

Ratios of SOC to total N were equal in soils of the two vegetation types. The C:N ratios in the active SOM pool were also equal in both *A* horizons and in the 0- to 5-cm depth of both vegetation types (table 2). However, active-pool SOM of cheatgrass soils had much lower C:N ratios in upper subsurface horizons (fig. 7) and in the 5- to 20-cm depth increment (table 2) than those of native shrub-steppe soils. These differences in active-pool C:N ratios are analogous to comparisons between grassland and cropland soils (DeLuca and Keeney 1993a; Schimel 1986). This pattern suggests conservative, "tight" N cycling dominated by immobilization in soils under shrub-steppe vegetation compared to more net mineralization in a "leaky" N cycle under cheatgrass-dominated vegetation. Smith and others (1994) found that soils beneath shrub-steppe vegetation had much tighter, more efficient N cycling compared to cropland, forest, and annual grass ecosystems they analyzed.

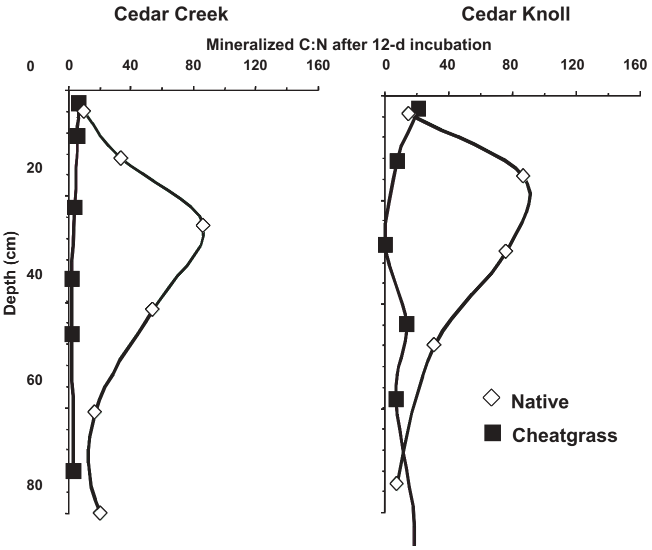


Figure 7—Active-pool C:N ratios (mineralized C:N after 12-d incubation) in paired soil profiles under cheatgrass-dominated and Wyoming big sagebrush-steppe vegetation at two of the seven study sites. Active-pool C:N ratios followed similar trends at six of the seven study sites.

Conclusions

This research contributes basic knowledge about how extensive annual grass invasion alters soil properties recognized as foundations of ecological stability and resilience (Coleman and others 1983). Our results suggest that conversion of diverse native plant communities to cheatgrass, which is now the dominant vegetation on most of three major physiographic provinces in the Western United States, leads to losses of SOM and changes in its composition and distribution. These changes may be analogous to changes brought about by crop cultivation in central grasslands of North America, which are known to have altered basic ecosystem functions such as cycling of C, N, and water. These basic ecosystem functions are even more difficult to restore in the arid and semiarid West because inherent fragility of altered ecosystems (Tausch and others 1993) makes reversal uncertain and very expensive. The magnitudes of these changes may intensify with the time that cheatgrass dominates, limiting the prospects for restoring these areas. Our results suggest that successful restoration of diverse native vegetation in cheatgrass-dominated areas may require use of transition species that are capable of competing with cheatgrass while contributing slow-pool SOC to the soil.

References

Aguilar, R.; Kelley, E. F.; Heil, R. D. 1988. Effects of cultivation of soils in Northern Great Plains rangeland. Soil Science Society of America Journal. 52: 1081–1085.

Angers, D. A.; Caron, J. 1998. Plant-induced changes in soil structure: processes and feedbacks. In: van Breeman, N., ed. Plant-induced soil changes: processes and feedbacks. Dordrecht, The Netherlands: Kluwer Academic Publishers: 55–72.

Arredondo, J. T.; Johnson, D. A. 1999. Root architecture and biomass allocation of three range grasses in response to nonuniform supply of nutrients and shoot defoliation. New Phytologist. 143: 373–385.

Belnap, J.; Phillips, S. L. 2001. Soil biota in an ungrazed grassland: response to annual grass (*Bromus tectorum*) invasion. Ecological Applications. 11: 1261–1275.

Blake, G. R.; Hartge, K. H. 1986. Bulk density. In: Klute, A., ed. Methods of soil analysis. Part 1: physical and mineralogical methods. 2d ed. Madison, WI: American Society of Agronomy: 363–375

Bolton, H., Jr.; Smith, J. L.; Wildung, R. E. 1990. Nitrogen mineralization potentials of shrub-steppe soils with different disturbance histories. Soil Science Society of America Journal. 54: 887–891.

Bowman, R. A.; Reeder, J. D.; Lober, R. W. 1990. Changes in soil properties in a Central Plains rangeland soil after 3, 20, and 60 years of cultivation. Soil Science. 150: 851–857.

Coleman, D. C.; Reid, C. P. P.; Cole, C. V. 1983. Biological strategies of nutrient cycling in soil systems. Advances in Ecological Research. 13: 1–55.

D'Antonio, C. M.; Vitousek, P. M. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annual Review of Ecology and Systematics. 23: 63–87.

Daubenmire, R. 1968. Plant communities: a textbook of plant synecology. New York: Harper & Row, Publishers. 300 p.

Davidson, E. A.; Ackerman, I. L. 1993. Changes in soil carbon inventories following cultivation of previously untilled soils. Biogeochemistry. 20: 161–193.

DeLuca, T. H.; Keeney, D. R. 1993a. Soluble organics and extractable nitrogen in paired prairie and cultivated soils of central Iowa. Soil Science. 155: 219–228.

DeLuca, T. H.; Keeney, D. R. 1993b. Glucose induced nitrate assimilation in prairie and cultivated soils. Biogeochemistry. 21: 167–176.

Ehrenfeld, J. G.; Scott, N. 2001. Invasive species and the soil: effects on organisms and ecosystem processes. Ecological Applications. 11: 1259–1260.

Evans, R. D.; Rimer, R.; Sperry, L.; Belnap, J. 2001. Exotic plant invasion alters nitrogen dynamics in an arid grassland. Ecological Applications. 11: 1301–1310.

Gill, R. A.; Burke, I. C. 1999. Ecosystem consequences of plant life form changes at three sites in the semiarid United States. Oecologia. 121: 551–563.

Gill, R. A.; Burke, I. C.; Milchunas, D. G.; Lauenroth, W. K. 1999. Relationship between root biomass and soil organic matter pools in the shortgrass steppe of eastern Colorado. Ecosystems. 2: 226-236.

Hart, S. C.; Stark, J. M.; Davidson, E. A.; Firestone, M. K. 1994. Nitrogen mineralization, immobilization, and nitrification. In: Weaver, R. W.; Angle, S.; Bottomley, P., eds. Methods of soil analysis. Part 2: microbiological and biochemical properties. Madison, WI: Soil Science Society of America: 985–1018.

Knapp, P. A. 1996. Cheatgrass (*Bromus tectorum* L) dominance in the Great Basin Desert. Global Environmental Change. 6: 37–52.

Knick, S. T. 1999. Requiem for a sagebrush ecosystem? Northwest Science. 73: 53–57.

Knick, S. T.; Rotenberry, J. T. 1997. Landscape characteristics of disturbed shrubsteppe habitats in southwestern Idaho (U.S.A.). Landscape Ecology. 12: 287–297.

Kuske, C. R.; Ticknor, L. O.; Miller, M. E.; Dunbar, J. M.; Davis, J. A.; Barns, S. M.; Belnap, J. 2002. Comparison of soil bacterial communities in rhizospheres of three plant species and the interspaces in an arid grassland. Applied and Environmental Microbiology. 68: 1854–1863.

Loeppert, R. H.; Suarez, D. L. 1996. Carbonate and gypsum. In: Sparks, D. L., ed. Methods of soil analysis. Part 3: chemical methods. Madison, WI: Soil Science Society of America: 437–474.

Mack, R. N. 1981. Invasion of *Bromus tectorum* L. into Western North America: an ecological chronicle. Agro-Ecosystems. 7: 145–165.

Monaco, T. A.; Johnson, D. A.; Norton, J. M.; Jones, T. A.; Connors, K. J.; Norton, J. B.; Redinbaugh, M. B. 2003. Contrasting responses of Intermountain West grasses to soil nitrogen. Journal of Range Management. 56: 282–290.

Norton, J. B.; Monaco, T. A.; Norton, J. M.; Johnson, D. A.; Jones, T. A. [In press]. Soil morphology and organic matter dynamics under cheatgrass and sagebrush-steppe plant communities. Journal of Arid Environments.

NRCS. 1993. Soil survey manual. Washington, DC: USDA Natural Resource Conservation Service.

Parton, W. J.; Schimel, D. S.; Cole, C. V.; Ojima, D. S. 1987. Analysis of factors controlling soil organic matter levels in Great Plains grasslands. Soil Science Society of America Journal. 51: 1173–1179.

Samson, F. B.; Knopf, F. L. 1994. Prairie conservation in North America. BioScience. 44: 418–421.

Schimel, D. S. 1986. Carbon and nitrogen turnover in adjacent grassland and cropland ecosystems. Biogeochemistry. 2: 345–357.

Schlesinger, W. H. 1999. Carbon sequestration in soils. Science. 284: 2095.

Smith, J. L.; Halvorson, J. J.; Bolton, H. J. 1994. Spatial relationships of soil microbial biomass and C and N mineralization in a semi-arid shrub-steppe ecosystem. Soil Biology Biochemistry. 26: 1151–1159.

Smith, S. D.; Bunting, S. C.; Hironaka, M. 1987. Evaluation of the improvement in sensitivity of nested frequency plots to vegetational change by summation. Great Basin Naturalist. 47: 299–307.

Svejcar, T.; Sheley, R. 2001. Nitrogen dynamics in perennial- and annual-dominated arid rangeland. Journal of Arid Environments. 47: 33–46.

Tausch, R. J.; Wigand, P. E.; Burkhardt, J. W. 1993. Viewpoint: plant community thresholds, multiple steady states, and multiple successional pathways: Legacy of the Quaternary? Journal of Range Management. 46: 439–447.

Whisenant, S. G. 1990. Changing fire frequencies on Idaho's Snake River Plains: ecological and management implications. In: McArthur, D. E.; Romney, E. M.; Smith, S. D.; Tueller, P. T., eds. Proceedings of the symposium on cheatgrass invasion, shrub die-off, and other aspects of shrub biology and management; 1989 April 5–7; Las Vegas, NV. Gen. Tech. Rep. INT-GTR-276. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 4–10.

Zibilske, L. M. 1994. Carbon mineralization. In: Weaver, R. W.; Angle, S.; Bottomley, P., eds. Methods of soil analysis. Part 2: microbiological and biochemical properties. Madison, WI: Soil Science Society of America: 15–40.

Response of Lewis Flax Seedlings to Inoculation With Arbuscular Mycorrhizal Fungi and Cyanobacteria

R. L. Pendleton
B. K. Pendleton
G. L. Howard
S. D. Warren

Abstract: Forbs comprise an important though understudied component of western rangelands. Little is known about the dependence of forb species on associated soil microorganisms such as arbuscular mycorrhizal fungi. In 1996 and 1998, we conducted two experiments examining the response of Lewis flax (*Linum lewisii* Pursh) to inoculation with arbuscular mycorrhizal fungi under a variety of soil conditions. Lewis flax was found to be highly dependent on mycorrhizae when grown in sandy soils, regardless of soil nutrient levels. Mycorrhizal plants had 10 times the root biomass and 16 times the shoot biomass of nonmycorrhizal controls. The addition of mycorrhizae also significantly decreased root:shoot ratios and significantly increased plant tissue concentrations of P, K, and Zn. The addition of cyanobacterial inoculum to the soil increased plant survival at low soil fertility, but had no effect on seedling growth. In the second experiment, three accessions of flax were grown in sand, peat, and a sand and peat mixture fertilized with high levels of a slow-release fertilizer. All three flax accessions responded positively to mycorrhizae in the sand and mixed soils, growing five and three times larger, respectively. In contrast, no significant response was observed in the peat soil. These findings indicate that mycorrhizal dependence is complex, and can be influenced by a number of factors, including soil nutrient status and organic matter content.

Introduction

Native forb species are prized both for their colorful contribution to western landscapes and for their importance in the diets of many herbivorous wildlife species. While early revegetation efforts focused primarily on the use of grass and shrub species, the use of herbaceous flowering plant seed in revegetation mixes has become increasingly common. As a result, the establishment requirements of forbs are becoming a research priority (Kitchen 1994).

North American Lewis flax (*Linum lewisii*) has wide distribution over the western half of the United States, Canada, and Northern Mexico (Mosquin 1971). Lewis flax and its close relative, *L. perenne*, have been used in revegetation and restoration plantings and show horticultural potential in xeriscaped gardens (Kitchen 1995; McArthur 1988). Other flax species are known to benefit from mutualistic associations with arbuscular mycorrhizal fungi (Thingstrup and others 1998). The purpose of this research was to examine the relative response of Lewis flax seedlings to inoculation with arbuscular mycorrhizal fungi (AMF) under a variety of soil conditions, including inoculation with biological soil crust organisms.

Methods

Experiment 1

Olympian 300XL pots (Hummert Int., Earth City, MO) were filled with a low-fertility bank sand that had been amended to one of three fertilizer levels. The sand was steam sterilized at 65 °C for 1 hour to kill any indigenous mycorrhizal fungi that might be present, and 2.4 g ammonium nitrate per 30 gallons of sand was added to raise the nitrogen level to 10 ppm. Medium and high fertilizer levels were amended with Osmocote 17-7-12 (The Scotts Company, Marysville, OH), formulated for 12 to 14 months continuous fertilization, applied at a rate of 5 and 9 ounces per cubic foot, respectively. Each pot received one of four inoculation treatments: algal inoculation, mycorrhizal inoculation, dual inoculation of both algae and mycorrhizae, and a noninoculated control. Mycorrhizal inoculation consisted of 1 teaspoon (approximately 100 spores) of pot-cultured mycorrhizal inoculum applied 1 to 2 inches below the soil surface. The inoculum was produced from soil collected from

---

In: Hild, Ann L.; Shaw, Nancy L.; Meyer, Susan E.; Booth, D. Terrance; McArthur, E. Durant, comps. 2004. Seed and soil dynamics in shrubland ecosystems: proceedings; 2002 August 12–16; Laramie, WY. Proceedings RMRS-P-31. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

R. L. Pendleton and B. K. Pendleton are Research Ecologists, USDA Forest Service, Rocky Mountain Research Station, 333 Broadway SE, Suite 115, Albuquerque, NM 87102-3497, U.S.A. FAX: (505) 724-3688, e-mail: rpendleton@fs.fed.us. G. L. Howard is Research Biologist, U.S. Army Corps of Engineers, Construction Engineering Research Laboratory, Champaign, IL. S. D. Warren is Research Scientist, Center for Environmental Management of Military Lands, Colorado State University, Fort Collins, CO 80523-1500.

a mixed desert shrub community near Toquerville, UT, that had been planted with ornamental corn seed (Carpenter Seed Co., lot 125). Nonmycorrhizal pots received an equal amount of inoculum that had been sterilized by autoclaving. Soil crust inoculum consisted of pelletized algal inoculum of the genera *Microcoleus* and *Nostoc* (Buttars and others 1998) ground to the consistency of cornmeal using a wheat grinder and applied at a rate of 1.6 g per pot, sprinkled by hand over the top of the soil at the time of planting.

Pots were sown with flax seed collected near Potosi Pass, west of Las Vegas, NV. Flax plants were thinned to one plant per pot upon emergence and grown for 15 weeks in a thoroughly cleaned, temperature-controlled greenhouse. At harvest, shoots were excised, dried, weighed, and ground for analysis of mineral content. Tissue samples were analyzed at the Soil and Plant Analysis Laboratory, Brigham Young University, Provo, UT, using atomic absorption and micro-Kjeldahl procedures (Johnson and Ulrich 1959). Results are only reported for plants grown at high soil fertility, as nonmycorrhizal plants at medium and low fertility produced insufficient biomass for mineral analysis. Roots were washed free of sand, dried at 60 °C, weighed, and stored at room temperature pending examination of mycorrhizal colonization (Tarkalson and others 1998).

Data were analyzed using the General Linear Models procedure on SAS, version 6.11 (SAS Institute 1993). Soil fertility, algal treatment, and AMF treatment were used as main effects in the model. Because of significant interaction terms involving soil fertility, the effects of algal and AMF inoculation treatments were also analyzed separately by soil fertility level. Survival data were analyzed using a 3 x 2 x 2 contingency table, later subdivided by soil fertility level.

Experiment 2

Seeds of three accessions of native Lewis flax (Potosi Pass, NV; Provo, UT; and Asotin, WA) were sown into SC-10 Super Cells (Stuewe & Sons, Corvallis, OR) containing one of three soil mixtures: (1) low-fertility bank sand that had been steamed for 2 hours at 77 °C, (2) a peat-based commercial potting soil, and (3) a mixture composed of half sand and half commercial potting soil. Mycorrhizal inoculum of the species *Glomus intraradices*, obtained from Tree of Life Nursery, Capistrano, CA, was added to one-half of the cells approximately 2 inches below the soil line, at a rate of 1 tablespoon per cell.

Fourteen replicate cells were used for each of the 18 soil/accession/inoculum combinations. Plants were thinned to one plant per cell and grown for 18 weeks in a temperature-controlled greenhouse. Each cell (plant) was fertilized using 1 tablespoon of Osmocote 17-7-12 (The Scotts Company, Marysville, OH). Plant height was recorded at the end of 9, 14, and 18 weeks growth. After 18 weeks, shoots were excised, dried, and weighed. Roots were washed free of soil, dried at 60 °C, weighed, and stored at room temperature for later examination of mycorrhizal colonization.

Data were analyzed using the General Linear Models procedure on SAS, version 6.11 (SAS Institute 1993). Soil type, plant accession, and AMF treatment were used as main effects in the model. Data were also analyzed by soil type and accession.

Results

Experiment 1

Survival of experimental plants was influenced by soil fertility level and algal inoculation ($X^2 = 47.8$; $P < 0.001$). Overall, survival was greatest at low fertility, followed by medium fertility (fig. 1). Inoculation with algae significantly improved survival at low fertility ($X^2 = 12.6$; $P < 0.001$), but significantly decreased survival at high fertility ($X^2 = 11.1$; $P < 0.001$).

Growth of flax plants was significantly affected by both soil fertility and inoculation with mycorrhizal fungi (table 1).

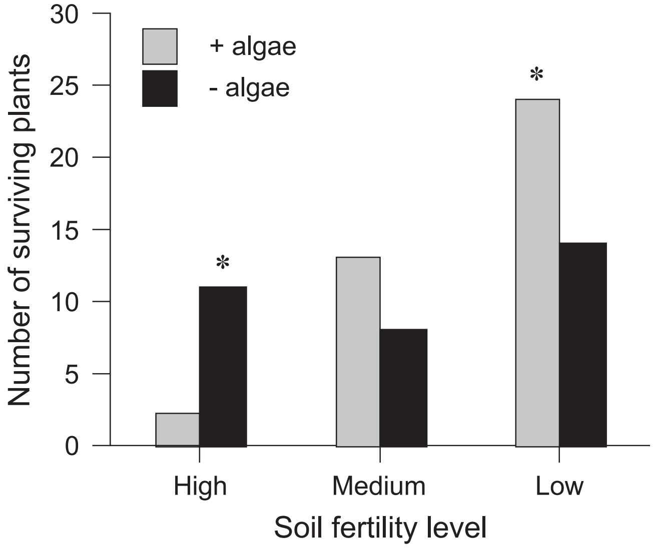


Figure 1—Effect of algal treatment on survival of Lewis flax plants (experiment 1). Bars marked with an asterisk indicate significant differences ($P \leq 0.05$) in plant survival.

Table 1—Attained significance values for treatment effects on Lewis flax growth measures by fertilizer level. Data are from experiment 1.

Fertility/source	Shoot biomass	Root biomass	r:s ratio
High fertility			
AMF inoculation	0.0135[a]	0.0895	0.0025[b]
Algal inoculation	NE[c]	NE[c]	NE[c]
AMF x algae	NE[c]	NE[c]	NE[c]
Medium fertility			
AMF inoculation	.0028[b]	.0043[b]	.0003[b]
Algal inoculation	.7954	.8350	.1068
AMF x algae	.7169	.8195	.3659
Low fertility			
AMF inoculation	.0001[b]	.0001[b]	.1395
Algal inoculation	.0588	.1693	.0226[a]
AMF x algae	.1386	.2598	.9970

[a] Significant at $P \leq 0.05$.
[b] Significant at $P \leq 0.01$.
[c] NE = nonestimable due to missing data.

Shoot biomass was significantly greater for mycorrhizal plants at all soil fertility levels (fig. 2). Root biomass was also significantly greater at medium and low soil fertility. Root: shoot ratios increased with decreasing soil fertility, but were consistently lower for mycorrhizal plants. Mycorrhizal plants also had higher tissue concentrations of P, K, Zn, and Mn (table 2). Calculated values for mycorrhizal dependence of flax (Plenchette and others 1983) ranged from 72 to 98 percent.

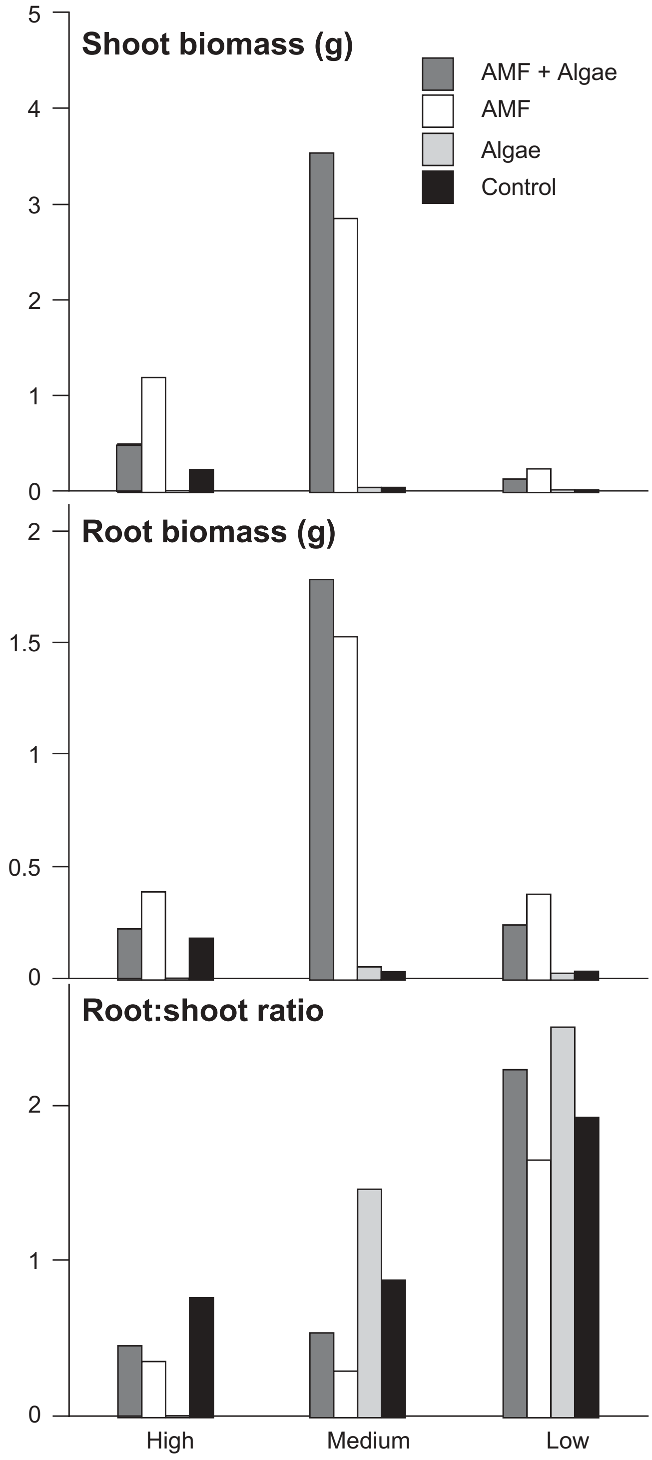


Figure 2—Effect of inoculation treatments on growth of Lewis flax plants (experiment 1).

Inoculation with blue-green algae increased root:shoot ratios at low and medium fertility levels (table 1; fig. 2), suggestive of some competition between plants and microorganisms. Algal inoculation also significantly increased plant tissue concentrations of K (2.06 versus 1.45 percent; *F* = 9.2; P = 0.01).

Experiment 2

While flax accessions differed in inherent growth rate, all accessions grew better with the addition of mycorrhizal inoculum when grown in either the sand or sand and peat mixture (fig. 3). Mycorrhizal plants were significantly taller and had greater shoot and root biomass (table 3), as well as total biomass, in these two soils. Mycorrhizal dependency values for these soils ranged from 78 to 96 percent, indicating that Lewis flax is strongly dependent on the fungus. In contrast, no significant differences in growth occurred in the peat-based potting soil. Dependency values in the peat soil ranged from 1 to 7 percent, indicating little or no dependence under these growing conditions.

Conclusions

1. Lewis flax may be characterized as mycorrhizal dependent. In inorganic media, growth of flax was significantly enhanced by inoculation, having dependency values ranging from 78 to 98 percent. The congener, *L. usitatissimum*, is also mycorrhizal dependent, exhibiting increased growth, reproduction, and resistance to pathogens in the presence of the fungus (Dugassa and others 1996; Thingstrup and others 1998).
2. In contrast, dependency values in organic soil ranged from 1 to 7 percent. The addition of organic matter through the peat-based potting mixture in many ways mimicked the response to P fertilization reported in previous studies. Mycorrhizal dependency may be influenced by a number of soil factors, including nutrient level, soil microorganisms, and organic matter content (Hetrick and others 1986; Schweiger and others 1995).
3. Inoculation with crust-forming algae increased survival at low soil fertility, but also increased root:shoot ratios. A shift in biomass allocation toward increased root mass suggests an increase in belowground competition for soil resources. Some competition between plant roots and soil microorganisms is likely, particularly during crust establishment.

Acknowledgments

This work was supported by grant MIPR W52EU260390969 from the U.S. Army Corps of Engineers, Construction Engineering Research Laboratory, Champaign, IL. Thanks are extended to Bruce N. Smith of Brigham Young University for providing student assistance, and to S. Garvin, D. Tarkalson, and B. St. Clair for technical support.

Table 2—Elemental tissue concentrations for mycorrhizal and nonmycorrhizal Lewis flax growing at high soil fertility. Nonmycorrhizal plants growing at medium and low fertility yielded insufficient biomass for elemental analysis. Attained significance values (P) from statistical analyses are given below. Significant differences are in boldface. Data are from experiment 1.

	n	N	P	K	Ca	Mg	Zn	Fe	Mn	Cu	Na
				percent					*ppm*		
+ AMF	4	4.16	0.33	2.01	2.73	0.69	17.47	203.1	67.3	10.83	743.5
– AMF	2	3.85	.11	.91	3.07	.78	4.43	280.3	128.5	10.47	740.3
P value		.3851	**.0147**	**.0389**	.5799	.4601	**.0310**	.2994	**.0082**	.8881	.9922

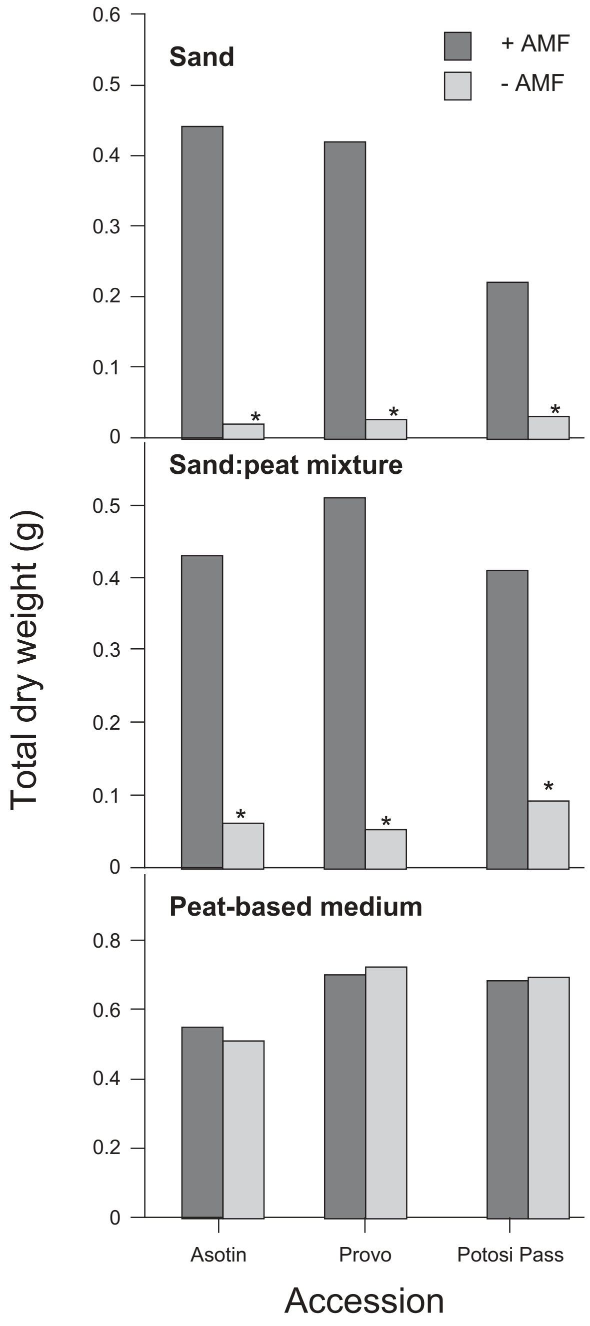


Figure 3—Effect of mycorrhizal fungi on growth of Lewis flax in three contrasting growth media (experiment 2). Bars marked with an asterisk indicate significant differences ($P \leq 0.05$) between mycorrhizal and nonmycorrhizal plants.

Table 3—Attained significance values from ANOVAs on growth measures of three accessions of mycorrhizal and nonmycorrhizal flax plants grown in sand, a peat-based potting soil, and a 1:1 mixture of the two. Data are from experiment 2.

Soil/accession	Height	Shoot biomass	Root biomass	Total biomass	Root/shoot ratio
	cm	- - - - - - - -	*g*	- - - - - - - -	
Sand					
Asotin	0.0001	0.0035	NS	0.0300	NS
Provo	.0001	.0051	.0043	.0038	NS
Potosi Pass	.0001	.0180	.0076	.0078	NS
Sand:peat					
Asotin	.0001	.0001	.0004	.0001	.0005
Provo	.0001	.0001	.0001	.0001	.0009
Potosi Pass	.0006	.0046	.0111	.0055	.0001
Peat					
Asotin	NS[a]	NS	NS	NS	NS
Provo	NS	NS	NS	NS	NS
Potosi Pass	NS	NS	NS	NS	NS

[a] Not significant at the 0.05 level.

References

Buttars, S. M.; St. Clair, L. L.; Johansen, J. R.; Sray, J. C.; Payne, M. C.; Webb, B. L.; Terry, R. E.; Pendleton, B. K.; Warren, S. D. 1998. Pelletized cyanobacterial soil amendments: laboratory testing for survival, escapability, and nitrogen fixation. Arid Soil Research and Rehabilitation. 12: 165–178.

Dugassa, G. D.; von Alten, H.; Schönbeck, F. 1996. Effects of arbuscular mycorrhiza (AM) on health of *Linum usitatissimum* L. infected by fungal pathogens. Plant and Soil. 185: 173–182.

Hetrick, B. A. D.; Kitt, D. G.; Wilson, G. T. 1986. The influence of phosphorus fertilization, drought, fungal species, and nonsterile soil on mycorrhizal growth response in tall grass prairie plants. Canadian Journal of Botany. 64: 1199–1203.

Johnson, C. M.; Ulrich, A. 1959. Analytical methods for use in plant analysis. California Agricultural Experiment Station Bull. 766: 30–33.

Kitchen, S. G. 1994. Perennial forb life-history strategies on semiarid rangelands: implications for revegetation. In: Monsen, S. B.; Kitchen, S. G., comps. Proceedings—ecology, management and restoration of annual rangelands; 1992 May 18–22; Boise, ID. Gen. Tech. Rep. INT-GTR-313. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 342–346.

Kitchen, S. G. 1995. Return of the native: a look at select accessions of North American Lewis flax. In: Roundy, B. A.; McArthur, E. D.; Haley, J. S.; Mann, D. K., comps. Proceedings: wildland shrub and arid land restoration symposium; 1993 October 19–21; Las Vegas, NV. Gen. Tech. Rep. INT-GTR-315. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 321–326.

McArthur, E. D. 1988. New plant development in range management. In: Tueller, P. T., ed. Vegetation science applications for rangeland analysis and management. Boston, MA: Kluwer Academic Publishers.

Mosquin, T. 1971. Biosystematic studies in the North American species of *Linum*, section *Adenolinum* (Linaceae). Canadian Journal of Botany. 49: 1379–1388.

Plenchette, C. J.; Fortin, A.; Furlan, V. 1983. Growth response of several plant species to mycorrhiza in a soil of moderate P fertility. I. Mycorrhizal dependency under field conditions. Plant and Soil. 70: 191–209.

SAS Institute. 1993. SAS/STAT user's guide, version 6, fourth edition. Cary, NC: SAS Institute, Inc. 1686 p.

Schweiger, P. F.; Robson, A. D.; Barrow, N. J. 1995. Root hair length determines beneficial effect of a *Glomus* species on shoot growth of some pasture species. New Phytologist. 131: 247–254.

Talkalson, D. D.; Pendleton, R. L.; Jolley, V. D.; Robbins, C. W.; Terry, R. E. 1998. Preparing and staining mycorrhizal structures in dry bean, sweet corn, and wheat using a block digester. Communications in Soil Science and Plant Analysis. 29: 2263–2268.

Thingstrup, I.; Rubaek, G.; Sibbesen, E.; Jakobsen, I. 1998. Flax (*Linum usitatissimum* L.) depends on arbuscular mycorrhizal fungi for growth and P uptake at intermediate but not high soil P levels in the field. Plant and Soil. 203: 37–46.

Heterogeneity in Soil C and N in Late- and Mid-Seral Sagebrush-Grass Rangeland

J. D. Reeder
D. W. Grant
G. G. Jezile
R. D. Child

Abstract: Development of criteria and indicators that can be used to evaluate nutrient cycling among plants, animals, and the soil is essential for evaluating rangeland health and sustainability, as well as for developing proper rangeland management practices. The distribution of nutrients in space and time has been identified as a useful criterion for evaluating the integrity of rangeland nutrient cycles and energy flow in rangelands. Spatial distributions of soil organic carbon (C) and organic and mineral nitrogen (N) were measured in both mid- and late-seral stages of a sagebrush-grass association. Vegetation cover differed between the two seral stages, with grass cover significantly higher (15 versus 3 percent), and bare ground area significantly lower (56 versus 69 percent) for the late-seral compared to mid-seral plant communities. The spatial distributions of soil organic C and N differed between the two seral stages and corresponded to differences in vegetation cover. The proportion of total soil N in the nitrate form was significantly higher in mid-seral soil than in late-seral soil, suggesting less efficient capture of available N by the fragmented mid-seral plant community and an uncoupling of the N cycle. Soil nitrate-N shows promise as a sensitive indicator of seral stage in sagebrush-grass plant communities.

Introduction

In developing a recommended approach for evaluating the ecological health of rangeland ecosystems, the National Research Council (1994) recognized the fundamental importance of nutrient cycling to ecosystem health, and recommended that any comprehensive evaluation of rangeland health and sustainability include indicators of the integrity of nutrient cycles. They suggested that the best indicator of rangeland nutrient cycling integrity is an assessment of the distributions of nutrients in space and time. Soil organic matter (SOM) is the primary source of plant-available nitrogen (N), the nutrient that most frequently limits primary and secondary productivity in rangeland ecosystems (Woodmansee and others 1978). The distribution and turnover of SOM is therefore a major determinant of ecosystem health and stability (Follett 2001).

Historically, rangeland studies have focused on the aboveground components of the ecosystem, and relatively few studies have evaluated belowground components and processes. Basic knowledge is therefore limited concerning the processes governing SOM distribution and turnover, and the response of these processes to management or disturbance. Additionally, detection of change in the mass or distribution of SOM as an indication of change in rangeland health is difficult because rangeland ecosystems are generally characterized by a high degree of spatial heterogeneity in SOM (Burke and others 1999; Tongway and Ludwig 1994). The magnitude of change expected as the result of disturbance or change in management is small relative to the large SOM pool size and its spatial heterogeneity across the landscape (Reeder 2002).

To address these limitations in our understanding of rangeland nutrient cycling and change in cycle integrity in response to management or disturbance, we compared soil and vegetation characteristics of two seral stages of a sagebrush-grass range to test the hypothesis that the distributions and forms of SOM carbon (C) and N differ between late- and mid-seral stages of a sagebrush-grass plant community. The objectives were to (1) characterize and quantify differences in soil C and N in late- and mid-seral stages of a Dry Mountain Loam sagebrush-grass range; and (2) to identify forms of soil C and/or N that are sensitive indicators of seral stage.

Methods and Materials

Study Site Description

The study was conducted on a Dry Mountain Loam Range Site south of Walden, CO, at an elevation of 2,500 m on the Cabin sandy loam soil series (fine loamy over sandy or sandy-skeletal, mixed Argic Cryoboroll). Average annual temperature is 2.8 °C, and average annual precipitation is 240 mm, with about two-thirds of annual precipitation falling as rain during the growing season (NRCS 1981). The Dry Mountain Loam Range Site consists of cool season grasses and forbs that form a sparse stand beneath an open

---

In: Hild, Ann L.; Shaw, Nancy L.; Meyer, Susan E.; Booth, D. Terrance; McArthur, E. Durant, comps. 2004. Seed and soil dynamics in shrubland ecosystems: proceedings; 2002 August 12–16; Laramie, WY. Proceedings RMRS-P-31. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

J. D. Reeder is a Soil Scientist and D. W. Grant a Biological Science Technician, USDA-ARS, 1701 Centre Ave., Fort Collins, CO 80526, U.S.A. FAX: (970) 492-7310, e-mail: jeanreeder@ars.usda.gov. G. G. Jezile was a Graduate Student and D. W. Child is a Professor of the Department of Rangeland Ecosystem Science, Colorado State University, Fort Collins, CO 80521, U.S.A.

stand of big sagebrush (*Artemisia tridentata* Nutt.). Estimated annual production ranges from 450 to 700 kg ha^{-1} (NRCS 1981).

Soil and vegetation sampling was conducted on two seral stages (mid-seral and late-seral) with different management histories. The areas selected for this study were based on the range condition classification outlined by the Natural Resource Conservation Service (NRCS 1981), and seral stages assigned in 1997 by the Owl Mountain Partnership, Walden, CO.

Historic grazing management of the late-seral stage consisted of decades of heavy-to-moderate season-long grazing prior to 1988, when the Bureau of Land Management implemented an allotment improvement program to improve livestock distribution and provide rest periods from grazing. Since 1988, grazing management has consisted of light-to-moderate grazing using a rotational grazing system that limits annual grazing to 3 to 6 weeks per year, with the season of grazing cycling annually among early season (beginning in mid June), mid season (beginning in early to mid July), and late season (beginning in mid August or early September). Soil and vegetation sampling was conducted 12 years after implementation of the new grazing management, at which time the plant community had improved from “fair” to “good” condition (NRCS 1981). At the time of sampling, late-seral vegetation was composed of streambank wheatgrass (*Agropyron dasystachyum*), sheep fescue (*Festuca ovina*), junegrass (*Koeleria macrantha*), sandberg bluegrass (*Poa secunda*), muttongrass (*Poa fendleriana*), needlegrass (*Stipa* spp.), squirretail (*Sitanion hystrix* Nutt.), bluebunch wheatgrass (*Pseudoroegneria spicata*), big sagebrush, snake weed (*Gutierrezia sarothrae* Pursh), pussytoes (*Antennaria rosea*), stonecrop (*Sedum lanceolata*), hoods phlox (*Phlox hoodii* Richards), moss phlox (*Phlox bryoides*), five fingers (*Potentilla diversiflora*), sedges (*Carex* spp.), lupine (*Lupinus* spp.), false buckwheat (*Eriogonum jamesii*), clover (*Trifolium* spp.), prickly gilia (*Leptodactylon pungens*), narrow leaved mertensia (*Mertensia lanceolata*), and other forbs.

Mid-seral plant species were similar to those of the late seral, but differed in abundance. Mid-seral vegetation consisted of increased big sagebrush, the warm season grass blue grama (*Bouteloua gracilis* H.B.K., Lag. Ex Steud.), and less palatable forbs, while cool season grasses were infrequent (NRCS 1981). Current and historic grazing management of the mid-seral stage consists of moderate-to-heavy nonrotational grazing.

Field Plot Establishment and Sampling

Three 100-m transects were established in both seral stages. Transect sites were selected on the basis of standard soil classification techniques to assure that all transects were positioned on the same soil series (Cabin sandy loam). Species composition at peak production (late June) was determined from visual estimates of ground cover from twenty 0.1-m^2 rectangular quadrats spaced 5 m apart along each transect (Jezile and others, in press). The amounts of bare ground, gravel, stones, ground litter, and standing litter were recorded for each quadrat. Species cover was expressed as a percentage of total cover, and estimates of percentage composition of each species were used to calculate an NRCS range condition rating. Herbage yield was estimated by randomly selecting and harvesting five of the 20 quadrats along each transect. For both seral stages, clipped plant material was separated by dominant species, dried for 48 hours at 60 °C and then reweighed to determine the percentage dry weight of the dominant species (Jezile and others, in press).

Soil samples were collected from two of the three transects of both seral stages. Cores were obtained at the five randomly selected 0.1-m^2 quadrat locations where herbage yields had been sampled. At each coring location along each transect, separate cores were obtained from three landscape microsites: bare ground, within a grass patch, and under a sagebrush canopy. Soil samples were taken with a 76.2-mm-diameter coring tube. Each soil core was partitioned into three depth increments: 0 to 5, 5 to 10, and 10 to 20 cm. Estimates of soil bulk density were obtained by the double-cylinder coring method described by Blake and Hartge (1986) from three equally spaced locations along each transect. Soil samples were placed in sealed plastic bags, and transported in coolers to the laboratory for processing.

Laboratory Analyses

Soil samples were passed through a 2-mm screen to remove plant crowns and visible roots. A subsample of field-moist soil was taken for analyses of gravimetric water content and field-moist water soluble organic C (WSOC); the remaining soil was air dried and used for all other analyses. Total C and N were determined by dry combustion with a Carlo Erba NA 1500 automatic carbon-nitrogen analyzer as described by Schepers and others (1989). Inorganic C was analyzed by a modified pressure-calcimeter method (Sherrod and others 2002), and soil organic C was calculated by subtracting inorganic C from total C. WSOC was determined by the procedure of Davison and others (1987) with the following modifications: the extraction ratio used was 5 mL deionized water to 1 g soil, and filtrates were analyzed with a Shimadzu TOC-5050A Soluble C analyzer. Exchangeable nitrate (NO_3–N) and ammonium (NH_4–N) were extracted with 2 M KCl and determined with an auto analyzer (Keeney and Nelson 1982).

Statistical Methods

Differences in soil C and N among landscape microsites (bare ground, beneath grass, and beneath shrub canopy) were analyzed by depth and by cumulative depth with analysis of variance and mean separation by least significant differences (LSD, $P \leq 0.05$) (Steele and Torrie 1980). Differences in soil C and N between the two seral stages were determined by depth and by cumulative depth with paired t-tests (Steele and Torrie 1980).

Results

Vegetation

Based on estimates of plant species composition, calculated NRCS range condition ratings were 35 percent (“fair” condition) for the mid-seral, and 57 percent (“good” condition) for the late-seral stages (NRCS 1981). Jezile and others (in press) reported that late-seral vegetation covered 44 percent of the soil surface (21 percent shrubs and canopy, 15 percent grasses, and 7 percent forbs), while the remaining 56 percent of the soil surface was comprised of exposed bare soil, gravel, or litter-covered soil. In comparison, mid-seral vegetation cover was 31 percent (23 percent shrubs, 3 percent grasses, 5 percent forbs), and 69 percent exposed soil, gravel, or litter-covered soil. Mid-seral grass cover and total forage (grasses + forbs) cover were significantly lower ($P < 0.10$), and bare ground significantly higher, than in the late-seral stage (Jezile and others, in press).

Soil Properties

Masses of SOM-C and SOM-N in the late-seral stage were significantly lower in bare areas than in grass or shrub areas, whereas C and N in the mid-seral stage were not significantly different among the three landscape microsites (table 1). Spatial distribution of total SOM-C differed between the two seral stages, with significantly more C associated with bare-ground areas, and less associated with grass areas, in the mid-seral than in the late-seral landscape (fig. 1). Similar distribution patterns were observed for total SOM-N (data not shown).

Labile fractions of soil C and N differed between the two seral stages. WSOC was significantly lower, and nitrate-N significantly higher, in the mid-seral compared to the late-seral landscape (table 1). Similar trends were observed in the proportion of total SOM-C in water soluble forms (fig. 2), and the proportion of total N in nitrate-N form (fig. 3). In both the late- and mid-seral landscapes, mass of nitrate-N was not significantly different among the three landscape

Table 1—Masses of carbon and nitrogen in the soil profile (0 to 20 cm) of late- and mid-seral stages of a sagebrush-grass plant community.

	Total soil organic C, Mg ha^{-1}		
	Late-seral	Mid-seral	p [a]
Bare	29.0	37.3	<0.01
Grass	37.3	40.6	.20
Shrub	40.4	41.8	.30
LSD (0.05)	3.4	ns	
	Total soil organic N, Mg ha^{-1}		
	Late-seral	Mid-seral	p [a]
Bare	2.62	3.43	<0.01
Grass	3.22	3.51	.17
Shrub	3.32	3.39	.37
LSD (0.05)	0.33	ns	
	Water soluble organic C, kg ha^{-1}		
	Late-seral	Mid-seral	p [a]
Bare	2.16	1.84	<0.01
Grass	3.36	2.28	<0.01
Shrub	3.94	3.02	<0.01
LSD (0.05)	.51	.33	
	Nitrate N, kg ha^{-1}		
	Late-seral	Mid-seral	p [a]
Bare	.98	3.10	<0.01
Grass	.85	2.87	<0.01
Shrub	.97	2.72	<0.01
LSD (0.05)	ns	ns	

[a] Comparison of late- and mid-seral values (paired t-test).

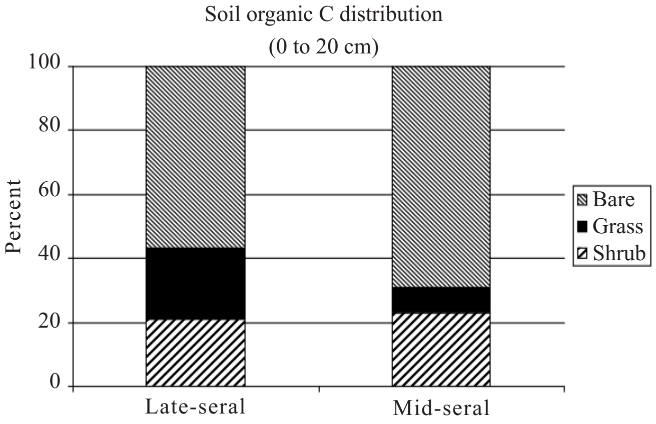


Figure 1—Spatial distribution of soil organic C in late- and mid-seral landscapes. (The two seral stages differ ($P < 0.01$) in mass of soil C in bare and grass areas.)

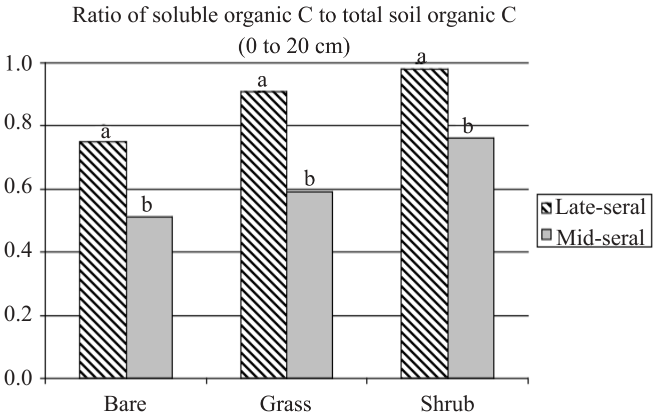


Figure 2—The ratio of mass of water soluble organic C to mass of total organic C (x 10^4) in the 0- to 20-cm soil profile.

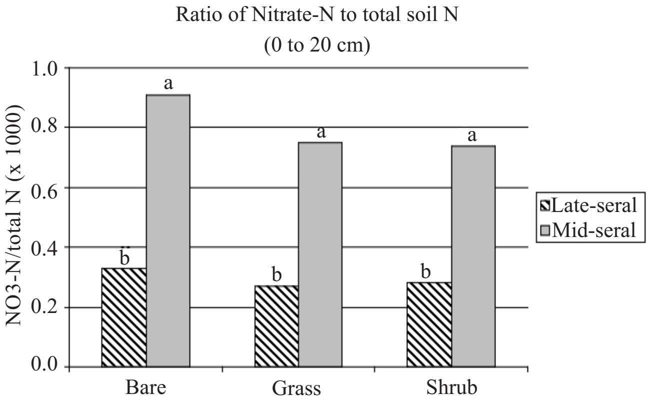


Figure 3—The ratio of mass of nitrate-N to mass of total soil N (x 10^3) in the 0- to 20-cm soil profile.

microsites, but mass of WSOC was lowest in bare ground areas, intermediate in grass areas, and highest beneath shrub canopies (table 1).

Discussion

Jezile and others (in press) reported that SOM-C and SOM-N concentrations were not significantly different between late- and mid-seral stages of this sagebrush-grass plant community. When converted to a mass basis, we found that levels of SOM-C and SOM-N were comparable between late- and mid-seral landscapes in grass and shrub areas, but levels of C and N were lower in bare-ground areas of the late-seral landscape than in the mid-seral landscape (table 1). These data, plus visual field observations, suggest that the late-seral landscape had experienced more historic soil loss by erosion than had the mid-seral landscape.

Similar to the trends in C and N concentrations observed by Jezile and others (in press), we found that total SOM-C and SOM-N masses were not good indicators of seral stage. Soil properties such as SOM are the result of millennia of soil-forming processes (Jenny 1980). Thus, even though significant changes in the plant community may be observed in response to a particular management history spanning decades, corresponding changes in most soil properties usually will not be observed unless erosional soil losses are substantial (Lal and others 1999).

Although SOM consists primarily of a large stable pool of C and nutrients that is resistant to decomposition, it also includes small subpools of more readily decomposable or labile organic compounds (Collins and others 1997) that may be easily changed in response to perturbation such as grazing, or to grazing-induced changes in plant community composition (Burke and others 1997; Reeder and others 2001). Assessing the integrity of nutrient cycles as an indicator of change in rangeland health (NRC 1994) can therefore be more readily accomplished by measuring the quality rather than the quantity of SOM C and N in the soil. We selected WSOC as an indicator of the labile pool of SOM-C because it is a measure of root exudates that provide a readily available C source for soil microorganisms (Cheng and others 1993, 1996), and is strongly correlated with microbial biomass and microbial activity (Burford and Bremner 1975; Davidson and others 1987). We selected the mineral forms of N in the soil, ammonium (NH_4–N), and nitrate (NO_3–N), as indicators of the labile pool of soil N, because these forms are easily measured, are the end products of the microbial mineralization processes that decompose SOM-N (Bartholomew 1965), and are the forms of soil N that are available for direct uptake by plants (Harmsen and Kolenbrander 1965).

We found that while comparisons of total masses of SOM-C and N were not good indicators of seral stage and thus of rangeland health, the proportions of total SOM-C and N that were in labile forms clearly separated late-seral from mid-seral landscapes in this sagebrush-grass plant community. The proportion of total SOM-C that was soluble was consistently higher (fig. 2), and the proportion of soil N that was in the nitrate form consistently lower (fig. 3) in the late-seral compared to the mid-seral landscape. These data suggest that the N cycle is more tightly coupled in the late-seral landscape. The higher level of WSOC observed in the late-seral soil suggests a higher level of root exudation and associated increase in microbial activity to utilize the readily available C (Cheng and others 1996). Stimulation of microbial activity by C-rich root exudates results in a N-limited environment in which microorganisms immobilize soil N (Kuzyakov 2002); thus levels of nitrate-N in the late-seral soil are low. In the mid-seral landscape, higher levels of nitrate-N and lower levels of WSOC indicate a loss of integrity, or uncoupling, of the N cycle. The mid-seral landscape is characterized by a higher percentage of bare-ground area and a more fragmented grass and forb plant community. In bare-ground and sparse-plant areas, warmer soil surface temperatures in combination with pulsed rainfall events enhance microbial decomposition of SOM (Bowman and others 1990). In the absence of growing plants or in areas of sparsely growing plants, root exudation of WSOC compounds is low, so less stimulation of microbial activity by C-rich root exudates occurs, resulting in net mineralization rather than net immobilization of soil N, and nitrate-N accumulation in the absence of sufficient plants to take up excess mineral N.

Rangeland ecosystems continually respond to temporary changes in both physical and biotic conditions. An assessment of change in rangeland health must be able to distinguish between changes that result in the crossing of an ecological threshold from those that are temporary and the result of normal fluctuations in physical and biotic conditions (NRC 1994). Our results demonstrate that assessments of labile forms of SOM, and of the landscape-level spatial distribution of SOM-C and SOM-N, distinguished a mid-seral from a late-seral stage of this sagebrush-grass plant community. Measurement of soil nitrate shows promise as an indicator of the integrity of the N cycle and change in successsional stage. Future studies are needed to evaluate the seasonality of differences in nitrate-N content between different seral stages, and to evaluate whether a change in nitrate-N can serve as an early indicator of change in rangeland health.

Acknowledgments

We thank Ernest Taylor and Lucretia Sherrod for their laboratory assistance with this research.

References

Bartholomew, W. V. 1965. Mineralization and immobilization of nitrogen in the decomposition of plant and animal residues. In: Bartholomew, W. V.; Clark, F. E., ed. Soil nitrogen. Madison WI: American Society of Agronomy: 287–308.

Blake, G. R.; Hartge, K. H. 1986. Bulk density. In: Klute, Arnold, ed. Methods of soil analysis. Part 1. Madison, WI: American Society of Agronomy: 363–375.

Bowman, R. A.; Reeder, J. D.; Lober, R. W. 1990. Changes in soil properties in a central plains rangeland soil after 3, 20 and 60 years of cultivation. Soil Science. 150(6): 851–857.

Burford, J. R.; Bremner, J. M. 1975. Relationships between the denitrification capacities of soils and total, water-soluble and readily decomposable soil organic matter. Soil Biology Biochemistry. 7: 389–394.

Burke, I. C.; Lauenroth, W. K.; Milchunas, D. G. 1997. Biogeochemistry of managed grasslands in central North America. In: Paul, E. A.; Paustian, L.; Elliott, E. T.; Cole, C. V., ed. Soil organic matter in temperate agroecosystems: long-term experiments in North America. Boca Raton FL: CRC Press: 85–102.

Burke, I. C.; Lauenroth, W. K.; Riggle, R.; Brannen, P.; Madigan, B.; Beard, S. 1999. Spatial variability of soil properties in the shortgrass steppe: the relative importance of topography, grazing, microsite and plant species in controlling spatial patterns. Ecosystems. 2: 422–438.

Cheng, W.; Coleman, D. C.; Carroll, C. R.; Hofman, C. A. 1993. In situ measurement of root respiration and soluble C concentrations in the rhizosphere. Soil Biology Biochemistry. 25(9): 1189–1196.

Cheng, W.; Zhang, Q.; Coleman, D. C.; Carroll, C. R.; Hoffman, C. A. 1996. Is available carbon limiting microbial respiration in the rhizosphere? Soil Biology Biochemistry. 28(10/11): 1283–1288.

Collins, H. P.; Paul, E. A.; Paustian, K.; Elliott, E. T. 1997. Characterization of soil organic carbon relative to its stability and turnover. In: Paul, E. A.; Paustian, L.; Elliott, E. T.; Cole, C. V., eds. Soil organic matter in temperate agroecosystems: long-term experiments in North America. Boca Raton, FL: CRC Press: 51–72.

Davidson, E. A.; Galloway, L. F.; Strand, M. K. 1987. Assessing available carbon: comparison of techniques across selected forest soils. Communications in Soil Science and Plant Analysis. 18(1): 45–64.

Follett, R. F. 2001. Organic carbon pools in grazing land soils. In: Follett, R. F.; Kimble, J. M.; Lal, R., eds. The potential of U.S. grazing lands to sequester carbon and mitigate the greenhouse effect. Boca Raton, FL: Lewis Publishers: 65–86.

Harmsen, G. W.; Kolenbrander, G. J. 1965. Soil inorganic nitrogen. In: Bartholomew, W. V.; Clark, F. E., eds. Soil nitrogen. Madison WI: American Society of Agronomy: 43–92.

Jenny, H. 1980. The soil resource. New York: Springer-Verlag. 377 p.

Jezile, G. G.; Reeder, J. D.; Grant, D. W.; Child, R. D. [In press]. Soil and vegetation relationships on late- and mid-seral sagebrush-grass range.

Keeney, D. R.; Nelson, D. W. 1982. Nitrogen—inorganic forms. In: Page, A. L., ed. Methods of soil analysis. Part 2. Chemical and microbiological properties. Madison, WI: Americal Society of Agronomy: 643–698.

Kuzyakov, Y. 2002. Review: factors affecting rhizosphere priming effects. Journal of Plant Nutrition and Soil Science. 165: 382–396.

Lal, R.; Mokma, D.; Lowery, B. 1999. Relation between soil quality and erosion. In: Lal, Rattan, ed. Soil quality and soil erosion. Boca Raton, FL: CRC Press: 237–258.

National Research Council. 1994. Rangeland health: new methods to classify, inventory and monitor rangelands. Washington, DC: National Academy Press. 180 p.

Natural Resource Conservation Service. 1981. Soil survey of Jackson County Area, Colorado. U.S. Department of Agriculture, Natural Resources Conservation Service and Colorado Agricultural Experiment Station. Washington, DC: U.S. Government Printing Office. 159 p.

Reeder, J. D. 2002. Overcoming spatial variation in measuring soil carbon stocks and sequestration potential of native rangelands in the Western U.S. Proceedings of the OECD expert meeting on soil organic carbon indicators for agricultural land; 2002 October 15–18; Ottawa, Canada: 193–200.

Reeder, J. D.; Franks, C. D.; Milchunas, D. G. 2001. Root biomass and microbial processes. In: Follett, R. F.; Kimble, J. M.; Lal, R., eds. The potential of U.S. grazing lands to sequester carbon and mitigate the greenhouse effect. Boca Raton, FL: Lewis Publishers: 139–166.

Schepers, J. S.; Francis, D. D.; Thompson, M. T. 1989. Simultaneous determination of total C, total N, and ^{15}N on soil and plant material. Communications in Soil Science and Plant Analysis. 20: 949–959.

Steele, R. G. D.; Torrie, J. H. 1980. Principles and procedures of statistics: a biometrical approach. 2d ed. New York: McGraw-Hill. 593 p.

Sherrod, L. A.; Dunn, G.; Peterson, G. A.; Kolberg, R. L. 2002. Inorganic carbon analysis by modified pressure-calcimeter method. Soil Science Society of America Journal. 66: 299–305.

Tongway, D. J.; Ludwig, J. A. 1994. Small-scale resource heterogeneity in semi-arid landscapes. Pacific Conservation Biology. 1: 201–208.

Woodmansee, R. G.; Dodd, J. L.; Bowman, R. A.; Clark, F. E.; Dickinson, C. E. 1978. Nitrogen budget of a shortgrass prairie ecosystem. Oecologia. 34: 363–376.

Monitoring Rangeland Health: Using a Biological Soil Crust Stability Index

Roger Rosentreter
David J. Eldridge

Abstract: Monitoring of rangeland health has recently transitioned from the taking of simple grass biomass measurements to a more integrated plant biodiversity and soil surface condition evaluation. One component being measured is the composition and cover of biological soil crusts (bsc). The bsc cover has been shown to correlate with soil stability. The bsc index is conducted in arid lands with clumped vegetation along a 20-m line intercept. The bsc stability index stratifies the bsc into one or more of three morphological categories, records that category by cover class, and then calculates a quantitative index. The bsc index is measured only in the plant interspaces. This index allows for comparison with other sites and for trend evaluation at the specific site over time. This bsc index readily rates the stability of the plant interspace soil and requires little analysis time or delay.

Keywords: monitoring, crusts, lichens, health, rangelands

Background

Biological soil crusts are integral components of rangeland soils on many continents. These complex assemblages of lichens, liverworts, mosses, cyanobacteria, and algae dominate the first few millimeters of the soil surface. Because of their close association with surface soils, crusts play an important role in the regulation of water, sediment, and nutrient flows, and provide favorable sites for the germination and establishment of some rangeland plants (Eldridge and Rosentreter 1999; West 1990).

Biological soil crusts are generally regarded as indicative of healthy landscapes due to the resistance they impart to the soil surface against wind and water erosion. Despite this, however, nonvascular plants have rarely been included in broad-scale inventories or assessments of rangeland health (West 1990). Biological soil crust organisms have traditionally been very difficult to identify, even to genus or family level, because of their small size, lack of definitive morphological features, and the fact that some species are separated on the basis of their chemistry.

Techniques that use biological soil crusts to assess soil health were pioneered in the semiarid woodlands of Eastern Australia in the early 1980s (Tongway and Smith 1989). Biological soil crust cover, along with other soil surface features, provides an indication of the extent to which the soil cycles nutrients, accepts rainfall, and resists erosion (Tongway and Smith 1989). Despite the incorporation of biological soil crusts into rangeland health assessment, there has been a reluctance to use crusts as indicators due to the problems discussed above. Eldridge and Rosentreter (1999) proposed crust monitoring at the level of morphological groups, rather than using a species-based approach. Morphological groups can be useful indicators of soil surface stability due to the strong association between morphology and function. This association provides an indication of the degree to which single or groups of organisms can resist perturbation.

Landscapes where the soil surface supports an extensive cover of biological soil crusts are known to be relatively resistant to wind and water erosion. Erosion, by removing part of the soil surface horizon, is an indicator of a rangeland's declining health (Davenport and others 1998; Dormaar and Willms 1998). Erosion reduces the productive potential of the soil by decreasing soil organic matter, cation exchange capacity and hence structural stability, and by reducing the capacity of the soil to accept infiltration. Ultimately, depauperate soils have lower infiltration rates and excessive overland flow, thereby reducing their structural stability and production capacity.

Soil Crust Index

A Biological Soil Crust Stability Index (BSCSI) integrating the surface cover of biological soil crusts with their ability to protect the soil against erosion has been developed for patterned grasslands and shrublands where cryptogamic crusts are a major component of the interspace soil matrix. This index ranks morphological groups of cryptogamic taxa in terms of their increasing dimensionality and hence their resistance to erosion. This is a practical system of monitoring that simplifies and unifies previous methods in order to encourage wider use and application. Even morphological groups are sometimes difficult for observers to determine during field survey. The soil crust index system

---

In: Hild, Ann L.; Shaw, Nancy L.; Meyer, Susan E.; Booth, D. Terrance; McArthur, E. Durant, comps. 2004. Seed and soil dynamics in shrubland ecosystems: proceedings; 2002 August 12–16; Laramie, WY. Proceedings RMRS-P-31. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Roger Rosentreter is Botanist, U.S. Department of the Interior, Bureau of Land Management, 1387 S. Vinnell Way, Boise, ID 83709, U.S.A. E-mail: roger_rosentreter@blm.gov. David J. Eldridge is Senior Research Scientist, Department of Sustainable Natural Resources, School of Biological, Earth and Environmental Sciences, University of NSW, Sydney, 2052, NSW, Australia; e-mail: deldridge@unsw.edu.au

simplifies taxa even further according to their dimensionality, characterizing cyanobacteria and algae as one dimensional; crustose, squamulose and foliose lichens and liverworts as two dimensional; and fruticose lichens and mosses as three dimensional.

Increasing dimensionality is considered indicative of greater erosion control and increasing rangeland health. One-dimensional soil crusts occur within the soil matrix and may be difficult to see, but they resist raindrop impact and hold the soil together, therefore protecting it from surface waterflow and wind erosion. Their impact is most marked on sandy soils where they often provide the only biological soil protection. Two-dimensional soil crusts are similar in their protection from erosion, but because they are generally larger and grow on top of as well as within the soil, they provide greater protection from raindrop impact, and the small cracks between crust organisms may act as traps for wind- and water-borne sediment. Three-dimensional soil crusts are generally larger than two-dimensional crusts, and their three-dimensional structure can capture and accumulate windblown dust and nutrients more effectively than two-dimensional crust types.

In patterned vegetation communities in Idaho, U.S.A., and western NSW, Australia, a 20-m line-intercept method has been used to determine the BSCSI. These measurements are often made in conjunction with other assessments of rangeland health, which involve measurements of the size and arrangement of vegetation patches.

The proportion of the various dimension types is multiplied by a rating value, which reflects the relative value of the crust type to resist erosion, or deformation. Research is currently underway to refine these stability ratings for various dimensional types. For example, we are subjecting the three crust types (1-D, 2-D, 3-D) to a range of laboratory tests to examine their ability to resist stress (Emerson aggregate test, water drop test), trap sediment (laboratory simulations of microwind erosion), retain water (immersion and drying tests), and withstand deformation (consistency and coherency tests). Empirical data from these laboratory tests will be subjected to multivariate analyses to determine overall relative differences in effectiveness of the three-dimensional types at stabilizing the soil surface. Preliminary results suggest that the 3-D surfaces are about 10 to 15 times more effective than 2-D surfaces, which are about 3 to 5 times more effective than 1-D surfaces (table 1).

Table 1—Dimensionality of biological soil crusts in relation to morphological group and stability rating.

Crust dimenstion type	Morphological groups	Stability rating value
1-D	Cyanobacteria, fungi, and algae	1
2-D	Crustose, squamulose and foliose lichens, and liverworts	3 to 5
3-D	Tall and short mosses, fructicose lichens	10 to 15

An overall rating for a site is calculated by multiplying the stability rating value for each crust type in each interspace by a value that reflects its cover, and expressing that number as a percentage out of 60, the maximum possible score. This has the effect of relativizing sites and therefore enables comparison between sites. The system is still under refinement and has yet to be tested in other environments.

Discussion

Although this system is still being tested and revised, it appears to be of value regardless of the vegetation type as long as the native vegetation is clumped or patterned (Rosentreter and Eldridge 2002). Results to date have shown strong relationships between the index and an independent assessment of health of the rangelands (fig. 1). The Biological Soil Crust Stability Index may underestimate crust contribution to total soil stability. However, this is a good system for comparing sites over time in a relative sense. The Index provides a rapid method of assessing the structure and condition of interspaces in shrublands and grasslands. This system should prove a useful tool for monitoring temporal and spatial changes in soil crust communities in patchy environments.

The Biological Soil Crust Stability Index is an efficient method because it requires less training, provides rapid and statistically powerful data analyses, and allows for rapid field measurements. Trampling impacts to the vegetation and cryptogamic crusts are focused in the interspaces of patterned arid vegetation. Therefore, impacts and changes in range condition are first measurable in the interspaces between plant clumps.

This Index evaluates microphytic vegetation and its impact without losing the small-scale structural features that influence hydrologic and watershed stability. This system is proposed as a rapid and efficient technique for monitoring

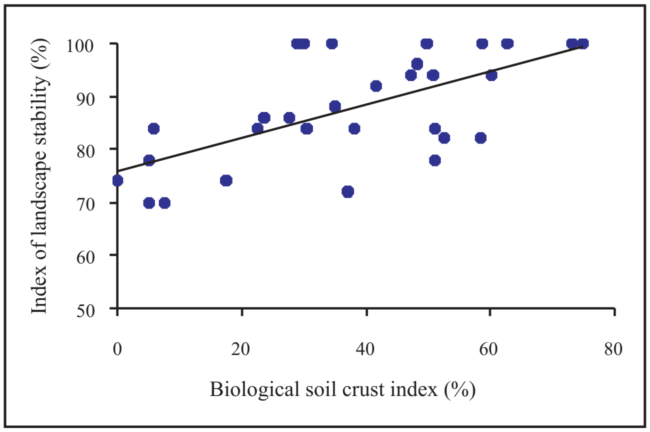


Figure 1—The relationship between the Biological Soil Crust Stability Index (BSCSI) and an index of landscape stability for *Artemisia* shrublands in Idaho.

erosion hazard potential, temporal and spatial changes in the quality of plant and animal habitat, and wildfire risk.

References

Davenport, D. W.; Breshears, D. D.; Wilcox, B. P.; Allen, C. D. 1998. Viewpoint: sustainability of pinyon-juniper ecosystems—unifying perspective of soil erosion thresholds. Journal of Range Management. 51: 231–240.

Dormaar, J. F.; Willms, W. D.; 1998. Effect of forty-four years of grazing on fescue grassland soils. Journal of Range Management. 5: 122–126.

Eldridge, D. J.; Rosentreter, R. 1999. Morphological groups: a framework for monitoring microphytic crusts in arid landscapes. Journal of Arid Environments. 41: 11–25.

Rosentreter, R.; Eldridge, D. J. 2002. Monitoring biodiversity and ecosystem function: grasslands, deserts and steppe. In: Nimis, P. L.; Scheidegger, C.; Wolseley, P., eds. Monitoring with lichens—monitoring lichens. NATO Science Series. The Hague, Netherlands: Kluwer Academic Publishers: 223–237.

Tongway, D. J.; Smith, E. L. 1989. Soil surface features as indicators of rangeland site productivity. Australian Rangeland Journal. 11: 15–20.

West, N. E. 1990. Structure and function of microphytic soil crusts in wildland ecosystems of arid and semi-arid regions. Advances in Ecological Research. 20: 179–223.

Shrub Mounds Enhance Water Flow in a Shrub-Steppe Community in Southwestern Idaho, U.S.A.

David J. Eldridge
Roger Rosentreter

Abstract: In the Western United States, substantial areas of shrub-steppe have been replaced by annual exotic grasses during the past century. These structural changes have been accompanied by functional changes in the landscape in relation to the ability of the landscape to capture essential resources such as water and sediments. Surface waterflow was measured in three contrasting shrub-steppe communities (sagebrush, winterfat, and rabbitbrush) on mound and interspace surfaces using disc permeameters. Waterflow was substantially greater (2 to 6 times) under shrubs compared with the shrub-free, microphytic-dominated interspaces. The ratio of sorptivity under ponding to sorptivity under tension, which is a useful index of the macropore (pores > 0.75 mm in diameter) status of the soil, demonstrated that mounds were characterized by a significantly greater amount of macropores compared with interspaces. The dense cover of the moss *Tortula ruralis*, which grows below *Artemisia* canopies, intercepted approximately 14 L of water m^{-2} and enhanced the infiltration capacity of shrub mound soils. The results reinforce the notion that these shrub-steppe communities are partitioned into moisture-rich mounds separated from moisture-deprived interspaces that are critical for the transfer of water to the shrub mounds. Disturbance of the interspaces ultimately leads to a reduction in water reaching the mounds and a decline in shrubland function.

Introduction

Since the late nineteenth and early twentieth centuries, extensive and uncontrolled livestock grazing has resulted in substantial changes to the composition and structure of many native shrub-steppe communities. The combined impact of grazing and invasion of annual Eurasian weeds (Mack 1981), primarily cheatgrass (*Bromus tectorum* L.) and medusahead (*Taeniatherum caput-medusae* ssp. *asperum* L.), have increased the risk of wildfire in shrub communities (Wambolt and others 2001). Consequently, increased frequency of wildfire has resulted in conversion of substantial areas of *Artemisia* shrub-steppe to annual grasslands, which in turn burn at intervals of less than 10 years (Whisenant 1990). This increasing cycle of fire, conversion to annual grasslands, and more fire has increased unabated, and now large areas of grassland exist in former shrub-steppe communities.

The dramatic change from shrublands to annual grasslands has resulted in substantial changes in landscape function at both local and regional scales. Changes in landscape structure have resulted in major impacts on biodiversity, including loss of overstory and understory flora, declines in many faunal taxa, and invasion of exotic species (Wambolt 2001, 2002; West 1993). Spatial heterogeneity in many shrub-steppe communities worldwide is characterized by a matrix of microphytic crust-dominated soils (the interspaces) on which are superimposed soil mounds colonized by perennial shrubs (shrub mounds). The microphytic crusts of the interspaces comprise cyanobacteria, bacteria, algae, mosses, and lichens (Hilty and others 2004; West 1990). Cyanobacterial polysaccharides bind together the surface of the interspace soils, giving it a tight microstructure that generally repels water (Eldridge and others 2000). In contrast, the surface soil of the shrub mound lacks the microphytic crust and is covered with loose soil particles. On functional shrub-steppe landscapes, these contrasting surfaces result in the concentration of water and nutrients within the nutrient-enriched shrub patches at the expense of the nutrient- and water-deprived interspaces (Blark and Small 2003; Schlesinger and others 1990; Thiery and others 1995; Tongway and Ludwig 1994). This patchiness exists at a range of spatial scales from whole catchments and subcatchments to individual plants.

Efficient, sustainable production of arid shrublands is dependent upon the movement of water, sediments, seed, and soil from the interspace to the shrub mounds. When these shrublands become degraded, resources are no longer trapped within the shrub mounds, and the landscape becomes dysfunctional (Ludwig and Tongway 1995). Healthy soils within shrub mounds are characterized by a high degree of macroporosity, that is, a large number of pores, generally biological in nature, greater than about 0.75 mm in diameter. These pores are important for capturing excess water generated from the interspaces. These macropores or biopores are destroyed by trampling, disturbance, and cultivation. Waterflow through soils over small spatial scales can

---

In: Hild, Ann L.; Shaw, Nancy L.; Meyer, Susan E.; Booth, D. Terrance; McArthur, E. Durant, comps. 2004. Seed and soil dynamics in shrubland ecosystems: proceedings; 2002 August 12–16; Laramie, WY. Proceedings RMRS-P-31. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

David J. Eldridge is Senior Research Scientist, Department of Sustainable Natural Resources, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney 2052, NSW, Australia, Fax: 62 9385 1558, e-mail: d.eldridge@unsw.edu.au. Roger Rosentreter is Botanist, Bureau of Land Management, 1387 S. Vinnell Way, Boise, ID 83709, U.S.A., e-mail: Roger_Rosentreter@blm.gov

be quantified using disc permeameters (White 1988). Using the permeameters, a measure of the ratio of waterflow under ponding to flow under tension can be obtained. This ratio gives an indication of the relative health of the soil. Other indicators of soil health include the relative differences in infiltration between mound and interspace soils, as well as the total infiltration capacity of the soil.

The aims of the research reported here are threefold. Firstly, we wished to examine relative differences in infiltration on three soil types supporting three different shrub-steppe communities common on the Snake River Plain. Secondly, we wished to test whether there were significant differences in infiltration between shrub mounds and adjoining interspaces in order to learn more about the consequences of shrub removal on the surface movement of water. Thirdly, we were interested in examining the relative effect of mosses growing below the shrub canopy on the interception, storage, and infiltration of water. We addressed these questions by applying water to shrub mound and intershrub (interspaces) areas using disc permeameters.

Methodology

Study Sites

Three sites were selected for detailed infiltration measurements: Bowns Creek (116°18'00"W, 43°12'00"N) approximately 48 k southeast of Boise, Cindercone Butte (115°56'30"W, 43°20'30"N) approximately 56 km southeast of Boise, and Kuna Butte in the Birds of Prey Reserve (116° 25'32"N, 43°25'59"W) approximately 20 km southwest of Boise, ID. These sites were chosen because they contained typical examples of three different types of shrub morphologies on different soils (loam, sand, and silt, respectively) at sites close to Boise. Further, the sites were not adversely impacted by encroachment of exotic annual grasses such as cheatgrass and medusahead. All sites were on level (less than 1 percent) slopes. A description of the biotic and abiotic features of the sites is given in table 1.

Waterflow

The soil body consists of a matrix of soil, minerals, air, and organic matter through which a network of pores of various size and shape pass. Large soil pores (macropores), generally greater than 0.75 to 1.00 mm in diameter, are important in the transfer of water and nutrients through the soil (Bouma 1991) and are generally biological in origin. Macropores are formed by plant roots and soil fauna (Oades 1993), and as pore size increases, capillary tension declines and waterflow increases. Smaller pores (micropores or matrix pores) are also present between individual mineral grains and between soil particles, but are not formed by soil biota.

The early phase of waterflow (2 to 10 minutes after water is applied) is termed sorptivity, during which water enters the soil in response to potential gradients of water potential (influenced by soil dryness and pore structure), and gravitational potential (pore size, distribution and continuity; White 1988). The sorptivity phase is largely governed by the capillary properties of the soil, particularly when it is dry. As the soil wets up, gravitational forces become more important (White 1988). The second phase of infiltration is known as the steady-state phase. In uniform soils, a time is reached where the flow rate from the source (in our case the disc permeameter) stabilizes over time. This steady-state flow rate or steady-state infiltration is governed by capillarity, gravity, the area of the disc permeameter in contact with the soil, and the pressure at which the water is supplied to the soil surface (CSIRO 1988).

Both sorptivity (mm $h^{-0.5}$) and steady-state infiltration (mm h^{-1}) were measured with disc permeameters at supply potentials of –40 mm (tension) and +10 mm (ponded) (Perroux and White 1988). When a negative pressure or tension is applied to the soil using the disc permeameter, water is prevented from entering macropores, and water only flows through matrix pores. However, when infiltration is measured with a positive pressure, water flows through both macropores and matrix pores. As these two tensions measure the contribution by different pore sizes, the ratio of sorptivity at +10 mm to flow at –40 mm is a useful index of the relative contribution of macropores to total waterflow. This is an extremely informative measure, as macropores are indicative of healthy, highly conductive soils, and a loss of ecosystem function in terms of waterflow can be attributed in a large part to a loss of this macroporosity.

At each of the three sites, five replicate measurements of waterflow were made at two microsites (shrub mound and interspace). The ponded permeameter was placed on a steel ring of 220 mm internal diameter, which was gently pressed into the soil to a depth of about 7 to 10 mm, and sealed with moistened soil along the outside edge to prevent leakage of water. Both permeameters were placed alongside each other and run for approximately 30 minutes, by which time steady-state had been achieved. At each supply potential, sorptivity

Table 1—Description of three sites.

Description	Bowns Creek	Cindercone Butte	Kuna Butte
Dominant vegetation community	Wyoming big sagebrush (*Artemisia tridentata* subsp. *wyomingensis*)	Rabbitbrush (*Chrysothamnus nauseosus*)	Winterfat (*Krascheninnikovia lanata*) with scattered Wyoming big sagebrush
Soil type	Loamy to clay loam Xerollic Durargids and Xerollic Haplargids	Loamy fine sand overlying sandy loams; Xerollic Camborthids	Silts and silty loams; Durinodic Haplocalcid
Shrub density (ha^{-1})	7,140	81,600	30,200
Grazing status	Ungrazed	Intermittently grazed	Ungrazed exclosure

was calculated according to the method of Cook and Broeren (1994), and steady-state infiltration according to White (1988).

Impact of Mosses on Infiltration

Tortula ruralis, the dominant tall moss in sagebrush steppe, is common in sheltered microsites beneath shrub canopies (Rosentreter 1994) where it forms extensive mats on the soil surface (Hilty and others 2003). In order to measure the impact of this thick cover of moss on waterflow, infiltration was remeasured, at the Bowns Creek site only, at each of the exact same mound locations after all moss had been carefully removed from the soil surface. We carefully removed all of the moss without damaging the soil, then allowed 5 days for the soil to equilibrate to its preinfiltration level of soil moisture. Ponded infiltration was then remeasured over 25 minutes. The amount of infiltration into the soil is the difference between the volume of water leaving the permeameter and the volume of water intercepted and stored by the moss. We removed the moss samples from below the permeameters, transported them back to the laboratory, and saturated them with water in order to calculate the amount of water intercepted by mosses. Excess water was allowed to drip off over a period of 20 minutes before the samples were weighed.

Soil Surface Morphology

At Bowns Creek, Cindercone Butte, and Kuna Butte we measured the percentage cover of each of five surface morphology types (Hilty and others 2003) adjacent to each of the five infiltration locations along two 5-m transects using the line-intercept method (Canfield 1941). A detailed description of the five soil surface morphological types (coppice, coppice bench, microplain, playette, disturbed), which have been adapted from Eckert and others (1978), is given in Hilty and others (2003).

Data Analyses

General Linear Models were used to test for differences in sorptivity, steady-state infiltration, and soil surface morphology between the three sites and between the two microsites and their interactions, after checking for homogeneity of variance (Levene's test) using Minitab (1997). We used a split-plot model with sites fixed and locations within a site random. This enabled us to account for the variability between the mound and nonmound microsites among the five replicate locations at each site.

Results

Soil Surface Morphology

Overall, coppice, coppice bench, and microplain surface morphologies accounted for about 90 percent of the surface of the soils across all sites. Although there were few differences in the proportion of most surface cover types between the three sites, there was a significantly greater cover of coppice bench at Bowns Creek compared with the other sites ($F_{4,48} = 17.64$, $P < 0.001$; fig. 1).

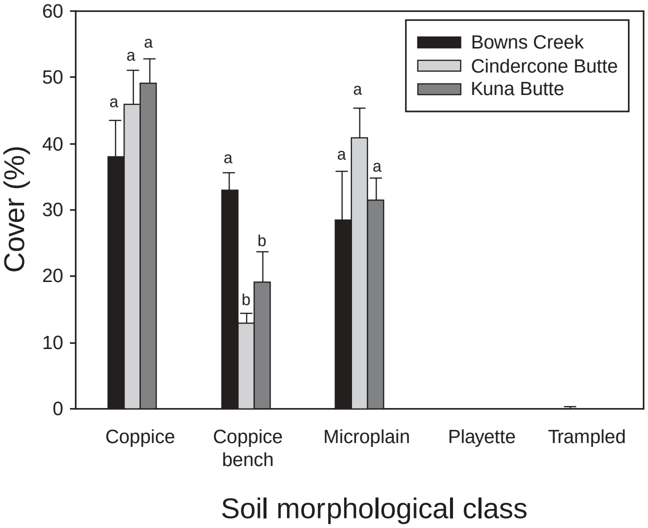


Figure 1—Cover of the five morphological classes at the three sites. Different letters within a class indicate a significant difference in that class between the three vegetation communities.

Infiltration

There were no significant differences in sorptivity or steady-state infiltration under tension between the three sites or between mound and interspace microsites (table 2; fig. 2). Under ponded conditions, both sorptivity and steady-state infiltration were significantly greater at Cindercone Butte compared with the other sites ($F_{2,12} = 6.9$ and 20.6, respectively) (table 2; fig. 2). Both sorptivity and steady-state infiltration were significantly greater in soil below the shrubs compared with in the interspaces ($F_{1,12} = 28.1$ and 22.7, respectively; $P < 0.001$). The greatest differences between shrub and interspace soils occurred at Bowns Creek where steady-state infiltration under the shrubs was more than 6.6 (± 1.1 SEM) times that in the interspaces. Infiltration through the mounds at Cindercone Butte and Kuna Butte was about twice that in the interspaces (fig. 2).

As indicated above, the ratio of sorptivity under ponding to sorptivity under tension is a useful index of the macropore status of the soil (White 1988). This ratio was significantly greater on the shrub mounds (range 8.0 at Kuna Butte to 20.0 at Cindercone Butte) compared with the interspaces (range 2.0 to 8.1; $F_{1,12} = 16.8$, $P = 0.01$), indicating the abundance of macropores below the shrub mounds.

The rate of infiltration was generally more variable in the presence of the moss *Tortula ruralis*. At about 17 minutes after commencement of water application, infiltration in the presence of moss cover significantly exceeded infiltration with moss removed (fig. 3). Over the surface area of the permeameter (220 cm^2), *Tortula ruralis* intercepted a substantial amount of water (0.5 L), and by the cessation of infiltration measurements, total infiltration of water in the presence of moss (5.15 L) was 42 percent greater than that without moss (2.99 L).

Table 2—Breakdown of site and microsite effects on sorptivity and steady-state infiltration under tension and ponding, and the macropore status of soils.

