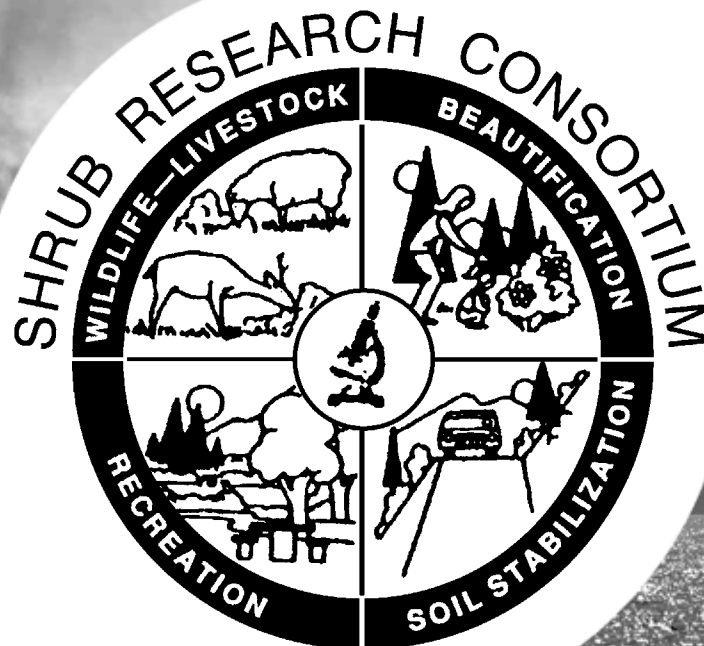


Proceedings: Shrubland Dynamics—Fire and Water

Lubbock, TX, August 10-12, 2004



United States Department of Agriculture
Forest Service
Rocky Mountain Research Station



Proceedings RMRS-P-47
July 2007

Sosebee, Ronald E.; Wester, David B.; Britton, Carlton M.; McArthur, E. Durant; Kitchen, Stanley G., comps. 2007. **Proceedings: Shrubland dynamics—fire and water; 2004 August 10-12; Lubbock, TX.** Proceedings RMRS-P-47. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 173 p.

Abstract

The 26 papers in these proceedings are divided into five sections. The first two sections are an introduction and a plenary session that introduce the principles and role of the shrub life-form in the High Plains, including the changing dynamics of shrublands and grasslands during the last four plus centuries. The remaining three sections are devoted to: fire, both prescribed fire and wildfire, in shrublands and grassland-shrubland interfaces; water and ecophysiology shrubland ecosystems; and the ecology and population biology of several shrub species.

Keywords: wildland shrubs, fire, water, ecophysiology, ecology

The use of trade or firm names in this publication is for reader information and does not imply endorsement by the U.S. Department of Agriculture or any product or service.

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.

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 series number.

Publishing Services

Telephone	(970) 498-1392
FAX	(970) 498-1122
E-mail	rschneider@fs.fed.us
Web site	http://www.fs.fed.us/rmrs
Mailing address	Publications Distribution Rocky Mountain Research Station 240 West Prospect Road Fort Collins, CO 80526

Rocky Mountain Research Station
Natural Resources Research Center
2150 Centre Avenue, Building A
Fort Collins, CO 80526

Proceedings: Shrubland Dynamics—Fire and Water

Lubbock, TX, August 10-12, 2004



Wyoming Big Sagebrush, Sweetwater County, Wyoming
Photo by E. Durant McArthur

Compilers

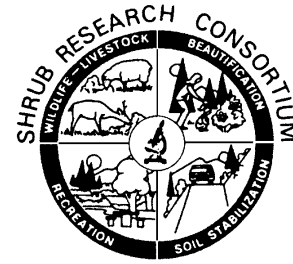
Ronald E. Sosebee, Department of Range, Wildlife and Fisheries Management, Texas Tech University,
Lubbock, TX

David B. Wester, Department of Range, Wildlife and Fisheries Management, Texas Tech University,
Lubbock, TX

Carlton M. Britton, Department of Range, Wildlife and Fisheries Management, Texas Tech University,
Lubbock, TX

E. Durant McArthur, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station,
Shrub Sciences Laboratory, Provo, UT

Stanley G. Kitchen, 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, Jason L. Vernon

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, Barry L. Perryman

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, Vernon, R. J. (Jim) Ansley

Texas Tech University, Lubbock, David B. Wester

USDA Agricultural Research Service, High Plains Grassland Research Station, Cheyenne, Wyoming,
D. Terrance Booth

USDA Agricultural Research Service, Jordana Experimental Range, Las Cruces, New Mexico, Mary E. Lucero

USDA Agricultural Research Service, Forage and Range Laboratory, Logan, Utah, Thomas A. Monaco

USDA Forest Service, Rocky Mountain Research Station, Forestry Sciences Laboratory, Albuquerque,
New Mexico, Rosemary L. Pendleton

USDA Forest Service, Rocky Mountain Research Station, Great Basin Ecology Laboratory, Reno, Nevada,
Robin J. Tausch

University of Utah, Salt Lake City, James R. Ehleringer

Weber State University, Ogden, Utah, Barbara A. Wachochki

Battelle Pacific Northwest Laboratories, Richland, Washington, Janelle L. Downs

Bechtel Nevada, Las Vegas, Nevada, 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 charter had three principal objectives: (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 13th in the series. The 12 previous symposia are listed on the next page. Proceedings of all publications to date have been published by the U.S. Department of Agriculture, Forest Service, Intermountain Research Station and Rocky Mountain Research Station. 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. Available from Rocky Mountain Research Station.
- 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 the 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. Available from the Rocky Mountain Research Station.
- 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 the 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. Proceedings RMRS-P-21. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 365 p. Available from the Rocky Mountain Research Station.
- Twelfth: Hild, A. L.; Shaw, N. L.; Meyer, S. E.; Booth, D. T.; McArthur, E. D., compilers. 2004. Seed and soil dynamics in shrubland ecosystems: proceedings; 2002 August 12-16; Laramie, WY. Proceedings RMRS-P-31. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 216 p. Available from the Rocky Mountain Research Station.

Contents

Introduction.....	1
Plenary Session.....	3
Shrubland Ecosystems: Importance, Distinguishing Characteristics, and Dynamics ...	3
<i>E. Durant McArthur and Stanley G. Kitchen</i>	
Grassland Ecosystems of the Llano Estacado	11
<i>Eileen Johnson</i>	
The Southern High Plains: A History of Vegetation, 1540 to Present	24
<i>David B. Wester</i>	
Prescribed Fire to Restore Shrublands to Grasslands.....	48
<i>Carlton M. Britton, David B. Wester and Brent J. Rancher</i>	
Role of Summer Prescribed Fire to Manage Shrub-invaded Grasslands.....	52
<i>Charles A. Taylor</i>	
Fire Session	
Management of South Texas Shrublands with Prescribed Fire.....	57
<i>C. Wayne Hanselka, D. Lynn Drawe, and D.C. Ruthven, III</i>	
Hydrology, Erosion, Plant, and Soil Relationships after Rangeland Wildfire.....	62
<i>Kenneth E. Spaeth, Frederick B. Pierson, Peter R. Robichaud and Corey A. Moffet</i>	
Using Relative Humidity to Predict Spotfire Probability on Prescribed Burns	69
<i>John R. Weir</i>	
Mesquite Cover Responses in Rotational Grazing/Prescribed Fire Management Systems: Landscape Assessment Using Aerial Images	73
<i>R. J. Ansley, W. E. Pinchak and W. R. Teague</i>	
Modeling Erosion on Steep Sagebrush Rangeland Before and After Prescribed Fire .	79
<i>Corey A. Moffet, Frederick B. Pierson and Kenneth E. Spaeth</i>	
Water and Ecophysiology Session	
Germination Responses to Temperature and Soil Moisture in Three Species of the Subfamily <i>Caragana</i> and Their Implications Toward Restoration in Loess-gully Region, China	85
<i>Zhao Xiaoying and Ren Jizhou</i>	
Saltcedar Control and Water Salvage on the Pecos River, Texas, 1999 to 2003	89
<i>Charles R. Hart, Larry D. White, Alyson McDonald and Zhuping Sheng</i>	
Mesquite Root Distribution and Water Use Efficiency in Response to Long-term Soil Moisture Manipulations.....	96
<i>R. J. Ansley, T. W. Boutton and P. W. Jacoby</i>	
Response of Seedlings of Two Hypogeal Brush Species to CO₂ Enrichment.....	104
<i>Charles R. Tischler, Justin D. Derner, H. Wayne Polley and Hyrum B. Johnson</i>	
Shrub Biomass Production Following Simulated Herbivory: A Test of the Compensatory Growth Hypothesis.....	107
<i>Terri B. Teaschner and Timothy E. Fulbright</i>	
Soil Responses to Human Recreational Activities in a Blackbrush (<i>Coleogyne ramosissima</i> Torr.) Shrubland	112
<i>Simon A. Lei</i>	
Influence of Shrubs on Soil Chemical Properties in Alxa Desert Steppe, China.....	117
<i>Hua Fu, Shifang Pei, Yaming Chen and Changgui Wan</i>	

Fungal Genomes that Influence Basic Physiological Processes of Black Grama and Fourwing Saltbush in Arid Southwestern Rangelands	123
<i>J.R. Barrow, M. Lucero, P. Osuna-Avila, I. Reyes-Vera and R.E. Aaltonen</i>	

Ecology and Population Biology Session

Estimating Aboveground Biomass of Mariola (<i>Parthenium incanum</i>) from Plant Dimensions	132
<i>Carlos Villalobos</i>	
Shrub Establishment in the Presence of Cheatgrass: The Effect of Soil Microorganisms	136
<i>Rosemary L. Pendleton, Burton K. Pendleton, Steven D. Warren, Jeffrey R. Johansen and Larry L. St. Clair</i>	
Differences in Volatile Profiles Between Populations of <i>Ceratoides lanata</i> var. <i>subspinosa</i> (Rydb.) J.T. Howell	142
<i>Mary Lucero, Rick Estell, Dean Anderson, Ed Fredrickson and Marta Remmenga</i>	
Emergence and Growth of Four Winterfat Accessions in the Presence of the Exotic Annual Cheatgrass	147
<i>Ann L. Hild, Jennifer M. Muscha and Nancy L. Shaw</i>	
Seed Germination Biology of Intermountain Populations of Fourwing Saltbush (<i>Atriplex canescens</i>: Chenopodiaceae)	153
<i>Susan E. Meyer and Stephanie L. Carlson</i>	
Efficacy of Exclosures in Conserving Local Shrub Biodiversity in Xeric Sandy Grassland, Inner Mongolia, China	163
<i>Feng-Rui Li, Zhi-Yu Zhou, Li-Ya Zhao, Ai-Sheng Zhang and Ling-Fen Kang</i>	
Intraspecific Variation in Leaf Anatomy of Blackbrush (<i>Coleogyne ramosissima</i> Torr.)	170
<i>Simon A. Lei</i>	

Introduction

The Southern High Plains of Texas (also known as the *Llano Estacado*) are in the southernmost subdivision of the High Plains section of the Great Plains Physiographic Province. Most of the Southern Great Plains is comprised of upland sites that were once grasslands dominated mostly by shortgrass plains that supported large herds of native buffalo. However, topographic diversity on the Southern High Plains is subtle and important: sandy soils were characterized by tall grass prairie or sand shinnery oak; major drainages (or draws) that cross the Southern High Plains from the northwest to the southeast provide the setting for plant communities that support considerable shrub diversity; and the escarpments that border the Southern High Plains historically have supported a rich complex of woody species.

Following European settlement in the 1500s, the grasslands of the Southern High Plains underwent vegetation change characterized by invasion by shrubs and trees. Invasion of woody plants cannot be attributed to any single environmental factor, although overgrazing by domestic livestock is often cited as the reason shrubs and trees have become dominant in the grasslands. Weather cycles and changing fire regimes have been perhaps as important as any other factor in contributing to the increase in woody plants. Woody plants are now a dominant species that must be reckoned with if the Southern Great Plains is ever again to become grassland.

The C₃, warm-season shrubs and trees, mostly *Juniperus* sp. and honey mesquite (*Prosopis glandulosa*), are commonly thought of as “using” large quantities of water that would otherwise be available for grass production if the woody plants were not present. Certainly, woody plants must have water to live just as does any other plant. However, the amount of water that is consumed by invasive woody plants is often misunderstood and/or misrepresented. Although many of the invasive woody plants have been referred to as “extravagant” water “users” or water “thieves,” these plants growing on dry sites (for example, shallow soils, upland sites, sloping hillsides) usually do not have access to large quantities of soil water. Therefore, like their grass counterparts, they are adapted to the semi-arid conditions under which they have evolved.

Fire is a natural part of the environmental conditions of the southern Great Plains. However, man has changed the fire

regime and vegetation changes that this area has experienced are also a consequence of changes in the historical fire regime. Some ecologists have suggested that there is no such thing as a grassland climax. In this view, fire played an important role either in eliminating woody species within the grasslands or in keeping woody plants suppressed, allowing grasses to dominate.

The theme of the Thirteenth Wildland Shrub Symposium was developed to examine the “pristine” vegetation of the Southern High Plains of Texas and the use of controlled fire, or prescribed burns, to manipulate the woody vegetation and return the grasslands to the more desirable grasses that once dominated the region. We also included a review of water use by woody vegetation from a scientific rather than an emotional viewpoint that is often found in popular opinion. As always, a wider array of topics was encouraged to broaden one’s knowledge of shrub dominated rangelands.

In addition to both oral and poster presentations of scientific data on shrublands, a field trip provided an opportunity to view shrub invasion of some of the formerly- dominated grasslands of the Southern High Plains and Panhandle of Texas. The field trip included stops with presentations at a saltcedar (*Tamarix gallica*)-infested riparian site, a sand shinnery oak (*Quercus havardii*)-dominated rangeland, and a mesquite-dominated grassland. The final stop of the field tour provided an opportunity to view native shrub communities on an escarpment along tributaries of the Red River in Texas at Caprock Canyons State Park.

The symposium provided an excellent opportunity for presentations of scientific changes in vegetation throughout geologic and recorded history of the Southern High Plains and an opportunity to see some of these changes in the field. It also provided an opportunity to broaden our knowledge concerning shrub ecology and general shrub biology. It was an excellent educational experience.

We would like to extend our thanks to the landowners who graciously allowed us to visit their properties. Special thanks go to the staff at Caprock Canyons State Park for hosting our final stop and for providing a pleasant site for a delightful meal at the end of our trip. We would also like to thank the presenters and moderators whose participation in this symposium made it a success.

Ronald E. Sosebee and David B. Wester

Plenary Session

Shrubland Ecosystems: Importance, Distinguishing Characteristics, and Dynamics

E. Durant McArthur¹
Stanley G. Kitchen²

Abstract: The importance of shrub species and shrubland ecosystems gained considerable impetus about 30 years ago with the establishment of the USDA Forest Service Shrub Sciences Laboratory and a series of workshops and symposia that preceded and accompanied the establishment of the Laboratory. Since that time, the Shrub Research Consortium and other forums have addressed various aspects of wildland shrub ecosystem biology and management. Shrubs occur in most vegetation types but are dominants only in those habitats that place plants under considerable stress. Three primary, often interacting factors, that promote shrubby habitats are drought or aridity, nutrient-poor soils, and fire. Other stress factors that may also be interactive that contribute to the shrubby habitat are shade, poor soil aeration, winter cold, short growing season, and wind. Most of these conditions frequently occur in semi-arid, temperate, continental climates. The principal shrubland ecosystems of the western United States are sagebrush, chaparral, mountain brush, coastal sage, blackbrush, salt desert, creosote bush, palo verde-cactus, mesquite, ceniza shrub, shinnery, and sand-sage prairie. Similar as well as distinctively different shrubland ecosystems occur at other locations around the world. Shrubland ecosystems have different human and wildlife values and have, and are, subject to changing environmental conditions including different fire regimes. Fragmentations of these ecosystems, for example the sagebrush ecosystems, are of concern since some ecosystem components are at critical risk. Shrubland ecosystem changes have become more apparent in recent decades posing significant ecological and management problems. The challenge for land managers and ecologists is to understand the fluidity of the ecosystems and to be proactive and sensitive to the needs of healthy, productive landscapes.

Introduction

Shrubs and shrubland ecosystems are valued differently by natural resource professionals and pastoralists depending on their backgrounds, experience, geographical location, and the economic impact of those shrublands on their livelihood. The contrasting values or points of views about shrubs were stated by Everist (1972) in the context of Australian shrublands, which could be extrapolated generally: “wildland shrubs have greatest importance on ... grazing lands, mostly as useful species but sometimes as invaders of and competitors with plants (more useful) ... for animal ... survival or productivity.” In North America, shrubs have been referred to as a neglected resource (McKell 1975; 1989) or contrastingly as an impediment to productive land use practice (Herbel 1979). In Africa and Asia, their value has long been appreciated and often over-exploited (Badresa and Moore 1982; Cloudsley-

Thompson 1974). In Australia, shrubs have been recognized alternately as valuable, sustainable forage and as a system that is more productive when it is converted to a disclimax herbaceous state (Williams and Oxley 1979).

The importance of shrub species and shrubland ecosystems gained considerable impetus about 30 years ago with the establishment of the U.S. Forest Service Shrub Sciences Laboratory and a series of workshops and symposia that preceded and accompanied the establishment of the Laboratory (McKell and others 1972, Stutz 1976). Since its charter in 1983 (McArthur 2001; Tiedemann 1984), the Shrub Research Consortium (SRC), lead by the project leaders of the Shrub Sciences Laboratory, has sponsored a series of symposia on the biology and management of shrubland ecosystems. The SRC symposia have generally focused on the positive values of shrubs in shrubland ecosystems but have also addressed management issues where shrubs were considered as

In: Sosebee, R.E.; Wester, D.B.; Britton, C.M.; McArthur, E.D.; Kitchen, S.G., comp. 2007. Proceedings: Shrubland dynamics—fire and water; 2004 August 10-12; Lubbock, TX. Proceedings RMRS-P-47. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 173 p.

Table 1—Shrub Research Consortium Wildland Shrub Symposia series.

Number	Date held	Title and location	Proceedings publication
1	1982	Research and Management of Bitterbrush and Cliffrose in Western North America—Salt Lake City, Utah	Tiedemann and Johnson 1983
2	1983	The Biology of Atriplex and related Chenopods—Provo, Utah	Tiedemann and others 1984
3	1984	The Biology and Management of Artemisia and Chrysothamnus—Provo, Utah	McArthur and Welch 1986
4	1985	Plant—Herbivore Interactions—Snowbird, Utah	Provenza and others 1987
5	1987	Shrub Ecophysiology and Biotechnology—Logan, Utah	Wallace and others, 1989
6	1989	Cheatgrass Invasion, Shrub Die-off, and other Aspects of Shrub Biology and Management—Las Vegas, Nevada	McArthur and others 1990
7	1991	Ecology and Management of Riparian Shrub Communities—Sun Valley, Idaho	Clary and others 1992
8	1993	Wildland Shrub and Arid Land Restoration—Las Vegas, Nevada	Roundy and others 1995
9	1995	Shrubland Ecosystem Dynamics in a Changing Environment—Las Cruces, New Mexico	Barrow and others 1996
10	1998	Shrubland Ecosystem Ecotones—Ephraim, Utah	McArthur and others 1999
11	2000	Shrubland Ecosystem Genetics and Biodiversity—Provo, Utah	McArthur and Fairbanks 2001
12	2002	Seed and Soil Dynamics in Shrubland Ecosystems—Laramie, Wyoming	Hild and others 2004
13	2004	Shrub Dynamics: Fire and Water—Lubbock, Texas	Sosebee and others—this proceedings

ecological or management problems (table 1). The two symposia that focused more on shrub control management issues rather than positive values were numbers 9 and 13 in the series which were held in the Southwest where shrubs have displaced grasses in historic time over large acreages (Barrow and others 1996; Herbal 1979, Sosebee and others—this proceedings). A series of wildland shrub workshops, each emphasizing various shrub taxa and communities (especially for land management professionals), were held in both Wyoming (1972-1988) and Utah (1981-1991)—see Fisser (1990), Johnson (1990), and McArthur (2001) for lists of these proceeding publications and more details on the process.

Although shrubs are an important and widespread life form, they are difficult to circumscribe. Individual species may be shrubs in some circumstances and trees in other circumstances. Other species may alternatively be shrubs or herbaceous plants depending on certain circumstances, for example, climate or soil fertility (Francis 2004). Shrubs do not comprise a cohesive phylogenetic unit, but derive from many lineages (McArthur 1989; Stebbins 1972; 1976). The shrub habit is more of a growth form than a phylogenetic unit. However, some taxonomic lines are wholly shrubby as might be expected depending upon the point of establishment of the shrub growth habit (table 2). Simmonds (1976) identified 168 principal crop plants of which 12 are shrubs. These 12 crop shrubs (tea, hazel, blueberries, cassava, currants and gooseberries, wattles, roselle, guava, pomegranate, raspberries and blackberries, coffees, and peppers) represent 12 different families (McArthur 1989). Francis (2004) analyzed the Natural Resources Conservation Service (USDA 2003) “Plants” database and determined that there were 5,281 species in the United States and territories that carry the growth habit designations “shrub” or “sub-shrub.” These species represent 166 families (table 3). Note that the West (especially the Southwest), Southeast, Hawaii, Puerto Rico, and Virgin

Islands are more species-rich than other areas, such as Alaska, the North Central States, and New England.

Shrubs occur in many vegetation types. Shrubs ordinarily have more than one main stem caused by branching below or above ground level, are perennial, and are lignified (Francis 2004). Often shrubs are thought of as midway between a tree and herb with adaptive advantages of both life forms that sustain the shrub habit in some unique situations (Stutz 1989). Shrubs have near relatives that are herbs and/or trees (table 2). Shrubs are dominant, but for the most part, only in habitats that place plants under considerable stress such as drought or aridity, nutrient-poor soils, fire, shade, poor soil aeration, winter cold, short growing seasons, and wind (McArthur 1989; Stebbins 1972; 1975). Many of these conditions are met in semi-arid continental climates (McArthur 1989; McKell and others 1972). For example, shrubs are widely distributed in the United States (fig. 1), but are dominants from a continental-scale perspective in the semiarid west (McArthur 1984). Table 4 is an analysis of shrub importance as determined from Kùchler’s (1964) map and manual. Significant dominance of shrubs is manifest only in the western shrublands and western shrub and grasslands. Shrubs as subdominants are important to a greater or lesser degree in nearly all vegetative types (table 4). The same general patterns of shrubs rising to dominance are evident in other semiarid and arid climatic regimes on other continents (Le Honérou 2000; McKell 1989; McKell and others 1972; Walter and Box 1976; West 1983; Wilson and Graetz 1979).

We conclude this section with a few comments about some shrub species that characterize the western North American landscapes. Whereas shrubs are widely distributed and are components of many ecosystems and community types, they give landscapes their primary character in areas that they dominate, such as the interior North American West (Francis 2004; McArthur 1984; 1989). McArthur (1989) identified 12

Table 2—Numbers of genera and species including example species and growth forms of selected families (after McArthur 1984 and McArthur and Tausch 1995).

Family ^a	Representative Genera	Number of shrub Genera ^b	Number of species from Western United States (all growth forms) ^c	Number of species (World total, all growth forms)	Growth habits ^d
Anacardiaceae	<i>Rhus</i>	1	9	150	S, T
Asteraceae	<i>Artemisia</i> <i>Baccharis</i> <i>Brickella</i> <i>Chrysothamnus</i> <i>Happlopappus</i> <i>Tetradymia</i>	18	126	2546	H, S
Caprifoliaceae	<i>Lonicera</i> <i>Sambucus</i> <i>Symphoricarpos</i>	5	28	317	S
Chenopodiaceae	<i>Atriplex</i>	8	29	441	H, S
Ericaceae	<i>Arctostaphylos</i> <i>Vaccinium</i>	14	82	1211	S, T
Ephedraceae	<i>Ephedra</i>	1	10	40	S
Fabaceae	<i>Acacia</i> <i>Dalea</i> <i>Mimosa</i>	19	70	3276	H, S, T
Fagaceae	<i>Quercus</i>	3	20	700	S, T
Fouquieriaceae	<i>Fouquieria</i>	1	1	9	S, T
Lamiaceae	<i>Salvia</i>	5	24	1175	H, S
Polygonaceae	<i>Eriogonum</i>	1	20	250	H, S
Rhamnaceae	<i>Ceanothus</i>	6	68	295	S
Rosaceae	<i>Amelanchier</i> <i>Prunus</i> <i>Rosa</i> <i>Rubus</i>	23	81	760	H, S, T
Scrophulariaceae	<i>Mimulus</i> <i>Penstemon</i>	4	22	454	H, S
Zygophyllaceae	<i>Larrea</i>	2	2	22	S

^a Families selected on the basis of at least one species included by a dominant by Küchler 1964.

^b Number of shrub genera in the United States west of 100° W longitude.

^c Total number of species in the United States west of 100° W longitude.

^d Growth habits of congeneric relatives: H = herbs, S = shrubs, T = trees.

Table 3—Most important families with shrub representatives in the United States and its territories (after Francis 2004).^a

Family	Number of shrub species
Asteraceae	618
Rosaceae	510
Fabaceae	342
Cactaceae	193
Ericaceae	189
Scrophulariaceae	182
Rubiaceae	165
Malvaceae	148
Euphorbiaceae	128
Lamiaceae	124
Polygonaceae	123
Companulaceae	112
Boraginaceae	106
Ramnaceae	103

^a There are 152 additional families with from one to 82 species each.

successful Western North American shrub species complexes (table 5). These species complexes demonstrate the variety of important entities in widespread and dominant shrubs inasmuch as they represent 8 families, a mix of polyploid systems versus diploid only chromosome numbers, a mix of wind and insect pollination, different degrees of dominance in their respective plant communities (table 5). The group is primarily outcrossing. The principal shrubland ecosystems of the western United States are sagebrush, chaparral, mountain brush, coastal sage, blackbrush, salt desert, creosote bush, palo verde-cactus, mesquite, ceniza shrub, shinnery, and sand-sage prairie (Küchler 1964, McArthur and Ott 1996). As an example of these important shrublands, we briefly discuss some of the characteristics of sagebrush, an American West icon (fig. 2). Sagebrush (the subgenus *Tridentatae* of *Artemisia*) occupies vast tracts of land west of the 100th meridian west longitude (McArthur and Sanderson 1999). As such, it gives the land its character, serves as habitat for resident wildlife, and

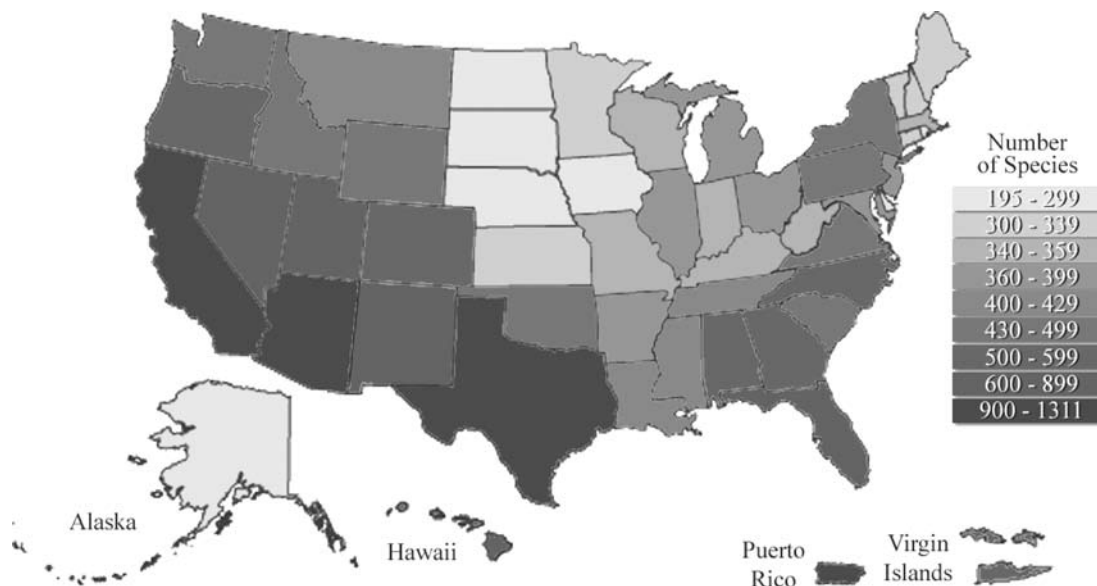


Figure 1. Numbers of shrub species in the States and Territories of the United States (Francis 2004).

contributes to livestock ranges (McArthur and Stevens 2004; Welch in press). Other *Artemisia* species of other subgenera are important landscape dominants in Eurasia (Vallès and McArthur 2001; West 1983). For additional details on western North American dominant shrub species complexes we recommend the first three wildland shrub symposium proceedings—McArthur and Welch (1986), Tiedeman and Johnson (1983), and Tiedemann and others (1984) (table 1); Francis (2004); and chapters on shrub species in Monsen and others (2004a)—McArthur and Mosen (2004), McArthur and

Stevens (2004), Mosen and others (2004b), and Shaw and others (2004).