	Site effects[a]		Microsite effects[b]	
Parameter	**Trend**	***P***	**Trend**	***P***
Sorptivity under tension	B = K = C	P = 0.19	M = I	P = 0.110
Sorptivity under ponding	C > (B = K)	P < 0.01	M > I	P < 0.001
Steady-state infiltration under tension	B = K = C	P = 0.79	M = I	P = 0.220
Steady-state infiltration under ponding	C > (B = K)	P < 0.01	M > I	P < 0.001
Macropore status[c]	C > (B = K)	P = 0.04	M > I	P < 0.001

[a] B = Bowns Creek, K = Kuna Butte, C = Cindercone Butte.
[b] M = shrub mound, I = interspace.
[c] Ratio of sorptivity under ponding (+10 mm) to sorptivity under tension (–40 mm).

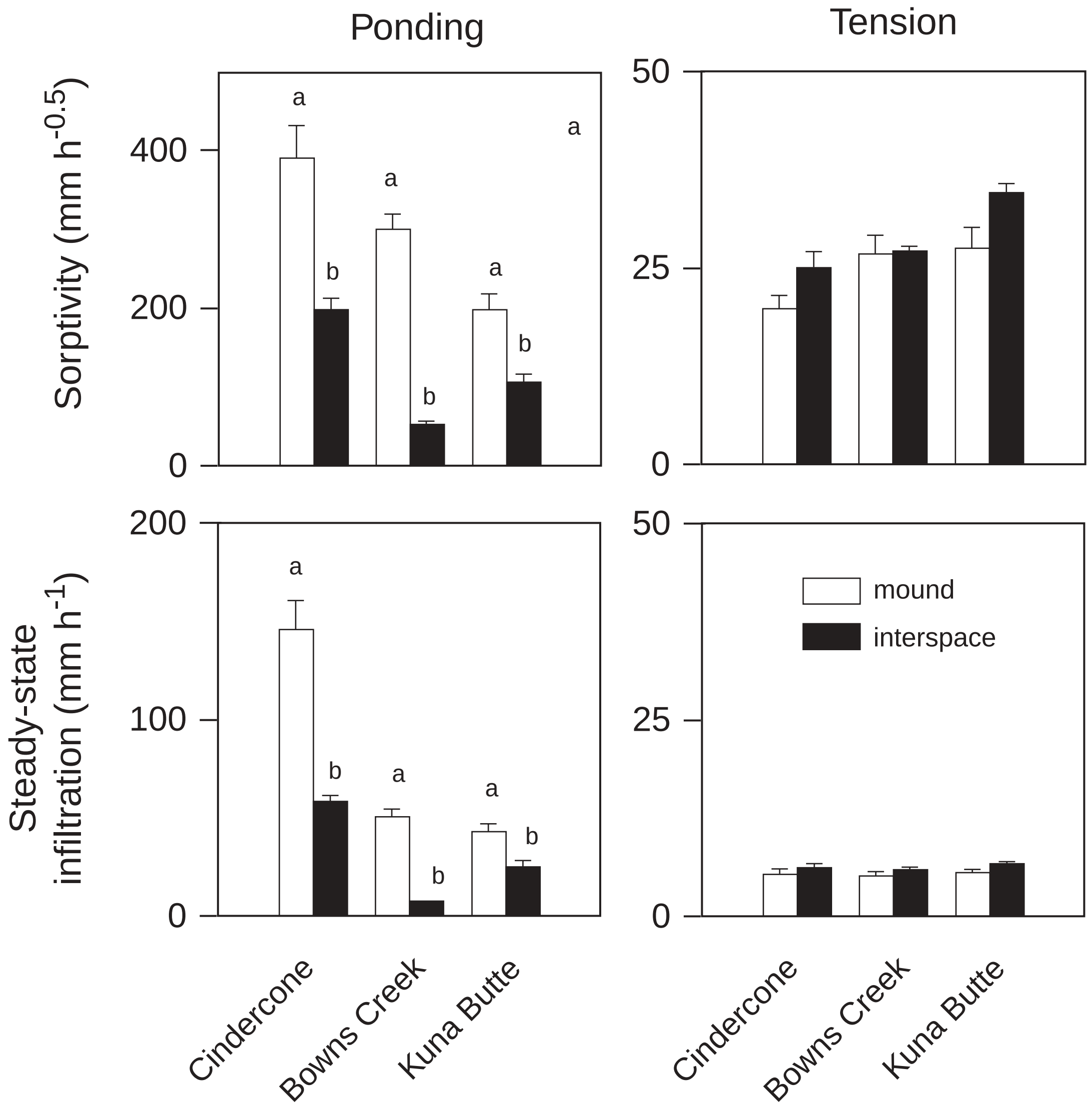


Figure 2—Mean (± standard error of the mean) sorptivity and steady-state infiltration under ponding and tension on mound and interspace microsites at the three sites. Different letters at a site indicate a significant difference at $P < 0.05$.

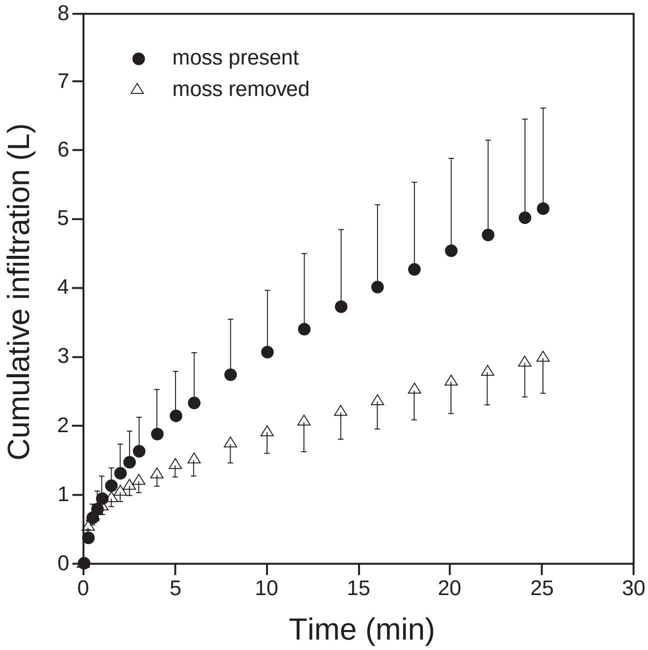


Figure 3—Mean (+ standard error of the mean) cumulative infiltration (L) on five mounds with *Tortula ruralis* intact and later removed. A significant difference in cumulative infiltration occurs after about 17 minutes.

Discussion

In our study, infiltration under the shrubs was two to six times greater than infiltration in the interspaces (fig. 2). We attribute the major difference in infiltration to structural differences in the two microsites, and in particular, differences in the macroporosity status of each microsite. Soil surface morphology was relatively similar between sites (fig. 1), and higher sorptivity and infiltration at the Cindercone site is attributed to the coarser (sandier) texture at that site (table 1).

Increased infiltration under shrubs has been demonstrated in a range of desert and semidesert environments. Scholte (1989) showed that the rate of infiltration under shrubs was 20 times greater than adjacent nonshrub surfaces, while greater flow under woody plants can be attributed to differences in macropores (Devitt and Smith 2002). Greene (1992) demonstrated tenfold greater infiltration rates in mulga (*Acacia aneura*) groves compared with adjacent sparsely populated runoff slopes. Our results emphasize the importance of shrubs for enhancing infiltration, reinforcing the notion that in these environments shrubs act as "fertile islands" (Parsons and others 2003).

A number of factors contribute to the different hydrologic response near shrubs (Dunkerley 2000). Direct plant effects include absorption of raindrop energy by the plant canopy (Whitford and others 1997), which often changes soil water levels and influences the microclimate of the surface, a greater abundance of roots near the surface creating macropores that facilitate waterflow (Beven and Germann 1982), and changes in soil litter cover and plant cover in the vicinity of shrubs that influence the retention and absorption of water (Geedes and Dunkerley 1999). Shrubs can also influence waterflow indirectly by altering adjacent physical and chemical properties of the soil, making the soil more conducive to soil invertebrates (Dunkerley 2000).

Despite the marked differences in sorptivity and steady-state infiltration under ponding, we failed to find any differences under tension when flow was restricted to pores between individual soil particles (matrix pores). There were no site effects nor any differences between shrub mounds and interspaces (fig. 2). This indicates to us that the matrix pore capacity of these soils is very similar, and that the soils have a relatively similar inherent ability to conduct water, which, in the absence of macropores, was quite low (fig. 2). Thus, infiltration rates in these soils are largely driven by macropores, and the greater infiltration under shrubs compared with the interspaces is due to the higher density of biologically derived macropores, probably plant root and faunal holes.

The movement of surface water is the critical process in semiarid and arid landscapes where essential resources are patchily distributed in the landscape. Some zones (source or runoff zones) respond rapidly to rainfall by shedding runoff water, directing it to adjoining patches which absorb water (sink zones). The result is a series of fertile patches or "islands" with enhanced soil moisture at levels greater than that which they would normally receive through natural rainfall (Yair 1994). In healthy landscapes these sinks cover about 30 percent of the surface (Tongway 1990). The marked differences in infiltration capacity between the shrub mounds and interspaces reinforces our view that these shrublands are strongly patterned into two distinct geomorphic zones: (1) a water shedding interspace and (2) a water accreting shrub mound (Ludwig and Tongway 1995).

On the sparsely vegetated interspaces, cryptogamic crusts create a matrix of small runoff zones (Hilty and others 2003) separated by the tussocks of small grasses, principally *Poa secunda*, which function as localized sites for water accumulation. These *Poa* microhummocks, while contributing to patchiness at small spatial scales, are thought to result from previous periods of degradation, and may be a sign of a recovering landscape (M. Pellant 2000, personal communication). During very small rainfall events, the *Poa* microhummocks hold most of the runoff water that is generated off the relatively hydrophobic (water repelling) cryptogamic crusts. However, larger rainfall and intense storms are likely to generate runoff, which is captured in the shrub mounds (Wainwright and others 1999) that have the capacity to absorb substantial volumes of runoff. Our infiltration measurements indicate that the shrub mounds are capable of soaking up substantial quantities of surface runoff, functioning as "ecological straws" in high rainfall years.

Some of this water retention in our study was due to the extensive cover of the moss *Tortula ruralis* below the shrubs (fig. 3). *Tortula ruralis* is generally restricted to shrub canopy and grass microsites (Rosentreter 1984) where it forms extensive mats on the soil surface. *Tortula ruralis* is well adapted to prolonged desiccation (Longton 1992) and quickly rehydrates after rainfall. Our study showed that *Tortula* can store about 0.5 liters of water over an area of 0.038 m^2, or 14.2 liters m^{-2}. The destruction of moss cover after fire (Hilty and others 2004) has the capacity therefore to reduce substantial amounts of water, which may be important for invertebrates resident within shrub-steppe ecosystems.

Shrub patches receiving enhanced water and nutrients would be expected to have higher levels of soil nutrients, particularly organic carbon and nitrogen, and greater populations of soil biota, and would be expected to be preferred sites for germination and survival of vascular plants compared with the interspaces. The *Chrysothamnus* site at Cindercone showed evidence of invasion by annual grasses, particularly cheatgrass, and the shrub mounds were poorly developed in comparison with the finer textured soils at Kuna Butte and Bowns Creek (table 1). Nevertheless, landscape patchiness appears to be governed by the distribution of shrubs, particularly *Chrysothamnus* and *Artemisia* spp., which show evidence of deep deposition of litter under the canopy.

Disturbance of the well-developed microphytic crust in the interspaces, particularly at Bowns Creek and Kuna Butte, is likely to lead to increased infiltration in the interspaces, invasion of the interspaces by annual species such as cheatgrass, and reduced redistribution of runoff to the shrub mounds. The breakdown in patchiness means that annual rainfall alone (in the absence of runon) may be insufficient to sustain the growth of perennial shrubs. Reduced infiltration through the mounds is likely to lead to a change in the composition of vascular plants to one dominated by weedy ephemerals. In the short-term, death of the perennial shrubs will result in reduced infiltration rates, erosion around the mound base, reduced trapping of wind- and water-borne sediments (dust), and eventually partial breakdown of the mounds (Offer and others 1998). The long-term effect of removal of the water-shedding crust is a disintegration of the mounds, and a general decline in rangelands productivity and condition (Eldridge and others 2000).

Conclusions

The results confirm the importance of landscape patchiness in controlling the distribution of water in shrub-steppe ecosystems. Shrub mounds represent a stable, healthy landscape, and their enhanced water status results in higher diversity and productivity. Activities that disturb the soil surface in the interspace have the capacity to reduce runoff to the shrub mounds and therefore reduce cover of the shrubs. Long-term management of desert shrublands should aim to maintain the integrity of both the mound and interspace, ensuring the efficient functioning of shrub and shrubland biota.

Acknowledgments

We thank Cleve Davis (Bureau of Land Management) for assistance with data collection, Terry Koen for statistical advice, and Ann and Teddy DeBolt for comments on the manuscript.

References

Beven, K.; Germann, P. 1982. Macropores and waterflow in soils. Water Resources Research. 18: l131–1325.

Blark, E. W.; Small, E. C. 2003. Associations between plant canopies and the spatial patterns of infiltration in shrubland and grassland of the Chihuahuan Desert, New Mexico. Ecosystems. 6: 185–196.

Bouma, J. 1991. Influence of soil macropores on environmental quality. Advances in Agronomy. 46: 1–37.

Canfield, R. H. 1941. Application of line interception in sampling range vegetation. Journal of Forestry. 33: 388–394.

Cook, F. J.; Broeren, A. 1994. Six methods for determining sorptivity and hydraulic conductivity with disc permeameters. Soil Science. 157: 2–11.

CSIRO. 1988. CSIRO disc permeameter instruction manual. Canberra, ACT, Australia: CSIRO Division of Environmental Mechanics.

Devitt, D. A.; Smith, S. D. 2002. Root channel macropores enhance downward movement of water in a Mojave Desert ecosystem. Journal of Arid Environments. 50: 99–108.

Dunkerley, D. L. 2000. Hydrological effects of dryland shrubs: defining the spatial extent of modified soil water uptake rates at an Australian desert site. Journal of Arid Environments. 45: 159–172.

Eckert, R. E.; Wood, M. K.; Blackburn, W. H.; Peterson, F. F.; Stephens, J. L.; Meurisse, M. S. 1978. Effects of surface-soil morphology on improvement and management of some arid and semiarid rangelands. In: Hyder, D. N., ed. Proceedings of the First International Rangelands Congress, Denver, CO: 299–302.

Eldridge, D. J.; Zaady, E.; Shachak, M. 2000. Infiltration through three contrasting biological soil crusts in patterned landscapes in the Negev, Israel. Catena. 40: 323–336.

Geedes, N.; Dunkerley, D. 1999. The influence of organic litter on the erosive effects of raindrops and of gravity drops released from desert shrubs. Catena. 36: 303–313.

Greene, R. S. B. 1992. Soil physical properties of three geomorphic zones in a semi-arid mulga woodland. Australian Journal of Soil Research. 30: 5569.

Hilty, J.; Eldridge, D. J.; Rosentreter, R.; Wicklow-Howard, M. 2003. Burning and seeding influence soil surface morphology in an *Artemisia* shrubland in southern Idaho. Arid Land Research and Management. 17: 111.

Hilty, J. H.; Eldridge, D. J.; Rosentreter, R.; Wicklow-Howard, M. C.; Pellant, M. 2004. Recovery of biological soil crusts following wildfire in Idaho. Journal of Range Management. 57: 89–96.

Longton, R. E. 1992. The role of bryophytes and lichens in terrestrial ecosystems. In: Bates, J. W.; Farmer, A. M., eds. Bryophytes and lichens in a changing environment. London: Oxford University Press: 32–76.

Ludwig, J.; Tongway, D. J. 1995. Spatial organisation of landscapes and its function in semi-arid woodlands, Australia. Landscape Ecology. 10: 51–63

Mack, R. N. 1981. Invasion of *Bromus tectorum* L. into Western North America: an ecological chronicle. Agro-Ecosystems. 7: 145–165.

Minitab. 1997. References manual, release 10.1. Pennsylvania, PA: State College of Pennsylvania, Minitab Incorporated.

Oades, J. M. 1993. The role of biology in the formation, stabilization and degradation of soil structure. Geoderma. 56: 377–400.

Offer, Z. Y.; Zaady E.; Shachak, M. 1998. Aeolian particle input to the soil surface at the northern limit of the Negev Desert. Arid Soil Research and Rehabilitation. 12: 55–62.

Parsons, A. J.; Wainwright, J.; Schlesinger, W. H.; Abrahams, A. D. 2003. The role of overland flow in sediment and nitrogen budgets of mesquite dunefields, southern New Mexico. Journal of Arid Environments. 53: 61–71.

Perroux, K. M.; White, I. 1988. Designs for disc permeameters. Soil Science Society of America Journal. 52: 1205–1212.

Rosentreter, R. 1994. Displacement of rare plants by exotic grasses. In: Monsen, S. B.; Kitchen, S. G., comps. Proceedings of the ecology and management of annual rangelands. Gen. Tech. Rep. INT-GTR-313, Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 170–175.

Rosentreter, R. 1984. Compositional patterns within a rabbitbrush (*Chrysothamnus*) community of the Idaho Snake River Plain. In: McArthur, E. D.; Welch, B. L., comps. Proceedings—symposium on the biology of *Artemisia* and *Chrysothamnus*. Gen. Tech. Rep. INT-GTR-200. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 273–277.

Schlesinger, W. H.; Reynolds, J. E.; Cunningham, G. L.; Huenneke, L. E.; Jarrell, W. M.; Virginia, R. A.; Whitford, W. G. 1990. Biological feedbacks in global desertification. Science. 247: 1043-1048.

Scholte, T. S. 1989. Vegetation-soil relations in an area with sealed Chromic Luvisols, Kenya. Arid Soil Research and Rehabilitation. 3: 337–348.

Thiery, J. M.; D'Herbes, J. M.; Valentin, C. A. 1995. A model simulating the genesis of banded vegetation patterns in Niger. Journal of Ecology. 83: 497–507.

Tongway, D. J.; Ludwig, J. A. 1994. Small-scale patch heterogeneity in semi-arid landscapes. Pacific Conservation Biology. 1: 201–208.

Tongway, D. J. 1990. Soil and landscape processes in the restoration of rangelands. Australian Rangeland Journal. 12: 54–57.

Wainwright, J.; Parsons, A. J.; Abrahams, A. D. 1999. Rainfall energy under creasotebush. Journal of Arid Environments. 43: 111–120.

Wambolt, C. L.; Harp, A. J.; Welch, B. L.; Shaw, N.; Connelly, J. W.; Reese, K. P.; Braun, C. E.; Klebenow, D. E.; McArthur, D.; Thompson, J. G.; Torell, L. A.; Tanaka, J. A. 2002. Conservation of greater sage-grouse on public lands in the Western U.S.: implications of recovery and management policies. PACWPL Policy Paper SG-02-02: 1–41.

Wambolt, C.; Walhof, K.; Frisina, M. 2001. Recovery of big sagebrush communities after burning in south-western Montana. Journal of Environmental Management. 61: 243–252.

West, N. E. 1990. Structure and function of microphytic soil crusts in wildland ecosystems of arid and semi-arid regions. Advances in Ecological Research. 20: 179–223.

West, N. E. 1993. Biodiversity of rangelands. Journal of Range Management. 46: 2–13.

Whisenant, S. G. 1990. Changing fire frequencies on Idaho's Snake River Plains: ecological and management implications. In: McArthur, E. D.; Romney, E. M.; Smith, S. D.; Tueller, P. T., comps. Proceedings of a symposium on cheatgrass invasion, shrub die-off, and other aspects of shrub biology and management. Gen. Tech. Rep. INT-276. Ogden, UT: U.S Department of Agriculture, Forest Service, Intermountain Research Station: 4–10.

White, I. 1988. Tillage practices and soil hydraulic properties: why quantify the obvious? In: Loveday, J., ed. National Soil Conference Review Papers, Canberra, May 1988. Canberra, ACT, Australia: Society of Soil Science Incorporated: 87–126.

Whitford, W. G.; Anderson, J.; Rice, P. M. 1997. Stemflow contribution to the 'fertile island' effect in creosotebush, *Larrea tridentata*. Journal of Arid Environments. 35: 451–457

Yair, A. 1994. The ambiguous impact of climate change at the desert fringe: Northern Negev, Israel. In: Millington, A. C.; Pye, K., eds. Environmental change in drylands: Biogeographical and Geomorphological Perspectives. London: John Wiley and Sons: 199–227.

Edaphic Characteristics of Nitrogen Fixing Nodulation (*Actinorhizae*) by *Cercocarpus montanus* Raf. and *Purshia tridentata* (Pursh) DC

Stephen E. Williams
Joe D. Johnson
Larry C. Munn
Terry Nieder

Abstract: Edaphology, excavation techniques, nodulation and some nitrogen fixation characteristics of mountain mahogany (*Cercocarpus montanus* Raf.) and antelope bitterbrush (*Purshia tridentata* (Pursh) DC) were examined principally in southeastern Wyoming environments. Although critical levels of soil nitrogen and soil organic matter were not identified, relatively high levels of nitrate nitrogen (above 3 ug/g) and soil organic matter (above 2 to 4 percent) inhibit nodulation, whereas low levels of nitrate (less than 1 ug/g) and soil organic matter (less than 1 percent) are conducive to nodule formation. Excavation of these nodulated Rosaceous plants in the field requires care and attention to detail. Strategies for excavation should involve allowing sufficient time and input of energy into the excavation process, and excavation of mature plants may take even weeks to accomplish. Field observations and subsequent greenhouse studies strongly suggest that the agents responsible for nodulation of these plants (member of the actinomycete genus *Frankia*) is either not present or is inactive in surface soils. The paradox of stressing plants via sampling and the expectation that collected data represents normal response is discussed.

Introduction

Cercocarpus montanus Raf. and *Purshia tridentata* (Pursh) DC, mountain mahogany and antelope bitterbrush, respectively, are common shrubs in Western North America, being found mostly in the foothills topographically between grasslands and forested environments. Sometimes both are in the understory of lower elevation coniferous forest. These two plants, both in the family Rosaceae, are important as browse for many wildlife species and as cover for others, and both may periodically occupy deep soils, but mostly they can be found in areas of shallow soil where the lithic contact is within a meter of the surface. Usually the geological substrata, which best host both species, are sedimentary materials with limestone and sandstone; claystones and siltstone are less favored.

That these two plants are adaptable to a diversity of fairly harsh environments may well be a function of the relatively large variety of mutualistic symbiotic microorganisms known to occupy the root systems of both plants. Both plants are known nitrogen fixers, and are infected by bacteria of the Actinomycetales genus *Frankia*. These bacteria elicit development of root cortical hypertrophies (nodules and often called actinorhizae) that function to biologically fix atmospheric nitrogen. Further, both plants can be infected by mycorrhizal fungi including arbuscular mycorrhizal fungi expressed as an endomycorrhizal morphology as well as by fungi that are manifest as an ectomycorrhizal morphology (Williams 1979). It is highly probable that the capacity of these plants to host such a variety of known beneficial root microorganisms results in these plants being somewhat independent of essential soil nitrogen because they can fix their own. They also can benefit from the enhanced uptake function of mycorrhizal roots, which includes uptake of critical nutrients such as phosphorus and zinc (Allen 1991) as well as uptake of water (Stahl and others 1998). Ectomycorrhizal plants are also known to have some protection against root pathogens (for example, Marx 1972).

Mountain mahogany and antelope bitterbrush (*C. montanus* and *P. tridentata*) are two species among perhaps a dozen or more species spread across five or six genera in the Rosaceae that fix nitrogen via association with *Frankia*. The genera *Chamaebatia*, *Cowania*, *Dryas*, and perhaps *Rubus* are also known for their nitrogen fixing habit (Peterson and others 1991). It is not very well known how much nitrogen is commonly fixed by these associations, although speculation is that it is low especially in highly arid environments (Dalton and Zobel 1977; Kummerow and others 1978). Further, there remains speculation that even though these rosaceous plants have nodules and fix nitrogen that such activity is not very important to supplying nitrogen needed

---

In: Hild, Ann L.; Shaw, Nancy L.; Meyer, Susan E.; Booth, D. Terrance; McArthur, E. Durant, comps. 2004. Seed and soil dynamics in shrubland ecosystems: proceedings; 2002 August 12–16; Laramie, WY. Proceedings RMRS-P-31. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Stephen E. Williams and Larry C. Munn are Professors, Department of Renewable Resources, College of Agriculture, University of Wyoming, Laramie, WY 82071, U.S.A.; e-mail: sewms@uwyo.edu. Joe D. Johnson is District Conservationist, USDA-NRCS, Kewaunee, WI 54216, U.S.A. Terry Nieder is Technical Sales Representative, ADCON Telemetry, Santa Rosa, CA 95403, U.S.A.

by the plant. This general observation is based on observations by a number of researchers that these plants are not well nodulated or are often not nodulated in the field.

The objectives of this work are to (1) discuss soil properties that influence actinorhizae development on these two plants, (2) derive strategies for and show results of plant excavation to locate and quantify actinorhizae development on these two and similar plants, (3) report nodulation characteristics and nitrogen fixation activity for these species under various environmental conditions, and (4) discuss the uncertainty that arises from determining normal characteristics of plant activity when done destructively and where the plant is otherwise stressed to secure such characteristics.

Materials and Methods

Soil Properties That Influence Actinorhizae Development

Mountain mahogany and antelope bitterbrush have been excavated by the authors and associates since the mid-1970s mostly in southeastern and central Wyoming. In the early 1980s to about 1995, numerous plants were excavated and examined by excavation of the root system to a minimum depth of 30 cm to consolidated and immovable rock or to the extent of the root system. Plants of all ages were excavated; however, the majority of plants were less than 12 years of age. Here, excavation is used to mean that the entire root system of each plant was systematically unearthed, nodules counted, fresh and dry weights taken, and soils collected from nodule zones. If a plant bore no nodules, soil was still taken from that rooting zone of the plant where, from our experience, we would normally expect to find nodules. This zone was normally in the range of 30 to 60 cm from the soil surface. Numerous plants were taken from highly disturbed soils where top soil had been removed. We became aware early that such plants were much more likely to be nodulated than those on well developed soils.

Plants and soils were examined at approximately 50 sites throughout Wyoming. Bitterbrush was examined primarily in the Laramie Range, The Snowy Range foothills, the Wind River Range foothills, and the Absaroka Range foothills. Mountain mahogany samples were taken exclusively from the Laramie Range and the Snowy Range foothills.

Plants were examined visually for presence of nodules. Organic matter (Allison 1965), NO_3-N (Oien and Olsen 1969), pH (1:1 in water), available K (Bower and Wilcox 1965), available P (Wantanabe and Olsen 1965), and electrical conductivity (Bower and Wilcox 1965) were determined for each soil sample.

Strategies for Plant Excavation

Techniques—The tendency when looking for nodules on root systems is to take digging tools to the field and oftentimes indiscriminately and randomly sample from the soil around the base of the plant, relying mostly on chance that one will strike a cluster of nodules. This rather arbitrary method can be successful when nodules are needed for general examination or for a crude assay. It is particularly fruitful when looking for nodules on cultivated legumes, and can be successful when examining members of the genus *Alnus* in many riparian systems. However, when nodules are deep within soils, and when clusters are apparently rare, more methodical methods are used, and sufficient time must be allocated to fully excavate plant roots.

There are numerous problems encountered when quantitatively examining plant root systems. Actinomycete nodulated shrubs often have root systems that extend to considerable depth, the rooting medium may be obstreperous (for example, too clayey, too many large coarse fragments), roots of differing species make following the roots of the target individual difficult, roots of same species make following target individuals difficult, and plants can be in steep topographical positions that may defy examination.

We have used a variety of techniques to examine roots systems of shrubs. Herein we describe methodology for shrub excavation that can be used to quantitatively remove shrub root systems. The objectives and scale of research will dictate, to some degree, the intensity of excavation needed and the data that will be recorded. However, as the spatial and temporal development of plant roots are examined, as well as symbiotic associations between roots and a variety of mutualistic, pathogenic, and commensalic biota, roots systems will need to be more accurately and methodically excavated. There are a variety of reference materials that can be accessed that detail root excavation considerations and techniques. Two works from the archaeology literature are very much worth consideration especially for project level excavations (Joukowsky 1980; Roskams 2001).

Examination of Soil Taxa Associated With Nodulated Shrub Communities—During plant excavation to locate and quantify actinorhizae development, soils and plants were examined along a trenched transect that was made from a site occupied by mountain mahogany, through the boundary of the plant community, and into an associated soil type having no mountain mahogany and dominated primarily by grasses and forbs. The site was representative of a number of associations between mountain mahogany and adjacent vegetation and was located 10 km NNE of Laramie, WY, south of the mouth of Roger Canyon.

Soils and plants were examined also along a transect made at a site occupied by antelope bitterbrush, through the boundary of the antelope bitterbrush community, and into an associated soil type that was void of the shrub but dominated primarily by *Artemisia* sp. shrubs, grasses, and forbs. The transect was located 15 km ESE of Laramie, WY, adjacent to Blair Road. This transect was not trenched, but rather was examined by locating pits and observation of natural and manmade cuts that intersected the established transect.

The two transects indicated above were established primarily to determine if there were identifiable morphological features of soils associated with these two rosaceous shrub communities. Soils were classified in accordance with Soil Taxonomy (Soil Survey Staff 1999) and the Soil Survey of Albany County, WY (Reckner 1998).

Nodulation Characteristics and Nitrogen Fixation Activity

Actinorhizal Plants During Winter Months—Antelope bitterbrush and mountain mahogany were observed occasionally during winter seasons between 1988 and 1998. Observation years were categorized as dry winters or wet winters where dry winters had very little surface snow accumulation and the soil profile was generally dry. Wet winters were those where there was considerable surface accumulation of snow.

During one wet winter, 1988, antelope bitterbrush individuals were excavated from a site along the Happy Jack Road on Pole Mountain near Laramie, WY. Soils here were weakly developed with some organic matter accumulations in the upper 20 to 30 cm over an undeveloped coarse subsoil. Nodules were found in the coarse subsoil. Three plants were excavated in February of that year—a 1-year-old plant on a recently disturbed roadcut and two 5-year-old plants on an adjacent, but undisturbed site. Nodules were taken and incubated in a 10 percent atmosphere of acetylene to ascertain nodule nitrogen fixation via analysis of ethylene (Upchurch 1987). Incubation chambers were 450 ml volume, incubation time was up to 1 hour, and was done at ambient soil temperatures in the field. Gas samples from the incubation chambers were stored in vacutainers prior to analysis. Subsamples of 100 microliters each were analyzed via gas chromatography (Upchurch 1987). Observations of antelope bitterbrush and mountain mahogany during several winter seasons showed that during dry winters, nodules were very hard to find and that when found, they had no visual signs of activity. Nodules were usually brown to black including nodule tips. During wet winters and especially under snow pack, nodules were easier to find and often gave the visual appearance of considerable activity, that is, nodule tips were white and apparently turgid.

Biological Assay of Soil Materials for Nodulation Capacity—The field portion of this study was done in SE Wyoming, in Laramie County. Seven sites were located in two separate areas. Six of these sites were inhabited by mountain mahogany, and one site that did not have this plant provided soil materials as a control. Pits were excavated on each of these sites to the depth of consolidated bedrock or 1.8 m, whichever was less. Five-kg soil samples were taken from each horizon of each site. These were split, with half used in a greenhouse bioassay and half used for soil analysis. Soil analysis included texture (hand-textured according to Thien 1979). Soils were taxonomically described in the field.

Seeds were collected from plants at four of the seven sites. Tails were removed and the seeds submerged in a 0.525-percent sodium hypochlorite solution for 20 minutes to control fungi. Sterile water-rinsed seeds were placed in glass containers in wetted sterile vermiculite and refrigerated at 2 °C for 60 days, and then at 12 °C for 10 days. This treatment resulted in 90-percent germination.

Autoclaved (121 °C at 0.1035 MPa for 20 minutes) pottery shards were placed in the bottoms of plastic 30.5-cm-diameter pots to expedite drainage. Pots had been soaked overnight in a 0.525-percent sodium hypochlorite solution. Each pot was half filled with autoclaved sand. Soil from each horizon of the seven sites was each mixed 1:1 (weight to weight) with autoclaved sand. The sand-soil mixture from each specific horizon was used to layer 5 cm over the sand in each pot. Over this an additional 5-cm layer of a 1:1 sand to perlite mixture was added. Across the seven field sites, 23 different horizons were collected. Because two pots of diluted soil material were derived from each horizon, a total of 46 pots resulted. Two control pots were also constructed, where a 1:1 sand to perlite mixture was substituted for the 1:1 sand to soil mixtures. Pots were thoroughly watered (to near field capacity) and five germinated mountain mahogany seeds planted in the surface 2 cm of each container and lightly covered with the sand to perlite mixture. All plants were placed in a greenhouse in late April and misted daily during the emergence and establishment period of the plants. Pots were randomly placed, on 45-cm centers, in the greenhouse and rerandomized monthly. Damping-off fungi were problematic, and resulted in necessary replacement of some seedlings. Pots were watered as needed. Temperatures in the greenhouse averaged 20 to 22 °C during daylight hours and 7 to 8 °C during night. Plants remained in this environment for 10 months.

At the conclusion of this time, whole plants were removed from the rooting media and observed for nodulation. Tops and roots were separated and weighed individually.

Results

Soil Properties That Influence Actinorhizal Development

For both mountain mahogany and antelope bitterbrush, soil organic matter and extractable nitrate nitrogen are strongly related to the capacity of these plants to host the nitrogen fixing symbiont and consequent formation of actinorhizae (see Peterson and others 1991; and especially White and Williams 1985). Nodulated mountain mahogany and antelope bitterbrush had, respectively, 0.61 (standard deviation of 0.66) percent organic matter and 0.68 (0.59) percent organic matter in root zones as compared to non-nodulated plants that were 2.94 (1.37) percent and 3.73 (2.24) percent. These differences were statistically significant between nodulated and non-nodulated populations (within species) at 0.01 and 0.001, respectively, for mountain mahogany and antelope bitterbrush. Extractable nitrate nitrogen showed similar trends and significance levels—0.59 (0.50) ug/g and 0.92 (0.76) ug/g for nodulated mountain mahogany and antelope bitterbrush, respectively; and 2.81 (1.73) and 3.50 (2.35), respectively, for non-nodulating plants. Differences were statistically significant at 0.01 levels for both comparisons within species. Other soil parameters (pH, electrical conductivity, extractable P, and extractable K) were all significantly different between nodulated and non-nodulated mountain mahogany, but were not significant for antelope bitterbrush. These findings suggest that nodulation of these rosaceous plants is controlled by edaphic factors such as organic matter and nitrate levels. Given the high level of resources that a plant must invest in the acquisition of nitrogen from atmospheric sources, it makes sense that these plants would not allocate such resources if nitrogen is available in mineral forms (for example, as nitrate) or in organic forms (for example, from soil organic matter) at levels above a basal level needed for survival. Artificial fertilization of antelope bitterbrush (Tiedeman 1983) seedlings in a greenhouse study showed a positive response to

N, P, and S, but in the field, established mature plants did not respond to fertilization with N, P, and S, although associated understory plants did. Tiedeman's work did not examine the influence of fertilization on nodule formation.

Strategies for Plant Excavation

Techniques—Standard, nonstructured digging usually results in holes that are roughly conical shaped with the flat surface of the cone represented by the original surface of the soil. This geometry is a result reflective of enthusiastic excavation early and at the surface where digging is easy. This activity wanes with time as the digger's energy reserves dissipate, and earthy substrates become more consolidated.

Our experiences have taught us to be somewhat and sometimes opportunistic when seeking observations of the belowground plant parts, especially of deeply rooted species like mountain mahogany and antelope bitterbrush. Cuts and trenches made by digging machinery can be excellent places to observe roots of these plant species. Often these can be accessed opportunistically when new roads or pipelines are being constructed. It is possible and often desirable to then work from the surface, progressing down the face of the cut, excavating specific intervals of the substrate sequentially to the depth of the roots or to the depth of the trench or cut. For mature mountain mahogany and antelope bitterbrush it is often convenient to stake off a distinct zone where the shrub stem is roughly in the middle of the zone. We often use a full square meter designation, where one side of the square follows the edge of the cut or trench.

As excavation proceeds, it is usually necessary to remove the aboveground portion of the plant. Some excavation can be done with the plant in place, but this can be awkward. An alternative is to divide the surface meter square into half-meter or quarter-meter sectors and excavate those to depth. In such cases, the aboveground plant parts can often be left in place for part of the excavation.

We have generally found it expeditious to stake out the area to be trenched and proceed as rapidly as possible with the trenching. Certainly root observations can be made, but it is also an option to ignore observations and extend the trench to the length, depth, and width desirable. One should be sure that the trench face, which will become the working and access plane to the root system of the target plant, is sufficiently far from the target so that root disturbance of that individual is minimized. Having a level indicator for such an excavation is of value to be sure the functional side of the trench is vertical.

Before the careful excavation of the root system begins, one should decide at what intervals soils should be removed. It is often desirable to remove the soil by pedogenic horizon. Sometimes this does not make sense if such horizons are very thin, and at other times it may be desirable to subdivide a particularly thick horizon. Intervals of 20 cm are often convenient and seem to represent a scale that fits with the size of these organisms.

In working with the first or top interval of the profile, one can work from the surface of the exposed face back into substratum to the extent of the predetermined boundaries of the excavation. As this is done, photographs or maps of roots and associated phenomena can be made. Nodules can be observed and collected or tested (for example, acetylene or ^{15}N incubations). It is best to completely remove a defined volume of soil before moving to the next. It is usually best also to sieve that material to catch missed roots and nodules using a box sieve of usually 60 by 60 cm construction with sieve openings of 1.25 cm. The substratum can be placed on the sieve and agitated to pass through. Roots and nodules will be caught on the sieve and recovered. The ease and success of such an operation is very much connected with the integrity of the substratum. Sand or gravelly material is often easy to excavate and passes the sieve quickly and efficiently. Decomposing granites can also work fairly well and can be usually easily crushed to pass the sieve. High clay content materials often require washing to remove roots as do materials containing silts.

Usually as an excavation progresses to deeper depths, coarse fragments tend to increase. This is especially true in soils inhabited by mountain mahogany and antelope bitterbrush. Very coarse fragments are often very common especially in subsoils. Further, roots often do not abate when they encounter consolidated rock. Roots may penetrate cracks, and we have often come across nodules in cracks. Roots may extend a meter or more into such materials. Nodules may be found wherever roots go.

Examination of Soil Taxa Associated With Nodulated Shrub Communities—Soils identified along the trench that intersected the mountain mahogany community were Typic Haplustolls, loamy-skeletal, frigid under both the grassland community adjacent to mountain mahogany and under the mountain mahogany community. The soil solum under both vegetation types consisted of noncalcareous A and B horizons containing approximately 15 percent course fragments overlying calcareous, skeletal C horizons. The soils in this association were more highly developed under the mountain mahogany than observed in other locations where mountain mahogany was examined. The major consideration at this site was a thin laminar petrocalcic horizon at the surface of the skeletal layer in the soil under the grassland community. The petrocalcic layer prevented root penetration into the lower, high course fragment containing C horizon. Under the mountain mahogany stand such a restrictive layer was not present, and roots penetrated to a considerable depth (to more than a meter). These soils developed in limestone colluvium.

In many cases, mountain mahogany grows in very small lenses of soil in cracks between rocks. From a taxonomic standpoint these materials are essentially unconsolidated rock. In the Rogers Canyon site it was noted that none of the mountain mahogany whose roots were exposed in the trench had nodules in the A horizon (the zone of highest organic matter content); however, numerous plants whose root systems extended well below this horizon were nodulated in subsoil horizons below the A horizon. These horizons were very low in soil organic matter (less than 0.5 percent). In other sites where plants were growing essentially in contact with consolidated rock, nodules were seldom found; however, complete excavation of the root systems of these plants was usually not possible.

In the antelope bitterbrush transect, the soils under the adjacent sagebrush grassland mixture were Typic Argiustolls, fine-loamy, on upland sites grading into Cumulic Haploustolls, fine-loamy, on sites (drainages) where there was transport of soil material onto the site. Bitterbrush occupied Typic Torriorthents, loamy-skeletal, on the footslopes grading into Lithic Torriorthents, loamy-skeletal, and eventually to rock on steeper sites.

Antelope bitterbrush, as is usually the case with mountain mahogany, occupied sites of shallower rocky soil than associated vegetation (sagebrush and grasses). No nodules were found where plant roots were in contact with high organic matter soils (the A horizon). Nodules were found in subsoils below the A horizon, although even these on this site were sparse.

Nodulation Characteristics and Nitrogen Fixation Activity

Actinorhizal Plants During Winter Months—Nodules encountered during the 1988 winter season had visual signs (white tips, elastic and turgid) that suggested they were active. However, all plants displayed necrotic nodules (dark, shrunken, and brittle). Even the 1-year-old plant had necrotic nodules (0.08 g) associated with active nodules (0.05 g). The 5-year-old plants also had necrotic nodules (an average of 0.13 g per plant) as well as active nodules (average of 0.12 g dry weights 70 °C for 48 hours).

Ambient soil temperatures in the field and of the incubation chambers were just barely above the freezing point of water (about 2 °C). Acetylene reduction assay indicated that all nodules were inactive, even though some gave visual appearances of activity. Ethylene produced by these nodules was indistinguishable from background levels. Implications here are that soil temperatures were too cold and plants too inactive to provide photosynthate to accommodate nitrogen fixation. However, an argument could be made from the appearance of some nodules that they were poised to rapidly begin nitrogen fixation once conditions or temperature and photosynthate availability came more into functional ranges.

Biological Assay of Soil Materials for Nodulation Capacity—Essentially the sites examined came from two completely different parent materials. Sites 1, 2, and 3 were on igneous and metamorphic rocks in the western part of the county, whereas sites 4, 5, 6, and 7 were on sedimentary rocks in the northern part of the county (table 1). The sites were separated by approximately 40 m of elevation change and 51 km of lateral change. The soils were Haplustolls and Calciustolls on the upland, frigid sites (1, 2, and 3) and Haplustolls on the lower elevation, mesic sites (4, 5, and 6). Site 7 was a Torripsamment (Stevenson 2001).

Seedlings were susceptible to damping-off fungi. Although soil material was dispersed between two pots for each horizon tested, and a total of five seedlings were planted to each pot, approximately 80 percent of the plants were lost, although at least one plant survived in soil from each horizon tested (table 1). Plants harvested at the end of the 10-month period were observed for a variety of microbial manifestations on root systems, including the presence of nodules.

Roots were removed from the rooting media and stained using an acid fuchsin technique (Williams 1979). Ecto-mycorrhizal and endomycorrhizal (arbuscular fungi) were observed on all root systems. Infection density (mantled, swollen root tips for ectomycorrhizae and arbuscules, vesicles and characteristic hyphae for endomycorrhizae) was variable, ranging from light to very high in all horizons from sites 1 through 6. Infection was unrelated to horizon or depth below the surface. Mycorrhizal infections in roots exposed to the soil material collected at site 7, where mountain mahogany was absent from the flora, were present but the density was consistently light.

Very small nodules were observed on bioassay roots exposed to subsoils from sites 1, 2, and 4. No other nodules were observed.

After 10 months, most bioassay plants appeared stunted and had very low fresh-weight biomasses (less than 0.5 g). Large plants (greater than 1.0 g) were present, but were always in soil material derived from A horizons or A/C horizons. Some of these plants were more than 5.0 g fresh weight. Nodules were never observed, however, on any plants growing in A or A/C horizon materials. All nodules were on plants growing in subsoil material derived from C horizons. However, these nodulated plants were all small plants.

The data from table 1 suggests that there were factors present in the A horizons and sometimes the A/C horizons of most soils examined that allowed mountain mahogany to develop substantial growth. It is likely that these factors were higher soil fertility associated with higher soil organic matter in these horizons. However, sometimes a soil horizon tested would generate a large plant and a stunted plant (for example, site 1, horizon A generated plants of 5.64 and 0.39 g; see table 1). Genetic variability among plants could also account for these differences. Plants on materials derived from C horizons almost always were very small, although a few plants exceeded 0.5 grams and one plant exceeded 1.0 g in size. Table 1 shows these average differences; however, it does not show deviations from averages, many of which were as large as the mean.

Table 1 also suggests that whatever factor was the causative agent of nodule formation was found only in subsurface horizons (C material), but was inconsistent in those horizons or was incompatible with some test plants. It would be consistent with established theory that plants that became nodulated would be large and robust. Here we suspect that nodulated plants had not had sufficient time to respond to nodulation, or that the nodules were ineffective. Another season of growth may have resolved this issue, but this would have required that nodulated plants be identified as nodulated, a process that can only be done destructively.

Discussion

The work reported herein was conducted over several decades and focused on acquiring field data on nodulation of two Rosaceous shrubs, mountain mahogany, and antelope bitterbrush.

From field observations, it is hypothesized that soil properties influence nodule initiation on both plants. Available nitrogen, here as nitrate, and soil organic matter determine nodulation in both plants. Although critical levels of nitrogen and soil organic matter were not identified, relatively high levels of nitrate nitrogen (approximately 3 ug/g) and soil organic matter (2 to 4 percent) inhibited nodulation, whereas low levels of nitrate (less than 1 ug/g) and soil organic matter (less than 1 percent) were conducive to nodule formation. It is

Table 1—Sites, locations, soil descriptions, and results of bioassay for mountain mahogany soils from Laramie County, Wyoming. Soil material from each horizon was planted with mountain mahogany seedlings that were examined after 10 months of growth. A sand and perlite mixture (8) was planted as a control (see text).

Site	Horizon	Depth	Surviving plants	Nodulation[a]	Mycorrhizae[b]	Average plant fresh weight[c]
		- - - *cm* - - -				- - - - - *g* - - - - -
1. On calcareous igneous colluvium (41°11’5” N.; 105°10’48” W.; 2,128 m, 15 percent north slope). Native vegetation: *Achnatherum hymenoides*, *Yucca glauca*, *Cercocarpus montanus* (nodulated extensively).	A	0 to 8	2	None	Variable From light to very high	3.01
	AC	8 to 30	2	None		.21
	C1	30 to 61	2	Yes		.08
	C2	61 to 91	3	Yes		.84
2. On mixed calcareous alluvium (41°11’5” N.; and 105°10’48”W., 2,134 m, 3 percent southwest slope). Native vegetation: *Agropyron* spp. and *C. montanus* (nodulated)	A	0 to 20	2	None	Variable From light to very high	4.56
	Bw	20 to 46	1	None		1.21
	C1	46 to 102	1	Yes		.06
	C2	102 to 152	2	None		.40
3. On red sandstone over white sandstone (41°11’5” N.; 105°10’48” W., 2,164 m, 20 percent west slope). Native vegetation: *C. montanus* (no nodules). Cr is hard, white sandstone.	A	0 to 8	2	None	Variable From light to very high	1.59
	AC	8 to 30	3	None		.08
	C	30 to 56	2	None		.05
	Cr	56+				
4. On very fine, noncalcareous sandstone (41°26’44” N., 104°40’22” W., 1,740 m, 20 percent north slope). Native vegetation: *Yucca glauca*, *Eriogonium* spp., *Phlox* spp., and nodulated *C. montanus*.	A	0 to 15	2	None	Variable From light to very high	.73
	AC	15 to 51	2	None		.25
	C1	51 to 122	1	Yes		.41
	C2	122 to 183	1	None		.31
5. On semicalcareous sandstone (41º26’44” N., 04º40’22” W., 1,749 m, 30 percent west slope). Native vegetation: *Yucca glauca*, *Phlox* spp., and nodulated *C. montanus*. Cr is semi-calcareous sandstone .	A	0 to 8	2	None	Variable From light to very high	.28
	AC	8 to 28	2	None		.42
6. On white sandstone (41°26’44” N.; 104°40’22” W., 1,750 m, 15 percent north slope). Native vegetation: *Bouteloua gracilis*, *Ribes* spp., *Gutierrezia* spp., and nodulated *C. montanus*. Cr is hard, calcareous sandstone.	A	0 to 8	2	None	Variable From light to very high	.38
	AC	8 to 66	1	None		.24
	C	66 to 102	1	None		.39
	Cr	102+				
7. On slightly calcareous sandstone (41°26’44” N.; 104°40’22” W., 1,747 m, 10 percent southeast slope). Native vegetation: mainly *Bouteloua gracilis* and *Yucca glauca*. No *C. montanus*. Cr is hard, calcareous sandstone.	A	0 to 15	2	None	Light Infection only	.39
	AC	25 to 30	2	None		1.37
	C	30 to 122	1	None		.07
	Cr	122+				
8. Sand; perlite mixture.	Control		2	None	No infection	.06

[a] None, no nodules. Yes, nodules on at least one plant.
[b] Ectomycorrhizae and endomycorrhizae were observed. Data not shown.
[a] Fresh weight of whole plants.

quite likely that the inhibitory effects of soil organic matter and nitrate are closely related. Formation of nodules and supplying them with photosynthate require considerable energy inputs from the plant. It is likely that when sufficient available nitrogen is present that feedback mechanisms in the plant block nodule formation. The presence of soil organic matter, which can be viewed as a form of potential labile nitrogen, may also block nodule formation. It has also been demonstrated that phenolic compounds, which are common components of soil organic matter, often inhibit activity of *Frankia*, the microbial causative agents of nodulation (Perradin and others 1983).

Excavation of these nodulated Rosaceous plants in the field needs to be done with care and attention to detail. Strategies for excavation should involve allowing sufficient time and input of energy into the excavation process, and excavation of mature plants may take even weeks to accomplish.

Often recording accurate morphological data of roots and nodules in the field can be done with some accuracy even if the plant is being destroyed. Certainly the value of such data is less with time as roots die, turgidity is lessened, and colors are muted. However, to claim that a plant is responding normally under such extreme conditions of stress is unjustified. Certainly, physiological data such as nitrogen fixation activity, root uptake function, or photosynthesis cannot be assumed to occur at normal rates while the plant is being stressed during excavation. However, what roots do in soil and what they do in unconsolidated or consolidated rock are likely different. Nodules often and perhaps most likely on some plants (for example, those of this report) occur very deep below the soil surface. Mycorrhizal associations may also occur very deeply in substrates. This poses a dilemma of how to observe belowground biological phenomena in field settings so that physical, chemical, and biological characteristics can be taken that are undistorted by the stress imposed on the biological system. Conversely, if a plant is minimally sampled to minimize or even eliminate stress on that plant, then there is uncertainty that the physical, chemical, or biological observations being made are accurate.

Nodules observed and acetylene reduction made of bitterbrush during the winter months indicated that although nodules gave visual appearance of activity, physiologically they were not active in nitrogen fixation. Given the time of year (winter), cold soil temperatures, and absence of photosynthetic organs on the plant tops (leaves), it is not surprising that the physiological function of the nodules was nil. However, given that excavation of the plant was not a normal condition of these plants, did excavation-induced stress mask the physiological phenomena? Given the low temperatures and shortened day length, it seems unlikely that physiological response was being masked by plant stress. A case might be made that plant physiological response may be more unfettered by excavation-induced stress during these winter months than during any other time of the year.

Evidence from the study where mountain mahogany was grown in soil materials derived from pedogenic horizons complements the work done and reported above, and suggests that soil properties (nitrate and soil organic matter) inhibit nodulation. The work corroborates the observation that mountain mahogany does not nodulate when in the presence of soil materials having high organic matter. However, it provides a little evidence that active factor(s) that cause nodulation reside within subsurface horizons very low in soil organic matter. Members of the genus *Frankia* are very slow growing (Callaham and others 1978; Stowers 1987). The fact that they would exist deep in soils, under low carbon regimes and in zones of low microbial activity and competition, is consistent with what we know about their growth habit in controlled cultures. However, the results of this part of the study really suggest only a hypothesis, not currently adequately challenged: *Frankia*, responsible as the microbial agent in nodulation of Rosaceous shrubs, are active only in subsoils low in carbon and nitrogen.

A principle that has emerged from this particular work is that there is a question that physiological measurements represent normal plant response when the plant is being stressed by the sampling process. Simultaneously, there is a question that an adequate sample has been collected, especially of root parameters, if the stress due to sampling is minimized or eliminated. Paradoxically, accurate measurements belowground that are reflective of a normal plant, cannot be made because the plant must be stressed to make such measurements. If the relationship between carbon fixation and nitrogen fixation can be determined, then monitoring carbon fixation during the excavation of the plant can, at least theoretically, provide a means to correct nitrogen fixation levels.

References

Allen, M. F. 1991. The ecology of mycorrhizae. Cambridge Studies in Ecology (series). Cambridge University Press. 184 p.

Allison, L. E. 1965. Organic carbon. In: Black, C. A., ed. Methods of Soil analysis. Agronomy 9: 1367–1378.

Bower, C. A.; Wilcox, L. V. 1965. Soluble salts. In: Black, C. A., ed. Methods of soil analysis. Agronomy. 9: 933–951.

Callaham, D.; Tredici, P. Del; Torrey, J. G. 1978. Isolation and cultivation *in vitro* of the actinomycete causing root nodulation in *Comptonia*. Science. 199: 899–902.

Dalton, D. A.; Zobel, D. B. 1977. Ecological aspects of nitrogen fixation by *Purshia tridentata*. Plant and Soil. 48: 57–80.

Joukowsky, M. 1980. A complete manual of field archaeology, tools and techniques of field work for archaeologists. Prentice-Hall, Inc. 630 p.

Kummerow, J.; Alexander, J. V.; Neel, J. W.; Fishbeck, K. 1978. Symbiotic nitrogen fixation in *Ceanothus* roots. American Journal of Botany. 65: 63–69.

Marx, D. H. 1972. Ectomycorrhizae as biological deterrents to pathogenic root infections. Annual Review of Phytopathology. 10: 429–454.

Oien, A.; Olsen, A. R. 1969. Nitrate determination in soil extracts with the nitrate electrode. Analyst. 94: 888–884.

Perradin, Y.; Mottet, M. J.; Lalonde, M. 1983. Influence of phenolics on in vitro growth of *Frankia* strains. Canadian Journal of Botany. 61: 2807–2814.

Peterson, G. A.; Williams, S. E.; Moser, L. E. 1991. Chapter 18. Inorganic fertilizer use and its effects on semiarid and arid region soils. In: Skujins, J., ed. Semiarid lands and deserts: soil resource and reclamation. Marcel Dekker: 543–580.

Reckner, R. 1998. Soil survey of Albany County area, Wyoming. U.S. Department of Agriculture, Natural Resource Conservation Service, Forest Service, and Bureau of Land Management; and The University of Wyoming Agricultural Experiment Station. 540 p. plus maps.

Roskams, S. 2001. Excavation. Cambridge manuals in archaeology. Cambridge University Press. 311 p.

Soil Survey Staff. 1999. Soil taxonomy: a basic system of soil classification for making and interpreting soil surveys, 2d ed. Agric. Handb. 436. Washington, DC: U.S. Government Printing Office.

Stahl, P. D.; Schuman, G. E.; Frost S. M.; Williams, S. E. 1998. Arbuscular mycorrhizae and water stress tolerance of Wyoming big sagebrush seedlings. Soil Science Society of America Journal. 62: 1309–1313.

Stevenson, A. 2001. Soil survey of Laramie County, Western Part. U.S. Department of Agriculture, Natural Resource Conservation Service; and The University of Wyoming Agricultural Experiment Station. 355 p. plus maps.

Stowers, M. D. 1987. Chapter 2. Collection, isolation, cultivation, and maintenance of *Frankia*. In: Elkans, G. H., ed. Symbiotic nitrogen fixation technology. Marcel Dekker, Inc.: 29–53.

Tiedemann, A. R. 1983. Response of bitterbrush and associated plant species to broadcast nitrogen, phosphorus, and sulfur fertilization. In: Tiedemann and Johnson, eds. Proceedings—research and management of bitterbrush and cliffrose in Western North America. Gen. Tech. Rep. INT-152. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station: 240–254.

Thien, S. J. 1979. A flow diagram for teaching texture-by-feel analysis. Journal of Agronomy. 8: 54–55.

Upchurch, R. G. 1987. Chapter 12. Estimation of bacterial nitrogen fixation using acetylene reduction. In: Elkan, Gerald H., ed. Symbiotic nitrogen fixation technology. Marcel Dekker, Inc.: 289–305.

Wantanabe, F. S.; Olsen, R. S. 1965. Test of an abscorbic acid method for determining phosphorus in water and $NaHCO_3$ extracts from soil. Proceedings: Soil Science Society of America. 29: 677–678.

White, J. A.; Williams, S. E. 1985. Symbiotic N2-Fixation by Frankia: Actinorrhizae establishment on disturbed lands. Proceedings. Denver, CO: American Society of Surface Mining and Reclamation, National Conference: 289–297.

Williams, S. E. 1979. Vesicular-arbsucular mycorrhizae associated with actinomycete-nodulated shrubs, *Cercarpus montanus* Raf. and *Purshia tridentata* (Pursh) DC. Botanical Gazette. 140(s): S115–S119.

Germination and Seedling Establishment

Ipomopsis spicata ssp. *robruthii*

Illustration on the reverse side is by Walt Fertig. In: Wyoming Natural Diversity Database. 2000. Available at: http://www.uwyo.edu/wyndd (Accessed 12/18/03).

Cultural Methods for Enhancing Wyoming Big Sagebrush Seed Production

D. T. Booth
Y. Bai
E. E. Roos

Abstract: Demand for sagebrush seed is expanding, but wildland harvesting is impaired by several factors including loss of stands to weed invasions and fire. To increase the potential for seed production, sagebrush seed harvests were compared among cultural treatments for stands on a coal mine near Glenrock, WY. Sagebrush in the study were mature plants on unmined rangeland (age unknown) and 5- to 20-year-old plants on reclaimed land. Plants on mined land protected by 1- by 1- by 1-m fence of 2.5-cm wire net had a 3-year average seed yield of 20.7 g per plant compared to 5.2, 1.4, and 0.9 g per plant from plants on unmined-fenced, mined-unfenced, and unmined-unfenced rangelands. Fencing prevented browsing by herbivores and had a beneficial influence on plant microclimate. Seed weight was greater where mulch or other treatments mitigated environmental stress. We conclude that the quantity and quality of Wyoming big sagebrush seed harvest can be increased for existing stands, particularly those on mined land, by protecting the plants from large-animal herbivory and by using methods such as windbreaks and fabric mulch to mitigate the effects of drought.

Introduction

Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* [Beetle & Young]) is used for ecological restoration of areas disturbed by fire, mining, cropping and other situations requiring artificial revegetation with native shrubs. That use has made Wyoming big sagebrush seed a regionally important specialty crop with a history of sustained demand over more than a decade (R. Dunne, CEO, Wind River Seed, personal communication; J. Johansen, Natural Resource Specialist, BLM Regional Seed Warehouse - Boise District, personal communication). While the demand for seed has been steadily increasing, native stands suitable for seed harvesting have been steadily decreasing due to fire and invasion by weeds. The situation suggests a need to manage selected sagebrush stands, such as those on reclaimed mined lands, for improved seed production. Here we review work conducted to access the quality and quantity of seed that could be harvested from existing stands of sagebrush at the Dave Johnston Coal Mine near Glenrock, WY (Booth and others 2003).

Study Site Description

The Dave Johnston Coal Mine is 40 km east of Casper, WY, at an elevation of 1,646 m. The mean annual precipitation is 328 mm and the mean annual temperature is 8.8 °C (Martner 1986; Owenby and Ezell 1992) with an average 123 frost-free days per year. Soil parent material is Cretaceous clay shale (Young and Singleton 1977). Five sites were located on the mine where mined-land sagebrush stands were in close proximity to stands of sagebrush on unmined rangeland. These sites ranged in age from 5 to more than 20 years at the start of the study (table 1).

Experimental Design and Treatments

The experimental design was a split plot, 2 by 2 factorial replicated among the five sites with whole plots being mined and unmined land at each site and subplots being cultural treatments. Cultural treatments were assigned to single sagebrush plants selected for uniformity and are described as follows: (1) understory plants were cut to ground level, and a 1-m^2 piece of fabric mulch (Appleton and others 1990) was installed around the base of the plant; (2) a windbreak of fabric mulch was erected on the north and west side of the plant, (3) both mulch and a windbreak were installed, and (4) the selected plant was not treated (neither windbreak nor mulch). Three subsamples (individual plants) were used for each treatment combination. Treatments were installed in July 1995.

A 1-m^2 by 1-m-high fence of 2.54-cm wire net was placed around plants selected for treatment. Fenced plants were paired with a similar-size, unfenced, untreated adjacent plant (table 1). Our test included an evaluation of any effects of the wire net because we needed to protect experimental plants from browsing wildlife, and we needed to measure the effect of our protective measures.

Soil moisture was measured using gypsum blocks buried to 10 cm below the soil surface and beneath the canopy of treated plants. The blocks were read midmonth, May through

---

In: Hild, Ann L.; Shaw, Nancy L.; Meyer, Susan E.; Booth, D. Terrance; McArthur, E. Durant, comps. 2004. Seed and soil dynamics in shrubland ecosystems: proceedings; 2002 August 12–16; Laramie, WY. Proceedings RMRS-P-31. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

D. T. Booth is a Rangeland Scientist, USDA-ARS, High Plains Grasslands Research Station, 8408 Hildreth Road, Cheyenne, WY 82009, U.S.A., e-mail: tbooth@lamar.colostate.edu. Y. Bai is an Assistant Professor, Department of Plant Sciences, University of Saskatchewan, 51 Campus Drive, Saskatoon, Saskatchewan S7N 5A8, Canada. E. E. Roos is Assistant Area Director, USDA-ARS, Northern Plains Area, 1201 Oakridge Dr., Fort Collins, CO, 80525, U.S.A., formerly Research Leader and Plant Physiologist, National Seed Storage Laboratory.

Table 1—Experimental variables used in sagebrush seed production study.

Variable (number and identification)
Sites (5; Fuel Island, Entry 50, 110 School, 60 Badger, 4 School)
Whole plots (2; mined and unmined)
Subplots (4 treatments x [3 subsamples + 3 paired plots] = 24 as indicated below)
Mulch plots with paired untreated and unfenced plots (3 + 3)
Windbreak plots with paired untreated and unfenced plots (3 + 3)
Mulch + windbreak plots with paired untreated and unfenced plots (3 + 3)
Control plots with paired untreated and unfenced plots (3 + 3)

September 1996 through 1998. The data were analyzed by month across the 3 years of the study.

Seeds were harvested annually in late October or early November 1996 through 1998. Data collected included number of seed stalks and bulk weight of seeds produced per plant; and seed weight, moisture content at harvest, germination, and seedling vigor. Seed quality tests used 20 seeds per plant or the maximum number of seeds available if less than 20. The methods used for seed-quality testing are described elsewhere (Bai and others 1997; Booth and Griffith 1994; Booth and others 2003). We used the "Mixed" procedure in SAS to test for differences among variables and the "differences" option to compare least-square means (Littell and others 1996; SAS 1996). Protective fencing was evaluated in separate analyses as a subplot effect (table 2).

Results

Seed Yield

To our surprise, more seed was harvested from mined land than from adjacent unmined rangeland. There was no difference between mined and unmined land in the number of seed stalks counted at seed harvest, but plants on mined land yielded more seed in all 3 years of the study. The extent of the harvest was a factor of protective fencing. Fence-protected plants produced greater seed stalk numbers (table 3), and greater seed yield per plant (bulk weight). Protected plants on mined land yielded 3 to 6 times more seed than protected plants on unmined land (fig. 1).

Compared to the effects of land type and fencing, mulch and windbreak had a relatively minor effect on yield. Mulch was a significant ($P \leq 0.10$) factor in only 1 year and then as part of a three-way interaction (table 4). Windbreak interacted with other factors to have a significant influence ($P \leq 0.10$) on seed yield in 2 of the 3 years.

Seed Quality

Fenced plants produced heavier seeds in 1996 and 1997, but not in 1998 (table 3). Average seed dry weight had some influence of land x mulch in 1997 and mulch in 1998 (table 5). Seed moisture at harvest was similar among cultural treatments, but fenced plants consistently had higher seed moisture than unfenced plants (table 3). This may indicate residual food storage activity in the seeds, and may account for the trend for fenced plants to produce heavier seeds.

We found no differences in germination or dormancy due to treatments, fencing, or types of land. Mean germination percentages ranged between 39 and 92 percent from unmined land, and between 77 and 92 percent from mined land. Percentage dormant seeds (those that did not germinate but remained firm throughout the test period) ranged from 3.5 to 23.7 percent in 1996, 1.0 to 6.8 percent in 1997, and 1.2 to 8.4 percent in 1998. (Note the tendency for a correlation between increasing seed dormancy with lower seed yield [compare dormancy range with fig. 1]. It would be interesting to learn if this apparent correlation is real.)

Means for seedling axial length in our test of seed vigor ranged from 23 to 34 mm. There were no differences due to land or fencing in 1997 or 1998 ($P \geq 0.57$), and in 1996 there were not enough seeds harvested to compare treatments.

Table 2—Example programs, with model statements, as submitted to SAS for fenced, and fenced-versus-unfenced plot analysis.

Fenced

```
Proc mixed;
Class site land mulch windbreak replication;
Model bulk weight =
   Land
   Mulch
   Land x mulch
   Land x windbreak
   Land x mulch x windbreak;
Random site; site x land
lsmeans land mulch x windbreak
   Land x mulch x windbreak/difference; run
```

Fenced versus unfenced

```
Proc mixed;
Class site land fence replication;
Model bulk weight =
   Fence
   Land
   Land x fence;
Random site; site x land
lsmeans fence land x fence/difference; run
```

Table 3—Effect of protective fencing on means of sagebrush seed stalks per plant, weight of sagebrush seeds, and seed moisture 1996 to 1998. The observed significance level is given for each pair of means.

	1996		1997		1998	
Variable	**Fenced**	**Unfenced**	**Fenced**	**Unfenced**	**Fenced**	**Unfenced**
Number seed-stalks	22	4	56	10	76	15
OSL[a] (df = 48)	$P < 0.01$		$P < 0.01$		$P < 0.01$	
Seed weight (mg per seed)	0.1507	0.0708	0.2483	0.1422	0.2325	0.1916
OSL[a] (df = 48)	$P = 0.01$		$P < 0.01$		$P = 0.29$	
Seed moisture (percent)	3.9	1.3	5.6	3.1	4.0	2.5
OSL[a] (df = 48)	$P < 0.01$		$P < 0.01$		$P = 0.02$	

[a] Observed significance level.

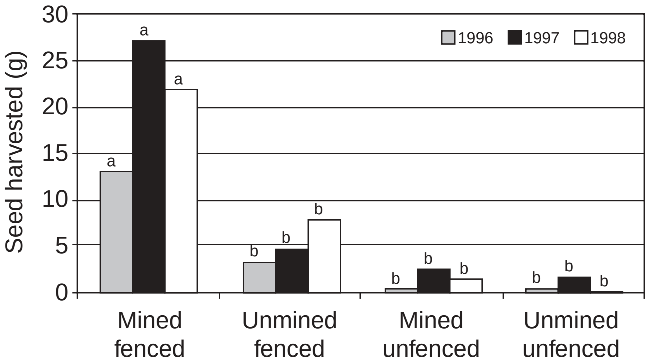


Figure 1—Mean bulk weight of sagebrush seeds per plant by year as affected by type of land and protective fencing. The OSL for the land x fence interaction was $P = 0.03$, 0.03, and 0.05 in 1996, 1997, and 1998. Means within a year followed by the same letter are not different at $P \leq 0.05$ as indicated by differences in least square means within the "Mixed" statistical procedure (SAS 1996).

Table 4—Mean bulk weight of sagebrush seeds per fenced plant by year as affected by type of land, mulch, and windbreak[a].

Year	Land status	Mulch	Windbreak	Bulk weight seeds
				- - *g* - -
1996	Mined	yes	No	25.5a
	Mined	No	Yes	21.8ab
	Mined	No	No	13.0b
	Mined	Yes	Yes	12.7b
	Unmined	Yes	Yes	4.3b
	Unmined	Yes	No	3.9b
	Unmined	No	No	3.1b
	Unmined	No	Yes	2.4b
1997	Mined	–	No	29.9a
	Mined	–	Yes	20.1b
	Unmined	–	Yes	8.6b
	Unmined	–	No	6.0b
1998	Mined	–	–	19.1 ($P = 0.10$)
	Unmined	–	–	4.4

[a] Observed significance level: 1996 land x mulch x windbreak $P = 0.06$; 1997 land x windbreak $P = 0.07$; and 1998 land $P = 0.10$; df: land = 4, windbreak = 102, mulch = 102, interactions = 104. Means within a year followed by the same letter are not different at $P < 0.05$ as indicated by differences in least-square means within the "Mixed" statistical procedure (SAS 1996).

Soil Moisture (Fenced Plants Only)

Soil moisture in May was influenced by site x land x mulch ($P = 0.05$), land x mulch x windbreak ($P < 0.01$), year x mulch ($P < 0.05$), year x land ($P < 0.01$, and year x site ($P < 0.01$). The interactions with site and year were expected. The three-way interactions (table 6) reveal that mined-land soils had soil moisture equal to or greater than that of unmined lands. The greatest soil moisture occurred on mined land with mulch and windbreak.

June soil moisture interactions were site x land ($P = 0.02$), year x mulch ($P = 0.04$), and year x site ($P < 0.01$). The site x land data again indicated that mined-land soil moisture was equal to, or greater than that of unmined lands (table 7). There were no differences in main effects or interactions for July ($P \geq 0.83$), and year x site was the only significant interaction in August and September ($P < 0.01$ for both months).

Plant Mortality

There were three mined-land plants in the study that died at 110 School (12.5 percent) and 11 that died at 60 Badger (46 percent). (Note the high soil moisture for mined land at 60 Badger [table 7].) All mortality during the 3 years occurred on mined land; there was no mortality at any of the other study sites.

Table 5—Seed quality: mean weight of sagebrush seeds by year as affected by land type and mulch[a].

Year	Land status	Mulch	Seed weight	OSL[b]
			- - -*mg* - - -	
1996	Mined	–	0.21	$P = 0.22$
	Unmined	–	0.11	
1997	Unmined	Yes	0.33a	$P = 0.09$
	Mined	Yes	0.28ab	
	Mined	No	0.27ab	
	Unmined	No	0.24b	
1998	–	Yes	0.28	$P = 0.09$
	–	No	0.24	

[a] Multiple means within a year followed by the same letter are not different at $P < 0.05$ as indicated by differences in least-square means using the "Mixed" statistical procedure (SAS 1996). Degrees of freedom: land = 4, mulch = 104, windbreak = 104, interactions = 104.

[b] OSL = Observed significance level.

Table 6—Mean percentage soil moisture for May averaged over 5 years and as affected by land, mulch, and windbreak.

Windbreak	Mulch	Mined	Unmined	OSL[a] for land
		- - - - *percent* - - - -		
Yes	Yes	72.8	62.6	<0.01
Yes	No	59.6	55.6	.09
	OSL for mulch	<0.01	<0.01	
No	Yes	69.3	66.5	.29
No	No	69.7	58.4	<0.01
	OSL for mulch	.87	<0.01	

[a]Observed significance level.

Table 7—Mean percentage soil moisture for June averaged over 3 years as affected by site and land.

Site	Mined	Unmined	OSL[a] for land
	- - - - - - *percent* - - - - - - -		
Fuel Island	20	16	0.55
Entry 50	36	27	.16
110 School	31	37	.36
60 Badger	70	45	<0.01
4 School	35	21	.03

[a]Observed significance level.

Discussion

Why Were Seed Yields Greater on Mined Versus Unmined Land?

Seed yields from fenced plants on mined land were consistently greater than for other treatment combinations. This may have been due to soil moisture, which was usually greater under mined-land plants in May and June. Why these soils contained more moisture is a matter for speculation. Conceivably plant density—either of shrubs or of all plants—was lower on mined land. Plant density often affects seed yield and differences in soil moisture may be only one aspect of that affect (Henderson and others 2000; Holen and others 2001; Lopez-Bellido and others 2000; USDA 1961). Given that seed quality as measured by seed weight, seed moisture, germination, and seedling vigor (axial length) was not affected by land status, the greater seed yield for mined land suggests seed producers might wish to direct cultural efforts to mined-land stands.

Fenced and Unfenced Plants

It is clear that large herbivores reduced seed production by eating seed stalks (table 4). Wagstaff and Welch (1991) also reported that protected sagebrush plants produce significantly more seed stalks than plants not protected from grazing animals. We recognize that protective fencing modified the environment in favor of the protected plants. However, the report of Gores (1995), and personal observations of the effects of wildlife on mined-land shrub stands suggest the bias was relatively insignificant and should not be used to underrate wildlife herbivory as a factor limiting seed production of mined-land sagebrush.

Environmental Modification by Fence, Windbreak, and Mulch

We found that surrounding a sagebrush plant with wire netting (fenced) resulted in a beneficial modification of its environment as evident by greater seed weights from protected plants (table 4). This was not expected, especially with the large (2.54-cm) net used. The fencing affect may account for the minimal effect of mulch and windbreak on seed production and quality. Mulch and windbreak did influence seed production and quality, but these effects were not consistent. The mulch, due to its small size (1 m^2), did not always result in greater soil moisture (table 7). A larger piece of fabric would have shown a more consistent benefit to soil moisture, shrub growth, and seed production (Booth, unpublished data).

Conclusions and Recommendations

Wyoming big sagebrush on reclaimed mined lands similar to those of the Dave Johnston Coal Mine have the potential to produce more seeds than plants from adjacent unmined land. However, the mined-land seed-production advantage will be realized only when the plants are protected from browsing wildlife. Environmental modification—particularly the use of fabric mulch—can also improve seed production and some factors of seed quality, but these efforts are viewed as secondary to that of excluding browsing animals.

Acknowledgments

The work was supported in part by the Abandoned Coal Mine Lands Research Program at the University of Wyoming. Support was administered by the Wyoming Department of Environmental Quality from funds returned to Wyoming from the Office of Surface Mining of the U.S. Department of the Interior. The authors thank C. Skilbred, Sr., Environmental Scientist for Glenrock Coal Company for cooperation in this study and L. W. Griffith for technical assistance.

References

Appleton, B. L.; Derr, J. F.; Ross, B. B. 1990. The effect of various landscape weed control measures on soil moisture and temperature, and tree root growth. Journal of Arboculture. 16: 264–268.

Bai, Y.; Booth, D. T.; Roos, E. E. 1997. Effect of seed moisture on Wyoming big sagebrush seed quality. Journal of Range Management. 50: 419–422.

Booth, D. T.; Bai, Y. 1999. Effects of imbibition temperature on seedling vigor: comparison among crops and rangeland shrubs. Journal of Range Management. 52: 534–538.

Booth, D. T.; Bai, Y.; Roos, E. E. 2003. Wyoming big sagebrush seed production from mined and unmined rangelands. Journal of Range Management. 56: 542–546.

Booth, D. T.; Gores, J. K.; Olson, R. A.; Schuman, G. E. 1999. Shrub densities on pre-1985 reclaimed mine lands in Wyoming. Restoration Ecology. 7: 24–32.

Booth, D. T.; Griffith, L. W. 1994. Measuring post-germination growth. Journal of Range Management. 47: 503–504.

Gores, J. D. 1995. The evaluation of big sagebrush and fourwing saltbush establishment on pre-1985 Wyoming reclaimed mine sites. Laramie: University of Wyoming. 150 p. Thesis.

Henderson, T. L.; Johnson, B. L.; Schneiter, A. A. 2000. Row spacing, plant population, and cultivar effects on grain amaranth in the Northern Great Plains. Agronomy Journal. 92: 329–336.

Holen, D. L.; Bruckner, P. L.; Martin, J. M.; Carlson, G. R.; Wichman, D. M.; Berg, J. E. 2001. Response of winter wheat to simulated stand reduction. Agronomy Journal. 93: 364–370.

Littell, R. C.; Milliken, G. A.; Stroup, W. W.; Wolfinger, R. D. 1996. SAS system for mixed models. Cary, NC: SAS Institute, Inc.

Lopez-Bellido, L.; Fuentes, M.; Castillo, J. E. 2000. Growth and yield of white lupine under Mediterranean conditions. Agronomy Journal. 92: 200–205.

Lyford, M. E. 1995. Shrub establishment on drastically disturbed lands. Laramie: University of Wyoming. 84 p. Thesis.

Martner, B. E. 1986. Wyoming climate atlas. Lincoln: University of Nebraska Press.

Owenby, J. R.; Ezell, D. S. 1992. Monthly station normals of temperature, precipitation, and heating and cooling degree days, 1961–1990 for Wyoming. Asheville, NC: National Climatic Data Center.

SAS. 1996. SAS/STAT software: changes and enhancements through release 6.11. Cary, NC: SAS Institute, Inc.

USDA. 1961. Seeds—the yearbook of agriculture. Washington, DC: U.S. Government Printing Office.

Wagstaff, F. J.; Welch, B. L. 1991. Seedstalk production of mountain big sagebrush enhanced through short-term protection from heavy browsing. Journal Range Management. 44: 72–74.

Young, J. F.; Singleton, P. C. 1977. Wyoming general soil map. Wyoming Agricultural Experiment Station Bulletin. Research Journal 117. Laramie: University of Wyoming.

Seeds of Success and the Millennium Seed Bank Project

Ann DeBolt
Carol S. Spurrier

Abstract: The Bureau of Land Management (BLM) entered into an agreement with the Royal Botanic Gardens, Kew (RBG, Kew), to collect seeds from native plants in the Western United States. This program, initiated in 2000, is called "Seeds of Success." It is an offshoot of the international "Millennium Seed Bank" project. The goal of the Millennium Seed Bank project is to collect seed from10 percent of the world's dryland flora and place it in long-term storage. For the BLM, this was an opportunity to evaluate additional native pant materials for restoration projects and to place seed in long-term storage for conservation. Collection targets included native species: of known forage or browse value, widespread regional endemics, wild relatives of cultivated or economically important species, species with significance to Tribes, monotypic species, relatives of rare species, relatives of nonnative invasive species, species of known pollinator importance, and flagship species such as State flowers and trees. RBG, Kew, and the BLM developed a seed collecting protocol at the population level. In 2002, the first collecting season, BLM gathered seed from 375 taxa in 11 States. Seed is currently in long-term storage at RBG, Kew, and the USDA National Seed Storage Laboratory in Fort Collins, CO.

Introduction

The Royal Botanic Gardens, Kew (RBG, Kew), has initiated a worldwide seed collection program called the "Millennium Seed Bank" project. It is a multiyear project funded by the United Kingdom Millennium Trust with a goal of collecting and conserving at least 10 percent of the world's flora (approximately 24,000 species) by the year 2010. Fourteen countries around the world are currently participating in the project. The Bureau of Land Management (BLM) participates with the RBG, Kew, and the Plant Conservation Alliance in an offshoot program named "Seeds of Success." The goal of Seeds of Success is multifold. Establishing a high-quality, accurately identified, and well-documented native seed collection at the USDA National Seed Storage Laboratory (NSSL) in Fort Collins, CO, with a backup collection at the Millennium Seed Bank, is a major objective. Additional, equally important objectives are to identify important native species for restoration of public lands, and to obtain information on the quality, viability, and germination requirements of those species.

The BLM was an obvious choice for RBG, Kew, to contact given the extensive arid regions the agency manages. The BLM and RBG, Kew, participate in the Seeds of Success program under the terms of a cooperative agreement signed by both parties in May 2000. The BLM agreed to collect seeds for the project and to grant access to the lands they manage for collection; to grant prior informed consent to RBG, Kew, for study and long-term storage of these seeds; and to send all seeds and vouchers to Kew. RBG, Kew, agreed to clean, process, test, and store all seed sent by the BLM; to return half of each collection to the United States for long-term storage; to provide the BLM with all testing results; to fund a fixed-term coordinator position in BLM to develop the collection program; and to provide training and advice to BLM during the project.

RBG, Kew, is interested in seed banking a range of species for long-term conservation of genetic material in support of the Convention on Biodiversity, and because their funding is partly provided by their ability to seed bank at the species level. Given that seeds from the majority of arid land plants in the United States are expected to survive conventional germplasm bank conditions (that is, drying to low moisture content and freezing at –20 °C), land managers can rely on conserved seed samples for use in plant conservation and restoration programs. As BLM collects seeds for restoration across the range of the species, they work with local seed growers to ensure that private businesses are given the opportunity to use and market native plant materials originating from the project.

As a multiple-use agency, the BLM has a need for native plant materials for many different programs. One of the goals set forth in the BLM's mission statement is to restore at-risk resources and to maintain or improve functioning ecosystems. In 1999 and 2000, wildfires burned more than 3 million acres, creating a demand that far exceeded the supply of native species. Fires often increase establishment of exotic, invasive species, and vast acreages are in need of restoration. Native seed is needed for BLM's fuels reduction program, for prescribed fire planning and implementation, and for the Great Basin Restoration Initiative. Wildlife enhancement programs, particularly those for threatened or endangered species, require native seed. Supplying energy is currently a priority activity for BLM, and native plant materials are needed for mitigation in mining reclamation and oil and gas exploration activities, and for nonenergy-related rights-of-way restoration such as communication lines and new roads. The newly designated national monuments have requirements for the use of native plant species

---

In: Hild, Ann L.; Shaw, Nancy L.; Meyer, Susan E.; Booth, D. Terrance; McArthur, E. Durant, comps. 2004. Seed and soil dynamics in shrubland ecosystems: proceedings; 2002 August 12–16; Laramie, WY. Proceedings RMRS-P-31. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Ann DeBolt is Botanist at the U.S. Forest Service, Rocky Mountain Research Station, 316 East Myrtle, Boise, ID 83702, U.S.A.; e-mail: a.debolt@fs.fed.us. Carol S. Spurrier is Botany Program Lead at BLM's Washington Office, 1849 C Street NW, Washington, DC 20240, U.S.A.

inside monument boundaries. Seeds of Success can help to successfully build a native plant materials program across the United States. It will also enhance the seed conservation capacity currently available within the United States, principally at the USDA NSSL in Fort Collins, CO.

Methods

The collecting focus for Seeds of Success is on species needed for ecological restoration of public lands, native plant material development, and conservation of widespread species. Target species lists were developed using The Nature Conservancy's ecoregions and included native species of known forage or browse value, widespread regional endemics, wild relatives of cultivated or economically important species, species with significance to Tribes, monotypic species, relatives of rare species, relatives of nonnative invasive species, species of known pollinator importance, and well-known species that the public can easily identify, such as State flowers and trees.

According to Brown and Marshall (1995), at least one copy of 95 percent of the alleles occurring in a population at frequencies of greater than 0.05 can be achieved by sampling from:

1. 30 randomly chosen individuals in a fully outbreeding sexual species, or
2. 59 randomly chosen individuals in a self-fertilizing species.

Because the reproductive biology of most target species has not been studied, and the capture of rarer alleles would require a markedly increased sample size, collectors are advised to sample from in excess of 50 individuals within a single population, and to look for populations with larger numbers of plants. For Seeds of Success, it was determined that an "ideal" collection would be from 100 to 500 individuals and contain 10,000 to 20,000 seeds. Each Western State was assigned a target number of species to collect during the first year. To help accomplish this, the Student Conservation Association (SCA) partnered with BLM and hired teams of three to four interns to work with botanists in five States, including California, Idaho, Oregon, Nevada, and Utah (fig. 1). The BLM also entered into a cooperative agreement with the Center for Plant Conservation to use their seed collection expertise in reaching BLM's goal of collecting 2,000 species over the next 10 years.

Once target species were identified, but before seed could be collected, potential sites were visited to assess the population size, collect a herbarium voucher for species verification (nomenclature follows Kartesz and Meacham 1999), evaluate presence of insect damage, and estimate seed production and maturation date. Seed collection protocols are as follows:

1. Carefully examine a small, representative sample of seeds using a cut test to estimate the frequency of empty or damaged seeds, and to confirm that the majority of seeds are mature. Repeat cut tests throughout the sampling to ensure seed quality across the population.
2. Collect mature, dry seeds into either cloth or brown paper bags. Large collections could be made using plastic buckets, for later transfer.
3. If seeds can be liberated from their fruits quickly and easily, do so and record this on the data form. Cleaning should generally be left to RBG, Kew, staff.
4. Collect fleshy fruits into plastic bags and allow to aerate. Contact RBG, Kew, right away for specific advice on ripening and cleaning, as these fruits decompose rapidly and poor storage can lead to mold-infested seed.
5. Sample equally and randomly across the extent of the population, maintaining a record of the number of individuals sampled.
6. Collect no more than 20 percent of the viable seed available on the day of collection.
7. Collect from populations that allow removal of 10,000 to 20,000 viable seeds.
8. For each collection, estimate and record the viable seed production per fruit, per individual, and per population.

Figure 1—Student Conservation Association interns collecting seed in Idaho for the Bureau of Land Management Seeds of Success program.