Dynamics

Like all plant species, communities, and ecosystems, shrub species and their attendant plant communities or ecosystems are not static. Evolutionary forces and environmental change have been active over geological time in leading to present day species, communities, and ecosystems. Two recent wildland

Table 4—Dominant and subdominant shrub species occurrence in the principal vegetative types of the conterminous United States (after McArthur 1989).

Vegetative type	N	Dominant species			Subdominant species			All shrubs ($\bar{X}$ + se)
		All species	Shrubs		All species	Shrubs		
		$\bar{X}$ + se	$\bar{X}$	%	$\bar{X}$ + se	$\bar{X}$	%	
Western needleleaf forests	24	2.3 + 0.2	0.04	1.7	10.0 + 1.1	3.9	39.0	3.9 + 0.6
Western broadleaf forests	3	1.3 + 0.3	0	0	10.0 + 2.3	3.7	37.0	3.7 + 1.8
Western broadleaf and needleleaf forests	5	5.6 + 0.7	0.2	3.6	16.4 + 3.0	7.6	46.3	7.8 + 2.1
Western shrublands	13	2.7 + 0.6	1.9	70.4	13.6 + 1.9	8.7	63.9	10.6 + 1.7
Western grasslands	8	3.6 + 0.8	0	0	11.6 + 2.0	1.6	13.8	1.6 + 0.6
Western shrubs and grasslands	6	3.2 + 0.4	1.3	40.6	17.0 + 2.5	3.8	22.4	5.2 + 1.0
Central and eastern grasslands	17	2.9 + 0.3	0	0	14.2 + 1.4	1.4	9.8	1.4 + 0.4
Central and eastern grasslands and forests	15	3.4 + 0.5	0	0	17.2 + 2.5	1.7	9.9	1.7 + 0.3
Eastern needleleaf forests	5	2.4 + 0.2	0	0	6.8 + 0.8	2.0	29.4	2.0 + 0.7
Eastern broadleaf forests	8	3.1 + 0.7	0	0	14.9 + 2.1	1.1	7.4	1.1 + 0.7
Eastern broadleaf and needleleaf forests	11	4.0 + 0.5	0.09	2.2	13.4 + 2.3	1.9	14.2	2.0 + 0.4
Total	115	—	—	—	—	—	—	—
$\bar{X}$		3.1 + 0.5	0.3	9.7	13.2 + 1.9	3.4	25.8	3.7 + 0.9

Table 5—Twelve successful Western North American shrub complexes (McArthur 1989)^a.

Shrub complex	Polyploidy	Breeding system	Dominance characteristics
Manzanita— <i>Artostaphylos</i> spp. (Ericaceae)	yes	Outcrossing, insect	Many dominant species in communities
Sagebrushes—subgenus <i>Tridentatae</i> of <i>Artemisia</i> (Asteraceae)	yes	Outcrossing (limited self), wind	Dominant by itself with occasional subordinate co-dominants
Saltbushes— <i>Atriplex</i> spp. (Chenopodiaceae)	yes	Outcrossing, wind	Usually dominant by self or with other congeners and chenopods ^b
Buckbrushes— <i>Ceanothus</i> spp. (Rhamnaceae)	no	Outcrossing (limited self in some species), insect	Many dominant species in communities
Mountain mahoganies— <i>Cercocarpus</i> spp. (Rosaceae)	no	Outcrossing (limited amount of self), wind	Few dominant species aside from <i>Cercocarpus</i>
Rabbitbrushes— <i>Chrysothamnus</i> spp. (Asteraceae) ^c	no	Self (limited outcrossing), insect	Usually a sub or co-dominant
Blackbrush— <i>Coleogyne</i> (Rosaceae)	no	Outcrossing, wind ^d	Usually dominant by self
Cliffrose and bitterbrush— <i>Purshia</i> spp. ^e (Rosaceae)	no	Outcrossing, insect	Usually a sub or co-dominant
Mormon tea or joint fir— <i>Ephreda</i> spp. (Ephredaceae)	no	Outcrossing, wind	Usually a co-dominant
Bursage— <i>Ambrosia</i> (Asteraceae)	yes	Outcrossing, wind	Usually a co-dominant
Creosote bush— <i>Larrea</i> (Zygophyllaceae)	yes	Outcrossing, insect	Usually a co-dominant
Oakbrush— <i>Quercus</i> spp. (Fagaceae)	no	Outcrossing, wind	Usually a co-dominant

^a Documenting references in McArthur (1989) except as noted in additional footnotes.

^b Including greasewood (*Sarcobatus* spp.) which has been recently segregated into its own family (Sanderson and others 1999).

^c Taxonomy in the rabbitbrushes is under scrutiny; some or all are alternately treated as *Ericameria* (Anderson 1995).

^d Confirmed by Pendleton and Pendleton (1998).

^e The former independent generic standing of cliffrose (*Cowania*) has been submerged into *Purshia* (Hendrickson 1986; Reichenbacher 1994)



Figure 2. Wyoming big sagebrush, Sweetwater County, Wyoming (photo by E. Durant McArthur).

shrub symposia addressed these issues: McArthur and Fairbanks (2001), Shrubland Ecosystem Genetics and Biodiversity and Barrow and others (1996), Shrubland Ecosystem Dynamics in a Changing Environment. Johnson (this proceeding) addressed these issues for the Southern High Plains. These changes in shrub communities (in other words, community structure and species evolution) are on distinct time scales. Both time scales are ordinarily very long in terms of the human lifespan perspective. Species evolution is ordinarily the longer of the two phenomena. Betancourt (1996) and Tausch and others (1993) reviewed climatic influences that have led to current vegetation communities. Since settlement of the American West by Euro-Americans, especially in recent decades, shrubland vegetation communities have changed rapidly. Consensus is that these changes have been driven not only by global warming, but also by management activities, especially livestock grazing, and by a change in the frequency of wildfires mediated by the higher fine fuel loads of exotic annual grasses such as cheatgrass. Two contrasting examples of changed communities are the fragmentation of sagebrush communities in the Intermountain West as a result of agricultural conversions, brush control projects, and increased fire frequency (Knick 1999; Welch 2005; Whisenant 1990) and the expansion of woody shrubs (principally mesquite—*Prosopis* spp., tarbush—*Flourensia cernua*, and creosote bush—*Larrea tridentata*) into warm desert grasslands in the Southwest as a result of overgrazing and climate change (Havstad and Schlesinger 1996; Herbel 1979). The likelihood is that changes will continue, even accelerate, with climate change, industrial activities, and intensive land management (Neilson and Drapek 1998). The challenges for land managers and ecologists is to understand the fluidity of the system and to be proactive and sensitive to the needs of healthy, productive landscapes.

Acknowledgments

We thank Ron Sosebee and his Texas Tech University colleagues for their tireless efforts to lead in the organization and conduct of the symposium and field trip. This paper is the result and reflection of our involvement in a series of wildland shrub symposia. We appreciate the participation of many colleagues over the course of this symposia series. This paper reflects that long involvement. We thank Burton V. Barnes, John K. Francis, and Stewart C. Sanderson for constructive comments on an earlier version of the manuscript.

References

- Anderson, L. C. 1995. The *Chrysothamnus-Ericameria* connection (Asteraceae). Great Basin Naturalist. 55: 84-88.
- 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.
- Betancourt, J. L. 1996. Long- and short-term climate influences on Southwestern shrublands. In: 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: 5-9.
- Bhadresa, R.; Moore, P. D. 1982. Desert shrubs; the implications of population and pattern studies for conservation and management. In: Spooner, B.; Mann, H. S., eds. Desertification and development: dryland ecology in social perspective. London, United Kingdom: Academic Press: 269-276.
- 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.
- Cloudsley-Thompson, J. L. 1974. The expanding Sahara. Environmental Conservation. 1: 5-13.
- Everist, S. L. 1972 Australia. In: McKell, C. M.; Blaisdell, J. P.; Goodin, J. R., tech. eds. Wildland shrubs—their biology and utilization: an international symposium; 1971 July 12-16; Logan, UT. General Technical Report INT-1. Ogden, UT; U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station: 16-25.
- Fisser, H. G., ed. 1990. Wyoming shrublands: aspen, sagebrush, and wildlife management: proceedings of the seventeenth Wyoming Shrub Ecology Workshop; 1988 June 21-22; Jackson, WY. Laramie, WY: University of Wyoming, Department of Range Management. 76 p.
- Francis, J. K. 2004. Wildland shrubs. In: Francis, J. K., ed. Wildland shrubs of the United States and its territories: thamnisc descriptions: volume 1. San Juan, PR and Fort Collins, CO, U.S. Department of Agriculture, Forest Service, International Institute of Tropical Forestry and Rocky Mountain Research Station: 1-11.
- Havstad, K.; Schlesinger, W. 1996. Reflections on a century of rangeland research in the Jornada Basin of New Mexico. In: 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: 10-15.
- Hendrickson, J. 1986. Notes on Rosaceae. Phytologia. 60: 486.
- Herbel, C. H. 1979. Utilization of grass- and shrublands of the south-western United States. In: Walker, B. H., ed. Management of semi-arid ecosystems. Amsterdam, Netherlands: Elsevier Scientific Publishing Company: 161-203.
- Hild, A. L.; Shaw, N. L.; Meyer, S. E.; Booth, D. T.; McArthur, E. D., compilers. 2004. Seed and soil dynamics in shrubland ecosystems: proceedings; 2002 August 12-16; Laramie, WY. Proceedings RMRS-31. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 216 p.
- Johnson, K. L., ed. 1990. Proceedings of the fifth Utah Shrub Ecology Workshop, the genus *Cercocarpus*; 1988 July 13-14; Logan, UT. Logan, UT: Utah State University, College of Natural Resources. 105 p.
- Knick, S. T. 1999. Requiem for a sagebrush ecosystem? Northwest Science. 73: 53-57.
- Küchler, A. W. 1964. Potential natural vegetation of the conterminous United States (map and manual). Special Publication 36. New

- York, NY: American Geographical Society. 116 p (map scale 1: 3,168,000).
- Le Houérou, H. N. 2000. Utilization of fodder trees and shrubs in the arid and semiarid zones of West Asia and North Africa. *Arid Soil Research and Rehabilitation*. 14: 101-135.
- McArthur, E. D. 1984. Natural diversity of Western range shrubs. In: Cooley, J. L.; Cooley, J. H., eds. *Natural diversity in forest ecosystems; proceedings of the workshop*; 1982 November 29-December 1; Athens, GA. Athens, GA: Institute of Ecology, University of Georgia: 193-209.
- McArthur, E. D. 1989. Breeding systems in shrubs. In: McKell, C. M., ed., *The biology and utilization of shrubs. The biology and utilization of shrubs*. San Diego, CA: Academic Press, Inc.: 341-361.
- McArthur, E. D. 2001. The Shrub Sciences Laboratory at 25 years: retrospective and prospective. In: McArthur, E. D.; Fairbanks, D. J., compilers. *Shrubland ecosystem genetics and biodiversity; proceedings*; 2000 June 13-15; Provo, UT. *Proceedings RMRS-P-21*. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 3-41.
- McArthur, E. D.; Fairbanks, D. J., compilers. 2001. *Shrubland ecosystem genetics and biodiversity; proceedings*; 2000 June 13-15; Provo, UT. *Proceedings RMRS-P-21*. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 365 p.
- McArthur, E. D.; Monsen, S. B. 2004. Chenopod shrubs. In: Monsen, S. B.; Stevens, R.; Shaw, N. L., compilers. 2004a. *Restoring western ranges and wildlands. General Technical Report RMRS-GTR-136-vol. 2*. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 467-491.
- 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.
- McArthur, E. D.; Ott, J. E. 1996. Potential natural vegetation in the 17 conterminous Western United States. In: 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: 16-28.
- 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.
- McArthur, E. D.; Sanderson, S. C. 1999. Cytogeography and chromosome evolution of subgenus *Tridentatae* of *Artemisia* (Asteraceae). *American Journal of Botany*. 86: 1754-1775.
- McArthur, E. D.; Stevens, R. 2004. Composite shrubs. In: Monsen, S. B.; Stevens, R.; Shaw, N. L., compilers. 2004a. *Restoring western ranges and wildlands. General Technical Report RMRS-GTR-136-vol. 2*. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 295-698.
- McArthur, E. D.; Tausch, R. J. 1995. Genetic aspects of the biodiversity of rangeland plants. In: West, N. E., ed. *Biodiversity on rangelands; proceedings of the symposium*; 1993 February 16; Albuquerque, NM. Logan, UT: Natural Resources and Environmental Issues Volume IV, College of Natural Resources, Utah State University: 5-20.
- 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.
- McKell, C. M. 1975. Shrubs—a neglected resource of arid lands. *Science*. 187: 803-809.
- McKell, C. M. 1989. *The biology and utilization of shrubs*. San Diego, CA: Academic Press, Inc. 656 p.
- McKell, C. M.; Blaisdell, J. P.; Goodin, J. R., tech. eds. 1972. *Wildland shrubs—their biology and utilization: an international symposium*; 1971 July 12-16; Logan, UT. *General Technical Report INT-1*. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 494 p.
- Monsen, S. B.; Stevens, R.; Shaw, N. L., compilers. 2004a. *Restoring western ranges and wildlands. General Technical Report RMRS-GTR-136-vol. 2*. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 295-698.
- Monsen, S. B.; Stevens, R.; Shaw, N. L. 2004b. Shrubs of other families. In: Monsen, S. B.; Stevens, R.; Shaw, N. L., compilers. 2004a. *Restoring western ranges and wildlands. General Technical Report RMRS-GTR-136-vol. 2*. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 597-698.
- Neilson, R. P.; Drapek, R. J. 1998. Potentially complex biosphere responses to transient global warming. *Global Change Biology*. 4: 505-521.
- Pendleton, B. K.; Pendleton, R. L. 1998. Pollination biology of *Coleogyne ramosissima* (Rosaceae). *Southwestern Naturalist*. 43: 376-380.
- 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.
- Reichenbacher, F. W. 1994. Identification of *Purshia subintegra* (Rosaceae). *Great Basin Naturalist*. 54: 256-271.
- Sanderson, S. C.; Stutz, H. C.; Stutz, M.; Roos, R. C. 1999. Chromosomeres in *Sarcobatus* (Sarcobataceae, Caryophyllales). *Great Basin Naturalist*. 59: 301-314.
- Squires, V. R. 1989. Australia: distribution, characteristics, and utilization of shrublands. In: McKell, C. M., ed. *The biology and utilization of shrubs*. San Diego, California: Academic Press, Inc.: 69-92.
- Shaw, N. L.; Monsen, S. B.; Stevens, R. 2004. Rosaceous shrubs. In: Monsen, S. B.; Stevens, R.; Shaw, N. L. 2004a. *Restoring western ranges and wildlands. General Technical Report RMRS-GTR-136-vol. 2*. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 539-596.
- Stebbins, G. L. 1972. Evolution and diversity of arid-land shrubs. In: McKell, C. M.; Blaisdell, J. P.; Goodin, J. R., tech. eds. *Wildland shrubs—their biology and utilization: an international symposium*; 1971 July 12-16; Logan, UT. *General Technical Report INT-1*. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station: 111-120.
- Stebbins, G. L. 1976. Shrubs as centers of adaptive radiation and evolution. In: Stutz, H. C., ed. *Proceedings, symposium and workshop on the occasion of the dedication of the U.S. Forest Service Shrub Sciences Laboratory*; 1975 November 4-6; Provo, UT. Provo, UT: Brigham Young University, College of Biology and Agriculture: 120-140.

- Stutz, H. C., ed. 1976. Proceedings, symposium and workshop on the occasion of the dedication of the U.S. Forest Service Shrub Sciences Laboratory; 1975 November 4-6; Provo, UT. Provo, UT: Brigham Young University, College of Biology and Agriculture. 168 p.
- Stutz, H. C. 1989. Evolution of shrubs. In: McKell, C. M., ed., The biology and utilization of shrubs. The biology and utilization of shrubs. San Diego, CA: Academic Press, Inc.: 323-340.
- 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.
- Tiedemann, A. R. 1984. Shrub Research Consortium formed. *Great Basin Naturalist* 44: 182.
- 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.
- 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.
- 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.
- USDA Natural Resources Conservation Service. 2003. Plants database. <http://plants.usda.gov/>. [not paged].
- Vallès, J.; McArthur, E. D. 2001. *Artemisia* systematics and phylogeny: cytogenetic and molecular insights. In: McArthur, E. D.; Fairbanks, D. J., compilers. 2001. Shrubland ecosystem genetics and biodiversity; proceedings; 2000 June 13-15; Provo, UT. Proceedings RMRS-P-21. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 67-74.
- Wallace, A. R.; 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.
- Walter, H.; Box, E. 1976. Global classification of natural terrestrial ecosystems. *Vegetatio*. 32: 75-81.
- West, N. E., ed. 1983. Ecosystems of the world 5, temperate deserts and semi-deserts. Amsterdam, Netherlands: Elsevier Scientific Publishing Company. 522 p.
- Welch, B. L. 2005. Big sagebrush: a sea fragmented into lakes, puddles, and ponds. General Technical Report-RMRS-GTR-144. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 210 p.
- 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., compilers. 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: 4-10.
- Williams, O. B.; Oxley, R. E. 1979. Historical aspects of the use of chenopod shrublands. In: Graetz, R. D.; Howes, K. M. W., eds. Studies of the Australian arid zone. IV. Chenopod shrublands. Melbourne, Australia: Division of Land Resources Management, Commonwealth Scientific and Industrial Research Organization: 5-16.
- Wilson, A. D.; Graetz, R. D. 1979. Management of the semi-arid and arid rangelands of Australia. In: Walker, B. H., ed. Management of semi-arid ecosystems. Amsterdam, Netherlands: Elsevier Scientific Publishing Company: 83-111.

The Authors

¹Program Manager and Research Geneticist, USDA Forest Service, Rocky Mountain Research Station, Shrub Sciences Laboratory, Provo, UT. dmcarthur@fs.fed.us

²Research Botanist, USDA Forest Service, Rocky Mountain Research Station, Shrub Sciences Laboratory, Provo, UT.

Grassland Ecosystems of the Llano Estacado

Eileen Johnson¹

Abstract: The Llano Estacado, or Southern High Plains, has been a grassland throughout the Quaternary. The character of this grassland has varied through time, alternating between open, parkland, and savannah as the climate has changed. Different lines of evidence are used to reconstruct the climatic regimes and ecosystems, consisting of sediments and soils, vertebrate and invertebrate remains, phytolith and macrobotanical remains, isotope data, and radiocarbon ages. Binding or key indicator species throughout the late Pleistocene and Holocene are bison, pronghorn antelope, and prairie dog. Depending on time period, hackberry, cottonwood, sumac, honey mesquite, and Texas walnut are among the native trees and shrubs growing in the valleys and around upland basins. The middle Pleistocene is characterized as a sagebrush grassland whereas that of the late Pleistocene is a cool-climate pooid-panicoid dominated grassland. Focusing on the Holocene, this dynamic period experiences climatic changes, the early rise of the short-grass ecosystem, and modulations to that ecosystem.

The Llano Estacado and Distribution of Localities

The last synthesis of the Quaternary vegetation of the Llano Estacado, based on pollen data, was more than 40 years ago (Wendorf 1961). A hallmark of this seminal study was its multidisciplinary research effort to examine the paleoecology. Since then, research has generated several lines of evidence leading to an increased database from an expanded number of localities representative of the major geomorphic landforms across the region. Refinements in pollen processing and greater understanding of post-depositional processes have led to increased interpretive ability that calls into question the validity of the earlier pollen diagrams and interpretation. Other lines of evidence, generally concordant with each other, are not in agreement with the earlier pollen record and regional interpretation. This current synthesis, then, is an update based on an expanded record that presents a different perspective on the past vegetation and ecosystems of the Llano Estacado.

The Llano Estacado, or Southern High Plains, is a flat, expansive plateau in northwestern Texas and eastern New Mexico covering 130,000 km² (fig. 1). Part of the High Plains, a subdivision of the Great Plains province (Fenneman 1931; Hunt 1967; Holliday and others 2002), the Llano Estacado is in the southern portion of the province. Escarpments define the region along the north, west, and east sides. The northern escarpment overlooks the Canadian River Valley that separates the Southern High Plains from the rest of the High Plains section. The Pecos River Valley section is to the west and southwest and includes the Mescalero Plains along with the Monahans Dunes and Mescalero Dunes that abut the southwestern escarpment. Bordering the eastern escarpment is the Osage Plains of the Central Lowland province. To the south, the region merges with the Edwards Plateau without an obvious break. Superimposed over, but not coincident with all

of the High Plains, is the short-grass ecosystem or short-grass steppe (Lauenroth and Milchunas 1992).

The Southern High Plains (Llano Estacado) of today has a continental climate. The region experiences a large temperature range that is not influenced by the ocean or other large bodies of water (Johnson 1991). Rainfall occurs throughout the year, but highs are in the spring and fall as a result of frontal lifting of warm moist air. Summer droughts are common due to high pressure that dominates the region during this time. Summer rains, then, occur mainly through intense thunderstorms that depend on daytime heating and the weakening of the high pressure cell. Winter snowfall is minimal, but extended periods of below freezing are normal (Barry 1983; Haragan 1983:67; Bomar 1995:10). The Southern High Plains is dry and classified as semi-arid. It grades into the deserts of the Trans Pecos and southeastern New Mexico, the Rocky Mountain foothills of northeastern New Mexico, and the savannahs of the southern Central Lowlands (Osage Plains).

The modern vegetation of the Llano Estacado is a short-grass prairie dominated by blue grama (*Bouteloua gracilis*) and buffalograss (*Buchloe dactyloides*) with patches of honey mesquite (*Prosopis glandulosa*). Historically, how one viewed and used this vast landscape was a matter of cultural perspective. In 1839, an Anglo trader and explorer returning to the East from Santa Fe described the Llano Estacado as “an open plain...which was one of the most monotonous I have ever seen, there being not a break, not a valley, nor even a shrub to obstruct the view. The only thing which served to turn us from a direct course pursued by the compass, was the innumerable ponds which bespeckled the plain, and which kept us at least well supplied with water” (Gregg 1954:252). Despite that acknowledgement of water, he also noted the Llano Estacado as “that immense desert region,” “dry and lifeless” and “sterile” (Gregg 1954:357, 362). In the 1850s, government-backed Anglo explorers reported that the area was “the Zahara of North America” (Marcy 1850:42) with “no inducements to

In: Sosebee, R.E.; Wester, D.B.; Britton, C.M.; McArthur, E.D.; Kitchen, S.G., comp. 2007. Proceedings: Shrubland dynamics—fire and water; 2004 August 10-12; Lubbock, TX. Proceedings RMRS-P-47. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 173 p.

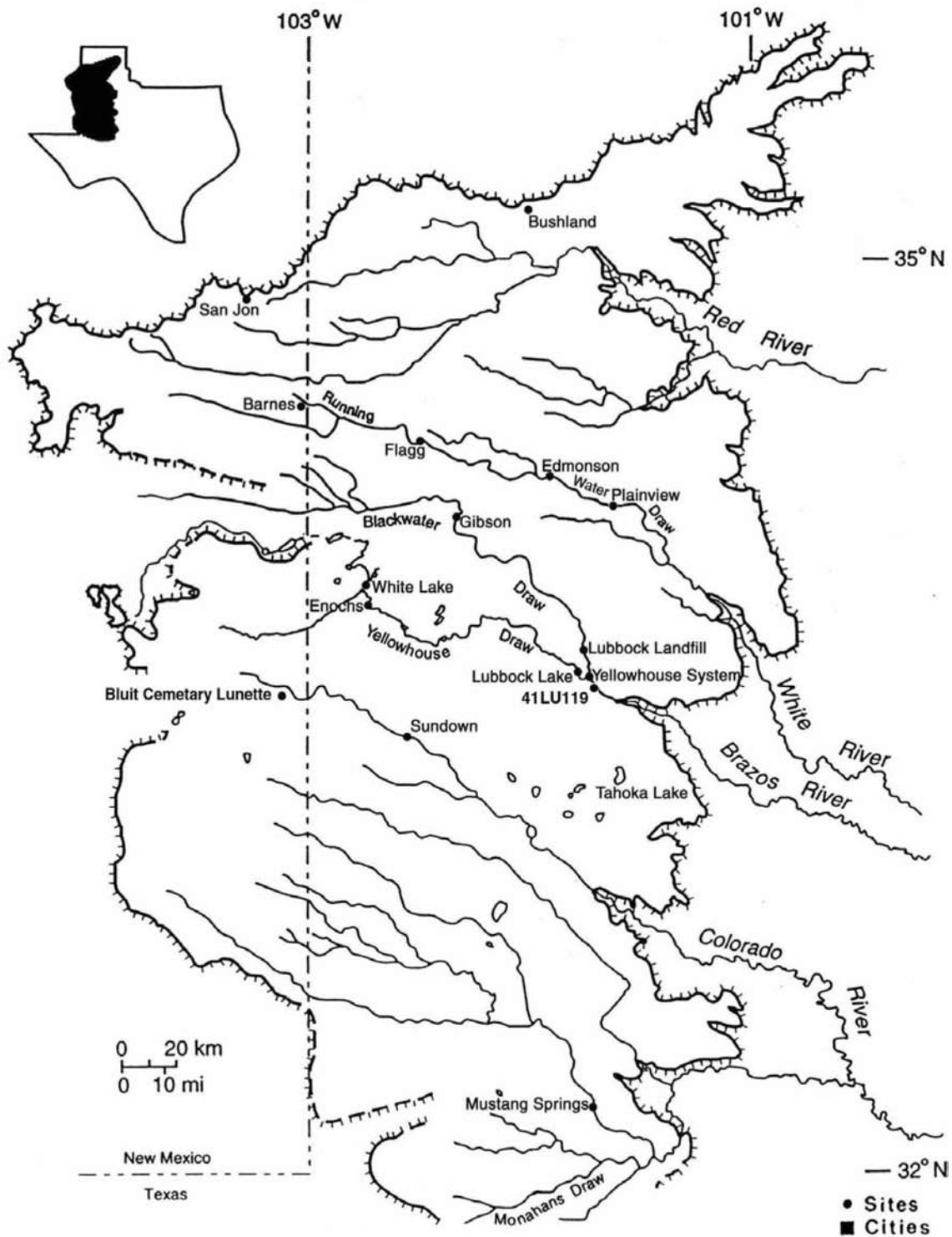


Figure 1. Localities on the Llano Estacado yielding paleovegetation data (direct evidence).

cultivation” (Pope 1855:9). Yet, 20 years later in the 1870s, the Pastores (Hispanic shepherders from New Mexico and the first non-indigenous settlers of the region) saw the territory as a vast, well-watered grassland ideal for expansion first through transhumance and then through year-round sedentary village pastoralism (Hicks and Johnson 2000). They called the western escarpment *La ceja de Dios* or “God’s eyebrow”

(Cabeza De Baca 1954). This appellation imparted a much different sentiment from that of the Anglo statements.

A synthesis of the development of the late Quaternary grassland ecosystems of the Llano Estacado from the Last Glacial Maximum (LGM) to historic times is based on the data from more than 20 localities across the region (table 1; fig. 1). These localities occur in the principal landforms (valleys, lake basins,

Table 1—Localities on the Llano Estacado yielding paleovegetation data (direct evidence).

Locality	Geomorphic setting	Stratum/sge	Evidence	Reference
Bluitt Cemetery Lunette	lunette	LGM	phytoliths	Fredlund and others 2003
Bushland Playa	upland playa	LGM	phytoliths, pollen	Fredlund and others 2003
White Lake	salina	LGM	phytoliths	Fredlund and others 2003
San Jon	upland playa	stratum 1	phytoliths	Fredlund and others 2003
		stratum 2	phytoliths	Fredlund and others 2003,
		8,000 B.P.	phytoliths, charcoal	Fredlund and others 2003,
				Johnson unpublished data
Barnes Playa	upland playa	stratum 1	phytoliths	Fredlund and others 2003
		stratum 2	phytoliths	Fredlund and others 2003
		8,000 B.P.	phytoliths	Fredlund and others 2003
Lubbock Lake Landmark	valley	stratum 1	phytoliths, seeds, preserved wood,	Fredlund and others 2003, Thompson 1987, Robinson 1982
		stratum 2	phytoliths, pollen, impressions, seeds	Fredlund and others 2003, Hall 1995, Thompson 1987, Robinson 1982
		8,000 B.P.	phytoliths	Fredlund, unpublished data
		stratum 3	seeds	Thompson 1987
		stratum 4	seeds	Thompson 1987
		stratum 5	seeds, charcoal	Thompson 1987, Johnson unpublished data
Yellowhouse system ^a	valley	stratum 1	seeds, charcoal	Johnson unpublished data
		stratum 2	phytoliths, seeds, charcoal	Johnson unpublished data
		stratum 3	phytoliths, seeds, charcoal	Johnson unpublished data
		stratum 4	phytoliths, seeds, charcoal	Johnson unpublished data
		stratum 5	phytoliths, seeds, charcoal	Johnson unpublished data
Mustang Springs	valley	stratum 1	phytoliths	Bozarth 1995
		stratum 2	phytoliths	Bozarth 1995
		stratum 4	phytoliths	Bozarth 1995
		stratum 5	phytoliths	Bozarth 1995
Plainview	valley	stratum 2	pollen	Hall 1995
Edmonson	valley	8,000 B.P.	phytoliths	Bozarth 1995
Gibson	valley	stratum 3	phytoliths	Bozarth 1995
Enochs	valley	stratum 3	phytoliths	Bozarth 1995
Lubbock Landfill	valley	stratum 4	phytoliths	Bozarth 1995
Sundown	valley	stratum 4	phytoliths	Bozarth 1995
Flagg	valley	stratum 5	phytoliths	Bozarth 1995
41LU119	uplands	stratum 5	seeds	Johnson unpublished data
Tahoka Lake	salina	stratum 5	seeds, charcoal	Johnson unpublished data

^aRepresents a compilation of more than 10 localities within a 20 km stretch of the Yellowhouse system.

dunes). Some localities are stratified, providing a record for several time periods in one place, whereas others represent only a single time period. Some provide multiple lines of evidence for past plant communities whereas others produced only one. Taken together, these localities cover the region and the late Quaternary using multiple lines of evidence to view these changing ecosystems.

The Llano Estacado has been a grassland since Miocene-Pliocene times (Fox and Koch 2003). Despite previous

interpretations of a boreal forest during latest Pleistocene times (Hafsten 1961; Wendorf 1961, 1970, 1975; Oldfield and Schoenwetter 1975), the Llano Estacado throughout the Quaternary has been a grassland (Holliday 1987). Interpretations based on pollen data have proven to be untenable (Holliday 1987; Holliday and others 1985; Hall and Valastro 1995). As the climate changed, the character of the Llano Estacado grassland has varied through time, alternating between open, parkland, and savannah, with isolated to small stands of deciduous trees.

Lines of Evidence

The synthesis is based on both direct and indirect lines of evidence that form the basis for interpretation. Direct evidence is composed of the vestiges of plants themselves represented by phytoliths, pollen, or macrobotanical specimens. Phytoliths are hydrated silica-bodies produced by grasses and certain other monocotyledon and dicotyledon families as well as some spore-producing families (Piperno 1988). The phytolith record generally is well-preserved on a regional basis (Bozarth 1995; Fredlund 2002; Fredlund and others 2003) and is thought to indicate what was growing in the local environs.

Based primarily on phytoliths, three major grass subfamilies have been identified in the record. Pooid grasses are C_3 plants that are short-day grasses, having limited available sunshine for growing and flowering. They generally prefer cool to cold climates with a sufficient moisture regime during the growing season. Limiting factors are available moisture and temperature. Panicoideae grasses are composed of both C_3 and C_4 plants that are long-day grasses, having maximum available sunshine. They generally prefer moist, humid tropic to subtropic conditions. They have the same limiting factors as pooid grasses. Chloridoideae grasses are C_4 plants that are long-day grasses. They generally prefer warm, dry climates.

The pollen record for the Southern High Plains is generally considered unreliable due to the lack of duplication or notably dissimilar nature of pollen diagrams within the same locality, very low counts, grain corrosion, and other preservation problems (Bryant and Schoenwetter 1987; Hall 1981; Hall and Valastro 1995). The few dependable records are included in the synthesis. Because of the ease of wind transport and dispersal, pollen records may be a mix of the local environs, regional vegetation, and extraregional plants.

Macrobotanical remains consist of seeds, charcoal, preserved wood, and preserved impressions (fig. 2). Carbonized seeds and charcoal are the most pervasive of the four types, having been recovered from throughout the late Quaternary stratigraphy. Preserved wood and impressions are rare and, to date, have been found only in late Pleistocene fluvial (wood) and early Holocene lacustrine (impressions) environments.

Indirect evidence providing proxy data on vegetation communities includes sediments and soils, radiocarbon and stable-carbon isotope data, and vertebrate records. The regional sediments and soils reflect the influence of climate, environmental factors, and biota (Buol and others 1973; Birkland 1999; Holliday 2004). Well over 325 radiocarbon dates are available that provide a solid chronology. Many of these are assays from organic-rich sediments that also provide $\delta^{13}C$ values as a result of routine measurement along with radiocarbon dating. This isotopic value reflects the C_3 and C_4 plant biomass. A positive correlation exists between $\delta^{13}C$ and the proportions of C_3 and C_4 biomass and $\delta^{13}C$ values (Cerling 1984; Bowen 1991; Nordt 2001). The C_3 plants have a lighter isotopic composition. This group is comprised of cool season grasses, most aquatic plants, and trees. The C_4 plants have a heavier isotopic composition and are composed of primarily warm season grasses. Each per mil change represents a shift

of about 7 percent in the ratio of C_3 to C_4 biomass (Bowen 1991).

Although less than half the available radiocarbon dates with $\delta^{13}C$ values have been analyzed, an initial pattern has emerged that indicates both a shift from lighter (C_3 plants) to heavier (C_4 plants) isotopic composition and a time-transgressive nature of the shift across the Southern High Plains from

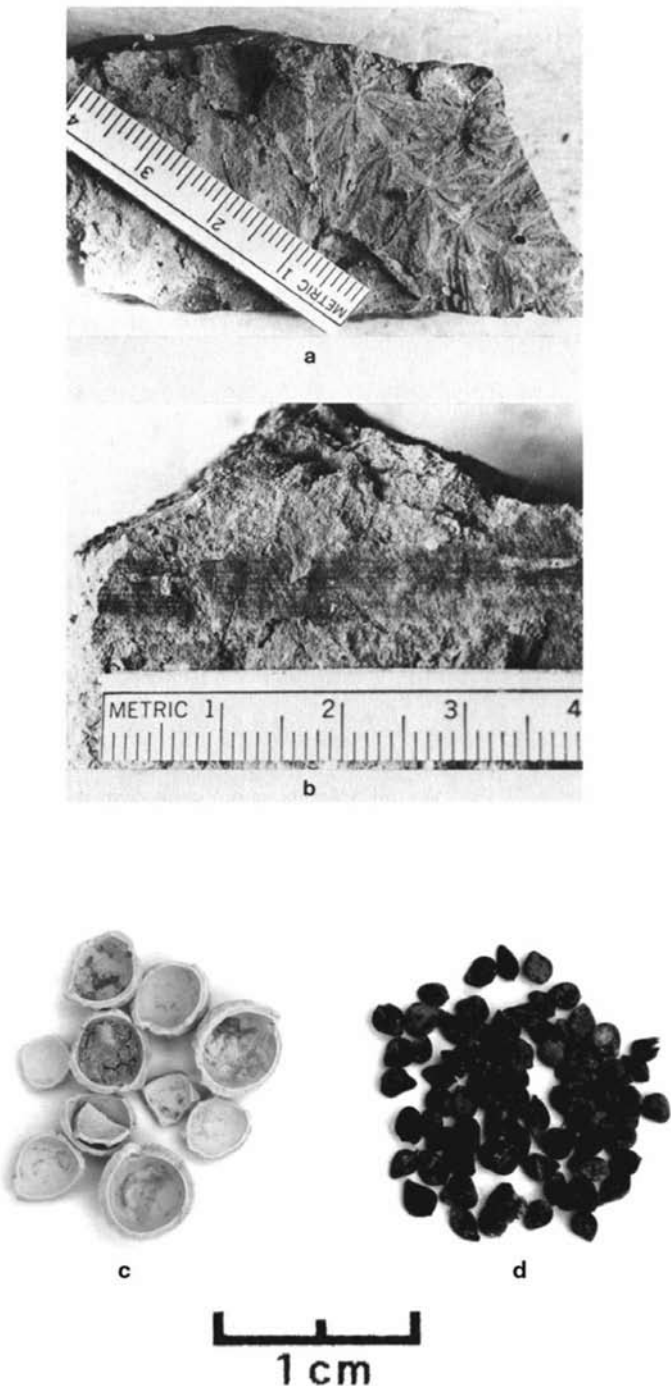


Figure 2. Macrobotanical evidence from localities on the Llano Estacado: a) preserved impression of musk-grass (*Chara*); b) preserved impression of horsetail (*Equisetum*); c) fossil net-leaf hackberry (*Celtis reticulata*) seeds; and d) fossil bulrush (*Scirpus*) seeds.

ca. 8,800 to 8,200 B.P. (Holliday 1995a). This difference in timing could reflect localized conditions or be an artifact of sampling.

The best and longest record (Lubbock Lake Landmark; Holliday 1995a:57) covers the Holocene and indicates both change and stability. Lighter isotopic values dominate from ca. 10,000 to 8,200 B.P. An abrupt shift from lighter to heavier isotopic composition occurs ca. 8,200 B.P., with ca. 28 percent C_4 grasses in the earliest Holocene. The C_4 grasses dominate throughout the middle Holocene between 7,000 to 4,500 B.P., with ca. 79 percent C_4 grasses. That pattern holds for most of the late Holocene between 4,500 to 500 B.P., with ca. 79 percent C_4 grasses. Around 500 B.P., a shift to lighter composition (C_3 plants) occurs, with only ca. 19 percent C_4 grasses. This high frequency of C_3 plants (ca. 81 percent) most likely reflects the aquatic plants of the extensive marsh at this time in the valley floor. Based on this record, grasses indicative of cooler conditions dominate the valleys of the Llano Estacado in the earliest Holocene and were replaced by grasses of warmer conditions by the end of the early Holocene. These warm season grasses continue throughout the middle and late Holocene.

Stable-carbon isotope data from lunettes on the uplands of the central Llano Estacado provide a regional perspective with a lengthier and compatible but incomplete record that indicates broad trends (Holliday 1997:63-64, 66). From 25,000 to 15,000 B.P., a gradual shift toward lighter isotope values indicates an increase in cooler, temperate-climate plants. Between 15,000 and 13,000 B.P., both lighter and heavier values occur, with a shift to heavier values from 13,000 to 10,000 B.P. A shift back to lighter values occurs from 10,000 to 8,000 B.P., with a shift at 8,000 B.P. back to heavier values that is maintained throughout the rest of the Holocene. The shift to post-LGM warmer conditions is most dramatic from 13,000 to 10,000 B.P., with a second shift to warmer conditions around 8,000 B.P.

Major physiographic features and indicator plants and animals bind the grasslands together over the vast Great Plains (Coupland 1992). The regional late Quaternary vertebrate record is known, and is particularly extensive for the late Pleistocene and early Holocene (Johnson 1986, 1987). A number of forms are environmentally sensitive or characteristic of certain ecosystems or vegetation communities. The vertebrate binding or key indicator species for grasslands are bison, pronghorn antelope, and prairie dog. These species are common on the Llano Estacado throughout the late Quaternary.

Framework

The Ogallala Formation and the Blackwater Draw Formation are the principal units responsible for the flat, almost featureless, constructional surface of the Llano Estacado. The upper Ogallala Formation (Miocene-Pliocene), the principle geologic bedrock of the Llano Estacado, was a stable land surface for hundreds of thousands of years, resulting in a well-developed soil. The ca. 2 m thick highly

resistant calcrete at the top of the Ogallala Formation is a remnant of that soil. This pedogenic calcrete unit primarily is responsible for the configuration and size of the Llano Estacado, the prominent escarpments around its margin, and contributes to the topographic flatness.

The landforms and Quaternary soils and sediments form the framework for examining the past ecosystems of the region. The Blackwater Draw Formation (Pleistocene) was formed by deposition of episodic, thick, and widespread aeolian sediments laid down starting sometime in the early Pleistocene up to about 50,000 years ago (Holliday 1989a; Reeves 1976). Originating in the Pecos River Valley, these sediments draped the region and blanketed all underlying units and geomorphic features (including the drainage system and basins). The sediments were altered by soil formation under dry and warm conditions. This deposit and its associated soils represent the major surficial deposit of the Llano Estacado.

Landforms

Modern geomorphic features have cut into or through, or rest upon the Blackwater Draw Formation. The surface of the Llano Estacado has been modified by three geomorphic forms. Two of these, basins and dunes, occur on the uplands.

About 25,000 small lake basins (locally known as playas) and 40 saline depressions (locally known as salinas) cover the landscape, occurring primarily on the High Plains surface (Sabin and Holliday 1995). Playas are inset into the Blackwater Draw Formation and formed primarily through erosional processes. They usually are freshwater sources. Most playas began forming in the late Pleistocene. Some basins were filled completely and no longer have a surface expression. Salinas are large, irregularly shaped basins probably formed through dissolution and collapse into the Ogallala Formation. They appear to be subsidence basins where long-term infiltration of ground water has caused point-source dissolution of the Permian salts (Reeves 1991). Although freshwater springs are associated with some salinas, the basins contain salt deposits and lake waters are brackish (Wood and others 2002).

Dune fields and lunettes rest on the Blackwater Draw Formation throughout the Llano Estacado. Extensive dune fields occur in three areas on the western side of the Southern High Plains. They are coincident with three major reentrant valleys on the western escarpment that acted as ramps or channels for sediments blowing off the Pecos River Valley in an incursion onto the Llano Estacado. Elsewhere along the western edge, large dune fields built up against the escarpment.

Lunettes are lee side dunes formed on the downwind side of drying playa and salina lake basins. Not all playas have lunettes, but of those that do, the lunettes generally are on the east and southeast side of the playa basin. Lunettes along playas form a single dune ridge. Those around the larger salinas typically occur as three dune ridges (Holliday 1997; Rich and others 1999).

The northwest-southeast trending now-dry river valleys (locally known as draws) are tributaries of the Red, Brazos,

and Colorado rivers that flow through the Osage Plains and into the Gulf of Mexico or the Mississippi River. Generally, these valleys have cut through the Blackwater Draw Formation to the Ogallala Formation except where the drainages have intercepted late Pliocene (Blanco Formation) or Pleistocene lake sediments. Final down cutting that resulted in the modern drainage system began sometime after 20,000 years with aggrading and infilling of the valleys starting around 12,000 years ago (Holliday 1995a).

Numerous springs, active since at least the late Pleistocene (Holliday 1995a, 1995b), flowed in various reaches of the valleys prior to the 1930s, with both ponds and free-flowing water available (Brune 1981). These springs were not distributed throughout the draws but rather were concentrated and confined to certain reaches of the valley system where the aquifer had been breached by valley downcutting. Today, the valleys generally are dry due to the dropping water table, and the playas and salinas contain the only naturally impounded, although generally seasonal, surface water for the region.

Quaternary Stratigraphy

Soil characteristics provide information on the vegetation community or ecosystem under which they developed. A boreal forest imparts distinctive pedologic characteristics to the soils, all of which are absent in the buried and surficial soils of the Southern High Plains (Holliday 1987, 1989a). The Blackwater Draw Formation is the aeolian mantle that covers the Southern High Plains and forms the surficial sediment. It contains several buried soils, the oldest of which was buried ca. 1.5 million years ago. Sedimentation ceased around 50,000 years ago and the regional surface began developing (Holliday 1989a). All buried soils virtually are identical to surface soils. What this means is that the late Quaternary vegetation represents that of most of the Quaternary. At no time during the Quaternary were boreal forests or coniferous woodlands present on the Llano Estacado. Rather, the region has been dominated by grassland, albeit varying in grass composition.

The late Quaternary stratigraphic record for the Southern High Plains is contained in the three landforms, although primarily in the valley system. Generally, late Holocene aeolian sediments over Blackwater Draw Formation occur in the upland areas between playas, salinas, and dune fields. Dune formation is a Holocene feature. Deposition of sand sheets began in the early Holocene, with episodic development in the middle and late Holocene (Holliday 1995b, 2001a; Muhs and Holliday 2001).

Few playas or salinas are stratified. Salinas contain discontinuous stratigraphic records. Early and middle Pleistocene playas occur below some of the recent playas (Gustavson and others 1995; Holliday and others 1996). Playas can contain thick (average 3 to 5 m) fills of lake mud and some aeolian sediments that span the late Pleistocene and Holocene and provide a lengthy record of shifting waters in the basin through time (Hill and others 1995; Holliday and others 1996). Lunettes, a late Pleistocene to Holocene feature, are stratified and

typically contain buried soils indicative of episodic accretion (Holliday 1997). Lunettes around salinas occur in three bands representing different time periods (late Pleistocene, middle Holocene, late Holocene) and wind directions (Holliday 1997; Sabin and Holliday 1995).

Valley fills provide the most extensive regional record (Holliday 1995a). The valley fill stratigraphy is composed of five major stratigraphic units within which a number of buried soils are contained. Subunits are defined within the major units as well as facies. Although the five major units are well-represented throughout the valley system, no one location contains the entire record of units, subunits, and facies. The most complete record is at Lubbock Lake (Holliday 1985; Holliday and Allen 1987) in Yellowhouse Draw. Although local subunit and facies designations have been maintained, they are correlated with the regional terminology (table 1). Although some boundaries regionally are time-transgressive (Holliday 1995a), Lubbock Lake's geochronology provides a general framework in which to view the hydrologic and landscape changes through time.

The lowest stratum of valley fill is stratum 1 consisting of a basal sand and gravel unit (substratum 1A), cross-bedded sand (substratum 1B), and locally, an overlying clay drape (substratum 1C). Stratum 1 is interpreted as a meandering stream deposit with point bar sediments and overbank deposits. Deposition of stratum 1 generally ended about 11,000 B.P., although in some reaches flowing water continued as late as 10,000 years ago. The climate was cool and humid (maritime conditions) with enhanced rainfall in the winter (Johnson 1987, 1991).

Stratum 2 is primarily a lacustrine and marsh deposit found along the valley axis. Substratum 2A contains beds of pure diatomite that represent periods of standing water with interbedded peaty muds indicating marshy conditions. Substratum 2B overlies 2A and contains a homogeneous layer of organic-rich silt and clay representing a slowly aggrading marsh. A sandy shore facies is found in a narrow zone along the valley margin while a sandy, aeolian facies with some slopewash and interbedded marsh sediments is found along the outer valley margin. Deposition of stratum 2 began about 11,000 B.P. and the 2A-2B transition occurred about 10,000 B.P. Aggradation of 2B ceased about 8,500 B.P. and the Firstview Soil formed on a stable surface from about 8,500 to 6,400 B.P. Elsewhere in the valley system, the Firstview Soil was buried earlier than at Lubbock Lake (Holliday 1995a) and at one locality, stratum 2 started accumulating as early as 11,300 B.P. (Holliday 1995a:13). The climate was warming with a shift in rainfall pattern. Rainfall levels and a lower evaporation rate led to more effective moisture reflective of continuing wet conditions (Johnson 1987). Nevertheless, the first signs of Holocene drought (less available moisture) occurred during the period 10,900 to 10,200 B.P. (Holliday 2000).

Stratum 3 lies conformably on top of stratum 2 and is composed of a moderately calcareous, sandy aeolian deposit along the western valley margin and a highly calcareous, silty lacustrine unit found along the valley axis. Stratum 3 represents an alkaline lake or marsh along the valley floor with considerable aeolian additions along the valley margin. Stratum 3

deposition and formation of the Yellowhouse Soil occurred between about 6,400 to as late as 5,000 B.P. Elsewhere in the valley system, stratum 3 deposition occurred perhaps as early as 10,000 B.P. and internal buried A-horizons locally occur within stratum 3 (Holliday 1995a). Stratum 3 denotes a time of increasing temperatures, decreasing rainfall, and lower humidity (Johnson 1987).

Stratum 4 is composed of alluvial and marsh deposits found only along the valley axis (4A), and a sandy aeolian deposit that blankets the valley (4B) with a clayey marsh facies (4m) found along the valley axis. The Lubbock Lake Soil formed in substratum 4B under well-drained conditions and is well-developed with prominent A and B horizons and often multiple calcic horizons. Deposition of 4A occurred between 5,500 and 5,000 B.P. and 4B between 5,000 and 4,500 B.P. The Lubbock Lake Soil began forming around 4,500 to around 1,000 B.P. when it locally was covered by stratum 5. Elsewhere in the valley system, stratum 4 is buried as early as 3,900 B.P. (Holliday 1995a). Where not buried by stratum 5 sediments, soil formation continues today. Stratum 4 represents the culmination of the warming trend, with increasingly hot, dry, and dusty conditions known as the Altithermal (Holliday 1989b). The climate is very xeric. By 4,500 B.P., the modern continental climate emerges with a return to cooler and mesic conditions (Johnson 1987; Holliday 1989b).

Stratum 5, the uppermost stratum, is represented by marsh deposits and upslope, valley margin facies composed of layers of aeolian sand and slopewash sand and gravel, burying stratum 4. Buried soils occur locally. Deposition of lower 5 began around 750 to 600 B.P. and continued to about 450 B.P. when a soil began to form locally. Deposition of upper 5 began about 300 B.P. A weakly developed soil began to form locally about 100 B.P. and is exposed locally at the surface today. Elsewhere in the valley system, deposition of stratum 5 valley margin sands begins as early as 3,900 B.P. and valley axis marsh muds by 3,200 B.P. (Holliday 1995a). By 2,000 B.P., an episodic drought cycle begins that continues today as part of the modern climatic pattern. The intensity and frequency of droughts varies through time, alternating between more mesic and less mesic conditions (Johnson 1987; Holliday 1995a).

The Record

The various localities across the Southern High Plains (fig. 1) provide a composite of the floral and faunal communities from the Last Glacial Maximum (LGM) to the latest Holocene. That composite is segmented by time and stratigraphy, with any one time period represented by three to six localities. Each locality, as well as stratigraphic units within a locality, varies in terms of the type of direct and indirect evidence available (table 2). The data come from two primary sources—those that are published (Bozart 1995; Hall 1995; Hall and Valastro 1995; Holliday 1995a; Johnson 1986, 1987b; Thompson 1987) and those that are unpublished. Unpublished data either have been presented at professional meetings (Fredlund 2002; Fredlund and others 2003) or are those of

Table 2—Correlation of valley fill stratigraphic terminology for the Lubbock Lake Landmark with the regional stratigraphy.

Lubbock Lake stratigraphy ^a	Regional stratigraphy ^b
stratum 5	stratum 5
substratum 5B	stratum 5s2 and 5gs
substratum 5Bm	stratum 5m
substratum 5A	stratum 5s1 and 5g1
substratum 5Am	stratum 5m
substratum 5m	stratum 5m
stratum 4	stratum 4
substratum 4B (upper/A-horizon)	stratum 4s
substratum 4B	stratum 4s
substratum 4A	stratum 4m
substratum 4m	stratum 4m
stratum 3	stratum 3
substratum 3c (upper/A-horizon)	stratum 3c
substratum 3c	stratum 3c
substratum 3m	stratum 3m
substratum 3e	stratum 3s
stratum 2	stratum 2
substratum 2s	stratum 2s
2s local bed c	stratum 2s
2s local bed b	stratum 2s
2s local bed a	stratum 2s
substratum 2e	stratum 2s
substratum 2B (upper/A-horizon)	stratum 2m
substratum 2B	stratum 2m
2B cienega	stratum 2m
substratum 2A	stratum 2d
2A local bed 5	stratum 2d
2A local bed 4	stratum 2d
2A local bed 3	stratum 2d
2A local bed 2	stratum 2d
2A local bed 1	stratum 2d
stratum 1	stratum 1
substratum 1C	stratum 1
substratum 1B	stratum 1
substratum 1A	stratum 1

^aBased on Holliday (1985), Holliday and Allen (1987), and field notes on file at the Museum of Texas Tech University.

^bBased on Holliday (1995a).

the author's. Nevertheless, the overall record is robust with a clear dominance of grasslands and grassland vertebrate forms throughout.

The late Quaternary period is subdivided into late Pleistocene and Holocene epochs. Discussion of the late Pleistocene begins with the LGM, ca. 20,000 to 18,000 B.P., and continues through post-glacial time to the Pleistocene-Holocene boundary at 11,000 B.P. Climatic changes and large-scale extinctions occurring at the end of the Pleistocene and around 11,000 B.P. mark the biotic and ecosystemic end of Wisconsinian conditions on the Southern High Plains. This time period is used as the boundary between the Pleistocene and Holocene rather than the geologic convention of using an arbitrary 10,000 B.P. as the boundary (Hageman 1972; Holliday 2001b).

Late Pleistocene Background

The LGM is represented by three localities dating from 21,865 to 17,710 B.P. (table 1) that are associated with playas or salinas on the uplands. Data indicate a grassland composed of sagebrush (*Artemisia*), grasses (Poaceae), ragweed (*Ambrosia*), daisy-sunflower-aster family (Asteraceae), Chenopods (chenopods and amaranth), and juniper (*Juniperus*). A rare component of the flora consists of hackberry (*Celtis*), Liguliflorae (herbs such as wild lettuce [*Lactuca*]), wild buckwheat (*Eriogonum*), carrot or parsley family (Apiaceae), greasewood (*Sarcobatus*; a chenopod shrub), amaranth family (Amaranthaceae), evening primrose family (Onagraceae), yucca (*Yucca*), cactus family (Cactaceae), and bluebell-lobelia family (Campanulaceae). Aquatic plants indicative of wet ground to open water are the sedge family (Cyperaceae), ditch grass (*Ruppia*; submersed vegetation in alkaline lakes), common cattail (*Typha latifolia*; emergent vegetation), and colonies of the freshwater algae (*Botryococcus* and *Pediastrum*). Ditch grass is known only from White Lake, reflecting the brackish waters of that salina.

Little is known of the fauna at this time. The presence of mammoth (*Mammuthus* spp.), ancient horse (*Equus* spp.), and ancient bison (*Bison antiquus*) (Evans and Meade, 1945) is indicative of grasslands. The records denote a sagebrush grassland with high amounts of composites. This grassland is an herbaceous prairie community under an equitable, cooler, and humid climate with no modern analog (Hall and Valastro 1995:244).

Late Pleistocene stratum 1 times are represented by five localities dating from 12,500 to 11,000 B.P. (table 1) that are associated with upland playas and the valley system. Pooid grasses, including needlegrass or wintergrass (*Stipa*; cool-moist season), dominate with a very low component of panicoid grasses and chloridoid grasses. Almost no C_4 grasses are present and sagebrush is absent. Other floral elements reflecting the valley system are seepweed (*Suaeda*), gromwell (*Lithospermum*), devil's claw (*Proboscidea louisianica*), and net-leaf hackberry (*Celtis reticulata*). Aquatic plants indicative of wet ground to open water are bulrush (*Scirpus*; emergent vegetation) and spikerush (*Eleocharis*; emergent vegetation).

A highly diverse herd herbivore fauna, indicative of grasslands, is complimented by an equally diverse carnivore guild (table 3). The larger carnivores are dependent upon these herbivores and preyed upon and scavenged their carcasses (Matheus 1995, 2003; Matheus and others 2003). Other grassland forms are as varied (table 3). The tiger salamander and meadow vole, in particular, reflect the riparian habitat along the streams. Sedge beds, reflected in the macrobotanical remains, are the preferred habitat of meadow voles (Findley and others 1975; Thompson 1965). Equally of note is the prairie dog town community (prairie dog, ground squirrels, grasshopper mouse, burrowing owl, western hognose, and ground snakes) reflected in these smaller grassland forms and some of the town's predators (rattlesnake, turkey vulture, ferruginous hawk).

Table 3—Late Pleistocene (stratum 1) grassland fauna of the Llano Estacado.