After collecting, seeds were kept in a cool, dry place prior to shipping to the seed bank. Voucher specimens and data forms were shipped with the seed to RBG, Kew, typically within a few days. Data recorded for each population included species name, collector name(s), location (narrative description plus latitude/longitude), elevation, habitat, landform, parent material, slope, soil texture, number of plants sampled, an estimate of the total population size and area, and the number of duplicate voucher specimens made. The location of each population was recorded with a Global Positioning System (GPS) unit, and digital photos of each species and its seed were taken. After cleaning and testing, half of each sample shipped to the RBG, Kew, seed bank will return to the United States for native plant materials development or long-term storage.

Results

Seed from 375 native taxa were collected in 2002, the first year of implementation for Seeds of Success (table 1). Taxa collected in more than one state are listed as such. Student Conservation Association intern teams assisted in five of the 11 States where collections were made, and

Table 1—Taxa and State of origin for 2002 native seed collections for the Bureau of Land Management's Seeds of Success program. Seed is currently in long-term storage at RBG, Kew, as part of the international Millennium Seed Bank project, or in the Bureu of Land Management's native plant materials development program.

Family	Genus	Species	State
Aceraceae	*Acer*	*negundo*	UT
Anacardiaceae	*Rhus*	*trilobata*	UT
Anacardiaceae	*Rhus*	*trilobata* v. *trilobata*	CO
Apiaceae	*Angelica*	*kingii*	NV
Apiaceae	*Cnidium*	*cnidiifolium*	AK
Apiaceae	*Heracleum*	*lanatum*	CA
Apiaceae	*Lomatium*	*dissectum*	ID
Apiaceae	*Lomatium*	*grayi*	ID
Apiaceae	*Lomatium*	*macrocarpum*	CA
Apiaceae	*Lomatium*	*nudicaule*	CA
Apiaceae	*Lomatium*	*nuttallii*	CO
Apiaceae	*Lomatium*	*triternatum*	CA
Apiaceae	*Osmorhiza*	*berteroi*	OR
Apiaceae	*Perideridia*	*bolanderi*	OR
Asclepiadaceae	*Asclepias*	*cryptoceras*	OR
Asclepiadaceae	*Asclepias*	*speciosa*	ID
Asteraceae	*Achillea*	*millefolium*	CA
Asteraceae	*Achillea*	*millefolium* v. *occidentalis*	OR
Asteraceae	*Agoseris*	*glauca* v. *glauca*	OR
Asteraceae	*Agoseris*	*heterophylla*	OR
Asteraceae	*Ambrosia*	*eriocentra*	NV
Asteraceae	*Antennaria*	*monocephala*	AK
Asteraceae	*Arnica*	*chamissonis* ssp. *foliosa*	CA
Asteraceae	*Arnica*	*cordifolia*	OR, UT
Asteraceae	*Arnica*	*lessingii* ssp. *lessengii*	AK
Asteraceae	*Arnica*	*longifolia*	UT
Asteraceae	*Artemisia*	*tridentata* v. *tridentata*	UT
Asteraceae	*Artemisia*	*arctica* ssp. *arctica*	AK
Asteraceae	*Artemisia*	*suksdorfii*	CA
Asteraceae	*Artemisia*	*tilesii* ssp.*elatior*	AK
Asteraceae	*Aster*	*pauciflorus*	NV
Asteraceae	*Baccharis*	*pilularis*	OR
Asteraceae	*Balsamorhiza*	*hookeri*	ID
Asteraceae	*Balsamorhiza*	*macrophylla*	UT
Asteraceae	*Balsamorhiza*	*sagittata*	CA, ID
Asteraceae	*Balsamorhiza*	*serrata*	OR
Asteraceae	*Bebbia*	*juncea*	NV
Asteraceae	*Blepharipappus*	*scaber*	CA, OR
Asteraceae	*Brickellia*	*incana*	NV
Asteraceae	*Brickellia*	*oblongifolia*	NV
Asteraceae	*Chaenactis*	*douglasii*	ID
Asteraceae	*Chrysothamnus*	*humilis*	OR
Asteraceae	*Cirsium*	*cymosum*	CA
Asteraceae	*Cirsium*	*mohavensis*	NV
Asteraceae	*Crepis*	*acuminata*	ID
Asteraceae	*Encelia*	*virginensis*	NV
Asteraceae	*Erigeron*	*bloomeri*	ID
Asteraceae	*Erigeron*	*disparipilus*	ID
Asteraceae	*Erigeron*	*glaucus*	CA
Asteraceae	*Erigeron*	*peregrinus*	AK
Asteraceae	*Erigeron*	*pumilus*	ID
Asteraceae	*Erigeron*	*speciosus*	UT
Asteraceae	*Eriophyllum*	*lanatum* v. *grandiflorum*	CA
Asteraceae	*Eriophyllum*	*lanatum* v. *integrifolium*	CA
Asteraceae	*Eriophyllum*	*staechadifolium*	CA
Asteraceae	*Eurybia*	*radulina*	OR
Asteraceae	*Eurybia*	*sibirica*	AK
Asteraceae	*Grindelia*	*squarrosa*	UT
Asteraceae	*Helianthella*	*uniflora*	UT
Asteraceae	*Heterotheca*	*villosa*	CO, UT
Asteraceae	*Hieracium*	*triste*	AK

(con.)

Table 1—(Con.)

Family	Genus	Species	State
Asteraceae	*Hymenoxys*	*cooperi*	NV
Asteraceae	*Isocoma*	*drummondii*	UT
Asteraceae	*Iva*	*acerosa*	UT
Asteraceae	*Microseris*	*troximoides*	ID, OR
Asteraceae	*Petasites*	*hyperboreus*	AK
Asteraceae	*Peucephyllum*	*schottii*	CA, NV
Asteraceae	*Psilocarphus*	*oregonus*	CA
Asteraceae	*Rudbeckia*	*laciniata* v. *ampla*	CO
Asteraceae	*Rudbeckia*	*occidentalis*	UT
Asteraceae	*Senecio*	*atratus*	CO
Asteraceae	*Senecio*	*spartioides* v. *spartioides*	NV
Asteraceae	*Solidago*	*canadensis*	UT
Asteraceae	*Solidago*	*multiradiata* v. *multiradiata*	AK
Asteraceae	*Solidago*	*spathulata* v. *spathulata*	CA
Asteraceae	*Stephanomeria*	*exigua*	OR
Asteraceae	*Stephanomeria*	*pauciflora*	NV
Asteraceae	*Symphyotrichum*	*spathulatum*	ID
Asteraceae	*Taraxacum*	species not yet determined	AK
Asteraceae	*Tetradymia*	*canescens*	ID
Asteraceae	*Tetradymia*	*spinosa*	ID
Asteraceae	*Townsendia*	*florifer*	ID
Asteraceae	*Tripleurospermum*	*maritimum* ssp. *phaeocephalum*	AK
Asteraceae	*Wyethia*	*amplexicaulis*	ID
Asteraceae	*Wyethia*	*mollis*	CA
Asteraceae	*Wyethia*	*scabra*	UT
Asteraceae	*Xylorhiza*	*tortifolia*	NV
Berberidaceae	*Mahonia*	*aquifolium* ssp. *aquifolium*	OR
Betulaceae	*Betula*	*occidentalis*	UT
Bignoniaceae	*Chilopsis*	*linearis*	NV
Boraginaceae	*Cryptantha*	*circumscissa*	ID
Boraginaceae	*Heliotropium*	*curassavicum*	NV, OR
Boraginaceae	*Lithospermum*	*ruderale*	ID
Boraginaceae	*Mertensia*	*ciliata*	UT
Brassicaceae	*Draba*	*verna*	ID
Brassicaceae	*Lepidium*	*dictyotum*	CA
Brassicaceae	*Polyctenium*	*fremontii*	OR
Brassicaceae	*Stanleya*	*pinnata*	NV
Cactaceae	*Opuntia*	*whipplei*	NV
Campanulaceae	*Downingia*	*bacigalupii*	CA
Campanulaceae	*Downingia*	*bicornuta*	OR
Campanulaceae	*Downingia*	*insignis*	CA
Caprifoliaceae	*Lonicera*	*hispidula*	OR
Caprifoliaceae	*Lonicera*	*involucrata*	UT
Caprifoliaceae	*Symphoricarpos*	*oreophilus*	UT
Chenopodiaceae	*Atriplex*	*canescens*	NV
Chenopodiaceae	*Atriplex*	*confertifolia*	NV
Chenopodiaceae	*Grayia*	*spinosa*	CA
Chenopodiaceae	*Nitrophila*	*occidentalis*	NV
Chenopodiaceae	*Suaeda*	*torreyana*	NV
Cornaceae	*Cornus*	*nuttallii*	OR
Cornaceae	*Cornus*	*sericea*	CO
Crassulaceae	*Sedum*	*spathulifolium*	OR
Cupressaceae	*Juniperus*	*communis*	NV
Cupressaceae	*Juniperus*	*osteosperma*	NV
Cupressaceae	*Juniperus*	*occidentalis*	ID
Cucurbitaceae	*Cucurbita*	*palmata*	NV
Cyperaceae	*Carex*	*alma*	NV
Cyperaceae	*Carex*	*aurea*	NV
Cyperaceae	*Carex*	*interior*	UT
Cyperaceae	*Carex*	*microptera*	NV
Cyperaceae	*Carex*	*nebrascensis*	UT
Cyperaceae	*Carex*	*pellita*	UT
Cyperaceae	*Carex*	*praegracilis*	NV, UT

(con.)

Table 1—(Con.)

Family	Genus	Species	State
Cyperaceae	*Cladium*	*californicum*	NV
Cyperaceae	*Eleocharis*	*palustris*	ID
Cyperaceae	*Eleocharis*	*parishii*	NV
Cyperaceae	*Eleocharis*	*rostellata*	UT
Cyperaceae	*Fimbristylis*	*thermalis*	NV
Cyperaceae	*Schoenoplectus*	*acutus*	UT
Cyperaceae	*Schoenoplectus*	*americanus*	NV, UT
Cyperaceae	*Schoenoplectus*	*maritimus*	NV
Cyperaceae	*Schoenoplectus*	*pungens* v. *longispicatus*	UT
Cyperaceae	*Schoenoplectus*	*tabernaemontani*	NV
Cyperaceae	*Schoenus*	*nigricans*	NV
Cyperaceae	*Scirpus*	*microcarpus*	OR
Cyperaceae	*Trichophorum*	*alpinum*	AK
Elaeagnaceae	*Shepherdia*	*argentea*	UT
Ephedraceae	*Ephedra*	*californica*	CA
Ericaceae	*Arctostaphylos*	*canescens* ssp. *canescens*	OR
Ericaceae	*Arctostaphylos*	*columbiana*	OR
Ericaceae	*Arctostaphylos*	*patula*	OR
Ericaceae	*Harrimanella*	*stelleriana*	AK
Ericaceae	*Phyllodoce*	*glanduliflora*	AK
Ericaceae	*Rhododendron*	*camtschaticum* ssp. *spathulata*	AK
Ericaceae	*Vaccinium*	*ovatum*	CA, OR
Ericaceae	*Vaccinium*	*parvifolium*	OR
Fabaceae	*Acacia*	*greggii*	NV
Fabaceae	*Astragalus*	*alpinus*	AK
Fabaceae	*Astragalus*	*filipes*	ID
Fabaceae	*Astragalus*	*lentiginosus*	CA
Fabaceae	*Astragalus*	*lentiginosus* v . *floribundis*	CA
Fabaceae	*Astragalus*	*obscurus*	ID
Fabaceae	*Astragalus*	*preussii* ssp. *preussii*	UT
Fabaceae	*Astragalus*	*purshii* ssp. *purshii*	CA
Fabaceae	*Astragalus*	*utahensis*	UT
Fabaceae	*Astragalus*	*whitneyi*	CA
Fabaceae	*Cercis*	*orbiculata*	NV
Fabaceae	*Glycyrrhiza*	*lepidota*	UT
Fabaceae	*Hedysarum*	*alpinum*	AK
Fabaceae	*Lathyrus*	*littoralis*	CA
Fabaceae	*Lupinus*	*arbustus*	CA
Fabaceae	*Lupinus*	*argenteus*	CA, UT
Fabaceae	*Prosopis*	*gladulosa*	NV
Fabaceae	*Prosopis*	*gladulosa* v. *torreyana*	NV
Fabaceae	*Prosopis*	*pubescens*	NV
Fabaceae	*Prosopis*	*velutina*	AZ
Fabaceae	*Sophora*	*stenophylla*	UT
Fabaceae	*Thermopsis*	*californica* v. *argentea*	CA
Garryaceae	*Garrya*	*elliptica*	OR
Gentianaceae	*Gentiana*	*glauca*	AK
Grossulariaceae	*Ribes*	*cereum* v. *cereum*	CA
Grossulariaceae	*Ribes*	*cruentum* v. *cruentum*	OR
Grossulariaceae	*Ribes*	*sanguineum* v. *glutinosum*	CA
Grossulariaceae	*Ribes*	*sanguineum* v. *sanguineum*	OR
Hydrangeaceae	*Whipplea*	*modesta*	OR
Hydrophyllaceae	*Eriodictyon*	*angustifolium*	NV
Hydrophyllaceae	*Phacelia*	*capitata*	OR
Hydrophyllaceae	*Phacelia*	*humilis* ssp. *humilis*	CA
Iridaceae	*Iris*	*douglasiana*	CA
Iridaceae	*Iris*	*missouriensis*	CA, CO
Iridaceae	*Sisyrinchium*	*demissum*	UT
Iridaceae	*Sisyrinchium*	*halophilum*	NV
Iridaceae	*Sisyrinchium*	species not yet deterrmined	NV
Juncaceae	*Juncus*	*alpinus*	UT
Juncaceae	*Juncus*	*balticus*	ID, NV, UT
Juncaceae	*Juncus*	*breweri*	CA

(con.)

Table 1—(Con.)

Family	Genus	Species	State
Juncaceae	*Juncus*	*castaneus*	AK
Juncaceae	*Juncus*	*cooperi*	NV
Juncaceae	*Juncus*	*drummondii*	AK
Juncaceae	*Juncus*	*effusus* v. *brunneus*	OR
Juncaceae	*Juncus*	*longistylis*	UT
Juncaceae	*Juncus*	*mertensianus*	AK
Juncaceae	*Juncus*	*nodosus*	NV, UT
Juncaceae	*Juncus*	*saximontanus*	UT
Juncaceae	*Juncus*	*torreyi*	UT
Juncaceae	*Luzula*	*parviflora*	AK
Juncaginaceae	*Triglochin*	*concinna*	NV
Juncaginaceae	*Triglochin*	*maritimum*	UT
Lamiaceae	*Agastache*	*urticifolia*	CA, UT
Lamiaceae	*Hedeoma*	*nana*	NV
Lamiaceae	*Lepechinia*	*calycina*	CA
Lamiaceae	*Mentha*	*arvensis*	UT
Lamiaceae	*Monardella*	*odoratissima*	CA, UT
Lamiaceae	*Salvia*	*sonomensis*	CA
Lamiaceae	*Stachys*	*ajugoides* v. *rigida*	CA
Lamiaceae	*Stachys*	*palustris*	UT
Liliaceae	*Allium*	*acuminatum*	ID, OR, UT
Liliaceae	*Calochortus*	*macrocarpus*	OR
Liliaceae	*Camassia*	*leichtlinii*	OR
Liliaceae	*Camassia*	*quamash*	OR
Liliaceae	*Lilium*	*columbianum*	OR
Liliaceae	*Lilium*	*pardalinum* ssp. *pardalinum*	OR
Liliaceae	*Maianthemum*	*stellatum*	NV
Lillaceae	*Veratrum*	*viride*	AK
Lillaceae	*Zigadenus*	*elegans*	AK
Lillaceae	*Zigadenus*	*venenosus* v. *venenosus*	CA
Loasaceae	*Eucnide*	*urens*	NV
Loasaceae	*Mentzelia*	*albicaulis*	ID
Loasaceae	*Mentzelia*	*lacinata*	NV
Malvaceae	*Sphaeralcea*	*grossulariifolia*	ID
Malvaceae	*Sphaeralcea*	*munroana*	UT
Malvaceae	*Sphaeralcea*	*parviflora*	UT
Myricaceae	*Morella*	*californica*	OR
Nyctaginaceae	*Abronia*	*latifolia*	OR
Oleaceae	*Fraxinus*	*velutina*	NV
Onagraceae	*Clarkia*	*gracilis*	CA
Onagraceae	*Epilobium*	*ciliatum*	UT
Onagraceae	*Epilobium*	species not yet determined	AK
Orchidaceae	*Epipactis*	*gigantea*	NV
Orchidaceae	*Platanthera*	*dilatata*	AK
Papaveraceae	*Argemone*	*hispida*	CO
Plumbaginaceae	*Armeria*	*maritima* v. *californica*	CA
Poaceae	*Achnatherum*	*hymenoides*	UT
Poaceae	*Achnatherum*	*nelsonii*	CA
Poaceae	*Achnatherum*	*thurberianum*	CA, ID
Poaceae	*Andropogon*	*glomeratus*	NV
Poaceae	*Aristida*	*purpurea*	UT
Poaceae	*Bromus*	*carinatus*	OR
Poaceae	*Bromus*	*marginatus*	CA
Poaceae	*Bromus*	*vulgaris*	OR
Poaceae	*Calamagrostis*	*nutkaensis*	CA
Poaceae	*Danthonia*	*californica*	CA, OR
Poaceae	*Distichlis*	*spicata*	NV
Poaceae	*Elymus*	*spicata*	CA
Poaceae	*Festuca*	*californica*	CA, OR
Poaceae	*Melica*	*californica*	CA
Poaceae	*Muhlenbergia*	*asperifolia*	NV, UT
Poaceae	*Muhlenbergia*	*rigens*	NV
Poaceae	*Panicum*	*virgatum*	NV

(con.)

Table 1—(Con.)

Family	Genus	Species	State
Poaceae	*Pluchea*	*sericea*	NV, UT
Poaceae	*Poa*	*fendleriana*	NV
Poaceae	*Poa*	*macrantha*	CA
Poaceae	*Poa*	*secunda*	NV
Poaceae	*Sporobolus*	*airoides*	NV, UT
Poaceae	*Stipa*	*comata*	UT
Poaceae	*Stipa*	*lettermanii*	CO
Polemoniaceae	*Collomia*	*grandiflora*	CA
Polemoniaceae	*Polemonium*	*foliosissimus*	UT
Polygonaceae	*Eriogonum*	*bifurcatum*	NV
Polygonaceae	*Eriogonum*	*caespitosum*	CA
Polygonaceae	*Eriogonum*	*corymbosum*	NV
Polygonaceae	*Eriogonum*	*latifolium*	CA
Polygonaceae	*Eriogonum*	*lobbii*	NV
Polygonaceae	*Eriogonum*	*niveum*	WA
Polygonaceae	*Eriogonum*	*nudum* v. *auriculatum*	OR
Polygonaceae	*Eriogonum*	*racemosum*	UT
Polygonaceae	*Eriogonum*	*sphaerocephalum* v. *halimioides*	CA
Polygonaceae	*Eriogonum*	*umbellatum* ssp. *nevadense*	CA
Polygonaceae	*Eriogonum*	*umbellatum* v. *polyanthum*	CA
Polygonaceae	*Oxyria*	*digyna*	AK
Polygonaceae	*Rumex*	*arcticus*	AK
Portulacaceae	*Lewisia*	*rediviva*	ID
Primulaceae	*Dodecatheon*	*redolens*	NV, UT
Primulaceae	*Primula*	*parryi*	WY
Primulaceae	*Samolus*	*ebracteatus*	NV
Ranunculaceae	*Aconitum*	*columbianum*	UT
Ranunculaceae	*Aconitum*	*delphiniifolium* ssp. *delphiniifolium*	AK
Ranunculaceae	*Anemone*	*parviflora*	AK
Ranunculaceae	*Aquilegia*	*formosa*	CA
Ranunculaceae	*Caltha*	*leptosepala*	UT
Ranunculaceae	*Clematis*	*ligusticifolia*	UT
Ranunculaceae	*Thalictrum*	*fendleri*	UT
Rhamnaceae	*Rhamnus*	*betulifolia*	NV
Rosaceae	*Amelanchier*	*alnifolia*	ID
Rosaceae	*Cercocarpus*	*ledifolius* v. *intermontanus*	NV
Rosaceae	*Cercocarpus*	*ledifolius*	UT
Rosaceae	*Cercocarpus*	*montanus*	CO
Rosaceae	*Dryas*	*drummondii*	AK
Rosaceae	*Dryas*	*octopetala* ssp. *octopetala*	AK
Rosaceae	*Fallugia*	*paradoxa*	UT
Rosaceae	*Geum*	*rossii*	AK
Rosaceae	*Geum*	*triflorum*	CA
Rosaceae	*Luetkea*	*pectinata*	AK
Rosaceae	*Potentilla*	*gracilis*	CA
Rosaceae	*Potentilla*	*uniflora*	AK
Rosaceae	*Prunus*	*virginiana*	ID
Rosaceae	*Purshia*	*glandulosa*	NV
Rosaceae	*Purshia*	*mexicana*	UT
Rosaceae	*Purshia*	*tridentata*	UT
Rosaceae	*Rosa*	*pisocarpa*	OR
Rosaceae	*Rosa*	*woodsii*	CO
Rosaceae	*Rubus*	*parviflorus*	CA
Rosaceae	*Sanguisorba*	*canadensis*	AK
Rosaceae	*Spiraea*	*douglasii*	OR
Rosaceae	*Spiraea*	*stevenii*	AK
Rutiaceae	*Thamnosma*	*montana*	NV
Salicaceae	*Populus*	*angustifolia*	UT
Salicaceae	*Salix*	*exigua*	ID, UT
Salicaceae	*Salix*	*lemmonii*	ID
Salicaceae	*Salix*	*lucida*	UT
Salicaceae	*Salix*	*lutea*	ID, UT
Santalaceae	*Commandra*	*umbellatum*	NV

(con.)

Table 1—(Con.)

Family	Genus	Species	State
Saururaceae	*Anemopsis*	*californica*	CA, NV
Saxifragaceae	*Boykinia*	*occidentalis*	OR
Saxifragaceae	*Parnassia*	*kotzebuei*	AK
Saxifragaceae	*Saxifraga*	*bronchialis*	AK
Saxifragaceae	*Saxifraga*	*lyallii*	AK
Saxifragaceae	*Saxifraga*	*odontoloma*	UT
Saxifragaceae	*Tellima*	*grandiflora*	OR
Saxifragaceae	*Tiarella*	*trifoliata* ssp. *unifoliata*	OR
Scrophulariaceae	*Castilleja*	*applegatei* ssp. *pinetorum*	CA
Scrophulariaceae	*Castilleja*	*linariifolia*	CA, UT
Scrophulariaceae	*Castilleja*	*minor* ssp. *minor*	UT
Scrophulariaceae	*Castilleja*	*pruinosa*	OR
Scrophulariaceae	*Castilleja*	*unalaschcensis*	AK
Scrophulariaceae	*Lagotis*	*minor*	AK
Scrophulariaceae	*Mimulus*	*aurantiacus*	CA
Scrophulariaceae	*Mimulus*	*guttatus*	CA, UT
Scrophulariaceae	*Penstemon*	*acuminatus*	ID
Scrophulariaceae	*Penstemon*	*albomarginatus*	NV
Scrophulariaceae	*Penstemon*	*cyananthus*	UT
Scrophulariaceae	*Penstemon*	*cyaneus*	ID
Scrophulariaceae	*Penstemon*	*deustus*	ID
Scrophulariaceae	*Penstemon*	*fruticiformis*	NV
Scrophulariaceae	*Penstemon*	*fruticosus*	ID
Scrophulariaceae	*Penstemon*	*laevis*	UT
Scrophulariaceae	*Penstemon*	*palmeri*	UT
Scrophulariaceae	*Penstemon*	*platyphyllus*	UT
Scrophulariaceae	*Penstemon*	*roezlii*	CA
Scrophulariaceae	*Scrophularia*	*californica*	CA
Scrophulariaceae	*Veronica*	*peregrina* ssp. *xalapensis*	CA
Scrophulariaceae	*Veronica*	*wormskjoldii*	AK
Typhaceae	*Typha*	*angustifolia*	UT
Valerianaceae	*Valeriana*	*sitchensis*	AK
Zygophyllaceae	*Larrea*	*tridentata*	NV

Center for Plant Conservation botanists collected in two States. Table 2 includes both target and the actual number of taxa collected by State. In general, where interns or other assistance was provided, targets were exceeded, as the additional workload was difficult to accomplish otherwise. Drought conditions in the Western United States limited seed production for some species; however, because flexibility is built into the program, alternate species could usually be identified for collection.

Table 2—2002 targeted and actual number of taxa collected by the Bureau of Land Management for the Millenium Seed Bank project and Seeds of Success program.

State	Number of species targeted	Number of species collected
AK	20	45
AZ	25	1
CA[a]	50	73
CO	25	11
ID[a]	50	37
MT	20	0
NV[a]	50	77
NM	20	0
OR[a]	50	52
UT[a]	50	79
WY	30	0
Total	**390**	**375**

[a] States that had Student Conservation Association intern teams.

Seed collecting protocols, shipping forms, proposed species lists, and a database of collected taxa are available at http://www.nps.gov/plants/sos and http://www.rbgkew.org.uk/seedbank. Digital photographs of each species and its seed were also taken in 2002. These photographs are housed at RBG, Kew, and each participating BLM office, and may eventually be available online.

Conclusions

In 2002, in partnership with RBG, Kew, and as part of the international Millennium Seed Bank project, the Bureau of Land Management implemented a native seed collecting program deemed "Seeds of Success." Seed from 414 populations representing 375 taxa were collected for long-term storage at RBG, Kew, and the USDA National Seed Storage Laboratory in Fort Collins, CO, and for use in native plant materials development. As a multiple-use agency, the BLM has a need for native plant materials for many different programs in order to meet its goal of restoring at-risk resources and maintaining or improving functioning ecosystems. The Seeds of Success program facilitates development of native plant materials from local genetic sources, and provides valuable information on germination and viability of native plant species that are currently in short supply. Additional information on Seeds of Success and the Millennium Seed Bank project is available at http://www.nps.gov/plants/sos and http://www.rbgkew.org.uk/seedbank.

References

Brown, A. H. D.; Marshall, D. R. 1995. A basic sampling strategy: theory and practice. In Guarino, L; Ramanatha Rao, V.; Reid, R. Collecting plant genetic diversity. Technical Guidelines. CAB International.

Kartesz, J. T.; Meacham, C. A. 1999. Synthesis of the North America Flora, Version 1.0. North Carolina Botanical Garden, Chapel Hill, NC.

Recruitment Failure of Chenopod Shrub Populations in the Great Basin

Susan C. Garvin
Susan E. Meyer
David L. Nelson

Abstract: The salt desert shrub ecosystem has suffered increasing invasion by exotic annual weeds, especially cheatgrass, for the last 25 years or longer. After the extensive shrub dieoffs of 1982 to 1984 in the Great Basin and Colorado Plateau, many shadscale (*Atriplex confertifolia*) and winterfat (*Ceratoides lanata*) populations failed to regenerate. Several facultatively pathogenic fungi were isolated from the rhizosphere of shadscale. Levels of soil *Fusarium* and pythiaceous fungi in intact and dieoff shrubland areas were measured with positive correlation between fungal density and dieoff severity of shadscale in one study and winterfat in a separate study. Shadscale seedings in three shadscale sites invaded by annual weeds in the Utah western desert resulted in significant seedling emergence followed by 100 percent establishment failure. Seedlings with wilt symptoms were observed in each of these studies. In each case soil moisture was adequate for seedling establishment. A greenhouse test was conducted to study seedling establishment of these two species in 10 valley bottom soils, four from recruiting shrub populations and six from defunct shrub sites invaded by cheatgrass or halogeton. Autoclaved and fungicide-treated soil treatments significantly increased winterfat seedling survival ($P > 0.001$) in soils from weed-invaded sites. No effect of soil treatment was seen in shadscale seedling numbers in this study. Winterfat seedling weight was not affected by soil treatment and did not differ between soil sites. Shadscale seedling weight was significantly increased by soil treatment in intact soils but not in weedy soils. In a separate emergence study shadscale fruits were planted in soil from two intact and two weed-invaded shadscale sites. After moist chilling at 2 °C, more than twice as many live seedlings were observed in the two soils from intact sites as in the two soils from weed-invaded sites. Work in progress will attempt to isolate a causal organism from dying shadscale seedlings. Shadscale sensitivity to fungicides will also be investigated.

Introduction

The salt desert shrub ecosystem in Western North America is second in area only to the sagebrush ecosystem. It covers over 17 million ha of lowlands, with the dominant perennial plants being shrubs from the chenopod family (West 1994). During the last 25 to 50 years increasing invasion of alien grasses and other annual plants has led to recurring fires and expanding invasion of weeds; in many cases the native shrub communities have not returned.

An extensive shrub dieoff occurred in the Great Basin and Colorado Plateau in the early 1980s, coinciding with a series of “El Niño” years that resulted in record high precipitation. This dieoff affected chenopod shrubs, particularly shadscale (*Atriplex confertifolia*) in most Great Basin valleys. The Bureau of Land Management (BLM) estimated that more than 280,000 ha of shadscale were lost in Utah alone (Nelson and others 1989). This dieoff was followed by a massive invasion of annual weeds and a subsequent series of wildfires. Shadscale recruitment in most burned dieoff areas was, and remains, almost nonexistent. It is common for shadscale populations to experience cyclic dieoff and recruitment events, made possible by a long-lived soil seed bank (Sharp and others 1990), but the recruitment phase of that cycle has failed to occur in many populations, and shadscale seed banks may have become depleted. Widespread decline and recruitment failure of winterfat (*Ceratoides lanata*), a shrub second only to shadscale in abundance in salt desert shrubland, has also occurred in many Great Basin valleys (Kitchen 2001; Nelson and others 1989). Thus substantial decreases of two major shrubs have resulted in large acreages of valley bottoms susceptible to invasion by cheatgrass (*Bromus tectorum*), halogeton (*Halogeton glomeratus*), and other weeds.

Previous Research

This paper will review published studies explaining the causes of this phenomenon and describe more recent preliminary studies carried out in our laboratory. Studies carried out during and shortly after the 1980s El Niño investigated, among other factors, the role of pathogenic fungi in the dieoff. Shadscale roots were exhumed, and fungal isolations were made from surface-sterilized tap and secondary roots, as well as crowns and stems (Nelson and others 1990). Hundreds of fungi were isolated, pure-cultured, and identified to genus and often species level. Fungi with pathogenic potential were frequently isolated from surface sterilized root material. *Fusarium* was the most frequently isolated genus, from both healthy and necrotic

---

In: Hild, Ann L.; Shaw, Nancy L.; Meyer, Susan E.; Booth, D. Terrance; McArthur, E. Durant, comps. 2004. Seed and soil dynamics in shrubland ecosystems: proceedings; 2002 August 12–16; Laramie, WY. Proceedings RMRS-P-31. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Susan C. Garvin is Biological Technician, Susan E. Meyer is Ecologist, and David L. Nelson is Retired Plant Pathologist, U.S. Department of Agriculture Forest Service, Shrub Sciences Laboratory, Provo, UT, U.S.A. FAX: (801) 375-6968; e-mail: sgarvin@fs.fed.us

root material and at every plant position. Facultatively parasitic plant pathogens are common in this genus; this class of fungi can survive and multiply saprophytically on organic substrates, but can also induce plant disease, especially when plant host defense mechanisms are lowered because of environmental stress (Nelson and others 1990). Some *Fusarium* species commonly induce both vascular wilt and root rot in susceptible plants. Other genera commonly isolated were *Alternaria*, known to cause leaf spot and twig blight, *Cephalosporium*, also capable of causing vascular wilt, and *Sclerotium*, *Rhizoctonia*, and *Pythium*, all of which can cause root rot or "damping-off" of seedlings.

As a part of these dieoff studies, soil samples were collected from the rhizosphere of shadscale and other dying shrubs, and populations of fungi closely related to *Pythium* (referred to hereafter as pythiaceous fungi) were counted on selective agar media. A very strong correlation between small secondary rootlet mortality and dieoff severity ($r = –0.99$, $P = <0.01$) and a significant correlation between number of pythiaceous fungi and dieoff severity on a site ($r = 0.64$, $P = <0.01$) was observed (fig. 1). The number of pythiaceous propagules was quite variable and ranged from 163 to 2,931 per gram of soil in sites with a low dieoff severity to 1,416 to 6,056 per gram of soil in sites with complete shadscale dieoff.

Harper and others (1996) reported on a winterfat dieoff occurring on the Desert Experimental Range in southwestern Utah. Winterfat was being replaced by halogeton in a valley bottom, the site of a known overland waterflow. In an adjacent site winterfat was recruiting successfully as openings occurred. Soil samples were collected from both the winterfat dieoff area and adjacent healthy winterfat area; half the soil was fumigated with methyl bromide, and winterfat seeds were sown in pots in the greenhouse. Results from that study (Harper and others 1996) showed that fumigation increased winterfat recruitment in halogeton-affected soil but not in soil from the healthy winterfat site.

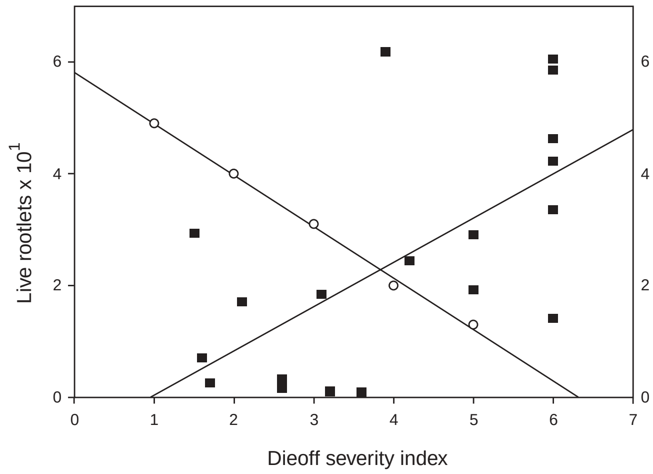


Figure 1—Correlation of dieoff severity at shadscale sites with number of live rootlets present on 30 plants excavated from each severity class and with number of pythiaceous fungi isolated from rhizosphere soil of 10 plants from each of 20 sites. Each site was ranked by averaging plant dieoff class (1 to 6) at 10-m intervals along three 100-m transects, so a site with dieoff severity of 6 consisted of all dead plants (Nelson and others 1990).

Further work on these soils carried out in our laboratory was designed to determine if density of pathogenic fungi correlated with lack of winterfat recruitment. Surface soil samples were collected in three areas: dieoff areas replaced by halogeton, dieoff areas not yet invaded by halogeton, and areas where winterfat was successfully recruiting. Soil samples were diluted and plated on two agar media, selective for either *Fusarium* species or pythiaceous species, and number of colonies was determined, with each colony representing a reproductive propagule. In winterfat dieoff soils *Fusarium* numbers were 3.4 times higher than in soils from intact winterfat areas ($P > 0.001$) (table 1). Pythiaceous fungal numbers were more than 10 times higher in winterfat dieoff soil than in intact winterfat soil ($P > 0.001$). This trend continued and intensified in areas where winterfat had been replaced by halogeton (David L. Nelson, unpublished data).

Ramsey and others (1995) presented results of a study conducted in 1992 to 1994 on an *Atriplex* seedling failure in northeastern New Mexico. A selection of an *Atriplex* hybrid of *A. canescens* X *A. obovata* repeatedly failed to become established after seeding in a nonmined site. Soil from the site and a commercial soil mix were planted with the same seed source under greenhouse conditions, and establishment was compared. Seedlings emerged in both soils, but most of the seedlings in the native soil died of "damping-off." Most seedlings in the commercial mix survived.

Diluted soil samples from the planting site and a nearby stockpile soil were plated on selective agar media designed to inhibit all but pythiaceous fungi. The planting site soil averaged 1,230 pythiaceous fungi per gram of soil, compared to 20 pythiaceous fungi per gram from the stockpile soil. Seeds treated with the fungicide Captan® (Drexel Chemical Co.) and untreated seeds were planted in a pot experiment. Seedling mortality in the soil from the failed planting site was 87 percent using untreated seed and 27.5 percent with the Captan® treated seed. A subsequent seeding at the same site using Captan®-treated seeds increased seedling survival 100-fold.

New Research

Shadscale Seedling Establishment Studies

In the course of our studies on shadscale germination biology (Garvin and others 1995; Garvin and Meyer 2003;

Table 1—Enumeration of *Fusarium* and pythiaceous fungi in soil from a winterfat dieoff site in western Utah. Numbers are fungal propagules per gram of soil.

Soil source	*Fusarium*	Pythiaceous fungi
Healthy winterfat area	517	105
Winterfat dieoff area	1,771	1,152
Halogeton invaded dieoff area	4,775	1,765

Meyer and others 1998), we carried out several field tests to evaluate seedling emergence and establishment. These studies were carried out in two western Utah valleys in 1991, 1997, and 2000. The 1991 study was conducted in northeastern Rush Valley with eight populations of shadscale fruits in emergence strips 8 ft long by 1 ft wide; each population was replicated eight times. A total of approximately 19,200 filled fruits were planted 1 cm deep. The study in 1997 consisted of four populations, planted in square-meter plots, replicated eight times, with approximately 32,000 filled fruits planted. A third study was carried out in 2000 using seed already in the seed bank, so total fruit density is not known. Emergence and establishment results are shown in table 2. In each test, a considerable fraction of seeds germinated and emerged; 3 months later only a small fraction of emerged seeds survived, and by the following spring none of the seedlings remained alive. Each time we counted seedlings we observed typical damping-off symptoms, even though soil moisture was adequate for survival.

Greenhouse Seedling Establishment of Winterfat and Shadscale

In 1999 we began a preliminary greenhouse pot study to determine the effect of different soils on seedling establishment. We collected soil (upper 5 to 10 cm) from each of 10 sites in four valley bottoms in western Utah, attempting to match weed-invaded sites with equivalent intact sites. Soil was either autoclaved to eliminate all microorganisms, treated with Banrot® (The Scotts Company) as a drench at the rate of 12 ounces per 100 gallons) or untreated. Rectangular pots (10 cm by 15 cm by 7.5 cm) were filled with soil, watered to saturation, and planted either with 25 winterfat seed or 25 shadscale seedlings germinated in Petri dishes in moist chill. Each soil treatment x species combination was replicated eight times. Seedling emergence was evaluated every 3 days initially and once a week after the first 2 weeks. After 3 months, plants were harvested by clipping at the soil line, dried, and weighed. We compared weedy and intact soils and different soil treatments using SAS PROC GLM Analysis of Variance.

The effect of fungicide treatment on plant survival and size is shown in figure 2. Autoclaved soil treatment results are similar. Winterfat seedling survival was significantly higher in fungicide treated and autoclaved soil treatments from weedy sites, but little effect was seen on survival in soil from intact sites. Most death of winterfat seedlings occurred 10 to 21 days after emergence with little additional seedling death after that point. We found no significant effect of soil treatment on shadscale seedling numbers. Percentage survival of transplants was similar in all three soil treatments.

Little difference in plant weight of winterfat was measured overall, although in most soils either autoclaving or drenching (but often not both) produced significantly greater plant growth than in untreated soil. The ratio of shadscale plant weight in fungicide treated soil compared to untreated soil from nonweedy sites was significantly increased by a factor of 2 (P > 0.001). No significant effect of fungicide or autoclave treatment was seen on shadscale plant weight when plants were grown in weedy soil.

Table 2—Number of seedlings emerged in early spring, established in late spring, and established 1 year later after a late fall planting.

	Early spring seedlings	Late spring seedlings	Year-old plants
Rush Valley	807	118	0
Skull Valley North	1,029	24	2
Skull Valley South	896	114	0

Shadscale Seedling Survival During Moist Chilling

A second preliminary study was carried out in a cold room and growth chamber. This study used four soil collections, two from a weed-invaded site and two from a nearby intact site in two western Utah valleys. Four different methods of fungus control, including biological control organisms, were tested. Subdue® (Ciba-Geigy) fungicide was applied at the recommended high rate as a drench; soil was steamed at 60 °C for 30 minutes; Kodiak® (commercial *Bacillus subtilis* GBO3 inoculum obtained from Gustafson) was applied to fruit before planting; and commercial *Gliocladium* inoculum (Soilguard®) from Gardens Alive! was pre-applied to fruit in combination with a half dosage of Subdue® fungicide applied as a soil drench. Afterripened shadscale fruits were planted in the rectangular pots as described in the previous study, watered to saturation, placed in closed plastic bags to maintain soil saturation, and incubated at 2 °C for 12 weeks. Treatments were replicated 15 times. Pots were removed from the cold, germinated seedlings were counted in each pot, and pots were moved to the growth chamber, set to approximate early spring temperature and light conditions. Unfortunately, the experiment was terminated prematurely due to overheating of the growth chamber and death of most seedlings, so only main effect means were analyzed statistically.

Results of the seedling count are summarized in table 3. This data is a measure of seedling emergence and survival during moist chilling. The steamed soil treatment is not shown since almost no germination occurred in any treatment. There was a strong indication in our data that shadscale seedlings may have been damaged before emergence by the high rate of Subdue® fungicide, since seedling emergence in the fungicide treated soil was only 31.7 percent of the control, and only 56 percent of emerged seedlings survived, compared with 71 to 76 percent survival in the other soil treatments. Emergence of plants grown in the soil treated with only one-half the high fungicide dosage (with SoilGuard®) was significantly less than emergence of plants grown in the untreated soil (P > 0.05); plant survival after emergence was not significantly reduced by the half dosage of fungicide. More than twice as many seedlings emerged and survived in soils collected from intact shadscale sites as in soils from weed-invaded sites (P > 0.01). No other differences between fungus control treatments could be determined.

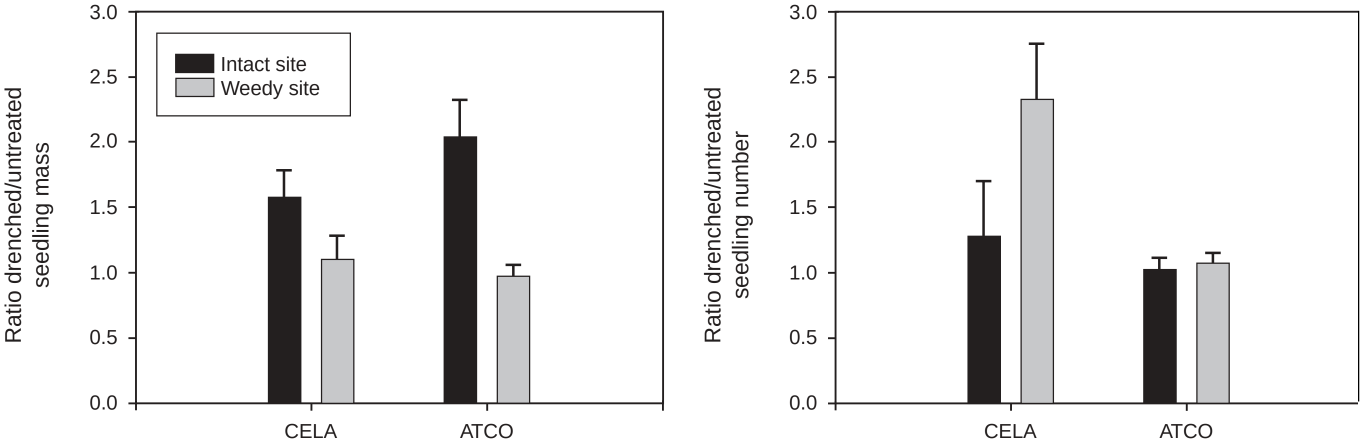


Figure 2—Means of the ratio of fungicide drench weight or seedling number to untreated values for soils from four intact sites versus soils from six weedy sites in the greenhouse pot experiment. Larger ratios indicate more effect of fungicide, with values of 1.0 indicating no effect.

Discussion

Because shadscale seed was not germinated in the presence of soil fungi in the greenhouse study, it is not surprising that seedling numbers were little affected by soil treatment. Damping-off organisms are often attracted to germinating seeds (Schroth and Cook 1964) so seedlings that might have become infected in the test soils during this period survived. Pathogens in the test soils seldom killed shadscale seedlings after emergence. Increased survival of winterfat seedlings in treated weedy soils can be interpreted to mean that a group of pathogenic fungi was suppressed by fungicide and autoclaving. The interpretation of the shadscale weight data becomes more problematic. If pathogens were responsible for inhibited plant growth we would expect that soil treatments that decrease numbers of facultative soil fungi would increase plant weight. We found this to occur in the soil from intact shadscale sites but surprisingly not in the soil from weedy sites. One interpretation might be that fungicide treatment suppressed endemic low levels of pathogens (root nibblers) and promoted more growth in intact soils but was ineffective against a different pathogen or pathogens in weedy soil. These arguments lead to the possibility of several different pathogens affecting chenopod shrubs, in both weed-invaded and intact soils, and at different stages of plant growth. Other evidence for this scenario comes from Nelson's (1990) studies, which show the presence of several facultative fungal pathogens in root and stem tissue of shadscale plants. It is difficult to test for pathogenicity of these organisms because plants must be stressed in some way to lead to the infection process.

Some likely confounding effects of autoclaving soil include the production of toxic organic compounds during heating and the increase in available nutrients due to the death of

Table 3—Mean fraction of shadscale seedling survival and number of emerged seedlings (live and dead) after 2 months in moist chilling at 2 °C in pots with soils from two intact and two weedy shadscale sites[a].

Soil source	Untreated	Fungicide	Kodiak®	SoilGuard®+1/2 F[b]	Site means	Weediness means
Fraction of surviving shadscale seedlings						
Dugway intact	0.671	0.588	0.690	0.702	0.663	
Rush intact	.658	.687	.861	.773	.745	.704a
Dugway weedy	.850	.609	.682	.792	.733	
Rush weedy	.658	.357	.628	.778	.605	.669a
Treatment means	.709ab	.560b	.715ab	.761a		
Number of emerged seedlings						
Dugway intact	70	17	71	47	51.25	
Rush intact	117	30	79	44	67.50	59.38a
Dugway weedy	40	23	22	24	27.25	
Rush weedy	38	14	43	18	28.25	27.75b
Treatment means	66.25a	21.00c	53.75ab	33.25bc		

[a] Main effect means followed by the same letter are not significantly different at the $P < 0.05$ level (LSD).

[b] 1/2 F = One-half the full dosage of fungicide. See text for details on soil treatments and sources of biological control treatments.

the microbial population; these factors were not controlled in our test and probably explain some of the variability between soils and inconsistent results within soils. Another disadvantage of steaming or autoclaving soils high in clay content is apparent in our study on seedling emergence during moist chilling: the heated soils lost all structure and apparently became either toxic or impenetrable to seedlings. Soil fumigation might lead to clearer results, although fumigation, as well as autoclaving, can cause a flush of available nitrogen after soil biota are killed.

Another confounding factor is that fungicide treatment of soil may be toxic to some plant species (Leach and MacDonald 1978). If the clay fraction of the soil is lower than in agricultural soil, less fungicide is bound by the clay fraction. Conversely, if the clay fraction is higher than in most agricultural soils, more fungicide may be bound by clay particles and not available for killing fungal pathogens. Soil organic matter can also immobilize fungicide, so increased organic matter in weed-infested soils may bind more fungicide than in soils from intact shrub sites. More research needs to be carried out to discover effective rates of application of fungicide on chenopod shrubs and in different desert soils. Because we do not know which fungi are acting as pathogens, we may not have used an appropriate fungicide. We are currently engaged in studies on shadscale seeds designed to isolate possible pathogens from infected shadscale seedlings. Candidate fungi will then be tested by inoculating shadscale fruits and re-isolating the fungus from infected seedlings. We will also determine appropriate rates of fungicide application for the valley bottom soils from our study sites and test these rates for toxicity to shadscale germination and seedling stages.

The massive chenopod shrub dieoff associated with record precipitation and subsequent invasion of annual weeds has also resulted in changes in the soil. Harper and others (1996) measured increased salinity in the surface soil of halogeton-infested winterfat sites. Increased salinity probably cannot account for the death of mature shrubs, but plants in the germination and young seedling stage are far more susceptible to increased salinity, so this could be a factor in recruitment failure.

Ewing and Dobrowolski (1992) characterized soil factors such as moisture and salinity in the plant communities in Puddle Valley, UT, where shadscale dieoff was extensive in the early 1980s. They found that dead shadscale was negatively correlated with slope and elevation; the greatest density of dead shrubs was found in flat valley bottoms. Shadscale death was positively correlated with increased clay content and increased soil moisture, both conditions leading to enhancement of favorable sites for fungus proliferation. Sites with higher salinity had greater rates of survival. The leading edge of shadscale dieoff was followed from 1987 to 1989; the authors concluded that the dieoff was continuing even after precipitation levels returned to normal.

Topsoil organic matter and surface litter also increase in annual weed-infested sites, which is likely to increase the populations of facultatively parasitic fungi, such as *Fusarium* and *Pythium*. Other soil biotic changes may also occur, as shown by Evans and Belnap (1999), such as decreased nitrogenase and ammonia mineralization activity in sites with disturbed cryptobiotic crust. Belnap and Phillips (2001) found that plant pathogenic fungi increased in cheatgrass-invaded perennial grass sites in Canyonlands National Park. Bolton and others (1993) measured increased surface soil microbial biomass carbon and nitrogen, soil respiration, dehydrogenase, and phosphatase activity in cheatgrass invaded soil compared to soil under sagebrush, perennial grass, and cryptobiotic crust. The changes to soil biota and chemistry caused by annual weed invasion have only begun to be studied; effective measures to restore native communities need to consider changes within as well as above the soil.

References

Belnap, J.; Phillips, Susan L. 2001. Soil biota in an ungrazed grassland: response to annual grass (*Bromus tectorum)* invasion. Ecological Applications. 11: 1261–1275.

Bolton, H., Jr.; Smith, J. L.; Link, S. O. 1993. Soil microbial biomass and activity of a disturbed and undisturbed shrub-steppe ecosystem. Soil Biology and Biochemistry. 25: 545–552.

Evans, R. D.; Belnap, J. 1999. Long-term consequences of disturbance on nitrogen dynamics in an arid ecosystem. Ecology. 80: 150–160.

Ewing, K.; Dobrowolski, J. P. 1992. Dynamics of shrub die-off in a salt desert plant community. Journal of Range Management. 45: 194–199.

Garvin, S. C.; Meyer, S. E.; Carlson, S. G. 1996. Seed germination studies in *Atriplex confertifolia* (Torr. & Frem.) Wats. In: McArthur, E. D.; Barrow, J. R.; Sosebee, R. E.; Tausch, R. J., comps. Proceedings—shrubland ecosystem dynamics in a changing environment; 1995 May 23–25; Las Cruces, NM. Gen. Tech. Rep. INT-GTR-338. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 165–169.

Garvin, S. C.; Meyer, S. E.; Clement, S. 2003. Multiple mechanisms for seed dormancy regulation in shadscale (*Atriplex confertifolia*: Chenopodiaceae). Canadian Journal of Botany. 81: 601–610.

Harper, K. T.; Van Buren, R.; Kitchen, S. G. 1996. Invasion of alien annuals and ecological consequences in salt desert shrublands of western Utah. In: Barrow, J. R.; McArthur, E. D.; Sosebee, R. E.; Tausch, R. J., comps. Proceedings—shrubland ecosystem dynamics in a changing environment; 1995 May 23–25; Las Cruces, NM. Gen. Tech. Rep. INT-GTR-338. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 58–65.

Kitchen, S. 2001. Winterfat decline and halogeton spread in the Great Basin. In: McArthur, E. D.; Fairbanks, D. J., comps. Proceedings—shrubland ecosystem genetics and biodiversity; 2000 June 13–15; Provo, UT. Gen. Tech. Rep. RMRS-P-21. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 200–203.

Leach, L. D.; MacDonald, J. D. 1978. Greenhouse evaluation of seed treatment fungicides for control of sugar beet seedling diseases. In: Zehr, Eldon I., ed. Methods for evaluating plant fungicides, nematicides, and bactericides. St. Paul, MN: American Phytopathological Society: 23–25.

Meyer, S. E.; Carlson, Stephanie L.; Garvin, Susan C. 1998. Seed germination regulation and field seed bank carryover in shadscale (*Atriplex confertifolia*: Chenopodiaceae). Journal of Arid Environments. 38: 255–267.

Nelson, David L.; Harper, Kimball T.; Boyer, Kenneth C.; Weber, Darrell J.; Haws, B. Austin; Marble, James R. 1989. Wildland shrub dieoffs in Utah: an approach to understanding the cause. In: Proceedings—symposium on shrub ecophysiology and biotechnology; 1987 June 30–July 2; Logan UT. Gen. Tech. Rep. INT-276. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 119–135.

Nelson, D. L.; Weber, D. J.; Garvin, S. C. 1990. The possible role of plant disease in the recent wildland shrub dieoff in Utah. In: McArthur, E. Durant; Romney, Evan M.; Smith, Stanley D.; Tueller, Paul T., comps. Proceedings—symposium on cheatgrass invasion, shrub die-off, and other aspects of shrub biology and management; 1989 April 5–7; Las Vegas, NV. Gen. Tech. Rep. INT-276. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 84–90.

Ramsey, T.; Stutz, H. C.; Nelson, D. 1995. Seedling failure in Atriplex (Chenopodiaceae) due to "damping-off." In: Schuman, Gerald E.; Vance, George F., eds. Proceedings of national meeting of the American Society for Surface Mining and Reclamation; 1995 June 5–8, Gillette, WY. Princeton, WY: American Society for Surface Mining and Reclamation: 757–761.

Sharp, L. A.; Sanders, K.; Rimbey, N. 1990. Forty years of change in a shadscale stand in Idaho. Rangelands. 12: 313–328.

Schroth, M. N.; Cook, R. J. 1964. Seed exudation and its influence on pre-emergence damping-off of bean. Phytopathology. 54: 670–673.

West, Neil E. 1994. Effects of fire on salt-desert rangelands. In: Monsen Stephen B., Kitchen, Stanley G., comps. Proceedings—symposium on ecology, management, and restoration of Intermountain annual rangelands; 1992 May 18–22; Boise ID. Gen. Tech. Rep. INT-313. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 71–74.

Annual Brome Seed Germination in the Northern Great Plains: An Update

M. R. Haferkamp
M. D. MacNeil

Abstract: Japanese brome (*Bromus japonicus* Thunb) and downy brome (*B. tectorum* L.), alien weedy cool-season annual grasses, have invaded thousands of hectares of grass and shrub communities in the Northern Great Plains, Great Basin, and Columbia Basin. Abundance of brome is dependent upon availability of seed, amount and distribution of rainfall, temperature, and availability of soil nitrogen. More than 10,000 annual brome seeds can be present in a square meter in the mixed-grass prairie of the Northern Great Plains. A large portion of ripe seeds will generally germinate over a wide range of temperatures and osmotic potentials that often occur in late summer and autumn, but soils usually must be moist for 3 to 5 days for seeds to germinate. However, a percentage of seeds that do not germinate by late September can become dormant when water is taken up at or below 0 °C. This dormant state can last through the next winter, spring, and summer. These characteristics aid annual brome's persistence on rangelands.

Introduction

Japanese brome (*Bromus japonicus* Thunb) and downy brome (*B. tectorum* L.), alien weedy cool-season annual grasses, have invaded thousands of hectares of grass and shrub communities in the Northern Great Plains (Haferkamp and others 1993; Hewlett and others 1981; Whisenant 1990), Great Basin (Mack 1981; Young and Evans 1972), and Columbia Basin (Daubenmire 1970; Hulbert 1955). Although annual bromes can produce large quantities of nutritious spring forage, they can have a negative impact on associated perennial forage species and performance of grazers (Haferkamp and others 1994b, 1997, 1998, 2001a,b; Rummell 1946). Forage production is erratic from year to year (Gartner and others 1986; Haferkamp and others 1993, 2001a), and due to early maturation of the annual bromes (Vallentine and Stevens 1994) compared to perennial grasses, their presence can alter seasonal patterns of forage production and cause relatively rapid declines in forage quality on infested rangelands (Haferkamp and others 1994b, 2001b).

Abundance of brome is dependent upon the seedbank (Karl and others 1999), temperature, and amount and distribution of rainfall (Haferkamp and others 1993; Mack and Pyke 1983; Whisenant 1990). Karl and others (1999) reported that more than 10,000 germinable annual brome seeds can be present in a square meter in the mixed-grass prairie of the Northern Great Plains. Thus, the potential for dense populations of annual brome seedlings is great. We have developed a better understanding of the dynamics of seed germination for Japanese brome through a series of studies conducted at the Fort Keogh Livestock and Range Research Laboratory, Miles City, MT (Haferkamp and others 1994a, 1995a,b).

Temperature

The influence of temperature on germination was investigated on Japanese brome seed collected on native rangeland in eastern Montana (Haferkamp and others 1995b). The objective was to determine temperature profiles for germination of Japanese brome seeds, representative of those disseminated from seed heads during the period spanning late summer to early autumn.

Methods

Seeds were collected on eight dates during July and August 1990 and 1991. Seeds were stored in paper sacks in the laboratory at about 21 °C until germination trials were run in Reno, NV, 3 to 9 months after collection.

Four replications of 25 seeds from each collection date were incubated for 4 weeks in closed petri dishes on 1-mm-thick filter paper moistened with distilled water. Dishes were arranged in a randomized complete-block design, in 10 dark incubators. Constant incubator temperatures included 0, 2, 5, and all 5 °C increments through 40 °C. Alternating temperature regimes were attained by moving dishes between incubators using 16 hours at each constant temperature plus 8 hours at all possible higher temperatures. For example, 35 °C was alternated with 40 °C, while 0 °C was alternated with 2, 5, 10, 15, 20, 25, 30, 35, and 40 °C. Germination counts were taken weekly, and seeds were considered germinated when the radicle was at least 5 mm long.

Data from each base temperature and its alternating temperature regime were used to develop regression equations of quadratic response surfaces with estimated germination means and confidence intervals at the 5-percent level of probability. A number of germination parameters were

---

In: Hild, Ann L.; Shaw, Nancy L.; Meyer, Susan E.; Booth, D. Terrance; McArthur, E. Durant, comps. 2004. Seed and soil dynamics in shrubland ecosystems: proceedings; 2002 August 12–16; Laramie, WY. Proceedings RMRS-P-31. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

M. R. Haferkamp is a Rangeland Scientist and M. D. MacNeil is a Research Geneticist, USDA-ARS, Fort Keogh Livestock and Range Research Laboratory, 243 Fort Keogh Road, Miles City, MT 59301-4016, U.S.A., FAX: (406) 232-8209, email: marshall@larrl.ars.usda.gov

synthesized from these quadratic response surfaces to assist in interpretation of germination temperature profiles.

Results and Discussion

Mean germination of Japanese brome seed from the 55 temperature profiles averaged across the eight collection dates represented in figure 1 was 71 ± 4.0 percent. Some germination occurred in 96 ± 1.4 percent of the temperature regimes, and the mean germination for regimes where some germination occurred was 74 ± 4.0 percent. Optimum temperatures for germination of Japanese brome seed were constant 20 °C and several alternating (16 hours of minimum with 18 hours of maximum) temperatures. The optimum alternating regimes were 2 through 10 °C minimums with 15 °C maximum, 0 through 15 °C minimums with 20 °C maximum, 5 through 20 °C minimums with 25 °C maximum, and 15 °C minimum with 30 °C maximum. Over 75 percent of the collections produced optimum germination (defined as germination not lower than the maximum observed minus one-half of its confidence interval at 0.05 level of probability) in these regimes. Maximum germination of Japanese brome seed occurred at moderate and cold seedbed conditions with germination being somewhat depressed in very cold and warmer than moderate temperatures. Young and Evans (1985) report that at least some germination of downy brome seed is possible with temperatures as low as 0 °C and as high as 40 °C.

A wide range of temperature conditions occur in autumn on seedbeds in the Northern Great Plains region. Findings of this study suggest that while Japanese brome seeds collected in Montana are sensitive to temperature, germination in excess of 50 percent occurs over a wide range of temperature regimes. Thus, there is an excellent potential for continued invasion of this species on these Northern Great Plains rangelands. The high level of germination exhibited by afterripened Japanese brome seeds suggest that a large portion of the disseminated seeds will germinate completely with available water during late summer and early autumn.

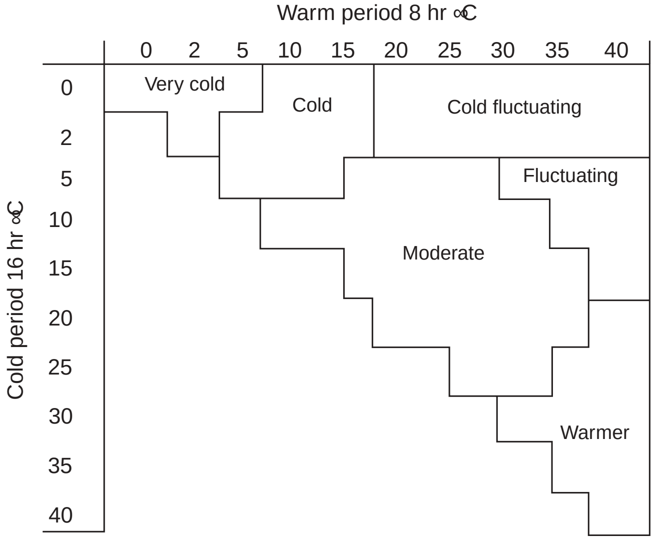


Figure 1—Temperature regimes reflecting seedbed environments occurring across a wide array of geographic locations. Regimes are based on monitoring studies.

Secondary Dormancy

We previously collected data that suggested up to 72 percent of Japanese brome seeds disseminated after mid-September in eastern Montana may enter a secondary dormancy state when they imbibe water at or near 0 °C (Haferkamp and others 1994a). These findings agree with Baskin and Baskin (1981) for Japanese brome in north-central Kentucky and with Hull and Hansen (1974) for downy brome in Utah and Idaho. We further investigated the potential for onset of secondary dormancy in Japanese brome (Haferkamp and others 1995a) by designing a study to determine which Japanese brome seed collections obtained from mid-June to late January were receptive to induction of secondary dormancy when imbibed at 0 °C.

Methods

Japanese brome seeds, collected on 17 dates from June 18, 1992, to January 28, 1993, were hand threshed and stored in near ambient outside conditions in a warehouse. In early February 1993, eight replications of 100 seeds of each collection were incubated in 9-cm petri dishes. Each dish contained two pieces of a thick medium speed filter paper with high water retention supported on a polyurethane foam disc. Distilled water was supplied to the paper (Haferkamp and others 1994a). Seeds were incubated initially for 10 days in alternating 12-hour periods of 0 and 10 °C and then transferred and incubated for an additional 18 days in alternating 12-hour periods of 8 and 23 °C. Light was supplied with cool-white fluorescent bulbs (PAR = 30 µmoles m^{-2} sec^{-1}) during each 12-hour 10 or 23 °C period. One set of seeds, the wet regime, was moistened on day 1, and another set, the dry regime, was not moistened until day 11, when seeds were transferred to the 8 and 23 °C temperature regime. Germinated seeds were counted on days 11, 14, 21, and 28, and removed from the dishes when the radicle and coleoptile were at least 5-mm long. Dishes were arranged in a randomized block design. Analysis of variance was used to detect differences in total germination data resulting from varying seed collection dates and moisture regimes. Separate analyses were conducted for each count date. Means were separated by Least Significant Difference ($P \geq 0.05$).

Results and Discussion

No seeds had germinated by day 11 (table 1). By day 14 less than 5 percent of the seeds germinated in the dry regime, but up to 69 percent germinated in the wet regime. Seed collected from June to January germinated readily in the dry regime by day 21 (92 percent) and day 28 (97 percent), and seed collected from June through mid-September germinated 94 percent by day 21 and 96 percent by day 28 in the wet regime. Germination, however, declined in the wet regime beginning with the late September collection to

Table 1—Total germination of Japanese brome seeds (includes all but moldy seeds) collected from June 1992 to January 1993 near Miles City, MT, U.S.A., and incubated for 10 days at 0 and 10 °C and 18 days at 8 and 23 °C. Dry seeds were moistened on day 11 and wet seeds were moistened on day 1.

Collection date	Count days[a]					
	14		21		28	
	Dry	Wet	Dry	Wet	Dry	Wet
	- - - - - - - -	- - - - - - - -	- - - - *percent*-	- - - - - - - -	- - - - - - - -	- - - - - - - -
Brown seed						
6/18/92	0.0^{A}_{a}	39.7^{B}_{c}	98.4^{A}_{a}	97.7^{A}_{b}	99.2^{A}_{a}	98.5^{A}_{a}
Green seed						
6/19/92	$.0^{A}_{a}$	19.3^{B}_{efg}	90.1^{A}_{ab}	84.8^{A}_{b}	94.5^{A}_{ab}	87.9^{A}_{b}
7/02/92	$.0^{A}_{a}$	68.3^{B}_{a}	97.5^{A}_{ab}	98.0^{A}_{a}	98.0^{A}_{ab}	98.8^{A}_{a}
7/15/92	1.0^{A}_{a}	69.4^{B}_{a}	99.4^{A}_{ab}	98.3^{A}_{a}	97.6^{A}_{ab}	99.2^{A}_{a}
7/30/92	$.0^{A}_{a}$	57.6^{B}_{b}	96.7^{A}_{ab}	95.8^{A}_{a}	98.9^{A}_{a}	96.1^{A}_{a}
8/13/92	$.8^{A}_{a}$	63.2^{B}_{ab}	97.7^{A}_{ab}	93.9^{A}_{a}	99.0^{A}_{a}	95.0^{A}_{ab}
8/27/92	4.0^{A}_{a}	56.4^{B}_{b}	98.8^{A}_{a}	96.8^{A}_{a}	98.8^{A}_{a}	97.4^{A}_{a}
9/10/92	2.5^{A}_{a}	27.5^{B}_{cde}	98.8^{A}_{a}	89.9^{B}_{ab}	98.8^{A}_{a}	92.8^{A}_{ab}
9/24/92	$.5^{A}_{a}$	19.5^{B}_{defg}	97.9^{A}_{a}	72.1^{B}_{c}	98.1^{A}_{ab}	74.4^{B}_{c}
10/08/92	$.8^{A}_{a}$	12.8^{B}_{efgh}	98.2^{A}_{a}	50.4^{B}_{e}	99.2^{A}_{a}	56.1^{B}_{d}
10/22/92	$.0^{A}_{a}$	6.0^{A}_{fgh}	95.9^{A}_{ab}	59.0^{B}_{d}	97.8^{A}_{ab}	73.8^{B}_{c}
11/05/92	$.0^{A}_{a}$	12.3^{A}_{efgh}	90.3^{A}_{ab}	46.9^{B}_{e}	95.0^{A}_{ab}	53.6^{B}_{d}
11/19/92	$.0^{A}_{a}$	$.6^{A}_{h}$	69.4^{A}_{c}	32.4^{B}_{g}	93.1^{A}_{ab}	54.2^{B}_{d}
12/02/92	$.0^{A}_{a}$	4.6^{A}_{fgh}	75.3^{A}_{c}	32.5^{B}_{fg}	90.8^{A}_{b}	42.3^{B}_{e}
12/17/92	$.0^{A}_{a}$	6.5^{A}_{fgh}	88.0^{A}_{b}	46.0^{B}_{ef}	96.9^{A}_{ab}	53.9^{B}_{d}
12/31/92	$.0^{A}_{a}$	3.5^{A}_{gh}	89.2^{A}_{b}	46.8^{B}_{e}	95.9^{A}_{ab}	60.0^{B}_{d}
1/28/93	$.0^{A}_{a}$	4.1^{A}_{fgh}	81.8^{A}_{bc}	19.0^{B}_{h}	95.5^{A}_{ab}	28.2^{B}_{f}

[a] Paired moisture treatment means within collection date and count day followed by the same superscript do not differ significantly (P > 0.05). Collection date means within a moisture treatment and count day followed by a similar subscript do not differ significantly (P > 0.05).

an average of 45 percent by day 21 and 55 percent by day 28 for seed collected from late September to January.

Timing of seed dissemination is determined by seed maturation and factors such as wind, rain, and disturbance by birds, insects, and mammals. These results suggest that 26 to 72 percent of the seeds that were not disseminated until after mid-September may enter secondary dormancy. These seeds that enter secondary dormancy may enter the seed bank and germinate the following autumn or later. Allowing this large percentage of seeds to overwinter will potentially enhance proliferation and perpetuation of Japanese brome on Northern Great Plains rangelands.

Water Stress

Seed germination is controlled by the availability of soil water at an adequate temperature. Pyke and Novak (1994) found that germination of downy brome occurred over a normal range of soil water contents, and germination was not inhibited by soil water potentials of –1.5 MPa. Downy brome seed tend to respond to intermittent moisture with minimal delay in germination rate (Allen and others 1994). Time to germination of downy brome seed may increase as soil water potential becomes more negative (Evans 1961; Evans and Young 1972). Our objective was to determine the impact of water stress on seed germination of Japanese and downy brome. Alternately, were differences between species in germination pattern sufficient to explain the dominance of downy brome on drier sites in years following relative dry autumns?

Methods

Japanese and downy brome seed were collected in July 1992 from native rangeland near Miles City, MT. Seeds were initially stored in paper sacks in an unheated warehouse until July 1993 when they were brought into the laboratory and stored at about 21 °C. Seeds were germinated in 9-cm petri dishes containing 30 ml of the appropriate solution. Osmotic solutions were prepared with 20,000 MW polyethylene glycol and distilled water. In Trial 1 osmotic potentials ranged from –0.05 to –1.3 MPa, and in Trial 2 osmotic potentials ranged from –0.03 to –0.99 MPa. Solution osmotic potentials were measured at the beginning and end of the study with a vapor pressure osmometer. Each dish contained one piece of a thick medium-speed filter paper with high retention supported on a polyurethane foam disc (Haferkamp and others 1994a). The filter paper was continually moistened via a cotton wick inserted through the center of the foam disc. Once filter paper was saturated, 100 seeds of each collection were placed on the filter paper, and covered dishes were placed individually into a polyethylene bag. Seeds were germinated for 28 days at alternating 8/23 °C with illumination during the 12 hours at 23 °C. Dishes were arranged in a randomized complete-block design with eight replications. Replications were run over time, with two replications placed in the germinator at 2-day intervals in Trial 1 and 7-day intervals in Trial 2, until all eight replications were being incubated. Germination was counted every 2 days in Trial 1 and every 7 days in Trial 2. Seeds were considered germinated when coleoptiles and radicals were 5 mm long.

In Trial 1, a sigmoidal time-dependent response function was fit to data from each dish. Resulting parameters were subject to analysis of variance to determine osmotic potential effects on germination patterns. In Trial 2, the sampling interval precluded fitting a sigmoid-shaped curve to the data. Thus, the counts of seeds germinated at each sampling point were subject to analysis of variance directly.

Results and Discussion

In Trial 1 no Japanese brome seed germinated in osmotic potentials ranging from –0.9 to –1.3 MPa (fig. 2). Maximum seed germination was >95 percent in –0.05 to –0.23 MPa. Seed germination declined to <35 percent in –0.63 MPa. Days to 50 percent of maximum germination ranged from 5 to 9 days for –0.05 to –0.23 MPa to 22 days for –0.63 MPa (fig. 3). In Trial 2 Japanese brome seed germination was <15 percent in –0.99 MPa (fig. 4), >90 percent in –0.03 to –0.29 MPa, and <90 percent but >75 percent in –0.5 MPa and >35 percent in –0.71 MPa. Japanese and downy brome seed germinated similarly in –0.03 to –0.16 MPa (figs. 4 and 5). Maximum germination of downy brome seed was, however, up to 5.5 fold greater than germination of Japanese brome seed in –0.29 to –0.99 MPa.

Water stress can both reduce amount and rate of germination of Japanese brome seed. In addition we have observed years when seedlings that emerged from germinating seeds during late August perished due to lack of soil water in September. It appears that soils must be wet for 3 to 5 days for seeds to germinate. Mack and Pyke (1984) report that a series of successive days of >1 mm of precipitation during autumn appears adequate for germination of downy brome. Thill and others (1979) report that reductions in soil matric potential from –0.2 to –1.6 MPa markedly reduced the percentage and rate of germination of downy brome. They

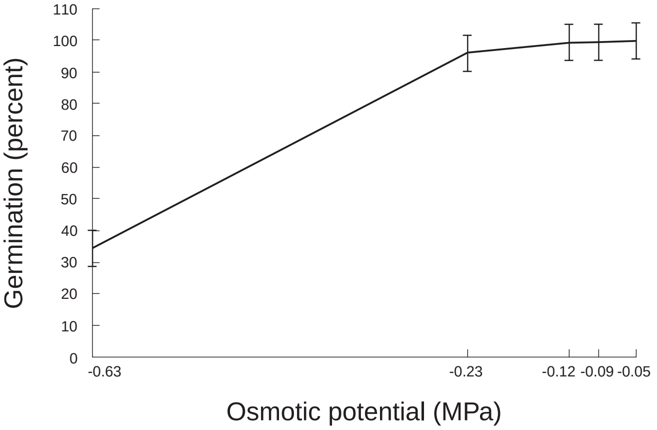


Figure 2—Effect of osmotic potential on maximum percentage germination of Japanese brome seed. Least square means ± standard error at P = 0.05 are presented.

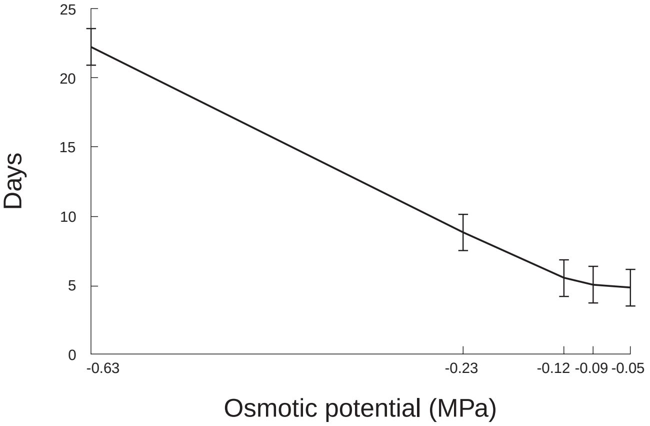


Figure 3—Effect of osmotic potential on days to 50-percent germination of Japanese brome seed. Least square means ± standard error at P = 0.05 are presented.

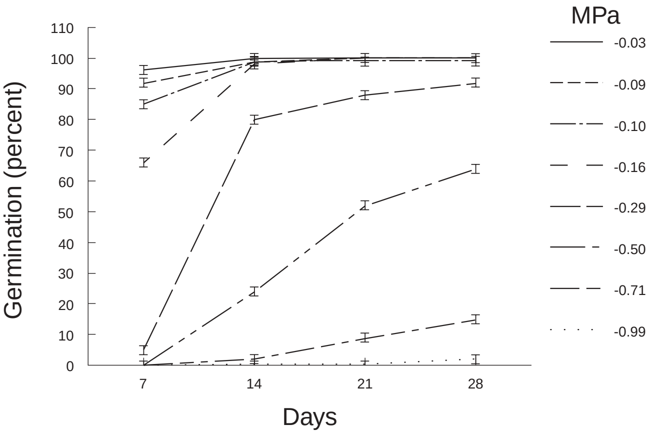


Figure 4—Effect of osmotic potential on percent germination of Japanese brome seed. Least square means ± standard error at P = 0.05 are presented.

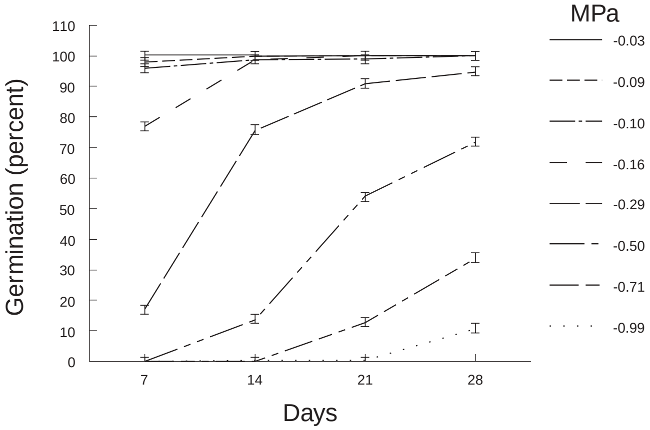


Figure 5—Effect of osmotic potential on percent germination of downy brome seed. Least square means ± standard error at P = 0.05 are presented.

found that downy brome is adapted to a wide range of temperatures and soil water conditions, and is limited mostly by cold soil or warm dry soil. Although seeds of both annual bromes germinated over a wide range of osmotic potentials in our study, the fact that downy brome seeds appeared to germinate with greater stress than Japanese brome seed helps explain why downy brome dominates on drier sites and in years preceded by dry autumns in the Northern Great Plains.

Conclusions

Annual bromes are clearly adapted to the Northern Great Plains. The high level of germination exhibited by after-ripened seeds suggests a large portion of the disseminated seeds will germinate with available water during late summer and early autumn. The secondary dormancy state attained by some seeds will also enhance the species persistence on rangelands, because seedlings emerging in August and September in any year likely come from two seed crops, the current and previous years.

Fluctuations in environmental conditions will continue to cause erratic fluctuations in annual brome populations on Northern Great Plains rangelands. However, due to the large seed banks and ability of seeds to germinate in variable environmental conditions, we think annual bromes will persist on these rangelands for many years in the future.

Acknowledgments

Authors express appreciation to cooperators Trudy Hentges, Caralea Leidholt, Debra Palmquist, James Young, Cheryl Murphy, and Bryon Bennet for assistance in these studies, and to Mary Ellen French for manuscript assistance.

References

Allen, P. S.; Debaene-Gill, S. B.; Meyer, S. E. 1994. Regulation of germination timing in facultatively fall-emerging grasses. In: Monsen, S. B.; Kitchen, S. G., comps. Proceedings—ecology and management of annual rangelands; 1992 May 18–21; Boise, ID. Gen. Tech. Rep. INT-GTR-313. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 215–219.

Baskin, J. M.; Baskin, C. C. 1981. Ecology of germination and flowering in the weedy winter annual grass *Bromus japonicus*. Journal of Range Management. 34: 369–372.

Daubenmire, R. 1970. Steppe vegetation of Washington. Bull. 62. Pullman: Washington Agricultural Experiment Station. 131 p.

Evans, R. A. 1961. Effects of different densities of downy brome (*Bromus tectorum*) on growth and survival of crested wheatgrass (*Agropyron desertorum*) in the greenhouse. Weeds. 9: 216–223.

Evans, R. A.; Young, J. A. 1972. Microsite requirements for establishment of annual rangeland weeds. Weed Science. 20: 350–356.

Gartner, F. R.; Butterfield, R. I.; Thompson, W. W.; Roath, L. R. 1986. Prescribed burning of range ecosystems in South Dakota. In: Hyder, D. N., ed. Proceedings 1st International Rangeland Congress; 1978 August 14–18; Denver, CO: Society for Range Management: 687–690.

Haferkamp, M. R.; Grings, E. E.; Heitschmidt, R. K.; MacNeil, M. D.; Karl, M. G. 2001a. Suppression of annual brome impacts rangeland: animal responses. Journal of Range Management. 54: 663–668.

Haferkamp, M. R.; Heitschmidt, R. K.; Grings, E. E.; MacNeil, M. D.; Karl, M. G. 2001b. Suppression of annual bromes impacts rangeland: vegetation responses. Journal of Range Management. 54: 656–662.

Haferkamp, M. R.; Heitschmidt, R. K.; Karl, M. G. 1997. Influence of Japanese brome on western wheatgrass yield. Journal of Range Management. 50: 44–50.

Haferkamp, M. R.; Heitschmidt, R. K.; Karl, M. G. 1998. Clipping and Japanese brome reduce western wheatgrass standing crop. Journal of Range Management. 51: 692–698.

Haferkamp, M. R.; Karl, M. G.; MacNeil, M. D. 1994a. Influence of storage, temperature, and light on germination of Japanese brome seed. Journal of Range Management. 47: 140–144.

Haferkamp, M. R.; MacNeil, M. D.; Karl, M. G. 1995a. Induction of secondary dormancy in Japanese brome (*Bromus japonicus*). In: West, N., ed. Proceedings 5th International Rangeland Congress, rangelands in a sustainable biosphere; 1995 July 23–28; Salt Lake City, UT. Denver, CO: Society of Range Management: 199–200.

Haferkamp, M. R.; Palmquist, D.; Young, J. A.; MacNeil, M. D. 1995b. Influence of temperature on germination of Japanese brome seed. Journal of Range Management. 48: 264–266.

Haferkamp, M. R.; Volesky, J. D.; Borman, M. M.; Heitschmidt, R. K.; Currie, P. O. 1993. Effects of mechanical treatments and climatic factors on the productivity of Northern Great Plains rangelands. Journal of Range Management. 46: 346–350.

Haferkamp, M. R.; Young, J. A.; Grings, E. E.; Karl, M. G.; Heitschmidt, R. K.; MacNeil, M. D. 1994b. Japanese brome in the Northern Great Plains. In: Monsen, S. B.; Kitchen, S. G., comps. Proceedings—ecology and management of annual rangelands; 1992 May 18–21; Boise, ID. Gen. Tech. Rep. INT-GTR-313. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 396–401.

Hewlett, D. B.; Johnson, J. R.; Butterfield, R. I.; Mosley, V. K. 1981. Japanese brome response to atrazine in combination with nitrogen fertilizer in the mixed prairie. Journal of Range Management. 34: 22–25.

Hull, A. C., Jr.; Hansen, W. T., Jr. 1974. Delayed germination of cheatgrass seed. Journal of Range Management. 27: 366–368.

Hulbert, L. C. 1955. Ecological studies of *Bromus tectorum* and other annual brome grasses. Ecological Monographs. 25: 181–213.

Karl, M. G.; Heitschmidt, R. K.; Haferkamp, M. R. 1999. Vegetation biomass dynamics and patterns of sexual reproduction in northern mixed-grass prairie. American Midland Naturalist. 141: 227–237.

Mack, R. N. 1981. Invasion of *Bromus tectorum* L. into Western North America: an ecological chronicle. Agro-Ecosystems. 7: 145–165.

Mack, R. N.; Pyke, D. A. 1983. The demography of *Bromus tectorum*: variation in time and space. Journal of Ecology. 71: 69–93.

Pyke, D. A.; Novak, S. J. 1994. Cheatgrass demography-establishment attributes, recruitment, ecotypes, and genetic variability. In: Monsen, S. B.; Kitchen, S. G., comps. Proceedings—ecology and management of annual rangelands; 1992 May 18–21; Boise, ID. Gen. Tech. Rep. INT-GTR-313. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 12–21.

Rummell, R. S. 1946. Some effects of competition from cheatgrass brome on crested wheatgrass and bluestem wheatgrass. Ecology. 27: 159–167.

Thill, D. C.; Schirman, R. D.; Appleby, A. P. 1979. Influence of soil moisture, temperature, and compaction on the germination and emergence of downy brome (*Bromus tectorum*). Weed Science. 27: 625–630.

Vallentine, J. F.; Stevens, A. R. 1994. Use of livestock to control cheatgrass—a review. In: Monsen, S. B.; Kitchen, S. G., comps. Proceedings—ecology and management of annual rangelands; 1992 May 18–21; Boise, ID. Gen. Tech. Rep. INT-GTR-313. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 202–206.

Whisenant, S. G. 1990. Postfire population dynamics of *Bromus japonicus*. American Midland Naturalist. 123: 301–308.

Young, J. A.; Evans, R. A. 1978. Germination requirements as determinants of species composition of *Artemisia* rangeland communities. In: Hyder, D. N., ed. Proceedings 1st International Rangeland Congress; 1978 August 14–18; Denver, CO: Society for Range Management: 366–369.

Fate of Fall-Sown Bitterbrush Seed at Maybell, Colorado

Robert Hammon
Gary Noller

Abstract: Approximately 50,000 acres of a nearly pure stand of bitterbrush, *Purshia tridentata* (Pursh), near Maybell, CO, has burned in the past 2 decades. Attempts at reclaiming bitterbrush stands by seeding burned land have been largely ineffective. A research project funded by the Colorado Division of Wildlife Habitat Partnership Program was initiated in the fall of 2000 to determine the causes of seeding failures. Initial observations on seeds planted in the fall of 1999 indicated that insects such as wireworms and cutworms may have been responsible in part for seeding failures. Seeds planted November 2000 had germinated by early April 2001, with little impact from insect or other predators noted during the 2000/2001 planting and establishment season. More than 90 percent of those seedlings died during the summer from drought. Only 1.25 percent of seeds planted in the fall of 2000 were still alive in October 2002, following the second year of drought. Seeds treated with insecticide and fungicide/rodent repellent and untreated seeds were planted in 10 seed caches on two dates (October 11 and November 15) in 2001. Samples taken on November 15 and December 19 showed that much of the seed planted on either date had already germinated. Several fungal pathogens were isolated in the fall from germinated seed. Rodents, possibly chipmunks, destroyed much of the November 15 planted seed at one site. Seedling emergence was 2 weeks to 1 month later in 2002 than 2001. Cutworms killed more than 25 percent of emerged seedlings at one site in April 2002. Most surviving seedlings were killed by drought during the summer of 2002, and by mid October, only 0.06 percent of fall 2001 planted seeds were still alive.