Taxon	Common name
<u>Herd herbivores</u>	
<i>Mammuthus columbi</i>	Columbian mammoth
<i>Bison antiquus</i>	ancient bison
<i>Equus mexicanus</i>	large, stout-legged horse
<i>Equus francisci</i>	small, stilt-legged horse
<i>Camelops hesternus</i>	yesterday's camel
<i>Capromeryx</i> spp.	extinct, 4-pronged antelope
<i>Hemiauchenia macrocephala</i>	large-headed llama
<i>Odocoileus virginianus</i>	white-tailed deer
<i>Antilocapra americana</i>	pronghorn antelope
<i>Platygonus compressus</i>	flat-headed peccary
<u>Carnivore guild</u>	
<i>Arctodus simus</i>	short-faced bear
<i>Smilodon fatalis</i>	saber-toothed cat
<i>Canis dirus</i>	dire wolf
<i>Canis lupus</i>	gray wolf
<i>Canis latrans</i>	coyote
<i>Vulpes velox</i>	swift fox
<i>Urocyon cinereoargenteus</i>	gray fox
<u>Other grassland forms</u>	
<i>Ambystoma tigrinum</i>	tiger salamander
<i>Scaphiopus</i> spp.	spade-foot toad
<i>Bufo cognatus</i>	Plains toad
<i>Kinosternon flavescens</i>	yellow mud turtle
<i>Elaphe guttata</i>	corn snake
<i>Gyalopion canum</i>	western hook-nosed snake
<i>Heterodon nasicus</i>	western hognose snake
<i>Lampropeltis triangulum</i>	common king snake
<i>Sonora semiannulata</i>	ground snake
<i>Thamnophis</i> cf. <i>sirtalis</i>	common garter snake
<i>Tropidoclonion lineatum</i>	lined snake
<i>Crotalus atrox</i>	western diamondback rattlesnake
<i>Carthartes aura</i>	turkey vulture
<i>Buteo regalis</i>	ferruginous hawk
<i>Athene</i> cf. <i>cunicularia</i>	burrowing owl
cf. <i>Pooecetes gramineus</i>	vesper sparrow
<i>Holmesina septentrionalis</i>	giant pampathere
<i>Glossotherium</i> (= <i>Paramylodon</i>) <i>harlani</i>	Harlan's ground sloth
<i>Lepus californicus</i>	black-tailed jack rabbit
<i>Spermophilus richardsonii</i>	Richardson's ground squirrel
<i>Spermophilus tridecemlineatus</i>	13-lined ground squirrel
<i>Spermophilus mexicanus</i>	Mexican ground squirrel
<i>Cynomys ludovicianus</i>	black-tailed prairie dog
<i>Geomys bursarius</i>	Plains pocket gopher
<i>Reithrodontomys montanus</i>	Plains harvest mouse
<i>Onychomys leucogaster</i>	Northern grasshopper mouse
<i>Neotoma micropus</i>	Southern Plains woodrat
<i>Microtus pennsylvanicus</i>	meadow vole
<i>Microtus ochrogaster</i>	prairie vole

These prairie dog towns existed within an overall dominant pooid grass prairie that was a parkland. Isolated hackberry trees to small groves grew along the streams in the valley system, continuing the presence of this native tree from the LGM. A lower mean annual temperature than today, cooler summers and warmer winters that lacked extended freezing conditions, more effective moisture, lower evaporation rate, and enhanced winter precipitation indicated an equitable, humid, and

maritime-like climate that lacked seasonal extremes (Johnson 1991). Nevertheless, a major environmental shift at 11,000 B.P. is represented in the draws by an abrupt hydrologic change from flowing to standing water, and on the uplands, by the onset of regional dune construction that heralds the Holocene.

Holocene Dynamics

Early Holocene stratum 2 times are represented by five localities dating from 10,800 to 8,200 B.P. (table 1) that are associated with upland playas and the valley system. While still dominant, pooid grasses, including needlegrass or winter-grass, are steadily decreasing. Chloridoid grasses show a continuing rise with a low but steady component of panicoid grasses including the short-grass threeawn (*Aristida*; warm season). Other floral elements reflecting the valley system are goosefoot (*Chenopodium*), buffalo bur (*Solanum rostratum*), guarra (*Guara*), devil's claw, ragweed, the daisy-sunflower-aster family, Liguliflorae, mustards (Brassicaceae), and the evening primrose family. A variety of emergent and submersed vegetation indicative of wet ground to open water include cattail, sedge (*Cyperus*), bulrush, spikerush, horsetail (*Equisetum*), musk-grass (*Chara*), and colonies of the fresh-water algae (*Botryococcus*).

Native trees in the valley are net-leaf hackberry, sumac (*Rhus*), and cottonwood (cf. *Populus*), with juniper (cf. *Juniperus*) and piñon-pine (cf. *Pinus edulis*) along the High Plains escarpment. The latter three are from pollen of questionable reliability (Hall 1995), but plausible. Juniper and an occasional piñon-pine grow along the western High Plains escarpment today and occasional cottonwoods grow in the lower reaches of the valley system. Sumac, like hackberry, is a shrub to small tree. Isolated, disjunct populations of littleleaf sumac (*R. microphylla*) occur today on the Llano Estacado, with a similarly isolated population of prairie sumac (*R. lanceolata*) just to the north of the region (Petrides and Petrides 1992:134, 137).

The diversity of herd herbivores, along with the carnivore guild, decreased considerably (table 4) due to the changes occurring around 11,000 B.P. and the collapse of the Pleistocene food web (Matheus and others 2003). Ancient bison became the dominant herd herbivore. Although some reduction in diversity occurred with the smaller grassland forms, variety was still maintained with some new taxa appearing (table 4). Both plant and animal forms indicated sedge beds around the marshy edges of the ponded waters in the valleys and later with the aggrading marshes, along with submersed vegetation in the ponds. A prairie dog town community continued along with the badger as its predators.

These prairie dog towns existed within an overall mixed grassland with an increase in C_4 grasses without sagebrush. The setting was that of a savanna. Low numbers of hackberry, sumac, and possibly cottonwood trees grew along the valley margins in the valley system. Equitable climatic conditions gave way to the onset of winters with at least occasional

Table 4—Early Holocene (stratum 2) grassland fauna of the Llano Estacado.

Taxon	Common name
<u>Herd herbivores</u>	
<i>Bison antiquus</i>	ancient bison
<i>Capromeryx</i> spp.	extinct 4-pronged antelope
<i>Odocoileus</i> spp.	deer
<i>Antilocapra americana</i>	pronghorn antelope
<u>Carnivore-guild</u>	
<i>Canis lupus</i>	gray wolf
<i>Canis latrans</i>	coyote
<i>Taxidea taxus</i>	badger
<u>Other grassland forms</u>	
<i>Ambystoma tigrinum</i>	tiger salamander
<i>Kinosternon flavescens</i>	yellow mud turtle
<i>Terrapene ornata</i>	western box turtle
<i>Phrynosoma cornutum</i>	Texas horned lizard
<i>Eumeces obsoletus</i>	Great Plains skink
<i>Coluber constrictor</i>	racer
<i>Sonora semiannulata</i>	ground snake
<i>Thamnophis</i> cf. <i>sirtalis</i>	common garter snake
<i>Tropidoclonion lineatum</i>	lined snake
<i>Circus cyaneus</i>	harrier
cf. <i>Eremophila alpestris</i>	horned lark
<i>Mimus polyglottis</i>	mockingbird
<i>Tympanuchus cupido</i>	prairie chicken
<i>Notiosorex crawfordi</i>	desert shrew
<i>Lepus californicus</i>	black-tailed jack rabbit
<i>Spermophilus tridecimlineatus</i>	13-lined ground squirrel
<i>Spermophilus mexicanus</i>	Mexican ground squirrel
<i>Cynomys ludovicianus</i>	black-tailed prairie dog
<i>Geomys bursarius</i>	Plains pocket gopher
<i>Chaetodipus hispidus</i>	hispid pocket mouse
<i>Dipodomys ordii</i>	Ord's kangaroo rat
<i>Reithrodontomys montanus</i>	Plains harvest mouse
<i>Onychomys leucogaster</i>	Northern grasshopper mouse
<i>Sigmodon hispidus</i>	cotton rat
<i>Neotoma</i> cf. <i>micropus</i>	Southern Plains woodrat
<i>Microtus pennsylvanicus</i>	meadow vole
<i>Microtus ochrogaster</i>	prairie vole

periods of freezing temperatures. Summers were warming and occasional droughts (less effective moisture) occurred (Holliday 2000). While conditions still were humid, rainfall pattern was shifting with an eventual decrease in rainfall, and mean annual temperature was rising (Johnson 1986, 1987b).

By around 8,000 B.P., the dynamics between climate, vegetation, and fauna were such that the character of the landscape is changing. Chloridoid grasses are dominant, most likely produced by a grama-buffalograss (*Bouteloua-Büchloe*) prairie. A low level of pooid and panicoid grasses that included short-grass threeawn continues. Based on phytolith data, the short-grass ecosystem emerges around 8,000 to 8,200 B.P., with modulations in that ecosystem into modern times (Fredlund and others 2003). The phytolith and stable-carbon isotope data, then, are in general agreement.

In tandem with this change but somewhat later, modern bison (*Bison bison*) emerged, not as a replacement species, but as the transformation of the ancient form into the modern form due to the plasticity of the bison genome (Lewis 2003;

Lewis and others 2001). Bison underwent a rapid decrease in body size during the period post-8,000 B.P. and before 6,500 B.P., most likely with fully modern bison emerging by 7,000 B.P. This decrease in size appeared correlated with the rise and spread of the short-grass ecosystem and the greater productivity, but less nutritive value of C_4 grasses.

Early middle Holocene stratum 3 times are represented by four localities dating from 7,000 to 5,500 B.P. (table 1) that are associated with the valley system. Chloridoid grasses, most likely produced by a grama-buffalograss prairie, are dominant, but some pooid and panicoid grasses continue. Wet ground to open water plants include emergent bulrush, submerged musk-grass, and the water lily family (Nymphaea). The native trees net-leaf hackberry and sumac persist.

In comparison to the faunal diversity in late Pleistocene to early Holocene times, the known Middle Holocene faunas in general are depauperate. Herd herbivores are modern bison and pronghorn antelope (*Antilocapra americana*), with the carnivore guild represented by gray wolf (*Canis lupus*) and coyote (*Canis latrans*). Other grassland forms include tiger salamander (*Ambystoma tigrinum*), Couchi's spadefoot toad (*Scaphiopus couchi*), yellow mud turtle (*Kinosternon flavescens*), western box turtle (*Terrapene ornata*), Texas horned lizard (*Phrynosoma cornutum*), bull snake (*Pituophis melanoleucus*), black-tailed jackrabbit (*Lepus californicus*), black-tailed prairie dog (*Cynomys ludovicianus*), Plains pocket gopher (*Geomys bursarius*), yellow-faced pocket gopher (*Cratogeomys castanops*), and cotton rat (*Sigmodon hispidus*). Despite the reduction in diversity, elements occur indicating the continuance of a prairie dog town community.

This prairie dog town community, as well as the other animals, represents basically a modern fauna adapted to an open short-grass prairie with some brushland. The occasional hackberry and sumac may have been more like shrubs than trees at this time. Warming and drying conditions occur, with a decrease in available moisture and humidity levels, greater seasonality, and aeolian sedimentation accumulation that indicates the beginning of a reduction in vegetation cover.

Middle and early Late Holocene stratum 4 times are represented by five localities that date from 5,500 to 2,000 B.P. (table 1) and are associated with the valley system. Chloridoid grasses increase in frequency and dominance throughout this time, most likely produced by a grama-buffalograss prairie. Some pooid grasses persist, including needlegrass or wintergrass, and panicoid grasses, including the short-grass threeawn.

In lower stratum 4, dating to the middle Holocene (5,500 to 4,500 B.P.), other floral elements are pigweed (*Amaranthus*), knotweed (*Polygonum*), buffalo bur, and the spurge family (Euphorbiaceae). Wet ground to open water plants include emergent bulrush and the water lily family. Native trees are net-leaf hackberry and honey mesquite.

Modern bison dominate the grassland fauna at this time as the herd herbivore. The carnivore guild is represented only by the coyote. Other grassland forms include long-nosed snake (*Rhinocheilus lecontei*), black-tailed prairie dog, yellow-faced pocket gopher, Ord's kangaroo rat (*Dipodomys ordii*), cotton rat, and white-throated woodrat (*Neotoma albigula*).

The grassland fauna was adapted to dry to desert conditions. Conditions had been warming since the early Holocene and this period is the height of the Altithermal (Holliday 1989b, 1995a, 1995b), a climatic episode of greatly reduced precipitation and available water, increased temperatures, and blowing dust. The setting most likely was a desert grassland with an occasional hackberry or mesquite shrub. Prairie dog towns persisted, although most likely reduced in size and scope. The short grass, herbaceous prairie dominated within a dry landscape of reduced vegetation.

In upper stratum 4, dating to the early part of the late Holocene (4,500 to 2,000 B.P.), floral elements in the short-grass prairie are buffalo bur and the spurge family. Net-leaf hackberry and honey mesquite are the native trees.

Herd herbivores are modern bison and pronghorn antelope, with the carnivore guild represented by gray wolf and coyote. Other grassland forms include tiger salamander, western box turtle, Texas horned lizard, 13-lined ground squirrel (*Spermophilus tridecemlineatus*), black-tailed prairie dog, and Plains pocket gopher.

By 4,500 B.P., the climate ameliorated, the landscape stabilized, and mesic and cooler conditions returned. Landscape stability heralded the establishment of basically modern conditions. Only the open prairie was reflected in the fauna and prairie dog towns existed in a short-grass, herbaceous prairie under essentially a continental climate.

Late Holocene stratum 5 times are represented by five localities dating from 2,000 to 200 B.P. (table 1) that are associated with both an upland salina and the valley system. Chloridoid grasses, most likely produced by grama-buffalograss prairies, continue to dominate. A low frequency of pooid grasses persist, including needlegrass or wintergrass, and panicoid grasses, including the short-grass threeawn. Crown grass (*Paspalum*; C_4 warm-season grass) joins the grass roster. Other floral elements are devil's claw, prickly poppy (*Argemone*), and buffalo bur. Only emergent bulrush represents wet ground to open water plants. Native trees are net-leaf hackberry, honey mesquite, and Texas walnut (*Juglans microcarpa*), another small tree to shrub. Isolated populations of the Texas walnut occur today on the Llano Estacado in the lower reaches of the canyons (Petrides and Petrides 1992:124; Cox and Leslie 1995).

The late Holocene fauna was more diverse than the middle Holocene fauna. The mainstay herd herbivores were modern bison and pronghorn antelope. The carnivore guild expanded to include gray wolf, coyote, badger (*Taxidea taxus*), and striped skunk (*Mephitis mephitis*). Other grassland forms were tiger salamander, Plains toad, yellow mud turtle, western box turtle, Texas horned lizard, ground snake (*Sonora semianulata*), checkered garter snake (*Thamnophis* cf. *marcianus*), western diamondback rattlesnake (*Crotalus atrox*), hawks (*Buteo* spp.), Say's phoebe (cf. *Sayornis saya*), northern mockingbird (*Mimus polyglottis*), Audubon cottontail (*Sylvilagus audubonii*), black-tailed jackrabbit, 13-lined ground squirrel, hispid pocket mouse (*Chaetodipus* cf. *hispidus*), black-tailed prairie dog, Plains pocket gopher, and cotton rat. A prairie dog town community continued, along with hawk and badger as its predators.

This prairie dog town community existed within a short-grass, herbaceous prairie in a savanna setting of occasional deciduous trees in the valley and mesquite along the upland lake basins. Despite the greater availability of moisture and less arid conditions than those of the middle Holocene, a cyclical drought pattern began around 2,000 B.P. that continues today. Periods of some aridity occurred through increased temperatures and decreased effective moisture. The droughts appeared not to have been severe enough to alter either the faunal community or the short-grass prairie significantly. Surface erosion from periodic denuding of the vegetation led to deposition and altered landscapes (Holliday 2001a; Muhs and Holliday 2001).

Summary Statement

Throughout the Quaternary, the Llano Estacado has always been a grassland, albeit the character of this grassland has changed through time. During the late Quaternary, it remains an herbaceous grassland. By the LGM, the region is a grassland steppe that was a sagebrush grassland in a cool-dry climate. During the latest Pleistocene (stratum 1), the grassland is a tall grass prairie in a cool-humid climate with a parkland setting in the valleys. By the beginning of the early Holocene (stratum 2), the grassland is a mixed prairie experiencing an increasing rise in C_4 grasses in a warming, less humid, and more seasonal climate with a savanna setting in the valleys. The emergence of the short-grass ecosystem occurs between 8,200 to 8,000 B.P. and is the dominant vegetation throughout the rest of the Holocene. Middle to late Holocene (strata 3 to 5) grasslands are short-grass prairies within a fluctuating climate that affected the ecosystem from a mesic to xerix to mesic grassland setting with a continued savanna setting in the valleys.

Various trees are native to the Llano Estacado, and most are deciduous. All but one of the deciduous trees can occur in a small tree to shrub form, making them more flexible in response to changing climatic conditions. Occurring primarily in the valley system, an occasional hackberry and mesquite were on the uplands around the lake basins depending on the period. Net-leaf hackberry is the most consistent tree, having persisted in the region since the LGM. Conifers are restricted to juniper and the occasional piñon-pine that grew along the western escarpment, primarily in the late Pleistocene and earliest Holocene. Today, junipers are thick along the western escarpment with again the occasional piñon-pine.

Key transformations take place that appear to involve climate and vegetation response. An early Holocene warming trend with greater seasonality and probable decrease in winter precipitation is coupled with a shift from the tall grass prairie to the mixed grass prairie. By 8,000 B.P., humid conditions have declined with a probable shift in rainfall pattern and increasing seasonality leading to less effective moisture than preceding periods. This situation is coupled with the rise of the short-grass ecosystem that maintains dominance through an increasingly arid period. Heat and drought tolerance are key characteristics of the short-grass prairie that maintained

this dominance then, and throughout the rest of the Holocene. The emergence of the continental climate around 4,500 B.P. provides more mesic but still semi-arid conditions and that climatic regime is modernized by the modification of a cyclical drought pattern starting around 2,000 B.P.

Bison, pronghorn antelope, and prairie dog are the binding grassland species. The transformation of ancient bison into modern bison appears to be in response to the rise of the short-grass ecosystem and its greater productivity but less nutritional value. The rapid size change reflects both a coping mechanism with the changing grassland composition and the flexibility of the bison genome. Pronghorn antelope browse on forbs and other herbaceous vegetation. Their presence throughout the late Quaternary underscores the continuance of the herbaceous aspect regardless of the character of the grassland. Prairie dogs also are adaptable and resilient, with a continuing prairie dog town community throughout, regardless of the character of the grassland.

The various lines of evidence are for the most part concordant and provide a solid foundation for examining the late Quaternary ecosystems of the region. Phytolith and macrobotanical remains have proven more informative and reliable than pollen. These lines of evidence are more reflective of local conditions and generally not influenced by extraregional factors. Explorations are on-going to expand the record and fill in the details. Of specific interest are the expansion of the upland record, an increased knowledge of the herbaceous nature of the grassland through time, and the relationship between prairie dog town communities (and, in particular, the prairie dog) and the health and status of a grassland.

Acknowledgments

Thanks are due to Dr. Ron Sosebee (Department of Range, Wildlife, and Fisheries Management, Texas Tech University) for his gracious invitation to participate in the opening plenary session of the 13th Wildland Shrub Symposium of the Shrub Research Consortium; Dr. Vance T. Holliday (Departments of Geoscience and Anthropology, University of Arizona) for sharing data and critical review of the manuscript; Dr. Glenn Fredlund (Department of Geography, University of Wisconsin – Milwaukee) for sharing data; and to Tara Backhouse (Museum of Texas Tech University) for the figures. This manuscript represents part of the ongoing Lubbock Lake Landmark regional research program (under the auspices of the Museum of Texas Tech University) into late Quaternary climatic and environmental change on the Southern High Plains.

References

- Barry, R. G. 1983. Late-Pleistocene climatology. In: Porter, Stephen C., ed. *The Late Pleistocene*. Minneapolis, MN: University of Minnesota Press: 390-407.
- Birkeland, Peter W. 1999. *Soils and Geomorphology*, 3rd ed. New York, NY: Oxford Press.

- Bomar, George W. 1995. *Texas Weather*, 2nd ed. Austin, TX: University of Texas Press. 275 p.
- Bowen, Robert. 1991. *Isotopes and Climates*. New York, NY: Elsevier Applied Science.
- Bozarth, Steven. 1995. Fossil Biosilicates. In: Holliday, Vance T. *Stratigraphy and paleoenvironments of Late Quaternary valley fills on the Southern High Plains*. Geological Society of America Memoir. 186:47-50.
- Bryant, Vaughn M. Jr.; Schoenwetter, James. 1987. Pollen records from Lubbock Lake. In: Johnson, Eileen, ed. *Lubbock Lake. Late Quaternary Studies on the Southern High Plains*. College Station, TX: Texas A&M University Press: 36-40.
- Brune, Gunnar. 1981. *Springs of Texas*. Ft. Worth, TX: Branch-Smith, Inc.
- Buol, S. W.; Hole, F. D.; McCracken, R. J. 1973. *Soil Genesis and Classification*. Ames, IA: Iowa State University Press. 360 p.
- Cabeza de Baca, Fabiola. 1954. *We Fed Them Cactus*. Albuquerque, NM: University of New Mexico Press. 186 p.
- Cerling, Thure E. 1984. The stable isotope composition of modern soil carbonate and its relationship to climate. *Earth and Planetary Science Letters*. 71:229-240.
- Coupland, Robert T. 1992. Overview of the grasslands of North America. In: Coupland, Robert T., ed. *Natural Grasslands: Introduction and Western Hemisphere*. Amsterdam: Elsevier: 147-149.
- Cox, Paul W.; Leslie, Patty. 1995. *Texas Trees*. San Antonio, TX: Corona Publishing Company. 374 p.
- Evans, Glen L.; Meade, Grayson E. 1945. *Quaternary of the Texas High Plains*. University of Texas Bureau of Economic Geology, Contributions to Geology. 4401:485-507.
- Fenneman, Nevin M. 1931. *Physiography of Western United States*. New York, NY: McGraw-Hill Book Company, Inc. 534 p.
- Findley, James S.; Harris, Arthur H.; Wilson, Don E.; Jones, Clyde. 1975. *Mammals of New Mexico*. Albuquerque, NM: University of New Mexico Press. 360 p.
- Fox, David L.; Koch, Paul L. 2003. Tertiary history of C4 biomass in the Great Plains, USA. *Geology*. 31(9):809-812.
- Freundlund, Glenn. 2002. Phytolith evidence for change in Late Pleistocene and Holocene grassland composition on the Southern High Plains. Paper presented at the 60th Plains Anthropological Conference, Oklahoma.
- Freundlund, Glenn; Holliday, Vance T.; Johnson, Eileen. 2003. Vegetation change on the Southern High Plains during the Pleistocene-Holocene transition. Paper presented at the XVI INQUA Congress, Reno.
- Gregg, Josiah. 1954. *Commerce of the Plains*. Norman, OK: University of Oklahoma Press.
- Gustavson, Thomas C.; Holliday, Vance T.; Hovorka, Susan D. 1995. Origin and development of playa basins, sources of recharge to the Ogallala aquifer, Southern High Plains, Texas and New Mexico. University of Texas at Austin, Bureau of Economic Geology, Report of Investigation. 229:1-44.
- Hafsten, Ulf. 1961. Pleistocene development of vegetation and climate in the Southern High Plains as evidenced by pollen analysis. In: Wendorf, Fred, assembler. *Paleoecology of the Llano Estacado*. Museum of New Mexico, Santa Fe, Ft. Burgwin Research Center Publication. 1:59-91.
- Hageman, B.P. 1972. Reports of the International Quaternary Association subcommission on the study of the Holocene. *Bulletin*. 6:1-6.
- Hall, Stephen A. 1981. Deteriorated pollen grains and the interpretation of Quaternary pollen diagrams. *Review of Paleobotany and Palynology*. 32:193-206.
- Hall, Stephen A. 1995. Pollen. In: Holliday, Vance T., *Stratigraphy and paleoenvironments of Late Quaternary valley fills on the Southern High Plains*. Geological Society of America Memoir. 186:53-54.
- Hall, Stephen A.; Valastro, Salvatore Jr. 1995. Grassland vegetation in the Southern Great Plains during the Last Glacial Maximum. *Quaternary Research*. 44:237-245.
- Haragan, Donald R. 1983. *Blue Northerners to Sea Breezes: Texas Weather and Climate*. Dallas, TX: Hendrick-Long Publishing Co. 98 p.
- Hicks, J. Kent; Johnson, Eileen. 2000. Pastores presence on the Southern High Plains of Texas. *Historical Archaeology*. 34(4):46-60.
- Hill, Matthew Glenn; Holliday, Vance T.; Stanford, Dennis J. 1995. A further evaluation of the San Jon site, New Mexico. *Plains Anthropologist*. 40(154):369-390.
- Holliday, Vance T. 1985. Archaeological geology of the Lubbock Lake site, Southern High Plains of Texas. *Geological Society of America Bulletin*. 96:1483-1492.
- Holliday, Vance T. 1987. A reexamination of Late-Pleistocene boreal forest reconstructions for the Southern High Plains. *Quaternary Research*. 28:238-244.
- Holliday, Vance T. 1989a. The Blackwater Draw Formation (Quaternary): a 1.4-plus-m.y. record of eolian sedimentation and soil formation on the Southern High Plains. *Geological Society of America Bulletin*. 101:1598-1607.
- Holliday, Vance T. 1989b. Middle Holocene drought on the Southern High Plains. *Quaternary Research*. 31:74-82.
- Holliday, Vance T. 1995a. Stratigraphy and paleoenvironments of Late Quaternary valley fills on the Southern High Plains. *Geological Society of America Memoir*. 186:1-131.
- Holliday, Vance T. 1995b. Late Quaternary stratigraphy of the Southern High Plains. In: Johnson, Eileen, ed. *Ancient Peoples and Landscapes*. Lubbock, TX: Museum of Texas Tech University: 289-313.
- Holliday, Vance T. 1997. Origin and evolution of lunettes on the High Plains of Texas and New Mexico. *Quaternary Research*. 47:54-69.
- Holliday, Vance T. 2000. Folsom drought and episodic drying on the Southern High Plains from 10,900-10,200 14Cyr B.P. *Quaternary Research*. 53:1-12.
- Holliday, Vance T. 2001a. Stratigraphy and geochronology of upper Quaternary eolian sand on the Southern High Plains of Texas and New Mexico, U.S.A. *Geological Society of America Bulletin*. 113:88-108.
- Holliday, Vance T. 2001b. Quaternary geoscience in archaeology. In: Goldberg, Paul; Holliday, Vance T.; Ferring, C. Reid, eds. *Earth Sciences and Archaeology*. New York, NY: Kluwer Academic/Plenum Publishers: 3-35.
- Holliday, Vance T. 2004. *Soils in Archaeological Research*. New York, NY: Oxford University Press. 448 p.
- Holliday, Vance T.; Allen, B. L. 1987. Geology and soils. In: Johnson, Eileen, ed. *Lubbock Lake. Late Quaternary Studies on the Southern High Plains*. College Station, TX: Texas A&M University Press: 14-21.
- Holliday, Vance T.; Hovorka, Susan D.; Gustavson, Thomas C. 1996. Lithostratigraphy and geochronology of fills in small playa basins on the Southern High Plains. *Geological Society of America Bulletin*. 108:953-965.
- Holliday, Vance T.; Johnson, Eileen; Hall, Stephen A.; Bryant, Vaughn M. 1985. *Lubbock Subpluvial. Current Research in the Pleistocene*. 3:53-54.

- Holliday, Vance T.; Knox, James C.; Running, Garry L. IV; Mandel, Rolfe D.; Ferring, C. Reid. 2002. The Central Lowlands and Great Plains. In: Orme, Antony R., ed. The Physical Geography of North America. Oxford: Oxford University Press: 335-362.
- Hunt, Charles B. 1967. Physiography of the United States. San Francisco, CA: W. H. Freeman and Company. 480 p.
- Johnson, Eileen. 1986. Late Pleistocene and Early Holocene vertebrates and paleoenvironments on the Southern High Plains. *Géographie Physique et Quaternaire*. 40:249-261.
- Johnson, Eileen. 1987. Paleoenvironmental overview. In: Johnson, Eileen, ed. Lubbock Lake. Late Quaternary Studies on the Southern High Plains. College Station, TX: Texas A&M University Press :90-99.
- Johnson, Eileen. 1991. Late Pleistocene cultural occupation on the Southern Plains. In: Bonnicksen, Robson; Turnmire, Karen L., eds. Clovis Origins and Adaptations. Corvallis, OR: Oregon State University: 215-236.
- Lauenroth, W. K.; Milchunas, D. G. 1992. Short-grass steppe. In: Coupland, Robert T., ed. Natural Grasslands: Introduction and Western Hemisphere. Amsterdam: Elsevier: 183-226.
- Lewis, Patrick. 2003. Metapodial Morphology and the Evolutionary Transition of Late Pleistocene to modern bison. Unpublished doctoral dissertation. Durham, NC: Duke University.
- Lewis, Patrick; Buchanan, Briggs; Johnson, Eileen. 2001. Late Quaternary bison evolution at the Lubbock Lake Landmark and its implications for hunter-gatherer research. Paper presented at the annual meeting of the Society for American Archaeology, New Orleans.
- Marcy, R. B. 1850. Report of the exploration and survey of the route from Fort Smith, Arkansas, to Santa Fe, New Mexico, made in 1849. 31st Congress, 1st session. House Executive Document 45, Public Document 577, Washington, D.C.
- Matheus, Paul E. 1995. Diet and co-ecology of Pleistocene short-faced bears and brown bears in Eastern Beringia. *Quaternary Research*. 44:447-453.
- Matheus, Paul E. 2003. Locomotor adaptations and ecomorphology of short-faced bears (*Arctodus simus*) in Eastern Beringia. *Palaeontology Program, Government of the Yukon, Occasional Papers in Earth Sciences*. 7:1-126.
- Matheus, Paul E.; Guthrie, R. Dale; Kunz, Michael L. 2003. Predator-prey links in Pleistocene East Beringia: evidence from stable isotopes. 3rd International Mammoth Conference, 2003: Program and Abstracts, *Palaeontology Program, Government of the Yukon, Occasional Papers in Earth Sciences* 5:80.
- Muhs, Daniel R; Holliday, Vance T. 2001. Origin of Late Quaternary dune fields on the Southern High Plains of Texas and New Mexico. *Geological Society of America Bulletin*. 113:75-87.
- Nordt, Lee C. 2001. Stable carbon and oxygen isotopes in soils: applications for archaeological research. In: Goldberg, Paul; Holliday, Vance T.; Ferring, C. Reid, eds. *Earth Sciences and Archaeology*. New York, NY: Kluwer Academic/Plenum Publishers: 419-448.
- Oldfield, Frank; Schoenwetter, James. 1975. Discussion of the pollen-analytical evidence. In: Wendorf, Fred; Hester, James J., eds. *Late Pleistocene environments of the Southern High Plains*. Southern Methodist University, Dallas, Ft. Burgwin Research Center Publications. 9:149-177.
- Petrides, George A; Petrides, Olivia. 1992. *A Field Guide to Western Trees*. Boston, MA: Houghton Mifflin Company. 308 p.
- Piperno, Dolores R. 1988. *Phytolith Analysis. An Archaeological and Geological Perspective*. San Diego, CA: Academic Press. 280 p.
- Pope, J. 1855. Report of the explorations near the thirty-second parallel of north latitude from the Red River to the Rio Grande, vol. 2. Report of the exploration and survey from the Mississippi River to the Pacific Ocean. 33d Congress, 2d session, Senate Executive Document 78, Washington, D.C.
- Reeves, C. C. Jr. 1976. Quaternary stratigraphy and geological history of the Southern High Plains, Texas and New Mexico. In: Mahaney, William C., ed. *Quaternary Stratigraphy of North America*. Stroudsburg, PA: Dowden, Hutchinson and Ross, Inc.: 213-234.
- Reeves, C. C. Jr. 1991. Origin and stratigraphy of alkaline lake basins, Southern High Plains. In: Morrison, Roger B., ed. *Quaternary non-glacial geology: coterminous U.S.* Geological Society of America Centennial. Volume K-2:484-486.
- Rich, Julie; Stokes, Stephen; Wood, Warren W. 1999. Holocene chronology for lunette dune deposition on the Southern High Plains, USA. *Zeitschrift für Geomorphologie, supplementband*. 16:165-180.
- Robinson, R. 1982. Phytoliths from the Lubbock Lake Landmark. Report on file at the Museum of Texas Tech University, Lubbock.
- Sabin, Tye; Holliday, Vance T. 1995. Morphometric and spatial relationships of playas and lunettes on the Southern High Plains. *Annals of the Association of American Geographers*. 85:286-305.
- Thompson, Daniel. 1965. Food preferences of the meadow vole (*Microtus pennsylvanicus*) in relation to habitat affinities. *American Midland Naturalist*. 74(1):76-86.
- Thompson, Jerome. 1987. Modern, historic, and fossil flora. In: Johnson, Eileen, ed. *Lubbock Lake. Late Quaternary Studies on the Southern High Plains*. College Station, TX: Texas A&M University Press: 26-35.
- Wendorf, Fred. 1961. *Paleoecology of the Llano Estacado*. Santa Fe, NM: Museum of New Mexico Press. 144 p.
- Wendorf, Fred. 1970. The Lubbock Subpluvial. In: Dort, Wakefield; Jones, J. Knox Jr., eds. *Pleistocene and Recent Environments on the Central Great Plains*. Lawrence, KS: University Press of Kansas: 23-36.
- Wendorf, Fred; Hester, James J. 1975. *Late Pleistocene environments of the Southern High Plains*. Southern Methodist University, Dallas, Publication of the Fort Burgwin Research Center. 9:1-290.
- Wood, Warren W.; Stokes, Stephen; Rich, Julie. 2002. Implications of water supply for indigenous Americans during Holocene aridity phases on the Southern High Plains, USA. *Quaternary Research*. 58:139-148.

The Author

¹ Quaternary Scientist and museum curator, Museum of Texas Tech University, Lubbock, TX. eileen.johnson@ttu.edu

The Southern High Plains: A History of Vegetation, 1540 to Present

David B. Wester¹

Abstract: Considerable documentary evidence is available about the historic vegetation of the Southern High Plains (SHP). Accounts spanning about 350 years (from the earliest European explorers in the 1540s to scientists working in the later 19th and early 20th centuries), however, lead to vague and sometimes contradictory conclusions about the nature of this vegetation. The earliest documents describe the SHP as vast grassland. The fact that native soils were Paleustolls supports this description. The earliest accounts also suggest considerable vegetation diversity in certain topographic settings (for example, in sandy soils and major draws that cross the SHP). It is also certain that the SHP supported vast populations of native herbivores (which were quickly replaced by large populations of domestic livestock); were subject to climatic variability; and were frequently burned. All of these factors interact with each other at several spatial and temporal scales to affect vegetation. Based on historic documentary evidence, it is difficult to describe the precise nature of the vegetation of the SHP when it was first encountered by European explorers. Although the dominant aspect of the vegetation was that of a grassland, woody species (primarily mesquite, *Prosopis glandulosa*) were either historically present but unrecorded by early explorers in upland sites because they had limited experience in these sites and/or because recurrent fires maintained populations; or mesquite was introduced in a novel way by domestic livestock beginning in the late 1870s and 1880s. In either of these scenarios, subsequent increases in woody vegetation during the 20th century likely involved changes in fire frequency, grazing history, and climate.

“Too Grande and Too Sublime to be Imagined”

(Pike 1832, in Haley 1968:23)

“The monotonous level or billowy swells of a sea of grass unrelieved by the presence of taller plants like a shrub or tree... could fasten upon the senses a conception of the power of a victorious vegetation...” (Bray 1906:92)

“If you w’d remain in ignorance of this region of the world read descriptions of it...if you would wish to appreciate the scale of its sublimity, on which all Nature is here arranged, come and see it.” (Gilpin 1836)

Introduction

The Southern High Plains (SHP) are a 130,000-km² plateau in Texas and eastern New Mexico (Holliday 1990). Also known as the Llano Estacado, this southernmost subdivision of the High Plains section of the Great Plains Physiographic Province is “essentially an isolated remnant of the Rocky Mountain piedmont alluvial plain” (Reeves 1965:182). The SHP are bordered on the east by the Caprock Escarpment and the upper Colorado, Brazos and Red Rivers in Texas, and on the west by the Pecos River Valley. The northern border of the SHP, abruptly delimited by the Canadian River Valley, contrasts with the gradual merging of its southern boundary with the Edwards Plateau (fig. 1).

The SHP are both extensive and remarkably flat, which has led many authors to rather expressive descriptions. For

example, Carroll and others (1986:186) wrote that the SHP are “almost absolutely flat and represent one of the largest tracts of level land in the world.” Morris (1997:2) described the Llano Estacado as “perhaps the largest isolated, non-mountainous area in North America” and elsewhere (p. 20) as “one of the world’s largest and flattest plains.” Hunt (1967:225) wrote that “...the Llano Estacado [is] one of the most nearly level parts of the United States.” A USGS web site states that the “Llano Estacado [is] one the largest expanses of near-featureless terrain” (<http://tapestry.usgs.gov/features/features/html>). Whereas slopes on the SHP average only 3 m per mile (Reeves 1965), several physiographic provinces in North American (for example, the Gulf Coastal Plains and the Atlantic Coastal Plains) are also relatively flat as well as larger in areal extent than the SHP, occupying about 10 percent of the land area of the U.S. (Hunt 1967).

In: Sosebee, R.E.; Wester, D.B.; Britton, C.M.; McArthur, E.D.; Kitchen, S.G., comp. 2007. Proceedings: Shrubland dynamics—fire and water; 2004 August 10-12; Lubbock, TX. Proceedings RMRS-P-47. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 173 p.

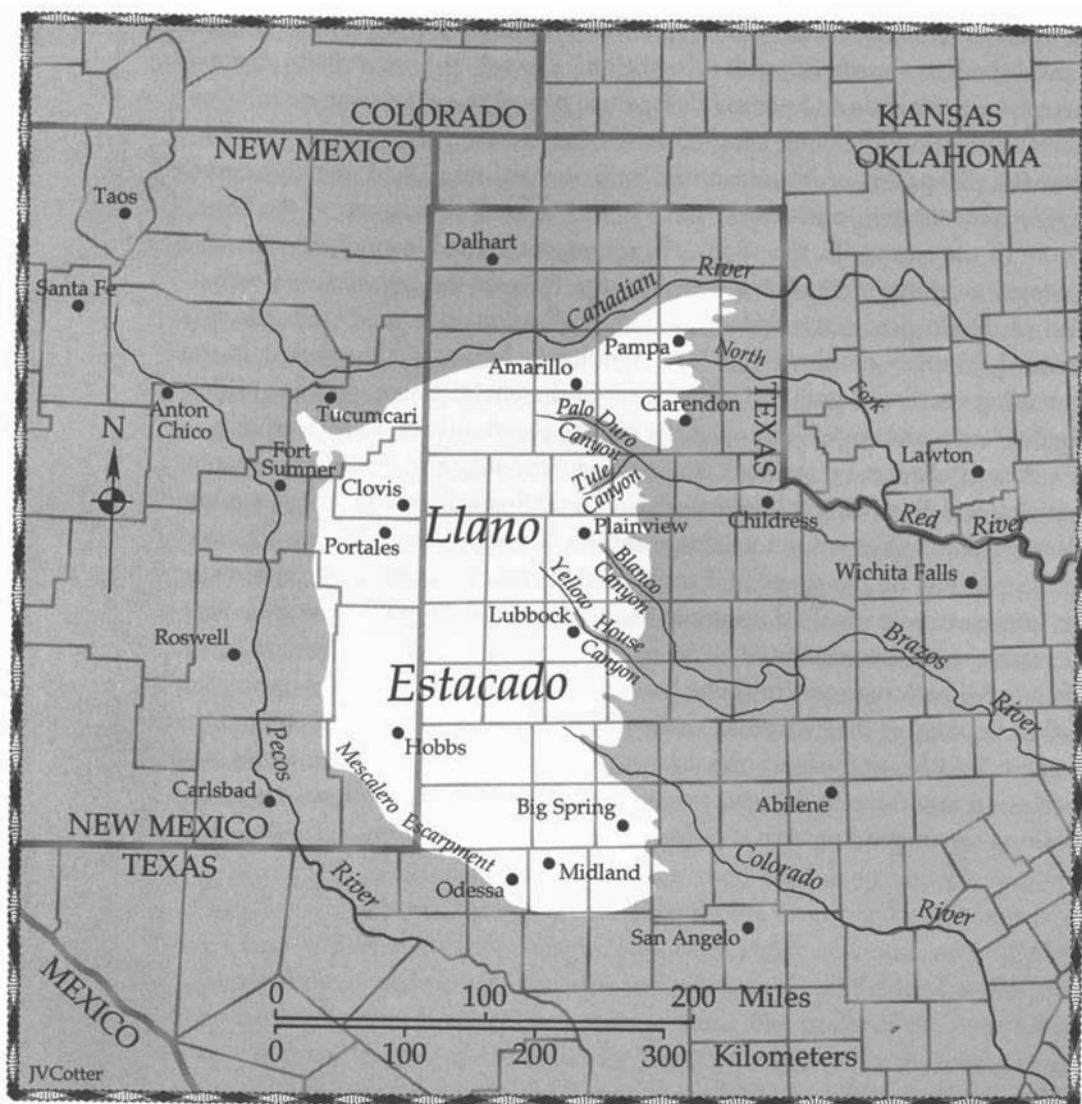


Figure 1. The Southern High Plains (from Morris 1997).

Geological History

Characterized by a semi-arid continental climate, this “virtually featureless, constructional surface” (Holliday 1989:74) is the most recent of as many as six well-developed but buried soils that comprise the Blackwater Draw Formation formed by multiple episodes of eolian sheet deposition separated by long periods of relative landscape stability over the past 1.4 million years (Holliday 1990). In fact, similarities between the Quaternary Blackwater Draw Formation and the underlying Miocene-Pliocene Ogallala Formation suggest that the SHP “has probably been a grassland or savanna grassland varying from perhaps an arid to a semi-arid or sub-humid environment for about 11 million years” (Holliday 1990:510). The topographic monotony of the SHP is relieved only by Holocene dune fields (formed during droughts of the Altithermal period) along its southwestern and western borders (Holliday 1989), thousands of playas scattered over its surface (Bolen and others 1989), over two dozen larger saline lakes, and several dry tributaries (or “draws”) of the Colorado, Brazos, and Red Rivers (Holliday 1990).

Grazing History

As part of the extensive grasslands of the North American Great Plains, the SHP have a long history of herbivory. Reviewing global patterns, Coughenour (1985:853) concluded that “extensive grasslands, grazers, and semiarid climates appeared almost simultaneously,” and suggested that many of the characteristics of grasses that are advantageous in semi-arid environments (for example, presence of basal meristems, small stature, high shoot density, deciduous shoots, below-ground storage of nutrients, and rapid growth) are also beneficial under grazing. In an influential paper, Stebbins (1981:84) concluded that “Coevolution of grasses and herbivores has progressed continuously on the North American grasslands ever since they first appeared as savannalike openings in the forest during the early part of the Tertiary period.” MacGinitie (1962:99, from Axelrod 1985:168) also suggested that “the regular association of grazing and browsing mammals on the High Plains from the Middle Miocene into the Pliocene supports the idea of a savanna-type vegetation.” Early fossil evidence in the Great Plains suggests that

cool season caespitose species (for example, *Stipa*, *Nassella*, *Piptochaetium*, and the extinct *Berrichloa*) were associated with horses and pronghorn antelope during Pliocene times. However, current dominant genera of the Great Plains (for example, *Andropogon*, *Schizachyrium*, *Bouteloua*, *Buchloe*, and *Panicum*) belong to different tribes than the Pliocene flora. Although it is uncertain when this transition occurred, Stebbins (1981) believed that the current dominant flora was absent or uncommon at the beginning of the Pleistocene glaciations. Further, he suggested that the current flora is of post-Pleistocene origin. After an extensive literature review, Axelrod (1985) agreed with MacGinitie (1962) that “most of the current formations of western North America, except possibly in the area south of Latitude 35°, are less than 10,000 years old” (MacGinitie 1962:99, from Axelrod 1985:168). The change from long-leaved caespitose species to stoloniferous shortgrasses reflects adaptations related to changes both in environment (increasing aridity) and in dominant grazers. In particular, grazers during the Pliocene were horses and pronghorn. However, *Bison latifrons*, a browser/grazer adapted to forest openings or woodlands, appeared between 500,000 and 125,000 years ago, peaked in abundance about 100,000 years ago during the Sangamon interglacial, survived until at least 30,000 to 20,000 years ago, and disappeared in late Wisconsin (10,000 years ago). *Bison antiquus*, a grazer/browser adapted to savanna or wooded steppe, probably appeared during the Sangamon interglacial and peaked during the late Wisconsin (10,000 years ago). *Bison bison*, primarily a grazer adapted to open grassland environments, appeared during the late Wisconsin and early Holocene; the southern subspecies (*B. bison bison*) reached maximum numbers about 2,500 years ago (McDonald 1981). Although about 75 percent of the megafauna of North America disappeared with the closing of the last ice age, bison numbers followed a different trend, reaching peak numbers from 9,000 to 6,000 years ago (Alford 1973).

It has been estimated that 100 million buffalo existed on the Great Plains. Buffalo hunting began in the Texas Panhandle in 1874. The southern buffalo herd was exterminated between 1874 and 1878, the northern herd was slaughtered by 1884, and by 1878, only 1,091 animals were left (McComb 1989:82-83). Almost simultaneous with the extermination of the buffalo was the removal of native Americans from the Panhandle of Texas with the battle of the Red River in 1874-1875. Carlson (1974:15) wrote that “More than most campaigns the Red River War made the immense northern border of the Llano Estacado safe for an advancing civilization.” Mexican sheep ranchers were the first graziers in the SHP (Taylor 1997). They were followed, however, and soon outnumbered by cattle ranchers. One of the first ranchers in this area, Charles Goodnight, brought 1,600 head of cattle to the Palo Duro Canyon area in 1876. By 1880, more than 100 other ranchers brought 100,000 cattle as well as 100,000 sheep into north-west Texas (Nall 1972). Thus, the native herbivores were exterminated and quickly replaced by domestic animals.

There were fewer than 500,000 cattle in Texas in 1830 (Fisher 1977:183). Cattle numbers increased thereafter

throughout the state, and by 1888 there were more than 9 million head of cattle (Brooks and Emel 2000:54). Cattle were not grazed on the SHP, however, until the 1880s (Carlson 1974). Further, the “boom” years of the SHP cattle industry did not last long. Two factors combined to lead to a collapse in the cattle industry. First, weather conditions in the years around 1870 were equable (following widespread drought conditions throughout much of the Great Plains in the early 1860s; Meko 1995:322-323; fig. 6 in Woodhouse and Overpeck 1998). Second, high livestock numbers led to overgrazing: before the worst overgrazing, 5 acres could support one steer, but by 1880, 50 acres were needed (White 1991, from Brooks and Emel 2000:55). With these two factors as background, an extremely harsh winter in 1885, and another in 1888, with “freezing temperatures and high winds...combined with loss of range due to overgrazing, [and] brought heavy losses...The cattle ranching that remained on the plains was just a remnant of the flourishing cattle trade of the late 1870s and early 1880s, never to recover the teeming numbers of that era” (Brooks and Emel 2000:55-56; also see Nall 1972; Taylor 1997). Britten (1993) indicated that millions of cattle perished following the droughts and blizzards of 1885 to 1887.

Today, the SHP are one of the most intensively-farmed areas in the United States, with 90 percent of its area in row-crop agriculture (on 11,880 farms; farm acreage is based on the following Texas counties: Deaf Smith, Randall, Parmer, Castro, Swisher, Bailey, Lamb, Hale, Floyd, Cochran, Hockley, Lubbock, Crosby, Yoakum, Terry, Lynn, Gaines, Dawson, Andrews, Martin; www.nass.usda.gov/census/census02/volume1/tx/st48_2_001.pdf, and www.census.gov/prod/2002pubs/00ccdb/dd00_tabB1.pdf). Cotton is the largest crop produced on the Llano Estacado. In fact, 15 percent of the cotton grown in the U.S. and 3.5 percent of the cotton grown world-wide is produced on the SHP (Brooks and Emel 2000:111). Texas produces more cattle (13.7 million head; Texas Farm Bureau) than any other state. The 26 counties surrounding Amarillo, Texas, have 25 to 30 percent of all cattle on feed in the U.S. (Evetts 2003).

Human History

The SHP are also remarkable for the records of human history they reveal. The earliest evidence of European people in southwestern North America (Chipman 1992:11) can be found in the descriptions of Alvar Núñez Cabeza de Vaca in the 1530s. The area is also among the earliest occupied by Native Americans – there are abundant archeological artifacts of human habitation 12,000 years ago at the Lubbock Lake Landmark site (Johnson 1987). The Paleo-Indian period on the SHP can be recognized in the following subdivisions: Clovis (11,500 to 10,000 years B.P.); Folsom (10,500 to 10,000 years B.P.); Plainview (around 10,000 years B.P.); and Firstview (from Plainview to about 8,000 years B.P.). Additional native American cultures of the Archaic Period (6,000 to 2,000 years B.P.), Woodland tradition (2,000 years B.P.), and Plains Village Culture (1,350 to 1,450 A.D.) existed on the

SHP. Early Spanish explorers encountered Apaches on the SHP. These native Americans were replaced by Comanches by 1775 (Brooks and Emel 2000:26-27, 30).

The SHP were one of the last regions settled by Texans after fighting with Native Americans ended with the Red River War in 1874-1875 (for example, Carlson 1974). Early farming settlements were simultaneous with the establishment of cattle ranches on the SHP (Nall 1972). The southern parts of the SHP were generally established earlier than the northern parts.

Several railroads (for example, the Denver & Fort Worth Railroad and the Southern Kansas Railway Company) were operating on the SHP by 1888 (Nall 1972). Big Spring began to develop around 1880 when rail service began in Howard County. Likewise, Miami began around 1887 with rail service, and Sutton and Floyd counties and the city of Lubbock were established in 1890. Although Deaf Smith County was established in 1879, it had no permanent settlers until 1887 (Burnett 1990:4). Census returns in 1880 showed a population of 5,388 residents in the 50 counties of the Llano Estacado. By 1910, the population had grown to 140,749 residents (Burnett 1990:4). In the Texas Panhandle, the population increased from 1,607 to 9,542 from 1880 to 1890 (Nall 1972). The first farm was established in 1879 in the town of Estacado (Crosby County, Texas). In 1886, Estacado became the county seat for Crosby County and Central Plains Academy, the first college on the SHP, was established in 1890 (<http://www.tsha.utexas.edu/handbook/online/articles/view/EE/hne27.html>). In 1900, 803 farms existed on the SHP. By 1910, this number swelled to 2001 farms. Continued growth was evident, with 4089 farms in 1920 and 6,161 farms in 1925 (Brooks and Emel 2000:69-70). As early as 1925, farm acreage occupied nearly 49 percent of the area of a 10-county region on the SHP (Bailey, Cochran, Crosby, Floyd, Hale, Hockley, Lamb, Lubbock, Parmer, and Potter counties; Brooks and Emel 2000:84).

In several respects, therefore, the SHP have a remarkably long history: first, with regard to relative geologic and climatic stability punctuated by periodic and sometimes devastating droughts; second, with regard to the presence of herbivores, both native and domestic; and third, with regard

to interaction with human cultures. All of these factors, whose combined influence has shaped the vegetation of the SHP, must be considered to more fully understand its dynamic history.

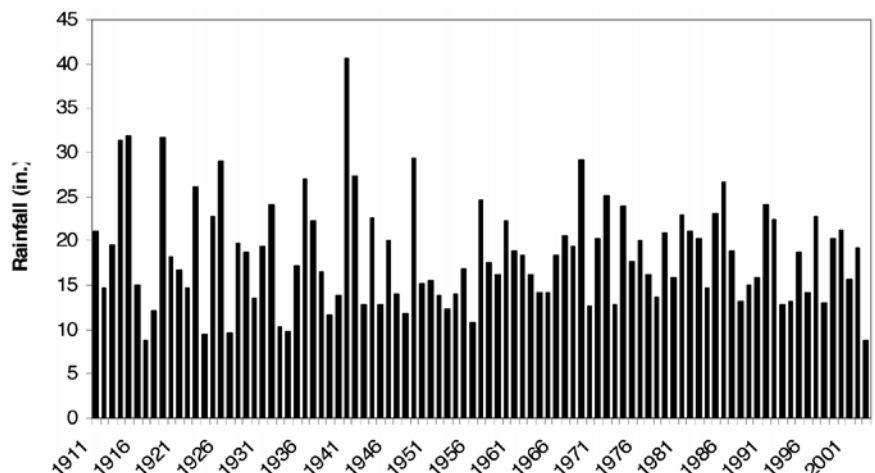
Environmental Characterization

Climate

Elevations on the SHP range from 823 m on the eastern border to 1,463 m on the west (Reeves 1965). A semi-arid or dry steppe climate with mild winters results from the combined influence of relatively high elevation, frequent intrusions of dry polar air masses, and distance from sources of moisture (NOAA 1982). Annual precipitation increases from 300 mm in the west to 500 mm in the east (Holliday 1990). The continental nature of the SHP climate, however, leads to considerable intra-annual (NOAA 1982) and inter-annual (Holliday 1990) variability in precipitation. The months of May and September typically have the highest rainfall, and the period from October to April is generally dry. In the northern SHP (Hereford, Randall County), annual rainfall averages 474 mm; May (54 mm), June (74 mm), August (82 mm) and September (57 mm) are the wettest months. In the central portion of the SHP (Lubbock, Lubbock County), annual precipitation averages 475 mm; May (59 mm), June (76 mm), August (60 mm) and September (65 mm) are the wettest months. In the southern portion of the SHP (Andrews, Andrews County), annual precipitation averages 384 mm; June (54 mm), July (57 mm), and September (56 mm) are the wettest months.

Annual precipitation also varies interannually (fig. 2). Droughts are recurring features of the climate of the SHP (for example, Woodhouse and Overpeck 1998; fig. 3). Holliday (1989) indicated that the warmer, drier conditions during the Altithermal, which initiated eolian sedimentation locally throughout the SHP between 8000 and 7000 BC, and affected all areas of the SHP between 3500 and 2500 BC, resulted in “more geomorphic change ... than any other equivalent period of time for which data are available” (Holliday

Figure 2. Annual rainfall, Lubbock, Texas (NOAA).



Palmer Drought Severity Index

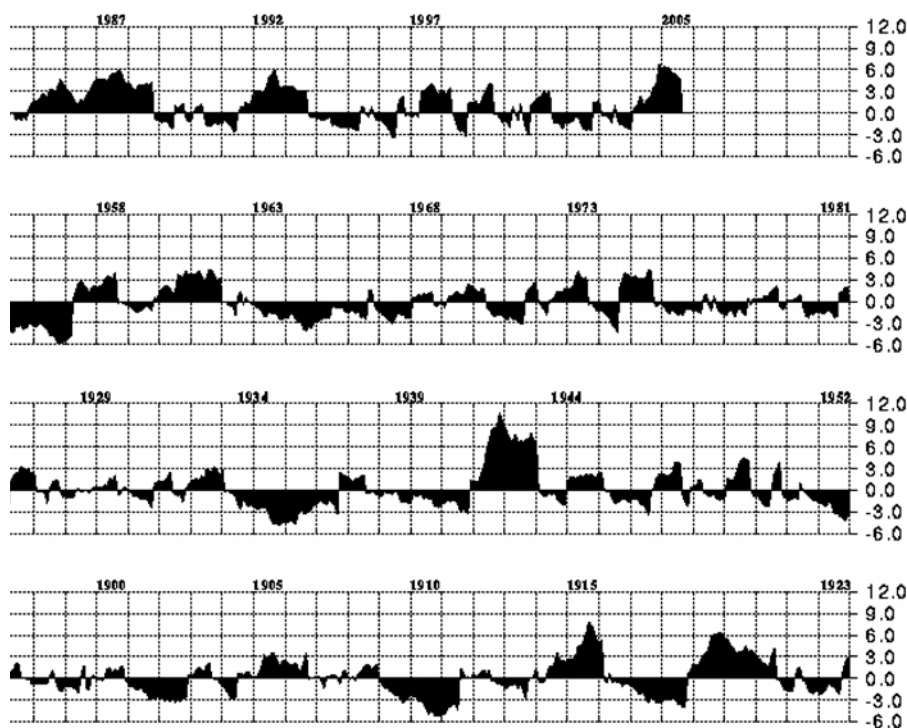


Figure 3. Palmer Drought Severity Index for the Southern High Plains, Texas (from www.ncdc.noaa.gov).

Texas - Division 01: 1895-2005 (Monthly Averages)

1889:80). In more recent times, droughts have been observed in at least some parts of the Great Plains in the last quarter of the 13th century (Woodhouse and Overpeck 1998); in the second half of the 16th century (Woodhouse and Overpeck 1998; Stahle and others 2000); and in the 1750s, early 1800s, 1820s, early 1850s to early 1860s, late 1880s to early 1900s, 1930s, and 1950s (Meko 1995; Woodhouse and Overpeck 1998) (fig. 3). It is interesting to note that (1) droughts in the 16th century evidently lasted longer than the drought of the 20th century; (2) there is little evidence of drought between the severe drought of the latter half of the 16th century and the latter half of the 18th century; and (3) despite the severity of the droughts of the 20th century, these periods were not drastic enough to cause regional mobilization of sand dunes (Woodhouse and Overpeck 2000:2696 and references therein; also see Muhs and Holliday 1995; Forman and others 2001). Periodic droughts have had significant effects of flora, fauna, and human activities.

Soils

The Blackwater Draw Formation, with a thickness that varies from a “feather-edge” in the southwest to “at least 27 m” in the northeast (Reeves 1976:217, in Holliday 1990:494) forms the surface of the SHP. This “sheet-like body of eolian sediment” (Holliday 1990:493), with the Pecos River Valley as its source, is comprised of sands to very fine sands in the southwest and finer sediments (silts and clays) toward the northeast (Holliday 1990). This pattern of textural variability

is “apparently the result of downwind sorting” (Holliday 1990:493). Additionally, the thickening of the Blackwater Draw Formation from the southwest to the northeast “is probably due to the sandy texture of the sediments in the southwest, which would be much more susceptible to wind deflation than the silty and clayey sediments in the northeast” (Holliday 1990:494). It is also likely that vegetative cover in the southwest was sparser than in the northeast because of drier conditions. This would render the southwestern portion more prone to wind deflation (Holliday 1990).