Introduction

The rangeland west of Maybell, CO (Moffat County), was at one time the largest continuous stand of bitterbrush, *Purshia tridentata* (Pursh), in North America. More than 50,000 acres of this stand has burned since 1980 (fig. 1). Bitterbrush is a primary winter browse source for many large game mammals, including a large elk herd that winters in the area. Winter browse has been in short supply since the fires, and elk are increasingly moving to private lands, where they are causing considerable damage to haystacks and pastures. The bitterbrush has not regenerated from seed on the burned lands, with several attempts at reseeding resulting in failure. The causes of the failures are not known, and a research project was funded in 2001 by the Colorado Division of Wildlife Habitat Partnership Program to determine the fate of fall-seeded bitterbrush at Maybell.

Maybell Rangeland

Maybell, CO, is located in the extreme northwest corner of the State in Moffat County. Maybell is located at 40 degrees N latitude, at an elevation 6,300 ft above sea level. Annual precipitation is 12 to 15 inches, with about half of the total moisture falling as snow. The years 2000, 2001, and 2002 have all received lower than normal precipitation (fig. 2). The average annual temperature is 42 °F. Winter temperatures are very cold, with numerous instances of –50 °F recorded. Climactic data for Maybell can be accessed at http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?comayb. The rangeland near Maybell is classified as "Sandhills" range, within Land Resource Area 34. The deep sandy soils are classified as Cotopaxi loamy sands. They vary from fine sandy loams in the swales to loamy fine sands on hills and upland areas.

The research site is dominated by bitterbrush in unburned areas. Other shrubs associated with bitterbrush are big and silver sagebrush, gray horsebrush, and low and rubber rabbitbrush. These shrubs are now abundant within the burned areas. The principal grasses are Indian ricegrass, needle and thread, sand dropseed, and Sandberg bluegrass. Cheatgrass is a dominant weed in burned areas.

Figure 1—Rangeland near Maybell, CO. The dark vegetation across the center of the photograph is a remnant unburned stand of bitterbrush.

In: Hild, Ann L.; Shaw, Nancy L.; Meyer, Susan E.; Booth, D. Terrance; McArthur, E. Durant, comps. 2004. Seed and soil dynamics in shrubland ecosystems: proceedings; 2002 August 12–16; Laramie, WY. Proceedings RMRS-P-31. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Robert Hammon, Western Colorado Research Center, 1910 L Road, Fruita, CO, U.S.A., e-mail: rhammon@lamar.colostate.edu. Gary Noller (Retired), Upper Colorado Environmental Plant Center, 5538 RBC #4, Meeker, CO 81641, U.S.A.

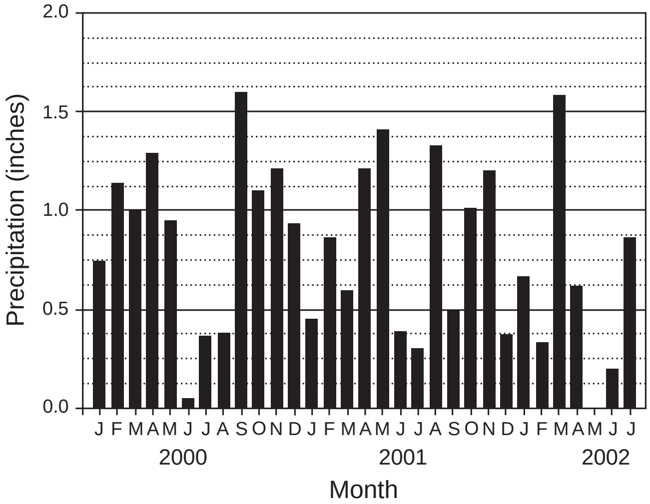


Figure 2—Precipitation at Maybell, CO, January 2000 to July 2002

Conspicuous forbs are hairy golden aster, buckwheat, lupine, loco, arrowleaf balsamroot, yarrow, death camas, scarlet globemallow, crypthantha, evening primrose, and daisy fleabane. Percent ground cover in unburned areas is about 25 percent, with ground cover generally less in burned areas.

Fall Planting Studies: 2000 and 2001

Fall 2000 Study

A simple nonreplicated seeding trial was planted in the fall of 2000, with the intention of observing seed fate and seedling behavior to use as a basis for more detailed studies in 2001. The studies were planted in two wildlife exclosures, denoted "Windmill" (N 40° 27.645'; W 108° 11.671'; elevation 6,354 ft) and "North" (N 40° 29.260'; W 108° 10.943'; elevation 6,314 ft). They are located approximately 5 miles west of the town of Maybell. Two hundred seeds were planted in each of two 10-foot-long strips at each site. One strip was planted with seed treated with imidocloprid (Gaucho 480 FS; 2 oz/cwt) and thiram (Thiram 42-S; 5 oz/cwt), and the other strip was planted with untreated seed. The Gaucho 480 FS is an insecticide intended to control soil inhabiting insects such as wireworms and white grubs and aboveground insect pests such as cutworms. The Thiram 42-S is primarily used as a fungicide, but also has rodent repellent characteristics when applied at high rates. The rate used in this study is recommended to repel rodents. The strips were planted on November 7, 2000. There were approximately 3 inches of snow on the ground at the time of planting, but the soils were not yet frozen. There was nearly continuous snow cover throughout the winter after planting.

The plots were visited on April 4, 2001, at which time many seedlings were observed. One foot of row from each strip was dug, and seeds recovered. Germination was calculated to be 79 percent. Seedling emergence was complete by mid-April 2001. A slight amount of insect and rodent feeding was noted on the seedlings during the spring observations, but the amount was insignificant. Feeding damage was observed in both treated and untreated strips. Significant mortality of emerged seedlings was observed during the summer of 2001, primarily due to drought. On May 1, 2002, 15 live seedlings were recorded at the Windmill site (3.75 percent survival of planted seeds), and three seedlings were found at the North site (0.75 percent survival). On October 7, 2002, nine seedlings were alive at the Windmill site and only one remained alive at the North site. The summer of 2002 was extremely dry (4.25 inches of precipitation through July), and mortality was attributed to drought.

Natural Reproduction of Bitterbrush: Spring 2001

Many natural bitterbrush seedlings were observed in the area during the spring of 2001. All seedlings observed appeared to be from rodent-distributed seed caches. The number of seedlings per cache varied from seven to 30. The seed caches were most easily found along the sandy edges of roadways near mature bitterbrush stands. No caches were observed more than 30 ft from mature bitterbrush stands. This is probably due to the limited range of the rodents responsible for burying the seed. There was a slight amount of insect and rodent feeding damage on natural seedlings, but it was rare. Significant mortality from drought occurred during the summers of 2001 and 2002, and by October 2002, natural caches that had emerged during 2001 were difficult to find.

Fall 2001 Study

The goal of the fall 2001 study was to evaluate planting date and seed treatments as factors influencing bitterbrush establishment. The sampling scheme was designed to determine the causes of seeding failure. The 2001 experiments were conducted in the same wildlife exclosures used in 2000. The 2001 experiment was a three-factor (planting date, seed treatment, location) randomized complete block design with four replications. The seed used in the experiments was produced in 1994 from Maybell Source plants at the Upper Colorado Environmental Plant Center near Meeker, CO. All seed was hand planted in 10 seed caches. A planting dibble was used to make a hole 1 to $1^{1}/_{2}$ inches in depth, into which the seed was placed. Plots were seeded on October 11 and November 15, 2001. The seed treatments were the same as used in 2000: Gaucho 480 FS (2 oz/cwt) plus Thiram 42-S (5 oz/cwt) or untreated. Twenty-five caches of each treatment were planted in each replication. The October 11 planting date was sampled on November 15, the day the second planting date was seeded. Both planting dates were sampled on December 19, 2001, April 9, 2002, and May 1, 2002. Five randomly chosen caches were dug on each sample date to determine seed fate. Samples were taken to the laboratory where seeds were removed and inspected for damage. Seed samples from the December 19 sample were sent to the Jefferson County Cooperative Extension Plant Diagnostic Clinic, Golden, CO, in December 2001 for pathogen identification after seed rots were observed. More samples from the same sample date were sent to the North Carolina State University Plant Pathogen Identification Laboratory, Raleigh, NC, for molecular characterization of the pathogens. Plots were evaluated again on June 18, 2002, and October 7, 2002, by randomly choosing five caches from each treatment per replication, and counting the live plants.

Results from fall 2001 and spring/summer 2002 sampling of the fall 2001 planted plots is displayed in tables 1 and 2. The most surprising aspect of the fall 2001 sampling is that much of the seed had germinated shortly after planting, instead of remaining dormant until spring. Seventy-seven percent of October 11 planted seed had begun the germination process by November 15. Germination of October 11 planted seed was significantly greater at the Windmill versus the North site, probably a result of drier soil conditions at the latter site. Seed treatments were responsible for a slight, but significant increase in germination, and reduction in damage of October 11 planted seed on the first sample date.

When the sites were visited on December 19, 2001, there were 2 to 4 inches of snow on the ground, and the soil was frozen. Five caches per treatment were sampled in one replication at each site, and data were not subjected to statistical analysis. Germination of October 11 planted seed was 92.6 percent on December 19, while that of November 15 planted seed was 13 percent. Seed planted on November 15 at the North site was destroyed by rodents between the time of planting and December 19. Only 20 percent of treated seed and 4 percent of untreated seed was recovered. Seed that was cracked and chewed upon was easily found in the samples. None of the intact seed recovered at the North site had germinated. Dry conditions, which were responsible in part for a shallow planting depth at the site, may have made the seed accessible to rodents. The holes made by the planting dibble tended to collapse before seed could be placed into them. This caused seeding depth to be less than 1 inch.

Five random seed caches from each treatment were dug from each replication on April 9 and again on May 1, 2002. No seedlings had emerged on April 9, 2002. In 2001, emergence was complete by that date. This difference may have resulted from differences between the 2 years in soil temperature. Seedlings had emerged on the May 1, 2002, sample date. Percent emergence, calculated by counting the number of seedlings divided by the number of seeds planted, was greatest for the October 11 planted seed at the North site, and least for the November 15 planted seed at that site. Differences in emergence at the Windmill site were slight, although there was significantly greater emergence of treated seed for the November 15 planting date than the October 11 planting date. On May 1, 6.8 percent of seeds at the Windmill site and 8.7 percent of seeds at the North site had emerged and were still alive. There was no significant impact of seed treatment on emergence, and interactions were not statistically significant for seed treatment x site or planting date

When the plots were visited on June 18, 2002, all emerged plants at the Windmill site were dead. Only two plants, in a

Table 1—Sample data from fall 2001. The November 15 sample was taken from only October 11 planted seed. The 19 December sample was nonreplicated, so not subjected to analysis of variance.

			Sample dates[a]				
Site	**Planting date**	**Seed treatment**	**Recovery Nov. 15, 2001**	**Germinated Nov. 15, 2001**	**Damage[b] Nov. 15, 2001**	**Recovery Dec. 19, 2001**	**Germinated Dec. 19, 2001**
			- - - - - - - - - - - -	- - - - - -	*Percent*	- - - - - -	- - - - - - - - - - - -
Windmill	October 11 only on first sample; both on second date	Both	65.0	83.4a	6.0	79	59.2
North		Both	70.3	70.4b	7.1	30.5	46.5
	***P*-value**		**NS**	**.0158**	**NS**		
Both	October 11	Both	67.6	76.9	6.6	57.5	92.6
Both	November 15	Both				52	13.0
Both	October 11 only on first sample; both on second date	Treated	72.5	82.2a	4.1B	56.0	54.7
Both		Untreated	62.8	71.6b	9.0A	53.5	51.0
	***P*-value**		**NS**	**.0373**	**.0727**		
Windmill	October 11	Treated	65.0	86.8	4.7	54	100
Windmill	October 11	Untreated	65.0	79.9	7.3	78	84.6
Windmill	November 15	Treated				90	22.2
Windmill	November 15	Untreated				94	29.8
North	October 11	Treated	80.0	77.6	3.4	60	96.7
North	October 11	Untreated	60.5	63.2	10.7	38	89.4
North	November 15	Treated				20	0
North	November 15	Untreated				4	0
	***P*-value**		**NS**	**NS**	**NS**		

[a] Means followed by the same lower case letter are not significantly different at $P = 0.05$; means followed by the same upper case letter are not significantly different at $P = 0.10$.

[b] Seed was considered damaged if it appeared abnormal in any way. Most damage was due to chewing by rodents or mold from fungal growth.

Table 2—Sample data from spring 2002.

			Sample dates[a]					
			April 9, 2002		May 1, 2002			
Site	Planting date	Seed treatment	Recovery	Germinated	Recovery	Germinated	Cutworm damage	Emergence
			Percent					
Windmill			83.1a	62.3a	72.1a	58.8a	25.1a	6.9
North			56.6b	39.9b	38.3b	36.5b	8.0b	8.8
	***P*-value**		**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**.0027**	**NS**
	October 15		80.9a	62.0a	65.6a	58.5a	18.8	10.9a
	November 15		58.9b	40.2b	44.8b	36.8b	14.3	4.8b
	***P*-value**		**<0.0001**	**.0001**	**.0001**	**<0.0001**	**NS**	**.0007**
Windmill	October 15		81.0a	59.6a	68.5ab	59.0a	27.7	5.3bc
Windmill	November 15		85.2a	65.0a	75.8a	58.5a	22.6	8.5b
North	October 15		80.7a	64.4a	62.8b	58.0a	9.9	16.5a
North	November 15		32.5b	15.4b	13.8c	15.0b	6.1	1.0c
	***P*-value**		**<0.0001**	**<0.0001**	**<0.0001**	**.0001**	**NS**	**<0.0001**
		Untreated	68.4	51.0	56.0	49.3	16.9	7.3
		Treated	71.4	51.1	54.4	46.0	16.2	8.4
	***P*-value**		**NS**	**NS**	**NS**	**NS**	**NS**	**NS**
Windmill		Untreated	81.3	62.7	72.5	58.4	20.9AB	6.3
Windmill		Treated	85.0	61.9	71.8	59.2	29.3A	7.5
North		Untreated	55.5	39.3	39.5	40.3	12.9BC	8.3
North		Treated	57.7	40.4	37.0	32.7	3.1C	9.3
	***P*-value**		**NS**	**NS**	**NS**	**NS**	**.0835**	**NS**
	October 15	Untreated	79.5	62.8	62.8A	60.0	18.3	10.8
	October 15	Treated	82.2	61.2	68.5A	57.0	19.4	11.0
	November 15	Untreated	57.3	39.2	49.3B	38.6	15.5	3.8
	November 15	Treated	60.5	41.1	40.3B	34.9	13.1	5.8
	***P*-value**	**NS**	**NS**	**.0860**	**NS**	**NS**	**NS**	
Windmill	October 15	Untreated	80.5	68.4a	66.5	63.2a	23.0	7.0cd
Windmill	October 15	Treated	81.5	50.7b	70.5	54.9a	32.4	3.5de
Windmill	November 15	Untreated	82.0	56.9ab	78.5	53.5a	18.9	5.5cde
Windmill	November 15	Treated	88.5	73.0a	73.0	63.5a	26.2	11.5bc
North	October 15	Untreated	78.5	57.1ab	59.0	56.8a	13.6	14.5ab
North	October 15	Treated	83.0	71.6a	66.5	59.2a	6.2	18.5a
North	November 15	Untreated	32.5	21.5c	20.0	23.7b	12.1	2.0de
North	November 15	Treated	32.5	9.2c	7.5	6.3c	0.0	0.0e
	***P*-value**		**NS**	**.0021**	**NS**	**.0309**	**NS**	**.0183**

[a] Means followed by the same lower case letter are not significantly different at $P = 0.05$; means followed by the same upper case letter are not significantly different at $P = 0.10$.

single cache, were found in the samples at the North site. The cause of death of seedlings that had been alive on May 1 was probably drought. Less than $^{1}/_{2}$ inch of precipitation had fallen between the time seedlings emerged and the sample date. The plots were evaluated again on October 7, 2002, and the survival was the same as on June 18. No seedlings were found at the Windmill site, and only two were found at the North site.

Insect Predators and Fungal Pathogens

Army cutworm, *Euxoa auxiliaris* (Grote), killed a significant number of seedlings at both sites; 25.1 percent of seedlings at the Windmill site and 8.0 percent at the North site were cut off by May 1, 2002. There were no statistical differences between planting dates or seed treatments. All recorded cutworm damage occurred between emergence and May 1.

All soil-inhabiting insects were collected from soil samples taken in the fall of 2001 and spring of 2002. Several species of ground beetles (Coleoptera: Carabidae) were found. While some of these are seed predators, it is not known if they prey upon bitterbrush seed. White grub larvae (Coleoptera: Scarabidae: *Phyllophaga* spp) were common in fall-collected samples, and adults were found in spring samples. These root-feeding insects are probably associated with grasses growing in the area. Seed predation by insects appeared to be of little significance to seedling establishment. Army cutworm was the only insect to affect bitterbrush establishment during this study. All specimens collected during the study are deposited in the Western Colorado Research Center insect collection at Fruita.

Two fungal pathogens were recovered from germinated seeds during the fall of 2001. They were cultured and initially identified as *Fusarium* spp. and *Rhizoctonia* spp. by the Jefferson County Plant Disease Diagnostic Laboratory, Golden, CO. Samples of rotted seed collected on December 19, 2001, were sent to The North Carolina State University Plant Pathogen Identification Laboratory, Raleigh, NC, for molecular characterization of the fungus. Two *Rhizoctonia*-like isolates were identified. The most common produced white mycelia and sclerotia after growth on PDA media. The other produced brown mycelia, but no sclerotia. Molecular analysis of these isolates showed that they were actually *Poculum* spp., probably unidentified species.

Two *Fusarium* species were also present, but not common. One produced a carmine red colony with cottony brown mycelia. The second isolate produced light pink to yellow colonies. One isolate was identified as *F. redolens*, and the second was determined to be an undescribed *Fusarium* species.

Thiram fungicide appeared to have some impact on protecting seedlings after emergence. Seed collected on December 19 was grown out in the greenhouse, and damping off type symptoms were more common on untreated seed than treated seed.

Seed Age and Dormancy

The seed used in both the fall 2000 and 2001 planting studies was produced in 1994 and stored since that time. Germination tests were conducted in June 1995, September 1997 and March 2002 by the Colorado Seed Laboratory, Fort Collins, CO. Results from that testing are displayed in figure 3. The percent live seed increased and the percentage of dormant seed decreased over time. It is interesting to note that the percent germination recorded in the fall 2001 planting was greater than that recorded in the 2002 seed test of the same seed lot. The lack of seed dormancy is responsible for the fall germination of 2001 planting. The 2000 planting did not experience fall germination because of cold soil temperatures when the plots were seeded.

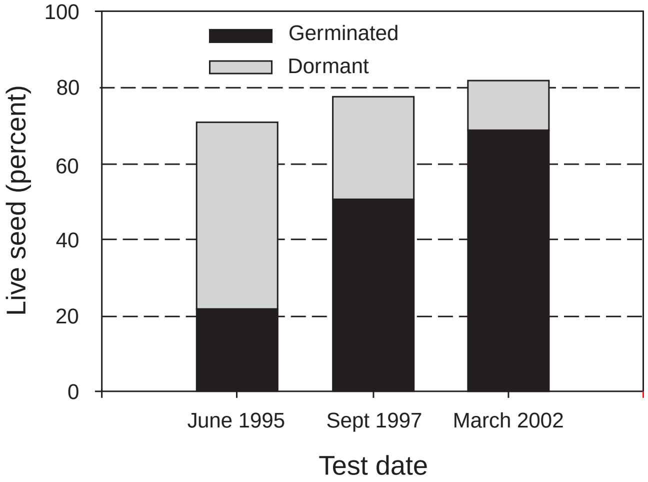


Figure 3—Germination tests conducted on 1994 produced seed used in experiments.

Conclusions

- Several factors affected bitterbrush establishment from seed in this study. Fungal pathogens impacted seed before emergence. Cutworms killed many plants after emergence. Drought killed most other plants.
- Moisture affected seeding depth and germination, and lack of moisture killed most seedlings in the first 4 months after emergence.
- Once seedlings have survived their first year, they are much more capable of surviving drought.
- Fall germination of seed may be important in pathogenicity of *Fusarium*- and *Rhizoctonia*-like organisms.
- Gaucho seed treatment was not effective in controlling insects. Thiram was marginally effective in controlling pathogens and seed predation by mammals. Other compounds may be more effective.

Comparative Seed Germination Biology and Seed Propagation of Eight Intermountain Species of Indian Paintbrush

Susan E. Meyer
Stephanie L. Carlson

Abstract: In chilling experiments with seeds of eight *Castilleja* species, seeds of all species were dormant at harvest and responded positively to moist chilling. Seeds of species from warmer, drier habitats had shorter chilling requirements, germinated more quickly during chilling, and were more likely to lose dormancy in dry storage than those of species from high elevation habitats with longer winters. Seed germination patterns within *Castilleja* were not affected by the hemiparasitic habit, but instead were similar to those of species of *Penstemon* from similar habitats. Seedlings of all eight species were readily produced in container culture, but outplanting success was greatly enhanced by potting the seedlings with a potential host plant for 6 to 8 weeks prior to transplanting outdoors.

Introduction

Indian paintbrush (*Castilleja*: Scrophulariaceae) species are among the most beautiful, well-known, and beloved Western native wildflowers, yet they are very seldom seen in cultivation. Published information on paintbrush propagation and cultural requirements is limited. In this investigation, we attempted to fill this information gap. Our study was carried out with two objectives in mind, namely to learn to propagate paintbrushes from seed as well as to understand something about their establishment ecology in the wild.

The chief obstacle to paintbrush cultivation is often thought to be their hemiparasitic nature. Paintbrushes are not true parasites, in the sense that they have chlorophyll and are capable of making their own food through photosynthesis. But most, if not all, paintbrushes apparently rely on a root connection with a host plant as a source of inorganic and organic nutrients as well as water, especially in more xeric habitats and during the dry season in mesic habitats (Press 1989). Because of this hemiparasitism, there seems to have been the assumption that paintbrush seeds would be difficult to germinate, perhaps requiring a signal from the host as in strict parasites such as *Striga* (Press and Graves 1995). Thus, reports of even the most straightforward chilling experiments with these species are lacking in the literature. In addition, it is not actually known which Intermountain species are hemiparasites, or whether the relationship with a host is an obligate one.

In this study, we use a comparative approach in exploring the relationship between habitat and paintbrush seed germination syndrome. This tactic has been successful for us in work with many Intermountain genera, including *Penstemon*, another large genus in the Scrophulariaceae (for example, Meyer and others 1995). The approach involves making multiple seed collections of related species, and populations within species, from as wide a range of habitats as possible, subjecting seeds to a standard array of laboratory germination tests, and relating their responses to habitat at the site of seed origin. This also provides valuable information for use in propagating these species from seed.

Materials and Methods

Fourteen seed collections representing eight species were made in the summers of 1997 (six species) and 1998 (*C. scabrida* and *C. miniata*; table 1). The collections were cleaned by screening and blowing, and seeds were stored in manila envelopes under laboratory conditions until the initiation of experiments 2 to 4 months later (depending on collection date).

The experiment had a completely randomized design and included six chilling treatments: 0, 4, 8, 12, 16, and 24 weeks of moist chilling at 2 °C in the dark. After chilling, dishes were transferred to a 10/20 °C alternating temperature regime (12 hours:12 hours), with cool white fluorescent light during the period at higher temperature. For each experimental treatment, there were four replications of 25 seeds per collection. Seeds were placed on the surface of two moistened germination blotters in plastic 10- by 100-mm petri dishes, and blotters were remoistened with water as necessary during the course of the experiment. Germinated seeds (that is, with radicles visible) were counted and removed periodically during chilling in the 24-week chilling treatment and weekly during the 4-week postchilling incubation period for all treatments. At the end of postchilling incubation, ungerminated seeds were scored

---

In: Hild, Ann L.; Shaw, Nancy L.; Meyer, Susan E.; Booth, D. Terrance; McArthur, E. Durant, comps. 2004. Seed and soil dynamics in shrubland ecosystems: proceedings; 2002 August 12–16; Laramie, WY. Proceedings RMRS-P-31. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Susan E. Meyer is a Research Ecologist and Stephanie L. Carlson is a Biological Technician, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Shrub Sciences Laboratory, 735 North 500 East, Provo, UT 84606, U.S.A., e-mail: smeyer@susna.com

Table 1—Collection information for 14 seed collections of *Castilleja* species included in study.

Species	Population	County	Habitat	Viability
C. exilis	Calf Creek	Garfield	Desert riparian	91.5
C. exilis	Utah Lake	Utah	Freshwater marsh	95.7
C. linariifolia	North of Boulder	Garfield	Pinyon-juniper woodland	90.0
C. linariifolia	North of Escalante	Garfield	Pinyon-juniper woodland	83.7
C. linariifolia	Boulder Mountain	Garfield	Mountain meadow	99.5
C. chromosa	North of Koosharem	Sevier	Sagebrush steppe	87.0
C. chromosa	Fishlake Pass	Wayne	Sagebrush steppe	92.7
C. chromosa	Santaquin Hill	Utah	Sagebrush steppe	86.7
C. scabrida	East of Zion	Kane	Pinyon-juniper woodland	88.0
C. flava	Soldier Summit	Utah	Mountain brush	96.5
C. miniata	Aspen Grove	Utah	Aspen parkland	87.0
C. applegatei	Bald Mountain Pass	Summit	Alpine meadow	96.0
C. rhexifolia	Albion Basin	Salt Lake	Subalpine meadow	95.8
C. rhexifolia	Mirror Lake	Duchesne	Alpine meadow	93.7

for viability using a cut test (that is, seeds with firm, white embryos were scored as viable). Mean germination percentages for each collection-treatment combination were calculated on the basis of total viable seeds. Viability was generally high (table 1; average 92 percent). Six of the collections included in this study were also part of a later study (Mogensen and others 2001) on the effects of chilling temperature on dormancy loss for species of *Castilleja*, *Penstemon*, and several other genera. These experiments were initiated in April 2000, approximately 3 years after harvest for the 1997 paintbrush collections and 2 years after harvest for the 1998 collections. To examine whether paintbrush seeds lose dormancy in dry storage, we compared our data for recently harvested seeds with the data in Mogensen and others (2001) for seeds laboratory stored for 2 to 3 years. To make the chilling temperatures comparable to our 2 °C chilling data, we averaged the data for the 1 and 3 °C chilling temperatures.

We analyzed the data for each seed collection in the chilling experiment with recently harvested seeds using one-way fixed effects analysis of variance (ANOVA), with chilling duration as the independent variable and germination percentage (proportion) as the dependent variable. Germination proportion was based on the number of viable seeds in each replicate, and was arcsine transformed to improve homogeneity of variance prior to analysis.

Results

Seeds of all eight species of Indian paintbrush were essentially completely dormant without chilling (table 2). Species and populations within species varied greatly in their response, but seeds of all species responded to chilling to at least some degree. In general, populations from warmer, low-elevation sites had shorter chilling requirements and more rapid germination during chilling than populations and species from higher, colder sites. But there were distinctive differences among species superimposed over this general pattern.

Table 2—Mean germination percentages (expressed as percentage of viable seeds) after chilling at 2 °C for 0 to 24 weeks followed by incubation at 10/20 °C for 4 weeks for 14 Utah seed collections belonging to eight Intermountain species of *Castilleja*.

		Chilling duration (weeks)[a]					
Species	**Population**	**0**	**4**	**8**	**12**	**16**	**24**
C. exilis	Calf Creek	0b	100a	98.8a	99.0a	100a	98.9a
C. exilis	Utah Lake	0b	99.0a	100a	100a	99.0a	100a
C. linariifolia	North of Boulder	3.0b	100a	100a	100a	100a	99.0a
C. linariifolia	North of Escalante	0c	90.6b	93.8b	98.7a	100a	100a
C. linariifolia	Boulder Mountain	0d	17.1c	22.6c	74.3b	100a	100a
C. chromosa	West of Koosharem	0d	6.5c	51.5b	88.3a	81.8a	81.0a
C. chromosa	Fishlake Pass	0c	5.9c	48.7b	83.0a	87.8a	84.9a
C. chromosa	Santaquin Hill	0c	1.3c	32.5b	72.7a	41.0b	66.3a
C. scabrida	East of Zion	6.7d	72.1ab	51.0c	57.2bc	56.6bc	84.1a
C. flava	Soldier Summit	0d	5.7cd	10.3c	56.3b	66.8b	85.9a
C. miniata	Aspen Grove	0b	14.7a	10.3a	11.3a	4.7ab	13.7a
C. applegatei	Bald Mountain Pass	0b	1.1b	5.3b	15.0a	14.3a	18.7a
C. rhexifolia	Albion Basin	0c	3.2c	11.7b	12.4b	10.0b	20.6a
C. rhexifolia	Mirror Lake	0a	0a	1.0a	2.2a	1.0a	6.7a

[a] Within a collection (row), means followed by the same letter are not significantly different according to a means separation test using the Student-Newman Keuls criterion following analysis of variance.

Castilleja exilis

This scarlet-flowered annual species of wetland habitats had a short chilling requirement, with full germination of seeds in postchilling incubation for both populations after only 4 weeks of chilling (table 2). There was no evidence for mechanisms, such as the presence of a chilling-nonresponsive fraction, that would promote seedbank carryover across years. The seeds of this species were very slow to germinate in chilling, however, particularly those of the northern Utah Lake lot (fig. 1). The Utah Lake seeds did not begin to germinate in chilling until 21 weeks, and germinated to less than 20 percent during chilling, while the southern Calf Creek lot began germinating in the cold at 18 weeks and reached about 80 percent by the end of chilling. The chilling periods required for any germination in the cold are much longer than those likely to be encountered by these seeds in their habitat of origin. The remaining seeds of both lots germinated rapidly and completely after transfer to the postchilling incubation regime. Germination during chilling may offer little advantage to this species, which grows in habitats where water is not limited during the growing season.

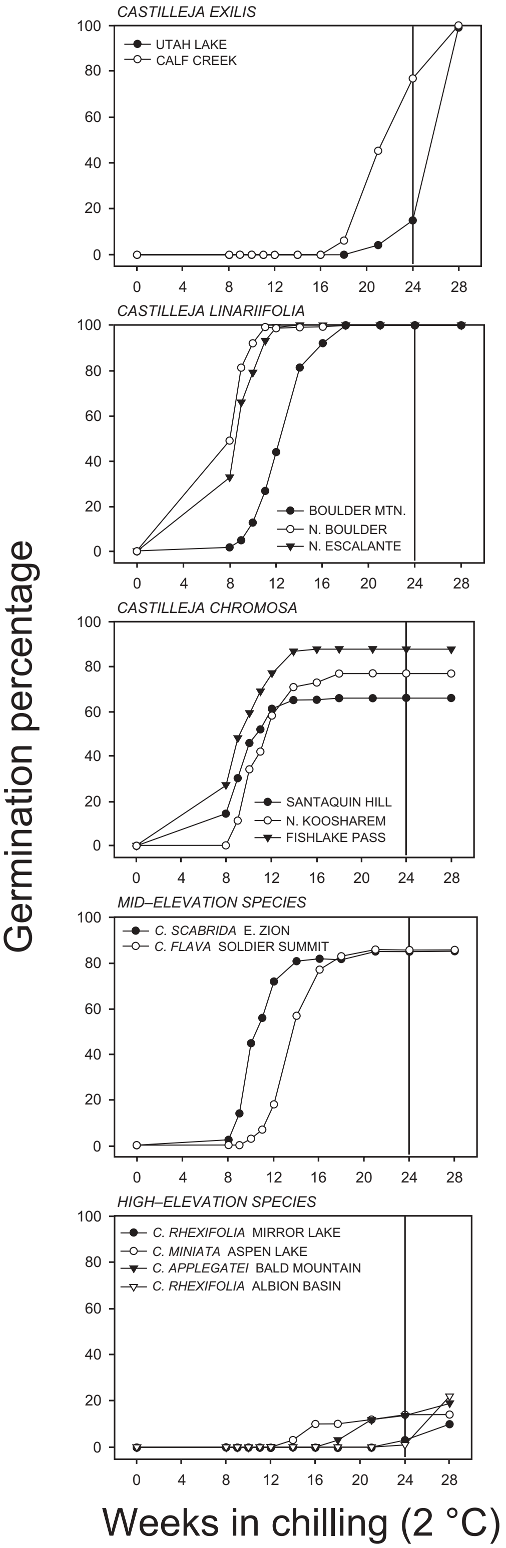


Figure 1—Time courses for germination during 24 weeks of chilling at 2 °C followed by 4 weeks of incubation at 10/20 °C for 14 *Castilleja* seed collections included in the study. Germination percentages are expressed as percentage of viable seeds. The vertical bars represent the point in time (24 weeks) when the seeds were transferred from chilling to postchilling incubation.

Castilleja linariifolia

C. linariifolia is a common scarlet-flowered summer species in sagebrush steppe, pinyon-juniper, mountain brush, and lower montane communities. The seeds from the three populations included in the study showed marked differences in germination response to chilling when recently harvested, and these differences were habitat related. The higher elevation Boulder Mountain population showed a pattern of incremental increase in germination percentage as a function of chilling duration up to 16 weeks, while the populations from pinyon-juniper woodland were largely or completely nondormant after only 4 weeks of chilling (table 2). The high-elevation collection also germinated much more slowly in the cold (fig. 1). All three lots germinated completely in the longer chilling regimes, and there was no evidence of any mechanism for seedbank carryover.

When the seeds of the high-elevation *C. linariifolia* collection were subjected to chilling 3 years after harvest, they showed a dramatic change in chilling response (fig. 2). Instead of the incremental increase in germination with chilling duration that was evident for recently harvested seeds, the 3-year-old seeds germinated to 100 percent after only 4 weeks of chilling, a response similar to that seen in recently harvested seeds of lower elevation collections. This change shows that seeds of this species of *Castilleja* can lose dormancy under dry conditions, a process known as dry after-ripening.

Castilleja chromosa

C. chromosa is the common scarlet-flowered spring paintbrush species of warm and cool desert shrublands, sagebrush steppe, and pinyon-juniper woodland in the Intermountain West. The seeds of all three collections of *C. chromosa* in this study were from sagebrush steppe habitats, and showed similar responses to chilling, although

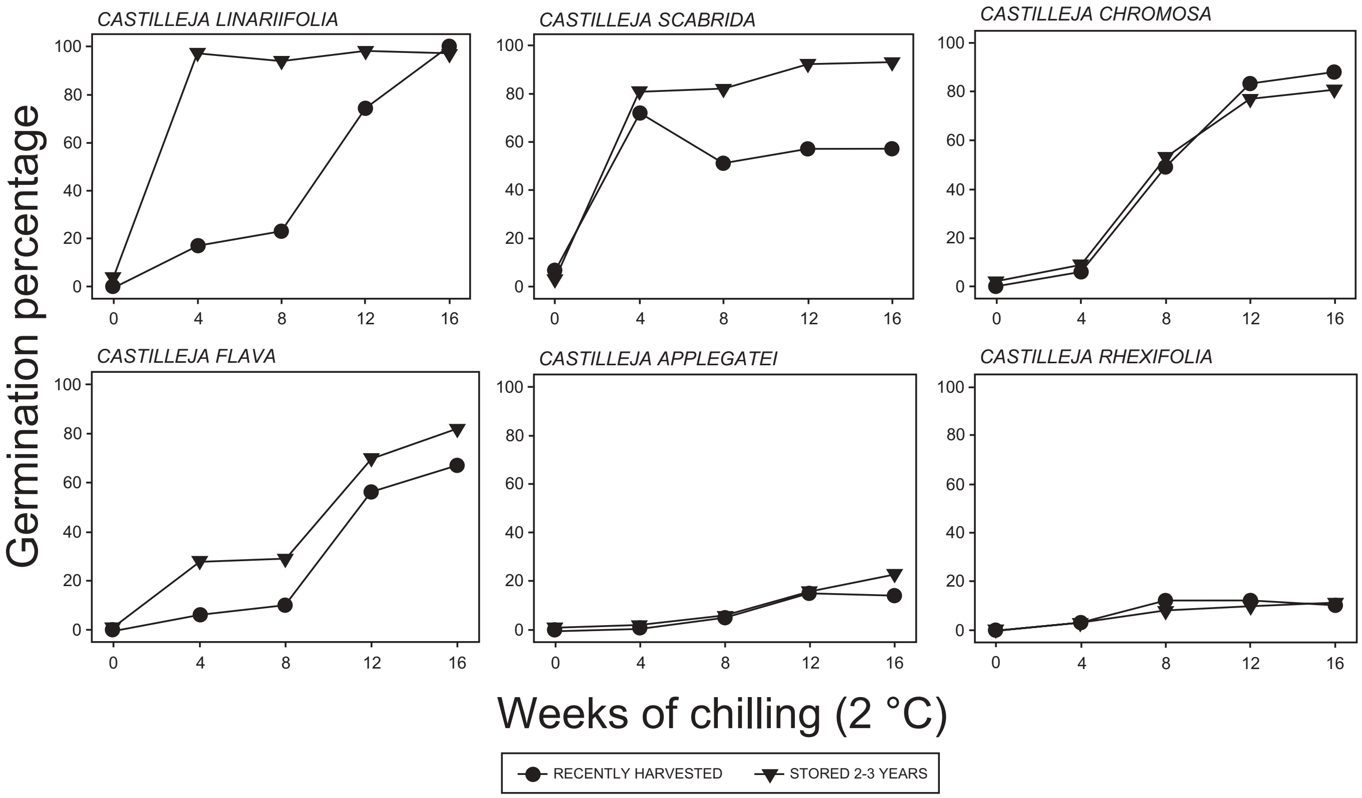


Figure 2—Changes in chilling responsiveness for six *Castilleja* seedlots during 2 to 3 years of laboratory storage. Data for recently harvested seeds are those presented for these lots in table 1, while data for seeds stored 2 to 3 years are from Mogensen and others (2001).

the more northern Santaquin Hill population was somewhat more dormant overall (table 2). The first substantial increase in germination took place in response to 8 weeks of chilling. The germinable fraction for the two southern populations increased with chilling duration up to 12 weeks, then leveled off between 80 and 90 percent. For the northern Santaquin Hill population, there was actually a significant drop in germination percentage between chilling periods of 12 weeks and 16 weeks. The remaining chilling nonresponsive seeds would have the potential to carry over across years as a persistent seedbank. Most of the seeds that became nondormant in chilling germinated in the cold soon after dormancy loss during the period from 8 to 12 weeks (fig. 1). This would place germination in the field in late winter in the sagebrush steppe habitats where these seeds originated.

Seeds from the Fishlake population tested after an additional 3 years in laboratory storage were largely unchanged in their chilling response, suggesting that dry after-ripening plays little role in dormancy regulation, at least for this population (fig. 2).

Castilleja scabrida

Seeds of this scarlet-flowered Colorado Plateau rock crevice specialist were less dormant than those of the closely-related species *C. chromosa*, germinating to over 70 percent after only 4 weeks of chilling (table 2). They showed decreased germination percentages at intermediate chilling periods of 8 to 16 weeks but germinated to a relatively high percentage after 24 weeks of chilling. Chilling durations in *C. scabrida* habitat in the field would never approach 24 weeks, so the information from shorter chilling durations is probably more ecologically relevant. The presence of a large chilling nonresponsive fraction under these intermediate chilling regimes is evidence for a mechanism for seedbank carryover. Germination response under continuous chilling was similar to that for *C. chromosa*, with most of the germination taking place between 8 and 12 weeks.

In contrast to those of *C. chromosa*, the seeds of *C. scabrida* definitely afterripened during dry storage for 2 years (fig. 2). The response to shorter chilling durations was similar for recently harvested and 2-year-old seeds, but the response to intermediate chilling durations was greatly increased for 2-year-old seeds.

Castilleja flava

Seeds of this golden-flowered mid-elevation mountain brush species showed incremental increases in germination percentage as a function of chilling duration up to 24 weeks, with 86 percent germination in response to 24 weeks of chilling (table 2). The fact that not all the seeds germinated even after this prolonged chilling treatment provides some evidence for seedbank carryover. This species showed an intermediate germination rate in chilling, with most of the seeds germinating between 12 and 16 weeks, soon after dormancy loss (fig. 1).

When the seeds of *C. flava* were retested after 3 years of laboratory storage, they showed evidence of after-ripening in dry storage, with approximately a 20 percent increase in germination percentage over chilling durations from 4 to 16 weeks (fig. 2).

Castilleja miniata

C. miniata is the common crimson-flowered mid-montane species of paintbrush throughout the southern Intermountain region and is found in aspen parkland, montane coniferous forest, and mountain meadow communities. The seeds of the *C. miniata* seedlot in our experiment were highly dormant, with a maximum germination of 15 percent and no incremental increase in response to increasing chilling duration (table 2). It was also relatively slow to germinate in chilling, with most of the seeds germinating between 14 and 16 weeks (fig. 1).

Castilleja applegatei

C. applegatei is a scarlet-flowered species found in rocky subalpine and alpine meadows. In our experiment, its seeds showed an incremental increase in germination percentage with increasing chilling duration, but the maximum germination was less than 20 percent (table 2). Most of the germination in the 24-week chilling treatment took place in the cold between 18 and 21 weeks (fig. 1). When this seedlot was retested 3 years later, its chilling response was largely unchanged (fig. 2).

Castilleja rhexifolia

C. rhexifolia is a pale yellow to crimson or purple-flowered species that is closely related to *C. miniata* and is found in similar habitats, but is more northerly in its distribution and ranges up into subalpine and even alpine communities. The two populations in our study were both from the upper elevational limits for the species and had highly dormant seeds. The Albion Basin collection germinated to a maximum of 20 percent, while the Mirror Lake population had a maximum germination of 7 percent (table 2). Both seedlots tended to show incremental increases in germination percentage with increasing chilling, but this increase was significant only for the Albion Basin collection. Neither collection germinated during chilling; the germination that did occur took place during postchilling incubation (fig. 1). These results, coupled with the fact that snow cover commonly lasts 8 to 9 months in high mountain habitats, suggest that our longest chilling duration was not long enough to obtain a maximum chilling response. This statement is also true for the two preceding species (*C. miniata* and *C. applegatei*). Longer chilling durations could be effective for these species.

Retesting the Albion Basin seed collection after 3 years of storage gave a chilling response essentially identical to the one for recently harvested seeds (fig. 2). It is therefore unlikely that dry after-ripening plays much of a role in dormancy regulation for this species.

Discussion

Comparative Germination Ecology

It is clear from our experiments that seed germination regulation in Intermountain species of *Castilleja* is not particularly impacted by the potentially hemiparasitic nature of these plants. The seeds are relatively easy to germinate, responding to moist chilling in a manner essentially similar to that of many other species of the Intermountain West. In fact, there are a great many parallels between the results reported here for *Castilleja* and those we have previously published for the related, nonhemiparasitic genus *Penstemon* (for example, Meyer and others 1995). The generally obligate requirement for some chilling, even in after-ripened seeds, is related to the fact that species of both genera have spring-emerging seedlings.

Variation in laboratory chilling responses can be tied to mechanisms for timing germination to occur appropriately in early spring in different habitats. If germination is delayed too long, the seedbed may dry out before the seedlings have a chance to become established, whereas if germination occurs too early, long before snowmelt, the newly germinated seedlings are at risk from pathogens that operate at low temperatures. This is why seeds of populations from warmer, drier, low-elevation habitats tend to respond to shorter chilling periods and to germinate more quickly in chilling than seeds of populations from high-elevation habitats with long winters.

These habitat-correlated differences are seen both within species with wide ecological amplitude, such as *C. linariifolia* in this study, and between species. For example, the three high-elevation species in this study had very long chilling requirements, so that even a 6-month chilling period resulted in relatively low germination percentages. This is not surprising given that chilling conditions under snow cover often last much longer than 6 months in these habitats. In contrast, species and populations from southern pinyon-juniper woodland, where long periods of chilling conditions are unlikely, respond to chilling periods as short as 4 weeks. Mid-elevation sagebrush steppe and mountain brush species and populations have intermediate chilling requirements that correspond to the chilling periods likely to be encountered in those habitats.

Most of the species of paintbrush in our study did not germinate fully even after 24 weeks of chilling. Seedlots of several of the mid-elevation species contained a sizeable chilling nonresponsive fraction that would not germinate even after prolonged chilling, in spite of the fact that the chilling responsive fraction became nondormant after much shorter chilling periods. The function of such a chilling nonresponsive fraction is probably to permit carryover of seeds across years, even in years when winter conditions result in longer than average periods of snow cover.

Although most are perennial, many paintbrush species have populations that turn over fairly rapidly, especially during cycles of drought. There are often scenarios, particularly at lower elevations, where establishment from a persistent seedbank is necessary for population survival. The chilling nonresponsive fraction makes this possible. The mechanism that renders these seeds chilling responsive in later years may be related to the dry after-ripening we observed in some of these seedlots. We also have some preliminary evidence that drying after inadequate chilling may render the seeds more responsive to chilling the following winter.

The summer annual wetland species *C. exilis* had a unique germination response pattern in our study. It had an obligate requirement for chilling that would function to prevent autumn emergence, but its chilling requirement was short, only 4 weeks or less. Once the seeds were rendered nondormant in chilling, they remained ungerminated even after several months in the cold. This is in contrast to the other species with relatively nondormant seeds, whose seeds germinated in chilling soon after they lost dormancy. *C. exilis* is a plant of relatively warm low-elevation habitats where the length of field chilling would be short, thus necessitating a short chilling requirement. But unlike low-elevation upland habitats, the wetland habitat does not pose the problem of a seedbed that dries rapidly in spring. There would therefore be no advantage to germinating during chilling for a wetland species, so it is not unexpected that nondormant *C. exilis* seeds do not germinate in the cold.

Seed Propagation

The first steps of seed propagation for species of *Castilleja* are essentially similar to those for any native species whose seeds require moist chilling. The individual seeds within a lot often have different chilling requirements, and because the seeds tend to germinate in chilling soon after losing dormancy, it is difficult to obtain uniform emergence when ungerminated chilled seeds are planted. By the time most of the seeds are nondormant, a large fraction has already germinated, and germinated seeds that remain in the cold tend to become stringy and difficult to plant successfully. On the other hand, if the seeds are planted as soon as the first few begin to germinate, most of the seeds are still dormant and poor stands are obtained. We can solve this problem on a small scale by planting the seeds as they germinate in the cold, while the radicles are still very short, and returning the remaining seeds to chilling. This results in seedlings of staggered age, which could be a problem in commercial production. If seeds are not in short supply, it may be possible to chill enough so that large batches of seedlings of each age can be obtained. The germinants are planted carefully in shallow depressions and covered with a thin (2 to 4 mm) layer of soil. Paintbrush seeds and germinants are very small, so it is important not to plant them too deeply. Poor emergence of newly germinated seedlings usually results either from planting too deeply or from allowing the surface to dry out during emergence. The germinants should be planted into well-watered potting medium, and the surface should be misted daily, especially if conditions are sunny, until emergence is complete. At this point it is best to water less often but more thoroughly, making sure that the soil is wetted to its full depth each time. Young paintbrush plants in containers are not as drought hardy as those of most native species, and it is important to pay careful attention to the watering. Paintbrushes, perhaps because of their hemiparasitic nature, tend to have relatively little root biomass in relation to their shoot biomass. Plants that have wilted from lack of water sometimes recover by resprouting from the base, but the resulting plants are not as sturdy as plants that have been watered consistently.

We prefer a relatively fast-draining potting medium for *Castilleja* propagation. Planting containers that produce a long, narrow root mass, such as root trainers (Spencer-Lemaire, Edmonton, Alberta) or Ray Leach Conetainers (Steuwe and Sons, Corvallis, OR), work best for paintbrushes, as they do for most other native herbaceous perennials. The plants can be grown in these containers for 3 to 4 months, depending on growing conditions and container volume. At this point, when other plants would normally be hardened for outplanting or potted up individually into larger containers, our propagation procedure deviates from the usual pattern.

While we do not have quantitative data to substantiate our recommendations, we have found through experience that small paintbrush stock planted out on its own usually exhibits poor survival, even when planted early in the spring and even in a garden setting. We have much higher success rates if we pot the paintbrush seedling up with a potential host plant and let the two plants grow together for 6 to 8 weeks, then harden them off and outplant them as a unit. Paintbrush species are not host specific, and we have had success using shrubs, grasses, and other perennial herbs as host plants. We particularly like aesthetically pleasing and ecologically appropriate combinations, such as planting *C. chromosa* with various species of sagebrush, the plants with which it is most often associated in the wild. Paintbrushes planted out with big sagebrush often live for many years in gardens and freely self-seed, so that as the shrub begins to overgrow the paintbrush, more small paintbrushes are produced around its periphery.

In a naturalized garden or restoration project, most species of paintbrush are easily obtained through direct seeding as long as the seed source used is adapted to the planting site. If sufficient seed is available, this is clearly the simplest and least labor-intensive way to establish these plants. Obviously, autumn planting will be necessary in order to ensure that the seeds receive the chilling they require in order to germinate and establish the following spring.

Acknowledgments

We would like to thank Darrin Johnson and Bettina Schultz for help in obtaining seed collections. Alisa Ramakrishnan provided invaluable technical assistance.

References

Meyer, S. E.; Kitchen, S. G; Carlson, S. L. 1995. Seed germination timing patterns in Intermountain *Penstemon*. American Journal of Botany. 82: 377–389.

Mogensen, S. H. A. C.; Allen, P. S.; Meyer, S. E. 2001. Prechill temperature and duration are important in determining seed quality for 12 wildflowers. Seed Technology. 23: 145–150.

Press, M. C. 1989. Autotrophy and heterotrophy in root hemiparasites. Trends in Ecology and Evolution. 4: 258–263.

Press, M. C.; Graves, J. D. 1995. Parasitic plants. London: Chapman and Hall.

Effects of Biological Soil Crusts on Seedling Growth and Mineral Content of Four Semiarid Herbaceous Plant Species

R. L. Pendleton
B. K. Pendleton
G. L. Howard
S. D. Warren

Abstract: A growing body of evidence indicates that biological soil crusts of arid and semiarid lands contribute significantly to ecosystem stability by means of soil stabilization, nitrogen fixation, and improved growth and establishment of vascular plant species. In this study, we examined growth and mineral content of *Bromus tectorum*, *Elymus elymoides*, *Gaillardia pulchella*, and *Sphaeralcea munroana* grown in soil amended with one of three levels of biological soil crust material: (1) a low-fertility sand collected near Moab, UT, (2) sand amended with a 1-cm top layer of excised soil crust, and (3) crushed-crust material. Plants were harvested after 10 weeks growth, dried, weighed, and leaves were ground for nutrient analysis. Root architecture was also quantified. Soil crust additions significantly affected nearly all variables examined. Both aboveground and belowground biomass were significantly increased in the presence of crust material. The effect of soil crust additions is likely due to the increased nitrogen content of the crusts. Nitrogen tissue content of all four species was greatly enhanced in crusted soils. All species showed a decline in root/shoot ratios with crust additions, indicating a shift in plant allocation patterns in response to improved soil fertility. The proportion of fine feeder roots, as measured by specific root length, also declined with the addition of soil crust material. These data support other studies suggesting that soil crusts have a positive effect on establishment of associated vascular plant species.

Introduction

Biological soil crusts are a common surface feature of arid and semiarid lands throughout the world (West 1990). While the ecological role of these crusts varies according to their composition (Belnap and others 2001; Evans and Johansen 1999), available information indicates that biological crusts contribute to a variety of ecological functions, including soil stabilization, nitrogen (N) fixation, nutrient availability, and vascular plant establishment. We examined the effects of biological crust additions on the growth, N content, and root architecture of four plant species: *Elymus elymoides*, *Gaillardia pulchella*, *Sphaeralcea munroana*, and *Bromus tectorum*. Complete results of the study are available in Pendleton and others (2003).

Methods

We transplanted 2-week-old seedlings into 6-inch pots containing one of three soil treatments: (1) a steam-sterilized low-fertility sand collected near Moab, UT, (2) crushed soil crust material, and (3) 6-inch circles of intact soil crust placed over the low-fertility sand. We also inoculated plants with spores of the arbuscular mycorrhizal fungus *Glomus intraradices* obtained from Brokow Nursery in Saticoy, CA, at the time of transplanting. Plants were grown in a greenhouse and bottom watered as needed using a capillary mat system.

Seedlings were harvested after 10 weeks growth in the treatment media. Shoots and roots were separated, dried, and weighed. Ground leaf and stem tissue was analyzed for N content at the Soil-Plant Analysis Laboratory, Brigham Young University, Provo, UT, using a micro-Kjeldahl procedure. Dried root tissue was rehydrated and fixed in 70 percent ethanol. Total root length was calculated using a modified line intersect method (Tennant 1975), and specific root length was calculated as meters root length per gram dry root weight. We also confirmed colonization of all plants by mycorrhizal fungi (Koske and Gemma 1989).

Statistical analyses were performed using SAS version 8.1 for personal computers (SAS Institute 1999–2000). Variables were analyzed separately by species, first using a MANOVA procedure to determine the significance of treatment effect, followed by univariate analyses using a one-way ANOVA or GLM procedure.

In: Hild, Ann L.; Shaw, Nancy L.; Meyer, Susan E.; Booth, D. Terrance; McArthur, E. Durant, comps. 2004. Seed and soil dynamics in shrubland ecosystems: proceedings; 2002 August 12–16; Laramie, WY. Proceedings RMRS-P-31. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

R. L. Pendleton and B. K. Pendleton are Research Ecologists, USDA Forest Service, Rocky Mountain Research Station, 333 Broadway SE, Suite 115, Albuquerque, NM 87102-3497, U.S.A.; FAX: (505) 724-3688; e-mail: rpendleton@fs.fed.us. G. L. Howard is Research Biologist, U.S. Army Corps of Engineers, Construction Engineering Research Laboratory, Champaign, IL, U.S.A. S. D. Warren is Research Scientist, Center for Environmental Management of Military Lands, Colorado State University, Fort Collins, CO 80523-1500, U.S.A.

Results and Discussion

Soil treatment had a significant effect on growth and N content of all four plant species (table 1). Plants grown in the crushed-crust medium were 6 to 8 times the size of plants growing in sand only. Significant differences also occurred between plants grown in the crust-over-sand and sand treatments. Plants grown in crusted soils were larger and had higher N concentrations in their stem and leaf tissue. Total uptake of N by plant shoots, calculated as biomass x concentration, was without exception greatest in the crushed-crust medium, followed by the crust-over-sand treatment. Other studies have reported increased growth and mineral content, especially N, of plants grown in crusted soils as compared to blow sand (Belnap and others 2001).

The relative allocation between root and shoot biomass was also affected by the addition of crust material (table 1). Root/shoot ratios of all species decreased with increasing crust additions, indicating that plants invested proportionately fewer resources in root tissue as nutrient availability increased (Kachi and Rorison 1989). Values for specific root length, which measures the relative proportion of fine feeder roots to larger conducting roots, were also lower in crusted soils, again indicating less biomass investment in fine feeder roots for plants growing in higher nutrient soils.

Biological soil crusts contain a large reservoir of bioessential elements that slowly become available for plant growth. The high concentration of nutrients relative to the underlying soil comes from the active fixation of nitrogen and carbon, as well as the accumulation of small dust particles (Belnap and others 2001; Harper and Pendleton 1993). Crust material used in this experiment was high in organic matter, N, calcium, and magnesium. Next to water, N is the factor most limiting to plant growth in arid environments (Evans and Belnap 1999). Mycorrhizal plants in particular may benefit from the fixation of atmospheric N by soil crusts. Considerable evidence indicates that mycorrhizal fungi play an important role in N uptake (Hodge and others 2001).

In the Colorado Plateau region, trampling or other compressional disturbance when crusts are dry and brittle destroys the integrity of the crust, causing a short-lived flush of nutrients similar to that experienced by plants growing in the crushed-crust treatment. A rapid increase in nutrient availability could disrupt community dynamics, resulting in differential establishment and increased reproductive success of exotic annual species such as *Bromus* sp. (McLendon and Redente 1991). Subsequent loss of the crust community through wind and water erosion reduces the number of mycorrhizal propagules and other microorganisms associated with the crust layer (Harper and Pendleton 1993). The resulting reduction in soil fertility and stability of such a degraded ecosystem could have profound and lasting consequences (Evans and Belnap 1999).

Acknowledgments

This work was supported by grants MIPR 94N107 and MIPR W2V5AA51113582 from the U.S. Army Corps of Engineers, Construction Engineering Research Laboratory, Champaign, IL. Technical assistance was provided by Susan Garvin, Jeff Ott, David Tarkalson, and Cari York.

Table1—Growth measures and tissue nitrogen content of plants grown in different soil treatments. Letters following means denote significant treatment differences at P < 0.05 using the Student-Newman-Keuls multiple range test.

	Shoot biomass	Root biomass	Root/shoot ratio	Specific root length	Nitrogen concentration	Total shoot N
	- - - - - - - - - *g* - - - - - - - -			*m/g*	*percent*	*mg*
Sphaeralcea munroana						
Crushed crust	3.91a	0.86a	0.21a	7,848a	2.39a	0.925a
Crust over sand	.51b	.29b	.57b	9,434b	2.49a	.127b
Sand	.30c	.25b	.84c	13,054c	1.99b	.059c
P value	<0.0001	<0.0001	<0.0001	<0.0001	.0254	<0.0001
Gaillardia pulchella						
Crushed crust	4.66a	1.14a	.26a	9,622a	1.30ab	.566a
Crust over sand	.83b	.36b	.45b	10,927a	1.45a	.122b
Sand	.62c	.31b	.51b	10,846a	1.11b	.067c
P value	<0.0001	<0.0001	<0.0001	.3900	.0433	<0.0001
Elymus elymoides						
Crushed crust	1.48a	.26a	.18a	9,731a	1.66a	.241a
Crust over sand	.30b	.14a	.44b	16,442b	1.65a	.051b
Sand	.16c	.06a	.46b	20,997b	1.44a	.023c
P value	.0073	.1621	.0051	.0137	.3900	.0101
Bromus tectorum						
Crushed crust	3.19a	.90a	.26a	14,496a	1.64a	.477a
Crust over sand	.79b	.40b	.54b	24,238b	1.09b	.083b
Sand	.40c	.22c	.58b	24,422b	.96c	.037c
P value	.0004	.0099	<0.0001	.0051	<0.0001	<0.0001

References

Belnap, J.; Kaltenecker, J. H.; Rosentreter, R.; Williams, J.; Leonard, S.; Eldridge, D. 2001. Biological soil crusts: ecology and management. BLM/ID/ST-01/001+1730, Technical Reference 1730-2. Denver, CO: National Science and Technology Center, Bureau of Land Management. 110 p.

Evans, R. D.; Belnap, J. 1999. Long-term consequences of disturbance on nitrogen dynamics in an arid ecosystem. Ecology. 80: 150–160.

Evans, R. D.; Johansen, J. R. 1999. Microbiotic crusts and ecosystem processes. Critical Reviews in Plant Sciences. 18: 183–225.

Harper, K. T.; Pendleton, R. L. 1993. Cyanobacteria and cyanolichens: can they enhance availability of essential minerals for higher plants? Great Basin Naturalist. 53: 59–72.

Hodge, A.; Campbell, C. D.; Fitter, A. H. 2001. An arbuscular mycorrhizal fungus accelerates decomposition and acquires nitrogen directly from organic material. Nature. 413: 297–299.

Kachi, N.; Rorison, I. H. 1989. Optimal partitioning between root and shoot in plants with contrasted growth rates in response to nitrogen availability and temperature. Functional Ecology. 3: 549–559.

Koske, R. E.; Gemma, J. N. 1989. A modified procedure for staining roots to detect mycorrhizae. Mycological Research. 92: 486–488.

McLendon, T.; Redente, E. F. 1991. Nitrogen and phosphorus effects on secondary succession dynamics on a semiarid sagebrush site. Ecology. 72: 2016–2024.

Pendleton, R. L.; Pendleton, B. K.; Howard, G. L.; Warren, S. D. 2003. Growth and nutrient content of herbaceous seedlings associated with biological soil crusts. Arid Land Research and Management. 17(3): 271–281.

SAS Institute. 1999–2000. SAS/STAT user's guide, release 8.1. Cary, NC: SAS Institute Inc. 1028 p.

Tennant, D. 1975. A test of a modified line intersect method of estimating root length. Journal of Ecology. 63: 995–1001.

West, N. E. 1990. Structure and function of microphytic soil crusts in wildlife ecosystems of arid to semiarid regions. Advances in Ecological Research. 20: 179–223.

Seeding Time and Method for Winterfat in the Semiarid Region of the Canadian Prairies

Michael P. Schellenberg

Abstract: Seeding recommendations for winterfat (*Krascheninnikovia lanata* (Pursh) A.D.J. Meeuse & Smit) are to seed in fall. A 3-year establishment study (1997 to 1999) of this semishrub at the Semiarid Prairie Agricultural Research Centre indicated that year-to-year variation occurs. After-ripened seed from New Mexico was seeded in fall or in spring. Seeding techniques compared were drill, broadcast, and broadcast followed by packing in cultivated land. Seedling counts and dry matter yield data for the establishment and the second year were obtained. Year-by-year statistical analysis revealed variation in seeding time benefits for number of seedlings. Broadcasting resulted in best establishment of winterfat (as found in the literature), but packing had a negative impact.

Introduction

Winterfat (*Krascheninnikovia lanata*) has been recognized as a valuable forage source since the 1890s (Van Dersal 1938). Anecdotal information indicates that cattle drives from Texas to the Canadian Prairies followed the winterfat northward. Also, Canadian ranchers have found that their best producing winter pastures often had higher winterfat populations than less productive winter pastures.

Improved economic viability for ranchers in the Northern Great Plains is associated with increased grazing period with a potential 56 percent increase in economic efficiency (Saskatchewan Agriculture and Food, Extension Agrologist, J. Graham, personal communication). This requires a forage source with good nutritional value in the fall when most forage sources are nutritionally deficient. Crude protein for many species falls below 7 percent, while winterfat maintains crude protein values above 7 percent (Clarke and Tisdale 1945), which is sufficient for winter grazing (Smoliak and Bezeau 1967). As a result, there has been an increased interest in this shrub due to its good nutritional composition and late season grazing potential. Interest, in part, has resulted in increased seed production as well as development of Northern adapted ecological varieties. With increased seed availability, the need for proper planting methods has been realized.

The present recommendation for seeding is fall broadcast seeding (Romo and others 1997; Stevens and others 1996).

Objectives

1. Under southwest Saskatchewan climatic conditions, is fall seeding required?
2. Would placement on the surface of a furrow or packing after broadcasting improve establishment?

Methods and Materials

A fully randomized factorial design study was seeded 3 years in succession from 1997 to 1999 using seed obtained from New Mexico (Wind River Seeds) and after-ripened for a 30-day period. The seeding took place at the Semiarid Agricultural Research Centre (SPARC), Swift Current (50° 17' N, 107° 41' W), Saskatchewan, Canada, on typic Haploboroll soil (Swinton loam soil [Orthic brown chernozem; Ayres and others 1985]). Each seeding site had four replicates. The factors examined in this paper were (1) fall (dormant seeding; late October to November) or spring (late May to early June) seeding; and (2) seeding method: surface seeded into a furrow, broadcast, and broadcast followed by packing.

Data on seedling counts for seeding year and the second year, as well as dry matter yields for second year, were collected in September of each year. Meteorological data were obtained from an Environment Canada weather station. Precipitation and potential evaporation (U.S. Weather Bureau Class A pan) were totalled for the month. The precipitation deficit was calculated as total potential evaporation minus total monthly precipitation. Long-term weather data were obtained from long-term records maintained at SPARC. Data were analyzed using SAS GLM (SAS Institute Inc. 1990).

Results and Discussion

Meteorological Data

Growing season precipitation exceeded the 114-year average for most years of the study (fig. 1). Potential available moisture also increased from 1998 to 2000 (fig. 2). Precipitation for 1998 and 1999 was lower than 2000 in the winter months, suggesting less insulative cover (fig. 1). The precipitation for the winter months of 2000 (fig. 1) and mean monthly temperature (fig. 3) were higher than those of

---

In: Hild, Ann L.; Shaw, Nancy L.; Meyer, Susan E.; Booth, D. Terrance; McArthur, E. Durant, comps. 2004. Seed and soil dynamics in shrubland ecosystems: proceedings; 2002 August 12–16; Laramie, WY. Proceedings RMRS-P-31. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Michael P. Schellenberg is a Forage Plant Ecologist, Semiarid Prairie Agricultural Research Center, Agriculture and Agri-Food Canada, Box 1030, Swift Current, SK, S9H 3X2, Canada. Phone: (306) 778-7247, FAX: (306) 773-9123, e-mail: schellenberg@agr.gc.ca

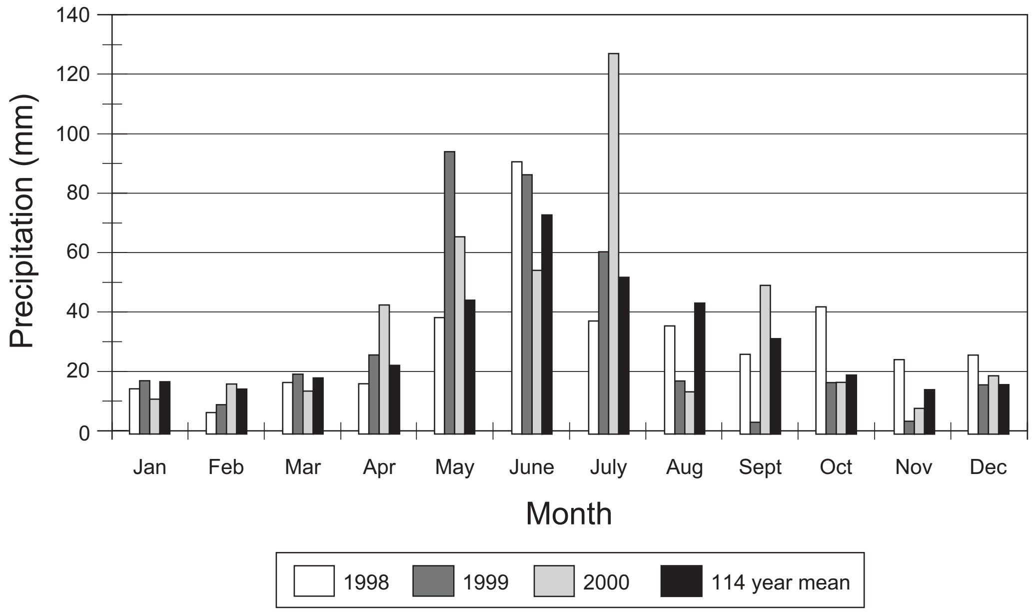


Figure 1—Monthly precipitation for 1998 to 2000 and 114-year mean.

previous years. Mean monthly temperatures in the fall of 1997 (fig. 3) were warmer than the following years, resulting in premature germination and seedling death prior to spring 1998, thus resulting in better 1998 spring seedling establishment (table 1).

Time of Seeding

Spring or fall seeding appears to be year dependant (table 1) with first-year seedling counts, indicating no multiple-year benefits for either spring or fall seeding. With increasing annual growing season precipitation (figs. 1 and 2), fall seeding failed to provide a benefit (table 1). In the wettest year (2000), no difference between spring or fall seeding occurred for seedling establishment. Plant counts for the year following establishment indicate that the effect of fall seeding continues beyond the seedling year (table 1). The dry matter yield per plant was better for fall-seeded plants (table 1). The additional time for growth from earlier germination is most likely the primary factor.

Method of Seeding

Furrows provide a microenvironment with potentially increased moisture (Bellotti and Blair 1989) and decreased wind. However, these potential benefits were negated by burial of surface-seeded winterfat as indicated by lower plant counts and dry matter yield (table 2). Broadcasting and packing failed to result in increased seedling numbers, although there may have been benefit for dry matter yield

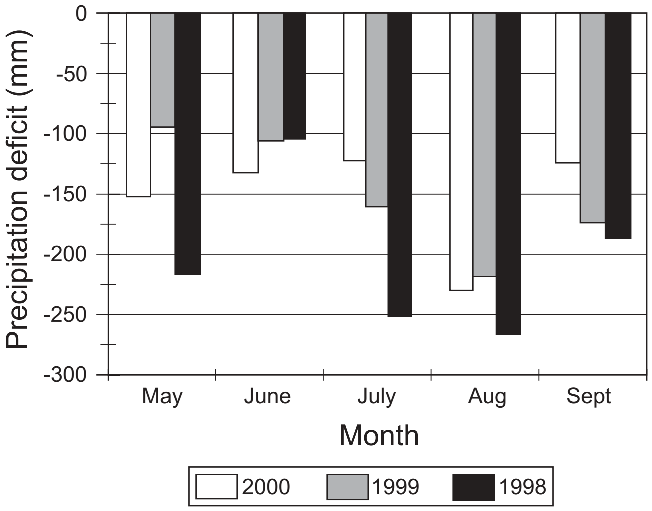


Figure 2—Precipitation deficit (Pan "A") evaporation-precipitation) for 1998 to 2000 growing seasons.

Table 1—Dry matter yields, plant counts for first year and second year of establishment for time of seeding factor for three seeding years.

	Seeding site		
	1997–1998	**1998–1999**	**1999–2000**
Year 1 fall plant count (m^{-2})			
Fall seeding	2.4	2.2[a]	1.3
Spring seeding	5.8[a]	1.5	1.4
Year 2 plant count (m^{-2})			
Fall seeding	na[b]	1.5	1.4
Spring seeding	na[b]	1.2	1.8
Year 2 dry matter yield (g $plant^{-1}$)			
Fall seeding	20.2[a]	14.3[a]	na[b]
Spring seeding	9.4	8.4	na[b]

[a] Statistically significant (P > 0.05).
[b] na = data not available.

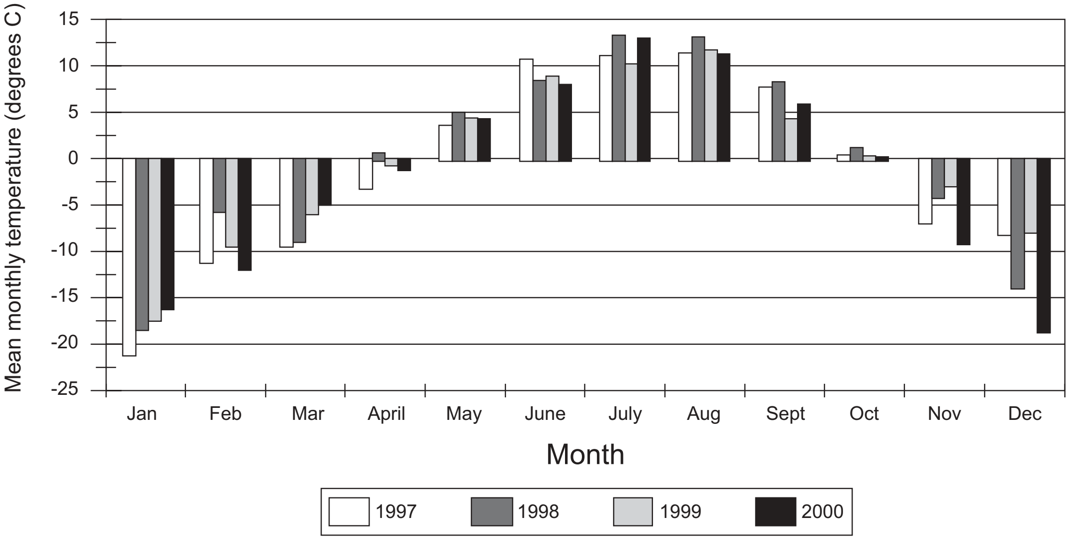


Figure 3—Mean monthly minimum temperature.

(table 2). The increased dry matter yield may have resulted from improved moisture retention or decreased seedling competition, as a result of lower number of seedlings. Further research is needed to determine exact cause.

Conclusions

Benefits of fall or spring seeding for winterfat seedling establishment depended on the prevailing environmental conditions during the establishment year. The variation in year could be due to available moisture. The availability of water, winter temperatures, and available insulative cover appear to affect the optimum time of seeding. Further research is required to establish the relationship of water and temperature.

Table 2—Dry matter yields, plant counts for first year and second year of establishment for seed method factor for three seeding years.

	Seeding site		
	1997–1998	1998–1999	1999–2000
Year 1 fall plant count (m^{-2})			
Furrow	2.0[a]	0.9[a]	0.4[a]
Broadcast	5.8	2.3	2.0
Broadcast and packed	4.6[b]	2.3	1.6[b]
Year 2 plant count (m^{-2})			
Furrow	na[c]	0.8[a]	0.6[a]
Broadcast	na[c]	1.9	2.2
Broadcast and packed	na[c]	2.0	2.0
Year 2 dry matter yield (g $plant^{-1}$)			
Furrow	12.8	11.6	na[c]
Broadcast	14.6	10.6	na[c]
Broadcast and packed	17.1	11.8	na[c]

[a] Statistically significant ($P > 0.05$) difference from broadcast treatments determined with single degree of freedom contrast.

[b] Statistically significant ($P > 0.05$) difference from broadcast alone treatment determined with single degree of freedom contrast.

[c] na = data not available.

Fall seeding did result in greater per plant dry matter production, although dry matter yields were unaffected by seeding method. Manipulation of microclimate using furrows did not result in increased seedling establishment. Broadcasting of winterfat seed resulted in better seedling establishment compared to seeding in a furrow, but packing following broadcasting tended to have a negative impact on seedling numbers.

Acknowledgments

This work was possible with funding support from the Saskatchewan Agricultural Development Fund and Agriculture and Agri-Food Canada. Technical support from J. Bolton, B. Hedger, and numerous summer students, especially C. Neufeld, was greatly appreciated. Poster development was with the assistance of D. Schott.

References

Ayres, K. W.; Acton, D. F.; Ellis, J. G. 1985. The soils of Swift Current map 725 Saskatchewan. Publ. 56. Saskatoon, SK: University of Saskatchewan, Saskatchewan Institute of Pedology. 22 p.

Bellotti, W. D.; Blair, G. J. 1989. The influence of sowing method on perennial grass establishment. II. Seedbed microenvironment, germination and emergence. Australian Journal Agricultural Research. 40: 313–321.

Clarke, S. E.; Tisdale, E. W. 1945. The chemical composition of native forage plants of southern Alberta and southwestern Saskatchewan. Tech. Bull. 46. Ottawa, Ontario: Dominion of Canada, Department of Agriculture.

Romo, J. T.; Booth, D. T.; Bai, Y.; Hou, J.; Zabek, C. 1997. Seedbank requirement and cold tolerance of winterfat seedlings: an adapted forage for the Canadian prairies. Saskatchewan Agricultural Development Fund Report prepared by: Department of Crop Science and Plant Ecology, University of Saskatchewan, Saskatoon, SK. 101 p.

SAS Institute, Inc. 1990. SAS users guide: statistics. Cary, NC: SAS Institute, Inc.

Smoliak, S.; Bezeau, L. M. 1967. Chemical composition and in vitro digestibility of range forage plants of the *Stipa-Bouteloua* prairie. Canadian Journal of Plant Science. 47: 161–167.

Stevens, R.; Jorgensen, K. R.; Young, S. A.; Monsen, S. B. 1996. Forb and shrub seed production guide for Utah. Logan: Utah State University Extension Service. 51 p.

Van Dersal, W. R. 1938. Native woody plants of the United States: their erosion-control and wildlife value. Washington, DC: U.S. Government Printing Office. 362 p.

New Native Plant Releases From the USDA-NRCS, Aberdeen, ID, Plant Materials Center

L. St. John
P. Blaker

Abstract: The Plant Materials Center at Aberdeen, ID, is operated by the United States Department of Agriculture, Natural Resources Conservation Service. The purpose of the Plant Materials Center is to evaluate and release plant materials for conservation use and to develop and transfer new technology for the establishment and management of plants. The Center serves portions of Nevada, Utah, California, Oregon, and Idaho. In 1995, two selected ecotypes of penstemon were released. The Richfield Selection of firecracker penstemon has bright red flowers on upright racemes. The Clearwater Selection of Venus penstemon has bright lavender flowers on narrow panicles. Native penstemon species provide soil stabilization, plant diversity, and beautification. 'Bannock' thickspike wheatgrass was released in 1995 to be used as a component of seed mixes for rangeland and pasture seedings. In 2001, Snake River Plains fourwing saltbush Selected Class Germplasm and Northern Cold Desert winterfat Selected Class Germplasm were released. Both of these shrubs are important species on many ecological sites in the Intermountain West and have potential for use in erosion control, rangeland restoration, livestock and big game browse, and wildlife plantings.

The Plant Materials Center (PMC) at Aberdeen, ID, is part of the national plant materials program operated by the United States Department of Agriculture, Natural Resources Conservation Service. The purpose of the plant materials program is to develop and transfer new technology for the establishment, use, and management of plants.

Plant Materials Centers assemble, evaluate, and release plant materials for conservation use. The Aberdeen PMC was established in 1939 and has been the primary breeder and releasing organization for 15 cultivars and 27 alternative releases, and has cooperated in the release of 12 additional cultivars. The Aberdeen PMC serves portions of Nevada, Utah, California, Oregon, and Idaho. The PMC works cooperatively with private landowners as well as State and Federal land management agencies. The PMC Farm is owned by the South Bingham Soil Conservation District and is leased to the PMC.

In 1995, the PMC in cooperation with the Idaho Agricultural Experiment Station released two selected ecotypes of *Penstemon*. Except for one minor species, the genus *Penstemon* does not occur naturally outside of North America. There are approximately 150 species and most are found in the Western United States. Penstemons are perennial plants with opposite leaves, and usually showy, often two-lipped flowers. The conservation values of penstemon are soil stabilization, plant diversity, and beautification of many different sites. The two penstemons were selected from a collection of 119 penstemons that were evaluated at the PMC from 1981 to 1985. They were chosen for their natural beauty, hardiness, and seed production.

The Richfield Selection of Firecracker penstemon (*Penstemon eatonii*) was collected near Richfield, UT. Its natural habitat is the sagebrush, juniper, and ponderosa pine zones at 3,000 to 8,000 ft (914 to 2,438 m) elevation and an annual precipitation zone from 10 to 16 inches (254 to 406 mm). It is best adapted to loamy, well-drained soils and can survive full sunlight, but will not tolerate hot, dry areas. It is not adapted to areas with poor drainage. Firecracker penstemon is a perennial, cool-season forb with a fibrous root system, and the stems are often decumbent or reclining. The leaves are large and slightly pubescent. The flowers are bright red on upright racemes 24 to 36 inches (60 to 91 cm) tall.

The Clearwater Selection of Venus penstemon (*Penstemon venustus*) was collected near the Dworshak Reservoir on the Clearwater River in northern Idaho. Its natural habitat is at elevations of 1,000 to 6,000 ft (305 to 1,829 m) and an annual precipitation zone from 20 to 35+ inches (508 to 889+ mm). Venus penstemon is best adapted to loamy, well-drained soils and can survive full sunlight on open, rocky slopes, but does not do well in areas with poor drainage. It is a perennial, cool-season forb, 12 to 24 inches (30 to 60 cm) tall with a strong taproot and woody base. The leaves are oblong and sharply serrate. The flowers are bright lavender to purple-violet and appear in one or more narrow terminal panicles 12 to 20 inches (30 to 51 cm) long.

The PMC and the Idaho Agricultural Experiment Station cooperatively released 'Bannock' thickspike wheatgrass (*Elymus lanceolatus* ssp. *lanceolatus*) in 1995. Bannock is a composite of six seed collections from Washington, Oregon, and southeast Idaho. The best performing plants were selected, isolated, and increased to create Bannock. The grass was developed to be used as a component of a seed mix for rangeland and pasture seedings. Bannock is especially adapted to sandy areas with a minimum of 8 inches (200 mm) annual precipitation. It also provides wildlife cover and nesting.

In: Hild, Ann L.; Shaw, Nancy L.; Meyer, Susan E.; Booth, D. Terrance; McArthur, E. Durant, comps. 2004. Seed and soil dynamics in shrubland ecosystems: proceedings; 2002 August 12–16; Laramie, WY. Proceedings RMRS-P-31. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

L. St. John is Plant Materials Center Team Leader and P. Blaker is Administrative Assistant, United States Department of Agriculture, Natural Resources Conservation Service, Plant Materials Center, P.O. Box 296, Aberdeen, ID 83210, U.S.A.; e-mail: stjohn@id.usda.gov

Bannock has been thoroughly tested and compared to other varieties of thickspike wheatgrass in the Western United States. It was named in honor of the Bannock Indian Tribe that inhabited the Great Basin. Bannock is a long-lived, leafy, rhizomatous, vigorous, sod-producing, cool-season grass. Thickspike wheatgrass is native to most of the Northern and Western United States and Southern Canada. The PMC has been granted Plant Variety Protection (PVP) for Bannock so that seed can be marketed only as a class of certified seed. This will help protect and maintain the characteristics for which it was released.

Snake River Plains fourwing saltbush (*Atriplex canescens*) Selected Class Germplasm was released in 2001 by the Aberdeen PMC, Pullman, WA, PMC, and the Idaho Agricultural Experiment Station. It is a composite of four seed collections made in 1976 on the Snake River Plains in Power, Owyhee, and Elmore Counties, Idaho. These were compared to 79 other collections evaluated at the PMC from 1977 to 1986. The four original collections were selected for their superior tolerance to cold temperatures.

Fourwing saltbush is one of the most widely distributed and important native shrubs on rangelands in the Western United States. Snake River Plains fourwing saltbush is an erect shrub that can grow to 6 ft (1.8 m) under ideal soil and moisture conditions. Leaves are simple, alternate, and linear to oblong $^{1}/_{2}$ to 2 inches (1.2 to 5.1 cm) long. The species is mostly dioecious, having separate male and female plants. Male flowers are red to yellow and form dense spikes at the end of branches. Female flowers are nondescript in axillary clusters. The seed is enclosed in a four “winged” membranous utricle.

Snake River Plains fourwing saltbush is potentially adapted to the northern portion of the Intermountain Western United States where annual precipitation averages 8 to 16 inches (200 to 400 mm). It can be used for erosion control; rangeland restoration; livestock and big game browse; and wildlife plantings in dry, moderately saline or alkaline areas.

The PMC and the Idaho Agricultural Experiment Station released Northern Cold Desert Winterfat (*Krascheninnikovia lanata*) Selected Class Germplasm in 2001. It is a composite of five seed collections made from 1974 to 1977 and compared to 40 other collections at the PMC from 1978 to 1986. The five original seed collections were selected for their superior tolerance to cold temperatures. Source locations of the original collections selected were Carbon, Emery, Kane, and Washington Counties in Utah, and Rio Blanco County, Colorado.

Winterfat is a widely distributed native shrub ranging from Saskatchewan and Manitoba, Canada, and northern Washington to western Nebraska, Colorado, west Texas to southern California. It is found from near sea level to 10,000 ft (3,000 m) elevation. Northern Cold Desert winterfat is an erect shrub that can grow to 3 ft (0.9 m). Leaves are simple, alternate, narrowly linear, flat, with rolled under edges and densely hairy. Winterfat is monoecious with both male and female flowers on the same plant. The fruit is a utricle and the pericarp is thin and covered with fine, white, silky hairs $^{1}/_{8}$ to $^{1}/_{4}$ inch (30 to 60 mm) long.

Northern Cold Desert winterfat is potentially adapted to the northern portion of the Intermountain Western United States where annual precipitation averages 7 to 16 inches (175 to 400 mm). It can be used for erosion control; rangeland restoration; livestock and big game browse; and wildlife plantings in dry, moderately saline or alkaline areas.

Predicting Seedling Emergence Using Soil Moisture and Temperature Sensors

Jeffrey R. Taylor
Bruce A. Roundy
Phil S. Allen
Susan E. Meyer

Abstract: Hydrothermal time models are often used to predict seed germination rates. In this study, soil water potential data from three resistance-type sensors (Colman cells, Watermark brand sensors, and Delmhorst gypsum blocks) and from a time-domain reflectometry (TDR) probe (Campbell Scientific 615) were input into a hydrothermal time model to predict seedling emergence in a growth chamber experiment for six desert grass species, including *Brachypodium distachyon*, *Bromus fasciculatus*, *Crithopsis delilianus*, and *Stipa capensis* from the Negev Desert, and naturalized downy brome (*Bromus tectorum*) and bottlebrush squirreltail (*Elymus elymoides*) from the Great Basin Desert. Seeds were sown in a structureless sandy loam soil that was irrigated approximating 0.58, 1.25, 1.50, and 2.00 times field capacity volumetric water content and allowed to dry in a growth chamber programmed to simulate spring temperatures in Provo, UT. Colman cells and Delmhorst gypsum blocks indicated more rapid soil surface drying than did Watermark sensors and TDR probes. Inputs provided by the sensors correctly predicted seedling emergence of these rapidly germinating grasses when water potential was high, but incorrectly predicted emergence when rapidly decreasing water potentials inhibited emergence. These results suggest that more accurate measurement or prediction of seed zone water potentials may be necessary before hydrothermal time models can effectively predict seedling emergence in the field.