Surface soils of the SHP are very well developed. Paleustalfs are common in the central and southwestern SHP, and Paleustolls are common in the central and northeastern SHP. The Paleustolls of the central SHP are similar to the Paleustalfs of the southwestern SHP except for the presence of a mollic epipedon. The Paleustolls of the northeastern SHP additionally possess a clay to clay loam argillic horizon with prismatic structure (Holliday 1990). The complex pattern of Paleustalfs and Paleustolls in the central SHP is most likely the result of wind erosion. The “native soils were most likely Paleustolls, given the native vegetation of the region. Eolian erosion could very effectively remove much of the mollic epipedon, resulting in a soil with an ochric epipedon, but otherwise not affecting the subsurface horizons...it is possible that the soil pattern is a historic feature, resulting from many periods of dust storm activity” during recent times or the middle Holocene (Holliday 1990:498). The Paleustolls of the northeastern SHP differ from those of the central SHP because of the presence of a darker color in the upper solum and finer

textures. The finer textures are due to downwind fining. One explanation for the darker solum is that it is a “pachic epipedon, the result of slow aggradation of the surface.” As the original A horizon became buried, it was converted to a Bt horizon (Holliday 1990:501). The darker color also may have resulted in part from more vegetation biomass as a consequence of higher effective precipitation and cooler temperatures in the northeastern SHP (Holliday 1990).

Another noteworthy feature of the landscape and soils of the SHP is the relative lack of evidence of erosion compared with other parts of the High Plains. No streams have deeply incised the SHP (Loomis 1938), leaving its surface “almost untouched by erosion” (Fenneman 1931:14). Mead and Brown (1970:47) described the Llano Estacado as “the best preserved of the [Great] plains, for they have been little dissected....”

Vegetation

Early Descriptions (1540s to 1850s)

Any description of the historic southwest must begin with Álgar Núñez Cabeza de Vaca and his celebrated journey in the 1530s. Historians disagree (for example, Chipman 1987) about the exact route that de Vaca and his three companions followed. Some authors place his route as far north as Big Spring (Hallenbeck 1940, from Olson and others 1997), Midland, Texas (Terrell 1962), or Lubbock, Texas (Bryan 1956). Others suggest a more southerly route (for example, Chipman 1987, 1992; Olson and others 1997; Krieger 2002).

In Chapter 30 of his *Relación de los Naufragios* (“Account of the Disasters”), de Vaca described meeting a group of Native Americans whom he called “the cow nation:”

“...They are people with the best bodies that we saw and the greatest liveliness and ability and who understood us best and responded to what we asked them. We call them those of the cows, because most of them [the bison] die [are killed?] near here. And up that river more than 30 leagues they go killing many of them” (Krieger 2002:86, bracketed text supplied by Krieger).

Morris (1997:14-15) places this encounter on the southern margins of the SHP, perhaps near the Pecos River that flows parallel to the SHP, or alternatively near the Rio Grande River. Others, notably Davenport and Wells (1918, 1919) and Krieger (2002) located “the people of the cows” near the confluence of the Rio Concho and Rio Grande rivers near present-day Presidio, Texas and Ojinaga, Mexico. Despite these differences in location, many authors (for example, Terrell 1962; Morris 1997; Krieger 2002) have suggested that de Vaca and his companions nevertheless encountered the “Llano culture.” It was in this general area that their native guides told the travelers that:

“...there were no people that way [either] (that is, to the north), except very far away, and nothing to eat, nor water to be found... (Krieger 2002:80; text in parentheses added).

Morris (1997:14) observed that this may well have been a description of the SHP: “it is vast; it is arid; it is low in traditional foods; and it has no permanent settlements.” In the quotation above describing the “cow nation,” Hodge (1907:103, footnote 4) suggested that the phrase “near here” probably did not refer to the “immediate” vicinity of the encounter between de Vaca and the so-named native peoples, because de Vaca and his companions:

“...decided to go in search of the maize and we did not want to follow the way to the cows because this was to the North. And this was for us a great detour...” (Krieger 2002:99).

Morris (1997:15) likewise concluded that de Vaca avoided the Llano Estacado proper. Nevertheless, the encounter with the cow nation was significant. Terrell (1962:207) provided an evocative image:

“They listened to talk and tales about things of which they had never heard. To the north were endless plains, plains so unchanging, so flat and treeless, that not a mound, not a stick or bush rose to disfigure their smooth flow to the horizons. Where they ended, no one could say. They ended in the sky. On them the herds of cattle roamed in countless numbers, herds so immense that they took several suns to pass, herds that covered the earth like ragged blankets as far as a man could see and crawled like the shadows of the clouds that journeyed to nowhere.”

The description of the SHP that we can draw from de Vaca’s travels is noteworthy in two respects. First, the Llano Estacado was an extensive, featureless plain with no trees or shrubs to relieve the dreary monotony of its level landscape. Second, the SHP was the home of immense herds of native grazers. Thus, our first description of the SHP is that of a grassland, and one that was, at least at times, heavily grazed.

The impressions about the SHP that can be gathered from de Vaca’s *Relación* are important, but are unfortunately vicarious. Most historians agree that de Vaca did not observe first-hand the Llano Estacado proper. His experiences nevertheless stimulated additional interest in the southwest: Don Francisco Vasquez de Coronado’s exploration of the SHP was organized partly in response to the stories told by de Vaca and his companions about the mysteries of the New World. Prior to leading his entire expedition to the SHP, Coronado dispatched Captain Hernando de Alvarado and 20 soldiers as an advance party to explore the “buffalo plains” (Winship 1964:77). Their journey took them past present-day Pecos, New Mexico, and then east southeast to present-day Santa Rosa, New Mexico, where they crossed the Pecos River (Morris 1997:20):

“After Alvarado had sent an account of this river to Francisco Vasquez, he proceeded forward to these plains, and at the borders of these he found a little river which flows to the southwest [perhaps a tributary of the Canadian (Bolton 1964:188)], and after four day’s

march he found the cows, which are the most monstrous in the way of the animals which has ever been seen or read about...There is such a quantity of them that I do not know what to compare them with, except with the fish in the sea, because in this journey, as also on that which the whole army afterwards made when it was going to Quivira, there were so many of them that many times when we started to pass through the midst of them and wanted to go to the other side of them, we were not able to, because the country was covered with them" (Winship 1964:355-356; bracketed text added).

The description of the geography of this expedition does not explicitly indicate that this advance party actually ascended the SHP proper. It seems reasonable, however, from the abundance of bison sighted that they may well have been on the Llano Estacado. Although the accounts of this journey do not contain a description of the vegetation of the SHP, chroniclers of Coronado's main expedition to the SHP were fulsome in their descriptions.

Coronado and his vast expedition departed from near present-day Bernanillo, New Mexico, in April, 1541 for the distant "buffalo plains." Morris (1997:26-28) suggested that his party may have crossed the Pecos River somewhere between present-day Tecolotito (San Miguel County) and Colonia (Guadalupe County), New Mexico. Meyers (2003:147) suggested that they reached and crossed the Pecos River at Anton Chico (San Miguel County). The expedition then traveled east with the escarpment of the Llano Estacado to their south. Morris (1997:28) suggested that they ascended the caprock onto the Llano Estacado proper between present-day Ragland and San Jon (Quay County), New Mexico (also see Chipman 1992:38). Meyers (2003:148) suggested that the army ascended the Llano Estacado possibly at Puerto del Arroyo (in southeastern Quay County, New Mexico) or at Agua del Piedro (near Adrian, Texas).

Pedro Castañeda, "the historian of the Coronado expedition" (Winship 1964:13), provided vivid images of the SHP. He described "such great numbers of cows [that is, bison] that it already seemed something incredible" (Winship 1964:235). He recounted how a Spaniard "got lost who went off hunting so far that he was unable to return to camp, because the country is very level" (Winship 1964:235). He told how, searching for an errant advance party, "it was impossible to find tracks in this country, because the grass straightened up again as soon as it was trodden down" (Winship 1964:235). Coronado "sent some of his companions to guide the army to that place, so that they should not get lost, although he had been making piles of stones and cow dung for the army to follow. This was the way in which the army was guided by the advance guard" (Winship 1964:235). Elsewhere, Castañeda wrote:

"Who could believe that 1,000 horses and 500 of our cows and more than 5,000 rams and ewes and more than 1,500 friendly Indians and servants, in traveling over those plains, would leave no more trace where they passed than if nothing had been there—nothing—so that it was necessary to make a pile of bones and cow dung

now and then, so that the rear guard could follow the army. The grass never failed to become erect after it had been trodden down, and, although it was short, it was fresh and straight as before" (Winship 1964:302).

Coronado himself described the SHP to King Charles V of Spain:

"I traveled...until I reached some plains, with no more landmarks than as if we had been swallowed up in the sea, when they strayed about, because there was not a stone, nor a bit of rising ground, nor a tree, nor a shrub, nor anything to go by. There is much very fine pasture land, with good grass...[we went] many days without water, and cooking food with cow dung, because there is not any kind of wood in all these plains, away from the gullies and rivers, which are very few" (Winship 1964:367-368).

Even the native guides who directed the return route of Coronado's army back to New Mexico needed help navigating across this featureless landscape. Castañeda wrote:

"... these people [that is, native American guides] are always roaming over this country in pursuit of animals and so know it thoroughly. They keep their road this way: In the morning, they notice where the sun rises and observe the direction they are going to take, and then shoot an arrow in its direction. Before reaching this they shoot another over it, and in this way they go all day toward the water where they are to end the day" (Winship 1964:241).

The writings of Coronado and his chroniclers leave an unmistakable image of the Llano Estacado. It was a treeless, shrubless sea of grass, and the monotony of this featureless landscape was not relieved by any structural vegetation diversity at all.

Spanish exploration of the SHP continued after Coronado's first historic journey, and later descriptions corroborated the images that Castañeda painted. In 1599, Vincente del Zaldívar, sent out by Don Juan Pérez Oñate, an early colonizer of New Mexico, explored the northern portion of the SHP in the vicinity of the Canadian River. Along the margins of the northern SHP timber was found in abundance. Describing the Llano Estacado, however, Zaldívar wrote, "These cattle have their haunts on some very level mesas which extend over many leagues...The mesas have neither mountain, nor tree, nor shrub, and when on them they were guided solely by the sun" (Bolton 1946:230). The last major expedition in the 1600s (Morris 1997:147) was made by Juan Dominguez de Mendoza who, in the company of two Franciscan priests, found the southern part of the SHP between the Pecos River and the Middle Concho River, "all...a plain" (Bolton 1946:330). In some locations, the country was so destitute of "suitable timber" that a cross could not be erected, although there was nevertheless an abundance of mesquite (for example, Bolton 1946:328-329, 333). In the 1780s, José Mares entered

the Llano Estacado on its northwestern borders. He wrote, “I traveled very rapidly this day across a very wide plain which contains no landmarks other than an arroyo which runs to the east and which has two clumps of chinaberry trees” (Loomis and Nasatir 1967:291). Loomis and Nasatir (1967:291) and Morris (1997:173) suggested that Mares and his companions were following Tierra Blanca Creek, and eventually encountered Tule Creek, near present-day Tulia, where permanent water allowed cottonwoods and reeds to grow.

The Llano Estacado was explored by Spanish, French, and American adventurers from the mid 1500s well into the 1800s. In fact, by 1800, “generations of New Mexican buffalo hunters...had traversed [the Llano Estacado] thoroughly” (Morris 1997:153-154). Chipman (1992) and Morris (1997) provided a thorough and insightful summary of accounts of the SHP written throughout this period. It is remarkable that the basic description of the landscape and the vegetation of the Llano Estacado, as seen through the eyes of explorers from 1541 well into the 1800s, remains essentially the same. Quotations presented earlier from the writings of Castañeda, for example, can be compared to what Albert Pike, a lawyer and author, wrote in 1832:

“Imagine yourself, kind reader, standing in a plain to which your eye can see no bounds. Not a tree, not a bush, not a shrub, not a tall weed lifts its head above the barren grandeur of the desert; not a stone is to be seen on its hard beaten surface; no undulation, no abruptness, no break to relieve the monotony...Imagine then countless herds of buffalo” (Haley 1968:21-22).

Similarly, George Kendall, a newspaperman who accompanied the “Texas-Santa Fe Expedition” of 1841 (Morris 1997:229-230), wrote in 1856:

“Here we were again gratified by finding spread out before us a perfectly level prairie, extending as far as the eye could reach, and without a tree to break its monotony” (p. 216)...We were going forward at a rapid pace, the prairies before us presenting no other appearance than a slightly undulating but smooth appearance (p. 221)...Not a tree or bush, and hardly a weed could be seen in any direction. A green carpet of short grass, which even at this season was studded with innumerable strange flowers, was spread over the vast expanse, with naught else to relieve the eye” (Kendall 1856:225).

Thomas Falconer, who accompanied the expedition, wrote:

“We commenced the ascent to the grand prairie—the Llano Estacado of New Mexico. This was the great plain spoken of at San Antonio as too extensive to travel over; where we should be without timber, without water, and where many of our horses would perish...we found before us an extensive flat table-land stretching as far

as the eye could reach...Proceeding over this great prairie...[we] were out of sight of every tree and shrub. The grass was fresh and green...Though we had no wood, there was an abundance of dried buffalo chips (p. 443)...[as they approached the boundary of the Llano Estacado] below us we saw a wooded country” (Kendall 1856:445; bracketed text added).

A diary by Gallagher and Hoyle, also written in 1841, describes the Llano Estacado as “a vast level prairie as far as the eye could reach without a tree or a shrub” (Morris 1997:238). In 1844 Josiah Gregg wrote, “The high plains seem too dry and lifeless to produce timber” (Moorhead 1954:362). In one of the most famous descriptions of the SHP (near Adrain, Texas), Captain R.B. Marcy, a military explorer, wrote on June 14, 1849:

“When we were upon the high table land, a view presented itself as boundless as the ocean. Not a tree, shrub, or any other object, either animate or inanimate, relieved the dreary monotony of the prospect; it is a vast illimitable expanse of desert prairie—the dreaded ‘Llano Estacado’ of New Mexico; or in other words, the great Zahara of North America. It is a region almost as vast and trackless as the ocean...it spreads forth into a treeless, desolate waste of uninhabitable solitude” (Marcy 1850:42).

Many of the descriptions of the SHP emphasize its vastness, its absence of woody vegetation, and its dominance by short grasses. These descriptions led to an image of the SHP as the “Great Zahara of North America” (Marcy 1850:42), a perception that has been thoughtfully analyzed by a number of authors (for example, Lewis 1966; Fenton 1990; Morris 1997). The concept of the “Great American Desert” was introduced to the American public by Z. Pike in 1810: “Beyond the meridian 96° 30’ west Pike distinguished between the valley floors, which would prove to be cultivable, and the extensive upland plains, poor in soil, treeless, and desiccated for eight months of the year, which he predicted might in time become ‘as celebrated as the sandy deserts of Africa’” (Lewis 1966:35). Major S.H. Long, however, is often credited with introducing this idea after his 1820 exploration to the Rocky Mountains. The official map produced from this expedition, published in 1823, labeled the region that included the Texas Panhandle as well as Oklahoma and parts of Colorado as “Great American Desert” (Lewis 1966:35). Many historians and geographers have since suggested that Long’s assessment of the central and southern Great Plains (from the South Platte to the Canadian River) was culturally biased, or even a product of a vivid imagination (for example, Blackmar 1906, from Lawson and Stockton 1981). However, Lawson and Stockton (1981), on the basis of reconstructed climatic data, concluded that: “These years of abnormally low moisture culminated in extreme drought throughout the lower portion of the western interior. Long’s route passed through the core of this moisture deficiency. In relative terms, the region identified by Long as

the Great American Desert was experiencing drought stress exceeding that of the 1930s. Only one other period, that of the late 1720s, surpassed the intensity or extent of the drought witnessed by Major Stephen H. Long. When one considers the magnitude of this moisture anomaly, augmented by the pressures of overgrazing by buffalo, perhaps it is less reasonable to refer to the desert as an illusion. For Long and his scientific cadre, the ‘impress of geographic conditions’ represented a reality never since experienced by this cis-Rocky Mountain west” (Lawson and Stockton 1981:535).

It is also true, however, that early explorers described woody vegetation in draws, riverbeds, and ravines, most obvious around the periphery of the SHP (on all sides), but also evident in some of the more conspicuous canyons that penetrated the SHP from the eastern escarpment of the Llano Estacado. For example, Coronado’s army constructed a bridge to cross the Pecos River on the way to the SHP, clearly indicating that woody vegetation was abundant along waterways peripheral to the SHP along its northwest margin. After they had crossed the SHP, Coronado encountered the eastern escarpment of the Llano Estacado, perhaps in Tule Canyon (Chipman 1992:38; Morris 1997:56), where “colorful canyons...descended hundreds of feet to rough, scrubby flats and timbered headwater creeks far below...Where these streams poured into larger drainages...the combination of wood, water, and food were particularly pleasant. These fringing woods were cool and shady...” (Morris 1997:55-56). Morris (1997, Chapter 6) also suggested that Coronado’s army stopped at Blanco Canyon in Crosby County, where timber, water, and food were abundant, including plums, wild grapes, mulberries, and possibly hickories.

In addition, the country that lay “below” the SHP (on all sides) supported abundant woody vegetation including mesquite. In fact, it was in Union County, New Mexico, along a stream usually identified as “Major Long’s Creek” (which flows into the Canadian River near the Texas state line; McKelvey 1955:229; Thwaites 1966, Vol. XVI:85) that Edwin James, a botanist traveling with Major S. Long in his exploration of the headwaters of the Red River in 1820, provided an early written record of mesquite in the area of the SHP:

“...we found ourselves once more entering a vast unvaried plain of sand...Among the few scattered and shrubby trees met with in this district, are oaks, willows, and the cottonwood; also a most interesting shrub or small tree, rising sometimes to a height of twelve or fourteen feet. It has dioecious flowers, and produces a leguminous fruit, making in several particulars a near approach to gladetschia...The leaves are pinnated, and the trunk beset with spines, somewhat like a honey locust, but the spines are single” (Thwaites 1966, Vol. XVI:91-93).

Several military explorers provided valuable descriptions of vegetation on the periphery of the SHP. Lt. James Abert traveled eastward along the Canadian River in 1846. Throughout his report, he remarked on the abundance of mesquite as he

traveled across the Texas Panhandle. For example, in the general vicinity of Logan, New Mexico, Abert (1846) wrote:

“[The Canadian River]...has increased to 70 or 80 feet in width, with a deep and very rapid current, so that we could scarcely keep our feet whilst bathing...the [river] bottom in which we encamped is everywhere covered with various species of cactus, the sharp spines of which penetrated our moccasins, making it painful to walk about. There is a plant still more annoying, commonly called “Sand-bur.” This is a diminutive plant, lying close to the sandy surface, loaded with a profusion of little burs, which attach themselves to our clothes and blankets by their sharp prickles, and adhere with great tenacity. Amongst the sylvia, the hackberry, “Celtis crassifolia,” is quite common, and we observed, for the first time, an extensive grove of the pride of India, “Melia azederach”—a tree gifted with a beautiful form and dense foliage...The trees were every where loaded with heavy masses of grape vines, “Nitis aestivalis”...It was now the fruit season of the broad-leaved cactus, “C. opuntia,” and they were every where in great abundance...We saw to-day great quantities of the “musquit,” or muskeet, covered with its long-sabre-formed legumes. The creek is well-timbered...” (Abert 1846:29-30).

In 1849, Marcy traveled from Fort Smith, Arkansas, to Santa Fe, New Mexico, along the Canadian River, and then returned along the southern boundary of the SHP. Marcy generally corroborated Abert’s general vegetation description of the Canadian River (also see Marcy 1853, for example, Chapter 5). For example, he remarked on June 10 that: “We have passed over a high rolling prairie for the last three days, destitute of wood, except a narrow fringe of trees upon the borders of the ravines” (Marcy 1850:40). However, the following day, Marcy wrote: “We started this morning, our road continuing over the elevated plateau, destitute of water, until we reached here, where there is a fine spring creek, with a great abundance of wood and grass” (Marcy 1850:40). On June 13, he wrote: “We passed a great deal of small mesquite and numberless plants of the jointed cactus today” (Marcy 1850:41). It should be noted that despite using terms such as “high rolling prairie” and “elevated plateau,” Marcy was in fact traveling below the SHP. He did not ascend to the Llano Estacado proper until June 14 (quoted above).

Marcy (1850) returned to Fort Smith via a route across the southern boundary of the SHP. From Santa Fe, he traveled south along the Pecos River, and then turned east, crossed through the Monahans area (Ward and Winkler Counties, Texas), and reached the eastern escarpment of the Llano Estacado at Big Spring, Texas (Howard County, Texas). Along the Pecos River, Marcy wrote:

“After marching six miles further, we encamped again on the west bank of the river. Here we found the finest and most luxuriant grama grass we had seen, with

mezquite wood. Keeping down the right bank of the river, we found the valley covered in many places with a growth of small mezquite trees..." (Marcy 1850:60).

After crossing the Pecos River, Marcy wrote:

"There has been a chain of sand hills in sight to-day, running from north to south across our course, about twenty miles to the east of us, (upon the Llano Estacado,) in which our guide informs us that there is water, but that we are obliged to pass over the sandy road from some fifteen miles to get through them" (Marcy 1850:61).

Marcy crossed through the sandy country, now known as the Monahans Sand Dunes, and was surprised to find water, which his guide informed him was permanent. Having passed through the sand dunes, Marcy again encountered "hard prairie...There is good grass near the hills, and sufficient wood for fuel" (Marcy 1850:62). Although the species is not identified, it is likely that Marcy encountered mesquite to the northeast of the Monahans sand dunes. Marcy then "pushed out upon the high plain of the Llano Estacado" (Marcy 1850:62-63). He encountered Mustang Pond and then Laguna, or Salt Lake. Marcy wrote: "We marched twenty-three miles today...which brought us to the Laguna, or Salt Lake. The country has been similar to that of yesterday, over the high rolling table lands of the Mesa, with no wood except the small mezquite brush" (Marcy 1850:64). In another eight miles bearing northeast, Marcy encountered the eastern escarpment of the Llano Estacado near Big Spring. He wrote: "The mezquite trees are becoming larger as we descend from the high plain" (Marcy 1850:64). As Marcy moved east off the Llano Estacado and started towards Fort Smith, Arkansas, he described "...a perfectly level grassy glade, and covered with a growth of large mesquite trees at uniform distances, standing with great regularity, and presenting more the appearance of an immense peach orchard than a wilderness" (Marcy 1850:68).

Lt. A. Whipple explored the possibility of a railroad route along the northern SHP in 1853. He wrote:

"Ascending about two hundred and fifty feet, in about a mile from camp we reached the top of the Llano. Here, for the first time, we saw what one might call a prairie ocean; so smooth, level and boundless does it appear. It is covered with a carpet of closely cropped buffalo-grass, and no other green thing is to be seen (p. 87)... to the top of the Llano...towards the south, appears smooth, level, and of unlimited extent. It is covered with short buffalo-grass, but contains neither shrub nor tree to vary the landscape" (Whipple 1853:119-120).

Marcy explored the sources of the Big Wichita and Brazos Rivers in 1854, accompanied by W.B. Parker. Both men left descriptions of their travels. Parker (1854:160-161) described the vegetation of a spur of the Llano Estacado along the Brazos River as follows: "...and finally ascending over a steep and

dangerous road, came to a broad level plain, a spur of the Llano Estacado, covered with buffalo grass and mesquite, and extending as far as the eye could reach in a perfect level towards the dim, cloud-like mountains at the head of the Brazos." This description clearly mentions mesquite on the east-central Llano Estacado. Two additional observations, however, are pertinent: Marcy's description of this area (Marcy 1854:14) fails to mention mesquite on the Llano Estacado and Parker's description is accompanied by a footnote which states, in part, that the Llano Estacado "is...without a tree...throughout its entire surface" (Parker 1854:161). Thus, the conclusion that mesquite was dominant in this area remains ambiguous.

J. R. Bartlett traveled westward from Fredericksburg, Texas, to El Paso in October, 1850. He frequently described woody vegetation including live oak and mesquite along his route through the northern Edwards Plateau. In October, he described the vegetation near Antelope Creek, which he identified as on the tributaries of the Concho River. At this time, Bartlett was still on the Edwards Plateau:

"Our route today had been over a level prairie country, deficient of wood, save a few scattering mezquit trees of diminutive size, and light grass, indicating a poorer soil. We have noticed as we advanced westward, and ascended the high tableland of Texas [he was not on the Llano Estacado at this time], an inferior soil, and, as a necessary consequence, a more scanty herbage. The beautiful live-oak, which abounds in eastern Texas, and which grows luxuriantly in the valleys as far as the north fork of Brady's Creek, has not disappeared, save on the immediate banks of water courses. The mezquit, too, which grew large and thrifty on good soil, had not either disappeared or dwindles into a diminutive tree or mere shrub" (Bartlett 1854:74; bracketed text added).

As he approached the southern margins of the SHP near Mustang Pond, he wrote:

"The desert was not, as I supposed, a level surface, but a succession of slight elevations. Everything bore the appearance of extreme barrenness; not a tree could be seen. Mezquit chapporal, or bushes from three to five feet in height, were thinly scattered over the plain. The wild sage and Larrea Mexicana, the prickly pear and other kinds of cactus, constituted the vegetation of this desert region. Grama grass (Chondrosium) [Chondrosium?] grew in some spots, and, though completely dried up, was eaten with avidity by our animals" (Bartlett 1854:87; bracketed text added).

And at Mustang Pond, he wrote: "Finding a spot where there was plenty of dry grass, the train was stopped and the animals turned out to graze...they ate the withered grass and browsed on the twigs of mezquit bushes with eagerness" (Bartlett 1854:88).

There are, therefore, many descriptions of woody vegetation in the lower country surrounding the SHP. And despite

the poignancy of many of the early descriptions of the SHP proper as vast and featureless, it is important to appreciate that there was *some* relief to the dreariness of the Llano Estacado even between its western and eastern escarpments. Morris (1997:52ff; also see Bryan 1956:87) provided convincing evidence that before reaching the eastern escarpment, Coronado's expedition encountered Running Water Draw, which crosses the SHP in a southeasterly direction. While on the SHP probably in lower Hale County, Texas (Morris 1997:51), Coronado sent Captain Diego López on a reconnaissance trip along a bearing toward the sunrise, and along this path, Morris suggests that they encountered Running Water Draw, which provided fresh, running water. When the reconnaissance party reunited with the main army, López reported that "they had seen nothing but cows and the sky" (Winship 1964:235), clearly indicating they were on the SHP. Significantly, though, in the same area where López saw only "cows and sky," Castañeda writes that the two native Indians who had found López's party and led them back to the main army were in fact looking for fruit when they encountered López. Clearly, this part of the Llano Estacado was crossed by a draw that supported woody vegetation with fruits (Morris 1997:54). Coronado himself provided an interesting and important corroborating clue to vegetation patterns on the Llano Estacado when he wrote to King Charles V: "... [we were] going many days without water, and cooking the food with cow dung, because there is not any kind of wood in all these plains, away from the gullies and rivers, which are few" (Winship 1964:368). Similarly, José Mares, dispatched by Governor Cabello to reconnoiter a route across the Llano Estacado in the 1780s, encountered chinaberry trees along an arroyo that Loomis and Nashatir (1967:291) and Morris (1997:173) identify as upper Tierra Blanca Creek, which soon joined with running water near present-day Friona and Hereford, Texas; Mares also encountered Tule Creek, near present-day Tulia, which he described as "...permanent [with] cottonwood trees and many reeds [*tules*]" (Morris 1997:173). Additionally, mesquite occurred in certain edaphic settings. For example, Havard (1884:455) remarked that: "The most desolate parts of the Staked plains are the Sand hills—barren heaps of shifting sand. Between these are sometimes found large, vigorous mezquit shrubs." In 1901, Oberholser (Smithsonian Institution Archives, Record Unit 7176, Box 95, Folder 14) described *Rhus aromatica* and *Celtis occidentalis* on the sand dunes 45 miles south of Hereford. Finally, as indicated above, Marcy (1850) and Bartlett (1854) reported mesquite in the southern part of the Llano Estacado, north-east of the Monahans Sand Hills and near Big Spring.

Summary of Early Descriptions

For a period of about 300 years, a description of the vegetation of the SHP can be drawn, from many sources, that shares the same essential features. First, the escarpment itself, as well as the country "below" the Llano Estacado, supported abundant woody vegetation. The fact that Coronado could build a bridge across the Pecos River suggests perhaps

abundant cottonwood. In addition, Castañeda described a number of woody species (for example, *Prunus*, *Morus*, and probable *Carya illinoensis*; Morris 1997:80-81) in what Morris suggested was Blanco Canyon, which penetrates the SHP from the eastern escarpment in Crosby County. Finally, both the first record of mesquite (by James), as well as abundant references to the plant (by, for example, Abert and Marcy), provide ample evidence that this country supported abundant woody vegetation.