Introduction

Annual and perennial grasses influence arid land plant communities by affecting biomass production, soil erosion, plant and herbivore interactions, and fire frequency. In the Negev Desert, Israel, annual grasses (such as *Brachypodium distachyon*, *Bromus fasciculatus*, *Crithopsis delilianus*, and *Stipa capensis*) provide important forage for grazing animals. In the Great Basin Desert, United States of America, introduced downy brome (*Bromus tectorum*) can invade and disrupt native perennial communities (Billings 1994; D'Antonio and Vitousek 1992).

Successful germination and seedling establishment in desert ecosystems is often limited by species-specific seed germination responses to near-surface soil water potentials and temperatures. Frasier (1987) reported that seedling survival for five warm-season desert grasses depended upon the number of seedlings that successfully emerged after initial wetting, the number of nongerminated and viable seed that remain, and the time interval between wet and dry periods. For example, the ability of Lehmann lovegrass (*Eragrostis lehmanniana*) to retain a viable seedbank during erratic summer rainfall in the Sonoran Desert grassland allows it to establish better than some native grasses that germinate most of their seeds after initial rains and are then subject to seedling desiccation (Abbott and Roundy 2003).

Seed germination models using soil matric potential (Ψ) and temperature data can be used to accurately predict germination (Allen and others 1999; Bradford 1990; Finch-Savage and Phelps 1993; Roman and others 1999). Gummerson (1986) was the first to combine water potential and temperature data to model germination (hydrothermal time). Hydrothermal time has since been used to successfully model germination for a variety of species (Allen and others 1999; Christensen and others 1997; Finch-Savage and Phelps 1993; Roman and others 1999).

Electric resistance sensors and time-domain reflectometry (TDR) probes are used to estimate soil moisture conditions (Amer and others 1994; Baker and Allmaras 1990; Collins 1987; Roundy and others 1997, 2001). Various sensors have been compared to see how they respond to changes in soil moisture. Topp and Davis (1985) compared TDR and gravimetric sampling at various depths within the top meter of soil and found both techniques produced similar results. Collins (1987) compared gypsum blocks with Colman cells and found that Colman cells had poor sensitivity in dry soils as well as large differences among individual sensor resistances. When comparing gypsum blocks and Watermark sensors, Hanson and others (2000) reported that gypsum blocks did not indicate reductions in soil water matric potential until the surrounding media fell below a certain moisture threshold. In addition, they found that Watermark

---

In: Hild, Ann L.; Shaw, Nancy L.; Meyer, Susan E.; Booth, D. Terrance; McArthur, E. Durant, comps. 2004. Seed and soil dynamics in shrubland ecosystems: proceedings; 2002 August 12–16; Laramie, WY. Proceedings RMRS-P-31. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Jeffrey R. Taylor and Susan E. Meyer are, respectively, Range Technician and Ecologist at the Shrub Sciences Laboratory, Rocky Mountain Research Station, Forest Service, U.S. Department of Agriculture, Provo, UT 84606, U.S.A., e-mail: jrtaylor@fs.fed.us and smeyer@fs.fed.us. Bruce A. Roundy and Phil S. Allen are, respectively, Professor, Department of Integrative Biology, and Associate Professor, Department of Plant and Animal Sciences, Brigham Young University, Provo, UT 84602, U.S.A.

sensors were more responsive in drier soils. In a comparison between Colman cells, TDR, and gravimetric sampling, Amer and others (1994) found that Colman cells tended to indicate higher soil moisture content and exhibited more variation, but were more effective at measuring shallow depths because they measure moisture at points. A more thorough and simultaneous comparison among available sensors in soils with widely fluctuating soil water potentials would better determine their ability to provide meaningful data to predict seedling emergence.

Hydrothermal Time

Nondormant seeds germinate after being exposed to suitable temperatures and water potentials for an adequate period of time (Allen and others 1999; Bradford 1995; Finch-Savage and Phelps 1993; Gummerson 1986; Roman and others 1999). Hydrothermal time can be described by the equation (Gummerson 1986):

$$HT = (\Psi - \Psi_{b(g)})(T - T_b)t_{(g)}$$

At the time of germination:

$$\theta_{HT} = (\Psi - \Psi_{b(g)})(T - T_b)t_{(g)}$$

HT is the amount of hydrothermal time that has accumulated (expressed as MPa-°-hours or days). The amount of hydrothermal time required for germination is θ_{HT} (the amount of HT that satisfies the requirement for radicle emergence). Ψ is the water potential of the soil, and $\Psi_{b(g)}$ is the minimum or base water potential for (g) fraction of the seeds to germinate for a given population. T is the temperature of the soil, and T_b is the minimum seed germination temperature. The time required for g fraction of the seeds to germinate is $t_{(g)}$.

Hydrothermal time analysis requires that data be probit transformed (to linearize the typical cumulative time course for germination of a particular collection). Transformed data are used to compare germination time differences among the various fractions of the seed population. Base soil water matric potentials (Ψ_b) are assumed to vary normally within the population. The $\Psi_{b(g)}$ of a given germination fraction from a population of seeds with a known $\Psi_{b(50)}$ can be calculated using a formula:

$$\Psi_{b(g)} = \Psi_{b(50)} + (\sigma_{\Psi b} \times prob_{(g)})$$

where $\Psi_{b(g)}$ is the minimum or base water potential for g fraction of the seeds to germinate from a given population, $\sigma_{\Psi b}$ is the standard deviation of the base water potential, and $prob_{(g)}$ is the probit conversion of fraction g. Although the model can algebraically calculate $\Psi_{b(g)}$ for any fraction, fractions beyond 2 standard deviations of the mean are less likely to be normally distributed.

Thermal Time

We adapted the thermal time (TT) equation from the hydrothermal time (HT) equation. In seed germination studies, TT describes the influence of temperature on seed germination rates. It predicts that radicle emergence will occur more rapidly as germination temperature increases until a maximum temperature threshold is reached. Because thermal time assumes that matric potential has no effect (in other words, it has a value of 0):

$$TT = (0 - \Psi_{b(g)})(T - T_b)t_{(g)}$$

which can be simplified to:

$$TT = (-\Psi_{b(g)})(T - T_b)t_{(g)}$$

The TT equation and the HT equation incorporate the same parameters with the exception of soil water potential. This can be useful for germination modeling when there is abundant soil moisture but an accurate Ψ measurement is unavailable.

Methods

We had three objectives in this study. First, compare the drying response of four different soil moisture sensors near the soil surface with different irrigation treatments. The sensors we used were TDR probes (Campbell Scientific, Inc., Logan, UT), Watermark brand sensors (Irrometer Co., Inc., Riverside, CA), Delmhorst gypsum blocks (Delmhorst Instrument Co., Towaco, NJ), and Colman cells (Soiltest Inc., Lake Bluff, IL). Second, use soil moisture data from the different sensors as driving variables in a hydrothermal time model for 11 grass seed collections from the Negev Desert, Israel, and the Great Basin, United States of America. Third, compare predicted and observed emergence for these 11 grass seed collections.

Soil Moisture Release Curve

We used a structureless, nonsaline (electrical conductivity 0.4 mmhos cm^{-1}), sandy loam (74.8 percent sand, 15.2 percent silt, and 8.5 percent clay) for this experiment. Water content of six soil samples was measured at 0.01, 0.033, 0.1, 0.3, 0.7, and 1.5 MPa using pressure plate Soil Moisture Equipment Co. extractors. The relationship between volumetric water content and matric tension was modeled using log-linear regression (double-log) focusing on three data points in the crucial area:

$$\Psi = e^{-14.3195} / x^{4.74341}$$

where Ψ is soil water matric tension (MPa) and x is volumetric water content (fig. 1).

Sensors

We buried three resistance-type sensors and one TDR probe in plastic trays. Colman resistance cells were individually calibrated for drying soil water content (Roundy and others 1997) to reduce the effects of sensor variability, while standard calibration curves were used for Delmhorst gypsum blocks (CSI 1983), Watermark sensors (CSI 1996a), and TDR probes (CSI 1996b). Resistance cells or blocks were all 2 cm in height or diameter and were buried at a depth of 1 cm (zone of measurement 1 to 3 cm). The TDR probe had two 3.2 mm diameter rods 30 cm long and spaced 3.2 cm apart. Rods were buried at 3.5 cm with the effective measurement environment being 2.5 cm above and below the rods (zone of measurement = 0.5 to 5.5 cm). Soil temperatures were measured at the same depth as resistance sensors using

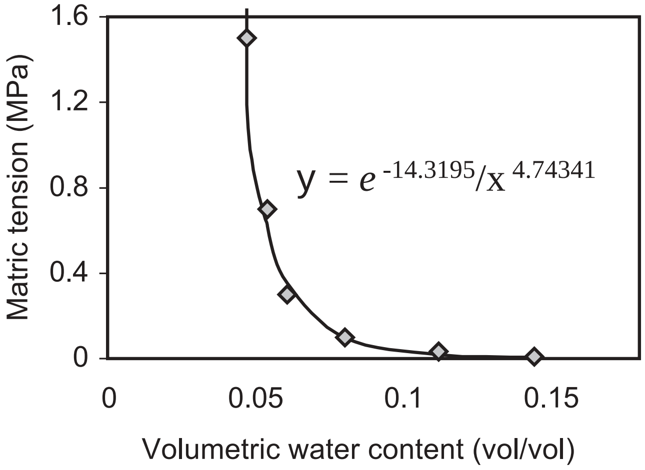


Figure 1—Moisture release curve for the sandy loam soil used in study. Data points indicate observed values; line is from equation.

thermocouples. Four resistance sensors of each type and one TDR probe were buried in each of eight trays (four blocks each receiving one of two irrigation treatments). Trays measured 60 cm long by 43 cm wide by 15 cm deep. We drilled holes in the bottoms of each tray to allow drainage. Sensors were read every minute with CR-10 microloggers (Campbell Scientific, Inc., Logan, UT), and hourly averages were recorded. We converted soil volumetric water content to soil water matric potential for the Colman cells and TDR probes using the moisture release curve (fig. 1).

Growth Chamber Experiment

Fifty seeds from 11 seed collections, including six species, were sown in each tray prior to irrigation. Collections came from the Negev Desert of Israel (*Brachypodium distachyon* [Brdi, 1996 and 1998], *Bromus fasciculatus* [Brfa, 1996 and 1998], *Crithopsis delilianus* [Crde, 1996 and 1998], and *Stipa capensis* [Stca 1997]) and the Great Basin of Utah (*Bromus tectorum* [Brte 15-Whiterocks, Utah, 1996, 1997–1999 Mix, Brte 18-Hobble Creek, Utah, 1996], and *Elymus elymoides* [Elel, 2000]). We sowed seeds of each collection at a depth of 3 to 5 mm with the exception of *Crithopsis delilianus*, which we sowed at a depth of 6 to 8 mm.

Trays were sequentially irrigated and allowed to dry on two occasions. Trays were initially assigned treatment one and two and received 1,363 and 2,934 mL of water, respectively (approximately 0.58 field capacity volumetric water content (fc) or 1.25 fc). Trays were later assigned treatments three or four and rewetted with 3,521 and 4,695 mL of water, respectively (approximately 1.50 fc or 2.00 fc). Trays were arranged in randomized blocks.

We counted seedlings daily and calculated emergence as a percentage of viable seeds. Seed viability for each collection was determined in preliminary germination tests with four replications. We placed 25 seeds from each collection in petri dishes lined with moist blotter paper. Dishes were then placed in incubation chambers programmed at 15, 20, and 25 °C. We considered a seed to have germinated when the radicle exceeded 2 mm. Time required for coleoptile emergence after germination was estimated by regressing the time required for coleoptiles to exceed 3 mm on the temperature of incubation (fig. 2). We estimated time for emergence after germination using the average thermocouple temperature reading within a tray during a corresponding irrigation and drying cycle.

Hydrothermal Time and Thermal Time Parameters

We assumed the hydrothermal time constant (θ_{HT}) and the base temperature (T_b) were constant for each nondormant seed collection (table 1). Hydrothermal parameters for fully after-ripened seeds of the collections were developed using repeated probit regression (Christensen and others 1996; Meyer and others 2000; Taylor and others, unpublished data on file).

Both the hydrothermal time and thermal time models used an average thermocouple temperature reading from four locations, each 3 cm deep, for each corresponding tray. Average soil water matric potential values for each resistance sensor type were calculated similarly while a single TDR probe provided soil water matric potentials for each tray.

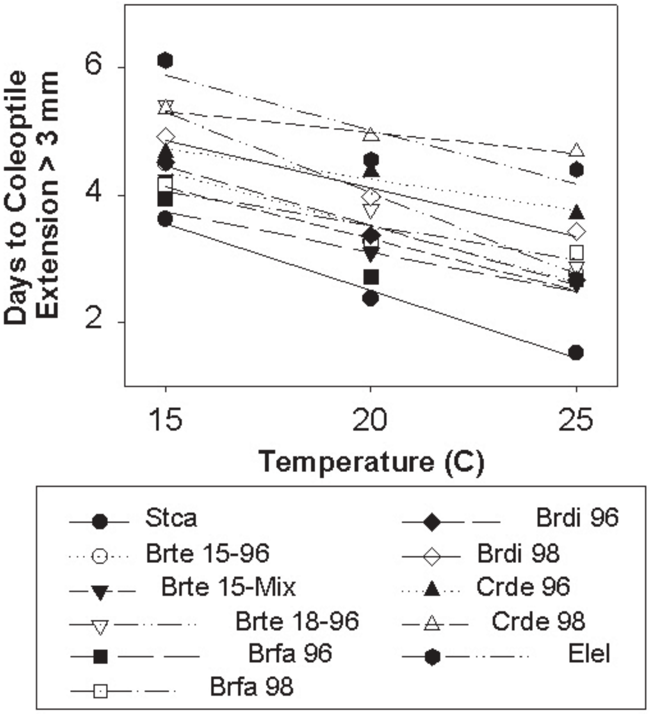


Figure 2—Days for coleoptile extension to more than 3 mm at different incubation temperatures. Coefficient of determination (r-squared) values ranged between 0.78 and 0.98.

Table1—Hydrothermal time parameters for each of the 11 seed collections[a].

Species	Year	θ_{HT} (MPa-°-hrs)	$\Psi_{b(50)}$ (MPa)	T_b (C)	$\sigma_{\Psi b}$ (MPa)
B. distachyon	1996	672	–0.85	2.2	0.328
B. distachyon	1998	864	–0.58	2	.372
B. fasciculatus	1996	744	–1.22	0.7	.326
B. fasciculatus	1998	480	–0.72	1	.315
B. tectorum-15	1996	744	–1.01	0	.337
B. tectorum-15	Mix[b]	744	–1.06	0	.337
B. tectorum-18	1998	672	–0.76	0	.377
C. delileanus	1996	1296	–1.08	4.4	.382
C. delileanus	1998	384	–0.57	10	.276
E. elymoides	2000	2500	–1.57	0	.277
S. capensis	1997	672	–1.23	0	.334

[a] From Taylor, Meyer, Allen, and Roundy, in preparation.
[b] Mix—includes seeds from 1997, 1998, and 1999.

Results and Discussion

All soil moisture sensors behaved consistently during the irrigation and drying cycles. Colman cells and gypsum blocks indicated more rapid drying than Watermark and TDR sensors (fig. 3). Colman cells responded to soil drying most rapidly. The drying pattern for gypsum blocks was similar to Colman cells, but readings usually lagged 1.5 to 2 days (fig. 3). Watermark sensors responded to the 0.58 fc and 1.25 fc treatments more slowly than the other sensors, but exhibited the least amount of variation between individual sensors within their limited range of sensitivity (0 to –0.2 MPa) (fig. 3). Compared with TDR, Colman cells measured soil moisture over a smaller soil volume. The depth interval of measurement of the TDR probes was 0.5 to 5.5 cm, making them the least sensitive to near-surface drying.

The hydrothermal time model and thermal time models generally predicted similar seedling emergence from water potential inputs or thermal inputs for each of the sensors, but usually predicted emergence sooner than actual emergence occurred (fig. 4). Slower actual than predicted emergence may be due to soil impedance of coleoptiles and by lower soil matric potentials in the seed zone than where the sensors were buried. The latter explanation is supported by the results from drier irrigation treatments (fig. 4—fc x 0.58, fc x 1.25, and fc x 1.50). In three of the irrigation treatments (0.58, 1.25, and 1.5 fc), both the hydrothermal time model and thermal time models incorrectly predicted at least 5 percent relative emergence for some or all of the seed collections before any corresponding seedlings emerged. With greater irrigation (fig. 4—fc x 2.00), the model overestimated time to 50 percent relative emergence for some collections, but correctly predicted time of emergence for most of the corresponding collections.

The similarity between hydrothermal time predictions and thermal time predictions (fig. 4) can be explained by two interrelated causes: the relationship between soil water

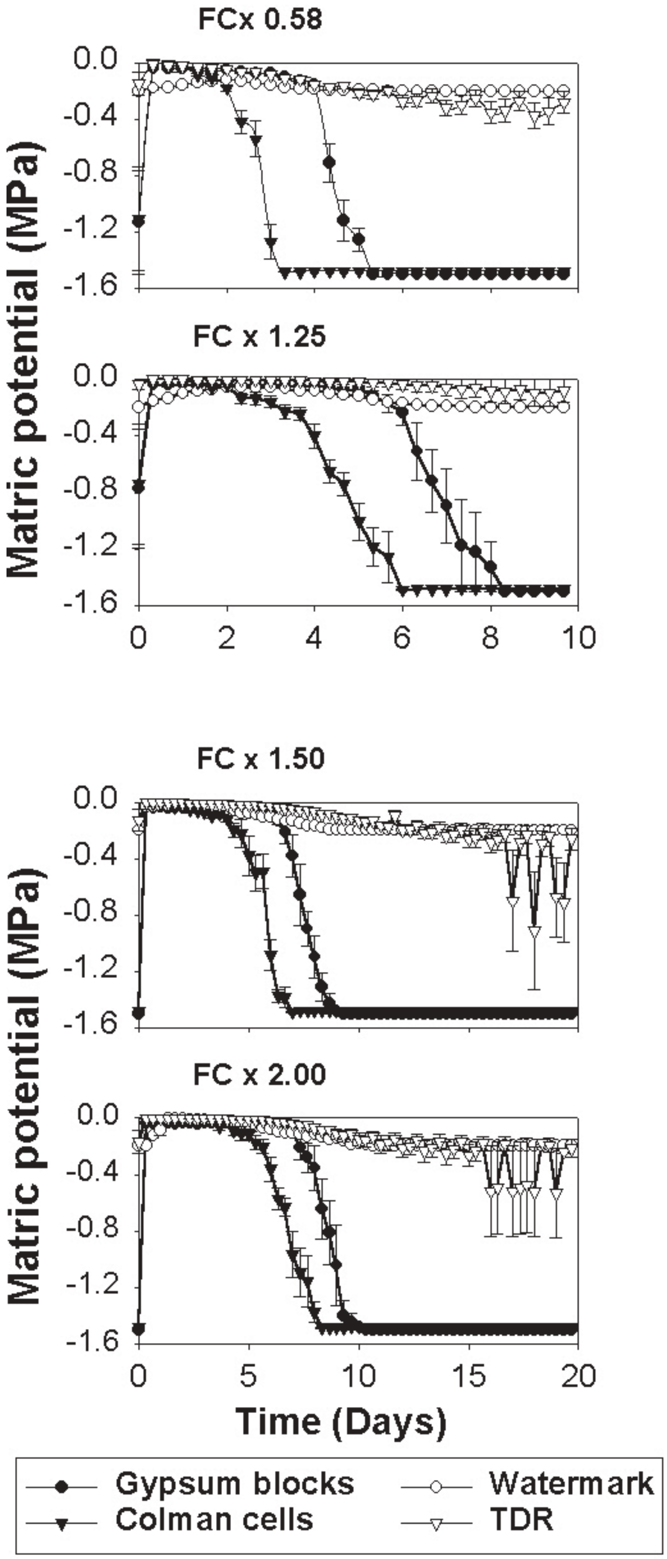


Figure 3—Soil matric potential measured at 1 to 3 cm below the soil surface for different sensors in soil subjected to four irrigation regimes (field capacity x 0.58, 1.25, 1.5, 2.0) and allowed to air dry. Error bars indicate standard error, n = 4.

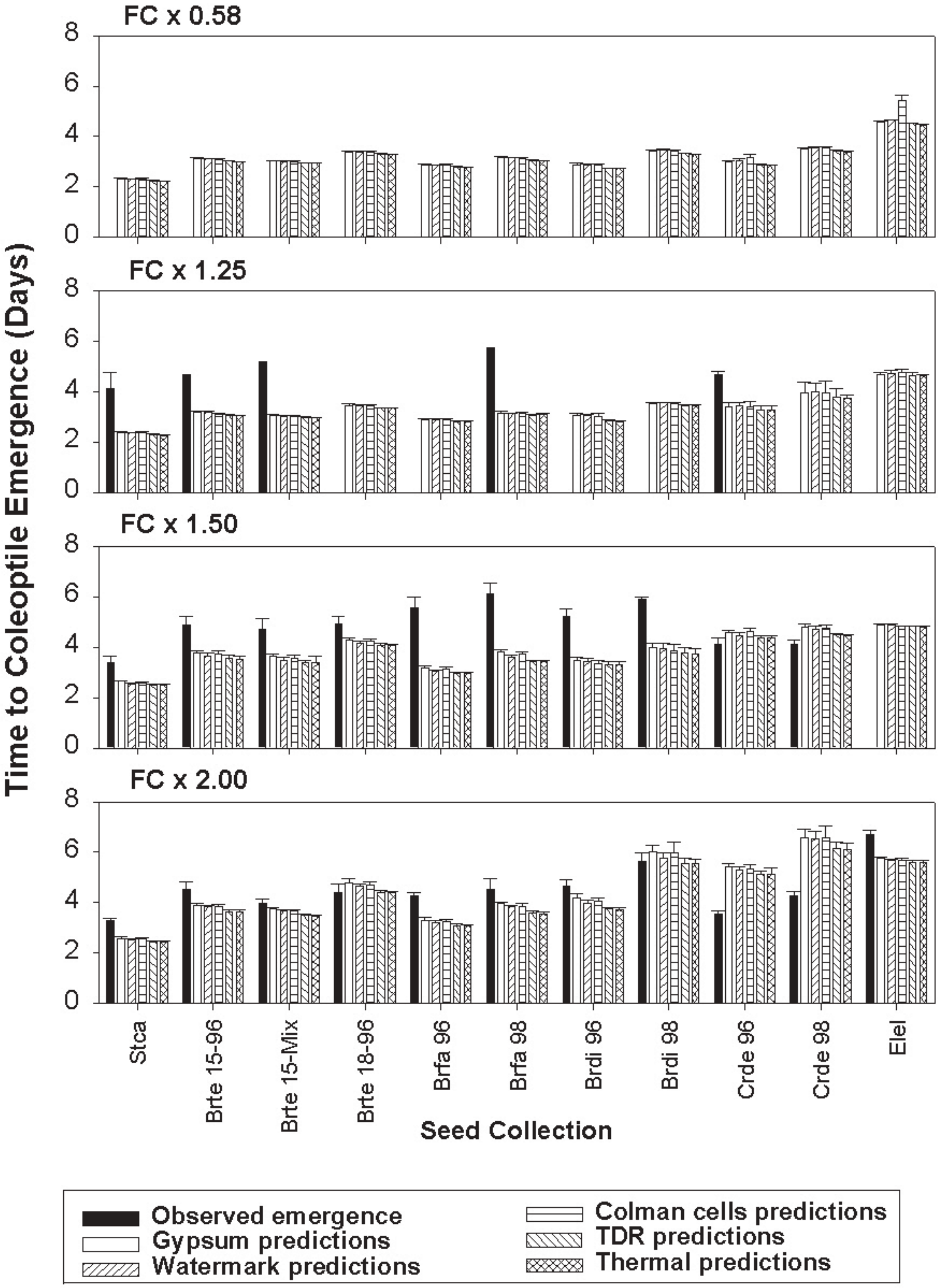


Figure 4—Observed and predicted time to coleoptile emergence. The models predicted 50 percent relative emergence when there was an observed emergence and 5 percent relative emergence when there was no observed emergence using matric potential and thermal inputs for either a hydrothermal time model (matric potential and thermal inputs) or a thermal time model (thermal inputs only) for each seed collection and irrigation regime. Error bars indicate standard error, n = 4.

matric potentials and the period when seeds were germinating and the nature of the hydrothermal and thermal time equations. Seeds germinated within the first 1 to 4 days after the 1.25, 1.50, and 2.00 fc irrigation treatments. During this period, the differences in soil matric potential measurements among the different sensors were minimal, and matric potential values were relatively high (fig. 3). As a result, the differences between ($\Psi - \Psi_{b(g)}$) among each sensor type were minimal. In addition, the influence of ($T - T_b$) was approximately 10 times greater than the influence of ($\Psi - \Psi_{b(g)}$) or ($-\Psi_{b(g)}$) for the hydrothermal and thermal time equations, respectively. This large difference in the relative contribution made by the thermal portion of the germination models essentially masked small differences in soil water matric potential as measured by each sensor type.

The ability of a hydrothermal time model to accurately predict emergence of seeds under slower germination and drying conditions requires sensors that more accurately measure water potential in the seed zone. Previous research has successfully created models using soil property related parameters to estimate daily soil moisture relationships. Models developed by Finch-Savage and Phelps (1993) are based on soil temperature and soil-type relationships, while Roman and others (2000) used weekly soil moisture averages from TDR sensors to develop near-surface soil moisture relationships. Currently, soil moisture sensors are unable to provide direct soil water potential inputs that accurately predict seedling emergence using a hydrothermal time model. Energy-based heat and waterflow models should be tested to see if they can predict near-surface water potential to provide accurate hydrothermal time predictions of seedling emergence.

Acknowledgments

We would like to thank Bruce Webb and the members of the Brigham Young University Soil and Plant Analysis Laboratory for helping us operate the soil pressure plate extractors, and Dr. Chris Grant, Associate Chair of the BYU Mathematics Department, for helping us model the relationship between volumetric soil water content and soil water matric potential.

References

Abbott, L. B.; Roundy, B. A. 2003. Available water influences field germination and recruitment of seeded grasses. Journal of Range Management. 56: 56–4.

Allen, P. S.; Meyer, S. E.; Khan, M. A. 1999. Hydrothermal time as a tool in comparative germination studies. In: Black, M.; Bradford, K. J.; Vasquez-Ramos, J., eds. Seed biology: advances and applications. CABI Publishing. 401–410.

Amer, S. A.; Keefer, T. O.; Weltz, M. A. 1994. Soil moisture sensors for continuous monitoring. Water Resources Bulletin. 30: 69–83.

Baker, J. M.; Allmaras, R. R. 1990. System for automating and multiplexing soil moisture measurement by time-domain reflectometry. Soil Science Society of America Journal. 54: 1–6.

Billings, W. D. 1994. Ecological impacts of cheatgrass and resultant fire on ecosystems in the western Great Basin. In: Monsen, S. B.; Kitchen, S. G., eds. Ecology and management of annual rangelands symposium, proceedings; 1992 May 18–22; Boise, ID. Gen. Tech. Rep. INT-313. Ogden, UT: U. S. Department of Agriculture, Forest Service, Intermountain Research Station: 22–30.

Bradford, K. J. 1990. A water relations analysis of seed germination rates. Plant Physiology. 94: 840–849.

Bradford, K. J. 1995. Water relations in seed germination. In: Kiegal, J.; Galili, G., eds. Seed development and germination. New York: Marcel Dekker: 351–395.

Christensen, M.; Meyer, S. E.; Allen, P. S. 1996. A hydrothermal time model of seed after-ripening in *Bromus tectorum* L. Seed Science Research. 6: 1–9.

Collins, J. E. 1987. Soil moisture regimes of rangelands: using datapods to record soil moisture. In: International conference on measurement of soil and plant water status: in commemoration of the centennial of Utah State: proceedings; 1987 July 6–10; Logan, UT: Utah State University: 219–225.

CSI. 1983. Model 227 Delmhorst cylindrical soil moisture block instruction manual. Logan, UT: Campbell Scientific, Inc.

CSI. 1996a. Model 253 and 253-L (Watermark 200) soil moisture sensor. Logan, UT: Campbell Scientific, Inc.

CSI. 1996b. CS615 water content reflectometry instruction manual. Logan, UT: Campbell Scientific, Inc.

D'Antonio, C. M.; Vitousek, P. M. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annual Review of Ecological Systems. 23: 63–87.

Finch-Savage, W. E.; Phelps, K. 1993. Onion (*Allium cepa* L.) seedling emergence patterns can be explained by the influence of soil temperature and water potential on seed germination. Journal of Experimental Botany. 44: 407–414.

Frasier, G. W. 1987. Soil moisture availability effects on seed germination and germinated seed survival of selected warm season grasses. In: Frasier, G. W.; Evans, R., eds. Seed and seedbed ecology of rangeland plants: proceedings; 1987 April 21–23; Tucson, AZ. Tucson, AZ: U.S. Department of Agriculture, Agricultural Research Service.

Gummerson, R. J. 1986. The effect of constant temperature and osmotic potentials on the germination of sugar beet. Journal of Experimental Botany. 37: 729–741.

Hanson, B.; Peters, D.; Orloff, S. 2000. Effectiveness of tensiometers and electrical resistance sensors varies with soil conditions. California Agriculture. 54(3): 47–50.

Meyer, S. E.; Debaene-Gill, S. B; Allen, P. S. 2000. Using hydrothermal time concepts to model seed germination response to temperature, dormancy loss, and priming effects in *Elymus elymoides*. Seed Science Research. 10: 213–223.

Roman, E. S.; Murphy, S. D.; Swanton, C. J. 2000. Simulation of *Chenopodium album* seedling emergence. Weed Science. 48: 217–224.

Roman, E. S.; Thomas, A. G.; Murphy, S. D.; Swanton, C. J. 1999. Modeling germination and seedling elongation of common lambsquaters (*Chenopodium album*). Weed Science. 47: 149–155.

Roundy, B. A.; Abbott, L. B.; Livingston, M. 1997. Surface soil water loss after summer rainfall in a semidesert grassland. Arid Soil Research and Rehabilitation. 11: 49–62.

Roundy, B. A.; Hegdar, H.; Watson, C.; Smith, S. E.; Munda, B.; Pater, M. 2001. Summer establishment of Sonoran Desert species for revegetation of abandoned farmland using line source sprinkler irrigation. Arid Land Research and Management. 15: 23–29.

Taylor, J. R.; Meyer, S. E.; Allen, P. S.; Roundy, B. A. [In preparation]. A hydrothermal germination model for germination of five desert annuals of the Negev Desert.

Topp, G. C.; Davis, J. L. 1985. Measurement of soil water content using time-domain reflectometry (TDR): a field evaluation. Soil Science Society of America Journal. 49: 19–24.

Community Ecology

Penstemon acaulis

Illustration on the reverse side is by Kaye H. Thorne. In: Fertig, W.; Refsdal, C.; Whipple, J. 1994. Wyoming rare plant field guide. Cheyenne: Wyoming Rare Plant Technical Committee. Available at: http://www.npwrc.usgs.gov/resource/distr/others/wyplant/species.htm (Accessed 12/18/03).

Antelope Bitterbrush Flowering, Survival, and Regeneration Following Ponderosa Pine Forest Restoration Treatments

Donald J. Bedunah
Kristi D. Pflug
Thad E. Jones

Abstract: To further understanding of the dynamics of antelope bitterbrush (*Purshia tridentata*) recruitment in a ponderosa pine (*Pinus ponderosa*) forest in western Montana, we measured bitterbrush seed viability and germination, flower numbers in 1997 and 1998, seed depredation, seedling survival between 1994 and 2002, and population changes between 1992 and 2002 on four forest restoration treatments. Treatments included a control, a shelterwood cut, a shelterwood cut followed by a low consumption burn, and a shelterwood cut followed by a high consumption burn. Bitterbrush flower numbers did not differ between treatments, but caged bitterbrush had greater flower numbers ($P < 0.001$) than their uncaged pairs, indicating that browsing reduced flower numbers. Seed depredation by rodents and birds caused a small reduction ($P < 0.050$) in seed crop in 1997. Bitterbrush seed viability and seedling survival (percent) were both high; although, the number of surviving bitterbrush seedlings averaged only 15 plants per treatment between 1994 and 2002. In the control treatment there has been a continual decline in bitterbrush numbers totaling 26 percent between 1992 and 2002; whereas, in the shelterwood cut and burn treatments bitterbrush numbers have stabilized since 1994. If bitterbrush stands are desired as a future part of this landscape, it seems clear that disturbance will be necessary. Failure to allow for disturbances that reduce forest overstory and increase mineral soil coverage may ultimately result in loss of bitterbrush from these stands.

Introduction

Antelope bitterbrush (*Purshia tridentata*) is a wide-ranging western shrub found from New Mexico to British Columbia, and from Montana to California in grasslands and open pine forests. In addition to its intrinsic value as an understory and grassland plant, bitterbrush is often an important winter browse species for mule deer (*Odocoileus hemionus*) and elk (*Cervus elaphus*). In a study by Austin and Urness (1983), bitterbrush was often the most heavily used browse species even when making up only 3 percent of the plant community. Moose (*Alces alces*), bighorn sheep (*Ovis canadensis*), yellow-pine chipmunk (*Eutamias amoenus*), deermice (*Peromyscus maniculatatus*), chipping sparrow (*Spizella passerina*), and blue grouse (*Dendragapus obscurus*) are among the other species that use bitterbrush for food and cover (Everett and others 1978; Matlock-Cooley 1993; Nord 1965).

During the last five decades, the lack of natural bitterbrush regeneration has become recognized as an increasing problem throughout much of its range (Clements and Young 1996; Fraas 1992; Peek and others 1978; Young and others 1997). For example, in a study of bitterbrush in six forest types in Utah from 1957 to 1980, "*Purshia* population densities declined in all forest types over the study period. Average density loss was 35.9 percent in 20 years. Photographs taken in the initial and the 1978 to 1980 periods demonstrate that many shrub individuals died and left no replacements" (Harper and Buchanan 1983).

Bitterbrush stands in western Montana have shown a similar lack of regeneration (Bunting and others 1985). Studies of the shrub-grass communities at and around the Mount Haggin Wildlife Management Area in southwestern Montana have repeatedly stressed the minimal amount of successful reproduction occurring in that region (Fraas 1992; Guenther 1989; Matlock-Cooley 1993). Such concerns have also been documented in the ponderosa pine forests of the Lick Creek Study Area in the Bitterroot National Forest of western Montana (Ayers 1995; Ayers and others 1999). Mature bitterbrush is an important component of the understory throughout much of this area; however, Ayers (1995) found only eight bitterbrush seedlings in the area during the combined field seasons of 1993 and 1994 raising concerns that seedling recruitment would not replace bitterbrush plants dying of natural causes or associated with forest restoration treatments (Bedunah and others 1999). Therefore, the major objectives of our study were to determine the cause of the low number of bitterbrush seedlings observed by Ayers (1995) at the Lick Creek study site and to monitor long-term changes in bitterbrush populations following ponderosa pine forest restoration treatments. To determine possible causes of the lack of regeneration, we measured (1) bitterbrush

---

In: Hild, Ann L.; Shaw, Nancy L.; Meyer, Susan E.; Booth, D. Terrance; McArthur, E. Durant, comps. 2004. Seed and soil dynamics in shrubland ecosystems: proceedings; 2002 August 12–16; Laramie, WY. Proceedings RMRS-P-31. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Donald J. Bedunah is Professor, and Kristi D. Pflug and Thad E. Jones are Graduate Research Assistants, School of Forestry, University of Montana, Missoula 59812, U.S.A. Fax: (406) 243-6645; e-mail: bedunah@forestry.umt.edu

flower numbers; (2) browsing impacts on flower numbers; (3) seed depredation by ungulates, rodents or birds, and insects; (4) differences in viability and germination between seeds collected from the site and seeds obtained from another local seed source, and (5) seedling survival and population changes between 1994 and 2002. Results from this study clarify factors associated with bitterbrush regeneration and population changes in the Lick Creek Study Area as well as provide information for the development of management prescriptions.

Study Area

Our study site is the Lick Creek Study Area of the Bitterroot National Forest located 21 km southwest of Hamilton, MT. Elevations range from 1,311 to 1,402 m. Mean annual precipitation is 56 cm, with approximately 50 percent in the form of snow. Soils are of granitic till parent material and are shallow to moderately deep, with some poorly drained areas and clay soils at the lowest elevations (Gruell and others 1982). Most of the habitat types (Pfister and others 1977) are Douglas-fir (*Pseudotsuga menziesii*) types. The dominant overstory before treatments was Douglas-fir and ponderosa pine. The potential site indexes for these two species average 16 m tall at age 50 (Gruell and others 1982; Pfister and others 1977). The Lick Creek area is considered an important local winter and spring range for mule deer and elk. White-tail deer and moose also occur but at much smaller numbers.

In 1991, the Bitterroot National Forest and Intermountain Forest Science Fire Laboratory initiated a project to examine the response of a ponderosa pine/Douglas-fir stand to a combination of prescribed fire and shelterwood cutting as ecological restoration management tools. Photographs of the study area in the early 1900s are of an open stand of large ponderosa pine with little shrub understory. Apparently, with fire suppression and subsequent logging practices, the area became dominated by dense stands of small diameter Douglas-fir. In 1992 personnel from the Intermountain Fire Sciences Laboratory divided the study site into 12 approximately equal 4-ha units. Each unit was assigned to one of the following four treatments: (1) a shelterwood cut (no burn), (2) a shelterwood cut and a high consumption burn (high consumption burn), (3) a shelterwood cut and a low consumption burn (low consumption burn), and (4) a control. The shelterwood cut was completed in the fall of 1992. Tree basal area was reduced by 53 percent to 13.1m^2. Before application of the shelterwood cut, the location of all bitterbrush within thirty-six 400-m^2 circular plots established in the control, shelterwood cut, low-consumption burn, and high-consumption burn treatments were permanently recorded. Prescribed burns were conducted in May 1993. Burn conditions and bitterbrush survival 2-years post-treatment are described in Ayers and others (1999).

Methods

Flower Production

In May 1997, fifteen 0.04-ha plots were chosen from each of the forest restoration treatments (five plots/replication) established in 1992 to undergo flower counts and seedling observations. We selected five plots because this was the minimum number of plots per replication that still contained live bitterbrush plants following the burning treatments. For those replicated treatments having more than five plots with live bitterbrush, selection was made by first eliminating plots with less than five remaining live plants, and then randomly selecting from the remaining plots. Bitterbrush flowers were counted for the 1997 and 1998 to determine if forest management treatments significantly affected flower production. Bitterbrush seedling survival and change in bitterbrush numbers between 1998 and 2002 were compared with pretreatment and post-treatment bitterbrush numbers. Flower counts were analyzed both as average number of flowers per hectare and average number of flowers per plant, as plant numbers varied across plots.

In the fall of 1994, previous researchers randomly selected 20 plants from each forest management treatment and paired plants of close proximity and with similar vigor and biomass, caging one plant from each pair in a 1.5-m-high wire cage (Ayers 1995). During May 1997, we located the original caged pairs to determine the difference in flower numbers between caged (unbrowsed) and uncaged (browsed) bitterbrush. Those pairs that had one or both members dead or missing were noted as such, and flower count was obtained only for those pairs, which were still viable during May of 1997 and 1998.

Seed Depredation

At the beginning of July 1997, we reviewed flower count data to identify those plants that produced at least 20 flowers. Of these, 15 plants per treatment were randomly selected for monitoring seed production and seed loss. Three plants per treatment were randomly selected to be caged with large square (4- by 7.5-cm opening) hardware cloth to exclude ungulates, three plants were covered with vexar netting to exclude all seed predators except insects, and three plants/treatments were unprotected (control). Seed count was recorded at the beginning of seed production (late June or early July), and again 3 weeks later (mid to late July), to determine the ratio of remaining seed count to original seed count. This ratio was then used to compare the amount of seed lost before seedfall among the three different sets of plants to assess whether ungulates, rodents and birds, or insects were harvesting or browsing seed before seedfall. In 1998, bitterbrush seeds had already ripened and fallen before our second seed count, likely a result of record high temperatures and extremely low levels of precipitation in July and August. Therefore, seed depredation measurements were not valid for the 1998 growing season and are not reported.

Seed Viability and Germination

Seed was collected from bitterbrush plants immediately outside the study plots during the last 2 weeks of July 1997. The seed were cleaned by hand, removing debris and the remnant flower parts, which contain germination inhibitors (Young and Young 1986). After hulling, black or spotted seeds were removed, as these are usually signs of insect infestation or not viable (Giunta and others 1978). Viability rates of Lick Creek seed were compared with viability of seed purchased from Bitterroot Restoration, Inc. (BRI). BRI bitterbrush seed was collected during the same season about 8 km south of our study site. The BRI seed had been cleaned and culled in a similar manner to ours and had produced healthy seedlings in previous greenhouse trials done by their seed biologist. Both sets of seeds were placed in dry cold storage (1 °C) until testing in the spring of 1998. Viability of seed was determined using a tetrazolium tests according to procedures of Grabe (1970) and Meyer and Monsen (1989). We used four replications of 30 randomly selected seeds from each seed source.

Germination tests were conducted using procedures of Young and Evans (1983), Young and Young (1986), and Meyer and Monsen (1989). Seeds were stratified in the dark for 6 weeks at 2 to 5 °C. Seeds were initially soaked in a 5-percent bleach solution for 2 minutes to kill bacteria or mold. Each replication of 30 seeds was divided into three equal subsets so that seeds could be spaced on petri dishes to prevent individual seeds contacting each other. Germination percent for each petri dish was determined as the ratio of seeds that germinated to the total number of seeds in that dish.

We also monitored germination and establishment of planted seeds in the control treatment by planting three plots of 10 seed groups in November 1997. The seed groups were planted at a depth of 2.5 cm under mineral soil in groups of five seeds to simulate natural germination conditions in rodent caches (Evans and others 1983; Matlock-Cooley 1993). The artificial caches were unmarked to avoid attracting rodents (Young and others 1997). Sites were inspected biweekly in May and early June 1998 to record the number of germinated seeds. Germination percentages were computed by the percent of seed groups that germinated out of the total number of seed groups. Seedling survival for the growing season was measured as the percentage of seedlings that were surviving in October out of the total number of germinated seedlings.

Data Analyses

All statistical analyses were conducted using SPSS software version 8.0 (SPSS 1997). Data were tested for normality and homogeneity of variances. In most cases, despite attempted transformations, most of the data did not meet assumptions of analysis of variance and necessitated the use of nonparametric tests. Number of flowers per plant and number of flowers per hectare between forest restoration treatments and years were compared using the Kruskal-Wallis test (Ott 1993) and the post-hoc comparisons of Tamhane, Dunnett and Games-Howell (Day and Quinn 1989). Because these tests would not allow a block by year, we also used a Kruskall-Wallis test for each year's data alone (flower counts), both with and without outliers. Flower number per plant was compared with all bitterbrush seedlings (any seedling documented between 1993 and 1998) and caged plants excluded from analyses. Flower count data between caged and uncaged plants and seed depredation treatments were tested with an approximate t-test (Day and Quinn 1989). Seed depredation involved comparing three populations using a two-sample t-test; we compared each one to the others by pairs (that is, big cage versus net; big cage versus no cage; no cage versus net). Comparisons of viability and germination rates between seed sources were conducted using an approximate t-test and the nonparametric Wilcoxon Rank Sum/Mann-Whitney test (Day and Quinn 1989; Norusis 1997) because there were too few data points to clearly ascertain normality. Survival of bitterbrush between treatments and years was tested using a two-way analysis of variance with treatments and years as factors.

Results and Discussion

Flower Numbers

Average flower count per hectare was not statistically different between restoration treatments ($P > 0.800$) or years (approximate t-test $P = 0.255$) (table 1). Average flower numbers per plant also did not differ between treatments ($P > 0.550$), but did differ between years ($P = 0.074$) (fig. 1). In 1997 and 1998, 57 and 44 percent of bitterbrush plants produced no flowers, but plants with several hundred to over 2,000 flowers were also found revealing high plant and plot variability (table 2). We believe the difference in flower production per plant between years was due to variations in climate, but was also affected by browsing pressure.

Flower numbers for caged bitterbrush compared to uncaged pairs were 3.4 and 6 times greater ($P < 0.001$) in 1997 and 1998, respectively. Caged plants had greater ($P < 0.05$) flower numbers than the uncaged plants in all treatments except for the control (fig. 2). The reduced flower numbers on uncaged plants revealed that browsing at the Lick Creek Study Area has a significant impact on flower production. We observed many plants during the late spring and early summer of 1997 that had bark slippage (stem segments stripped of cambium) on shoots 1 and 2 years old. Two-year-old leaders are heavily involved in flower production (Shaw and Monsen 1983). Even caged plants often had considerable twig breakage where ungulates had pushed their heads as far as possible through the

Table 1—Bitterbrush (*Purshia tridentata*) mean flower counts per hectare (95-percent confidence intervals) in 1997 and 1998 for the different forest restoration treatments at the Lick Creek Study Area.

Year	Control	No burn	Low-consumption burn	High-consumption burn
1997	7,064 ± 4,889	28,764 ± 25,125	5,579 ± 4,702	4,158 ± 2,606
1998	27,037 ± 19,278	45,005 ± 41,480	12,668 ± 9,645	12,035 ± 7,532

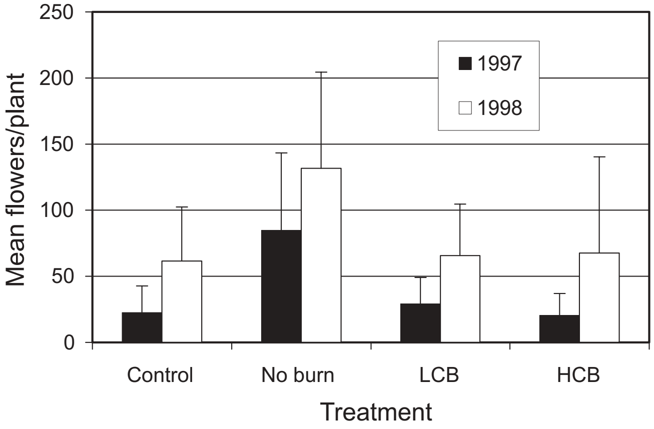


Figure 1—Mean bitterbrush (*Purshia tridentata*) flowers/plants in 1997 and 1998 in the control, no-burn (shelterwood cut only), low-consumption burn (LCB), and high-consumption burn (HCB) treatments at the Lick Creek Study Area.

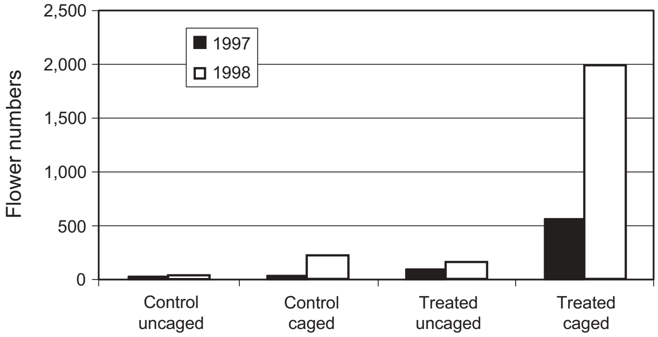


Figure 2—Mean number of bitterbrush (*Purshia tridentata*) flowers/plant for the control and restoration treatments combined for uncaged and caged (protected from browsing) pairs in 1997 and 1998 at the Lick Creek Study Area. Flower counts of caged bitterbrush were significantly different (P < 0.001) than uncaged pairs for all treatments except the control. The no burn, low-consumption burn, and high-consumption burn were combined into "treated," as there were no differences between these treatments and all were greater than for the control (P < 0.01).

tops of the cages. The lack of difference in flower numbers between caged and uncaged pairs for the control is likely related to low vigor of bitterbrush plants on the control treatment. Other researchers (Buwai and Trlica 1977; Guenther and others 1993) also found that browsing impacted bitterbrush stands, causing decreases in vigor and biomass. However, Tueller and Tower (1979) found a 70-percent reduction in bitterbrush forage production after 2 years of caging. Ferguson and Medin (1983) state that old bitterbrush will reduce leader growth and increase seed production if not browsed. Most caged plants on our study site were three to four times as tall as uncaged plants, and most of them completely filled their cage. These plants had been caged for four growing seasons before our initial flower counts, but were showing none of the reduction in vigor predicted by Tueller and Tower (1979) or Peek and others (1978) for unbrowsed plants. However, as stated previously a number of these caged plants displayed evidence of having been browsed where they extended through the cage at both top and sides. Perhaps this browsing stimulation was enough to keep the plants from becoming senescent. In light of the literature, and the fact that these caged and relatively lightly browsed plants were much more vigorous than the uncaged plants, we conclude that browsing is having a significant negative impact on bitterbrush flower production.

Seed Depredation Ratios of Caged, Netted, and Uncaged Plants

Seed depredation was decreased by netting, but increased by caging plants (P < 0.05). Ratios of remaining seeds to initial seeds were 0.75, 0.60, and 0.45 for the netted, uncaged, and large-caged plants, respectively. Apparently, nets kept rodents and birds from consuming seeds, while cages with large openings provided these animals with a safe, relatively predator-free place to feed. We observed a number of caged plants with new chipmunk holes directly under the plant. This bias created by possibly improving rodent habitat with these large cages makes it somewhat difficult to assess possible browsing trends on seed depredation. However, we do not think that ungulate browsing had much effect on these seed count ratios because ungulate populations at this time year are small, as most animals have migrated to their summer ranges. Some sources (Evans and others 1983; Young and Evans 1978) cite high seed depredation levels by ants. We observed

Table 2—Bitterbrush (percent) with no flowers, 1 to 10 flowers, 11 to 100 flowers, 101 to 500 flowers, and greater than 500 flowers in 1997 and 1998 for restoration treatments combined at the Lick Creek Study Area.

	Flower numbers				
Year	**None**	**1 to 10**	**11 to 100**	**101 to 500**	**Greater than 500**
			percent		
1997	57.0	14.5	16.9	8.7	3.0
1998	43.7	13.3	19.9	16.0	7.1

minimal ant activity on these plants during our seed count measurements. We conclude that since uncaged plants maintained 60 percent of their seed until seedfall, seed depredation was probably not a significant problem during 1997.

Laboratory Viability and Germination Rates

Comparisons of tetrazolium and laboratory germination test results revealed no difference in percent viability (P > 0.45) or germination percentages (P > 0.55) between the Lick Creek and Bitterroot Restoration, Inc. seed sources. Viability and germination percentages averaged 91 and 28 percent, and 91 and 33 percent, respectively for the Lick Creek and BRI seed sources. In theory, tetrazolium and laboratory germination tests should yield similar percentages (Grabe 1970; Meyer and Monson 1989; Meyer and others 1986). However, mold is frequently a problem in laboratory stratification and germination, causing some authors to recommend tetrazolium testing only (Grabe 1970; Meyer and others 1986). Once germination testing began we could not bleach or otherwise eliminate mold because the chemicals used would probably also have killed the embryos. This contamination problem is the reason for the lower germination percentages compared to viability. In our field germination trials, 75 percent of the seeds germinated, and 87 percent of these survived through the first growing season.

Seedling Recruitment and Change in Bitterbrush Numbers

Total seedling recruitment, measured as seedlings identified pre-1998 and still present in 2002, was 4, 32, 8 and 4 plants for the control, no burn, low-consumption burn, and high-consumption burn treatments, respectively. Seedling survival was 78 percent across treatments with no difference (P = 0.69) between treatments. Thus, the number of bitterbrush seedlings located has been small (and not significantly different between treatments), but survival has been high. The lack of seedlings is a concern in that the initial decrease in bitterbrush numbers following treatments averaged 34, 62, and 65 percent for the no burn, low-consumption burn, and high-consumption burn treatments (fig. 3). Seedling recruitment in these treatments has not been able to add significantly to the population losses caused by the initial treatments, with the no burn, low-consumption burn, and high-consumption burn treatments averaging 103, 106, and 99 percent of bitterbrush numbers found in 1994. However, bitterbrush in the control treatment has declined by 26 percent (P < 0.05) since the study began in 1992, showing significant mortality for untreated stands (fig. 3). The decrease in bitterbrush in the control treatment appears to be a relatively continuous decline, with 18-percent mortality between 1994 to 1998, and an additional 8-percent mortality between 1992 to 2002 (fig. 3). We believe this mortality is associated with the poor vigor of bitterbrush in these undisturbed forest stands and illustrates that a “no treatment” option is not a viable option for maintaining bitterbrush in the Lick Creek area.

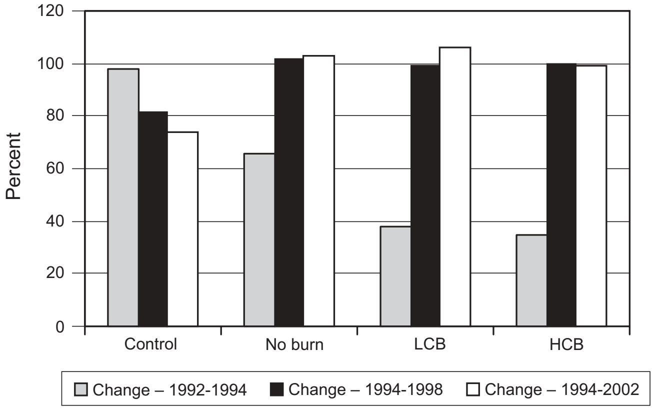


Figure 3—Change (percent) in bitterbrush (*Purshia tridentata*) numbers between 1992 to 1994, 1994 to 1998, and 1994 to 2002 for a control, no burn (shelterwood cut only), low-consumption burn (LCB), and high-consumption burn (HCB) at the Lick Creek Study Area. Pretreatment bitterbrush numbers were 184, 258, 259, and 490 for the control, no burn, low-consumption burn, and high-consumption burn treatments, respectively.

We examined historical photos taken of our study area during the past 90 years (some from Gruell and others 1982, others from the U.S. Forest Service Region 1 Headquarters, Missoula, MT) to determine the historical density and size of bitterbrush on this site. These pictures show mostly small, low-growing bitterbrush at low density for the areas photographed in 1909. These photographs were taken 14 years after the last recorded fire, which is within the 3- to 30-year fire interval for the site (Arno 1976). By the late 1920s, bitterbrush in the photographs are larger and the stands more dense. However, as the forest canopy closes no bitterbrush regeneration is visible, and stands appear less vigorous. When trees are removed in subsequent thinning, the bitterbrush stands appear to regain vigor. Photo interpretation indicates that bitterbrush were present on this site during the era of high-frequency, low-intensity fires although in smaller form and numbers (for example, see photo series accompanying USDA Forest Service photos 87357 and 86480). Therefore, the population levels of bitterbrush now found on the restoration treatments, although lower than before treatments, may represent more natural (pre-1900) levels of bitterbrush.

Summary and Management Implications

The primary goal of this study was to understand bitterbrush regeneration and survival following forest restoration treatments at the Lick Creek Study Area. The restoration treatments were designed to restore the area to an open ponderosa pine stand, similar to conditions prior to European settlement. Previous studies have shown high bitterbrush mortality on all treatments except the control and noted almost no bitterbrush flower production or seedlings

2 and 3-years post-treatment. We found no significant problems in bitterbrush seed viability, field germination, or seedling survival. Netting plants significantly reduced seed depredation; however, depredation of seeds on unprotected plants was only 40 percent and does not appear to be a major factor for the low seedling recruitment. Much higher flower numbers for caged bitterbrush compared to uncaged pairs shows that browsing by ungulates impacts flower numbers. It seems likely that more bitterbrush regeneration would occur if browsing pressure was reduced, especially where there is not a buildup of undecomposed organic matter and suitable sites for rodent caching and seed germination. Several studies have shown that a buildup of undecomposed organic matter reduces suitable sites for rodent caching and seed germination (Evans and others 1983; Ferguson and Medin 1983; Fraas 1992; Matlock-Cooley 1993).

The no burn, low-consumption burn, and high-consumption burn treatments resulted in 34, 62, and 65 percent bitterbrush mortality, respectively, following treatments (1992 to 1994). Bitterbrush mortality was found to be significantly related to mechanical damage class and burn severity (Ayers and others 1999). Since 1994, bitterbrush numbers have stabilized for these treatments, with the low consumption burn and no burn treatments having small increases in total plants (although not significantly different); however, for the control (no treatment) bitterbrush numbers decreased by 26 percent. Therefore, it is apparent that a “no treatment” is not a viable option for maintaining bitterbrush in the Lick Creek area. In addition, the potential of a high-intensity wildfire is much greater in stands with no treatment as compared to forest restoration treated stands. A high-intensity wildfire would likely result in extreme mortality of bitterbrush in this area. Land managers may want to consider a mosaic of different treatments on the landscape as a simulation of mosaics created by fires in the past. Such mosaics provide more diversity of habitat and species, both flora and fauna, and less potential for landscape-scale forest stand replacement by insects, disease, or fire (Camp and others 1996). A shelterwood cut with no burning would result in less bitterbrush plant loss compared to a treatment with understory burning. However, disturbances mimicking natural events, such as forest stand thinning and low-intensity burns, which maintain open ponderosa pine stands, should allow for bitterbrush maintenance and further reduce the potential of wildfires. The type of treatment chosen will depend on the specific management objectives for a given area, both in terms of bitterbrush stand condition and in terms of timber and other interests. However, it is apparent that if bitterbrush stands are desired as a future part of this landscape, some type of disturbance will be necessary to reduce forest overstory and increase mineral soil coverage on at least a portion of the landscape. Failure to provide or allow for these disturbances may ultimately result in long-term loss of bitterbrush from these stands, and for other species that also depend on disturbance for regeneration and maintenance.

References

Arno, S. F. 1976. The historical role of fire on the Bitterroot National Forest. Res. Pap. INT-187. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 29 p.

Austin, D. D.; Urness, P. J. 1983. Summer use of bitterbrush rangelands by mule deer. In: Tiedemann, A. R.; Johnson, K. L., comps. Proceedings: research and management of bitterbrush and cliffrose in Western North America. Gen. Tech. Rep. INT-152. Ogden, UT; U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station: 203–212.

Ayers, D. M. 1995. Response of bitterbrush and Scouler's willow to a shelterwood harvest and prescribed burn in western Montana. Missoula: University of Montana. 37 p. Thesis.

Ayers, D. M.; Bedunah, D. J.; Harrington, M. G. 1999. Antelope bitterbrush and Scouler's willow response to a shelterwood harvest and prescribed burn in western Montana. Western Journal of Applied Forestry. 14: 137–143.

Bedunah, D. J.; Harrington, M. G.; Ayers, D. M. 1999. Antelope bitterbrush and Scouler's willow response to a forest restoration project. In: McArthur, E. D.; Ostler, W. K.; Wambolot, C. L., comps. Proceedings: shrubland ecotones; 1998 August 12–14; Ephraim, UT. Proc. RMRS-P-11. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 256–259.

Bunting, S. C.; Neuenschwander, L. F.; Gruell, G. E. 1985. Fire ecology of antelope bitterbrush in the Northern Rocky Mountains. In: Fire effects on wildlife habitat, symposium proceedings. Gen. Tech. Rep. INT-186. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station.

Buwai, M.; Trlica, M. J. 1977. Multiple defoliation effects on herbage yield, vigor and total nonstructural carbohydrates of five range species. Journal of Range Management. 30: 164–171.

Camp, A. E.; Hessburg, P. F.; Everett, R. L. 1996. Dynamically incorporating late-successional forest in sustainable landscapes. In: Hardy, C. C.; Arno, S. F., eds. The use of fire in forest restoration. Gen. Tech. Rep. INT-GTR-341. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 20–23.

Clements, C. D.; Young, J. A. 1996. Influence of rodent predation on antelope bitterbrush seedlings. Journal of Range Management. 49: 31–34.

Day, R. W.; Quinn, G. P. 1989. Comparisons of treatments after an analysis of variances in ecology. Ecological Monographs. 59: 433–463.

Evans, R. A.; Young, J. A.; Cluff, G. J.; McAdoo, J. K. 1983. Dynamics of antelope bitterbrush seed caches. In: Tiedemann, A. R.; Johnson, K. L., comps. Proceedings: research and management of bitterbrush and cliffrose in Western North America. Gen. Tech. Rep. INT- 152. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station: 192–202.

Everett, R. L.; Meeuwig, R. 0.; Stevens, R. 1978. Deer mouse preference for seed of commonly planted species, indigenous weed seed, and sacrifice foods. Journal of Range Management. 31: 70–73.

Ferguson, R. B.; Medin, D. E. 1983. Long-term changes in an ungrazed bitterbrush plant community in southwest Idaho. In: Tiedemann, A. R.; Johnson, K. L., comps. Proceedings: research and management of bitterbrush and cliffrose in Western North America. Gen. Tech. Rep. INT- 152. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station: 107–116.

Fraas, W. W. 1992. Bitterbrush growth and reproductive characters in relation to browsing levels in southwest Montana. Bozeman: Montana State University. 137 p. Thesis.

Giunta, B. C.; Stevens, R.; Jurgensen, K. R.; Perry, A. 1978. Antelope bitterbrush. Publ. 78-12. Utah Division of Wildlife Research. 48 p.

Grabe, D. F., ed. 1970. Tetrazolium testing handbook for agricultural seeds. Contribution 29 to the handbook on seed testing. Association of Official Seed Analysis. 62 p.

Gruell, G. E.; Schmidt, W. C.; Arno, S. F.; Reich, W. J. 1982. Seventy years of vegetative change in a managed ponderosa pine forest in western Montana—implications for resource management. Gen. Tech. Rep. INT-130. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 42 p.

Guenther, G. E. 1989. Ecological relationships of bitterbrush communities on the Mount Haggin Wildlife Management Area. Bozeman: Montana State University. 73 p. Thesis.

Guenther, G. E.; Wambolt, C. L.; Frisina, M. R. 1993. Characteristics of bitterbrush habitats that influence canopy cover and mule deer browsing. Journal of Environmental Management. 36: 175–181.

Harper, K. T.; Buchanan, H. 1983. The ecology of shrubs in Bryce Canyon National Park with special reference to *Purshia tridentata*. In: Tiedemann, A. R.; Johnson, K. L., comps. Proceedings: research and management of bitterbrush and cliffrose in Western North America. Gen. Tech. Rep. INT-152. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station: 91–98.

Matlock-Cooley, S. J. 1993. Interaction between deermice, cattle and antelope bitterbrush. Bozeman: Montana State University. 84 p. Thesis.

Meyer, S. E.; Allen, P. S.; Wilson, G. R.; Davis; T. D.; Stevens, R.; Jorgensen, K.. 1986. Proposed rule for antelope bitterbrush *Purshia tridentata*. Association of Official Seed Analysts Newsletter. 69: 21–22.

Meyer, S. E.; Monsen, S. B. 1989. Seed germination biology of antelope bitterbrush (*Purshia tridentata*). In: Wallace, A.; McArthur, E. D.; Haferkamp, M. R., comps. Proceedings: symposium on shrub ecophysiology and biotechnology. Gen. Tech. Rep. INT-256. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 147–157.

Nord, C. C. 1965. Autecology of bitterbrush in California. Ecological Monographs. 35: 307–334.

Norusis, M. J. 1997. SPSS 7.5 guide to data analysis. New Jersey: Prentice-Hall. 553 p.

Ott, R. L. 1993. An introduction to statistical methods and data analysis. Belmont, CA: Duxbury Press. 1051 p.

Peek, J. M.; Johnson, F. D.; Pence, N. N. 1978. Successional trends in a ponderosa pine/bitterbrush community related to grazing by livestock, wildlife, and to fire. Journal of Range Management. 31: 49–53.

Pfister, R. D.; Kovalchik, B. L.; Arno, S. F.; Presby, F. C. 1977. Forest habitat types of Montana. Gen. Tech. Rep. INT-34. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 174 p.

Shaw, N. L.; Monsen, S. B. 1983. Phenology and growth habits of nine antelope bitterbrush, desert bitterbrush, Stansbury cliffrose, and Apache-plume accessions. In: Tiedemann, A. R.; Johnson, K. L., comps. Proceedings: research and management of bitterbrush and cliffrose in Western North America. Gen. Tech. Rep. INT-152. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station: 55–69.

Sherman, R. J.; Chilcote, W. W. 1972. Spatial and chronological patterns of *Purshia tridentata* as influenced by *Pinus ponderosa*. Ecology. 53: 294–298.

SPSS Inc. 1997. SPSS Base 8.0 syntax reference guide. Software available from: SPSS Inc., 444 N. Michigan Ave., Chicago, IL 60611.

Tueller, P. T.; Tower, J. D. 1979. Vegetation stagnation in three-phase big game exclosures. Journal of Range Management. 32: 258–263.

Young, J. A.; Clements, C. D.; Blank, R. R. 1997. Influence of nitrogen on antelope bitterbrush seedling establishment. Journal of Range Management. 50: 536–540.

Young, J. A.; Evans, R. A. 1978. Germination requirements as determinants of species composition of *Artemisia* rangeland communities. Proceedings, First International Rangelands Congress. Denver, CO: Society for Range Management: 366–369.

Young, J. A.; Young, C .G. 1986. Collecting, processing and germinating seeds of wildland plants. Portland, OR: Timber Press.

Effects of Elevated CO_2 on Growth Responses of Honey Mesquite Seedlings From Sites Along a Precipitation Gradient

Justin D. Derner
Charles R. Tischler
H. Wayne Polley
Hyrum B. Johnson

Abstract: We collected seeds from two honey mesquite (*Prosopis glandulosa* var. *glandulosa)* trees at each of three sites along an east-west precipitation gradient in Texas: Marlin (93.2 cm mean annual precipitation, MAP), Menard (62.0 cm MAP), and Bakersfield (36.6 cm MAP) to test the hypothesis that CO_2 enrichment would differentially affect plant responses along this gradient. However, significant interactions between CO_2 and the site of origin were not observed at either harvest (8- or 16-days postemergence). Growth responses of genotypes of honey mesquite collected from the east-west precipitation gradient were inconsistent with respect to the gradient. Significant growth responses to elevated CO_2 often were of small absolute and relative magnitude, especially at the 16-day harvest. If genetic differences exist among the genotypes used in this investigation, they do not affect growth responses to elevated CO_2 under well-watered conditions. Similar enhancement of seedling plant growth to elevated CO_2 in genotypes of honey mesquite from a wide precipitation gradient suggests that this invasive, woody plant will respond comparably to CO_2 enrichment regardless of precipitation at the site of origin. Whether this genetic potential is displayed in the field, however, is uncertain as existing environmental conditions may constrain responses to CO_2 enrichment. This invasive species likely will continue to be a problem species on rangelands in the future.

Introduction

Honey mesquite (*Prosopis glandulosa* var. *glandulosa*) is an invasive, leguminous shrub that has invaded arid and semiarid rangeland ecosystems and has become dominant on much of the southern mixed-grass and shortgrass prairies in the Great Plains (Ansley and others 2001; Archer 1989, 1990, 1995; Van Auken 2000). It has been proposed that elevated CO_2 may have a significant positive effect on woody plant species and that this is manifest in invasion by woody plants and subsequent thickening in grass-dominated ecosystems (Bond and Midgley 2000). Responses of honey mesquite to elevated CO_2 have been primarily conducted in response to soil water conditions (Polley and others 1996, 1999). Because there is genetic variation within species in responses to elevated CO_2 (Andalo and others 2001; Bezemer and others 1998; Curtis and others 1996; Klus and others 2001; Schmid and others 1996; Thomas and Jasienski 1996; Van der Kooij and others 2000), impacts of CO_2 enrichment on honey mesquite plant growth may be genotype-specific (for example, Mulholland and others 1998; Roumet and others 1999). This may be particularly important in the context of increasing shrub encroachment of rangelands, which encompass wide environmental gradients (Polley 1997; Polley and others 1997).

Species like honey mesquite that grow across wide environmental gradients likely differ genetically in ways that may affect growth responses to elevated CO_2. However, this area of research has received little attention. Three potential responses to elevated CO_2 include (1) similar responses to CO_2 by all genotypes from the environmental gradient, (2) greater responses to CO_2 by genotypes from more water-limiting environments because of increased soil water availability associated with elevated CO_2, or (3) greater responses to CO_2 by genotypes from sites with higher precipitation as they are more rapidly growing plants.

An underlying assumption of this study is that honey mesquite differs genetically at different points along an east-west precipitation gradient in western and central Texas. We tested the hypotheses that (1) growth of honey mesquite seedlings grown at ambient CO_2 increases as precipitation at the site of origin increases, and (2) CO_2 enrichment preferentially increases growth in genotypes that already grow most rapidly. Previous investigations have determined that CO_2 enrichment preferentially increased relative growth rate (Poorter 1993) and biomass (Bunce 1997) in species that had high growth rates. We addressed these potential responses in this investigation by growing seedlings of honey mesquite collected from the precipitation gradient in environmentally controlled glasshouses under optimal temperature and soil water conditions.

In: Hild, Ann L.; Shaw, Nancy L.; Meyer, Susan E.; Booth, D. -Terrance; McArthur, E. Durant, comps. 2004. Seed and soil dynamics in shrubland ecosystems: proceedings; 2002 August 12–16; Laramie, WY. Proceedings RMRS-P-31. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Justin D. Derner is a Rangeland Scientist, USDA-ARS, High Plains Grasslands Research Station, 8408 Hildreth Road, Cheyenne, WY 82009, U.S.A.; FAX: (307) 637-6124; e-mail: jderner@npa.ars.usda.gov. Charles R. Tischler, H. Wayne Polley, and Hyrum B. Johnson are Plant Physiologist, Research Leader, and Ecologist, respectively, USDA-ARS, Grassland, Soil & Water Laboratory, 808 East Blackland Road, Temple, TX 76502, U.S.A.

Materials and Methods

The CO_2 concentration of air in each of four glasshouse bays (31° 05´N, 97° 20´W) was measured at 4-minute intervals with a Li-Cor Model LI-6262 infrared gas analyzer (Li-Cor, Inc., Lincoln, NE). The CO_2 readings were corrected for atmospheric pressure measured with a Druck model DPI 260 pressure indicator (Druck, Inc., New Fairfield, CT). The infrared analyzer was calibrated daily against four CO_2 gas standards and weekly against a Li-Cor LI-610 dewpoint generator. Air temperature, manually set at 30 °C for both day and night in each bay, was measured in the center of each bay with fine-wire (25 µm diameter) thermocouples. Pure CO_2 gas was injected into appropriate bays as required to maintain the elevated CO_2 concentration. The CO_2 concentration of air in the ambient and elevated CO_2 treatments (two bays per treatment) averaged 366 and 702 $\mu mol\ mol^{-1}$, respectively. Photosynthetic photon flux density (PPFD) was measured on the glasshouse roof with a point quantum sensor (LI-190SB, Li-Cor) and within the bays with 1 m long line quantum sensors (LI-191SA, Li-Cor) mounted about plant height. On average, the daily integral of PPFD inside the bays was 70 percent of that measured above the glasshouse.

Seeds were collected in August 2000 from two individual trees (genotypes) of honey mesquite at each of three sites along a precipitation gradient in Texas: Marlin (93.2 cm mean annual precipitation, MAP), Menard (62.0 cm MAP), and Bakersfield (36.6 cm MAP), resulting in a total of six genotypes. Caution was taken to ensure that these trees were at least 2 km from any major road, and each was visually inspected to determine if the morphology of the trees was typical for the given area.

To prevent confounding influences of seed mass on initial seedling development (Villar and others 1998), seeds of each genotype were weighed prior to planting to ensure similar seed mass within a genotype. Two seeds of each genotype were planted to depth of 2 cm in each of 32, 0.05 m diameter by 1.60 m deep pots on July 20, 2001, for a total of 192 pots. Pots were constructed from polyvinyl chloride pipe cut longitudinally into two pieces of equal size to facilitate recovery of intact root systems. The two halves of each pot were taped together and secured at the base with a perforated cap. Pots were filled with a fine sandy loam soil (Pedernales series; fine, mixed, thermic typic Paleustalf; Huckabee and others 1977) with the following properties: pH = 7.1, organic carbon content = 0.57 percent, 76.2 percent sand, 16.2 percent silt, 7.6 percent clay, field capacity = 18 percent on a volumetric basis. Soil in the pots was wetted past field capacity prior to planting by adding one-half strength Hoagland's nutrient solution (Hoagland and Arnon 1950). Following planting, pots with each genotype were randomly assigned to one of four glasshouse bays, two maintained at ambient CO_2 and two at elevated CO_2, with eight pots per genotype in each bay. Full strength Hoagland's solution was added daily to each pot to maintain soil water content near field capacity. Seedlings were randomly thinned to one per pot following emergence.

One-half of the total number of seedlings were harvested at each harvest (8- or 16-days postemergence). Aboveground biomass was separated into stem and leaf components with the area of each leaf blade measured using a LI-3000A portable leaf area meter (Li-Cor, Inc., Lincoln, NE). Soil was manually washed from roots and the depth of deepest root penetration recorded. Roots were digitally scanned at high resolution (600 dpi) using the WinRHIZO software (Regent Instruments, Inc., Quebec, Canada, version 4.1c) and hardware (Hewlett Packard ScanJet 6100C scanner) to determine root length, surface area, and root volume. Roots were not stained prior to analyses, which resulted in underestimations (Bouma and others 2000), but these were minimized by using the WinRHIZO automatic threshold (that is, Lagarde's method) for pale roots with greater sensitivity. Aboveground tissues and roots were dried at 60 ºC for 72 hours prior to weighing.

Data were analyzed using ANOVA by harvest date using a split-split plot design with CO_2 as the split plot and the site of seed origin as the split-split plot in a balanced design (SAS Institute, Inc. 1994). Single degree freedom contrasts were used to compare the two genotypes within each site of seed origin. Means were separated by Duncan's multiple range test at the 0.10 level of significance. When needed to normalize residuals, data were logarithmically transformed before analysis; means and standard errors are reported after back transforming.

Results

Aboveground, but not belowground, variables of honey mesquite seedlings at 8 days postemergence were influenced by both the site of genotype origin and elevated CO_2 (table 1). However, significant interactions between the site of origin and CO_2 were not observed, indicating that growth responses to elevated CO_2 were similar for mesquite seedlings from along the precipitation gradient. Aboveground variables, with the exception of stem mass, were 20 to 110 percent greater for the genotypes from the site with greatest MAP compared to the two lower MAP sites, both of which did not significantly differ for the majority of aboveground responses. Belowground variables did not differ with respect to the site of genotype origin. There were no significant differences for aboveground or belowground growth responses between the two genotypes from each site of collection (data not shown). Elevated CO_2 increased all aboveground variables, but responses were significant for only other leaf area (excluding cotyledon and leaf pair 1) and mass, total leaf mass, and aboveground mass. Total plant mass was similar between CO_2 levels, however, as decreased root mass with elevated CO_2 offset the increased aboveground mass. In contrast to aboveground variables, belowground responses were generally reduced with elevated CO_2, but no significant effects were detected.

In contrast to observed results from the 8-day harvest, both changes in aboveground and belowground variables of honey mesquite seedlings at 16 days postemergence were influenced by the site of genotype origin and elevated CO_2 (table 2). Similar to the 8-day harvest, no significant interactions between CO_2 and the site of genotype origin were observed. Above- and belowground growth responses to the site of genotype origin decreased in magnitude at the 16-day harvest compared to the 8-day harvest. In general, growth responses were greater for genotypes from the wettest than

Table 1—Mean (± 1 SE) aboveground and belowground responses at 8-days postemergence for honey mesquite seedlings of genotypes from along an east-west precipitation gradient in Texas (Marlin [93.2 cm mean annual precipitation, MAP], Menard [62.0 cm MAP] and Bakersfield [36.6 cm MAP]) exposed to ambient and elevated CO_2 concentrations (366 and 702 μmol mol^{-1}, respectively).

	CO_2		MAP at site of genotype origin[a]		
Variable	**Ambient**	**Elevated**	**93.2**	**62.0**	**36.6**
			- - - - - - - - - -	*cm*	- - - - - - - - - -
Aboveground					
Cotyledon leaf area (cm^2)	2.13 (0.13)	2.27 (0.26)	2.85 (0.26)a	1.89 (0.20)b	1.85 (0.10)b
Cotyledon mass (g)	0.0144 (0.0009)	0.0158 (0.0021)	0.0180 (0.0025)a	0.0149 (0.0014)b	0.0128 (0.0009)b
Leaf pair 1 leaf area (cm^2)	2.27 (0.15)	2.34 (0.34)	2.82 (0.28)a	1.76 (0.33)b	2.19 (0.22)b
Leaf pair 1 mass (g)	0.0080 (0.0015)	0.0091 (0.0014)	0.0101 (0.0015)a	0.0069 (0.0008)c	0.0081 (0.0009)b
Other leaf area (cm^2)	2.28 (0.21)	2.86 (0.22)[b]	3.31 (0.63)a	1.91 (0.27)b	2.27 (0.24)b
Other leaf mass (g)	0.0093 (0.0009)	0.0176 (0.0048)[b]	0.0204 (0.0059)a	0.0081 (0.0013)b	0.0097 (0.0011)b
Stem mass (g)	0.0089 (0.0008)	0.0111 (0.0018)	0.0115 (0.0020)a	0.0094 (0.0022)a	0.0089 (0.0010)a
Total leaf area (cm^2)	6.68 (0.40)	7.48 (1.03)	8.97 (1.07)a	5.56 (0.73)b	6.31 (0.45)b
Total leaf mass (g)	0.0317 (0.0018)	0.0425 (0.0065)[b]	0.0485 (0.0075)a	0.0299 (0.0032)b	0.0305 (0.0019)b
Aboveground mass (g)	0.0406 (0.0022)	0.0537 (0.0077)[b]	0.0599 (0.0089)a	0.0393 (0.0048)b	0.0394 (0.0023)b
Belowground					
Root depth (cm)	51.6 (6.6)	49.6 (4.8)	49.8 (6.4)a	46.4 (10.8)a	53.5 (6.3)a
Root length (cm)	90.1 (12.2)	77.7 (7.8)	92.2 (8.6)a	75.2 (14.4)a	84.0 (14.4)a
Root surface area (cm^2)	17.5 (1.8)	14.8 (1.3)	17.4 (1.4)a	15.3 (2.7)a	16.1 (2.2)a
Root volume (m^3)	0.26 (0.03)	0.21 (0.02)	0.25 (0.02)a	0.23 (0.04)a	0.23 (0.03)a
Root mass (g)	0.0151 (0.0013)	0.0135 (0.0016)	0.0149 (0.0018)a	0.0132 (0.0025)a	0.0147 (0.0014)a
Whole plant					
Total plant mass (g)	0.0557 (0.0027)	0.0672 (0.0086)	0.0749 (0.0097)a	0.0524 (0.0067)b	0.0541 (0.0028)b

[a] Different letters among the MAP levels indicate a significant difference between means.

[b] Significant ($P < 0.10$) difference between ambient and elevated CO_2 means.

Table 2—Mean (± 1 SE) aboveground and belowground responses at 16-days postemergence for honey mesquite seedlings of genotypes from along an east-west precipitation gradient in Texas (Marlin [93.2 cm mean annual precipitation, MAP], Menard [62.0 cm MAP] and Bakersfield [36.6 cm MAP]) exposed to ambient and elevated CO_2 concentrations (366 and 702 μmol mol^{-1}, respectively).

	CO_2		MAP at site of genotype origin[a]		
Variable	**Ambient**	**Elevated**	**93.2**	**62.0**	**36.6**
			- - - - - - - - - -	*cm*	- - - - - - - - - -
Aboveground					
Cotyledon leaf area (cm^2)	2.39 (0.20)	2.57 (0.15)	2.93 (0.23)a	2.29 (0.20)b	2.08 (0.13)b
Cotyledon mass (g)	1.7553 (0.0011)	1.7585 (0.0010)[b]	1.7594 (0.0012)a	1.7569 (0.0015)b	1.7535 (0.0011)b
Leaf pair 2&3 leaf area (cm^2)	6.02 (0.40)	7.18 (0.39)[b]	7.38 (0.45)a	6.71 (0.55)a	5.44 (0.40)b
Leaf pair 2&3 mass (g)	1.7706 (0.0022)	1.7793 (0.0026)[b]	1.7778 (0.0023)a	1.7779 (0.0044)a	1.7680 (0.0023)b
Other leaf area (cm^2)	9.64 (0.97)	10.18 (1.20)	12.65 (1.52)a	8.70 (0.81)b	7.60 (0.57)b
Other leaf mass (g)	1.7826 (0.0047)	1.7901 (0.0062)	1.7985 (0.0076)a	1.7849 (0.0051)a	1.7723 (0.0025)b
Stem mass (g)	1.7652 (0.0040)	1.7756 (0.0036)	1.7743 (0.0064)a	1.7674 (0.0035)a	1.7666 (0.0027)a
Total leaf area (cm^2)	18.06 (1.48)	19.93 (1.54)	22.96 (2.07)a	17.70 (1.37)b	15.13 (0.72)b
Total leaf mass (g)	5.3085 (0.0074)	5.3280 (0.0086)[b]	5.3358 (0.0103)a	5.3196 (0.0101)a	5.2939 (0.0044)b
Aboveground mass (g)	7.0737 (0.0097)	7.1036 (0.0116)[b]	7.1100 (0.0146)a	7.0870 (0.0130)a	7.0605 (0.0067)b
Belowground					
Root depth (cm)	96.2 (5.7)	101.3 (5.0)	107.2 (6.8)a	93.9 (7.2)b	91.9 (5.3)b
Root length (cm)	201.2 (18.4)	240.3 (20.4)	250.9 (25.2)a	171.5 (17.4)b	218.0 (21.4)ab
Root surface area (cm^2)	32.5 (2.6)	40.1 (2.5)[b]	40.1 (3.4)a	31.5 (3.1)b	34.5 (2.8)ab
Root volume (m^3)	0.44 (0.04)	0.57 (0.04)[b]	0.55 (0.05)a	0.46 (0.06)a	0.45 (0.04)a
Root mass (g)	1.7861 (0.0044)	1.8024 (0.0055)[b]	1.7998 (0.0063)a	1.7955 (0.0085)a	1.7844 (0.0038)a
Whole plant					
Total plant mass (g)	8.8598 (0.0135)	8.9059 (0.0164)[b]	8.9098 (0.0135)a	8.8825 (0.0210)a	8.8449 (0.0102)b

[a] Different letters among the MAP levels indicate a significant difference between means.

[b] Significant ($P < 0.10$) difference between ambient and elevated CO_2 means.

driest site. Consistent with the 8-day harvest, there were no significant differences for aboveground or belowground growth responses between the two genotypes for each site of collection (data not shown). Elevated CO_2 increased all aboveground responses, but significant differences were observed for only leaf area and mass of leaf pairs 2 and 3, total leaf mass, and aboveground mass. The magnitude of these CO_2-induced growth responses was much reduced compared to the 8-day harvest. Belowground responses were greater with elevated CO_2, with significant increases at elevated CO_2 in root surface area, volume, and mass.

Discussion

Growth responses of honey mesquite genotypes collected from the east-west precipitation gradient were inconsistent with respect to the gradient, suggesting that our underlying assumption that honey mesquite differs genetically at different points along an east-west precipitation gradient in western and central Texas was incorrect, at least under well-watered conditions. In addition, this finding does not support our hypothesis that growth of seedlings grown at ambient CO_2 increases as precipitation at the site of origin increases. In general, genotypes from the wettest site (Marlin) had more leaf area, more mass, and greater root growth than genotypes from the driest site (Bakersfield), but growth responses of genotypes from the site with intermediate precipitation (Menard), however, were primarily responsible for the inconsistent growth response along the gradient. Growth responses of seedlings from this site were similar to those of genotypes from the wettest site for some variables and similar to genotypes from the driest site for other variables at the 16-day harvest. This inconsistency merits additional research attention, with a need to investigate additional genotypes from each site.

Elevated CO_2 increased aboveground variable responses at both harvest dates, while belowground variable responses to elevated CO_2 were inconsistent with decreases occurring at the 8-day harvest and increases at the 16-day harvest. Most of these responses, however, were not significant. Significant differences in response to elevated CO_2 often were of small absolute and relative magnitude, especially at the 16-day harvest. Significant interactions between CO_2 and the site of genotype origin were not observed for either the 8-day or 16-day harvest, indicating that observed growth responses to elevated CO_2 were similar for mesquite seedlings regardless of MAP at site of origin. Therefore, our hypothesis that elevated CO_2 would preferentially increase growth of the more rapidly growing plants from the sites with high than low precipitation was not supported for above- or belowground variables at either harvest date. If genetic differences exist among the genotypes used in this investigation, they do not affect growth responses to elevated CO_2 under well-watered conditions.