Second, the SHP proper was characterized by grassland vegetation over most of its vast, changeless expanse. Further, this grassland *evidently* supported no woody vegetation (but see below). Numerous quotations have been cited describing a landscape devoid of shrubs and trees, a topographic vacuum that demanded travelers to mark their routes with piles of buffalo dung to avoid disorientation and swallowed up those who strayed beyond the boundaries of the known. Third, despite the apparent monotony of the Llano Estacado, it is noteworthy that it was interrupted by vegetation diversity including woody species in and along major draws that crossed the SHP as well as in sandy soils. Coronado's telling phrase that there is not any kind of wood in all these plains, away from the gullies and rivers, which are few (Winship, 1964, p. 368), implies that the "gullies and rivers" in fact had woody species. Further, Coronado's Indian guides who found Captain Lopez were actually looking for fruit at the time, suggesting woody species in Running Water Draw in the northcentral part of the Llano Estacado. Finally, José Mares noted chinaberry trees along upper Tierra Blanca Creek (see earlier text).

Later 1800s to Early 1900s

Beginning in the late 1880s, with the "settling" of Texas, scientific interest in its natural resources spurred the commission of a biological survey of the state, including the SHP. The general descriptions of the vegetation of the SHP that have been gathered from the literature between 1541 and the 1850s are largely corroborated by Bailey's (1905) biological survey of Texas. Bailey's map of the distribution of mesquite in Texas and New Mexico (Bailey 1905, Plate III; see fig. 4) clearly showed that mesquite was absent from most of the SHP. In fact, Bailey defined the "plains" portion of the "Upper Austral Zone, Upper Sonoran Division" (Bailey 1905:33) (which included the SHP, see figure 3a in Schmidly 2002:43) by the "absence of mesquite and other shrubs of the surrounding Lower Sonoran Zone" (Bailey 1905:33; the "other shrubs" included species of *Acacia*, *Mimosa*, *Ziziphus*, *Condalia*, and *Lycium*; see Schmidly 2002:79). It is also significant that Bailey's map shows that mesquite was present along the southeastern portion of the Llano Estacado in the general area of Big Spring, which supports Marcy's (1850) and Bartlett's (1854) observations.

Bailey and his team of scientists left a wealth of valuable descriptions of the SHP and its surroundings. For example, Merritt Cary provided the following description of the Monahans area (Ward and Winkler Counties, Texas) in 1902:



Figure 4. Distribution of mesquite in Texas in 1905 (from Bailey 1905).

"Monahans is situated in a mesquite basin which is rimmed in on the southeast, south, southwest, and west sides by hard, limy ridges and on the northwest, north, northeast, and east by a range of high sandhills. A large portion of the basin is sandy, and supports a heavy growth of Ziziphus obtusifolia in addition to the mesquite. These are the only two shrubs occurring in the basin. Among smaller plants growing in the sandy soil are Mentzelia sp., Baccharis sp., and Artemisia sp. as well as Yucca stricta. The hard ridges support a heavy growth of range grasses, in addition to Larrea, Lycium berlandiera, Ziziphus, and a few mesquites... These sand hills are quite steep in some places, and are clothed with a more or less dense growth of "shin oak," except where the wind has formed "blow outs" (Smithsonian Institution Archives, Record Unit 7176, Box 93, Folder 13).

In 1892 B.H. Dutcher described the area around Stanton (southeast Martin County, Texas) as follows:

"Stanton is situated on the edge of the plateau top of the Llano Estacado or Staked Plains. Only a few miles east of the town the plain "breaks" down to the shelf that extends to the Colorado River. The surface of the country is gently undulating, is well-covered with grass and weeds, and supports a scattering growth of

mesquite trees, catclaws, etc. The trees and bushes seem to grow in groves, which are interspersed with excluded barren reaches...I was informed that the country lying to the north over the plains does not differ essentially in character from the country at Stanton" (Smithsonian Institution Archives, Record Unit 7176, Box 93, Folder 18).

Dutcher also reported:

"Mesquite. Common though not entirely covering the plains. Does not attain a height of over six or eight feet in the open. Juniperus virginiana. Common in groves along the edges of the plain overlooking the shelf below, on the red-soil mesquite plain" (Smithsonian Institution Archives, Record Unit 7176, Box 93, Folder 19).

Clay indicated that in the area of Stanton:

"Odessa, Warfield, and Stanton are situated alike on a high, grassy mesquite plain...In the vicinity of Stanton, however, there are very few mesquites, and large areas of open, grassy plain are frequent...The botany of the three localities is very similar. The principal shrubby plants noted were as follows: Ziziphus obtusifolia, Prosopis juliflora, Acacia sp., Opuntia arborescens (not noted east of Stanton), Cereus sp., Yucca stricta,

Ephedra nevadensis, *Baccharis* sp., *Grindelia*. A rank growth of range grasses obtains throughout the region” (Smithsonian Institution Archives, Record Unit 7176, Box 93, Folder 13).

In the northern half of the SHP, Bailey described the landscape surrounding Washburn, Texas (northeast corner of Armstrong County), in 1892 as:

“Washburn is on the Staked Plains...There is nothing to break the smooth, even monotony of almost level prairie, meeting the horizon on all sides...A low, thick growth of grass covers the country, giving an almost velvety smoothness of surface. Here and there a thistle, an *Aesclepias*, or *Euphorbia* rises a foot or so, but so scarce as to be hardly noticed. An occasional house, with windmill and fences, or cattle and horses grazing are all that break the monotony” (Smithsonian Institution Archives, Record Unit 7176, Box 92, Folder 13).

And describing a portion of Palo Duro Canyon (Armstrong County, Texas), Bailey wrote:

“Thirteen miles south of Washburn the Prairie Dog Fork of the Red River flows through an abrupt cañon of about 1,000 in depth...The top of the canyon is about a mile wide...The bottom is sandy and smooth. The river bed is small and now almost dry. The whole canon is lined with trees, brush and plants not found outside in the surrounding country, and furnishes the only timber for a long distance. Junipers are the most abundant and useful tree, being used for fence posts and fuel, and are very common along the sides of the cañon. A few cottonwoods grow along the bottom, also *Celtis* and chinaberry. *Prosopis* fills the canon and runs over the edge of prairie as also a little oak. *Lyssium* [*Lycium*?] is common, several species of *Rhus*, *Ptelia*, *Cercocarpos* [*Cercocarpos*?], *Atriplex canescens*, five species of cactus, *Yucca angustifolia*, *Artemisia* and others entirely new to me” (Smithsonian Institution Archives, Record Unit 7176, Box 92, Folder 13; bracketed text added).

Bailey added the following important note in a plant list of the area:

“*Prosopis glandulosa*, abundant in cañon, extending out along the top and a few small plants (rarely over two feet high) here and there over the prairie (Smithsonian Institution Archives, Record Unit 7176, Box 92, Folder 14).

Henry Oberholser described the landscape around Hereford in 1901 as follows:

“Hereford is located on the Staked Plains at an altitude of about 3,800 feet...For long distances in any direction from the town the country is a level or slightly rolling

grassy plain, at intervals interrupted by wide, scarcely abrupt and usually not very deep grassy valleys, or ‘draws’ as they are known in local parlance, which lead to the headwaters of the Red River, but contain water only after heavy rains. Close to the south side of Hereford there is, however, a spring-fed creek, the *Tierra Blanca*, which for some fifteen miles is a running though sluggish stream. Along the miles of its grassy valley there are frequent outcrops of friable white limestone appearing in low isolated cliffs usually close to the present stream bed. The margins of this creek are overgrown with a dense mass of cattails and rushes, while on the cliffs occurs the nearest approach to a natural growth tree [sic] anywhere to be found—a few scrubby bushes of *Celtis occidentalis*...Some 45 miles to the south of Hereford the general evenness of the country is broken by an extensive area of low sand hills. Here the soil changes from the dark colored loam of the environs of Hereford to the fine sand which supports a much less dense growth of grass. The highest of these hills probably is not much over 30 feet above the plain; and all are usually covered with a growth of rank weeds and bushes of *Rhus aromatica*, with sometimes a few low trees of *Celtis occidentalis*...after crossing them to the southeast the country more resembles that immediately about Hereford...The portion about Hereford is characterized by the absence of shrubby vegetation which begins to appear about 40 miles to the southward in the shape of scattered bushes of *Mimosa biuncifera*, this increasing in amount to the southwest until it forms in many places a low chaparral. About 50 miles south of Hereford scattered shrubby bushes of *Prosopis juliflora* begin to be observable, and continue to occur along the road leading southwest...” (Smithsonian Institution Archives, Record Unit 7176, Box 95, Folder 14).

Both Bailey and William Bray traveled from Gail, Texas, north to Amarillo in 1899. Bailey wrote:

“From Colorado [River] to 15 miles north of Gail the country is Colorado River valley and is characterized by an uneven, eroded surface of red beds and sand cover by a scattered growth of cactus, mesquite, etc. The escarpment of the real[?] Llano Estacado begins just west of Gail but our road does not rise onto it for about 15 miles farther north. The escarpment here is about 400 feet. To the north the country rises slowly but steadily to Lubbock, Hail [sic] Center, Canyon and Amarillo but appears as a flat plain, covered with short grass, free of bushes or trees...Most of the mesquites, thorn bushes, and cactus are left below the escarpment and soon disappear from the higher levels. Short grasses and low prairie, or plains, plants cover the top of the plains and give the characteristic smooth carpet appearance of the region. A few northern plants are met with that may be typical Upper Sonoran species

but the Upper Sonoran Zone of the top of the plains is marked rather by the absence of surrounding Lower Sonoran species than by a change from one set of plants to another...The country is mostly fenced up in pastures of enormous extent, often containing several hundred square miles, and cattle are scattered over the whole region. Except on areas where there has been no rain for a long time the range is not overstocked and the grass is abundant" (Smithsonian Institution Archives, Record Unit 7176, Box 92, Folder 16; bracketed text added).

Describing the area from the Colorado River to Gail, Bray wrote:

*"...the characteristic "red beds" formation continues. This is a country left rolling by erosion where stream ways occupy broad flat valleys which rise to picturesquely carved bluffs no where precipitous but for some areas of exposed rock. The gentler swells are covered with sandy loam and the valleys with more compact silt. On these flats the excellent range grass *Hilaria jamesii* was so abundant as to suggest a field of timothy hay. *Prosopis juliflora* is abundant over the flatland often covering the ground continuously with a large growth...On the flat stretch of some ten miles north of Gail before reaching the escarpment of the plains *Prosopis* is very abundant and still of large size. [About] ten miles north of Gail the road passes upon the Plains...Almost at once the biological character of the mesa indicates its individuality...The predominant botanical characteristic of the Staked Plains is this: A vast stretch of solid grass floor in which is an admixture of herbaceous vegetation from the south and another equally marked from the north"* (Smithsonian Institution Archives, Record Unit 7176, Box 93, Folder 8).

Bray continued in description of the "timber or shrubby vegetation of the Staked Plains:"

"Prosopis juliflora. This is a small tree of approximately normal size on the flat north of Gail. Never after ascending the escarpment $\pm$ 12 miles north of Gail does it exceed five feet in height, and is always a cluster of sprouts or very small trunks. In many places it is wholly absent for miles. At Lubbock there is still considerable mesquite one to two feet tall and the merest switches of stems. At Hale Center there is an occasional sprout of mesquite, but beyond this it disappears entirely. Going southeastward from Amarillo on the Denver City and Fort Worth line, short mesquite first appears at Goodnight station [between present-day Claude and Clarendon, Texas], sprouts two to three feet tall. Below the eastern escarpment a fairly large tree growth sets in. In general to the south and east mesquite stops at 3,500 ft... ." (Smithsonian Institution Archives, Record Unit 7176, Box 93, Folder 9; bracketed text added).

It is interesting to compare these comments (written in 1899) with Bray's description of mesquite in a 1904 publication:

"[Mesquite's] spread northward and eastward from the Rio Grande country during the past 50 years has been a marked phenomenon. By its invasion mile after mile of treeless plain and prairie have been won and reduced to the characteristic orchard-like landscape...It has pushed northward over the Staked Plains, covering half their area" (Bray 1904:34).

And in 1906, Bray provided the following poetical description of the vegetation of the Staked Plains:

"It is on these high grass plains that the complete masterfulness of the grass-land type of vegetation impresses one. The monotonous level or billowy swells of a sea of grass unrelieved by the presence of taller plants like a shrub or tree, such as the ungrazed plains presented, could fasten upon the senses a conception of the power of a victorious vegetation such as one might get in the depths of a virgin pine forest, or in the sun-beat chaparral jungle which are also the expression of dominant vegetation types" (Bray 1906:92).

It seems that Bray's descriptions of the woody vegetation of the SHP, gathered from his notes written in 1899 in conjunction with his work on the biological survey and his publications of 1904 and 1906, lack some consistency. Also, Bray's map (fig. 5), in contrast with Bailey's (fig. 4), shows that mesquite was present (although not abundant) in several counties along the southeastern border of the SHP (for example, Gaines, Dawson, Borden, Andrews, Martin, and portions of Lynn Counties).

Several vegetation descriptions in the early 20th century indicate that mesquite was present on the SHP. For example, in Clements' (1920:139-144) description of the Short-Grass Plains that extended into the Texas Panhandle, characterized by the *Buchl e-Bouteloua* association (which he later "down-graded" to the *Buchl e-Bouteloua* associates, a short-grass disclimax that resulted from overgrazing; Weaver and Clements 1936:524), Clements made no mention of mesquite. In his description of the Desert Plains in the grasslands of the southwest including New Mexico, Arizona, and Texas, characterized by the *Aristida-Bouteloua* association, Clements (1920:145) remarked that "Indeed, *Larrea* or *Prosopis* is scattered over so much [of this association] that it has often been regarded as mesquite rather than grassland." Clements explained that: "The desert plains are in close contact with but one other association of the grassland formation, namely, the short grass plains...The contact...is from Synder and Big Spring in the Staked Plains of Texas to Roswell and Socorro in New Mexico..." (Clements 1920:144-145). It is with this background that the following comment by Clements should be appreciated. He remarked: "Mesquite savannah lies typically in the desert plains, though the mesquite itself extends

northward into the short-grass association of the Stakes Plains” (Clements 1920:278).

In a description of vegetation types in the semiarid portion of the U.S., Aldous and Shantz (1924:103) included:

“Grama-Buffer, and Mesquite.—This is a very common type in the southern Great Plains of western Texas and eastern New Mexico, growing on hard lands. It is composed of an open sod of grama grass and buffalo grass, over which are scattered bunches of mesquite.”

However, Shantz and Zon (1924) mapped the Llano Estacado as short grass plains (“Grama-Buffer grass”), with tall grass prairie characterizing the sandy soils in the western portion of the SHP. “Mesquite and the desert grass savanna” was mapped in the Rolling Plains and Edwards Plateau regions to the east and south of the SHP. This latter description was also followed by Shantz (1938), where “Mesquite-Desert Grass Savanna (Desert Savanna)” was distinguished from the “Short Grass (Plains grassland)” “in that trees are scattered over a short-grass cover” (Shantz 1938:848).

Not all authors, however, recorded mesquite on the SHP. For example, in 1917 the Texas state forester, J.H. Foster wrote: “[Mesquite] is found in the Breaks of the Plains, but has gained no foothold on the high, level plains themselves, apparently being killed back by frosts” (Foster 1917:445). This is one of the few descriptions of the SHP that specifically mentions an absence of mesquite, and it stands in contrast to other quotations in this regard.

Interpretation

From the foregoing survey of the literature, an initial conclusion can be reached: although the landscape immediately surrounding the SHP was characterized by a mixture of grassland and woody species, the Llano Estacado proper supported a vast shortgrass plains grassland interrupted by woody species only in certain topographic settings (for example, in draws or on very sandy soils). This conclusion is based on the writings of Spanish explorers as well as later military explorers and naturalists, covers a period of approximately 300 years (1540s to 1850s), and is corroborated by vegetation maps of Bray (1896) and Bailey (1905).

It is also true, however, that this conclusion is contradicted by other evidence also recorded in the mid to latter 19th century. Marcy’s summary statement about mesquite, written in 1854, is important:

“...In the journeys I have made before upon the plains I had observed the mesquite tree extending over vast tracts of country...What the exact geographical range of the tree is we are as yet (with a great portion of our territory unexplored) unable to define; my own observations, however, warrant me in asserting confidently that it is only indigenous to the great plains of the west and south...Between the twenty-sixth and thirty-six parallels

of north latitude, with the ninety-seventh and one hundred and third meridian of longitude, it is found abundantly, often constituting vast tracts of wood land, and is, indeed, almost the only siloa [sic; silva?] of the section...In going north from the parallel of thirty-three degrees, (in the direction I have traveled,) the trees gradually become smaller and smaller; until at least they are mere bushes; and, finally, on arriving near the latitude of thirty-six degrees, they disappear entirely...It is a tree of short, shrubby growth, with stock averaging from four to fifteen inches in diameter, and seldom attaining a height, including its top, of more than twenty feet...[it] is often found upon the most elevated and arid prairies, far from water courses...” (Marcy 1854:25-26; bracketed text added).

When evaluating this important statement by one of the most successful military explorers of the SHP, it must be remembered that despite his lengthy expeditions, Marcy actually spent very little time on the SHP proper (which he alluded to in the above quotation when he wrote “with a great portion of our territory unexplored”). His travels from Fort Smith to Santa Fe in 1849 followed the Canadian River valley and ascended the Llano Estacado proper for only one day (June 14, 1849; Marcy 1850:12, 42). His return along the southern borders of the SHP likewise involved little time on the Llano Estacado proper (from September 28 to October 3, 1849, with one day of rest; Marcy 1850). In 1854, Marcy stated that “even the Indians do not venture to cross [the Llano Estacado] except at two or three points...” (p. 92). Thus, it might be suggested that although Marcy’s determination of the limits of the latitudinal range of mesquite was both accurate and based on extensive experience, it is not clear from his writings that he observed mesquite throughout the extent of the SHP.

Settlers in the Lubbock area described mesquite in the late 1800s. For example, Lou Stubbs arrived in Lubbock in the early 1890s and, after a wet June, noted a diverse flora of grasses and forbs as well as “green mesquite” (Burnett 1990:12). Bray’s notes recorded in 1899 described mesquite on the SHP at least as far north as Hale Center (Hale County). Slightly later, Clements (1920) remarked that mesquite extended into the shortgrass plains of the Llano Estacado, and Aldous and Shantz (1924) described a “grama-buffalo and mesquite” vegetation type as “very common” in the southern Great Plains (that is, “eastern New Mexico and western Texas”).

An inspection of a chronological sequence of maps of the distribution of mesquite, together with the written descriptions quoted above, suggests that whereas mesquite was evidently entirely absent from the SHP (figs. 4, 5, 6) or restricted to draws in the SHP in the mid and late 19th century (fig. 7), it had expanded its range into “upland” sites by the middle of the 20th century (figs. 7, 8), and virtually covered the SHP by the latter years of the 20th century (figs. 9, 10). (The distribution map in fig. 7 is from *Life Magazine* and obviously lacks the “credibility” of a refereed scientific publication, and it certainly fails to document the sources consulted for the construction of the map. Notwithstanding, it is curious that

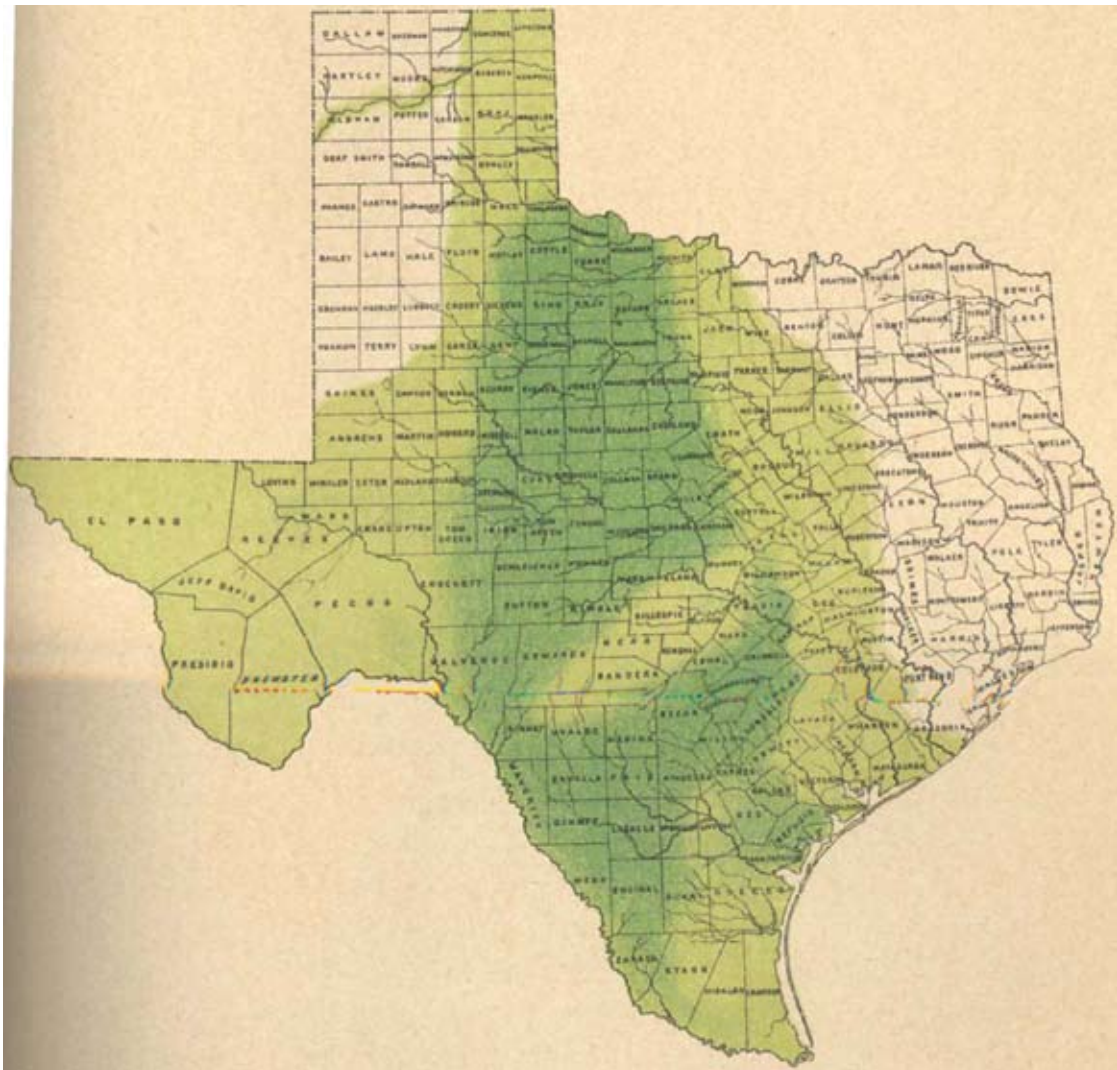


Figure 5. Distribution of mesquite in Texas in 1896 (from Bray 1896).

the distribution it shows for 1850 seems to be more consistent with the descriptions provided by the early explorers than the 1896 or 1905 distributions shown by Bray and Bailey, respectively. See Malin (1953:213) for a comment on the “authority” underlying this map.)

An Explanation

Some authors have suggested that mesquite has not expanded its range since the early 19th century, but rather it has increased in density so that plant populations are greater. Burkhart (1976:225) described *Prosopis* as a “primitive” genus that possibly originated in north Africa, and wrote: “Present distribution patterns of species of *Prosopis* do not exclude the possibility of an ancient desert flora common to both Americas which later divided and became widely separated into two centers, the Mexican-Texan center and the Argentine-Paraguayan-Chilean one...the fact that in both centers endemic species exist indicates their antiquity...”

Axelrod (1937) reported *P. pliocenica* in the Pliocene flora of southern California and observed that “Since the fossil species closely resemble their modern representatives, it is believed that the habitat implications of the fossil and living species are similar” (p. 138). He further described *P. pliocenica* as part of a “desert border element” whose modern equivalent is *P. juliflora* var. *glandulosa*. Malin (1953) advanced this interpretation with respect to the “floristic range” of mesquite generally. Johnston (1963) provided considerable supporting evidence, but limited his discussion to mesquite’s distribution in south Texas and northeastern Mexico (that is, areas “below 2,000 ft in elevation and south of the 29th parallel”; Johnston 1963:456). This explanation has been repeated by numerous authors (for example, Fisher 1977; Dahl 1982; Brown and Archer 1989, 1999; Jacoby and Ansley 1991), who, for the most part, discuss it in a general context. For example, “grassland and savanna systems” (for example, Brown and Archer 1999) or “the semiarid southwestern U.S.” (for example, Dahl 1982) are usually described without the distributional

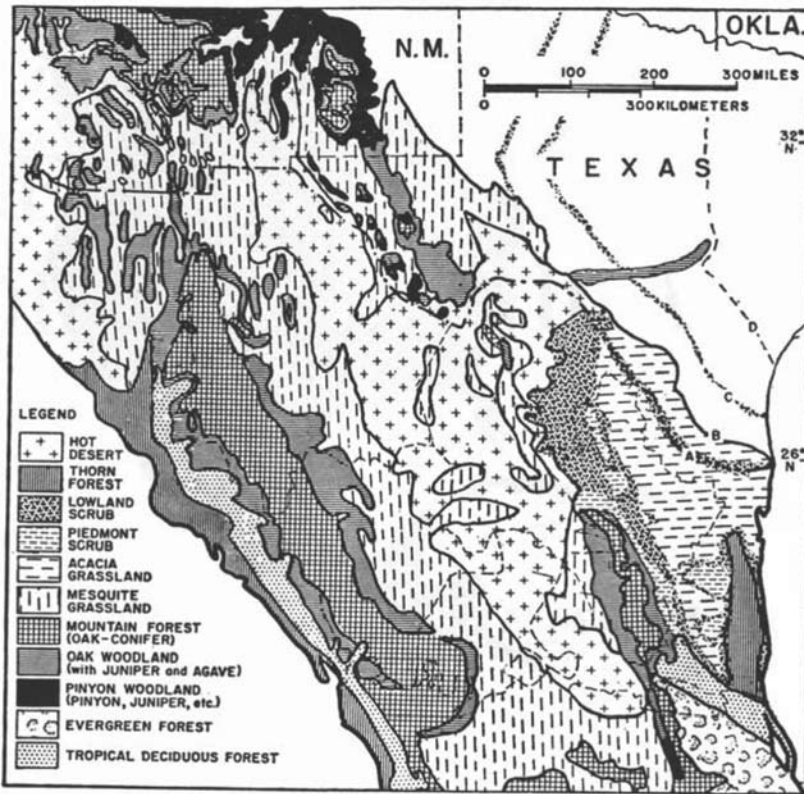


Figure 6. Probable distribution of mesquite grassland, *Acacia* grassland, and associated communities about A.D. 1600. *Acacia* grassland was believed to be present in the Rio Grande floodplain and adjacent areas (A) whereas mesquite extended to the line B. By 1923, the thorn shrubs had reached line C, and mesquite had reached line D (from Shelford 1964).

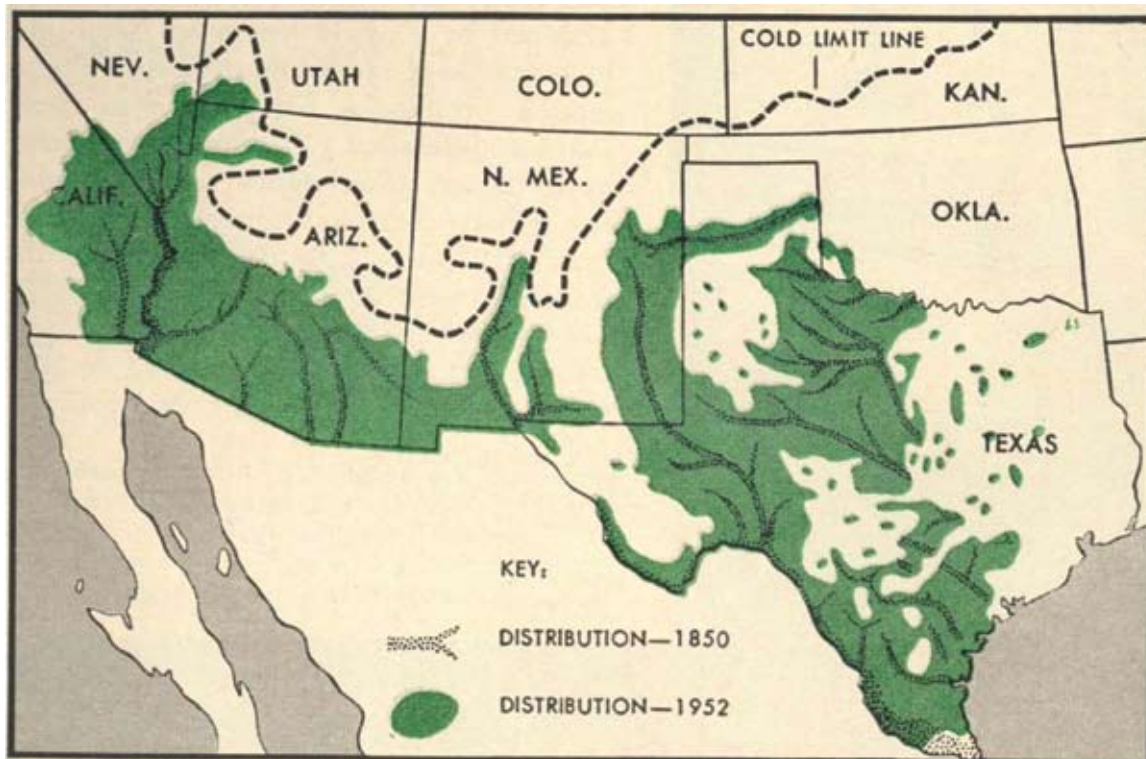


Figure 7. Distribution of mesquite (from Life Magazine 1952).