Inconsistent growth responses of aboveground and belowground variables to elevated CO_2 at the 8- and 16-day harvests are likely attributable to relative sink strengths and carbon allocation patterns of these honey mesquite seedlings. Increased aboveground, but decreased belowground, responses to elevated CO_2 at the 8-day harvest conform to priority of establishing sufficient photosynthetic machinery for seedling survival at the expense of root growth. The reduction in magnitude of aboveground response to elevated CO_2 at the 16-day harvest, and the associated increase in belowground response, indicate that photosynthetic machinery was quickly established and carbon allocation priorities shifted more belowground following the first harvest. Elevated CO_2 did not affect partitioning of dry matter between shoot and root of the grass *Dactylis glomerata* at high nitrogen, but at low nitrogen greater partitioning was observed into the shoot during early stages of growth (Harmens and others 2000). This suggests that in spite of daily additions of full-strength Hoaglands's solution, the inherently low nitrogen status and high leaching potential of the sandy loam soil resulted in low nitrogen availability to honey mesquite seedlings. Under limiting nutrient conditions, plant growth under elevated CO_2 is often negligible (Bernacchi and others 2000; Kimball and others 2002; but see Lloyd and Farquhar 1996).

Similar enhancement of early seedling plant growth in genotypes of honey mesquite from a wide precipitation gradient to elevated CO_2 suggests that this invasive, woody plant will respond comparably to CO_2 enrichment regardless of precipitation at the site of origin. Whether this genetic potential is displayed in the field, however, is uncertain, as existing environmental conditions may constrain responses to CO_2 enrichment. This invasive species likely will continue to be a problem species on rangelands in the future and may even increase competitiveness at the expense of warm-season grasses, which currently dominate the southern mixed-grass and shortgrass prairies, as these grasses are generally not as responsive to elevated CO_2 as is honey mesquite (Polley and others 1994).

Acknowledgments

Alicia Naranjo, Kyle Tiner, Holly Harland, Brooke Kramer, Jenny Fikes, and Dustin Coufal assisted with data collection and entry. Chris Kolodziejczyk maintained CO_2 and environmental control systems and data records.

References

Andalo, C.; Goldringer, I.; Godelle, B. 2001. Inter- and intragenotypic competition under elevated carbon dioxide in *Arabidopsis thaliana*. Ecology. 82: 157–164.

Ansley, J. R.; Wu, X. B.; Kramp, B. A. 2001. Observation: long-term increases in mesquite canopy cover in a north Texas savanna. Journal of Range Management. 54: 171–176.

Archer, S. 1989. Have southern Texas savannas been converted to woodlands in recent history? The American Naturalist. 134: 545–561.

Archer, S. 1990. Development and stability of grass/woody mosaics in a subtropical savanna parkland, Texas, U.S.A. Journal of Biogeography. 17: 453–462.

Archer, S. 1995. Tree-grass dynamics in a *Prosopis*-thornscrub savanna parkland: reconstructing the past and predicting the future. Ecoscience. 2: 83–99.

Bernacchi, C. J.; Coleman, J. S.; Bazzaz, F. A.; McConnaughay, K. D. M. 2000. Biomass allocation in old-field annual species grown in elevated CO_2 environments: no evidence for optimal partitioning. Global Change Biology. 6: 855–863.

Bezemer, T. M.; Thompson, L. J.; Jones, T. H. 1998. *Poa annua* shows inter-generational differences in response to elevated CO_2. Global Change Biology. 4: 687–691.

Bond, W. J.; Midgley, G. F. 2000. A proposed CO_2-controlled mechanism of woody plant invasion in grasslands and savannas. Global Change Biology. 6: 865–869.

Bouma, T. J.; Nielsen, K. L.; Koutstall, B. 2000. Sample preparation and scanning protocol for computerized analysis of root length and diameter. Plant and Soil. 218: 185–196.

Bunce, J. A. 1997. Variation in growth stimulation by elevated carbon dioxide in seedlings of some C_3 crop and weeds species. Global Change Biology. 3: 61–66.

Curtis, P. S.; Klus, D. J.; Kalisz, S.; Tonsor, S. J. 1996. Intraspecific variation in CO_2 responses in *Raphanus raphanistrum* and *Plantago lancelata*: assessing the potential for evolutionary change with rising atmospheric CO_2. In: Korner, C.; Bazzaz, F. A., eds. Carbon dioxide, populations, and communities. London: Academic Press: 13–22.

Harmens, H.; Stirling, C. M.; Marshall, C.; Farrar, J. F. 2000. Is partitioning of dry weight and leaf area within *Dactylis glomerata* affected by N and CO_2 enrichment? Annals of Botany. 86: 833–839.

Hoagland, D. R.; Arnon, D. I. 1950. The water-culture method for growing plants without soil. California Agricultural Experiment Station Circular. 347: 1–39.

Huckabee, J. W., Jr.; Thompson, D. R.; Wyrick, J. C.; Paulat, E. G. 1977. Soil survey Bell County Texas. Washington, DC: U.S. Department of Agriculture, Soil Conservation Service.

Kimball, B. A.; Kobayashi, K.; Bindi, M. 2002. Responses of agricultural crops to Free-Air CO_2 Enrichment. Advances in Agronomy. 77: 293–368.

Klus, D. J.; Kalisz, S.; Curtis, P. S.; Terri, J. A.; Tonsor, S. J. 2001. Family- and population-level responses to atmospheric CO_2 concentration: gas exchange and the allocation of C, N, and biomass in *Plantago lanceolata* (Plantaginaceae). American Journal of Botany. 88: 1080–1087.

Lloyd, J.; Farquhar, G. D. 1996. The CO_2 dependence of photosynthesis, plant growth responses to elevated CO_2 concentrations and their interactions with soil nutrient status. I. General principles and forest ecosystems. Functional Ecology. 10: 4–32.

Mulholland, B. J.; Craigon, J.; Black, C. R.; Colls, J. J.; Atherton, J.; Landon, G. 1998. Growth, light interception and yield responses of spring wheat (*Triticum aestivum* L.) grown under elevated CO_2 and O_3 in open-top chambers. Global Change Biology. 4: 121–130.

Polley, H. W. 1997. Invited synthesis paper: implications of rising atmospheric carbon dioxide concentration for rangelands. Journal of Range Management. 50: 562–577.

Polley, H. W.; Johnson, H. B.; Mayeux, H. S. 1994. Increasing CO_2: comparative responses of the C_4 grass *Schizachyrium* and grassland invader *Prosopis*. Ecology. 75: 976–988.

Polley, H. W.; Johnson, H. B.; Mayeux, H. S.; Tischler, C. R.; Brown, D. A. 1996. Carbon dioxide enrichment improves growth, water relations and survival of droughted honey mesquite (*Prosopis glandulosa*) seedlings. Tree Physiology. 16: 817–823.

Polley, H. W.; Mayeux, H. S.; Johnson, H. B.; Tischler, C. R. 1997. Viewpoint: atmospheric CO_2 soil water, and shrub/grass ratios on rangelands. Journal of Range Management. 50: 278–284.

Polley, H. W.; Tischler, C. R.; Johnson, H. B.; Pennington, R. E. 1999. Growth, water relations, and survival of drought-exposed seedlings from six maternal families of honey mesquite (*Prosopis glandulosa*): responses to CO_2 enrichment. Tree Physiology. 19: 359–366

Poorter, H. 1993. Interspecific variation in the growth response of plants to an elevated ambient CO_2 concentration. Vegetatio. 104/105: 77–97.

Roumet, C.; Laurnet, G.; Roy, J. 1999. Leaf structure and chemical composition as affected by elevated CO_2: genotypic responses of two perennial grasses. New Phytologist. 143: 73–81.

SAS Institute, Inc. 1994. SAS/STAT user's guide, release 6.03, 4th ed. Cary, NC: SAS Institute, Inc.

Schmid, B.; Birrer, A.; Lavigne, C. 1996. Genetic variation in the response of plant populations to elevated CO_2 in a nutrient-poor, calcareous grassland. In: Korner, C.; Bazzaz, F. A., eds. Carbon dioxide, populations, and communities. London: Academic Press: 31–50.

Thomas, S. C.; Jasienski, M. 1996. Genetic variability and the nature of microevolutionary responses to elevated CO_2. In: Korner, C.; Bazzaz, F. A., eds. Carbon dioxide, populations, and communities. London: Academic Press: 51–81.

Van Auken, O. W. 2000. Shrub invasions of North American semiarid grasslands. Annual Review of Ecological Systems. 31: 197–215.

Van der Kooij, T. A. W.; De Kok, L. J.; Stulen, I. 2000. Intraspecific variation in the response of *Arabidopsis thaliana* lines to elevated atmospheric CO_2. Phyton-annales Rei Botanicae. 40: 125–132.

Villar, R.; Veneklaas, E. J.; Jordano, P.; Lambers, H. 1998. Relative growth rate and biomass allocation in 20 *Aegilops* (Poaceae) species. New Phytologist. 140: 425–437.

Responses of Seedlings of Five Woody Species to Carbon Dioxide Enrichment

Charles R. Tischler
Justin D. Derner
H. Wayne Polley
Hyrum B. Johnson

Abstract: Encroachment of woody species into formerly productive rangeland is an immense problem in the Southwest. Effects of predicted global change scenarios on seedlings of such species are largely unstudied. Seedlings of five invasive woody legume species (honey mesquite [*Prosopis glandulosa*], huisache [*Acacia farnesiana*], honey locust [*Gleditsia triacanthos*], Eve's necklace [*Sophora affinis*], and Paloverde [*Parkinsonia aculeata*]) were grown for 23 days in glasshouses in Temple, TX, at ambient and twice ambient levels of atmospheric carbon dioxide. Plants were kept well watered and fertilized. Seedlings of all species responded positively to CO_2 enrichment, with significant differences in seedling mass observed 1 week after emergence. Mesquite and huisache responded most strongly to elevated CO_2. Other work from our laboratory suggests that at least for honey mesquite and huisache, seedling mortality is near zero beyond 3 weeks postemergence, even under water stress conditions. Thus, these invasive species will likely become even more problematic in the future as atmospheric CO_2 increases.

Introduction

It is now widely accepted that atmospheric CO_2 concentration has increased in the recent past and will continue to increase (Trabalka and others 1986). An environment enriched in CO_2 has direct stimulatory effects on plants with C_3 photosynthetic carbon metabolism (Bunce 1997), although moderate effects, as well as indirect effects, are noted in C_4 plants (Owensby and others 1993). Because most of the grasslands in the Southwestern United States consist of C_4 species that have been or are currently being invaded by C_3 woody species (Polley and others 1996), effects of this atmospheric change on growth and development of brush species merits study.

For most invasive species, success in the seedling stage is a critical factor influencing eventual success of that species. One reason for this is that woody species tend to be long-lived perennials that are avoided by livestock, and relatively resistant to environmental extremes, insects and pathogens, and other common causes of mortality. It has been proposed that elevated CO_2 may have a significant positive effect on woody plant species and that this is manifest in invasion by woody plants and subsequent thickening in grass-dominated ecosystems (Bond and Midgley 2000).

We studied effects of a twice ambient CO_2 atmosphere on the growth and development of five invasive woody legumes for the first 23 days after emergence in these experiments. These species differ markedly in invasive potential, and we hypothesize that positive effects of CO_2 would be most pronounced on the most invasive species. Mesquite (*Prosopis glandulosa*) and huisache (*Acacia farnesiana*) are found in almost pure stands on millions of acres of rangeland in Texas, with mesquite being cosmopolitan but more prevalent in the western portion of south-central and southwestern Texas, and huisache being more prevalent in south-central Texas and the eastern portion of the Rio Grande Plains, but not extending north beyond central Texas. Paloverde (*Parkinsonia aculeata*), honey locust (*Gleditsia triacanthos*), and Eve's necklace (*Sophora affinis*) are rare to common across the eastern half of Texas, generally never existing in pure stands, but being minor components of mixed woodlands. Occasionally Eve's necklace and Paloverde are used as ornamentals.

Materials and Methods

Seed of the five species used in this experimentation were harvested and scarified during the summer of 1996. Individual seed were weighed so that a narrow range of seed masses could be selected for each species, thus insuring relatively consistent cotyledonary leaf area for each species. The range of seed masses used for each species were Eve's Necklace 0.010 to 0.0800 g; Honey locust 0.0801 to 0.0900 g; Paloverde 0.1110 to 0.1160 g; mesquite 0.0451 to 0.0500 g; and huisache: 0.0651 to 0.0700 g. Planting dates were staggered to synchronize seedling emergence among species. Eve's necklace seed were planted on August 19, Honey Locust on August 26, and Paloverde, Mesquite, and Huisache were planted on August 27, with emergence for all species occurring on August 30 and 31, 1996.

In: Hild, Ann L.; Shaw, Nancy L.; Meyer, Susan E.; Booth, D. Terrance; McArthur, E. Durant, comps. 2004. Seed and soil dynamics in shrubland ecosystems: proceedings; 2002 August 12–16; Laramie, WY. Proceedings RMRS-P-31. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Charles R. Tischler, H. Wayne Polley, and Hyrum B. Johnson are Plant Physiologist, Research Leader and Ecologist, respectively, USDA-ARS Grassland, Soil & Water Research Laboratory, 808 E. Blackland Road, Temple, TX 76502, U.S.A.; FAX: (254) 770-6561; e-mail: ctischler@spa.ars.usda.gov. Justin D. Derner is a Range Scientist, USDA-ARS, High Plains Grasslands Research Station, 8408 Hildreth Road, Cheyenne, WY 82009, U.S.A.

Seed were planted at a depth of 1.5 cm in commercial potting mix in tapered plastic cones 25 cm deep and 6.25 cm in diameter. Total cone volume was 425 cm^3. Cones were watered at planting and weekly with full strength Hoagland's solution, and with tap water as necessary. As seedlings emerged, cones were transferred to interlocking racks, each with a capacity of 20 cones. Species were randomized within a rack, with four individuals of each species in a rack.

Two adjacent glasshouse bays at the Grassland, Soil, and Water Research Laboratory (Temple, TX) were utilized; CO_2 concentrations were 365 and 700 ppm. Air within each bay was sampled each 4 minutes with a Li-Cor Model LI-622262 infrared gas analyzer to determine CO_2 concentration. Pure CO_2 was injected into the 700 ppm glasshouse bay as needed to maintain the desired concentration, while in the 365 ppm bay, outside air was circulated through the glasshouse to maintain ambient conditions. Air temperature was maintained near that of outdoor temperature. The late summer of 1996 was dry with few clouds, and thus the seedlings received saturating levels of light most of the time.

Destructive harvests were made on days 3, 8, 13, 18, and 23. Root and shoot dry mass, and cotyledonary and true leaf dry mass and area were determined for seven plants of each species at each harvest. Data was analyzed by standard ANOVA techniques, with comparisons made only within a species and harvest date.

Results

Cotyledonary Mass

On days 8 and 13, some significant effects of elevated CO_2 on cotyledonary mass were observed (table 1). These effects were not observed later in development, probably because of the slow progression of the cotyledonary leaves to senescence, and the weight loss experienced by cotyledonary leaves before they abscise. With the exception of Paloverde, cotyledonary mass of all other species was at near maximum at day 3. This is because Paloverde is the only species that has significant expansion of cotyledonary leaves (6.13 cm^2 at day 13, compared to 2.6 cm^2 for mesquite at day 13, the next greatest area—both values for ambient atmosphere). Because of different developmental strategies between the woody species and differences in rates of development, detailed comparisons between the species are not meaningful.

Cotyledonary Leaf Area and True Leaf Mass and Area

When statistical differences were noted, cotyledonary leaf area and true leaf mass and area were greater for species in elevated versus ambient CO_2 atmospheres (data not presented). Because elevated CO_2 modifies plant phenology, we did not attempt to make comparisons of specific leaf weights, because these comparisons are not instructive.

Root Mass

By day 23, root mass for all species was numerically higher at elevated CO_2 (table 2). None of these differences reached statistical significance because of the great deal of variation in root mass from plant to plant. Larger sample sizes would be required to establish statistical significance.

Total Biomass

At day 23, total biomass was greater in every case for plants in enriched CO_2, although this difference was significant only for mesquite (table 3). However, we observed significant differences for Paloverde at days 8, 13, and 18; for Locust at days 8 and 18; for Mesquite additionally at days 3, 8, 13, and 18; for Huisache at days 8, 13, and 18, and for Eve's Necklace at day 13. These data suggest an overall significant effect of CO_2 on biomass accumulation, but point out a complicating factor often overlooked by investigators. This is the effect of "rests" or temporary lapses in growth (often concomitant with increases in complexity) as described by Stebbins (1976) and Vogel (1980). Comparisons between species become meaningless if one species is in a "rest" stage while a second is actively growing, as Stebbins (1976) demonstrated.

Table 1—Cotyledonary masses of five woody species at five sampling dates.

	Cotyledon mass[a]				
Entry	Day 3	Day 8	Day 13	Day 18	Day 23
	- - - - -	- - - - - - - - - -	*mg*	- - - - - - - - - -	- - - - -
Paloverde 350	0.028a	0.041b	0.050a	0.044b	0.043a
Paloverde 700	.026a	.057a	.057a	.053a	.051a
Locust 350	.016a	.012b	.010b	.010a	.010a
Locust 700	.016a	.015a	.011a	.009a	.010a
Mesquite 350	.018a	.023b	.021b	.017b	.018a
Mesquite 700	.018a	.031a	.038a	.033a	.027a
Huisache 350	.013a	.010b	.008a	.006a	.003a
Huisache 700	.014a	.014b	.008a	.005a	.004a
Eve's necklace 350	.015a		.012a		.015a
Eve's necklace 700	.016a		.015a		.018a

[a]Values for a species in a column followed by a different letter are significantly different (P ≤ 0.05), Duncan's Multiple Range Test.

Table 2—Root dry mass of five woody species at five sampling dates.

	Root mass[a]				
Entry	Day 3	Day 8	Day 13	Day 18	Day 23
	- - - - -	- - - - - - - - - -	*mg*	- - - - - - - - - -	- - - - -
Paloverde 350	0.017a	0.036a	0.043a	0.062a	0.081a
Paloverde 700	.016a	.034a	.050a	.067a	.087a
Locust 350	.016a	.016b	.029a	.049a	.067a
Locust 700	.015a	.020a	.034a	.054a	.075a
Mesquite 350	.010b	.015a	.017b	.033b	.047a
Mesquite 700	.012a	.016a	.023a	.046a	.070a
Huisache 350	.012a	.013a	.017a	.029b	.040b
Huisache 700	.012a	.249a	.023a	.039b	.058a
Eve's necklace 350	.013a		.017a		.041a
Eve's necklace 700	.013a		.023a		.045a

[a]Values for a species in a column followed by a different letter are significantly different (P ≤ 0.05), Duncan's Multiple Range Test.

Table 3—Total dry mass of five woody species at five sampling dates.

Species	CO_2	Total mass[a] Day 3	Day 8	Day 13	Day 18	Day 23
		- - - - - - - - - -	- - - -	*mg*	- - - -	- - - - - - - - - -
Paloverde	350	0.051b	0.077b	0.134b	0.166b	0.240a
Paloverde	700	.048a	.111a	.168a	.230a	.267a
Locust	350	.039a	.049b	.079a	.118b	.167a
Locust	700	.039a	.070a	.093a	.139b	.189a
Mesquite	350	.031b	.049b	.070b	.123b	.167b
Mesquite	700	.035a	.062a	.096a	.173a	.295a
Huisache	350	.028a	.042b	.059b	.091B	.125a
Huisache	700	.031a	.053a	.088a	.129a	.188a
Eve's necklace	350	.033a		.058b		.153a
Eve's necklace	700	.035a		.089a		.199a

[a] Values for a species in a column followed by a different letter are significantly different ($P \leq 0.05$), Duncan's Multiple Range Test.

Conclusions

Our data for five woody species vividly illustrate positive growth effects of elevated CO_2 early in the development of species. However, our glasshouse results probably grossly underestimate the effects of CO_2 in field or range situations. By increasing water use efficiency of all species in an ecosystem, elevated CO_2 alters water balance of the system, thus favoring seedling establishment. Although no data exists on this topic, it would also be logical to expect a positive influence of elevated CO_2 on reproductive output of shrub and brush species, thus enriching the seedbank of these invaders.

Obviously, cumulative effects of increasing CO_2 on rangeland ecosystems is an experiment in progress, whose result will not be completely chronicled for centuries. However, the data we present suggests that increasing CO_2 will favor shrub and brush invasion at the expense of grass communities.

References

Bond, W. J.; Midgley, G. F. 2000. A proposed CO_2-controlled mechanism of woody plant invasion in grasslands and savannas. Global Change Biology. 6: 865–869.

Bunce, J. A. 1997 Variation in growth stimulation by elevated carbon dioxide in seedlings of some C_3 crop and weed species. Global Change Biology. 3: 61–66.

Fenner, M. 1983. Relationships between seed weight, ash content and seedling growth in twenty-four species of Compositae. New Phytology. 95: 697–706.

Owensby, C. E.; Coyne, P. I.; Ham, J. M.; Auen, L. M.; Knapp, A. K. 1993. Biomass production in a tallgrass prairie ecosystem exposed to ambient and elevated CO_2. Ecological Applications: 3(4): 644–653.

Polley, H. W.; Johnson, H. B.; Mayeux, H. S.; Tischler, C. R. 1996. Are some of the recent changes in grassland communities a response to rising CO_2 concentrations? In: Korner, Christian; Bazzaz, Fakhri A., eds. Carbon dioxide, populations, and communities. New York: Academic Press: 177–195.

Stebbins, G. L. 1976. Seed and seedling ecology in annual legumes. I. A comparison of seed size and seedling development in some annual species. Oecologia Plantarum. 11: 321–331.

Tischler, C .R.; Polley, H. W.; Johnson, H. B.; Mayeux, H. S. 1998. Environment and seedling age influence mesquite response to epicotyl removal. Journal of Range Management. 51: 361–365.

Tischler, C. R.; Polley, H. W.; Johnson, H. B.; Pennington, R. E. 2000. Seedling response to elevated CO_2 in five epigeal species. International Journal of Plant Science. 161: 779–783.

Trabalka, J. R.; Edmonds, J. A.; Reilly, J. M.; Gardner, R. H.; Reichle, D. E. 1986 Atmospheric CO_2 projections with globally averaged carbon cycle models. In: Trabalka, J. R.; Reichle, D. E., eds. The changing carbon cycle: a global analysis. New York: Springer-Verlag: 534–560.

Vogel, de, E. F. 1980. Seedlings of dicotyledons. Pudoc, Centre for Agricultural Publishing and Documentation, Wageningen.

Soil Moisture Attributes of Three Inland Sand Dunes in the Mojave Desert

Simon A. Lei

Abstract: Soil moisture attributes were investigated in three active sand dunes in the Mojave Desert of southern Nevada and California. Soil water content increased significantly with increasing soil depth, and decreased when moving toward dune habitats. Path analysis revealed direct causal effects of soil depth and habitat type (dune and nondune) on soil water content. Among soil moisture variables, significant interaction was detected between habitat type and geomorphic surface (terrace and slope) for area of water spread (surface water runoff). When examining habitat type or geomorphic surface alone, significant differences were detected in all measured moisture variables. Significant differences were also found in site for water infiltration and depth of water penetration. The Kelso, Ash Meadows, and Death Valley dunes had different soil moisture attributes compared with adjacent *Larrea-Ambrosia* shrublands.

Introduction

Active sand dunes cover less than 1 percent of the North American deserts (Sharp 1966). Desert sand dunes are edaphically distinct from surrounding habitats in terms of extremely high percentage of sand, instability of sand substrates, and rate of sand movement. Long and dry seasons, low soil nutrient levels, high air and soil temperatures, as well as mobile and abrasive sand with coarse texture are characteristics of inland desert dunes (Bowers 1986; Pavlik 1985). Low soil moisture, low organic litter, and matter are also typical of dune environments (Barbour and others 1999; Bowers 1982). However, soil moisture increases with depth in the inland dunes (Bowers 1982; Prill 1968; Sharp 1966).

Although sand dune ecosystems appear simple, they are actually complex and delicately balanced (Bowers 1986). Sand dunes are unique continental islands isolated by their physical and biological properties or by factors related to the evolution of the landscape through geological time (Brown 1972). Because of low economic and agricultural values, dunes are one of the least studied ecosystems in the Southwestern United States. There have been a number of studies pertaining to the edaphic characteristics of eolian deposits in arid environments of the Southwest (Holiday 1990; Lancaster 1993, 1998; Lei 1998; McFadden and others 1987; Sharp 1966; Wells and others 1990). Yet, little attention has been focused on the soil surface and moisture characteristics of inland dunes in the Mojave Desert.

Despite limited economic and agricultural values, sand dunes are an important component of the Mojave Desert landscape, and are ecologically and edaphically interesting (Lei 1998). Two hypotheses were made prior to data collection: (1) soil moisture attributes would differ among the three dune sites, between dune and nondune habitats, and between two geomorphic surfaces (terrace and slope) within a habitat, and (2) gravimetric soil moisture would be partially influenced by habitat type and soil depth. These two hypotheses were tested by a combination of field and laboratory measurements of soil moisture attributes in the Kelso, Ash Meadows, and Death Valley dunes with their adjacent *Larrea tridentata-Ambrosia dumosa* (creosote bush-white bursage) shrublands (nondunes) in the Mojave Desert of southern Nevada and California.

Methods and Materials

Study Site

Field studies were conducted at three dune systems in southern Nevada and California (fig. 1) during the summer of 2001. The Kelso and Death Valley dunes are in southern California, and the Ash Meadows dunes are in southern Nevada (fig. 1). Elevations varied considerably, ranging from 85 m below sea level in Death Valley to 670 m above sea level in Kelso and Ash Meadows (table 1). Among the three active dunes, Death Valley has the highest mean monthly air temperature (fig. 2) and the lowest mean monthly precipitation (fig. 3).

The substrates were deep, unstable, and coarse grained on all three dunes. Within each dune system, variations in sand particles were observed. Sand particles, ranging from coarse to fine in texture, can be distinguished according to their particle size distribution and mean grain size (Lancaster 1993). Different sand occupies distinct areas of the dune field, suggesting that dunes represent a stacked sequence of sand deposition events (Lei 1998).

Atriplex spp. (saltbush) and *Larrea tridentata* commonly occur in dune and marginal dune habitats in the Kelso, Ash Meadows, and Death Valley dunes. Marginal dunes were located between active dunes and adjacent nondune areas, with sand more or less stabilized. Abundant vegetation may eventually cause soil to develop. *Larrea* plants are typically larger and taller in dune fields compared to its nondune

---

In: Hild, Ann L.; Shaw, Nancy L.; Meyer, Susan E.; Booth, D. Terrance; McArthur, E. Durant, comps. 2004. Seed and soil dynamics in shrubland ecosystems: proceedings; 2002 August 12–16; Laramie, WY. Proceedings RMRS-P-31. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Simon A. Lei is a Biology and Ecology Instructor, Department of Biology, WDB, Community College of Southern Nevada, 6375 West Charleston Boulevard, Las Vegas, NV 89146-1193, U.S.A. FAX (702) 257-2914; e-mail: salei@juno.com

Figure 1—Location of three inland sand dunes in southern Nevada and California. Dune systems are numbered as follows: 1 = Ash Meadows, 2 = Death Valley, and 3 = Kelso.

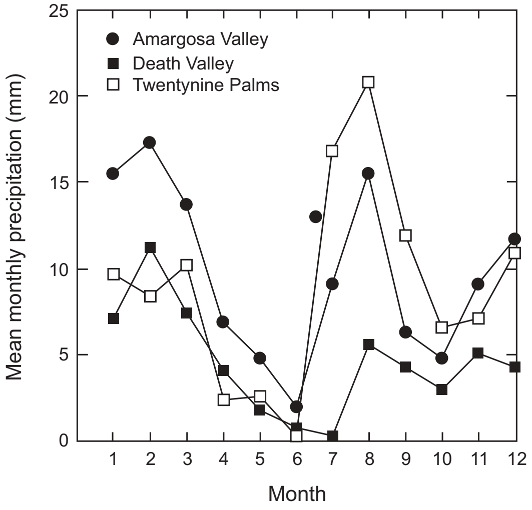


Figure 2—Mean monthly precipitation in Twentynine Palms, Amargosa Valley, and Death Valley (local climatological data, NOAA). Ash Meadows lies within the Amargosa Valley, while Kelso Dunes lies approximately 20 km northeast of Twentynine Palms. Weather data are not available in Kelso Dunes.

counterpart (Lei 1999). *Larrea* and *Ambrosia* are codominant shrub species occurring in the adjacent nondune habitats of the Kelso Dunes and Ash Meadows, while *Larrea-Atriplex* spp. form a common shrub association in Death Valley. *Hymenoclea salsola* (cheesebush) and *Salsola* spp. (Russian-thistle) are frequently found in dune habitats of Ash Meadows. *Achnatherum hymenoides* (Indian ricegrass) and *Astragalus lentiginosus* (locoweed) are herbaceous plants occurring in Kelso Dunes (Lei 1999).

Field and Laboratory Measurements

For each sand dune, 14 transects were established with each transect containing dune habitats, ecotone (marginal dune), and adjacent nondune shrublands. These 14 transects were randomly distributed around the entire dune area. Dune plots, with an area of 100 m^2, were located at least 200 m into the dune environments, whereas nondune plots were located 200 m from the nearest marginal dunes.

At the center of each adjacent nondune plot, one soil sample was extracted to depths of 5 cm and 20 cm only due to the presence of caliche layers near the surface. However, at the center of each dune plot, one soil sample was extracted at multiple depths—5, 20, 40, 90, and 130 cm. Soils were

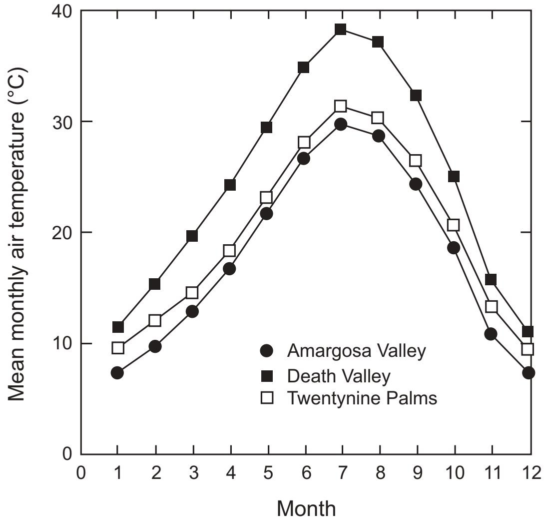


Figure 3—Mean monthly air temperature in Twentynine Palms, Amargosa Valley, and Death Valley (local climatological data, NOAA). Ash Meadows lies within the Amargosa Valley, while Kelso Dunes lies approximately 20 km northeast of Twentynine Palms. Weather data are not available in Kelso Dunes.

Table 1—Geographic characteristics of three inland sand dunes in the Mojave Desert.

Dune system	County, State	Latitude	Longitude	Elevation
		- - N - -	*- - W - -*	*- m -*
Ash Meadows	Nye, NV	36°20'	116°15'	670
Death Valley	Inyo, CA	36°35'	116°00'	< 85
Kelso	San Bernadino, CA	34°55'	115°40'	670

passed through a 2-mm sieve to remove large rocks and plant roots. A soil sieve also separated sand, silt, and clay from material larger than 2 mm such as gravels and cobbles. Soil samples were measured for gravimetric moisture. Soils were oven dried at 105 °C for 72 hours. Gravimetric soil moisture (soil water content) was determined by calculating the differences between fresh and oven-dried mass divided by dry mass. To ensure compatibility, air temperatures in the field were recorded concurrently when soil samples were collected.

Water infiltration rates were measured using a PVC pipe (cylinder), 5.5 cm in diameter and 9.5 cm tall. This cylinder was open at both ends, and was gently tamped into the dune and nondune soils to a depth of 2 cm to avoid leakage, and then 50 ml of water was ponded above the core inside of the cylinder (Brotherson and Rushforth 1983). Infiltration into the core was measured with a stopwatch as the number of seconds needed for the ponded water to disappear into the core (Brotherson and Rushforth 1983).

Approximately 1.5 L of water, serving as artificial rain, was manually poured through a perforated 13-cm disk, with perforations evenly spaced on a 0.1-cm grid. The disk was placed 1.0 m above ground. The total delivery time for the water to be dispensed on the dune or nondune soil was 60 seconds to create precipitation at a cloudburst level (Brotherson and Rushforth 1983). A sudden, heavy precipitation is significant due to its impacts on surface-water runoff and fluvial erosion. Depth of water penetration was immediately measured and recorded once the water had soaked into the soil.

Surface-water runoff was measured by recording the downslope and across-slope spread of water that was artificially rained onto study sites (Brotherson and Rushforth 1983). The area of water spread from these two slope measurements was computed using the formula for the area of an ellipse using the following equation: (πab), where a and b are radii of an ellipse (Larson and others 1994). Since surface water runoff did not form a perfect elliptical shape, measured areas were likely to be overestimates.

Soil movement was assessed by visually quantifying the amount of soil loss via fluvial erosion during a measured cloudburst. The following index was used at the spot of this cloudburst: 1 = no appreciable movement; 2 = moderate movement—up to 10 percent of soil particles being displaced, and 3 = heavy movement—between 10 and 20 percent of soil particles being displaced (Brotherson and Rushforth 1983).

Statistical Analyses

One-way Analysis of Variance (ANOVA; Analytical Software 1994) was used to detect significant effects of site (three dunes), habitat type (dune, marginal dune, and adjacent shrublands), and soil depth on soil water content. Tukey and Scheffe's multiple comparison tests (Analytical Software 1994) were used to compare site means when significant effects of habitat type and soil depth were detected. Pearson's Correlation (Analytical Software 1994) was conducted to correlate soil water content with site, habitat type, and geomorphic surface (terrace and slope). Path analysis includes a path diagram (fig. 4) with direct causal pathways whose strengths were indicated by partial regression coefficients (path coefficients), with arrows indicating the direction of causal connection from predictor (site, habitat type, and soil depth) to response (soil moisture) variables. A short, unlabeled (residual) arrow appeared in the path diagram, indicating that other abiotic factors would have some influence on the overall gravimetric soil moisture.

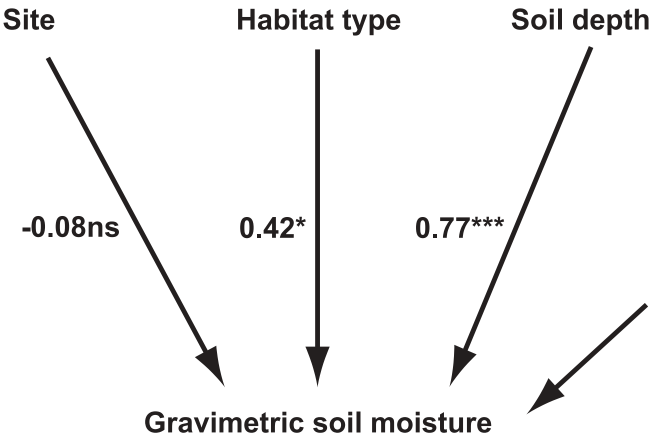


Figure 4—Path diagram depicting proposed causal influences of site, habitat type, and soil depth (environmental attributes) on gravemtrica soil moisture. The direct causal effect of each attribute (straight, one-headed arrow) on soil moisture is the standardized partial regression coefficient (path coefficient). A short, unlabeled (residual) arrow is shown to indicate that additional climatic, edaphic, and geomorphic factors may play a role in determining the overall soil moisture content.

Multivariate Analysis of Variance (MANOVA; Analytical Software 1994) was performed on soil moisture attributes with site, habitat type, and geomorphic surface as main effects. P-values equal to or less than 0.05 are reported as statistically significant.

Results

Gravimetric soil moisture were significantly different in site, habitat type, and soil depth ($P \leq 0.01$). Dune substrates had a significantly lower ($P \leq 0.001$) water content at the upper 20 cm than nondune substrates. Soil water content reached as high as 1.48 percent at 130 cm beneath the surface in the Ash Meadows dunes during midsummer.

Among the three dune fields, Death Valley dunes consistently exhibited the lowest soil water content at all depths (table 2). Mean summer precipitation fell below 5 mm (fig. 2), while mean summer air temperature exceeded 30 °C in Death Valley (fig. 3). In all three dunes, soil water content increased significantly as soil depth increased ($P \leq 0.001$; table 2). Path analysis revealed significant direct causal effects of soil depth and habitat type on soil water content (fig. 4). Despite more extreme monthly and annual weather conditions found in Death Valley, dune site had little direct effect on soil water content (table 3). According to path analysis, soil water content was significantly directly influenced by soil depth and

Table 2—Soil water content (percentages) at various depths in dune and adjacent nondune (*Larrea-Ambrosia*) habitats during July 2001 in the Mojave Desert (n = 14 per habitat in each dune system). Due to the presence of caliche layers near the soil surface, soil moisture was not examined beyond 20 cm in nondune habitats[a].

	Ash Meadows		Death Valley		Kelso	
Soil depth	**Dune**	**Nondune**	**Dune**	**Nondune**	**Dune**	**Nondune**
- - cm - -						
5	0.12aA	0.26aB	0.07aA	0.18aB	0.15aA	0.33aB
20	.34bA	.79bB	.15bA	.46bB	.39bA	.84bB
40	.64c	—	.41c	—	.59c	—
90	.98d	—	.74d	—	.92d	—
130	1.48e	—	1.08e	—	1.37e	—

[a] Mean values within each dune system (in rows) followed by different upper case letters are significantly different at $P \leq 0.05$. Mean values within each habitat (in columns) followed by different lower case letters are also statistically significant at $P \leq 0.05$.

Table 3—Relationship between three environmental variables and soil water content. The direct causal effect of each variable is the standardized partial regression coefficient (path coefficient). Total causal influence (Pearson's r-value) sums all direct and indirect pathways.

Variable	Direct causal	Indirect causal	Total causal
Site	–0.08[a]	–0.09[a]	–0.17[a]
Habitat type	.42[b]	.23[a]	.65[c]
Soil depth	.70[c]	.16[a]	.94[c]

[a] Nonsignificant
[b] Significance levels $P \leq 0.05$.
[c] Significance levels $P \leq 0.001$.

habitat type. Soil water content was subject to additional biotic and abiotic influences, representing by a residual arrow (fig. 4). Although not quantitatively examined in this study, other direct and indirect causal effects on soil water content may include absorption of water by plants, gravity, slope exposure, topography, macropore, soil compaction, soil particle size, air temperature, precipitation, evaporation, relative humidity, and amount of cloud cover.

Moreover, time for water infiltration and depth of water penetration increased significantly ($P \leq 0.001$; table 4) from the surrounding *Larrea-Ambrosia* shrublands to dune fields. Among the three dunes, Death Valley had a significantly shorter time for water infiltration and greater depth of water penetration. Downslope, across slope, and area of water spread were significantly smaller ($P \leq 0.001$; table 4) in dune than in nondune substrates. Water-born soil movement (fluvial erosion) was significantly greater at slope than at terrace sites ($P \leq 0.01$; table 4) regardless of habitat types.

Among the soil moisture regimes, significant interaction ($P \leq 0.001$; table 5) was detected between habitat type and geomorphic surface for area of water spread (surface water runoff) only. When examining habitat type or geomorphic surface alone, significant differences ($P \leq 0.05$; table 5) were found in all measured moisture variables. There were also significant differences ($P \leq 0.05$; table 5) in site for water infiltration and water movement into the soil.

Discussion

The Kelso, Ash Meadows, and Death Valley dunes in the Mojave Desert of southern Nevada and California were edaphically distinct in terms of soil moisture status from the surrounding *Larrea-Ambrosia* shrublands. In all dunes, soil water content increased with depth, and decreased from the surrounding *Larrea-Ambrosia* shrublands to dune fields.

Because of larger pore size, coarser particles, extremely high percent sand, and less organic matter, dune soils provide less moisture retention than nondune soils. In this study, soil moisture in the top 20 cm was less than 1 percent, but soil moisture increased significantly as depth increased in all three dunes during the midsummer season. Death Valley had significantly lower soil water content than Kelso Dunes and Ash Meadows, primarily due to a combination of higher evaporation and summer air temperature, lower summer precipitation, relative humidity, cloud cover, and lower elevation. Low moisture availability, usually less than 1 percent at or near the soil surface, is a common characteristic of inland sand dunes in Western America, including the Eureka, Mojave Desert dunes, and northeastern Colorado dunes (Bowers 1986; Lei 1998). Water does not store well in shallow soils, mainly due to rapid evaporation. Conversely, water is stored well in deep soils and can support perennial plants with deep roots. The loss of water in deep soils is primarily by percolation into groundwater, absorption of plant roots, and transpiration from plant leaves (Prill 1968). Moisture in dune sand comes from precipitation (Bowers

Table 4—Moisture characteristics of dune and adjacent nondune (*Larrea-Ambrosia* shrubland) soils in southern Nevada and California of the Mojave Desert (n = 14 per habitat in each dune system).

	Ash Meadows		Death Valley		Kelso	
Moisture parameter	**Dune**	**Nondune**	**Dune**	**Nondune**	**Dune**	**Nondune**
Infiltration rate			*seconds*			
Terrace	138.7	214.3	121.3	189.4	132.4	218.6
Slope	212.3	241.1	201.8	229.7	229.5	256.9
Depth of water penetration			*cm*			
Terrace	3.6	3.2	3.7	3.4	3.8	3.5
Slope	3.2	2.9	3.4	3.1	3.3	2.9
Downslope spread			*cm*			
Terrace	51.7	67.4	45.1	70.8	48.7	75.4
Slope	62.1	85.7	53.2	86.4	59.8	89.7
Across slope spread			*cm*			
Terrace	36.1	61.2	33.6	59.4	34.4	62.7
Slope	44.0	74.2	39.9	68.5	41.9	70.2
Area of spread			cm^2			
Terrace	933.2	2,062.4	757.7	2,012.8	837.6	2,363.8
Slope	1366.2	3,179.5	1,061.3	2,959.2	1,252.8	3,148.5
Soil movement			*fluvial erosion*			
Terrace	1.4	1.2	1.4	1.2	1.4	1.
Slope	1.6	1.4	1.7	1.4	1.7	1.3

Table 5—MANOVA results (P-values) of the effects of habitat type, geomorphic surface, site, and their interactions on six soil moisture attributes: water infiltration, depth of water penetration, downslope and across-slope water spread, area of water spread, and water-borne soil movement.

Source	Infiltration	Depth	Downslope	Across slope	Area	Soil
Habitat type (A)	0.0000	0.0000	0.0001	0.0000	0.0000	0.0001
Geomorphic surface (B)	.0005	.0000	.0137	.0001	.0000	.0006
Site (C)	.0005	.0295	.7024	.2750	.1663	.7065
A, B	.1497	.1372	.5041	.3752	.0028	.2562
A, C	.7301	.6726	.5942	.9868	.6100	.3743
B, C	.7118	.6014	.9770	.6710	.8228	.7065
A, B, C	.9153	.2372	.9689	.7804	.9396	.3641

1982). Shortly after a rain, moisture at the soil surface may be as high as 3 percent (Ramaley 1939). Sandy soils have large pores, which drain water downward by gravity after soils are moistened at the surface. Abundant water may be available in inland sand dunes below the surface layers, with the top 20 cm of dry sand insulating moister sand below from air exchange (Bowers 1982; Sharp 1966).

In this study, dune sand had considerably more available water than its sandy texture would suggest. For instance, percolating water can reach depths such that it is immune to evaporation but available to plant roots. Another process is vapor-phase addition of water to sand. This mechanism occurs as dew and mist that condense during the night on cold sand particles. As heating occurs during the day, some of this water evaporates into the atmosphere. A significant portion of water vapor, however, moves downward by diffusion to the cooler sand. The addition of moisture to sandy desert soils via this mechanism is essential. The hardpan restricts rooting in nondune sites. Because there are no root restriction zones in dunes, plants can root to much deeper depths so moisture stored at depth can be extracted.

Water percolated into dune soils significantly faster than into nondune soils in this study. The infiltration rate of South African soils is influenced by many factors, including organic matter, soil texture, and slope (Dean and Yeaton 1993). Significant interaction was found between habitat type and geomorphic surface for surface water runoff. Substantially higher water infiltration and greater depth of water penetration are expected on extremely sandy dune soils with terrace surface compared to adjacent nondune soils with slope surface, presumably due to a larger pore size, higher moisture leaching rate, and lower compaction.

Additionally, soil can be removed by the action of heavy rains or flash floods. In this study, dune soils exhibited a significantly lower surface-water runoff compared to nondune soils because dune soils absorbed more water during and shortly after a simulated cloudburst. With increased infiltration and reduced surface-water runoff, deeper penetration of water into the soil occurred at terrace than at slope sites. Nevertheless, a significantly greater fluvial erosion was detected at slope than at terrace sites in both dune and nondune soils. Although a short cloudburst did not create extensive fluvial erosion, some movement of soil particles occurred at the surfaces of slope sites when water traveled rapidly downslope by gravity. However, substantially more surface-water runoff and soil loss via fluvial erosion are likely to occur in both dune and nondune substrates if cloudbursts have longer duration, higher frequency, and/or greater intensity.

Active inland sand dunes occupy only a tiny fraction of the North America desert landscape. The Kelso, Ash Meadows, and Death Valley dunes of the Mojave Desert are different from the surrounding *Larrea-Ambrosia* shrublands in terms of soil moisture attributes. Compared to adjacent shrublands, sand dunes are edaphic islands that have water available at depth and that are important in shaping unique biogeographic patterns through time. Future research is required to investigate additional soil attributes, such as chemical nutrients and biological properties, in inland dunes of North America and on other continents.

Acknowledgments

I sincerely appreciate Steven Lei, David Valenzuela, and Shevaun Valenzuela for collecting soil samples and moisture data in the dune fields. Steven Lei assisted with statistical analyses. Scott Keiser provided stimulating discussions, and David Charlet provided helpful comments on earlier versions of this manuscript. The Department of Biology at the Community College of Southern Nevada provided logistical support.

References

Analytical Software. 1994. Statistix 4.1, an interactive statistical program for microcomputers. Minneapolis, MN: Analytical Software. 429 p.

Barbour, M. G.; Burk, J. H.; Pitts, W. D. 1999. Terrestrial plant ecology. 3d ed. Menlo Park, CA: Addison Wesley Longman, Inc.

Bowers, J. E. 1982. The plant ecology of inland dunes in Western North America. Journal of Arid Environments. 5: 199–220.

Bowers, J. E. 1986. Seasons of the wind. Flagstaff, AZ: Northland Press. 156 p.

Brotherson, J. D.; Rushforth, S. R. 1983. Influence of cryptogamic crusts on moisture relationships of soils in Navajo National Monument, Arizona. Great Basin Naturalist. 43: 73–78.

Brown, J. H. 1972. Species diversity of seed-eating desert rodents in sand dune habitats. Ecology. 54: 775–787.

Dean, W. R. J.; Yeaton, R. I. 1993. The effects of harvester ant *Messor capensis* nest-mounds on the physical and chemical properties of soils in the southern Karoo, South Africa. Journal of Arid Environments. 25: 249–260.

Holiday, V. T. 1990. Soils and landscape evolution of eolian plains: the southern High Plains of Texas and New Mexico. Geomorphology. 3: 489–515.

Lancaster, N. 1993. Kelso Dunes. National Geographic Research and Exploration. 9: 444–459.

Lancaster, N. 1998. The dynamics of star dunes: an example from the Gran Desierto, Mexico. Sedimentology. 36: 273–289.

Larson, R. E.; Hostetler, R. P.; Edwards, B. H. 1994. Calculus. Lexington, MA: D.C. Heath and Company.

Lei, S. A. 1998. Soil properties of the Kelso sand dunes in the Mojave Desert. Southwestern Naturalist. 43: 47–52.

Lei, S. A. 1999. Ecology of psammophytic plants in the Mojave, Sonoran, and Great Basin Deserts. In: McArthur, E. Durant; Ostler, W. Kent; Wambolt, Carl L., comps. Proceedings: shrubland ecotones. Proc. RMRS-P-11. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 212–216.

McFadden, L. D.; Wells, S. G.; Jercinovich, M. J. 1987. Influences of eolian and pedogenic processes on the origin and evolution of desert pavements. Geology. 15: 504–508.

National Oceanic and Atmospheric Administration (NOAA). 2001. Local climatological data: annual summary with comparable data. Ashville, NC: National Climatic Data Center.

Pavlik, B. M. 1985. Sand dune flora of the Great Basin and Mojave Deserts of California, Nevada, and Oregon. Madrono. 32: 197–213.

Prill, R. C. 1968. Movement of moisture in the unsaturated zone in a dune area, southwestern Kansas. U.S. Geological Survey Professional Paper 666D: 1–12.

Ramaley, F. 1939. Sand-hill vegetation of northeastern Colorado. Ecological Monographs. 9: 1–51.

Sharp, R. P. 1966. Kelso Dunes, Mojave Desert, California. Geological Society of America Bulletin. 77: 1045–1074.

Wells, S. G.; McFadden, L. D.; Schultz, J. D. 1990. Eolian landscape evolution and soil formation in the Chaco Dune field, southern Colorado Plateau, New Mexico. Geomorphology. 3: 517–546.

Leaf Temperatures of Blackbrush: Relationships With Air and Soil Surface Temperatures

Simon A. Lei

Abstract: Comparative diurnal and seasonal leaf temperatures of blackbrush (*Coleogyne ramosissima* Torr.) plants were quantitatively examined in the Clark Mountain of southeastern California. Path analysis revealed that seasonality and diurnal period were significant positive predictors of air, soil surface, and blackbrush leaf temperatures. Path analysis also indicated that air temperature was a significant positive predictor of soil surface and blackbrush leaf temperatures. Blackbrush leaf temperatures consistently remained at or near air temperatures throughout the day and year. Sunlit leaf temperatures were significantly warmer than shade leaf temperatures during the summer season only, but not during rest of the seasons. Soil surface temperatures were significantly warmer than air and blackbrush leaf temperatures irrespective of seasonality and diurnal period. Significant interactions were detected between seasonality and diurnal period for air and blackbrush leaf temperatures in the Mojave Desert of southeastern California.

Introduction

Plant species have adapted to survive various environmental stresses in deserts such as low precipitation, low relative humidity, low soil moisture and nutrients, intense solar radiation, and high air and soil temperatures. Solar radiation on plants growing in warm, arid environments may cause their death if plant temperatures rise well above a critical level (Gates and others 1968). Leaf temperatures exceeding the air temperature by 10 °C are common in the Great Basin Desert of southern Utah (Gates and others 1968). Xerophytes must prevent sunlit leaves from becoming too warm when air temperature exceeds 50 °C or more. Leaf temperatures of many xerophytic species in southern Utah are very close to air temperatures (Gates and others 1968). Many warm desert plants have small leaves compared to their closely related species living in more mesic environments. There are ecomorphological reasons why the temperature of small leaves stay near air temperature. Large, thin leaves have a greater surface area, absorb heat, and lose water via transpiration more rapidly compared to small, thick leaves.

Temperatures of the sunlit soil surfaces ranged from 12 to 28 °C above air temperatures of the Great Basin Desert in southern Utah (Gates and others 1968). Summer seasons have the largest daily and annual range of soil surface temperatures of any season. However, any litter, debris, and vegetation covering the ground would substantially reduce the diurnal and annual range of soil surface temperatures in southern Nevada (Lei and Walker 1997b). Relative to open substrate temperatures, Suzan and others (1996) reported a 15 °C decrease in summer maximum temperatures and an increase in winter minimum temperatures of 3 °C under shrubs in the Sonoran Desert. During the winter when the ground is continuously covered with snow, soil surface temperatures remain at or a few degrees below freezing because the insulating capacity of the snow traps heat radiating from the earth, thus protecting plants from extreme cold (Barbour and others 1999).

Leaf temperatures of some desert plant species were quantified (Gates and others 1968; Gibbs and Patten 1970; Smith 1978). Yet, possible interactions and correlations between air and soil surface temperatures in determining leaf temperatures of blackbrush (*Coleogyne ramosissima*) shrubs in southeastern California of the Mojave Desert have not been documented.

Methods

Study Site

Field studies were conducted during four 3-month intervals from March through December 2001 at the Clark Mountain (roughly 35°41'N and 115°32'W; elevation 1,475 m) near the Nevada State border. The months of March, June, September, and December represented the four distinct seasons. Summers display warm, arid conditions, with maximum air temperatures in the 40 °C range. Winter air temperatures, on the contrary, are generally mild and pleasant. Winter rainfalls are mild and may last up to several days (Rowlands and others 1977). Monsoonal precipitation occurs from July through mid-September, as thunderstorms of high intensity and short duration. Soil erosion, especially along wash edges, is evidence of the intensity of some of the thunderstorm activity. The spring and fall seasons are generally considered most ideal for blackbrush growth and development, although sharp temperature changes can occur during these months. A relative humidity of 20 percent or less is common in summer seasons (Lei and Walker 1997a,b). A combination of high air temperatures and high evaporation, as well as low relative humidity, cloud cover,

---

In: Hild, Ann L.; Shaw, Nancy L.; Meyer, Susan E.; Booth, D. Terrance; McArthur, E. Durant, comps. 2004. Seed and soil dynamics in shrubland ecosystems: proceedings; 2002 August 12–16; Laramie, WY. Proceedings RMRS-P-31. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Simon A. Lei is a Biology and Ecology Instructor, Department of Biology, WDB, Community College of Southern Nevada, 6375 West Charleston Boulevard, Las Vegas, NV 89146-1139, U.S.A. FAX (702) 257-2914; e-mail: salei@juno.com

and low precipitation create a typical arid environment, with an average annual rainfall of less than 200 mm at midelevations of the Clark Mountain (Lei, personal observations, 2001).

Blackbrush shrublands often are considered a floristically simple community, consisting primarily of monospecific blackbrush stands with other woody species scattered throughout. Many common herbaceous plants are members of the Asteraceae, Agavaceae, Brassicaceae, Fabaceae, and Poaceae families. Blackbrush shrublands share a broad lower ecotone with creosote bush-white bursage (*Larrea tridentata-Ambrosia dumosa*) shrubland, and a broad upper ecotone with pinyon-Utah juniper (*Pinus monophylla-Juniperus osteosperma*) woodland (Lei and Walker 1997a,b).

Field Observations

Diurnal and seasonal air temperatures were measured concurrently with soil surface and blackbrush leaf temperatures to ensure comparability. Air temperatures were measured with a mercury-in-glass thermometer placing at 1.6 m above ground surface. Soil temperatures were measured with a metallic soil thermometer placed at the surface in open substrates and beneath shrub canopies.

Blackbrush shrubs were tagged with a brightly colored yarn prior to leaf temperature measurements to facilitate repeated sampling throughout the day. Air, leaf, and soil surface temperatures were measured at predawn (0600 hours), and then at 3-hour intervals through 1800 hours. Temperatures of 100 leaves from 50 blackbrush shrubs were taken with a fine-wire (0.02-mm) copper-constantan thermocouple inserted into leaf tissues. These 100 leaves were subdivided evenly between the top and bottom layers of canopy from the same plants to represent sunlit and shade leaves, respectively. Individual leaves within each layer of canopy were randomly selected to avoid biased sampling.

Statistical Analyses

Two-way Analysis of Variance (ANOVA; Analytical Software 1994) was performed to determine if air temperatures differed by seasonality (spring and summer) and/or by diurnal period (hour of day). Three-way Analysis of Variance (ANOVA; Analytical Software 1994) was conducted to detect significant effects of seasonality, diurnal period, and habitat type (open substrate and beneath shrub canopy) on soil temperatures. This three-way ANOVA was also used to detect significant effects of seasonality, diurnal period, and canopy position (top and bottom) on leaf temperatures. Path analysis, expressed as path coefficient or partial regression analysis (Analytical Software 1994), was performed to determine if diurnal period and seasonality had direct causal effects on air, soil surface, and blackbrush leaf temperatures. Path analysis was also performed to determine if air temperature had a causal effect on soil surface and blackbrush leaf temperatures. Linear regression analysis (Analytical Software 1994) was used to correlate soil surface temperatures with blackbrush leaf temperatures. Statistical significance was tested at the 5-percent level.

Results

Air, soil surface, and blackbrush leaf temperatures were significantly directly affected by seasonality and diurnal period ($P \leq 0.001$; fig. 1). Soil surface and blackbrush leaf temperatures were also significantly directly influenced by air temperatures ($P \leq 0.001$; fig. 2). Soil surface temperatures were significantly positively correlated with blackbrush leaf temperature, expressed as a curved, two-headed arrow ($P \leq 0.001$; figs. 1 and 2).

For ease of visualization, air, soil surface, and blackbrush leaf temperature patterns were extremely similar between the spring and fall seasons, and only the spring season values were included graphically. Blackbrush leaf temperatures consistently remained at or near air temperature throughout the day and year (fig. 3). The air-sunlit leaf temperature difference in magnitude became greater around noon hours during the summer season (fig. 3). Sunlit leaves located at the top of canopies were warmer relative to shade leaves located deep inside the canopies (fig. 4). Soil surface temperatures were significantly warmer than air ($P \leq 0.01$; fig. 5) and blackbrush leaf (fig. 3) temperatures irrespective of diurnal period and seasonality. A similar trend in temperature differences was also observed between air and soil beneath blackbrush shrub canopy, between air and shade leaves, as well as between shade leaves and soil beneath canopy (data not shown).

Soil surface temperatures ranged from slightly below air temperature in December to nearly 16 °C above air temperatures in June (fig. 6). Within a single day, the soil-air

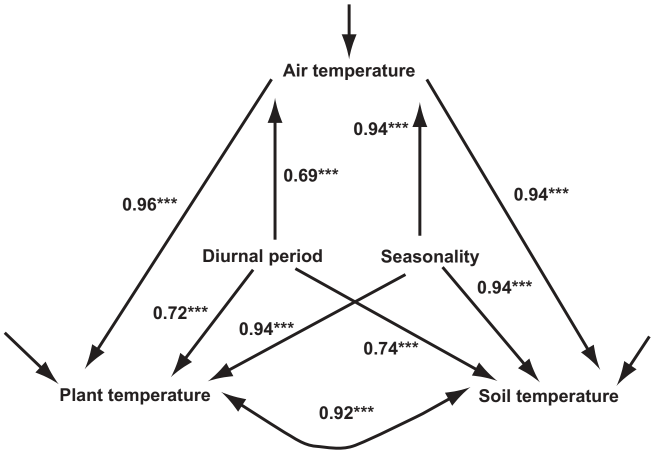


Figure 1—Path diagram depicting hypothesized relationships between blackbrush leaf temperatures and various environmental attributes. The direct causal effect of each attribute (straight, one-headed arrows) on blackbrush leaf temperature is the standardized partial regression coefficient (path coefficient). A short, unlabeled (residual) arrow is shown to indicate that additional biotic and abiotic factors may play a role in determining the overall leaf temperature. Soil temperatures were measured in open substrates, while leaf temperatures were measured at the top of the canopy exposed to prolonged direct sunlight. *** = P values less than 0.001.

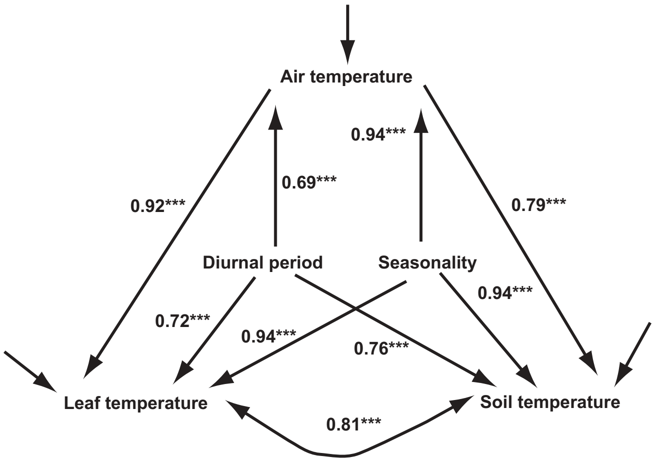


Figure 2—Path diagram depicting hypothesized relationships between blackbrush leaf temperatures and various environmental attributes. The direct causal effect of each attribute (straight, one-headed arrows) on blackbrush leaf temperature is the standardized partial regression coefficient (path coefficient). A short, unlabeled (residual) arrow is shown to indicate that additional biotic and abiotic factors may play a role in determining the overall leaf temperature. Soil temperatures were measured under shrub canopies. Leaf temperatures were measured at the bottom of the canopy, and leaves were shaded throughout much of the day. *** = P values less than 0.001.

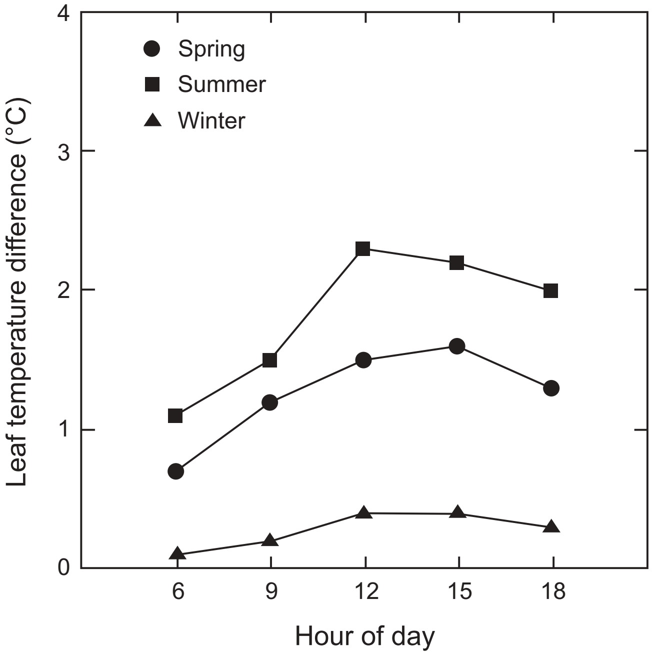


Figure 4—Temperature difference (n = 100 per diurnal period per season) between sunlit and shade leaves in the Clark Mountain of southeastern California. Shade leaves were located deep inside the canopy, and leaves were shaded throughout much of the day.

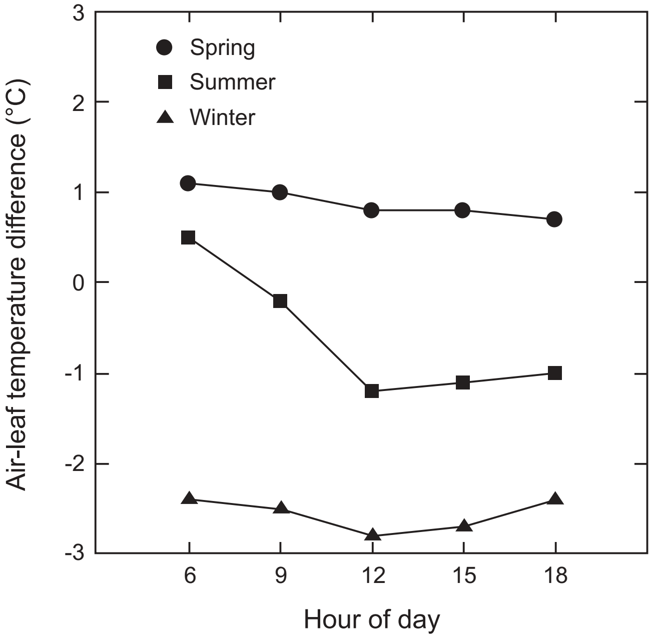


Figure 3—Temperature difference (n = 100 per diurnal period per season) between air and sunlit leaf exposed to prolonged, direct sunlight in the Clark Mountain of southeastern California.

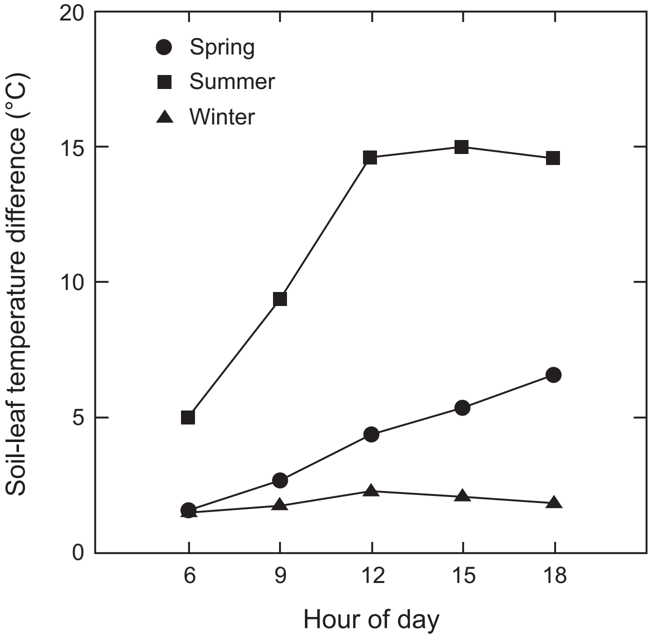


Figure 5—Temperature difference (n = 100 per diurnal period per season) between sunlit soil surface (open substrate) and sunlit leaves in the Clark Mountain of southeastern California.

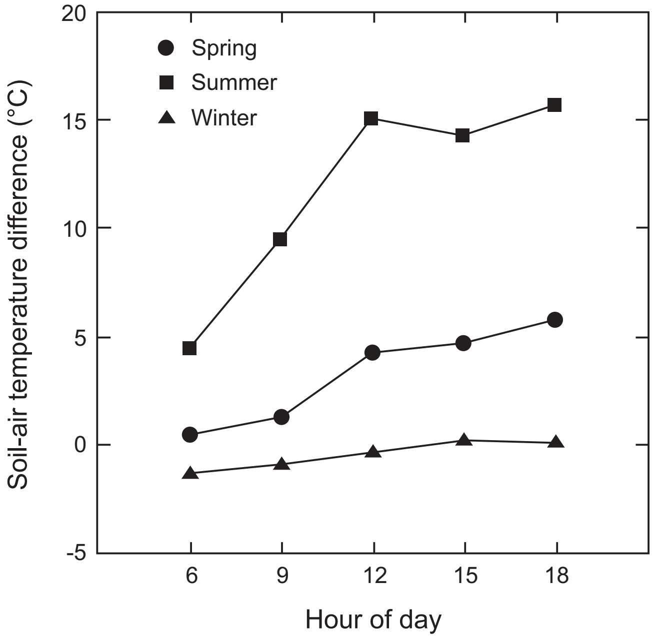


Figure 6—Temperature difference (n = 100 per diurnal period per season) between air and sunlit soil surface (open substrate) in the Clark Mountain of southeastern California.

temperature differences in magnitude became greater around midafternoon hours irrespective of seasonality (fig. 6). Soil surface temperatures in open substrate were significantly warmer ($P \leq 0.01$) than soil temperature under shrub canopies during the dry summer season, but were not significantly different during the snowy winter season (fig. 7).

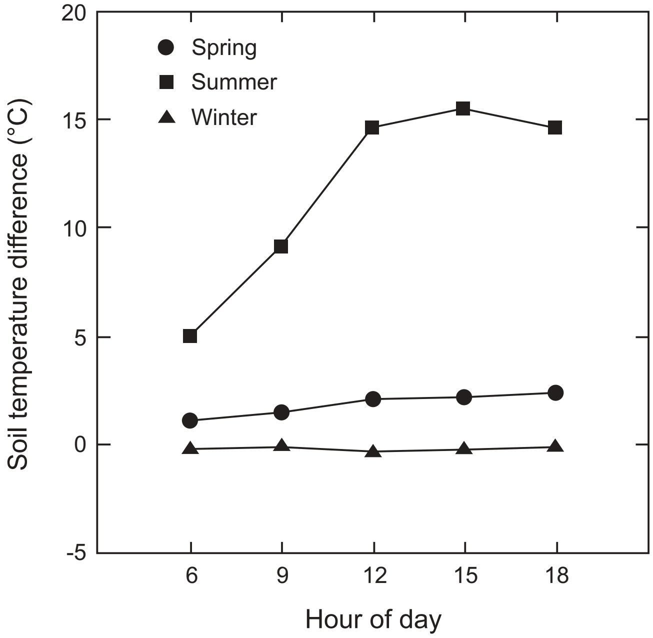


Figure 7—Temperature difference (n = 100 per diurnal period per season) between sunlit soil surface (open substrates) and soil beneath shrub canopies in the Clark Mountain of southeastern California.

Significant interactions were detected between seasonality and diurnal period for air and blackbrush leaf temperatures (table 1). Sunlit leaf temperatures were significantly warmer ($P \leq 0.05$; table 1) relative to shade leaf temperatures. All possible interactions (seasonality, diurnal period, and habitat type) were found to be significant for soil surface temperatures (table 1).

Discussion

Diurnal and seasonal temperature profiles were used to compare differences in magnitude of air, soil surface, and blackbrush leaves. Moreover, habitat type and canopy position are included as an additional variable for measuring soil surface temperatures and blackbrush leaf temperatures, respectively. The connections among environmental variables are represented in path diagrams by two types of arrows: a straight, one-headed arrow signifies a causal relationship between two variables, and a curved, two-headed arrow signifies a simple correlation between them (Loehlin 1998).

In this study, path analysis indicated that seasonality and diurnal period were significant positive predictors of air, soil surface, and blackbrush leaf temperatures. This analysis also revealed that air temperature was a significant positive predictor of soil surface and blackbrush leaf temperatures. Comparing to other seasons, the air-soil surface temperature difference in magnitude became substantially greater around midafternoon hours in open substrates during the dry summer season. Among all measured temperatures, the hottest temperatures were observed on soil surfaces in open substrates, exceeding both air and blackbrush leaf temperatures by as much as 15.8 °C in the summer season. Temperatures at soil surface in open substrates were significantly warmer, and experienced more seasonal extremes than temperatures at soil surface beneath shrub canopies in southern Nevada (Lei 1995; Lei and Walker 1997b) because the bare soil is a good heat absorber and it heats up much more rapidly.

According to the path diagram, a short, unlabeled (residual) arrow is pointed at air temperature, implying that variation in air temperature is subject to additional influences besides seasonality and diurnal period. Air and soil temperatures vary in a fairly parallel manner. Since air temperature is chiefly dependent on radiation and conduction from and to the ground, it follows that the diurnal and annual courses of the air temperatures and the ground temperatures should be similar (Shanks 1956).

A residual arrow is also pointed at soil surface temperatures in the path diagram. Soil surface temperatures are largely determined by a combination of air temperature, the presence of soil moisture and resulting evaporation, the presence of litter, debris, and/or vegetation cover, as well as the radiation regime incident upon the soil surface. During winter seasons, the presence of moisture at the soil surface and the resulting evaporation tends to give a low and uniform soil temperature (Shanks 1956). A persistent snow cover maintains the soil temperatures at or near 0 °C regardless of the air temperature, and even insulates the soil sufficiently to allow warmth from below to cause a slight rise in soil temperature. Conversely, a lack of snow cover allows

Table 1—Summary of two-way ANOVA showing the effects of seasonality, dirunal period, and their interactions on air temperatures. Summary of three-way ANOVA showing the effects of seasonality, diurnal period, habitat type or canopy position, and their interactions on soil surface and blackbrush leaf temperatures, respectively. df = 1 for seasonality, habitat type, and canopy position; df = 4 for diurnal period.

Variable	Air temperature		Soil temperature		Leaf temperature	
	F	P	F	P	F	P
Seasonality (A)	7,512.80	0.0000	14,668.39	0.0000	14,423.44	0.0000
Diurnal period (B)	347.71	.0000	775.93	.0000	560.71	.0000
Habitat type (C)	—	—	655.16	.0000	—	—
Canopy position (C)	—	—	—	29.88	.0000	—
A, B	13.17	0.0008	72.74	0.0000	24.41	0.0000
B, C	—	—	12.33	.0000	.12	.97
A, C	—	—	76.39	.0000	1.98	.18
A, B, C	—	—	3.07	0.0415	.51	.73

the soil temperature to average lower than the freezing point under frigid winter conditions (Shanks 1956).

Soil surface and blackbrush leaf temperature were significantly correlated with, and have a significant direct effect on, each other in this study. A dense vegetation cover or any covering on the soil considerably lessens the diurnal and annual surface temperature ranges. Due to the presence of dense blackbrush shrub canopies, soil surface temperatures under prolonged shade consistently remained at or near the air temperatures, with relatively little direct radiation reaching the ground. A large amount of solar radiation is absorbed by the vegetation rather than by the soil (Suzan and others 1996). In this study, soil temperatures beneath shrub canopies were 2.2 to 15.7 °C cooler than soil temperatures in adjacent open substrates during the summer month, but were only 0.9 to 2.4 °C warmer during the winter month. Shade decreases soil surface temperatures by 13.5 C to 15 °C in summer seasons, but increases soil temperatures by 1.2 to 3 °C in winter seasons in the Sonoran Desert (Franco and Nobel 1989; Suzan and others 1996). Shade is normally considered advantageous to seedling establishment in deserts of southeastern California because it moderates temperature extremes and water loss in microhabitats beneath shrub canopies (Walker and others 2001). Hence, shade creates cooler microhabitat temperatures and higher moisture regimes compared to adjacent open substrates.

Direct heating of the soil surface by solar radiation is important in considering the total heat load in the environment (Gibbs and Patten 1970). Heat is transferred from the soil to the plants by reradiation, convective air currents, and conduction by direct physical contact with the plants. Heat is also conducted from the soil surface to lower portions of plants where roots and soil exchange heat (Gibbs and Patten 1970). The tendency for canopies of blackbrush to occur near the ground surfaces allows the leaves to approach high temperature extremes. A combination of high leaf temperatures, low soil moisture, and low plant water content may play a vital role in determining the lower elevational limit of blackbursh in southeastern California of the Mojave Desert.

In this study, leaf temperatures of blackbrush consistently remained at or near air temperatures throughout the day and year because the leaves are small and dissipate heat primarily by convection. The dimensions of blackbrush leaves ranged from 0.5 to 1.4 cm in length, and were less than 1 cm in width. Temperatures of a leaf measuring 1 by 1 cm or less remain close to air temperatures (Gates and others 1968). They (1968) also discovered that temperatures of small leaves in shrubs and trees (*Artemisia*, *Ephedra*, *Juniperus*, and so forth) were within 3 °C of air temperatures in southern Utah, which is in agreement with this study.

Significant interactions were observed between seasonality and diurnal period for leaf temperatures. When evaluating individual variables alone, significant differences were observed in seasonality, diurnal period, and canopy position for blackbrush leaf temperatures. The coolest leaves were found within the leaf canopy, and were shaded from direct sunlight throughout much of the day. Early morning and late afternoon sunlight produces relatively less heat stress in plant tissues than midday sunlight in southern Nevada (Brittingham and Walker 2000). Reduced leaf temperature decreases heat damage to tissues, enhances stomatal functioning, maintains protein and membrane integrity, and lessens photoinhibition in summer dry seasons (Brittingham and Walker 2000; Singla and others 1997). Shading also decreases leaf temperature, thereby reducing water vapor concentration within intercellular air spaces, and reducing water vapor concentration gradient between intercellular air spaces and ambient air (Brittingham and Walker 2000).

In this study, leaf temperatures ranged from 2.8 °C below to 1.2 °C above air temperatures depending on seasonality, diurnal period, and canopy position, as well as on the intensity, duration, and frequency of direct sunlight. Sun leaves were considered those that were fully exposed to sunlight for most of the day. Conversely, shade leaves were located deeply inside the leaf canopy, mostly shaded during the day. Shade leaves ranged from 0.5 to 2.3 °C cooler than sun leaves of the same plants in this study.

Ecological Implications

The diurnal and seasonal fluctuations of air temperatures largely determined the fluctuations of soil surface and blackbrush leaf temperatures. Small leaves found in many desert plant species are important morphological adaptations in the regulation of leaf temperature. Due to high transpiration rates and high stomatal conductance, small leaves may act to reduce leaf temperatures to more optimal photosynthetic levels, particularly for rapid growth periods when water is abundant (Smith 1978). Without ample water supply and high transpiration rates, a larger leaf size that orients horizontally, exposed to prolonged sunlight and without pubescent layers, can contribute to warmer leaf temperatures, often well above air temperatures. Blackbrush is a typical microphyllous desert shrub species, so it is not surprising that leaf temperatures stay close to air temperatures. This phenomenon has been shown many times for microphyllous desert species. Thus, unusually high leaf temperatures for extensive periods can cause long-term or even permanent (irreversible) plant tissue damage in frequently stressful desert environments.

Acknowledgments

I gratefully acknowledge Steven Lei for collecting air, soil surface, and plant leaf temperature data in the field and for assisting with statistical analyses. David Charlet provided helpful comments on earlier versions of this manuscript. The Department of Biology at the Community College of Southern Nevada (CCSN) provided logistical support.

References

Analytical Software. 1994. Statistix 4.1, an interactive statistical program for microcomputers. St. Paul, MN: Analytical Software.

Barbour, M. D.; Burks, J. H.; Pitts, W. D. 1999. Terrestrial plant ecology. Menlo Park, CA: Addison Wesley Longman, Inc.

Brittingham, S.; Walker, L. R. 2000. Facilitation of *Yucca brevifolia* recruitment by Mojave Desert shrubs. Western North American Naturalist. 60: 374–383.

Franco, A. C.; Nobel, P. S. 1989. Effects of nurse plants on the microhabitat and growth of cacti. Journal of Ecology. 77: 870–886.

Gates, D. M.; Alderfer, R.; Taylor, E. 1968. Leaf temperatures of desert plants. Science. 159: 994–995.

Gibbs, J. G.; Patten, D. T. 1970. Plant temperatures and heat flux in a Sonoran Desert ecosystem. Oecologia. 5: 165–184.

Gibson, A. C. 1996. Structure-function relations of warm desert plants. Berlin, Germany: Springer.

Lei, S. A. 1995. A gradient analysis of *Coleogyne* communities in southern Nevada. Las Vegas: University of Nevada. Thesis.

Lei, S. A.; Walker, L. R. 1997a. Classification and ordination of *Coleogyne* communities in southern Nevada. Great Basin Naturalist. 57: 155–162.

Lei, S. A.; Walker, L. R. 1997b. Biotic and abiotic factors influencing the distribution of *Coleogyne* communities in southern Nevada. Great Basin Naturalist. 57: 163–171.

Loehlin, J. C. 1998. Latent variable models: an introduction to factor, path and structural analysis. Mahwah, NJ: Larrence Erlbaum Associates.

Rowlands, P. G.; Johnson, H.; Ritter, E.; Endo, A. 1977. The Mojave Desert. In: Barbour M.; Major, J., eds. Terrestrial vegetation of California. New York: John Wiley and Sons, Inc.

Shanks, R. E. 1956. Altitudinal and microclimatic relationships of soil temperature under natural vegetation. Ecology. 37: 1–7.

Singla, S. L.; Pareek, A.; Grover, A. 1997. Cellular responses to high temperature. In: Prasad, M. N. V., ed. Plant Physiology. New York: John Wiley and Sons, Inc.: 101–127.

Smith, W. K. 1978. Temperatures of desert plants: another perspective on the adaptability of leaf size. Science. 201: 614–616.

Suzan, H.; Nabhan, G. P.; Patten, D. T. 1996. The importance of *Olneya tesota* as a nurse plant in the Sonoran Desert. Journal of Vegetation Science. 7: 635–644.

Walker, L. R.; Thompson, D. B.; Landau, F. H. 2001. Experimental manipulations of fertile islands and nurse plant effects in the Mojave Desert, USA. Western North American Naturalist. 61: 25–35.

Impacts of Livestock Exclusion From Wyoming Big Sagebrush Communities

Jennifer M. Muscha
Ann L. Hild
Larry C. Munn
Peter D. Stahl

Abstract: Fenced exclosures are used by range scientists to determine the effects of livestock grazing on vegetation and soils. In the 1950s and 1960s numerous rangeland exclosures were established on previously grazed areas in Wyoming big sagebrush steppe. Current understanding suggests shrublands may not return to the pristine condition with livestock exclusion. In the summers of 2001 and 2002 we examined nine 30- to 45-year-old exclosures in Natrona, Fremont, Sweetwater, Bighorn, and Washakie Counties in Wyoming to compare vegetative cover and presence of biological soil crusts inside and outside exclosures. Bare soil was greater outside exclosures at three sites, and litter cover was greater inside the exclosure at three of the nine sites. Biological soil crust cover was greater inside only one of nine exclosures. Although shrub cover increased from original levels (data collected at time of exclosure establishment) both inside and outside exclosures at all sites, shrub cover was greater inside than outside at only one exclosure site. Our results are mixed with respect to impacts of livestock exclusion from Wyoming big sagebrush steppe, partially because original sagebrush levels were low in most exclosures, and because grazing use outside exclosures differed among the nine sites.

Introduction

Native rangeland protection is becoming increasingly important, as managers attempt to enhance and conserve biodiversity. Because a majority of our rangelands are under public ownership, management choices become controversial. Grazing of domestic livestock has been suggested as beneficial to semiarid rangelands in the Western United States (Vavra and others 1994), while others propose permanent removal of grazing by domestic livestock (Donahue 1999; Fleischner 1994; and others). The effects of grazing removal from already grazed systems in the West are not well documented.

Previous research on exclosures conducted in arid and semiarid regions document different vegetative responses to the exclusion of grazing. The most evident difference between grazed and ungrazed areas is greater density of aboveground vegetation inside the exclosure (Costello and Turner 1941). Although range managers once assumed that removal of grazing pressure from rangelands improved rangeland condition (Dyksterhuis 1949), several exclosure studies in arid environments demonstrate that recovery of degraded rangelands can be slow to nonexistent (Holechek and Stephenson 1983; Robertson 1971; West and others 1984). Other studies in arid and semiarid rangelands examining removal of livestock from an area report no change in vegetation (Johnson-Barnard 1995; West and others 1984**)**, an increase in herbaceous cover but not species richness (Anderson and Holte 1981), or an increase in shrub cover after removal of grazing (Brady and others 1989; Lang 1973), resulting in a more degraded state. In sagebrush systems, noticeable response of vegetation after grazing removal may not occur for many decades, and removal of grazing can increase density and cover of big sagebrush (Anderson and Holte 1981; Bock and others 1984; Lang 1973). If the grazing-free period has been short (less than 20 years; Brady and others 1989), shrub canopy may remain unchanged or increase greatly (sagebrush ground cover increased 293 percent inside and 30 percent outside an exclosure in northeastern Wyoming; Lang 1973).

Removal of livestock grazing from rangelands can be evaluated by using fenced grazing exclosures to compare vegetation inside with an adjacent grazed area. Long-term exclosures can reveal slow vegetative trends; however, several limitations of exclosures have been noted. Vegetative conditions between the grazed and protected area may have differed at the time of exclosure establishment (Costello and Turner 1941). The exclosure itself may act as a barrier to wind movement and affect soil and moisture deposition, altering temperature and humidity (Daubenmire 1940). Because exclosures were often constructed where vegetative change due to grazing had already occurred, these sites may not reflect the response of pristine vegetation. However, these sites do reflect the response of grazed vegetation to cessation of grazing by domestic livestock. Because range scientists are finding the Dyksterhuis (1949) view of range succession is not accurate where woody species dominate, Archer (1994) has distinguished that shrub-driven succession may deviate from grass-driven succession. Consequently, long-term

---

In: Hild, Ann L.; Shaw, Nancy L.; Meyer, Susan E.; Booth, D. Terrance; McArthur, E. Durant, comps. 2004. Seed and soil dynamics in shrubland ecosystems: proceedings; 2002 August 12–16; Laramie, WY. Proceedings RMRS-P-31. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Jennifer M. Muscha is a Graduate Student at the University of Wyoming. Ann L. Hild, Larry C. Munn, and Peter D. Stahl are Associate Professor, Professor, and Assistant Professor, Department of Renewable Resources, University of Wyoming, Laramie, WY 82071, U.S.A., Fax: (307) 766-6403, e-mail: annhild@uwyo.edu

exclosures in shrubland ecosystems can clearly demonstrate the impacts of grazing removal in much of the semiarid west. Finally, because biotic crusts are highly susceptible to soil surface disturbance such as trampling or offroad vehicles (Belnap and Gardner 1993), and their biomass and biotic activity are concentrated within 3 mm of the soil surface (Garcia-Pichel and Belnap 1996), they are usually influenced by domestic livestock use. Although biotic crusts are often more developed inside Great Basin exclosures (Kaltenecker and others 1999), little is known of their presence and richness in Wyoming shrublands. We selected nine 30- to 45-year-old rangeland exclosures within Wyoming sagebrush steppe and examined shrub and biological soil crust presence to better understand impacts of grazing cessation.

Materials and Methods

Exclosures in Wyoming

Between 1959 and 1965 approximately 100 rangeland exclosures were constructed in Wyoming for a cooperative study by the University of Wyoming, the Wyoming Agricultural Experiment Station Cooperative program, and the Bureau of Land Management (Fisser 1967, 1968). Studies of vegetational change by use of 0.6-m (2-ft) by 6.1-m (20-ft) and 1.2-m (4-ft) by 1.2-m (4-ft) plots were initiated in 1959 and 1960 (Fisser 1968). The study of vegetation change by use of permanent 30.3-m (100-ft) transects of 20 plots, each 0.3-m (1-ft) by 0.3-m (1-ft) square was initiated in 1965 (Fisser 1967). Some of these exclosures were sampled annually until the early 1970s, and all sampling using the original methods ceased after the early 1980s. A small number of these exclosures have been extensively studied since establishment (Garland 1972; Gdara 1977; Johnson-Barnard 1995; Uhlich 1982).

Site Selections and Description

Nine exclosure study sites were selected within Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle and Young) in Natrona, Fremont, Sweetwater, Bighorn, and Washakie Counties in Wyoming (fig. 1). Sites were selected to have comparable slope and elevation with minimal disturbance (no breaks in fences). Ages of exclosures ranged from 32 to 46 years (table 1) and ranged in size from 2.5 to 12.5 ha (1 to 5 acres). Dominant grass species found at exclosure sites were western wheatgrass (*Agropyron smithii* Rydb.), Sandberg bluegrass (*Poa secunda* Presl), bluebunch wheatgrass (*Agropyron spicatum* (Pursh) Scribn. & Smith), junegrass (*Koeleria macrantha* (Ledeb.) Schult.), needle and thread (*Stipa comata* Trin. & Rupr.), blue grama (*Bouteloua gracilis* (H.B.K.) Lag. ex Steud.), and Indian ricegrass (*Oryzopsis hymenoides* (R. & S.) Ricker) (table 1). Donlin was the only exclosure dominated by threadleaf sedge (*Carex filifolia* Nutt.). Cheatgrass (*Bromus tectorum* L.) was found at five of the nine sites: Poison Spider, Big Trails, Powder Rim D, Worland Cattle, and Sand Creek.

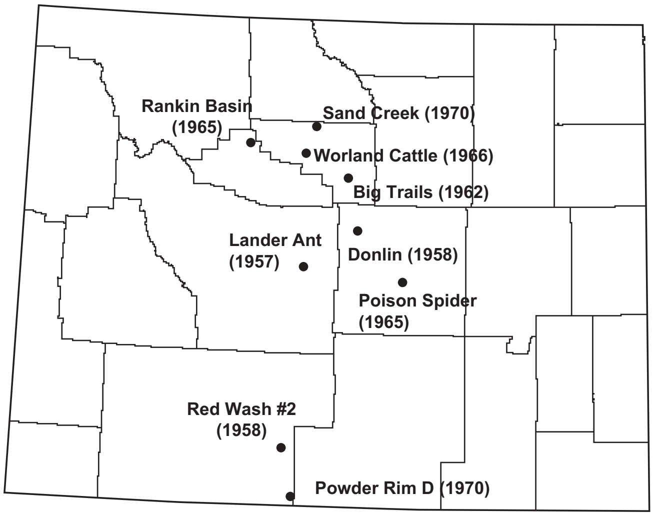


Figure 1—Locations of nine range exclosures sampled in Wyoming in 2001 and 2002 (year of establishment is indicated in parentheses).

Soil surface texture (Blake and Hartge 1986) was analyzed on soil samples retrieved from inside and outside exclosures. Grazing history at each exclosure site was maintained at the Bureau of Land Management Regional offices. Current grazing use and annual precipitation is reported in table 1. Seven exclosures in our study had sandy loam soil textures (table 1). The Poison Spider exclosure had 15 percent more sand content inside the exclosure than outside. Poison Spider and Big Trails have the greatest annual precipitation of the exclosures examined. Donlin and Powder Rim D have comparable annual precipitation and soil textures. Sand Creek and Worland Cattle also have comparable annual precipitation and soil texture, but are drier than Donlin and Powder Rim D sites. Rankin Basin and Red Wash #2 are the driest sites in our study because of low precipitation, and their soils have greater clay content than the other seven exclosures (table 1). Most exclosure sites are grazed in spring or in all seasons on a rotational basis. Rankin Basin site is different from other exclosures in its light grazing use only in winter.

Methods

In 2001 and 2002 we placed vegetative line transects 20 m in length at each exclosure. The number of transects (three to four inside and outside each exclosure) at each site was determined by the size of the exclosure. Basal and canopy cover was recorded on each transect. Transects were evenly spaced inside the exclosure and permanently marked on both ends with a metal stake. Outside the exclosure, transects were placed the same distance from the fence line as the inside transects. Basal and cover data at each site was analyzed using a two-group t-test (alpha 0.05) to compare grazed to grazing removal treatments. We compared our vegetative data to original records collected by Fisser at the time of exclosure construction. Because Fisser's initial samples included only a single transect in each exclosure and position (no replicates), we did not conduct analysis of variance on initial data sets. Some differences in vegetative cover between initial samples and our data may be partially

Table 1—Site characteristics of nine Wyoming shrubland exclosures sampled in 2001 and 2002.

Exclosure name	Established	Elevation	Annual precipitation	Dominant grass/ grasslike species (in order of abundance)	Soil texture	Domestic animal	Months grazed	Stocking rate
	year	*m*	*mm*					*Acres per AUM*
Big Trails	1962	1,515	348	Sandberg bluegrass, western wheatgrass, bluebunch wheatgrass, cheatgrass	Sandy loam	Cattle, horses	Nov. to Jan., first year April to June, second year Rested third year	3.0
Poison Spider	1965	1,758	303	Cheatgrass, Sandberg bluegrass, western wheatgrass, junegrass	Sandy loam	Cattle, sheep	March to June	5.5
Lander Ant	1957	1,621	221	Needle and thread, blue grama, Sandberg bluegrass, western wheatgrass	Sandy loam	Cattle	March to April Nov. to Feb.	10.0
Donlin	1958	1,879	285	Threadleaf sedge, needle and thread	Sandy loam	Cattle	April-June Sept. to Oct.	6.1
Powder Rim D	1970	1,939	277	Needle and thread, Sandberg bluegrass	Sandy loam	Cattle, sheep	Deferred rotation, all	10.0
Worland Cattle	1970	1,300	194	Needle and thread, cheatgrass, western wheatgrass	Sandy loam	Cattle, sheep	March to May, Oct. to Dec.[a]	9.0
Sand Creek	1966	1,333	194	Needle and thread, Sandberg bluegrass	Sandy loam	Cattle, sheep	March to May, Oct. to Dec.[a]	11.9
Rankin Basin	1958	1,932	172	Blue grama, needle and thread	Sandy clay loam	Cattle	Oct. to May	18.0
Red Wash #2	1965	1,576	258	Needle and thread, Indian ricegrass, bluebunch wheatgrass	Sandy clay loam	Cattle	Dec. to April	10.0

[a] Grazing use highly varied in this exclosure since established.

attributed to differences in sampling methods. However, because our data include only a single observer (Muscha) this effect is uniform across the nine exclosure sites.

Results

Exclosure sites represent environments with varieties of plant available moisture because of precipitation and soil disparities between sites (table 1). Consequently our tables and figures present the sites roughly ordered from most mesic (Big Trails and Poison Spider) to most xeric (Red Wash #2) based on precipitation and soil texture differences.

Basal cover differed between inside and outside positions at four of the nine exclosure study sites ($P < 0.05$). At Donlin, Big Trails, and Poison Spider, bare soil was greater, and litter cover was less outside than inside exclosures (fig. 2). In two of these sites (Poison Spider and Big Trails) litter was the dominant cover inside exclosures (76 percent and 64 percent, respectively), while at all other sites bare soil was the dominant cover inside exclosures. Litter in the Poison Spider exclosure was primarily due to invasion of cheatgrass at this site (fig. 3). Cheatgrass was also present at the Big Trails site, but absent from Lander Ant. Cheatgrass cover was greater inside Poison Spider and Big Trails exclosures. Powder Rim D exclosure was unique because it was the only site where cover of biological soil crusts differed between the two positions and was greater inside the exclosure. At all sites, biological soil crust cover was less than 10 percent regardless of position.

Vegetative canopy cover differed between positions (inside and outside) at Big Trails, Poison Spider, Powder Rim D, and Red Wash #2 sites (fig. 3). Native grass cover was greater inside the exclosure at Powder Rim D ($P < 0.05$); at Red Wash #2 and Poison Spider, native grass cover was greater outside the exclosures.

Only Poison Spider and Rankin Basin exclosures had initial shrub canopy cover more than 10 percent at the time of exclosure construction (figs. 4 and 5). In general, shrub cover increased from time of construction to present at all exclosure sites, regardless of position, and overall increases were greater inside exclosures than outside. In the most recent samples, shrub cover differed between positions (t-test, <0.05) only at Poison Spider (fig. 5).

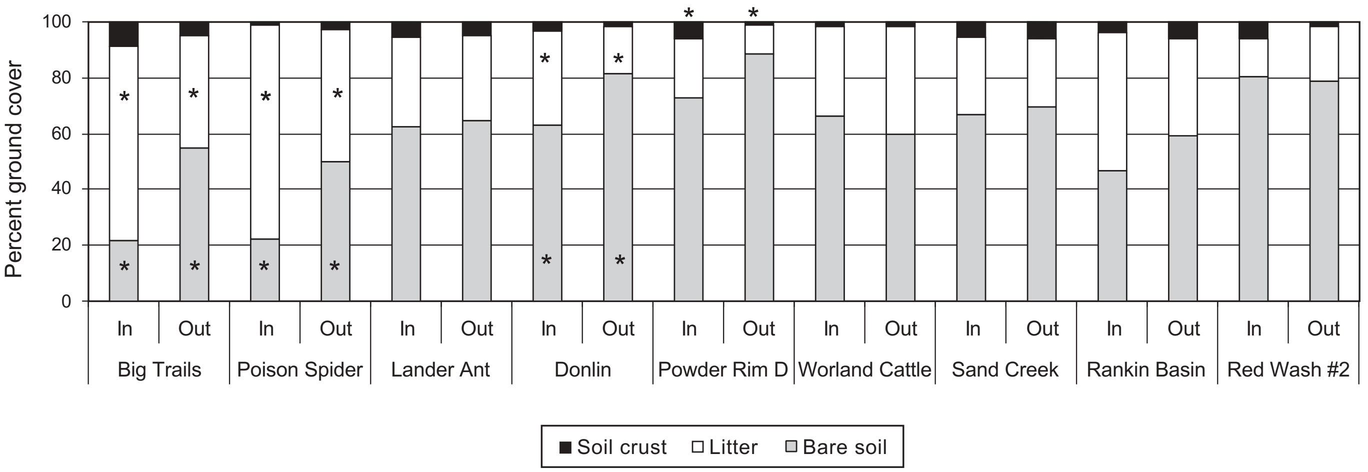


Figure 2—Soil cover (crusts, litter, and bare ground) in two positions (inside and outside grazing exclosures) at nine sagebrush study sites in Wyoming (within a site and cover type asterisks delineate significance at P < 0.05, t-test).

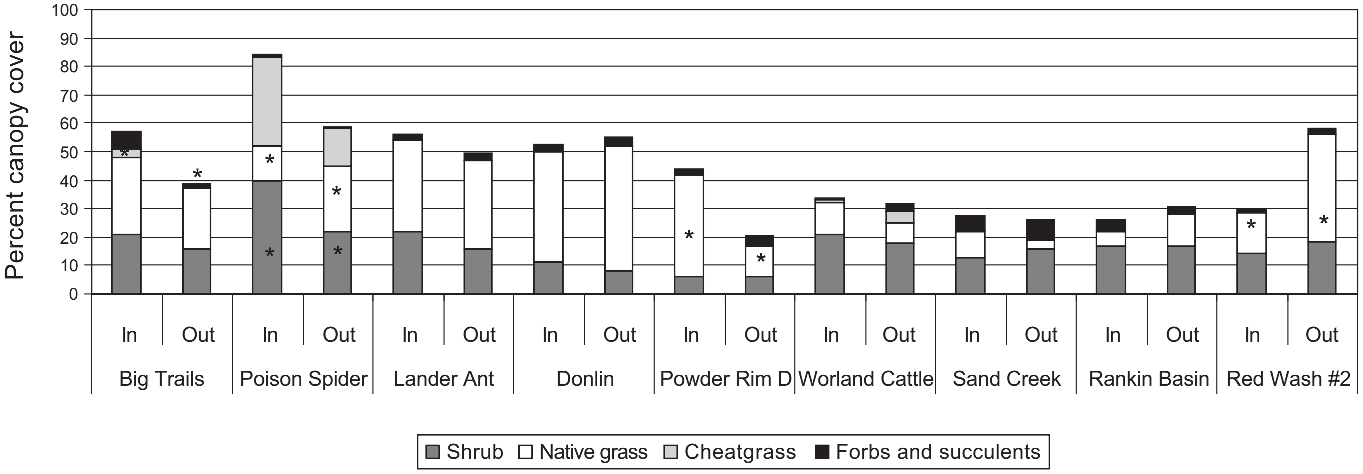


Figure 3—Canopy cover (shrub, native grass, cheatgrass, and forbs and succulents) in two positions (inside and outside grazing exclosures) at nine sagebrush study sites in Wyoming (within a site and cover type asterisks delineate significance at P < 0.05, t-test).

Discussion

Effects of Grazing Removal

The range of plant available moisture represented by the nine exclosure sites offered a variety of responses to removal of domestic stock from sagebrush steppe systems. Overall, at more xeric sites there were few differences inside and outside exclosures. Shrub cover increased both inside and outside exclosures as they aged, regardless of precipitation and soil differences. The Red Wash #2 site is unique in having more native grass cover outside the exclosure. This difference is likely due to a low stocking rate and use in winter months, allowing for favorable grass regrowth prior to our sampling in June. Other xeric sites were used in the spring, prior to sampling. In general, the most xeric sites have shown limited response to grazing removal so far. Moderately moist sites such as Powder Rim D seem to reflect more response to grazing removal, and the greatest response is seen in the most mesic sites (Big Trails and Poison Spider). The Lander Ant site may be unique in lack of response; however, this site differs from Big Trails and Poison Spider in its use only by cattle, lower stocking rate, and slightly lower precipitation. Additionally, cheatgrass is a large part of the vegetative cover in the Big Trails and Poison Spider sites and is absent from Lander Ant. The difference between positions at these two exclosures demonstrates the potential for transitions to shrub-driven succession as suggested by Archer (1994) and others. The unique interactions of available moisture, grazing animal, and season of use are impossible to separate in this study but provide important insight relative to the mechanisms involved in sagebrush increase. Additionally, none of the nine exclosures have been burned since establishment, and so generalizations relative to cheatgrass

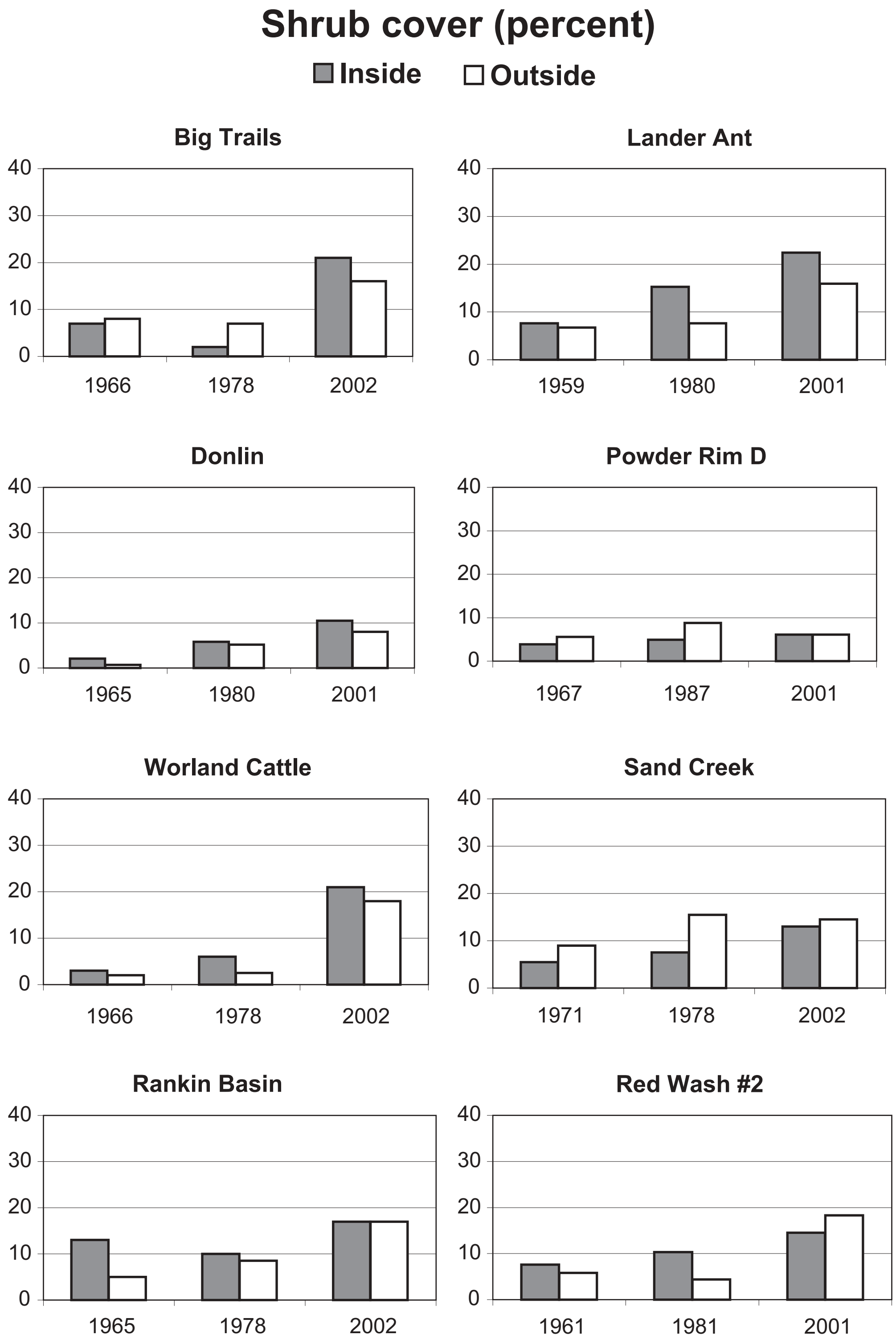


Figure 4—Shrub cover change at eight Wyoming exclosure sites from year of establishment to present (2001 or 2002 sampling dates). Order based on total canopy cover inside exclosures, soils, and precipitation (Poison Spider shown in fig. 5).

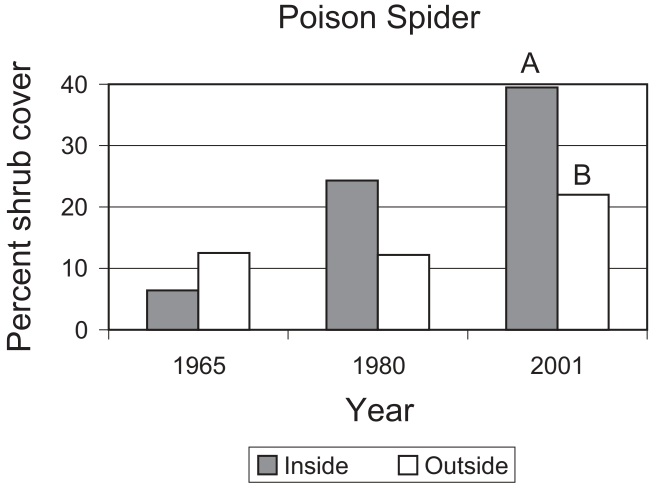


Figure 5—Shrub cover in Poison Spider exclosure from time of establishment to 2001 (within a year, columns with the same letter do not differ P > 0.05, t-test).

dynamics in Wyoming sagebrush steppe are speculative in the absence of fire.

Biological Soil Crusts

Biological soil crusts have received increased attention in arid land research, and our research has found that biological soil crusts are a visible presence in some shrubland ecosystems in Wyoming. Although we have no records of the cover of biotic crusts at time of exclosure establishment, we can only assume that they were similar across the sites prior to the time of fence construction. Although total cover of biological soil crusts was significantly greater inside only one exclosure (Powder Rim D; fig. 2), our data indicate a general trend of higher cover inside all exclosures. Additionally, crusts remain to be detailed for morphological characteristics or richness as suggested by Rosentreter (this proceedings). Several studies have shown biological soil crusts are negatively impacted by and highly susceptible to livestock trampling (Anderson and others 1982; Beymer and Klopatek 1992; Jeffries and Klopatek 1987; and others). Cover of biological soil crusts was less than 10 percent inside and outside exclosures at all sites even after more than 40 years of domestic livestock removal and do not appear to reflect stocking rate differences among our sites.

Conclusions

The small differences between the inside and outside positions at our nine exclosure sites indicate that some shrubland systems will not necessarily improve to a more productive system after 40 years of livestock exclusion. Our data demonstrate shrub cover will not always increase where stock are excluded at a greater rate than with livestock present. It is clear that the release of grazing pressure does not decrease shrub canopy; in some cases it may allow shrub canopy to increase. In most cases, shrub canopy cover increased comparably with or without domestic grazing livestock use. Explanation for these differential responses to grazing exclusion requires further examination.

References

Anderson, D. C.; Harper, K. T.; Holmgren, K. T. 1982. Factors influencing development of cryptogamic crusts in Utah deserts. Journal of Range Management. 35: 355–359.

Anderson, J. E.; Holte, Karl E. 1981. Vegetation development over 25 years without grazing on sagebrush-dominated rangeland in southeastern Idaho. Journal of Range Management. 34: 25–29.

Archer, S. 1994. Woody plant encroachment into southwestern grasslands and savannas: rates, patterns and proximate causes. In: Vavra, M.; Laycock, W. A.; Pieper, R. D. Ecological implications of livestock herbivory in the West. Denver, CO: Society for Range Management.

Belnap, J.; Gardner, J. S. 1993. Soils microstructure in soils of the Colorado Plateau: the role of cyanobacterium *Microcoleus vaginatus*. Great Basin Naturalist. 53: 40–47.

Beymer, J. D.; Klopatek, J. M. 1992. Effects of grazing on cryptogamic crusts in pinyon-juniper woodlands in Grand Canyon National Park. American Midland Naturalist. 127: 139–148.

Blake, G. R.; Hartge, K. H. 1986. Particle-size analysis. In: Klute, Arnold, ed. Methods of soil analysis. Part 1. Physical and mineralogical methods. Madison, WI: American Society of Agronomy, Inc.

Bock, C. E.; Bock, J. H.; Kenney, W. R.; Hawthorne, V. M. 1984. Responses of birds, rodents, and vegetation to livestock exclosure in a semidesert grassland site. Journal of Range Management. 37: 239–242.

Brady, W. W.; Stromberg, M. R.; Aldon, E. F.; Bohnam, C. D.; Henry, S. H. 1989. Response of a semidesert grassland to 16 years of rest from grazing. Journal of Range Management. 42: 284–288.

Costello, D. F.; Turner, G. T. 1941. Vegetation changes following exclusion of livestock from grazed ranges. Journal of Forestry. 39: 310–315.

Daubenmire, R. F. 1940. Exclosure technique in ecology. Ecology. 21: 514–515.

Donahue, D. 1999. The western range revisited: removing livestock from public land to conserve native biodiversity. Norman: University of Oklahoma Press. 388 p.

Dyksterhuis, E. J. 1949. Condition and management of rangeland based on quantitative ecology. Journal of Range Management. 2: 104–115.

Fisser, H. G. 1967. Exclosure studies with transects of permanent plots. 1965–1966 results. Science Rep. No. 69. Wyoming Agriculture Experiment Station.

Fisser, H. G. 1968. Long term exclosure studies with 2 x 20 ft and 4 x 4 ft permanent plots. 1959–1964 results. Science Rep. No. 131. Wyoming Agriculture Experiment Station.

Fleischner, T. L. 1994. Ecological costs of livestock grazing in Western North America. Conservation Biology. 8: 629–644.

Garcia-Pichel, F.; Belnap, J. 1996. The microenvironments and microscale productivity of cyanobacterial desert crusts. Journal of Phycology. 32: 774–782.

Garland, C. B. 1972. Ecology of arid land vegetation in western Wyoming. Laramie: University of Wyoming. Thesis.

Gdara, A. O. 1977. Interpretation of long term vegetation data from permanent quadrats on semiarid shrublands of western Wyoming. Laramie: University of Wyoming. Thesis.

Holechek, J. L.; Stephenson, T. 1983. Comparison of big sagebrush vegetation in north central New Mexico under moderately grazed and grazing excluded conditions. Journal of Range Management. 36: 455–456.

Jeffries, D. L.; Klopatek, J. M. 1987. Effects of grazing on the vegetation of the blackbrush association. Journal of Range Management. 40: 390–392.

Johnson-Barnard, J. 1995. Long-term vegetation changes at eight exclosures in the arid semi-desert of southwestern Wyoming. Laramie: University of Wyoming. Dissertation.

Kaltenecker, J. H.; Wicklow-Howard, M.; Rosentreter, R. 1999. Biological soil crusts in three sagebrush communities recovering from a century of livestock trampling. In: McArthur, E. D.; Ostler, W. K.; Wambolt, C. L., comps. Proceedings: shrubland ecotones. Proc. RMRS-P-11. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 222–226.

Lang, R. 1973. Vegetation changes between 1943 and 1965 on the shortgrass plains of Wyoming. Journal of Range Management. 26: 407–409.

Robertson, J. H. 1971. Changes on a sagebrush-grass range in Nevada ungrazed for 30 years. Journal of Range Management. 24: 397–400.

Uhlich. J. W. 1982. Vegetation dynamics of non-grazed and grazed sagebrush grassland communities in the Big Horn Basin of Wyoming. Laramie: University of Wyoming. Thesis.

Vavra, M.; Laycock, W. A.; Pieper, R. D., eds. 1994. Ecological implications of livestock herbivory in the West. Denver, CO: Society for Range Mangement.

West N. E.; Provenza, F. D.; Johnson, P. S.; Owens, M. K. 1984. Vegetation change after 13 years of livestock grazing exclusion on sagebrush semidesert in west central Utah. 37(3): 262–264.

Species Richness Inside and Outside Long-Term Exclosures

W. A. Laycock
D. L. Bartos
K. D. Klement

Abstract: Recent environmental literature contains claims that livestock grazing has caused reduction in species diversity on Western rangelands. Data of species richness (number of species) is presented from inside and outside 24 long-term exclosures in Montana, Utah, and Wyoming. For the average of all exclosures there was no difference between species richness inside and outside the exclosures. Overlap of species (those found both inside and outside of the exclosures) was high (69 to 72 percent), and the species found either inside only or outside only did not reveal any trend related to grazing or successional status. The areas inside and outside eight exclosures in Wyoming were sampled in 2 successive years. Growing season moisture was above normal the first year and far below normal the second. Species richness sampled was more than 40 percent lower in the second year than in the first. The rather small difference in species richness inside and outside all of the exclosures indicates that neither grazing nor lack of grazing has much long-term influence on species richness. However, growing season moisture can greatly influence how many species are encountered when sampling an area.

Introduction

Some conservation biology and environmental literature contains claims that livestock grazing has caused and continues to cause reduction in species diversity on Western rangelands: Livestock have greatly lowered plant diversity in most of the West (Jacobs 1991). One of the ecological costs of livestock grazing is the "reduction of species richness" (Fleischner 1994). Livestock grazing is the most insidious and pervasive threat to biodiversity on rangelands (Noss and Cooperrider 1994). Livestock grazing has altered and diminished the presettlement diversity of native fauna and flora on many Western rangelands (Donahue 1999). Ehrlich (1990), Wuerthner (1990), and Noss (1994) made similar statements. Wuerthner (1994) lumped farming and pastoralism (grazing) together and suggested that agriculture is the most serious threat to biodiversity in the Western United States. In most of these publications, only anecdotal information was presented to back up the claims that grazing reduces species diversity.

Authors have not always clearly defined terms (like biodiversity, diversity, and species diversity) used in their publications. Because of this, some definition of terms may be useful at this point. West (1993) defined "biological diversity" (or "biodiversity") as:

> ...the variety of life and its processes, including the variety of living organisms, the genetic differences among them, the communities, ecosystems and landscapes in which they occur, plus the interactions of these components.

This definition specifically includes diversity at the genetic, species, community, or ecosystem and landscape or regional level. In a later publication, West (1995) suggested that the culture and indigenous knowledge of local people engaged in sustainable lifestyles should also be added to the definition of biodiversity.

Species diversity is usually expressed in one of two ways: richness, which is the number of species present in an area; and evenness or equitability, which is a measure of the abundance of each species present (West 1993). This paper deals with only one element of diversity, that is, that of plant species richness.

This paper compares species richness (number of plant species) inside and outside 24 long-term exclosures in Utah, Wyoming, and Montana. Only species richness is reported because the data were collected by different methods in each area and, in some cases, species lists were pooled from more than one sampling method, and species evenness or other indices of diversity could not be calculated. Species richness inside and outside the eight exclosures in Wyoming also was compared over 2 years with substantially different amounts of growing season precipitation. This illustrated how such precipitation can influence the number of species encountered in sampling.

Methods

The central Utah study included eight exclosures with quaking aspen (*Populus tremuloides*) vegetation communities. One exclosure was established in 1934, and the other seven were established between 1947 and 1974. The exclosures ranged in size from 0.3 to 1.0 ha. Cover of understory vegetation by species was estimated on 0.1-m^2 quadrats in 1995 or 1996. Overstory tree species were not included in the species richness numbers unless the tree species occurred in

---

In: Hild, Ann L.; Shaw, Nancy L.; Meyer, Susan E.; Booth, D. Terrance; McArthur, E. Durant, comps. 2004. Seed and soil dynamics in shrubland ecosystems: proceedings; 2002 August 12–16; Laramie, WY. Proceedings RMRS-P-31. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

W. A. Laycock is a Rangeland Consultant, 3415 Alta Vista Drive, Laramie, WY 82072, U.S.A.; e-mail: blaycock@wyoming.com. D. L. Bartos is a Range Scientist, Rocky Mountain Research Station, USDA Forest Service, Logan, UT. K. D. Klement is a Rangeland Support Scientist, USDA Agricultural Research Service, Miles City, MT.

the understory. The overall comparisons for these exclosures were published by Kay and Bartos (2000), but the species richness data for each individual exclosure were obtained from file data.

In southwestern Wyoming, eight exclosures in sagebrush (*Artemisia tridentata* ssp. *Wyomingensis*) and/or salt desert shrub vegetation communities were studied. One was established in 1940, and the other seven exclosures were established between 1958 and 1963. The exclosures were either 0.4 or 0.8 ha in size. For shrubs, cover by species was sampled with line and belt transects. Herbaceous species were sampled with a point frame and density counts on 1.2-m^2 quadrats. Species lists from the various methods were pooled to calculate species richness. The same sampling methods were repeated by the same observer in 1993 and 1994. The species richness information for these exclosures were obtained from Johnson-Barnard (1995).

The southwestern Montana study included eight high-elevation exclosures: three in tall forb, three in open conifer, and two in mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) vegetation communities. Seven exclosures are 15.0 m^2 (0.02 ha) and were established in 1978. One of the open conifer exclosures is 0.09 ha in size and was established in 1960. For the open conifer type, only understory species were sampled, and the mature overstory tree species are not included in the number of species. Herbage production (biomass) by species was estimated in 1994 on 1.0-m^2 quadrats for sagebrush and 0.5-m^2 quadrats for other vegetation types. The species richness data for these exclosures were obtained from Klement (1997) and from file data.

All 24 exclosures had been protected from livestock grazing all or a majority of the time since establishment. The areas outside the exclosures had been grazed by livestock during the same seasonal period in each respective location: by cattle and/or sheep during the summer in Utah; by cattle and/or sheep either in summer or year round in Wyoming; and by sheep only during the summer in Montana. All areas were available for wildlife use. Plant species nomenclature follows that was used in each individual study.

Results and Discussion

Aspen Exclosures (Utah)

The understory plant communities in the aspen exclosures were not especially species-rich and had the fewest number of species of all the vegetation types studied (table 1). The average number of species detected by sampling was about the same both inside (9.3) and outside (9.1) the exclosures. Two exclosures had the most species found inside (12) and two different exclosures had the most species found outside (11). Three exclosures had more species inside the exclosure than outside, and four exclosures had more species outside the exclosure than inside. One exclosure had the same numbers of species inside and outside (table 2).

A total of 12 species were found inside one or more of the eight exclosures but not outside. Twelve species were found outside one or more of the eight exclosures but not inside (table 3). *Bromus ciliatus* and *Sitanion hystrix* were found inside but not outside at two exclosures, but these species were found both inside and outside at four other exclosures. All other species were found either inside only or outside only at just one exclosure.

The overlap of species, that is, the number of species found both inside and outside, averaged 7.5 species (69 percent) for

Table 1—Average number of plant species inside and outside aspen, shrub, and high-elevation exclosures.

		Vegetation type					
				High elevation (Montana)			
Location	Life form	Aspen (Utah)	Shrub (Wyoming)	Tall forb	Sagebrush	Open conifer	All exclosures
		Average number of species					
Inside exclosure	Shrub	1.9	7.0	0	2.5	0.3	0.8
	Grass	4.4	4.4	6.7	5.5	8.7	7.1
	Forb	3.0	2.6	27.7	21.5	22.0	24.0
	Total	9.3	14.0	34.4	29.5	31.0	31.9
Outside exclosure	Shrub	2.6	7.2	0	2.0	0	.5
	Grass	3.5	4.9	7.3	5.5	12.3	8.8
	Forb	3.0	2.4	29.0	24.5	25.7	26.6
	Total	9.1	14.5	36.3	32.0	38.0	35.9

Table 2—Number of exclosures with different numbers of species inside or outside for each vegetation type.

	Vegetation type					
			High elevation			
Location of different numbers of species	Aspen	Shrub	Tall forb	Sagebrush	Open conifer	All exclosures
	Number of exclosures					
More species inside than outside	3	3	1	0	0	1
More species outside than inside	4	4	2	2	3	7
Same number of species inside and outside	1	1	0	0	0	0

Table 3—Species found either inside or outside, but not both, for the eight aspen exclosures in Utah.

Species inside but not outside
Shrubs
- *Chrysothamnus viscidiflorus*

Grasses and grasslike
- *Bromus ciliatus*
- *Festuca idahoensis*
- *Festuca thuberi*
- *Sitanion hystrix*
- *Stipa comata*
- *Stipa lettermanii*

Forbs
- *Aquilegia coerula*
- *Galium* spp.
- *Potentilla gracilis*

Total species
- Inside but not outside = 12

Species outside but not inside
Shrubs
- *Artemisia tripartita*
- *Juniperus comunis*
- *Juniperus osteosperma*
- *Pushia tridentata*
- *Rosa woodsii*
- *Symphoricarops oreophilus*

Grasses
- *Muhlenbergia wrightii*
- *Poa pratensis*

Forbs
- *Antennaria microphylla*
- *Castilleja linariafolia*
- *Taraxacum officinale*

Total species
- Outside but not inside = 12

the eight exclosures (table 4). The lowest overlap was 58 percent, and the highest was 90 percent.

Species richness inside and outside the exclosures was almost identical and did not reveal any grazing effect. However, Kay and Bartos (2000) indicated that understory species composition of the aspen stands studied had been affected by ungulate herbivory. In the area available to mule deer but excluding livestock, tall forbs and shrubs were reduced, while grasses and unpalatable forbs increased. Cattle grazing tended to reduce grass cover. Both livestock and deer browsing affected aspen regeneration; aspen regenerated successfully in the livestock exclosure and combined use plots outside the exclosures only when mule deer populations were low. The species richness data did not reflect these composition changes in the vegetation in response to use by cattle and deer.

The aspen exclosures tended to be on drier sites, which may partially explain the low number of plant species sampled. A more detailed study of two aspen exclosures in Utah was published by Mueggler and Bartos (1977). One of these exclosures, Big Flat, was also sampled in 1995–1996 and was included in the Kay and Bartos (2000) study.

Shrub Exclosures (Wyoming)

The average number of species sampled was similar inside (14.0) and outside (14.5) the exclosures (table 1). Approximately half of the species were shrubs. The largest number of species found both inside and outside was 18 at different exclosures. More species were found inside the exclosure than outside at three exclosures, more species were found outside than inside at four exclosures, and the same number of species occurred inside and outside one exclosure (table 2).

When all eight exclosures were combined, 17 species were found inside but not outside a given exclosure, and 19 species were found outside but not inside. Most species were found only inside or only outside the exclosure at just one site, but one species was found inside only at two sites, one species was found outside only at two sites, and two species were found outside only at three sites.

One forb and two wheatgrass species were found inside only at one site and outside only at a different site. Five other forb species were found inside only at one exclosure, and one other forb species was found outside only at three exclosures. Two species of shrubs were found inside the exclosure only at one site and outside the exclosures only at two different sites. Six other species of shrubs were found inside one or more exclosures only but not outside, while seven completely different shrub species were found outside one or more exclosures only but not inside. Other than two wheatgrasses, no other grasses were found inside only, but five additional grass species were found outside only at one exclosure. The average overlap of species found both inside and outside was 11.9 species or 72 percent (table 4). The highest overlap of species occurring inside and outside the same exclosure was 83 percent, and the lowest overlap was 56 percent.

The number of species found either inside the exclosures only or outside only did not give any indication that grazing had a different effect on the vegetation of these shrub exclosures than 35 years of protection from grazing. Johnson-Barnard (1995) found no observable effect of grazing on cover, density, production, or species composition of shrub or

Table 4—Plant species overlap—average number of species per exclosure in common (present both inside and outside), found inside exclosures only and found outside exclosures only for the three vegetation types.

	Vegetation type					
			High elevation (Montana)			
	Aspen (Utah)	**Shrub (Wyoming)**	**Tall forb**	**Sagebrush**	**Open conifer**	**All exclosures**
	Number of species (percent)					
Species in common	7.5 (69)	11.9 (72)	30.7 (77)	26.0 (73)	26.7 (63)	28.0 (70)
Inside but not outside	1.8 (16)	2.1 (13)	3.7 (9)	3.5 (10)	4.3 (10)	3.8 (10)
Outside but not inside	1.6 (15)	2.6 (15)	5.7 (14)	6.0 (17)	11.3 (27)	7.9 (20)

herbaceous species for these exclosures. The only consistent difference between inside and outside was that shrub height was significantly (P = 0.05) greater inside all of the exclosures.

High-Elevation Exclosures (Montana)

The high-elevation exclosures in Montana had greater species richness than the Utah and Wyoming vegetation types sampled, averaging more than 30 species both inside and outside the exclosures (table 1). A great many of the species of grasses and forbs were the same in all three vegetation types for the high-elevation exclosures. The percentage of the total number of species made up by forbs was 68 to 81 percent for all of the vegetation types (table 1) (Klement 1997).

In the tall forb type, the highest number of species was 39 inside two exclosures and 42 outside one of the same exclosures. In the mountain big sagebrush type, one exclosure had 30 species inside and 32 species outside. This mountain big sagebrush type had more than twice the total number of species as the lower elevation Wyoming big sagebrush exclosures sampled in Wyoming.

In the open conifer type, the highest number of species was 41 outside and 38 inside the same exclosure. For all vegetation types, more species occurred outside than inside at seven of the exclosures (table 2), with an average of four more species outside. One of the tall forb exclosures had three more species inside than outside.

In spite of the rather large numbers of species found only inside or only outside the exclosures, the overlap (species found both inside and outside a given exclosure) was rather high for all of the high-elevation exclosures, ranging from an average 26.0 to 30.7 species in common, with an average overlap of 70 percent (table 4).

Even though more species generally were found outside of the exclosures than inside, species richness did not reveal any major differences in vegetation composition between the inside and the outside the exclosures in all three vegetation types. This agrees with Klement (1997) who, based on the biomass data, concluded that light summer grazing by sheep does not appear to be a factor in vegetation composition in these high-elevation vegetation types.

Effect of Growing Season Precipitation on Species Richness

The areas inside and outside the eight sagebrush and salt desert shrub exclosures in Wyoming were sampled by the same methods by the same observer in both 1993 and 1994. The 1994 data were summarized above. Late spring and early summer precipitation (May through July) from the nearest weather station (Kemmerer, WY) indicated that growing season precipitation in the 2 years were quite different. The long-term average for that period was 7.39 cm. Growing season precipitation was 31 percent above this average (9.70 cm) in 1993 and 73 percent below this average (2.77 cm) in 1994.

As might be expected, the number of shrub species sampled inside and outside were the same in 1993 and 1994. However the total number of herbaceous species sampled was 41 percent lower in 1994 than in 1993 (table 5) and the changes were similar both inside and outside the exclosures. The largest reduction in number of species was for forbs. The number of annual forb species sampled was 69 percent lower inside and 84 percent lower outside in 1994 than in 1993. The number of perennial forb species sampled was 48 percent lower inside and 45 percent lower outside. The reduction in number of grass species sampled in 1994 was smaller, 30 percent lower inside and 28 percent lower outside.

The species that were not found in 1994 presumably did not disappear from the community. The annual forb species may simply not have germinated in the dry conditions of 1994. The perennial forbs may have grown earlier when soil moisture was present but dried and were absent or unrecognizable at the time of sampling. The grass species absent in 1994 may have had so little growth that they were not recognizable at the time of sampling. The important point is that sampling in a year with low growing season precipitation can result in a lower number of species being detected than would be detected in a more favorable year. The 22 species that were present in 1993, but absent in 1994, inside exclosures at one or more sites and outside exclosures at one or more sites are listed in table 6.

Similar changes in numbers of species sampled as a result of differences in precipitation have been reported. On northern mixed grass prairie in North Dakota, Biondini and others (1998) reported an increase in the number of forb species sampled from 14 in 1988 at the end of a prolonged drought to 36 in 1995 after several years of above average precipitation. These changes occurred in pastures grazed moderately and heavily by cattle and also in exclosures. At the Cedar Creek Natural History Area in Minnesota, Tilman and El Haddi (1992) reported that the local species richness of four different grassland fields decreased an average of 37 percent during a 1988 drought. However, despite the return to more normal precipitation during the

Table 5—Sagebrush and salt desert shrub exclosures in Wyoming. Changes in richness of herbaceous species in 2 years with different precipitation.

Life form	1993 Inside	1993 Outside	1994 Inside	1994 Outside	1993–1994 change Inside	1993–1994 change Outside
	Average number of species					
Grass	6.3	6.8	4.4	4.9	–1.9	–1.9
Perennial forb	4.0	3.8	2.1	2.1	–1.9	–1.7
Annual forb	1.6	1.9	.5	.3	–1.1	–1.6
Total	11.9	12.5	7.0	7.3	–4.9	–5.2

Table 6—Sagebrush and Salt Desert Shrub Exclosures in Wyoming. Herbaceous species found in 1993 but not in 1994 inside exclosures at one or more different sites and outside exclosures at one or more different sites.

	Number of exclosures	
	Inside	Outside
Grasses		
Agropyron dasystachyum	5	6
Agropyron smithii	2	1
Agropyron spicatum	3	1
Oryzopsis hymenoides	1	1
Poa spp.	3	1
Poa canby	1	1
Poa fendleriana	1	1
Poa secunda	1	1
Sitanion hystrix	3	4
Stipa comata	1	2
Perennial forbs		
Allium textile	1	4
Antennaria dimorpha	2	2
Astragalus convallarius	1	1
Cryptantha fendleri	1	1
Eriogonum flavum	1	1
Eriogonum ovalifolium	1	1
Phlox hoodii	3	2
Phlox longifolia	3	3
Annual forbs		
Astragalus spp.	2	3
Descurainia pinnata	1	1
Halogeton glomeratus	1	1
Lappula redowskii	2	4

next 2 years, there was no significant recovery of species richness in the permanent plots. They concluded that "environmentally extreme conditions can limit species richness by causing the local extinction of rare species." However, they did not present long-term data to indicate that rare species had, indeed, become extinct in their permanent plots.

Conclusions

Because the sampling methods employed in this study were not primarily intended to compile a complete list of all species in the area, not every species present inside or outside each exclosure would have been encountered. To compile a comprehensive species list would have required sampling at different times during the growing season and additional searches for rare species outside the sample quadrats or lines. However, because the vegetation at each exclosure site was sampled by the same person, using the same methods and at the same time both inside and outside of each exclosure, comparisons of species richness between the two areas should be valid.

Species richness, by itself, may or may not be a good indicator of the effects of grazing on vegetation, depending on the situation. For the shrub areas in Wyoming and the high-elevation areas in Montana, the lack of difference in species richness inside and outside the exclosures agreed with the conclusions from analysis of cover or biomass data, that is, the vegetation inside and outside the exclosures was not different. However, for the aspen areas in Utah, the cover data revealed some differences caused by grazing or browsing by livestock or deer that the species richness comparison did not reveal.

The rather large impact that weather, mainly growing season precipitation, can have on the number of species encountered in a sample was shown by comparing samples taken in 2 successive years in Wyoming. The number of herbaceous species sampled in the dry summer of 1994 was more than 40 percent lower than the number sampled in the relatively wet summer of 1993. The majority of the species that were present in 1993 but not in 1994 were perennials that had not disappeared from the area. They either did not grow in 1994, or they may have been indistinguishable during sampling because they were too small or unidentifiable.

Collins (1987) reported that areas of tall grass prairie both burned and moderately grazed by cattle had the highest plant species diversity, while areas burned but not grazed had the lowest diversity. On shortgrass steppe vegetation in Colorado, Hart (2001) found that plant species diversity and evenness were greatest in lightly and moderately grazed pastures, least in exclosures, and intermediate in heavily grazed pastures. These pastures had been grazed by cattle at the same intensities for 55 years, and the exclosures had been protected from grazing during the same period.

Laycock (1994) suggested that either no grazing or very heavy grazing may reduce species diversity, but moderate grazing probably does not diminish diversity and may enhance diversity at both the species and landscape levels by promoting patchiness of vegetation.

Oba and others (2000) reviewed literature from African rangelands that suggested that grazing at moderate intensities on Mediterranean, sub-Saharan, and other subtropical rangelands increased plant species diversity and that, on Sahelan rangelands, neither continuous grazing nor long-term protection had a lasting effect on plant species diversity. Oba and others (2000) concluded that:

> Thus, the evidence suggests that the lack of grazing may degrade rangelands in sub-Saharan Africa. Long-term deferral of grazing results in either no significant changes in species composition or in lowered diversity caused by the disappearance of herbivory-adapted species. Therefore, if the removal of ungulate grazing results in the loss of principal species from the plant community, then this ecosystem may be considered to have been degraded in the absence of grazing.

The results of the present study agreed with published information summarized above that moderate livestock grazing does not cause plant species richness to decline. Thus, the claims that livestock grazing has reduced plant species richness on Western rangelands appear to be without merit at least for the vegetation types studied on these 24 sites.

Studies need to be conducted on many more rangeland vegetation types to determine the effects of livestock grazing on species richness or other elements of biodiversity. Previous studies have the potential to provide such information, but species richness or other measures of species diversity usually cannot be calculated from published results of grazing or exclosure studies because journals seldom allow the publication of complete species lists and often lump minor species as “Other.” Complete lists can be obtained from file data for previous studies or from complete species lists in unpublished theses or dissertations.

References

Biondini, M. E.; Patton, B. D.; Nyren, P. E. 1998. Grazing intensity and ecosystem processes in a northern mixed-prairie, USA. Ecological Applications. 8: 469–479.

Collins, S. L. 1987. Interaction of disturbances in tallgrass prairie: a field experiment. Ecology. 68: 1243–1250.

Donahue, D. 1999. The Western range revisited: removing livestock from public lands to conserve native biodiversity. Norman: University of Oklahoma Press. 388 p.

Ehrlich, P. R. 1990, Habitats in crisis: why should we care about loss of species: Forest Ecology and Management. 35: 5–11.

Fleischner, T. L. 1994. Ecological costs of livestock grazing in Western North America. Conservation Biology. 8: 629–644.

Hart, R. H. 2001. Plant biodiversity on shortgrass steppe after 55 years of zero, light, moderate or heavy cattle grazing. Plant Ecology. 155: 111–118.

Jacobs, L. 1991. Waste of the West: public lands ranching. Tucson, AZ: Lynn Jacobs. 602 p.

Johnson-Barnard, J. 1995. Long term vegetation changes at eight exclosures in the arid semi-desert of southwestern Wyoming. Laramie: University of Wyoming, Department of Rangeland Ecology and Watershed Management. Dissertation.

Kay, C. E.; Bartos, D. L. 2000. Ungulate herbivory on aspen communities on Utah aspen: assessment of long-term exclosures. Journal of Range Management. 53: 145–153.

Klement, K. D. 1997. Condition and trend analysis on subalpine rangeland grazed by sheep in the Centennial Mountains, Montana. Laramie: University of Wyoming, Department of Rangeland Ecology and Watershed Management. Thesis.

Laycock, W. A. 1994. Implications grazing vs. no grazing on today’s rangelands. In: Vavra, M.; Laycock, W. A.; Pieper, R. D., eds. Ecological implications of livestock herbivory in the West. Denver, CO: Society for Range Management: 250–288.

Noss, R. F. 1994. Cows and conservation biology. Conservation Biology. 8: 613–616.

Noss., R. F.; Cooperrider, A. Y. 1994. Saving nature’s legacy: protecting and restoring biodiversity. Washington, DC: Island Press.

Oba, G.; Stenseth, N. C.; Lusigi, W. J. 2000. New perspectives on sustainable grazing management in arid zones of sub-Saharan Africa. BioScience. 50: 35–51.

Tilman, D.; Haddi, A. El. 1992. Drought and biodiversity in grasslands. Oecologia. 89: 257–264.

West, N. E. 1993. Biodiversity of rangelands. Journal of Range Management. 46: 2–13.

West, N. E. 1995. Biodiversity on rangelands: definitions and values. In: West, N. E., ed. Biodiversity on rangelands. Logan: Utah State University, College of Natural Resources. Natural Resources and Environmental Issues. Volume IV: 1–4.

Wuerthner, G. 1990. The price is wrong. Sierra. (September): 38–43.

Wuerthner, G. 1994. Subdivision versus agriculture. Conservation Biology. 8: 905–908.

Vegetation Management for Sagebrush-Associated Wildlife Species

J. Kent McAdoo
Sherman R. Swanson
Brad W. Schultz
Peter F. Brussard

Abstract: It is obvious that the diverse array of wildlife species using sagebrush habitats has a similarly wide range of habitat requirements. Vegetation management for biological diversity on a landscape scale should take these diverse habitat requirements into consideration. Management for any one species may or may not provide the habitat requirements for other species. Creating a mosaic of habitats with multiple-aged stands of sagebrush and varying degrees of herbaceous and shrub cover would provide the diverse vertical and horizontal vegetation composition and structure required by diverse wildlife species.

Introduction

The sagebrush (*Artemisia* spp.)-dominated area of the West encompasses approximately 155.5 million acres (Paige and Ritter 1999). More specifically, there are two major regions of sagebrush dominance (West 1983a,b): (1) the "sagebrush steppe" that covers the northern portion of the Intermountain Region from eastern Washington and northern Nevada to the western two-thirds of Wyoming and northwest Colorado, and (2) the "sagebrush semidesert," the drier Great Basin sagebrush region that includes most of Nevada, parts of Utah and northern Arizona, and some areas of southwestern Colorado and northern New Mexico. The sagebrush semidesert is significantly drier and warmer than the sagebrush steppe and occurs between the sagebrush steppe and the drier salt-desert shrub region. Although sagebrush communities have undergone much change in modern history, the boundaries of sagebrush distribution have remained fairly constant.

Vale (1974) examined 29 historic journals and diaries from the early 19th century and concluded that presettlement vegetation in much of the Intermountain West was visually dominated by shrubs, with much of the area covered by thick brush stands. However, according to Miller and Eddleman (2001), fire influences caused plant composition to vary from dominant stands of sagebrush to grasslands. The authors speculated that much of the sagebrush steppe ecosystem during pre-settlement times was composed of open shrub stands with a substantial herbaceous cover component. Extreme weather conditions and insect outbreaks also affected the historic patterns of vegetation composition in sagebrush habitats.

Sagebrush-grass communities within these sagebrush regions vary markedly (Miller and Eddleman 2001; Tisdale and Hironaka 1981; West 1983a,b), but to one degree or another provide food, thermal cover, escape routes, and rearing sites for a variety of vertebrate wildlife species (McAdoo and Klebenow 1979). Some of these species inhabit sagebrush habitats year round, while others use them only seasonally or occasionally. Species that require sagebrush for some part of their life cycle are "sagebrush obligates." According to Paige and Ritter (1999), at least eight vertebrate species are considered to be sagebrush obligates: sage sparrow (*Amphispiza belli*), Brewer's sparrow (*Spizella breweri*), sage thrasher (*Oreoscoptes montanus*), sage grouse (*Centrocercus urophasianus*), pygmy rabbit (*Sylvilagus idahoensis*), sagebrush vole (*Lagurus curtatus*), pronghorn antelope (*Antilocapra americana*), and sagebrush lizard (*Sceloporus graciosus*). However, the latter species is also found in greasewood (*Sarcobatus* spp.) habitats (McAdoo and Klebenow 1979) and may not be a true "obligate." In parts of their range, gray flycatchers (*Empidonax wrightii*) and least chipmunks (*Eutamias minimus*) may also be considered sagebrush obligates. A number of other species have a broader amplitude of habitat adaptation, occurring not only in sagebrush but in other vegetation types as well. Sagebrush communities provide habitat for approximately 100 bird species and 70 mammal species (Braun and others 1976). Several species of lizards and snakes also inhabit these sagebrush areas (Fautin 1946).

Grazers, browsers, and seedeaters foraging within sagebrush- grass communities use the grasses, forbs, sagebrush, and/or other shrub species found there. In turn, many of

---

In: Hild, Ann L.; Shaw, Nancy L.; Meyer, Susan E.; Booth, D. Terrance; McAruthur, E. Durant, comps. 2004. Seed and soil dynamics in shrubland ecosystems: proceedings; 2002 August 12–16; Laramie, WY. Proceedings RMRS-P-31. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

J. Kent McAdoo is Area Rangeland Resources Specialist, University of Nevada Cooperative Extension, 1500 College Parkway, Elko, NV 89081, U.S.A., phone: (775) 738-7291; e-mail: mcadook@unce.unr.edu. Sherman R. Swanson is Professor of Range Science, University of Nevada-Reno, Reno, NV; Brad W. Schultz is Extension Educator, University of Nevada Cooperative Extension, Winnemucca, NV. Peter F. Brussard is Professor of Biology, University of Nevada-Reno, Reno, NV.

Authors' note: Portions of this paper have been previously presented and included as an expanded abstract in the non-peer-reviewed proceedings of the Restoration and Management of Sagebrush/Grass Communities Workshop, November 4–8, 2002, Elko, NV.

these species, including ungulates, rodents, hares and rabbits, small birds, reptiles, and insects are important as prey for predatory species living in or near sagebrush-grass communities.

Habitat Requirements of Sagebrush Obligates

Because of a West-wide decline in sage grouse populations and habitat, the sage grouse has been petitioned for listing as threatened or endangered, and much political attention has therefore been focused on this species. Sage grouse historically inhabited much of the western United States, including portions of 16 States and along the southern border of three western Canadian Provinces. This distribution closely parallels the range of sagebrush communities. The current core of sage grouse populations includes areas of Nevada, Oregon, Idaho, Colorado, Wyoming, and Montana, with remnant populations in other States. These birds require sagebrush for food and/or cover during each stage of their life cycle (Connelly and others 2000; Klebenow 2001). Although sage grouse depend on sagebrush vegetation for survival, they thrive best in areas with a mixture of sagebrush species, varying in age and cover classes. Optimal habitat includes a heterogeneous combination of diverse sagebrush communities, in other words, sagebrush stands with varying shrub heights and canopy cover and a diverse understory of perennial grasses and forbs. The proportion of sagebrush, perennial grasses, and forbs in an area varies with the species or subspecies of sagebrush, the ecological potential of the site, and condition of the habitat (Klebenow 2001). During the course of a year, sagebrush is quantitatively the most important component in the diet of sage grouse, comprising 60 to 80 percent of all food consumed. However, during spring and summer these birds (especially the juveniles) shift from a sagebrush-dominated diet to one of forbs and insects (Klebenow and Gray 1968).

Habitat requirements differ among the other sagebrush obligates. Sage sparrows, Brewer's sparrows, and sage thrashers all require sagebrush for nesting, with nests typically located in the sagebrush canopy. Sage thrashers usually nest in tall dense clumps of sagebrush within areas having some bare ground for foraging. Sage sparrows prefer large continuous stands of sagebrush, and Brewer's sparrows are associated closely with sagebrush habitats having abundant scattered shrubs and short grass (Page and Ritter 1999).

Pygmy rabbits live in areas with clumps of tall sagebrush in friable soils, whereas pronghorn antelope prefer lower growing sagebrush, presumably because of their keen eyesight adapted for detecting danger at long distances. Like sage grouse, both pygmy rabbits and pronghorns typically eat sagebrush almost exclusively during winter (Page and Ritter 1999). However, pronghorns depend primarily on forbs during much of the year. Sagebrush voles feed on green herbaceous plants in summer. They use the shredded bark of sagebrush to line their burrows and eat the bark and twigs of sagebrush during winter. Sagebrush lizards prey on insects found in sagebrush habitat, often climbing the shrubs in search of their prey.

Habitat Requirements of Other Sagebrush-Associated Species

Habitat requirements differ widely among other bird species associated with sagebrush grass communities. Some species, such as loggerhead shrikes (*Lanius ludovicianus*), nest primarily in the canopy of sagebrush and other shrubs. Others are primarily open ground and/or grass nesting species, requiring varying amounts of herbaceous cover. Such species include horned larks (*Eremophila alpestris*), vesper sparrows (*Pooecetes gramineus*), and western meadowlarks (*Sturnella neglecta*). Other species, like lark sparrows (*Chondestes grammacus*), are typically most abundant in areas with a diverse mixture of sagebrush and bunchgrass (McAdoo and Klebenow 1989). Horned larks and burrowing owls (*Athene cunicularia*) are adapted to more open areas, and both species often increase after wildfire or other disturbances that reduce dense sagebrush canopies.

In addition to pronghorn antelope, other ungulate big game species are dependent on sagebrush-grass communities to some extent. Mule deer (*Odocoileus hemionus*) are closely associated with sagebrush-grass communities in much of their range. Being primarily browers, any successional vegetation changes favoring shrubs may benefit mule deer populations. Many forbs and shrubs associated with sagebrush communities are important in mule deer diets, with grasses used primarily in spring. Forb use is highest in summer, and on many mule deer ranges, big sagebrush is the staple component in winter and early spring (Kufeld and others 1973). Elk (*Cervus elaphus*) generally depend on grasses for forage throughout much of their range, but they also eat shrubs, including big sagebrush, especially during fall and winter (Kufeld 1973). In parts of the Great Basin, elk use sagebrush-dominated habitats in other seasons as well. Bighorn sheep (*Ovis canadensis* spp.) also use sagebrush-grass communities in some areas, especially as winter range. Although grasses are typically the major component in the bighorn sheep diet, shrubs are important, and big sagebrush is a preferred shrub (McQuivey 1978).

Five species of hares and rabbits may occur in sagebrush-grass communities. The most common species in most areas is the black-tailed jackrabbit (*Lepus californicus*), an opportunistic feeder that selects for succulence. Blacktailed jackrabbits eat primarily grasses and forbs until winter, when they feed on shrubs, including the leaves and bark of big sagebrush. During population highs, this species can cause considerable damage to rangeland vegetation and cultivated crops (McAdoo and others 1987). Within sagebrush-grass habitats, blacktailed jackrabbits are typically associated with increasing shrub cover, whereas whitetailed jackrabbits (*L. townsendii*) are associated with increasing grass cover (Verts and Carraway 1998). Pygmy rabbits have already been identified (above) as sagebrush obligates. Two other rabbit species, desert cottontails (*Sylvilagus audubonii*) and mountain cottontails (*S. nuttallii*), are also found in some sagebrush-grass habitats.

Many rodent species (at least 28) inhabit sagebrush-grass communities, with the deer mouse (*Peromyscus maniculatus*) being typically most common. Unlike the sagebrush vole that was mentioned above as a sagebrush obligate, deer mice occur in a wide variety of vegetation types. Great Basin pocket mice (*Perognathus parvus*) are restricted primarily to sagebrush habitats in some areas (McAdoo and Klebenow 1979). Most rodent species are herbivores or granivores, but differ in specific habitat affinities. Rodents in general have a reputation for negative impacts on rangelands, but some species, such as kangaroo rats (*Dipodomys* sp.), can be quite beneficial in terms of seed dispersal and germination (McAdoo and others 1983).

At least nine bat species may be found within sagebrush habitats, but are more closely associated with caves, rock crevices, and water sources. The Merriam's shrew, an insect-eater, is sometimes a relatively common small mammal species in sagebrush basins (Ports and McAdoo 1986). Western rattlesnakes, gopher snakes, leopard lizards, horned lizards, and other reptiles also make their homes in sagebrush habitat, but amphibians are found only near water sources that may be surrounded by sagebrush or other upland habitat.

Although several mammalian predators use sagebrush habitats in search of prey, none are exclusively linked to sagebrush. The most common predator species using sagebrush habitats include coyotes, badgers, long-tailed and short-tailed weasels, bobcats, and mountain lions.

Vegetation Management Implications

Because habitat requirements for the many wildlife species in sagebrush-grass communities differ by species and even vary by season of use for many species, the spatial and temporal variability of sagebrush habitats becomes important in vegetation management. Before European settlement, "spotty and occasional wildfire probably created a patchwork of young and old sagebrush stands across the landscape, interspersed with grassland openings, wet meadows, and other shrub communities" (Paige and Ritter 1999). In drier regions, such as lower elevations in the Great Basin (that is, the sagebrush semidesert), fire probably had less influence. According to Miller and Eddleman (2001):

> The Wyoming big sagebrush and low sagebrush cover types, with less frequent disturbance events but slower recovery rates, and the mountain big sagebrush cover type, with more frequent disturbance but faster recovery rates, created a mosaic of multiple seral stages across the landscape. In addition, fire patterns were patchy, leaving unburned islands, particularly in Wyoming big sagebrush cover types because of limited and discontinuous fuels. Plant composition ranged from dominant stands of sagebrush to grasslands.

The authors went on to say that much of the sagebrush steppe ecosystem during presettlement times was probably composed of open shrub stands with a substantial component of long-lived perennial grasses and forbs.

The wildlife sightings by early explorers were a function of landscape ecology, the explorers' season of travel, and the time interval since the last fire. Based on anecdotal accounts, species like sage grouse seemed to be locally abundant, but regionally rare. According to Miller and Eddleman (2001), the range occupied by sage grouse is spatially diverse and temporally dynamic. By inference, since sage grouse distribution closely parallels the range of sagebrush communities in North America, the same principle holds for other sagebrush-associated vertebrate wildlife species. Inherent site potential, combined with such variables as the interspersion of varying shrub height and canopy cover, as well as herbaceous species composition, cover, and diversity, influence the regional diversity of wildlife species, the landscape level distribution of these species, and the local abundance of each species. Nothing, however, remains constant over time.

We can draw some inferences from the effects of sagebrush-grass community alteration on neotropical migrants (songbirds). Research conducted in northern and central Nevada (McAdoo and others 1989) showed that sagebrush removal from large acreages had initially negative impacts on shrub-nesting birds, especially sagebrush obligates such as sage thrashers, sage sparrows, and Brewer's sparrows. In those areas where crested wheatgrass (*Agropyron desertorum*) was planted after shrub removal, a corresponding increase was observed in ground and grass-nesting species like horned larks, western meadowlarks, and lark sparrows. However, as successional establishment of sagebrush occurred in these areas over time, shrub-nesting bird species returned and grass-nesting species remained. Bird species diversity increased as the complexity of the plant community increased (McAdoo and others1989). What are the implications of these bird population responses for wildlife species in general as related to sagebrush habitat management?

There exists an enormous challenge throughout much of the Intermountain West to revegetate large expanses of cheatgrass (*Bromus tectorum*) monocultures with native sagebrush-grass-forb communities that will support diverse wildlife communities. However, another habitat condition is perhaps being overshadowed by the cheatgrass problem. Namely, much of the Intermountain West contains large expanses of sagebrush habitat where shrub cover is so dominant that herbaceous cover is almost absent, with only sparse populations of remnant native grasses and forbs. To improve the site productivity of these areas for seasonal use by high profile species like sage grouse, proposals have been made to manage portions of these areas for reduced mature sagebrush cover, regeneration of young sagebrush, and increased native herbaceous cover. According to Klebenow (1969), reducing/thinning sagebrush cover in some areas can restore the balance of forbs and grasses, thereby enhancing sage grouse habitat. Connelly and others (2000) maintain that treatments such as prescribed fire, grazing, herbicides, and mechanical treatments may be used to restore sagebrush habitats, but caution that improper use of these tools can also result in the degradation or loss of such habitats.

Location, and especially size of treatments, must be carefully chosen, since wildlife species respond variously to scale of vegetation management treatments (Paige and Ritter 1999). For example, bird species in general are affected at the population level by vegetation management treatments covering thousands of acres, at the home range level by management of vegetation "stands" from 1 to thousands of acres in size, and at the individual/pair level by treatments on areas from less than 1 to hundreds of acres (Paige and Ritter 1999). For sage grouse specifically, Klebenow (2001) does not recommend sagebrush eradication over large areas, but suggests thinning sagebrush to about 15 percent cover to enhance forb and grass production. He also suggests that small burns in mountain big sagebrush can create a mosaic pattern to enhance forbs and increase sagebrush height diversity.

In lower elevation sites (dominated by Wyoming big sagebrush) where recovery of herbaceous vegetation is slower, fire should be used cautiously to reduce the threat of cheatgrass invasion. Some of these areas may require seeding with adapted perennial species to compete with cheatgrass, followed after establishment by interseeding of native shrubs, forbs, and grasses (Klebenow 2001). Connelly and others (2001) similarly recommend the seeding of “functional equivalents” (non-native plant species) where native forbs and grasses are unavailable. They also caution that prescribed fire (and fire surrogate treatments like herbicides) be used cautiously in Wyoming big sagebrush habitats, realizing that 30 years is the approximate recovery period for Wyoming big sagebrush stands. For populations of diverse bird species, Paige and Ritter (1999) recommend that prescribed burns to enhance vegetation diversity be kept relatively small (with patchy distribution), reseeded where necessary, and protected from livestock grazing until seeded species become established.

We propose that if such management strategies were properly implemented, a continuum of herbaceous, herbaceous-shrub, shrub-herbaceous, and shrub-dominated habitats could be created. We think that most wildlife species on a landscape scale would be largely benefited. Because of the diverse habitat requirements of various wildlife species, habitat for all sagebrush-associated wildlife species would be present in varying amounts on a landscape scale. In other words, creating landscape heterogeneity with multiple-aged stands of sagebrush and varying degrees of herbaceous and shrub cover would provide both the vertical and horizontal vegetation components of vegetation diversity required by diverse wildlife species. The value of each landscape parcel for various wildlife species would change over time with the dynamics of the initial natural or prescribed disturbance, environmental variability of secondary plant succession, and post-disturbance management.

State and transition models, imbedded into ecological site descriptions, offer the best tool for analyzing vegetation management hazards and opportunities, and determining management options and priorities (Bestelmeyer and others 2003; Laycock 1991, 1995; West 1999). Simply put, state and transition models reflect the idea that rangeland vegetation exhibits several “states” (recognizable complexes of soil and vegetation structure that are resistant to change and resilient to impacts). These models also present the idea that the various states have ecological phases through which the states progress over time, by pathways consisting of changes in plant species composition or community structure. On the other hand, almost irreversible “thresholds” or boundaries between states can be crossed in “transitions.” These transitions are reversible through reasonable management actions until an undesired threshold is crossed. Once such a threshold is crossed, change back toward a more desired state is irreversible unless extensive time, effort, and money are available to effect a change. For example, after a sagebrush-grass community has crossed the ecological threshold to dominance by cheatgrass or noxious weeds, the transition is virtually irreversible. But carefully built and easily understood state and transition models can help identify such ecological transitions at earlier stages, allowing appropriate changes in management actions to prevent the crossing of ecologically damaging thresholds.

The highest priorities for habitat treatments should be driven by the risk of crossing an ecological threshold (such as weed invasion) and the opportunity to apply an effective management treatment. Only adaptive management strategies (Macnab 1983) that follow up active vegetation management with monitoring and adjustment of strategies, if necessary, will ensure the perpetuation of a diverse and productive landscape. Success in establishing a heterogeneous mosaic of native plant communities across any rangeland landscape also complements sustainable rangeland management for multiple uses in addition to wildlife.

References

Bestelmeyer, B. T.; Brown, J. R.; Havstad, K. M.; Alexander, R.; Chavez, G.; Herrick, J. E. 2003. Development and use of state-and transition models for rangelands. Journal of Range Management. 56: 114–126.

Braun, C. E.; Baker, M. F.; Eng, R. L.; Gashwiler, J. S; Schroeder, M. H. 1976. Conservation committee report on effects of alteration of sagebrush communities on the associated avifauna. Wilson Bulletin. 88: 165–171.

Connelly, J. W.; Schroeder, M. A.; Sands, A. R.; Braun, C. E. 2000. Guidelines to manage sage grouse populations and their habitats. Wildlife Society Bulletin. 28: 967–985.

Fautin, R. W. 1946. Biotic communities of the northern desert shrub biome in western Utah. Ecological Monographs. 16(3): 251–310.

Klebenow, D. A. 2001. Enhancing sage grouse habitat…a Nevada landowner's guide. Northwest Sage Grouse Working Group Publication.

Klebenow, D. A. 1969. Sage grouse nesting and brood habitat in Idaho. Journal of Wildlife Management. 33: 649–662.

Klebenow, D. A.; Gray, G. M. 1968. Food habits of juvenile sage grouse. Journal of Range Management. 21: 80–83.

Kufeld, R. C. 1973. Foods eaten by Rocky Mountain Elk. Journal of Range Management. 26: 106–113.

Kufeld, R. C.; Wallmo, O. C.; Feddema, C. 1973. Foods of the Rocky Mountain mule deer. Res. Pap. RM-111. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 31 p.

Laycock, W. A. 1991. Stable states and thresholds of range condition on North American rangelands—a viewpoint. Journal of Range Management. 44: 427–433.

Laycock, W. A. 1995. New perspectives on ecological condition of rangelands: can state and transition or other models better define condition and diversity? In: Montes, L.; Olivia, G. E., eds. Proceedings—international workshop on plant genetic resources, desertification, and sustainability. Santa Cruz, Argentina: Centro Regional Patagonia Sur, INTA-EEA, Rio Gallegos: 140–164.

Macnab, J. 1983. Wildlife management as scientific experimentation. Wildlife Society Bulletin. 11: 397–401.

McAdoo, J. K.; Evans, C. C.; Roundy, B. A.; Young, J. A.; Evans, R. A. 1983. Influence of heteromyid rodents on *Oryzopsis hymenoides* germination. Journal of Range Management. 36: 61–64.

McAdoo, J. K.; Klebenow, D. A. 1979. Native faunal relationships in sagebrush ecosystems. In: The sagebrush ecosystem symposium. Logan: Utah State University: 50–61.

McAdoo, J. K.; Longland, W. S.; Cluff, G. J.; Klebenow, D. A. 1987. Use of new rangeland seedings by black-tailed jackrabbits. Journal of Range Management. 40: 520–524.

McAdoo, J. K.; Longland, W. S.; Evans, R. A. 1989. Nongame bird community responses to sagebrush invasion of crested wheatgrass seedings. Journal of Wildlife Management. 53: 494–502.

McQuivey, R. P. 1978. The desert bighorn sheep of Nevada. Biol. Bull. No. 6. Nevada Department of Fish and Game. 81 p.

Miller, R. F.; Eddleman, L. L. 2001. Spatial and temporal changes of sage grouse habitat in the sagebrush biome. Tech Bull. 151. Corvallis: Oregon State University Agricultural Experiment Station. 35 p.

Paige, C.; Ritter, S. A. 1999. Birds in a sagebrush sea: managing sagebrush habitats for bird communities. Boise, ID: Partners in Western Flight Working Group.

Ports, M. A.; McAdoo, J. K. 1986. *Sorex merriami* (Insectivora: Soricidae) in eastern Nevada. Southwest Naturalist. 31: 415–416.

Tisdale, E. W.; Hironaka, M. 1981. The sagebrush-grass region: a review of the ecological literature. Bull. 33. Moscow: University of Idaho, College of Forestry, Wildlife, and Range Sciences, Forest, Wildlife and Range Experiment Station.

Vale, T. R. 1975. Presettlement vegetation in the sagebrush-grass area of the Intermountain West. Journal of Range Management. 28: 32–36.

Verts, B. J.; Carraway, L. N. 1998. Land mammals of Oregon. Berkeley: University of California Press.

West, N. E. 1983a. Great Basin-Colorado Plateau sagebrush semi-desert. In: West, N. E., ed. Ecosystems of the World 5. Temperate deserts and semi-deserts. New York: Elsevier. Chapter 12 .

West, N. E. 1983b. Western Intermountain sagebrush steppe. In: West, N. E., ed. Ecosystems of the World 5. Temperate deserts and semi-deserts. New York: Elsevier. Chapter 13.

West, N. E. 1999. Synecology and disturbance regimes of sagebrush steppe ecosystems. In: Entwistle, P. G.; DeBolt, A. M.; Kaltenecker, J. H.; Steenhof, K., comps. Proceedings: sagebrush steppe ecosystems symposium. Boise, ID: Boise State University: 15–26.

Browsing Effects on Wyoming Big Sagebrush Plants and Communities

Carl L. Wambolt
Trista Hoffman

Abstract: The effect of likely yearlong browsing by several wild ungulate species on individual Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) plants and communities was studied. The investigation was conducted near Gardiner, MT, in the ungulate-rich boundary line area of the Northern Yellowstone Winter Range. Plant level responses were measured in this study and related to reported community responses. Individual sagebrush plants were significantly different ($P < 0.05$) in and out of an exclosure 35 years after it was constructed (1957) in regard to production, seedhead number, and leaf dry weight. Certain morphological characters of the same plants were not impacted by browsing. These results relate well to previously detailed plant community responses on this important ungulate range. The Wyoming big sagebrush has been greatly reduced in the study area by browsing.

Introduction

Big sagebrush (*Artemisia tridentata*) taxa are particularly important for ungulates as forage and often security and/or thermal cover in portions of the Northern Yellowstone Winter Range (NYWR) that are relatively free of snow. Under these conditions, the plants remain accessible for foraging throughout winter (Wambolt 1998). Twentieth-century naturalists (Cahalane 1943; Kittams 1950; Rush 1932; Wright and Thompson 1935) have commented on the conspicuous use of sagebrush for forage and cover by ungulates on the NYWR and expressed concern over what they considered excessive use of sagebrush in the winter diets of ungulates in Yellowstone National Park (YNP).

The effects of Yellowstone's large populations of ungulates on sagebrush taxa on the NYWR have been debated for more than 70 years (Rush 1932; Wright and Thompson 1935). The National Park Service (NPS) was concerned enough about sagebrush and other browse on the NYWR that they constructed ten 2-ha exclosures on the NYWR in 1957 and 1962 to investigate the relationships between ungulate foraging and plant communities.

We used a NPS exclosure erected in 1957 to test the hypothesis that Wyoming big sagebrush plants protected from browsing for 35 years would exhibit growth characteristics similar to browsed plants. These results were then related to plant community responses on the NYWR.

Study Area and Methods

The natural winter range provided by the Gardiner Basin is created by the orographic effects on precipitation of mountain peaks up to 3,353 m in elevation. Ideal winter range on extensive south- or west-facing aspects in the Gardiner Basin have been influenced by glacial scouring, morainal deposition, and outwash sediments. In the portion of the NYWR where this study was conducted, the sagebrush habitat is the Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*)-bluebunch wheatgrass (*Agropyron spicatum*) type.

Individual plant characteristics (table 1) were sampled from 20 plants randomly selected and then paired by size in and out of the 1957 exclosure. Seedheads were counted. Ten leaders were clipped per plant. Leaves were counted and dried at 65 °C, and dry weight was determined for each leader and its leaves. The Kolmogorov-Smimov test compared differences in distributions, and the Wilcoxon test compared distribution medians.

Sampling of community characteristics were made in and out of the above described exclosure (1957 construction) and a second similar exclosure constructed in 1962 approximately 300 yards from the first exclosure. This sampling included measurements of individual sagebrush plants for seedhead number and length, average cover, major and minor axes, crown depth, and overall height. These measurements estimated sagebrush productivity from models previously developed from Wyoming big sagebrush plants in

Table 1—Average differences between browsed and unbrowsed Wyoming big sagebrush plants.

Characteristic	Browsed[a]	Unbrowsed[a]
Production (g/plant)	10.0a	44.7b
Seedheads per plant	0.08a	60.3b
Leader length (mm)	22.9a	22.3a
Leader dry weight (g)	.02a	.02a
Leaves per leader	43.0a	44.0a
Leaf area (mm^2)	354.0a	354.0a
Leaf dry weight (g)	0.06a	0.08b

[a]Values followed by different letters are significant ($P \leq 0.05$).

In: Hild, Ann L.; Shaw, Nancy L.; Meyer, Susan E.; Booth, D. Terrance; McArthur, E. Durant, comps. 2004. Seed and soil dynamics in shrubland ecosystems: proceedings; 2002 August 12–16; Laramie, WY. Proceedings RMRS-P-31. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Carl L. Wambolt is a Professor of Range Science and Trista Hoffman is a Research Assistant, Montana State University, P.O. Box 172900, Bozeman, MT 59717, U.S.A. FAX: (406) 994-5589, e-mail: cwambolt@montana.edu

the Gardiner Basin (Wambolt and others 1994). Additional production information is reported in Wambolt and Sherwood (1999). Shrub density and line intercept (canopy cover) were determined for both young and old plants. Because the 2-ha exclosures contained considerable environmental variation, the sagebrush habitat within each exclosure was stratified (Hurlbert 1984) by separating topographic, soil, and micro-climatic variation into eight paired sites. With random sampling using paired sites (in and out of the exclosures), it is unlikely that comparable distributions of topo-edaphic positions would have been obtained regardless of sample size (Coughenour 1991). Sampling areas were paired in and out of each exclosure within four slope-aspect combinations (table 2). These areas were compared with students' t-tests.

Discussion

Because of heavy browsing, plants outside the exclosure had no terminal leader growth. However, the plants inside the exclosure were dominated by terminal growth, and axial long shoots were rare. Thus, for further investigation, it was necessary to compare the terminal leaders of protected plants inside the exclosure to axial long shoots on browsed plants.

Unbrowsed plants had consistently higher production than browsed plants (table 1). The average production per plant was 10 g with browsing and 45 g with protection. No measurements of dead crown were taken, but plants under protection appeared vigorous, whereas plants outside the exclosure had large amounts of dead crown.

The greatest difference between browsed and unbrowsed plants was in seedhead production. Seedheads overaged 0.08 per browsed plant and 60.3 per unbrowsed plant. Related studies confirm that stress, such as herbivory, may delay or prevent flowering for several years (Bazzaz 1987; Maschinski and Whitham 1989; McConnell and Smith 1977). The lower overall production of browsed sagebrush plants indicates that foliage loss results in reduced reproductive potential. Bilborough and Richards (1991) found that buds for flowering stems on mountain big sagebrush were located on short shoots at the distal end of the terminal leader. Because almost all terminal leaders were removed on browsed plants, flowering stems would have to be initiated from elsewhere. The loss in seedhead production from browsing on the NYWR has undoubtedly resulted in declines in reproduction for sagebrush because the taxon lacks any asexual means of reproduction.

A companion study found that the addition of average seedhead weight improved the capability of models to predict production of winter forage from the three NYWR big sagebrush subspecies (Wambolt and others 1994). However, these improved models could only be used for two of the taxa when they exhibited light use (browse form class). Heavily used plants produced few inflorescences; therefore, the addition of average seedhead weight to the model was most useful for predicting forage production from low-use plants (Wambolt and others 1994). The segregation of browse form classes and inclusion of average seedhead weight in the models acknowledge the impact browsing has had on the annual production and reproduction of NYWR sagebrush and relate well to our findings of individual plant characteristics.

Thirty-five percent of mountain big sagebrush (*A. t. vaseyana*) plants were killed by heavy browsing between 1982 and 1992 (Wambolt 1996). Many surviving plants developed a heavy-use browse form class with a high percentage of dead crown. The dead crown in the three big

Table 2—Percent canopy cover of Wyoming big sagebrush and number of big sagebrush plants (with a minimum canopy of 15 cm) per 60 m^2 at eight environmentally paired sites, either browsed or protected. The paired sites are associated with the exclosures established either in 1957 or 1962 (Wambolt and Sherwood 1999).

Site	Slope[a]	Aspect	Protected	Browsed	Probability > t
			- - - - - Canopy cover (percent)- - - - -		
Gardiner-57A	Flat	Flat	3.9	0.0	0.0001
Gardiner-57B	Steep	E	3.6	.1	.0004
Gardiner-57C	Gentle	SW	4.5	1.1	.0001
Gardiner-57D	Gentle	NWW	1.4	.4	.0073
Gardiner-62A	Moderate	NEE	21.8	.4	.0001
Gardiner-62B	Flat	Flat	17.6	4.3	.0000
Gardiner-62C	Very steep	NEE	2.4	.2	.0012
Gardiner-62D	Very steep	SE	6.8	.0	.0001
			- - - - - - Density (per 60 m^2) - - - - - -		
Gardiner-57A	Flat	Flat	9.0	.5	.0002
Gardiner-57B	Steep	E	8.1	.5	.0002
Gardiner-57C	Gentle	SW	15.1	5.0	.0005
Gardiner-57D	Gentle	NWW	7.7	1.0	.0001
Gardiner-62A	Moderate	NEE	36.0	1.2	.0001
Gardiner-62B	Flat	Flat	39.2	.2	.0001
Gardiner-62C	Very steep	NEE	2.2	.0	.0090
Gardiner-62D	Very steep	SE	6.9	.7	.0001

[a] Slope classes are: flat ≤ 3 percent, gentle = 4 to 15 percent, moderate = 16 to 29 percent, steep = 30 to 44 percent, very steep ≥ 45 percent.

sagebrush subspecies increased in proportion to the overall amount of browsing received by each taxon. The percentage of dead crown in live plants for mountain big sagebrush, Wyoming big sagebrush, and basin big sagebrush (*A. t.* ssp. *tridentata*) was 58.7, 45.4, and 30.1, respectively (Wambolt 1996).

A significant difference was found between the development of protected and browsed big sagebrush communities (table 2). Wambolt and Sherwood (1999), who studied mountain big sagebrush in addition to Wyoming big sagebrush, stated:

> Since the period of exclosure construction in 1957 and 1962, there has been a significant difference in the development of protected and browsed big sagebrush communities. Average big sagebrush canopy cover on protected sites was 202 percent greater ($P \leq 0.0027$) than on browsed sites over the nineteen-paired sites. The average big sagebrush cover for all 19 sites was 19.7 percent inside and 6.5 percent outside the exclosures. This relationship was universal on sites with Wyoming big sagebrush or mountain big sagebrush, flat to very steep topographies, and all aspects and precipitation levels.

However, the differences between in and out of the exclosures at the Wyoming big sagebrush sites discussed in this paper were much greater than at the mountain big sagebrush locations. The Wyoming big sagebrush sites under protection averaged almost 10 times more sagebrush cover than where browsing had continued following exclosure construction. Ungulate browsing also affected numbers of big sagebrush plants. Across the NYWR, big sagebrush plants were twice as numerous with protection as with browsing.

The production differential for Wyoming big sagebrush was great, but because browsed plants were so reduced in size, their growth parameters were not suitable for production models (Wambolt and others 1994). The response of the sprouting shrubs, green rabbitbush (*Chrysothamnus visidiflorus*), rubber rabbitbrush (*C. nauseosus)*, and gray horsebrush (*Tetradymia canescens*), as measured by canopy cover and density, was similar to that of big sagebrush across the NYWR.

Singer and Renkin (1995) and Wambolt and Sherwood (1999) found a large impact from browsing on the Wyoming big sagebrush in the Gardiner Basin (fig. 1). Wambolt and Sherwood (1999) considered the difference in impact between Wyoming big sagebrush and mountain big sagebrush with this statement: “Pronghorn and mule deer often forage heavily on big sagebrush taxa (Welch and McArthur 1979). Mule deer diets averaged 52 percent big sagebrush over a 10 year period (Wambolt 1996), only a couple of kilometers away from the eight Wyoming big sagebrush paired sites. A high degree of utilization is reflected in the great impact on Wyoming big sagebrush populations at these eight sites where elk may also be present with pronghorn and mule deer (Singer and Renkin 1995).”

Wambolt (1996) concluded that any of the four NYWR sagebrush taxa would be heavily browsed if severe winter conditions precluded ungulates from exercising their preferences. However, mountain big sagebrush was clearly the preferred taxon by mule deer and elk. The fact that Singer and Renkin (1995) and Wambolt and Sherwood (1999) found Wyoming big sagebrush to be more impacted than mountain big sagebrush was largely a function of snow depth limiting pronghorn and mule deer foraging over the larger distribution of mountain big sagebrush. The intensive competition from a large elk population also restricted the winter range of the smaller ungulates to the Wyoming big sagebrush habitat type.

Conclusions

The historical evidence and recent studies (Patten 1993; Wambolt 1998; Wambolt and Sherwood 1999) indicate a significant decline of NYWR sagebrush. This potentially impacts ungulates that rely on sagebrush habitat for meeting their nutritional needs and other requirements. Sagebrush taxa are highly nutritious and preferred forage for ungulates (Welch and McArthur 1979). They have been bred and selected to improve the forage values of rangelands (Welch and Wagstaff 1992). Sagebrush is particularly high in protein. Welch and McArthur (1979) found the midwinter crude protein content of 21 big sagebrush accessions averaged 12.4 percent (range = 10 to 16 percent).

Ungulates such as pronghorn are impacted as the loss of their highest winter protein source (sagebrush) continues (Welch and McArthur 1979). This loss will manifest itself in a decreasing ability to meet their nutritional needs and requirements for reproduction. The implications for other organisms are clear. In concert with the decline of the native vegetation (sagebrush and dependent species), it is reasonable to expect that numerous animals (Welch 1997) will be impacted.

The following points summarize our findings:

1. Wyoming big sagebrush shrubs that were protected from ungulate browsing produced significantly more forage than browsed shrubs.
2. Seedhead production was severely reduced by browsing. Heavily browsed stands may have difficulty regenerating.
3. Leaders on browsed shrubs have the same number of leaves as those on unbrowsed shrubs, but the mass of leaves is reduced.
4. Shrub composition of the Wyoming big sagebrush habitat type has been significantly changed by browsing on the NYWR.
5. Big sagebrush may be overused and severely damaged on big game winter ranges.

References

Bazzaz, F. A.; Chiariello, N. R.; Colley, P. D.; Ptielka, L. F. 1987. Allocating resources to reproduction and defense. Bioscience. 37: 58–67.

Bilbrough, C. J.; Richards, J. H. 1991. Branch architecture of sagebrush and bitterbrush: use of a branch complex to describe and compare patterns of growth. Canadian Journal of Botany. 69: 1288–1295.

Cahalane, V. H. 1943. Elk management and their regulation—Yellowstone National Park. Transactions of the North American Wildlife Conference. 8: 95–101.

Coughenour, M. B. 1991. Biomass and nitrogen responses to grazing of upland steppe on Yellowstone’s northern winter range. Journal of Applied Ecology. 28:71–82.

Hurlbert, S. H. 1984, Pseudoreplication and the design of ecological field experiments. Ecological Monographs. 54: 187–211.

Kittams, W. H. 1950. Sagebrush on the lower Yellowstone range as an indicator of wildlife stocking. Unpublished report on file at: Yellowstone National Park.

Maschinski, J.; Whitham, T. J. 1989. The continuum of plant responses to herbivory: the influence of plant association, nutrient availability and timing. The American Naturalist. 134: 1–19.

McConnell, B. R.; Smith, J. G. 1977. Influence of grazing on age-yield interactions in bitterbrush. Journal of Range Management. 30: 91–93.

Patten, D. T. 1993. Herbivore optimization and overcompensation: does native herbivory on western rangelands support these theories? Ecological Applications. 3: 35–36.

Rush, W. M. 1932. Northern Yellowstone elk study. Helena: Montana Fish and Game Commission.

Singer, F. J.; Renkin, R. A. 1995. Effects of browsing by native ungulates on the shrubs in big sagebrush communities in Yellowstone National Park. Great Basin Naturalist. 55: 201–212.

Wambolt, C. L. 1996. Mule deer and elk foraging preference for 4 sagebrush taxa. Journal of Range Management. 49: 499–503.

Wambolt, C. L. 1998. Sagebrush and ungulate relationships on Yellowstone's northern range. Wildlife Society Bulletin. 26: 429–437.

Wambolt, C. L.; Creamer, W. H.; Rossi, R. J. 1994. Predicting big sagebrush winter forage by subspecies and browse form class. Journal of Range Management. 47: 231–234.

Wambolt, C. L.; Sherwood, H. W. 1999. Sagebrush response to ungulate browsing in Yellowstone. Journal of Range Management. 52: 363–369.

Welch, B. L. 1997. Seeded versus containerized big sagebrush plants for seed-increase gardens. Journal of Range Management. 50: 611–614.

Welch, B. L.; McArthur E. D. 1979. Feasibility of improving big sagebrush (*Artemisia tridentata*) for use on mule deer winter ranges. In: Goodin, J. R.; Northington, D. K., eds. Arid land plant resources. Lubbock: Texas Tech University: 451–453

Welch, B. L.; Wagstaff, F. J. 1992. “Hobble Creek” big sagebrush vs. antelope bitterbrush as a winter forage. Journal of Range Management. 45: 140–142.

Wright, G. M.; Thompson, B. H. 1935. Fauna of the National Parks of the United States: wildlife management in the National Parks. Fauna Series 2. National Park Service.

Effects of Wildlife Utilization and Grass Seeding Rates on Big Sagebrush Growth and Survival on Reclaimed Mined Lands

Kristene A. Partlow
Richard A. Olson
Gerald E. Schuman
Scott E. Belden

Abstract: Ensuring Wyoming big sagebrush (*Artemisia tridentata* Nutt ssp. *wyomingensis* Beetle & Young) survival remains a challenge years after initial re-establishment on reclaimed mined lands. Wildlife utilization of big sagebrush can be a major factor influencing its survival. A wildlife-proof exclosure was erected on a portion of an existing sagebrush establishment research site initiated by Schuman and others (1998) in 1990 at the North Antelope/Rochelle Complex mine in northeastern Wyoming. Investigations focused on the effects of wildlife utilization of big sagebrush growth and survival as affected by grass seeding rates of the original study and the newly constructed exclosure. Results indicate no significant differences in big sagebrush density between grass seeding rates or inside versus outside the exclosure. Significantly greater leader growth of big sagebrush occurred inside compared to outside the exclosure. Mean leader length of big sagebrush inside the exclosure in April 2002, 10 months after construction, was 46.4 mm compared to 9.4 mm outside. Wildlife browsing occurred on 100 percent of the big sagebrush plants outside the exclosure in 2002. Utilization and mortality of the sagebrush plants was significantly higher at the lower grass seeding rates. Approximately 33 percent of the studied sagebrush plants outside of the exclosure died during the 15-month study period compared to 11 percent inside the exclosure. Findings of this study indicate that wildlife browsing on these sagebrush plants is significantly influencing their survival and growth.

Introduction

Wyoming big sagebrush (*Artemisia tridentata* Nutt ssp. *wyomingensis* Beetle & Young), if present in premined ecosystems, is required to be re-established according to the Surface Mining Control and Reclamation Act of 1977 and the Wyoming Environmental Quality Act of 1973 (Wyoming Department of Environmental Quality, Land Quality Division 1996). The process of re-establishing this shrub has been difficult for reclamation specialists. In 1990, Schuman and others (1998) initiated a study to evaluate the effects of various topsoil management, mulch type, and grass seeding rate treatments on re-establishment of Wyoming big sagebrush. The direct-placed topsoil treatment produced a higher big sagebrush seedling density than stockpiled topsoil in the first 2 years of the study. They believed this was due to consistently higher soil moisture in direct-placed topsoil plots. Their study demonstrated the positive benefits of direct-placed topsoil compared to stockpiled topsoil and various mulch treatments on big sagebrush re-establishment at North Antelope Coal Mine south of Gillette, WY.

However, ensuring big sagebrush survival remains a challenge years after initial re-establishment. Reclamation specialists are exploring other potential impacts to big sagebrush survival beyond edaphic and vegetative factors. Impacts of wildlife browsing may be a major factor on big sagebrush survival for some mines. Newly reclaimed coal mined lands often provide young, highly palatable and nutrient-rich plant communities that attract wildlife species such as mule deer (*Odocoileus hemionus*), pronghorn antelope (*Antilocapra americana*), cottontail rabbits (*Sylvilagus audubonii baileyi*), and jackrabbits (*Lepus townsendii* and *Lepus californicus melanotis*). Big sagebrush is a major diet component of many wildlife species because it provides a critical source of winter browse and cover (Beetle 1960). Since adjacent native rangelands usually contain older, mature shrubs of lower palatability and nutrient value, wildlife are attracted to reclaimed areas supporting greater herbaceous vegetation. Cool-season grasses and some shrub species, including big sagebrush, generally dominate reclamation seeding mixtures. The restriction of public access and prohibited hunting on mine property provides an environment that encourages habitual wildlife utilization of these reclaimed areas.

To investigate the influence of wildlife utilization on big sagebrush growth and survival, a wildlife-proof exclosure was constructed on half of the original North Antelope study site to provide comparative data on browsed versus unbrowsed big sagebrush, therefore, providing data on browsing impacts.

In: Hild, Ann L.; Shaw, Nancy L.; Meyer, Susan E.; Booth, D. Terrance; McArthur, E. Durant, comps. 2004. Seed and soil dynamics in shrubland ecosystems: proceedings; 2002 August 12–16; Laramie, WY. Proceedings RMRS-P-31. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Kristene A. Partlow is a Research Assistant and Richard A. Olson is a Professor at the University of Wyoming, Department of Renewable Resources, Laramie, WY 82071-3354, U.S.A., e-mail: rolson@uwyo.edu. Gerald E. Schuman is a Soil Scientist at the USDA-ARS High Plains Grasslands Research Station, Cheyenne, WY 82009, U.S.A. Scott E. Belden is a Senior Environmental Supervisor at Powder River Coal Co., North Antelope/Rochelle Complex, Peabody Energy Co., Gillette, WY 82716, U.S.A.

Browsing on vegetation can be positive, such as compensatory growth due to moderate use (McNaughton 1983), or negative, such as increased mortality from heavy use (Wambolt 1996).

Reclamation specialists have learned to successfully re-establish big sagebrush on reclaimed lands; however, developing successful management practices to ensure survival of these new seedlings must be addressed. Factors such as low seedling vigor, their inability to compete with herbaceous species, poor seed quality, and altered edaphic conditions can impact initial establishment and long-term survival of sagebrush (Cockrell and others 1995).When these factors are combined with intense wildlife browsing, sustaining big sagebrush re-establishment is challenging. Quantitative information on big sagebrush utilization and the effects of browsing impacts on long-term seedling survival are needed. Specific objectives of this project were to (1) determine long-term big sagebrush survival using data from the original study; (2) establish a new baseline data record of big sagebrush survival without wildlife influence using inside versus outside exclosure comparisons; (3) assess sagebrush density (plants m^{-2}) within various grass seeding rates, inside and outside the exclosure; (4) determine percent of big sagebrush plants browsed by grass seeding rates, inside and outside the exclosure; (5) examine seasonal (spring/summer, fall/winter) utilization rates of big sagebrush leader growth among grass seeding rates, inside/outside the exclosure; and (6) recommend potential management practices to enhance long-term big sagebrush survival on reclaimed mine lands.

Study Area

North Antelope Coal Mine is located in the Powder River Basin in northeast Wyoming, approximately 100 km south of Gillette, WY. Elevation ranges from 1,220 to 1,520 m. Climate is characterized as semiarid, temperate, and continental. Average annual temperature is 7 °C with January the coldest month (–6 °C) and July the warmest month (22 °C). Annual precipitation is 339 mm (1978 to 2000 average), with the greatest precipitation occurring in April, May, and June (Schuman and Belden 2002). The frost-free growing season averages 133 days (Glassey and others 1955).

The project area is approximately 1.2 ha in size. Native soils are broadly classified as Haplargids, Natrargids, and Torrorthents. Loamy and clayey soil textures comprise much of the basin (Young and Singleton 1977). Fresh direct-placed topsoil used at the research site included a complex of Shingle (loamy, mixed, calcareous, mesic, shallow, Ustic Torrorthents) and Samsil (clayey, montmorillinitic, calcareous, mesic, shallow, Ustic Torrorthents) series (Schuman and others 1998).

Topography is characterized as plains and low-lying irregular hills. Vegetation consists of low-growing shrubs, forbs, and short to midgrasses, primarily cool-season perennials. Prior to mining, the native vegetation primarily consisted of western wheatgrass (*Pascopyrum smithii* (Rybd.) A. Love), needleandthread grass (*Stipa comata* Trin. and Rupr.), prairie junegrass (*Koeleria macrantha* L. Pers.), big sagebrush, sandberg bluegrass (*Poa secunda* Presl), six-weeks-grass [*Vulpia octoflora* (Walt.) Rydb.], and cheatgrass (*Bromus tectorum* L.) (Western Water Consultants and Bureau of Land Management 1998). Species seeded on the reclaimed area were a mixture of native cool-season perennial grasses (Schuman and others 1998), including "Rosana" western wheatgrass [*Pascopyrum smithii* (Rybd.) A. Love], "San Luis" slender wheatgrass [*Elymus trachycaulus* (Link) Gould ex Skinner], and "Critana" thickspike wheatgrass [*Elymus lanceolatus* (Scribner & J.G. Smith) Gold].

The predominant land use in the area is domestic livestock grazing and habitat for big game, predators, small mammals, upland game birds, and nongame birds.

Methods and Materials

Experimental Design

The original big sagebrush re-establishment study design (Schuman and others 1998) initiated in August 1990 was used for this project and included the following treatments: topsoil management (fresh stripped/direct-placed and 5-year-old stockpiled topsoil), mulch type (stubble mulch, surface-applied straw mulch, stubble and surface-applied straw mulch, and no mulch), and grass seeding rate (no perennial grass seeded, 16 kg PLS [pure live seed] ha^{-1}, and 32 kg PLS ha^{-1}). All treatments were randomly assigned to a randomized block, split-split plot design with three replications (fig. 1). Topsoil treatment plots were 15 by 60 m with mulch subplots measuring 15 by 15 m and grass seeding rate sub-subplots measuring 15 by 5 m within each topsoil treatment main plot. Each of the four mulch types occurred within each of the three replications of fresh and stored topsoil treatments. The three grass seeding rates were randomly established within each of the four mulch treatments. Nine quadrats (1 m^2) were permanently staked in each of the grass seeding rate sub-subplots in three belts of three quadrats, lying in an east-west direction and located 1 m from the edge of each subplot.

In the original study, the direct-placed topsoil plots supported higher big sagebrush density than stockpiled topsoil in the first 2 years. Greater sagebrush seedling establishment in the direct-placed topsoil was due to consistently higher soil moisture observed in that treatment (Schuman and others 1998). Direct-placed topsoil also exhibits better chemical, physical, and biological properties than stockpiled topsoil (DePuit 1988; Stahl and others 1988; White and others 1989). The stockpiled topsoil treatment was excluded from this study because of the noted benefits of direct-placed topsoil. Stockpiled topsoil also no longer represented the original qualities because of the rapid inoculation by arbuscular mycorrhizae via wind and the many positive biogeochemical and physical changes that have occurred in the soil over 12 years.

Another addition to the original study was the construction of a wildlife-proof exclosure in June 2001 just prior to the first data collection. Exclosure dimensions are 90 by 30 m and 3.1 m tall, which enclosed half of each replicated direct-placed topsoil treatment plot. The same number of mulch treatment subplots and grass seeding rate sub-subplots were located inside and outside the exclosure. The exclosure fence was constructed of woven wire with 0.5 m

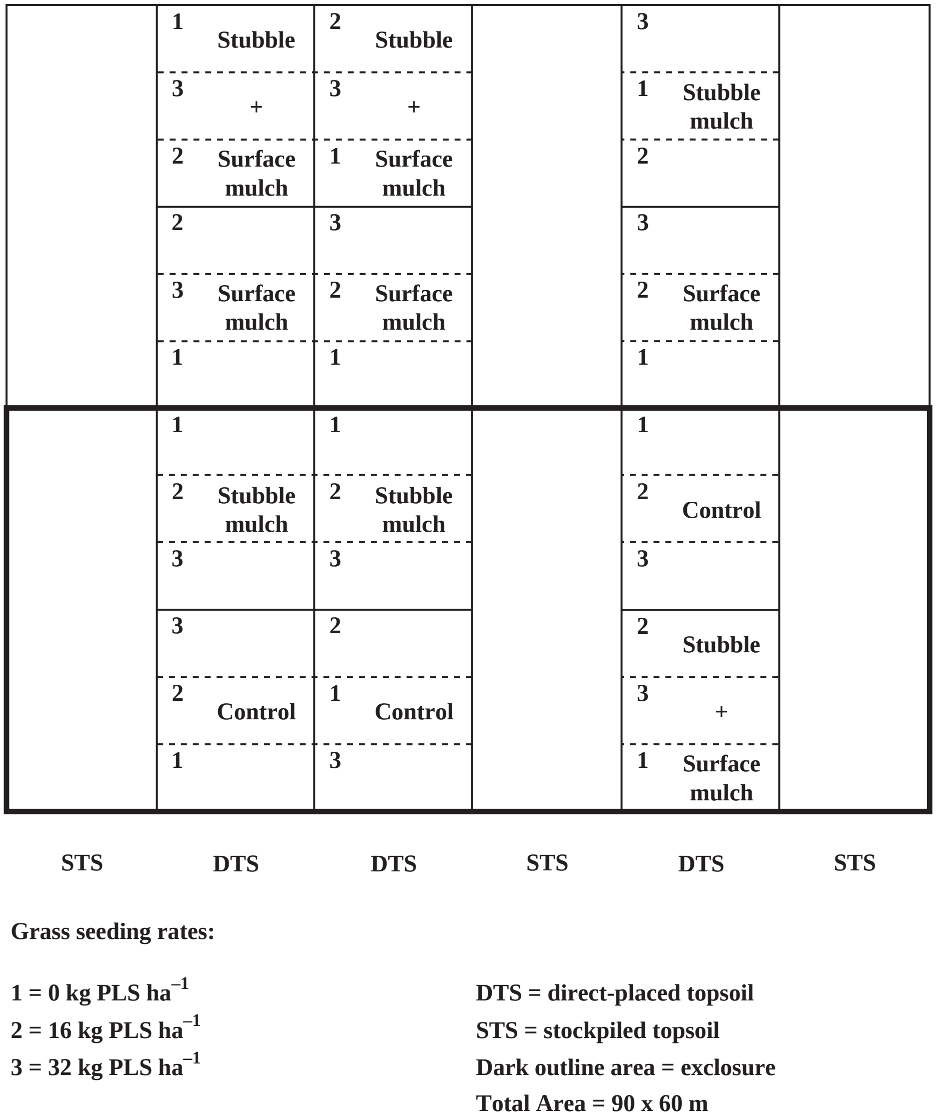


Figure 1—Study plot design including topsoil, mulch, and grass seeding rate treatments, North Antelope Coal Mine, Gillette, WY, 2001–2002.

high chicken wire extending along the ground surface to exclude rabbits and large rodents.

Big Sagebrush Density

Two methods of determining big sagebrush density were used. Permanent quadrats established in 1992 (Schuman and others 1998) were sampled to determine long-term big sagebrush survival. The number of live big sagebrush plants was counted in each of nine permanent quadrats within each grass seeding rate sub-subplot. Density was reported as the mean number of plants m^{-2} in each grass seeding rate inside and outside the exclosure.

Big sagebrush density was also assessed along a 2- by 12-m belt transect in each grass seeding rate sub-subplot, which provided another baseline record for evaluating big sagebrush survival inside and outside the exclosure. A 1-m^2 quadrat was placed alongside each belt transect, sagebrush plants were counted within the quadrat, then the quadrat was flipped to the next meter of the transect until all sagebrush plants were counted in the 24-m^2 area of the belt (12 m^2 on each side of the line). Density was summarized as the mean number of plants m^{-2} in each grass seeding rate inside and outside the exclosure.

Percent Browsed Big Sagebrush Plants

Within each grass seeding rate sub-subplot, four big sagebrush plants were selected near the outside corners of the permanent quadrats making a total of 144 plants (72 outside and 72 inside the exclosure). Each selected plant was marked by attaching a plastic locking zip tie at the base of the plant. Plant locations were mapped for easy relocation during subsequent sampling periods of the project. Each marked plant was inspected during sampling dates and recorded as browsed or unbrowsed to estimate percent of plants browsed.

Since the first sampling period (June 2001) immediately followed exclosure construction, some browsing had occurred prior to exclosure erection. Therefore, percent browsed plants were calculated inside and outside the exclosure in June 2001. In fall 2001, a small hole in the exclosure was discovered and repaired. Therefore, rabbit presence and potential utilization of sagebrush leaders was possible inside the exclosure until September 2001.

Big Sagebrush Leader Utilization

Differences in big sagebrush leader lengths of individually marked plants were evaluated to assess the degree of utilization. All leaders on marked plants were measured to the nearest 1 mm, and summarized as mean leader length per plant for each grass seeding rate inside and outside the exclosure. Nondistinctive leaders, such as those lacking woodiness or leaves extending from primary stems, were not considered leaders. Leader measurements excluded leaves extending from the terminal tip.

Big sagebrush leaders were measured in the spring and fall each year. Percent utilization was only calculated for the marked plants outside the exclosure because no browsing was observed inside the exclosure. The difference in mean leader length from spring to fall outside the exclosure provided percent summer utilization. Before new annual growth appeared the following spring, leader length was reassessed to provide the percent utilization during the late fall and winter period.

Data Analysis

Differences ($P \leq 0.10$) in mean big sagebrush density from permanent quadrats and belt transects, percent big sagebrush plants browsed, mean leader length, and percent utilization were evaluated between grass seeding rates inside and outside the exclosure using analysis of variance (ANOVA). Mean separations were evaluated using Tukey's pairwise comparison test (experimentwise $P \leq 0.10$) (Krebs 1999).

Results and Discussion

Big Sagebrush Density

Big sagebrush density (plants m^{-2}), measured in the permanent quadrats, increased in 1993 and 1994 following the 1992 seeding, but declined during subsequent years across all grass seeding rates (fig. 2) and mulch treatments (Schuman and Belden 2002). Mean big sagebrush density was generally highest in the 0 kg PLS ha^{-1} grass seeding rate across historical sampling years; therefore, percent survival was actually higher at the 16 and 32 kg PLS ha^{-1} grass seeding rates.

Big sagebrush densities inside and outside the exclosure were combined (averaged) in both 2001 and 2002 to compare to previous years. Although there were no differences in big sagebrush density among grass seeding rates in 2001 or 2002, there was a consistent decline in big sagebrush density for grass seeding rates over time. Future studies should evaluate long-term grass seeding rate influences on big sagebrush density and survival inside the exclosure where wildlife influences will not be a factor.

When examining 2001–2002 data only, mean big sagebrush density within the belt transects was highest in the 32 kg PLS ha^{-1} grass seeding rate inside the exclosure compared to other grass seeding rates, and significantly greater than the big sagebrush density in the same grass seeding rate outside of the exclosure (fig. 3). Big sagebrush density also exhibited a significant location by sample date interaction (fig. 4). Big sagebrush density was significantly higher inside

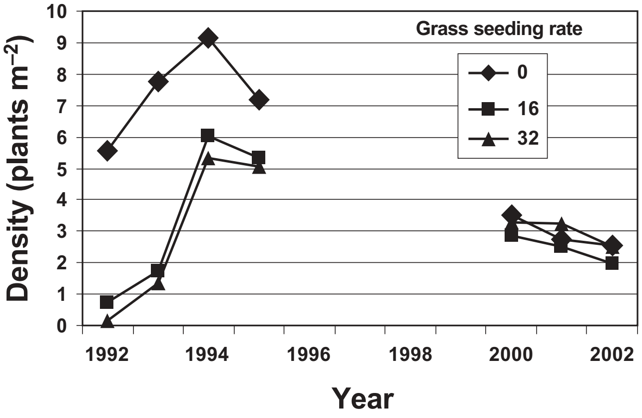
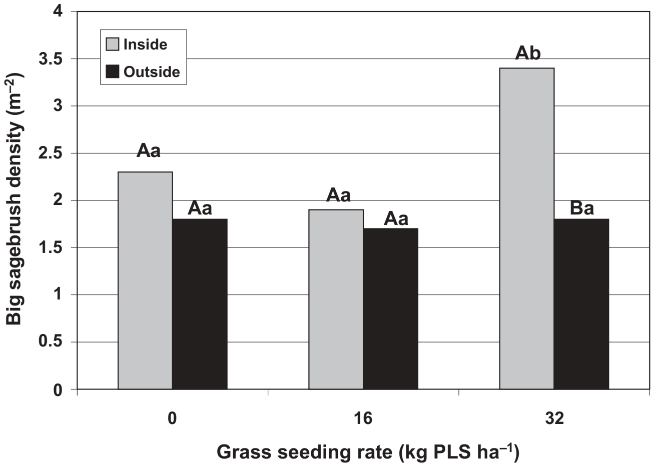


Figure 2—Historic and present mean big sagebrush density by grass seeding rates (kg PLS ha^{-1}) from permanent quadrat sampling, North Antelope Coal Mine, Gillette, WY.



Figue 3—Mean density of big sagebrush along belt transects by grass seeding rates inside and outside the exclosure, North Antelope Coal Mine, Gillette, WY, 2001–2002 (means within a grass seeding rate across locations with the same uppercase letter are not significantly different; means within a location across grass seeding rates with the same lower case letter are not significantly different, $P \leq 0.10$).

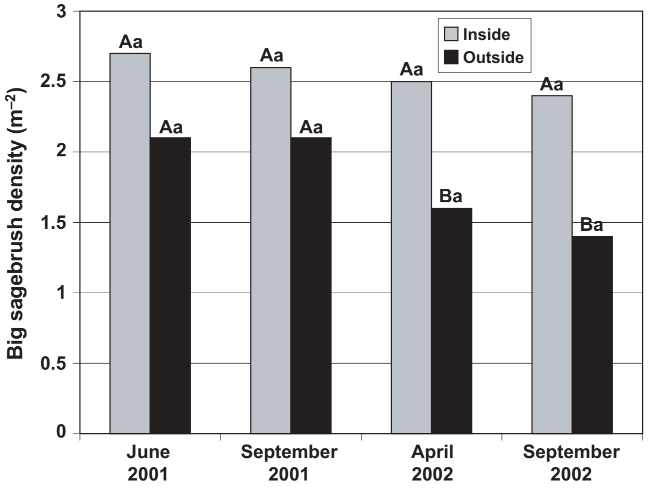


Figure 4—Density of big sagebrush along belt transects by sampling date inside and outside the exclosure, North Antelope Coal Mine, Gillette, WY, 2001–2002 (means within a sampling date across locations with the same uppercase letter are not significantly different; means within a location across sampling dates with the same lowercase letter are not significantly different, P ≤ 0.10).

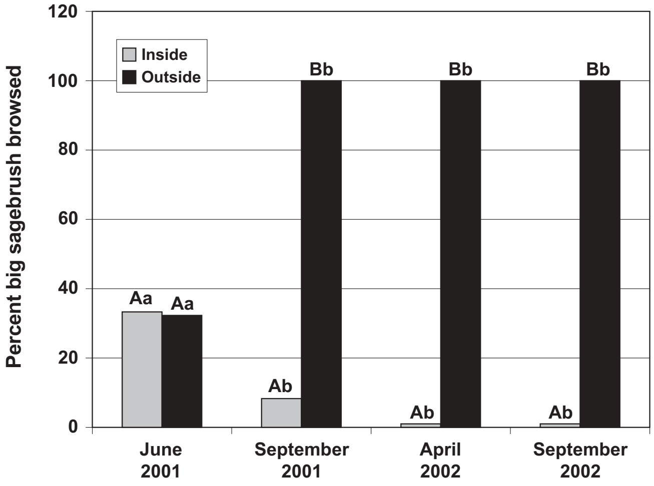


Figure 5—Percent big sagebrush plants browsed by sampling date inside and outside the exclosure, North Antelope Coal Mine, Gillette, WY, 2001–2002 (means within a sampling date across locations with the same uppercase letter are not significantly different; means within a location across sampling dates with the same lowercase letter are not significantly different, P ≤ 0.10).

the exclosure compared to outside of the exclosure in April and September 2002. No differences in density were observed inside the exclosure versus outside of the exclosure in 2001, which was anticipated since the exclosure was not constructed until June 2001.

Big sagebrush density was positively affected by wildlife exclusion 10 months (April 2002) after construction of the exclosure. Big sagebrush density outside the exclosure decreased more rapidly than inside, as evidenced by the number of dead marked plants during the study. Eight marked sagebrush plants inside the exclosure died compared to 24 plants outside of the exclosure. Mortality outside of the exclosure, among the marked plants, was 42 percent in the 0 kg PLS ha^{-1} grass seeding rate, 38 percent in the 16 kg PLS ha^{-1} grass seeding rate, and only 21 percent in the 32 kg PLS ha^{-1} grass seeding rate. Schuman and Belden (2002) also reported significantly greater sagebrush plant mortality in the 0 and 16 kg PLS ha^{-1} compared to the 32 kg PLS ha^{-1} grass seeding rate on these plots after 8 years. They hypothesized that this might be due in part to intraspecific competition and some sort of protective mechanism of the grass plants. Owens and Norton (1992) also reported that basin big sagebrush (*Artemisia tridentata* ssp. *tridentata*) seedlings experienced the greatest mortality in unsheltered areas of the landscape.

Percent Browsed Big Sagebrush Plants

Percent of big sagebrush plants browsed exhibited a significant interaction between location (inside versus outside exclosure) and sample date (fig. 5). There were no differences in the degree of big sagebrush plants browsed inside versus outside the exclosure in June 2001 due to the recent exclosure construction. However, percent of big sagebrush browsed decreased inside the exclosure from June 2001 to September 2002. Browsing inside the exclosure on the June 2001 sampling date occurred prior to construction of the exclosure about 10 days before the sampling date. All marked plants outside the exclosure exhibited browsing regardless of grass seeding rate. Across all grass seeding rates, April 2002 browsing data suggest that rabbits rather than big game were the primary browsers of the big sagebrush plants. However, the September 2002 browsing data indicate that big game and rabbit browsing was nearly equal. It is important to remember that identifying the browsing animal is limited to the most recent browser, because if a plant was browsed by big game and then browsed by a rabbit the data would only indicate it was browsed by a rabbit because of the methodology.

Utilization

Big sagebrush leader length exhibited a significant location by grass seeding interaction (fig. 6). Mean leader length was significantly greater in the 32 kg PLS ha^{-1} grass seeding rate compared to the lower grass seeding rates. This response cannot be explained. However, leader lengths were greater inside of the exclosure compared to outside the exclosure for all grass seeding rates. There were no differences in leader lengths among grass seeding rates outside of the exclosure. Big sagebrush leader length was also greater inside the exclosure for all sample dates (fig. 7). Big sagebrush leader length responded to the protection provided by the exclosure. Leader length inside the exclosure continued to increase, while unprotected plants outside the exclosure exhibited dramatic decreases in leader length due to wildlife browsing. Big sagebrush survival outside of the exclosure is threatened by continued intense wildlife utilization.

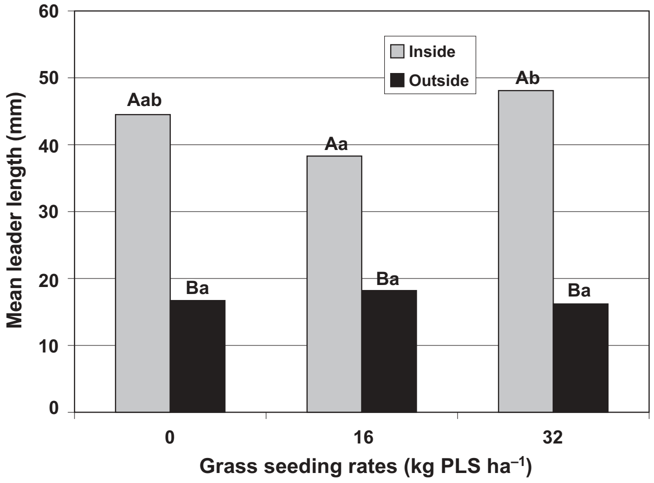


Figure 6—Mean leader length of marked big sagebrush by grass seeding rates inside and outside the exclosure, North Antelope Coal Mine, Gillette, WY, 2001–2002 (means within a grass seeding rate across locations with the same uppercase letter are not significantly different; means within a location across grass seeding rates with the same lower case letter are not significantly different, $P \leq 0.10$).

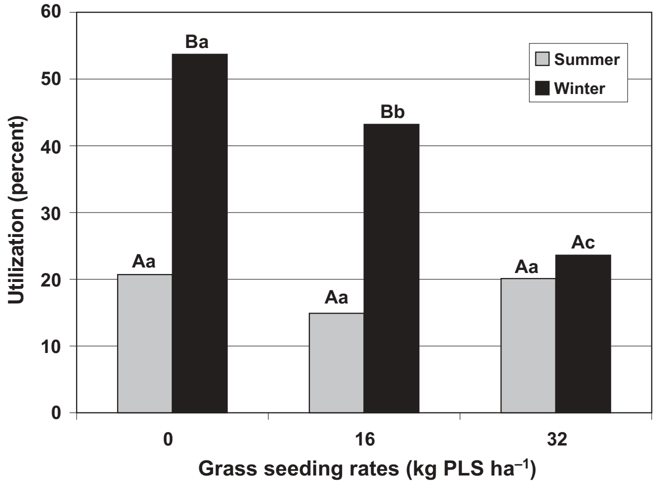


Figure 8—Seasonal percent utilization of marked big sagebrush plants by grass seeding rates outside the exclosure, North Antelope Coal Mine, Gillette, WY, 2001–2002 (means within a grass seeding rate across season with the same uppercase letter are not significantly different; means within a season across grass seeding rates with the same lower case letter are not significantly different, $P \leq 0.10$).

Seasonal utilization of marked sagebrush plants outside the exclosure exhibited a significant interaction between grass seeding rate and sample period (fig. 8). Summer wildlife utilization was consistent across grass seeding rates. However, winter utilization was significantly lower in the 32 kg PLS ha^{-1} grass seeding rate compared to both the 16 and 0 kg PLS ha^{-1} grass seeding rates. There was also significantly greater wildlife utilization in the winter compared to the summer period in the 0 and 16 kg PLS ha^{-1} grass seeding rates. The lower wildlife utilization during the winter months as grass seeding rate increased agrees with the sagebrush survival data presented by Schuman and Belden (2002) after 8 years, and also agrees with the survival and mortality data presented here 10 years after establishment (fig. 9). It appears that several things may be influencing the response sagebrush are exhibiting on this site. Austin and others (1994) evaluated the effects of deer and horse browsing on transplanted Wyoming big sagebrush survival. They found that plantings resulting in densities of 0.08 and 0.44 sagebrush plants m^{-2} were not influenced by the animals. However, the plant densities at our study site were severalfold higher and may have resulted in intraspecific competition for space, water, and nutrients. Owens and Norton (1994) found that sagebrush seedlings sheltered by other plants experienced less mortality than those growing in unprotected spaces. Based on their findings and those of Schuman and Belden (2002) it appears there are likely several factors affecting sagebrush survival on this reclaimed mined land. It is obvious from the significantly higher survival, lower mortality, and reduced wildlife utilization (fig. 9) of big sagebrush at the higher grass seeding rates that this is not a random response even though we cannot fully explain it.

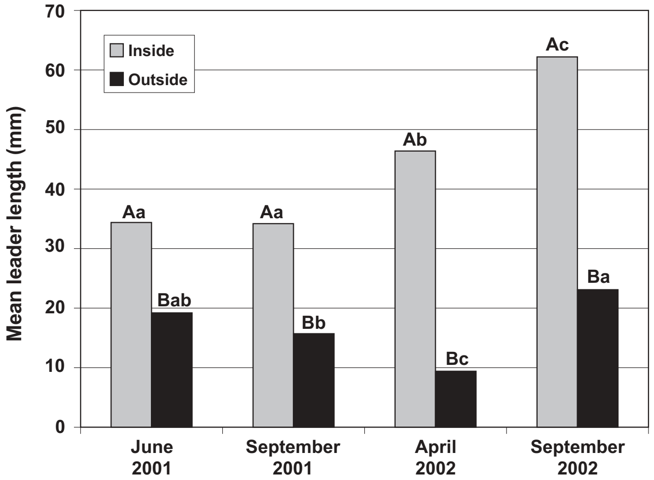


Figure 7—Mean leader length of marked big sagebrush plants by sampling period inside and outside the exclosure, North Antelope Coal Mine, Gillette, WY, 2001–2002 (means within a sampling date across locations with the same uppercase letter are not significantly different; means within a location across sampling dates with the same lowercase letter are not significantly different, $P \leq 0.10$).

Greater winter utilization was anticipated because browsing preference by big game (Craven 1983b; Schemnitz 1982; Welch and others 1981) and rabbits (Anderson and Shumar 1986; Craven 1983a; Knight 1982) intensify during the winter. Big sagebrush is a “starvation food” or necessary dietary component of winter months when nothing else is available (Welch and others 1981). Partial or complete defoliation of sagebrush leaders will not adversely affect growth,

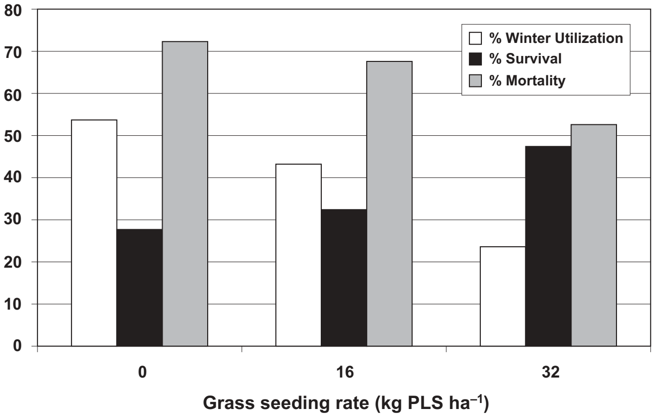


Figure 9—Relationship between percent winter utilization (2002), survival, and mortality of big sagebrush plants, North Antelope Coal Mine, Gillette, WY, 1994–2002.

vigor, and survival if leaf primordia and twigs are undamaged (Kelsey 1984). However, defoliation in our study was much more severe with considerable twig and primordia damage. Wildlife contributed to the death of about 33 percent of the marked sagebrush plants outside of the exclosure within 15 months.

For reclamation sites to provide adequate wildlife habitat, big sagebrush must be successfully established and maintained. Big sagebrush is included in the reclamation seed mix to satisfy State and Federal regulations for shrub reestablishment and land use. However, the intended land use (wildlife habitat) seems to be the very reason for threatened big sagebrush survival at this site. Our data indicate that high wildlife densities are impeding the successful long-term establishment and growth of the big sagebrush component of the reclaimed site. Both wildlife management and habitat manipulation may be necessary for successful reclamation of this site. Without proper wildlife and habitat management, big sagebrush densities could decline to less than 1 plant m^{-2} on these reclaimed areas, and not meet the required density for bond release (Wyoming Department of Environmental Quality, Land Quality Division 1996).

Management Implications

Because intense wildlife utilization has been shown to reduce big sagebrush survival on some mine sites, reclamation specialists should consider management practices to reduce wildlife herbivory impacts. Habitats on adjacent, native rangeland may be improved to attract wildlife away from reclamation sites, possibly enhancing big sagebrush survival. Prescribed burning, mechanical practices (mowing, roto-beating), and other treatments of adjacent native big sagebrush-dominated rangeland that increase herbaceous plant production, improve forage quality, and enhance plant diversity may help distribute wildlife. Interseeding perennial grasses and forbs, combined with management of overmature big sagebrush stands, could improve adjacent native landscape condition and improve big sagebrush survival on reclaimed areas by increasing wildlife distribution.

Improving wildlife distribution and enhancing rangeland forage quality may not be enough. Therefore, wildlife population management may also be necessary at some mines. Wildlife are attracted to reclamation areas for foraging on freshly seeded plant species, including big sagebrush seedlings. In addition, wildlife are provided protection from human disturbance by restricted public access and prohibition of hunting within the mine permit area. Wildlife populations might be better managed on theses reclaimed areas if mining companies would consider allowing limited harvesting (hunting) by methods compatible with the mine environment and considerations.

Evaluating the impacts of wildlife browsing on big sagebrush survival is necessary for all mines trying to reestablish big sagebrush and other shrub species. This study has additional value as a demonstration site for illustrating long-term differences between browsed (outside exclosure) and unbrowsed (inside exclosure) big sagebrush years after project completion. Recommendations to reduce wildlife browsing impacts on big sagebrush, as a byproduct of this research, will hopefully result in more successful reclamation by mining companies and provide improved wildlife habitat.

Acknowledgments

The authors would like to acknowledge the assistance of Matt Mortenson, Cliff Bowen, Lachlan Ingram, Krissie Peterson, Margaret Sharp, and Kelli Sutpfin in field data collection. We would also like to acknowledge Powder River Coal Co., North Antelope/Rochelle Complex, Peabody Energy Co., Gillette, WY, and Abandoned Coal Mine Land Research Program, Office of Research, University of Wyoming, and the Wyoming Department of Environmental Quality, Abandoned Mine Land Division, Cheyenne, WY, for partial funding of this research.

References

Anderson, J. E.; Schumar, M. L. 1986. Impacts of black-tailed jackrabbits at peak population densities on sagebrush-steppe vegetation. Journal of Range Management. 39: 152–156.

Beetle, A. A. 1960. A study of sagebrush: the section *tridentata* of *Artemisia*. Bull. 368. Laramie: Wyoming Agricultural Experiment Station. 83 p.

Cockrell, J. R.; Schuman, G. E.; Booth, D. T. 1995. Evaluation of cultural methods for establishing Wyoming big sagebrush on mined lands. In: Schuman, G. E.; Vance. G. F., eds. Decades later: a time for reassessment. Proceedings of 12th annual meeting, American Society for Surface Mining and Reclamation; 1995 June 5–8; Gillette, WY. Princeton, WV: 784–795.

Craven, S. R. 1983a. Cottontail rabbits. In: Timm, R. M., ed. Prevention and control of wildlife damage. Lincoln, NE: Great Plains Agricultural Council Wildlife Resources Committee and University of Nebraska Cooperative Extension Service: D69–D74.

Craven, S. R. 1983b. Deer. In: Timm, R. M., ed. Prevention and control of wildlife damage. Lincoln, NE: Great Plains Agricultural Council Wildlife Resources Committee and University of Nebraska Cooperative Extension Service: D23–D34.

DePuit, E. J. 1988. Shrub establishment on drastically disturbed lands. In: Fisser, H. G., ed. Proceedings of the seventeenth

Wyoming shrub ecology workshop; 1988 June 21–22; Jackson, WY. Laramie: University of Wyoming: 55–60.

Glassey, T. W.; Dunnewald, T. J.; Brock, J.; Irving, H. H.; Tippetts, N.; Rohrer, C. 1955. Campbell County soil survey, Wyoming. Soil Conservation Service, Number 22. Washington, DC: U.S. Department of Agriculture, United States Government Printing Office.

Kelsey, R. G. 1984. Foliage biomass and crude terpenoid productivity of big sagebrush. In: McArthur, E. D.; Welch, B. L., comps. Proceedings: symposium on the biology of *Artemisia* and *Chrysothamnus*; 1984 July 9–13; Provo, UT. Gen. Tech. Rep. INT-200. Ogden, UT: U.S. Department of Agriculture, Forest Service, Inermountain Research Station: 375–388.

Knight. J. E. 1983. Jackrabbits. In: Timm, R. M., ed. Prevention and control of wildlife damage. Lincoln, NE: Great Plains Agricultural Council Wildlife Resources Committee and University of Nebraska Cooperative Extension Service: D75–D80.

Krebs, C. J. 1999. Ecological methodology. New York: Harper and Row, Publishers.

McNaughton, S. J. 1983. Compensatory plant growth as a response to herbivory. Oikos. 40: 329–336.

Schemnitz, S. D. 1983. Pronghorn antelope. In: Timm, R. M., ed. Prevention and control of wildlife damage. Lincoln, NE: Great Plains Agricultural Council Wildlife Resources Committee and University of Nebraska Cooperative Extension Service: D1–D4.

Schuman, G. E.; Booth, D. T.; Cockrell, J. R. 1998. Cultural methods for establishing Wyoming big sagebrush on mined lands. Journal of Range Management. 51: 223–230.

Schuman, G. E.; Belden, S. E. 2002. Long term survival of direct seeded Wyoming big sagebrush on a reclaimed mine site. Arid Land Research and Management.16: 309–317.

Stahl, P. D.; Williams, S. E.; Christensen, M. 1988. Efficacy of native vesicular-arbuscular mycorrhizal fungi under severe soil disturbance. New Phytology. 110: 347–354.

Wambolt, C. L. 1996. Mule deer and elk foraging preference for four sagebrush taxa. Journal of Range Management. 49(6): 499–503.

Welch, D. L.; McArthur, E. D.; Davis, J. N. 1981. Differential preference of wintering mule deer for accessions of big sagebrush and for black sagebrush. Journal of Range Management. 32: 467-469.

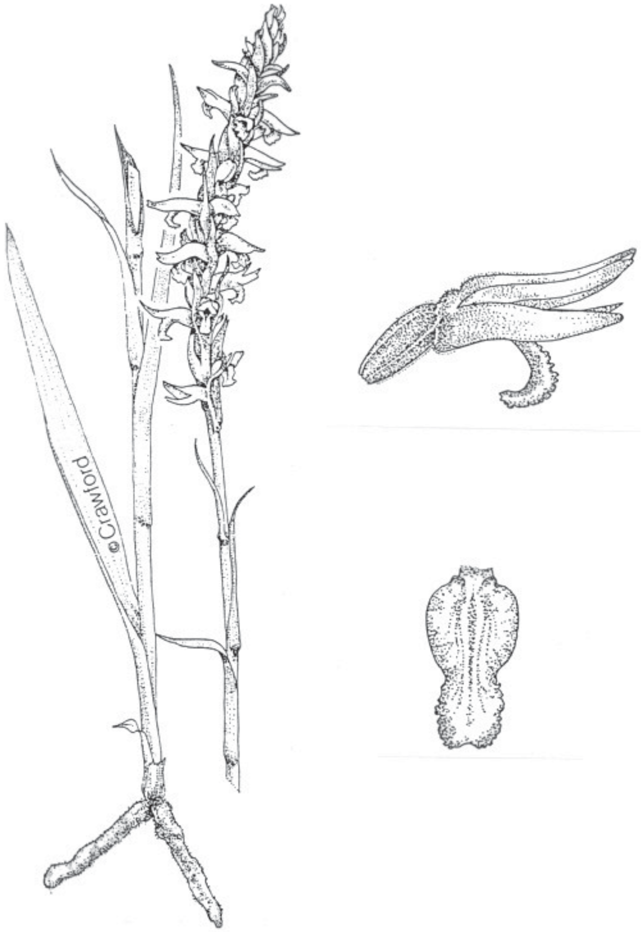
Western Water Consultants and Bureau of Land Management. 1998. Environmental impact statement for the Powder River Coal Lease Application and the Thundercloud Coal Lease Application. Sheridan, WY: Western Water Consultants; and Casper, WY: U.S. Department of the Interior, Bureau of Land Management.

White, J. A.; Munn, L. C.; Williams, S. E. 1989. Edaphic and reclamation aspects of vesicular-arbuscular mycorrhizae in Wyoming Red Desert soils. Soil Science Society of America Journal. 53: 86–90.

Wyoming Department of Environmental Quality, Land Quality Division. 1996. Coal rules and regulations. Chapter 4, Appendix A. Cheyenne: State of Wyoming.

Young, J. F.; Singleton, P. C. 1977. Wyoming general soil map. Research Journal 117. Laramie: University of Wyoming, Wyoming Agricultural Experiment Station.

Field Trips



Spirdiluv

Illustration on the reverse side is by Carolyn Crawford. In: Fertig, W.; Refsdal, C.; Whipple, J. 1994. Wyoming rare plant field guide. Cheyenne: Wyoming Rare Plant Technical Committee. Available at: http://www.npwrc.usgs.gov/resource/distr/others/wyplant/species.htm (Accessed 12/18/03).

Research at the High Plains Grasslands Research Station

D. T. Booth
J. D. Derner

Abstract: During the 12th Wildland Shrub Symposium, August 12 to 16, 2002, in Laramie, WY, field trip participants visited the High Plains Grasslands Research Station in Cheyenne. The Station is operated by the U.S. Department of Agriculture, Agricultural Research Service on land owned by the city of Cheyenne. The tour included a chance to visit the historic setting, tour facilities, and listen to presentations by Station scientists and cooperating investigators. Cooperators include the University of Wyoming and Colorado State University; U.S. Department of the Interior, Bureau of Land Management, Wyoming State Office; and the U.S. Department of Agriculture, Natural Resources Conservation Service, Grazing Lands Team.

Introduction

The High Plains Grasslands Research Station (HPGRS) is headquarters for the U.S. Department of Agriculture, Agricultural Research Service, Rangeland Resources Research Unit (RRRU). Besides the Cheyenne Station, the unit has field, office, and laboratory resources at the Central Plains Experimental Range (CPER), northeast of Nunn, CO, and offices and laboratories at the Crops Research Laboratory in Fort Collins, CO. The two field locations (HPGRS and CPER) are separated by less than 25 miles but have contrasting vegetation that greatly enhances research opportunities (table 1). The HPGRS is located at the southern end of the northern mixed-grass prairie, while the CPER is located at the northern edge of the shortgrass prairie. The CPER is also a part of worldwide Long-Term Ecological Research (LTER; http://lternet.edu). The research unit has a strong plant-animal-soil focus with a breadth of scientific expertise that has undergone some changes with two scientist retirements and two new scientists hired in 2002 (table 2).

History

In 1928, the 70th U.S. Congress authorized and directed the U.S. Department of Agriculture to establish an experimental station near Cheyenne, WY (Schuman 1989). To that end, 2,139 acres (a third of which was irrigable) were leased from the city of Cheyenne for 199 years at $1 per year. The station was named the Central Great Plains Field Station and was meant to complement the Northern Great Plains Field Station at Mandan, ND, and the Southern Great Plains Field Station at Woodward, OK. The first Superintendent at Cheyenne was Robert Wilson (1928 to 1930), and construction of the buildings began in June 1928. In 1930, A. C. Hildreth (1930 to 1959) became the Superintendent, the Station was renamed the Cheyenne Horticultural Field Station, and the first plantings of trees, shrubs, fruits, and vegetables were made.

The following year construction of the initial buildings was completed, and the first of numerous shelterbelts and landscape plantings were made on Federal, State, and local cooperating government lands. During the ensuing years of shelterbelt research, an additional 323 shelterbelts were planted on cooperating private farms in Wyoming, Colorado, Nebraska, Kansas, Utah, and South Dakota. This planting effort was facilitated by a Civilian Conservation Corp camp of 200 men opened on the Station in 1935. In its 7-year history the Corp constructed roads, water and septic systems, and over 2 miles of concrete-lined irrigation ditches, in addition to planting thousands of trees and shrubs.

Besides the shelterbelt research, over 1,300 varieties of fruit trees and 300 varieties of small fruits like raspberries, currants, gooseberries, and strawberries were included in varietal tests seeking strains adapted to the cold and drought of the High Plains. Many native strawberries (4,200 collections) were obtained from the Rocky Mountain area from Montana to New Mexico. These collections later led to the release of several strawberry varieties including Radiance, Ogallala, and Fort Laramie.

The Station's mission was broadened in 1936 to include forage crop research, and over 200 species and varieties of grass were established to evaluate their yield potential, hardiness, and nutritive value. The first horticultural findings from Station research were published that year, and in 1940 publication of the first Station grass research followed.

In 1942, Hildreth and others were temporarily reassigned to California to study the guayule plant as an alternative rubber source. Later Hildreth helped establish an agricultural experiment station in Afghanistan as part of his official duties. He retired in 1959, and L. A. Schaal became Superintendent in 1960. Schaal initiated a potato research program in 1961 in cooperation with the USDA station in Greeley, CO, and the University of Wyoming. In 1962 the Station published fruit-tree test results covering 28 years and 1,200 apple, 300 plum, 50 cherry, and 40 pear varieties. Gene Howard initiated carnation and chrysanthemum research after becoming superintendent in 1964. The Cheyenne Hardy Mums were named Cheyenne's official flower in

---

In: Hild, Ann L.; Shaw, Nancy L.; Meyer, Susan E.; Booth, D. Terrance; McArthur, E. Durant, comps. 2004s. Seed and soil dynamics in shrubland ecosystems: proceedings; 2002 August 12–16; Laramie, WY. Proceedings RMRS-P-31. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

D. T. Booth and J. D. Derner are Rangeland Scientists, U.S. Department of Agriculture, Agricultural Research Service, High Plains Grasslands Research Station, 8408 Hildreth Road, Cheyenne, WY 82009, U.S.A., e-mail: tbooth@lamar.colostate.edu

Table 1—Characteristics of research field locations.

Characteristics	High Plains Grasslands Research Station Cheyenne, WY	Central Plains Experimental Range Nunn, CO
Size	2,870 acres	15,500 acres
Annual precipitation	14.6 inches	12.8 inches
Rangeland type	Mixed-grass prairie	Shortgrass prairie
Annual production	1,380 pounds per acre	625 pounds per acre

Table 2—High Plains Grasslands Research Station scientists and field of expertise.

Name	Title	Research
Jack Morgan	Plant Physiologist	Carbon and water fluxes, global climate change
Gerald Schuman	Soil Scientist	Carbon sequestration, reclamation of degraded lands
Terrance Booth	Rangeland Scientist	Revegetation, remote sensing for rangeland monitoring
Jean Reeder	Soil Scientist	Nutrient cycling, belowground processes, carbon sequestration
Justin Derner[a]	Rangeland Scientist	Rangeland monitoring and health, grazing management
Dana Blumenthal[a]	Weed Ecologist	Invasive species, global change
Richard Hart, retired	Agronomist	Grazing management
Gary Frasier, retired	Hydrologist	Rangeland hydrology

[a] Newly hired.

1970. Then in 1974 Howard had the task of terminating the horticultural research program—fruits, flowers, vegetables, and shelterbelts—and of developing a program directed toward grazing management, water conservation, and mined-land reclamation. As part of the program redirection the Station was renamed the High Plains Grasslands Research Station and several new staff members were added.

Richard Hart became Location Leader (Superintendent) in l976, and the first papers derived from the Station's new grassland research mission were published. Additional land was acquired from F. E. Warren Air Force Base, enabling further development of livestock grazing research. In 1981, Gerald Schuman became the Location Leader and continued in that capacity until 1998. During that time grazing management and mined-land reclamation were the predominant research activities, and research findings contributed to improved stocking rate recommendations for rangelands, and to increasingly successful techniques for mined land reclamation. Jack Morgan assumed leadership responsibilities in 1998 and implemented new research with a focus on carbon sequestration, rangeland monitoring and health, management strategies for mitigation of global climate change, and invasive species.

New Changes to Meet the Challenges of the Twenty-First Century

Rangeland monitoring and health, invasive species, and improved land management strategies will be the primary research foci for the HPGRS in the early part of the new century. Research will continue to target systems-level questions that are pertinent to both private and public land issues (grazing, revegetation, weed management), but these practices will be addressed in the context of the ecological system and sustaining rangeland health. While research will continue at the HPGRS and CPER field sites, Station scientists will expand their research into the sagebrush steppe vegetation that is prominent throughout much of Wyoming. New research projects targeted to address public lands questions pertinent to the sagebrush steppe vegetation include determining above- and belowground carbon budgets following changes in land management and utilizing very large scale aerial (VLSA) imagery as a method to assess and monitor vegetation change.

The High Plains Grasslands Research Station has a long history of providing practical information for land managers and of reacting to the needs of local, State, and national customers. To this end, HPGRS scientists will continue to investigate innovative approaches to land management that combine emerging technologies and customer-oriented products. Our mission is to learn how plants, soil, water, atmosphere, weather, and management interact on grazing lands, and to use the resulting knowledge to promote sustainable and profitable management systems producing desired goods and services.

Reference

Schuman, G. E. 1989. Cheyenne Horticultural Field Station/High Plains Grasslands Research Station. In: Field, S. L., ed. History of Cheyenne, Wyoming-Laramie County. Vol. 2. Dallas, TX: Curtis Media Corporation: 55–56.

Appendix A: Agenda for Wildland Shrub Symposium Field Trip to the High Plains Grasslands Research Station

Wednesday, August 14, 2002

8:00 a.m.	Leave Laramie and travel to the High Plains Grasslands Research Station via Happy Jack Road
9:00	Welcome to the High Plains Grasslands Research Station by Jack Morgan, Research Leader
	Oral presentation in main office building.
9:10 & 10:00	Plant and animal responses to grazing systems at the High Plains Grasslands Research Station by Justin Derner and Jim Waggoner
	Poster presentations at picnic area (presenters will be at their posters until 11:20)
	Elevated CO_2 enhances production but reduces forage quality in perennial grasses of the shortgrass steppe - Jack Morgan
	Influence of livestock grazing on carbon sequestration in a semiarid mixed-grass and short-grass rangelands - Jean Reeder and Gerald Schuman
	Effect of interseeded Falcata alfalfa on carbon sequestration and production of a mixed-grass rangeland - Gerald Schuman
	Transplantable container for rangeland shrub revegetation - Terrance Booth
	Presentation at the airplane:
	Rangeland monitoring using very large scale imagery - Terrance Booth, Joe Nance, and Sam Cox
11:20	Break (visit labs, see Seed Growth Robot-2 and Wyoming big sagebrush seed orchard, or visit with staff)
12:00	Leave the High Plains Grasslands Research Station for Cheyenne's botanical garden and Lion's Park.
	A sack lunch will be served at Lion's Park followed by a tour of the botanical gardens or just enjoy the park.
1:30 p.m.	Leave Lion's Park for Terry Bison Ranch
2:00	Arrive Terry Bison Ranch and visit about ranch forage resources and grazing management.
3:00	Return to Laramie via I-80

Soils and Vegetation of the Snowy Range, Southeastern Wyoming Wildland Shrub Symposium Field Trip: Laramie to Woods Landing, Riverside, Libby Flats, and Centennial, Wednesday, August 14, 2002

Larry Munn
C. Lynn Kinter

Laramie, Wyoming, was established as a railroad construction town in May, 1868. The transcontinental railroad (Union Pacific) came across the Rockies in the late 1860s, across the then unsettled landscape that now contains Cheyenne and Laramie, after a southern route through Colorado was rejected because of the terrain. A relic of the Tertiary Ogallala formation called the “Gangplank” west of Cheyenne provided an access ramp across the mountains; this was the first place north of Denver where it was feasible to build the railroad. It was also the first place west of Missouri that railroad ties could be cut from the surrounding forests, and railroaders timbered for ties extensively in the Laramie and Snowy Ranges (about 3,000,000 ties were cut by 1870). The “tie hacking” continued until World War II. “Tie hacks” would cut mid-sized trees of 12 to 14 inches (30 to 35 cm) diameter in the winter, cutting flats on two opposing sides of the tree with a broad axe and piling 8-ft (2.4-m) lengths into creeks all winter, behind a temporary dam. In spring, when runoff waters were high, the dams were dynamited, and they had a log run! The fishery biologists are still trying to restore fish habitat in some of the drainages in the Snowy Range where channels were extensively gouged by these log runs.

Today, you can still see standing stumps from tie-hack activity in the Laramie and Snowy Ranges—often they are 3 to 4 ft (0.9 to 1.2 m) tall because the hacks were cutting in deep snow. These forests provided ties from Laramie to Rawlins and Rock Springs, 200 miles away, at which point ties were cut from the forests to the south of the track in the Uinta Range. At the peak of the steam engine period, the trains also used 2 million gallons of water each day from the Laramie River. Stops along the track where coal and water were available developed into towns, for example, Rawlins and Rock Springs. We left town heading southwest via Highway 230. Elevation at Laramie is 7,170 ft (2,185 m), and precipitation is 10.5 inches (26 cm), most of which falls in March through July.

Stop 1: University of Wyoming, Monolith Ranch by the fishing access to a Laramie River site with greasewood (*Sarcobatus vermiculatus*). This is an area that was farmed at the turn of the last century. In 1906, a grain elevator capable of loading 50,000 bushels onto railroad cars daily was built in Laramie. By 1920, failed farms were being consolidated into ranches. Greasewood, a highly salt-tolerant shrub, is increasing here between the Pioneer Canal (dug in 1890, visible along the hillside to the west and north) and the Laramie River to the southeast. The greasewood is expanding from canal seepage water that for the last hundred years has permeated the unlined canal into the underlying Niobrara formation (a Cretaceous age marine shale and sandstone). Other salt-tolerant plants include alkali sacaton (*Sporobolus airoides*) and saltbush (*Atriplex* sp.). Soils here are apparently increasing in salinity over time as a result of an accumulation of very soluble salts from the canal seepage water. The soils on this geomorphic surface are Aridisols (Calcids with frigid temperature regimes), which typically have calcic horizons and significant amounts of gypsum in the subsoil.

Stop 2: Fox Creek Road. Here we are on an alluvial fan extending from a canyon. The soils have a fairly thick profile; however, they are not well developed (no B horizons), but do have a mollic epipedon. Elevation at the site is 7,800 ft (2,377 m), and annual precipitation is approximately 16 inches (40 cm). There is a pronounced aspect effect here, between north- and south-facing slopes. Soils on the landscape are Mollisols (Haplustolls) on the drier south slopes; on the wetter, north-facing slopes the soils are Inseptisols (Dystrocryepts). There is also a pronounced aspect difference between north- and south-facing slopes in

---

In: Hild, Ann L.; Shaw, Nancy L.; Meyer, Susan E.; Booth, D. Terrance; McArthur, E. Durant, comps. 2004. Seed and soil dynamics in shrubland ecosystems: proceedings; 2002 August 12–16; Laramie, WY. Proceedings RMRS-P-31. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Larry Munn is Professor and Soil Scientist, Department of Renewable Resources, University of Wyoming, Laramie, WY; e-mail: LCMunn@uwyo.edu. C. Lynn Kinter is Botanist and Doctoral Candidate, School of Biological Sciences, Washington State University.

terms of the trees present: lodgepole pine (*Pinus contorta*), subalpine fir (*Abies lasiocarpa*), Englemann spruce (*Picea engelmannii*), and Douglas-fir (*Pseudotsuga menziesii*) on north-facing slopes; ponderosa pine (*Pinus ponderosa*), limber pine (*Pinus flexilis*), and Rocky Mountain juniper (*Juniperus scopulorum*) on the south-facing slopes. Dry open sites are dominated by mountain big sagebrush (*Artemisia tridentata* var. *vaseyana*), common rabbitbrush (*Chrysothamnus nauseosus*), and Idaho fescue (*Festuca idahoensis*). Narrowleaf cottonwood (*Populus angustifolia*), balsam poplar (*Populus balsamifera*), mountain alder (*Alnus incana*), willows (*Salix* spp.) and choke-cherry (*Prunus virginiana*) grow in the riparian area along Fox Creek. Chokecherries are an important food supplement for black bears; there are approximately 100 bears in the Snowy Range. This is an area that is used heavily by deer and elk as winter range, so you may see signs prohibiting offroad travel during the winter months.

Along the Highway: As we travel to higher elevations near the southern end of the Snowy Range, we drive past the road to the old sawmill settlement at Fox Park. At one time, the Forest Service had a small workstation there. The sawmill is closed now, and the area is largely private cabins.

The Fox Park area was extensively burned 150 to 200 years ago. It is a large area of fairly uniform lodgepole pine forest interspersed with moist shrub meadows along streams. In the coniferous forest, understory shrubs such as whortleberry (*Vaccinium scoparium*) and bearberry (*Arctostaphylos uva-ursi*) provide important forage for wildlife. Soils here are primarily Alfisols (Haplocryalfs), and in the meadows are wet Mollisols (Cryaquolls) or wet Inceptisols (Cryaquepts). This area of the Snowy Range was not glaciated, and the soils are relatively well developed (thicker Bt horizons) and contain more clay than soils on the younger, glaciated landscapes we will travel over later in the trip. Consequently, the water-holding capacity of these soils is greater, and the forests are more productive. Underlying geology here at the southern end of the Snowys is a complex of granitic, felsic, and hornblende gneiss, as well as amphibolite.

As we continue past Mountain Home we see several meadows with Wyoming big sagebrush (*Artemisia tridentata* var. *wyomingensis*). This is important habitat for wildlife that often finds limited food under the conifers. These areas also provide nesting habitat for numerous species of birds.

Next, the highway crosses briefly into northern Colorado. Here, we find larger openings of sagebrush grassland. You might notice on the surrounding hills that in the past, the Forest Service allowed rather large clearcuts. These are currently revegetated in aspen (*Populus tremuloides*) or young conifers, but are still clearly identifiable by the size of the trees. Today, logging cuts are more considerate of wildlife habitat needs, are generally smaller, and are done to create irregular contours and are thus less apparent in the early regrowth phase.

Our path has followed a former railroad track bed; the rails have now been removed. This railroad went from Laramie to North Park Colorado and was built in about 1910 to haul wood products from the Fox Park area and coal from a mine in North Park, Colorado. That coal mine has been shut down for almost 20 years now and the rails and ties were sold for scrap.

As we begin to turn north into Wyoming, on the slopes to the south of the road, remains a scar from a fairly large fire where an extensive stand of conifers burned about 10 to 15 years ago. That is a common story here in the Northern Rockies where through fire control we have allowed canopy closure in the forest on many sites that were probably more open historically. The first fire control plan was established on the Medicine Bow National Forest in 1912. These sites now are contributing to the fire problem in the West because current fires are typically hotter and extend over much larger areas than those that occurred prior to fire suppression.

On the north side of the road, there is an old copper mine. Though much more hard rock mining occurred in Colorado than in Wyoming, the Snowy Range does contain a series of gold mines and copper mines. Over in the Sierra Madres to the west of us, there was a copper mine with a smelter in Encampment, a town we will come to later in the trip.

As we pass the North Platte River we can see that it has fairly low flow this year, reflecting the drought we have been experiencing here in Wyoming for the past 3 to 5 years. As we drive along the Platte River Valley toward Saratoga, we see a landscape that is underlain by Tertiary age geologic materials (Upper Miocene, approximately 20 million years old). The geologic formation is the North Park Formation. There are small areas of older Eocene deposits along the southwest fringe of the basin. The small hills to the east along the highway are granite, and you may get some feeling of the filling of the basin with Tertiary valley fill materials. The geologic materials we are driving over were eroded from the top of the adjacent mountains as they were uplifted during the Tertiary. At several times during the Tertiary, the intermountain basins were largely filled with alluvium eroded off the rising mountains. Then, during periods of quietus in mountain uplift, the streams eroded much of the sediment from the basins toward the Gulf of Mexico. We are now apparently in a period when the uplift is relatively quiet and the basins are being exhumed slowly by geologic erosion. The light-colored sediments that show on hillsides along the road are exposures of the Tertiary valley fill.

We are now in a rolling vista of Wyoming big sagebrush (*Artemisia tridentata* var. *wyomingensis*) and several species of wheatgrass (*Agropyron* spp.). We also see areas where the sagebrush was sprayed for control—as shown by the delineations across the landscape.

Stop 3: We turn off at the Six Mile Road access to the National Forest. After traversing an area of private land, we reach a fishing access by the Platte River that is very important winter range for elk, deer, and bighorn sheep. The Wyoming Game and Fish Department estimates that there are approximately 6,500 elk and 250 bighorn sheep in the Snowy Range at present. About 600 elk and many of the sheep winter in this area.

The elevation at the Six Mile access to the Platte River is 7,500 ft (2,286 m). and the precipitation is about 16 inches (40 cm). This area was burned about 6 years ago for wildlife habitat improvement. Most burning is done in April to catch a window when the snow has melted from the sagebrush but is still present in the trees. This timing also prevents damage to root systems of shrubs like bitterbrush (*Purshia tridentata*), which sprout from the roots if the fires are not too hot. The road was used as a firebreak. Below the road and to the north up the slope you can see an area that was burned; the south side of the road represents the unburned condition. The burned area appears to have good regrowth of bitterbrush and shrubby cinquefoil (*Potentilla fruticosa*) and good recruitment of sagebrush seedlings. The soils here are Mollisols over the rolling topography with Inceptisols, and Entisols (Lithic Cryorthents) on the steeper slopes where the rocks are close to the surface.

Along the highway, driving north from the Six Mile access road, the areas without sagebrush were cleared for hay or wheat production. Much of the acreage formerly farmed with wheat in Wyoming has now been abandoned; the climate is too dry and cold, and the Conservation Reserve Program provided a good incentive for many farmers to revegetate back into rangeland.

Stop 4: Forest Service campground at Ryan Park. This area was the site of a Civilian Conservation Corps camp in the 1930s and was a prisoner of war camp during World War II. There was a rather short ski slope here also.

Medicine Bow National Forest via Highway 130. As we follow the creek you may see very telltale signs of glaciation. Ice collected on the north end of the Snowy Range on numerous occasions during the Pleistocene; and glaciers moved from the top of the range to the north, east, and west of Medicine Bow Peak. The ice carried glacial till across the landscape and down the major drainages. We are now driving along a moraine of Pinedale age (Late Wisconsin age; approximately 25,000 to 12,000 years before present). You can see the boulders imbedded in fine material jutting out of the roadcuts. Most of the soils on the moraines are Inceptisols because of their relatively young age, given the cool climate under the forest. Blocks of white rock are very distinctive in the till; they are the Medicine Peak quartzite from the highest crest of the Snowy Range. We will eventually drive beside the cliffs from which these rocks are derived; the rock was extracted by the ice and carried down the slopes in the French Creek watershed. The quartzite represents an old beach (2 billion years old!) and provides a good way to trace glacial activity from the north part of the range. The glaciers moved north, toward Elk Mountain; west, via French creek where we travel along the stream; and eastward, via Libby Creek toward the town of Centennial. French Creek was named for a family of Arcadians, the De La Sol family, who came here to prospect for gold. They did establish a productive claim, but the family eventually sold the mine and moved further north in Wyoming where they bought and leased a lot of land to create what is now the largest ranch in the State—the Sun Ranch. Another creek in the area, Pelton Creek, was named after a man who came to the area originally as a guest of the Wyoming Territorial Prison, but who later became a respected Laramie citizen and businessman (after his release).

Stop 5: Forest Service Riparian Area Walkway. The elevation here is 8,700 ft (2,652 m), and the precipitation is approximately 26 inches (65 cm). The riparian system here is dominated by willows (*Salix* spp.), sedges (*Carex aquatilis, Carex microptera*, and others), tufted hairgrass (*Deschampsia cespitosa*), and bluejoint (*Calamagrostis canadensis*). Across the road to the north you can see a good exposure of the moraine; the till contains, again, the white Medicine Peak quartzite boulders derived from the crest of the Snowy Range. You can see the peaks in the distance by looking up the highway. Soils in the willow bottom are primarily wet Inceptisols (Histic Cryaquepts), which have a thin layer of organic material over stratified alluvium. The beaver ponds along the creek act as important sediment traps and slow the runoff of snowmelt waters through the summer months. Generally Histosols are only found in very high water table areas in the riparian zones, and in kettle holes in the Pinedale moraine.

Stop 6: At the Forest Service observatory on top of the summit. Elevation here is 10,845 ft (3,305 m). The ice here was perhaps 800 to 1,000 ft (244 to 305 m) thick during Bull Lake glaciation (corresponding to the Illinoian glaciation of the mid-continent 175,000 to 140,000 years ago) and again later during the Late Pinedale glaciation (25,000 to 12,000 years ago). There were smaller glaciers several thousand years ago during the Neoglaciation, which started about 4,000 years before present. Ice accumulation during the Neoglaciation was simply a major sheet of ice that covered the north and east slopes of the crest. Blocks of rock, loosened from the exposed crest by frost action, slid along the ice sheet and formed pro-talus ramparts that are now several hundred yards from the rock wall—thus indicating the dimensions of the ice sheet. The landscape contains Nash dolomite as the underlying bedrock and quartzite blocks deposited in a thin smear of till across this landscape. The inclusion of blocks of the Nash dolomite in the till serves to buffer the pH of the soils developed here, and this effect carries all the way down the valleys on either side of the Range.

Medicine Bow Peak at 12,005 ft (3,661 m) is the highest peak in the Snowy Range. The dark band that parallels the ridgeline is a mafic intrusion that is much more easily weathered than the white quartzite. On October 6, 1955, a four-engine commercial airliner crashed into the peak at about the mafic intrusion, killing all 36 people on board. Several engines and other parts of the plane are still present at the base of the cliff, and in a few more years they will be protected by the Antiquities Act; now they are just junk!

Krummholtz trees, many of which are Engelmann spruce, are common at this elevation. The Krummholtz growth form is created by blowing ice crystals shearing the needles and branches from the trees. Other vegetation in this area includes common juniper (*Juniperus communis*), cascade and arctic willows (*Salix cascadensis, S. arctica*), alpine fescue (*Festuca ovina*), and tufted hairgrass.

Along the ridge above French Creek, you can see 50-year-old clearcuts that have not revegetated because of the blowing snow and extremely harsh growing conditions at this elevation. This highway closes to travel each winter beginning with the first heavy snows in September or October and reopens usually by Memorial Day, although it has sometimes been closed through part of June.

Stop 8: Fen in a Kettle Hole on the Sand Lake Road. Elevation is 8,600 ft (2,621 m). Present on the fen are bog birch (*Betula glandulosa*) and at least four different willows, including planeleaved willow (*Salix planifolia*) and shortfruited willow (*S. brachycarpa*). On drier ground around the fen, you'll find mountain silver sagebrush (*Artemisia cana* var. *viscidula*).

The soil here is a Cryofibrist. The pH of this organic soil is controlled by Nash dolomite rocks in the moraines around the kettle hole. As that rock has weathered, it buffers the pH of the system, both for the mineral forest soils in the upland and the organic soil. These soils all have nearly neutral pH. Normally you would expect fairly acidic soils under the trees and also in a bog setting like this. But because the Nash Dolomite occurred near the point of ice collection, blocks of it were carried here, causing the neutral pH.

Organic soils occur in sites with poor drainage and high water tables in the Snowy Range. Their use here is limited by the short growing season. In warmer climates, Histosols are prized for high value crops such as vegetables because of their generally excellent properties as a growing media. Organic soils have high water-holding capacities (200 to 600 percent by weight) and do not have problems with aluminum toxicity that is common for acid mineral soils. Organic soils present special management problems if they are drained: they subside as microbes accelerate decomposition of the organic material in the newly well-aerated soil. After drainage, they also are prone to wind erosion and burning. Histosols have extremely low bearing strength and are unsuitable foundations for houses and roads. The soil has a very thin Oa horizon (approximately 5 cm) over perhaps 3 m of Oi horizons, underlain by a 2C (Pinedale till). The soil is a Fibrist at the suborder level of *Soil Taxonomy* because the fibers hold up well when rubbed; the inference is that they are only slightly decomposed.

In the bottom of the Libbey Creek drainage we are driving through very classic Pinedale moraines, short steep slopes with a lot of stone showing in the road cuts. The ridges above us to the south have Bull Lake till on them. During the Pinedale, glaciers cut the deep canyons. The Bull Lake glacier carried till further out into the basin, and as we pass through the terminal Pinedale moraine we come to a more smooth and rounded topography that is the terminal moraine of the Bull Lake glacier. The landscape on the terminal moraine of the Bull Lake glacier has a more rounded form and is still studded with boulders of quartzite. Wyoming big sagebrush grows here on the terminal moraine and around the slopes on the igneous rock. Once you get out into the alluvium in the center of the valley, you lose the sagebrush.

Along the road in the Centennial area at 8,000 ft (2,440 m) elevation, we again see sedimentary rock exposed in hogback ridges. The ridge above Centennial was the terminal moraine for the Bull Lake glaciation. There is a veneer of Bull Lake till above Centennial and a large outwash plain below the town. Sedimentary rock exposed south and west of the town includes some very red rocks of Jurassic and Triassic age. These have a very distinctively bright red chroma. The exposed sedimentary rocks support mountain mahogany stands (*Cercocarpus montanus*), along with bitterbrush, willows, and chokecherry. On the east side of the Centennial Valley there is a similar uplifted banding of sedimentary rock against the flank of Sheep Mountain.

Stop 9: Petrocalcic horizon (caliche) on high alluvial surface above the Big Hollow. This stop shows the maximum expression of carbonate accumulation in Wyoming. The soil is Typic Petrocalcid, loamy-skeletal, carbonatic, frigid. Horizons are Ak, Bk, Bkm, Bk', and 2C. The surfaces where this soil occurs are all on the order of 1,600,000 years plus. This Bkm horizon material is what the locals refer to as "caliche" in the Southwest. The laminar layer at the top of the Bkm indicates that water no longer penetrates it at all. The original parent material here was quartzite-rich alluvium from the Little Laramie River, and the carbonate accumulation represents a tremendous accumulation of dust over time. These petrocalcic horizons are a very effective "armor" against erosion for the old valley floors. The high surfaces in the southern Laramie Basin are old alluvial valley floors, which are still extant because of the protection afforded them by the petrocalcic horizons and alluvial cobble channel deposits which occur on them. Plants here include winter fat (*Krascheninnikovia lanata*), ricegrass (*Oryzopsis hymenoides*), and wheatgrasses.

Along the Highway to Laramie: The Big Hollow is the largest deflation feature in North America, and you can see the entire rim around the Hollow. Apparently wind was channeled between Sheep and Jelm Mountains, and scoured out the hollow during Late Pleistocene time. The rims on either side are actually old alluvial valley floors, and the cobbles from the alluvium protected those surfaces on the north and south from erosion. The area where the basin lies would have been a small shale hill complex prior to the deflation. The shale hill in the distance is an example of the landscape before the topographic reversal. The shale hill was in place when the alluvial valleys were deposited on either side, but was much softer and eroded away, and so you now have a depression. Where the alluvial valley floors ran from the mountains toward Laramie on either side of that shale hill, the alluvium protected those surfaces from erosion. Today, they are still intact and stand high above the Hollow. The small pumping station is the southern end of the Quealy Dome oilfield. The pumping station reflects current oil prices; when prices are high (above $24 per barrel), the well is active, and when prices fall below that mark, the field is closed down.

The white rock that you can see in the distance is cretaceous Niobrara chalk formation. The Niobrara formation underlies the alluvial valley floor that we follow all the way into Laramie. Between here and town, ground water availability is poor, and livestock owners have dug stock ponds. By placing snow fence around the pond, they can successfully trap blowing snow in wet winters to collect stock water on these high surfaces for use in the summer.

Return to the University of Wyoming Campus.

References

Case, J. C.; Arneson, C. S.; Hallberg, L. L. 1998. Preliminary 1:500,000-scale digital surficial geology map of Wyoming: Wyoming State Geological Survey, Geologic Hazards Section Digital Map 98-1 (HDSM 98-1). Laramie: Wyoming State Geological Survey.

Hausel, W. D. 1993. Guide to the geology, mining districts, and ghost towns of the Medicine Bow Mountains and Snowy Range Scenic Byway. Public Inf. Circ. 32. Laramie: The Geological Survey of Wyoming. 53 p. plus maps.

Kim, H. B. 1993. Soil morphology and genesis along an elevational transect, Snowy Range and Laramie Basin, Wyoming. Laramie: University of Wyoming. Thesis.

Love, J. D.; Christianson, A. C. 1985. Geology of Wyoming. Reston, VA: U.S. Department of the Interior, U.S. Geologic Survey.

McCahon, T. J.; Munn, L. C. 1991a. Morphology and genesis of paleosols in the Medicine Bow Mountains, Wyoming. Soil Science. 152: 472–484.

McCahon, T. J.; Munn, L. C. 1991b. Soils developed in Late Pleistocene till, Medicine Bow Mountains, Wyoming. Soil Science. 152: 377–388.

Mears, B., Jr. 2001. Glacial records in the Medicine Bow Mountains and Sierra Madre of southern Wyoming and adjacent Colorado, with a traveler's guide to their sites. Public Inf. Circ. 41. Laramie: The Geological Survey of Wyoming. 26 p.

Mitchell, R. A. 1985. Characterization and interpretation of a buried paleocatena near Jelm Mountain, Wyoming. Laramie: University of Wyoming. Thesis.

Munn, L. C. 1987. Soil genesis associated with periglacial ice wedge casts, southcentral Wyoming. Soil Science Society of America Journal. 51: 1000–1004.

Munn, L. C. 1992. Periglacial features as sources of variability in Wyoming Aridisols. In: Kimble, J. M., ed. Proceedings of the sixth international correlation meeting (VI:ISCOM) characterization, classification and utilization of cold Aridisols and Vertisols. Lincoln, NE: Soil Conservation Service, National Soil Survey Center: 133–137.

Munn, L. C. 1993. Effects of prairie dogs on soils and associated plant communities. In: Oldemeyer, J. L.; Biggins, D. E.; Miller, B. J.; Crete, R., eds. Management of prairie dog complexes for the reintroduction of the black-footed ferret. Biological Rep. 13. Washington, DC: U.S. Department of the Interior, Fish and Wildlife Service: 11–17.

Munn, L. C.; Spackman, L. K. 1991. Soil genesis associated with periglacial ground wedges, Laramie Basin, Wyoming. Soil Science Society of America Journal. 55: 772.

Nelson, B. E. 1984. Vascular plants of the Medicine Bow Range. Laramie, WY: Jelm Mountain Press.

Rahman, S.; Munn, L. C.; Vance, G. F.; Arneson, C. 1997. Wyoming Rocky Mountain forest soils: mapping using an ARC/INFO geographic information system. Soil Science Society of America Journal. 61: 1730–1737.

Reider, R. G.; Gurley, S. R. 1975. Pre-Wisconsin paleosols and related soils on the South French Creek-Middle Fork (Little Laramie River) interfluve, Medicine Bow Mountains, Wyoming. Contributions to Geology. 14: 41–49.

Reider, R. G.; Kuniansky, N. J.; Stiller, D. M.; Uhl, P. J. 1974. Preliminary investigation of comparative soil development of Pleistocene and Holocene geomorphic surfaces of the Laramie Basin. In: Wilson, M., ed. Applied geology and archeology: the Holocene history of Wyoming. Geological Survey of Wyoming Rep. Invest. 10. Laramie: Wyoming Geological Survey: 27–33.

Soil Survey Staff. 1999. Soil taxonomy: a basic system of soil classification for making and interpreting soil surveys. 2d ed. USDA-SCS Agric. Handb. 436. Washington, DC: U.S. Government Printing Office.

Spackman, L. K.; Munn, L. C. 1984. Genesis and morphology of soils associated with formation of Laramie Basin (Mima-like) mounds. Soil Science Society of America Journal. 48: 1384–1392.

Thybony, S.; Rosenberg, R. G.; Rosenberg, E. M. 2001. The Medicine Bows, Wyoming's mountain country. Caldwell, ID: Caxton Press. 180 p.

You may order additional copies of this publication by sending your mailing information in label form through one of the following media. Please specify the publication title and number.

Fort Collins Service Center

Telephone	(970) 498-1392
FAX	(970) 498-1396
E-mail	rschneider/@fs.fed.us
Web site	http://www.fs.fed.us/rm
Mailing Address	Publications Distribution Rocky Mountain Research Station 240 Prospect Road Fort Collins, CO 80526

Pesticide Precautionary Statement

RMRS
ROCKY MOUNTAIN RESEARCH STATION

The Rocky Mountain Research Station develops scientific information and technology to improve management, protection, and use of the forests and rangelands. Research is designed to meet the needs of National Forest managers, Federal and State agencies, public and private organizations, academic institutions, industry, and individuals.

Studies accelerate solutions to problems involving ecosystems, range, forests, water, recreation, fire, resource inventory, land reclamation, community sustainability, forest engineering technology, multiple use economics, wildlife and fish habitat, and forest insects and diseases. Studies are conducted cooperatively, and applications may be found worldwide.

Research Locations

Flagstaff, Arizona
Fort Collins, Colorado*
Boise, Idaho
Moscow, Idaho
Bozeman, Montana
Missoula, Montana
Lincoln, Nebraska
Reno, Nevada
Albuquerque, New Mexico
Rapid City, South Dakota
Logan, Utah
Ogden, Utah
Provo, Utah
Laramie, Wyoming

*Station Headquarters, 240 West Prospect Road, Fort Collins, CO 80526