Figure 8. Distribution of mesquite in 1943 (from Allred 1949).



Figure 9. Distribution of mesquite in 1977 (from Fisher 1977).

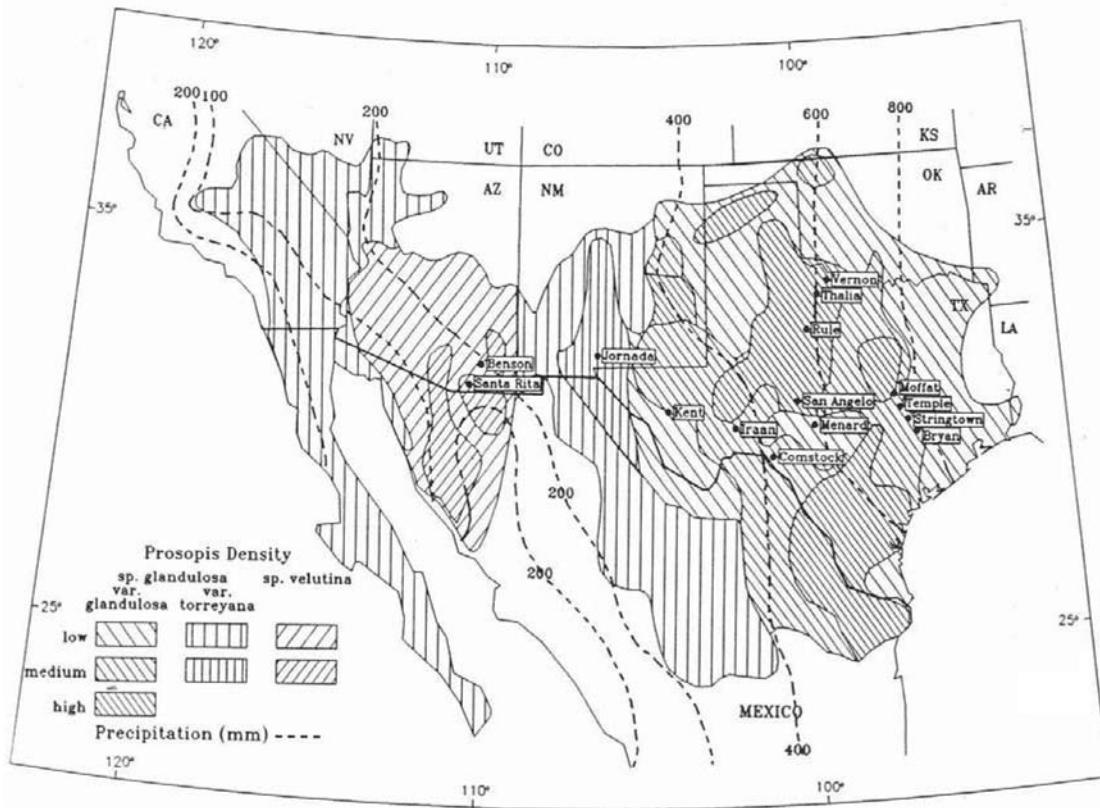


Figure 10. Distribution of mesquite in 1990 (from Johnson and Mayeux 1990).

limitations explicit in Johnston's (1963) paper (even though Johnson's paper is usually cited).

Many factors are probably involved in the population increase of mesquite, including changes in fire frequency, herbivory by both large mammals and rodents, and climate change. One of the most commonly-implicated factors is fire. In particular, many authors have suggested that periodic fires maintained relatively low mesquite population densities, and the reduction of fires allowed for increases in population densities. This explanation has a long history. For example, Cook (1908) wrote that:

"It is a matter of popular knowledge in south Texas that extensive regions which were formerly grassy, open prairies are not covered with a dense growth of mesquite...It differs locally only in the number of years since the bushes began to grow—thirty years, or twenty, or ten—subsequent to the establishment of the grazing industry on a large scale, the annual burning of the grass by cattlemen, and finally the fencing of the land for still more intensive grazing...Very often the old mesquite pioneers, the scattered trees which made the 'open mesquite country' of other decades, are still conspicuous among their much smaller progeny and the crowds of other camp-following species which now occupy the land to the almost complete exclusion of the grasses upon which the herds of former days were pastured. The change has come so gradually that even those who have the most intimate acquaintance with the

facts have not appreciated their significance...Before the prairies were grazed by cattle the luxuriant growths of grass could accumulate for several years until conditions were favorable for accidental fires to spread. With these large supplies of fuel the fires which swept over these prairies were very besoms of destruction not only for man and animals but for all shrubs and trees which might have ventured out among the grass...That such fires were evidently the cause of the former treeless condition of the southwestern prairies is also shown by the fact that trees are found in all situations which afford protection against fires [pp. 1-2]...Settlers in south Texas early adopted the practice of burning over the prairies every year; partly to protect their homes against the fires, partly to give their cattle readier access to the fresh growth of grass...While the grass was still abundant these annual burnings were able to keep the woody vegetation well in check, though no longer able to drive back the forest or even to prevent its slow advance. In spots where the grass is thin, seedling mesquites and oaks escape the flames and in a year or two begin to shade the ground and gain more protection against the dangerous proximity of the combustible grass; and even though the tops are killed by later fires the roots may send up sprouts again and again to improve the chances of becoming established [p. 3]..."

Johnston (1963:465) stated that: "It is emphasized that many 'grasslands' were infested with the ubiquitous mesquite...and

that the rapid takeover of the mesquite brush involved an increase in stature of the aerial parts of the plant and in density of stand, rather than invasion of previously brush-less areas. Most authors feel the control of fires explains the shrinkage of the grasslands. Nothing in this study contradicts such an explanation.” More recently, Dahl (1982:A-1) wrote: “Had fires not periodically swept southwestern grasslands, probably the entire area would have supported a woody overstory long before the first white men arrived in North America.” Brown and Archer (1989:25) wrote that one possible explanation for mesquite in southwestern grasslands is that: “*Prosopis* may have always been present in grassland, but recurring fires kept plants from developing in stature and producing seed.”

It may be difficult, however, to reconcile this explanation with the apparent *absence* of mesquite over most the SHP as depicted by the much of the literature reviewed here. If this explanation were true, it seems that *some* evidence of mesquite, perhaps present as small, stunted plants, would have been recorded by early explorers in upland sites, particularly in light of the fact that fire generally kills only very small mesquite plants (Havard 1884; Wright and Bailey 1982:149 and references therein). Additionally, it is noteworthy that mesquite seedlings are remarkably hardy, being tolerant of repeated top removal during the first growing season (Weltzin and others 1998) and capable of vegetative reproduction within 2 weeks of germination (Scifres and Hahn 1971). Although there are numerous statements in the literature about fires in the SHP (for example, Bolton 1946:330, 333; Hall 1947; Morris 1991:147), the only observation linking fire and the stature of mesquite discovered in the literature reviewed here was made by Bartlett (1854:75), who wrote about mesquite as he approached the southern margins of the SHP: “Where the prairies are frequently burned over, the tree is reduced to a shrubby state, a great number of small branches proceeding from one root, which goes on developing and attains a great size, though the portion above ground may not be more than four or five feet high.” In describing the grasslands of Arizona, Griffiths (1904:29) wrote: “A close examination of the broad, gentle, grassy slopes between the arroyos in this vicinity reveals a very scattering growth of mesquite...which is in the form of twigs 2 to 3 feet high with an occasional larger shrub in some of the more favorable localities...One cannot tell whether this growth indicates that this shrub is spreading or not. The present condition rather suggests this possibility” (from Turner and others 2003:xiii). The possibility exists that the small shrubs noted by Griffiths possibly had been held in check by repeated fires. In this connection, an anecdote reported by Kelton (1993:79-83) is noteworthy. Kelton recounted that O. Schwartz, who began farming in 1923 east of San Angelo, Texas (to the southeast of the SHP, which was “mostly open rangeland”, p. 79), would occasionally plow up an unseen mesquite stump that invariably had fire scars. Areas not broken out into farms later developed into dense stands of mesquite. Although this anecdote specifically relates to an area southeast of the SHP, it raises the possibility of like situations on the SHP, although no such remarks have been noted in the literature reviewed here.

A Second Explanation

A second explanation for the difference between the current and historical distributions of mesquite involves a combination of livestock grazing and fire considerations. In particular, it has been suggested that domestic livestock, which had consumed mesquite beans from trees growing along water courses, distributed these seeds through feces (see Fisher 1977 and references therein). [It should be appreciated, however, that mesquite seeds are an important food component for numerous small mammals, including kangaroo rat (*Dipodomys merriami* and *D. spectabilis*), *Perognathus hispidus*, hares (*Lepus*), and packrats (Mares and others 1977 and references therein). Additionally, Burkhardt (1976) and Mooney and others (1977) suggested that mesquite fruits evolved “to very effective endozoic diffusion through mammals and larger birds (owing to the succulent, edible legumes with hard seeds that escape digestion)” (Burkhardt, 1976, p. 225).] This mechanism of range expansion can then be combined with a reduction in intensity and frequency of fire, allowing for mesquite to establish populations in sites previously unoccupied by the species.

There are, therefore, two approaches to follow in explaining the differences between current and historical mesquite distributions over the SHP. The first approach suggests that woody vegetation (probably including mesquite) has been present on the SHP (at least since Europeans first explored the area, when written records begin), but plants went (largely?) unnoticed because recurrent fires maintained populations in a suppressed state. Further, mesquite’s current dominance, dramatic as it is, has not involved a range expansion, but rather a population explosion. The second explanation involves, first, a range expansion of woody species into a grassland (via introduction of domestic livestock), and second, a woody species population explosion.

It is likely that the factors involved in the population explosion are similar in both these scenarios and include changes in fire frequency, grazing history, and extreme climate events. Most range scientists have maintained that increases in woody plant populations require (1) a vector for seed dispersal (for example, herbivores spreading seed via defecation) and (2) a reduction in competition from herbaceous species (caused, for example, by heavy grazing or drought conditions) that provides gaps in an herbaceous stand for woody plant establishment as well as reduced competitive influence that allows for woody seedling growth. Additionally, these factors may be coupled with climatic events that favor the woody species, for example, episodically high rainfall promotes seed production and seed germination (for example, Turner and others 2003) (but see below).

It seems that an understanding of shrub dynamics on the SHP requires that a choice must be made between (i) an increase in the density of existing woody populations or (ii) an invasion of woody species into previously unoccupied areas, followed by an increase in population density. In an effort to evaluate these two scenarios, the following observations are offered.

1. *Woody vegetation (which presumably included mesquite) was recorded by the earliest explorers in the draws and the sandy soils of the SHP as well as in the landscape bordering the SHP. Johnson (this proceedings) reported that mesquite, sumac (Rhus sp.), and hackberry (Celtis sp.) were present and associated with the "valley system" of the SHP as early as 4,500 B.P., with additional records of these species together with Texas walnut (Juglans microcarpa) in the valley system as well as an upland salina dating from 2,000 to 200 B.P. Relative to vegetation dynamics throughout the Holocene, and with specific regard to native trees, Johnson (this proceedings) stated "Occurring primarily in the valley system, an occasional hackberry and mesquite were on the uplands around lake basins depending on the period."*

2. *Early explorers probably traveled across the SHP along paths of the existing drainages and not in haphazard directions that would have brought them across "upland" sites (see, for example, Morris 1997:47, 97; Meyers 2003). Thus, the absence of descriptions of woody vegetation on upland sites may be a result of lack of experience with upland sites by early explorers, rather than the absence of woody plants in these sites.*

3. *Early explorers remarked that there were trails from the (apparently shrub-less) "high plains" of the Llano Estacado down into the wooded canyons along the margins of the SHP that buffalo used to move from the Rolling Plains to the SHP (for example, Kendall 1856:228; Morris 1997:56).*

If domestic grazing animals are to be invoked as being responsible for moving seeds from woody plants (including mesquite) naturally growing in draws and canyons to upland sites through defecation (as in the second explanation, above), then it seems reasonable that buffalo, as well as numerous other large mammals and rodents, may have also fulfilled this role, leading to the possibility that native herbivores, prior to domestic livestock, may have distributed, to some extent, seeds of woody species from draws and canyons onto the SHP proper. However, Brown and Archer (1987) found no mesquite seedlings and fewer seeds in an ungrazed area compared to a grazed area in south Texas and concluded that domestic livestock were more effective agents of mesquite seed dispersal than native fauna in south Texas. These authors suggested that effective seed dispersers would be agents that "transplant large numbers of germinable seeds away from parent plants harboring host-specific seed predators and deposit them in grazed habitats where emergence and survival could be high" (Brown and Archer 1989:25). They concluded that "the apparently low densities of mesquite in grasslands prior to settlement may have been a consequence of limited dispersal or germination rather than biotic or abiotic constraints on establishment" (Brown and Archer 1987:79). Brown and Archer's characterization of an effective seed disperser is reasonable, and it is true that cattle fit this description. However,

an effective seed dispersal agent is one that would deposit a germinable seed "in areas where grasses ha[ve] been defoliated" (Brown and Archer 1989:19), and native fauna that do this also would be effective dispersal agents. With effective seed dispersal by native fauna, the absence of descriptions of woody vegetation in the literature reviewed here might then be explained by a lack of experience with these sites by early explorers, supplemented with the possibility that population densities were low and frequently-burned plants existed in a state of suppression and were thus not conspicuous to early travelers. If this reasoning is sound, then the conclusion is that woody vegetation was a natural component of the SHP, but its "dominance" as a community component was most apparent only in particular landscape settings (for example, the draws or valley systems). Further, on uplands where it may have been only occasionally present, woody vegetation was "held in check" by recurrent fires. Thus, its apparent neglect by early explorers may be explained in part by lack of experience and low populations in particular landscape settings.

In this regard, the results of Brown and Archer (1989, 1999) are pertinent. These authors showed in the Post Oak savanna of central Texas that, relative to non-defoliated plots, moderate grass defoliation increased mesquite seedling emergence by eight-fold. Further, there was no difference in seedling emergence between moderately and heavily-defoliated plots (Brown and Archer 1989). To the extent that mesquite emergence was enhanced by moderate defoliation, and because there was no difference between moderately and heavily-defoliated plots, these authors concluded that the competitive suppression that grasses may have on mesquite establishment was easily overcome; that is, "long-term and/or heavy grazing is [not] requisite for *Prosopis* encroachment into grasslands" (Brown and Archer 1989:19). In contrast, in south Texas, these authors showed that herbaceous biomass or density had no effect on mesquite seedling establishment. Instead, they documented relatively continuous mesquite seedling emergence that was also largely unaffected by moisture conditions (Brown and Archer 1999). Thus, whereas non-defoliated herbaceous vegetation was effective in reducing mesquite seedling emergence in central Texas, they concluded that "Historic grazing at [the south Texas] site appears to have altered herbaceous composition and reduced above- and belowground biomass production below the threshold level required for competitive exclusion of woody vegetation...[their] data suggest that rates and patterns of seed dispersal may be the primary determinants of *P. glandulosa* encroachment on present-day landscapes in semiarid regions" (Brown and Archer 1999:2385). These results suggest that (1) depending on past history, native vegetation unaltered by grazing may or may not be capable of excluding woody vegetation, and (2) seed dispersal is a prerequisite for woody plant invasion into grasslands.

The existence of well-developed ecotypes of mesquite extending from south Texas to central Oklahoma (Peacock and McMillan 1965; however, these authors did not study populations from the SHP proper) is also important in understanding the dynamics of this species. Although rates of evolutionary changes involved in the differentiation of ecotypes undoubtedly depend on the species and adaptive gradients in question,

Peacock and McMillan (1965:35) concluded that “Ecotypic differentiation over the northern part of its range adds weight to the historical evidence that mesquite has occupied its current distribution for a considerable period of time.”

An appreciation of the effects of (1) landscape setting (for example, draws and valley systems, or upland sites) on vegetation composition and structure, (2) both past and current grazing history on woody plant establishment, as well woody plant demographic phenomena involving both proximity of seed source and effectiveness of seed dispersal, and (3) fire, lie at the heart of understanding shrub dynamics in the SHP.

Summary

Despite considerable documentary evidence and the efforts of many ecologists, it is difficult to determine the precise nature of the vegetation of the SHP from the time of the first European explorers to the late 1800s. Based on accounts written during this time period, conclusions that can be drawn about this vegetation are vague and sometimes contradictory. For example, Coronado described a landscape with no trees or shrubs, and then added *except* away from the gullies and rivers. Marcy similarly described a landscape without trees or shrubs and then provided a delineation of the range of mesquite that included all of the SHP. Bray, in turn, wrote about the Llano Estacado as being unrelieved by the shrubs and trees, but also described mesquite as far north as Hale Center (Hale County).

There is little question that the earliest descriptions of the SHP indicate that it was a grassland interrupted by woody species only in certain topographic settings (for example, draws and canyons). The fact that “native soils [of the SHP] were most likely Paleustolls, given the native vegetation of the region” (Holliday 1990:498) suggests long-term landscape stability. It is equally clear that woody vegetation (including mesquite) was reported throughout most of the SHP by the 1890s. Finally, woody vegetation, including mesquite, has been recorded in the landscapes surrounding the SHP since 1820, and the presence of ecotypic differentiation suggests that mesquite populations surrounding the SHP have been in existence for a considerable time period. With specific regard to shrubs on upland sites of the SHP, and using mesquite as a case species, either mesquite has historically been present but went unrecorded prior to the 1890s because upland sites had low population densities, were not frequented, and/or because recurrent fires maintained populations inconspicuous, or mesquite was introduced in a novel way by domestic livestock that had been introduced in the late 1870s and 1880s. In either of these scenarios, subsequent increases in woody plant densities likely involved changes in fire frequency, grazing history, and climate.

Literature Cited

- Abert, J. W. 1846. Communicating a report of an expedition led by Lieutenant Abert, on the upper Arkansas and through the country of the Comanche Indians, in the fall of the year 1845. Washington, D.C.: 29th Congress, 1st Session, Senate Executive Document 438.
- Aldous, A. E.; Shantz, H. L. 1924. Types of vegetation in the semiarid portion of the United States and their economic significance. J. Agr. Res. 28:99-128.
- Alford, J. J. 1973. The American bison: An ice age survivor. Proc. Assoc. Amer. Geogr. 5:1-6.
- Allred, B. W. 1949. Distribution and control of several woody plants in Texas and Oklahoma. J. Range Management 2:17-29.
- Axelrod, D. I. 1937. A Pliocene flora from the Mount Eden beds, southern California, pp. 125-183. In: Miocene and Pliocene Floras of Western North America, Carnegie Institution of Washington Publ. No. 476 (dated 1938), Washington, D.C.
- Axelrod, D. I. 1985. Rise of the grassland biome, central North America. Bot. Rev. 51:163-201.
- Bailey, V. 1905. Biological Survey of Texas. North American Fauna No. 25. U.S.D.A. Biological Survey, Washington, DC. 222 p.
- Bartlett, J. R. 1854. Personal Narrative of Explorations and Incidents in Texas, New Mexico, California, Sonora, and Chihuahua. Volumes 1 and 2. The Rio Grande Press Inc., Chicago, 1965.
- Blackmar, F. W. 1906. The history of the desert. Trans. Kansas State Historical Soc. 9:101-102.
- Bolen, E. G.; Smith, L. M.; Schramm, H. L., Jr., 1989. Playa lakes: prairie wetlands of the Southern High Plains. Bioscience 39:615-623.
- Bolton, H. E. (ed.). 1946. Spanish Explorations in the Southwest, 1542-1706. Barnes and Noble Books, NY. 486 p.
- Bolton, H. E. 1964. Coronado, Knight of Pueblos and Plains. Univ. New Mexico Press, Albuquerque. 491 p.
- Bray, W. L. 1904. Forest resources of Texas. USDA Bur. For. Bull. 47. 71 p.
- Bray, W. L. 1906. Distribution and adaptation of the vegetation of Texas. Bulletin of the University of Texas, No. 82. 106 p.
- Britten, T. A. 1993. Changing land uses in Carson County: A microcosm of the Panhandle experience. Panhandle-Plains Historical Review LXVI:53-72.
- Brooks, L.; Emel, J. 2000. The Llano Estacado of the U.S. Southern High Plains, Environmental Transformation and the Prospect of Sustainability. United Nations University Press, Tokyo. 176 p.
- Brown, J. R.; Archer, S. 1987. Woody plant seed dispersal and gap formation in a North American subtropical savanna woodland: the role of domestic herbivores. Vegetatio 73:73-80.
- Brown, J. R.; Archer, S. 1989. Woody plant invasion of grasslands: establishment of honey mesquite (*Prosopis glandulosa* var. *glandulosa*) on sites differing in herbaceous biomass and grazing history. Oecologia 80:19-26.
- Brown, J. R.; Archer, S. 1999. Shrub invasion of grassland: recruitment is continuous and not regulated by herbaceous biomass or density. Ecology 80:2385-2396.
- Bryan, F. 1956. Early Texas Travelers. Central Texas Archeologist No. 7. 108 p.
- Burkhardt, A. 1976. A monograph of the genus *Prosopis* (Leguminosae Subfam. Mimosoideae). J. Arnold Arboretum 57:219-249, 450-525.
- Burnett, G. 1990. We Just Toughed It Out. The University of Texas, Southwestern Studies, No. 90. 55 p.
- Carroll, H. B.; Day, J. M.; Winfrey, D. H.; Siegel, S. 1986. Texas, pp. 184-200. In Collier's Encyclopedia, Vol. 22, Macmillan Educational Co., P. F. Collier, London. 763 p.
- Carlson, P. H. 1974. William R. Shafter, black troops, and the opening of the Llano Estacado, 1870-1875. Panhandle-Plains Historical Review XLVII:1-18.

- Chipman, D. E. 1987. In search of Cabeza de Vaca's route across Texas: An historiographical survey. *Southwestern Historical Quarterly* 91:127-148.
- Chipman, D. E. 1992. *Spanish Texas, 1519-1821*. University of Texas Press, Austin. 343 p.
- Clements, F. E. 1920. Plant Indicators: The Relation of Plant Communities to Process and Practice. Carnegie Institution of Washington Publication 290. 388 p.
- Cook, O. F. 1908. Change of vegetation on the south Texas prairies. U.S.D.A. Bureau of Plant Industry, Circular no. 14. 7 p.
- Coughenour, M. B. 1985. Graminoid responses to grazing by large herbivores: adaptations, exaptations, and interacting processes. *Ann. Missouri Bot. Gard.* 72:852-863.
- Dahl, B. E. 1982. Mesquite as a rangeland plant, p. A-1 to A-20. In: *Mesquite Utilization, 1982. Proceedings of a Symposium on Mesquite Utilization, held at Texas Tech University, October 29-30, 1982*. College of Agricultural Sciences, Texas Tech University.
- Davenport, H.; Wells, J. K. 1918, 1919. The first Europeans in Texas, 1528-1536. *Southwestern. Hist. Quart.* 22:111-142, 205: 205-259.
- Evelt, S. 2003. Irrigation methods, technology and management for increased water use efficiency. Annual report, 2003, ARS, USDA. (www.ars.usda.gov/research).
- Fenneman, N. M. 1931. *Physiography of the Western United States*. McGraw-Hill Book Co., NY. 534 p.
- Fenton, J. 1990. The desert myth dies slowly on the Staked Plains, 1845-1860. *Panhandle-Plains Historical Review*. LXIII: 45-74
- Fisher, C. E. 1977. Mesquite and modern man in southwestern North America, pp. 177-188. In: *Mesquite, Its Biology in Two Desert Shrub Ecosystems*, B.B. Simpson (ed.), US/IBP Synthesis Series No. 4. Dowden, Hutchinson and Ross, Inc., Stroudsburg. 250 p.
- Forman, S. L.; Oglesby, R.; Webb, R. S. 2001. Temporal and spatial patterns of Holocene dune activity on the Great Plains of North America: megadroughts and climate links. *Global and Planetary Change* 29:1-29.
- Foster, J. H. 1917. The spread of timbered areas in central Texas. *J. Forestry* 15:442-445).
- Gilpin, W. 1836. Letter to his mother, cited in G.M. Lewis, 1966. p. 41.
- Griffiths, D. 1904. Range investigations in Arizona. U.S.D.A. Bureau of Plant Industry Bulletin No. 67. Washington, D.C.
- Haley, J. E. 1968. Albert Pike's Journeys in the Prairie, 1831-1832. *The Panhandle-Plains Historical Society* 41:1-91
- Hall, C. V. 1947. The early history of Floyd County. *Panhandle-Plains Historical Review* XX:1-140.
- Hallenbeck, C. 1940. *Alvar Nunez Cabeza de Vaca: The journey and route of the first European to cross the continent of North America, 1534-1536*. Glendale, Arthur H. Clark Co. 326 p.
- Havard, V. 1884. The mezquit. *Amer. Nat.* XVIII:451-459.
- Hodge, F. W. (ed.). 1907. *Spanish Explorers in the Southern United States, 1528-1543. The Narrative of Alvar Nunez Cabeza de Vaca*. Charles Scribner's Sons, New York.
- Holliday, V. T. 1989. Middle Holocene drought on the Southern High Plains. *Quaternary Research* 31:74-82
- Holliday, V. T. 1990. Soils and landscape evolution of eolian plains: the Southern High Plains of Texas and New Mexico. *Geomorphology* 3:489-515.
- Hunt, C. B. 1967. *Physiography of the United States*. W.H. Freeman and Co., San Francisco. 480 p.
- Jacoby, P. W.; Ansley, R. J. 1991. Mesquite: Classification, distribution, ecology, and control, pp. 364-376. In: *Noxious Range Weeds*, L. F. James, J. O. Evans, M. H. Ralphs, and R. D. Child (eds.), Westview Press, Boulder. 466 p.
- Johnson, E. (ed.). 1987. *Lubbock Lake, Late Quaternary Studies on the Southern High Plains*. Texas A&M Univ. Press, College Station. 179 p.
- Johnson, H. B.; Mayeux, H. S. Jr. 1990. *Proposis glandulosa* and the nitrogen balance of rangelands: extent and occurrence of nodulation. *Oecologia* 84:176-185.
- Johnston, M. C. 1963. Past and present grasslands of southern Texas and northeastern Mexico. *Ecology* 44:456-466.
- Kelton, E. 1993. *Elmer Kenton Country, The Short Nonfiction of a Texas Novelist*. Texas Christian University Press, Fort Worth. 312 p.
- Kendall, G. W. 1856. *Narrative of the Texas Santa Fe Expedition, Comprising a Description of a tour through Texas, and Across the Great Southwestern Prairies...*. Harper and Brothers, Publ., NY, in two volumes (vol. 1, 452 p.; vol. 2, 442 p.)
- Krieger, A. D. 2002. *We Came Naked and Barefoot, The Journey of Cabeza de Vaca Across North America*, M.H. Krieger, ed. Univ. of Texas Press, Austin. 318 p.
- Lawson, M. P.; Stockton, C. W. 1981. Desert myth and climatic reality. *Ann. Assoc. Amer. Geogr.* 71:527-535.
- Lewis, G. M. 1966. William Gilpin and the concept of the Great Plains region. *Ann. Assoc. Amer. Geogr.* 56: 33-51
- Life Magazine, August 18, 1952. Man versus mesquite, Vol. 33: 69-70, 72.
- Loomis, F. B. 1938. *Physiography of the United States*. Doubleday, Doran and Co., Inc. NY. 350 p.
- Loomis, N. M.; Nasatir, A. P. 1967. *Pedro Vial and the Roads to Santa Fe*. Univ. of Oklahoma Press, Norman. 569 p.
- MacGinitie, H. D. 1962. The Kilgore flora: a late Miocene flora from northern Nebraska. *Univ. Calif. Publ. Geol. Sci.* 35:67-158.
- Malin, J. C. 1953. Soil, animal and plant relations of the grassland, historically reconsidered. *Sci. Monthly* 76:207-220.
- Marcy, R. B. 1850. In compliance with a resolution of the House of the 6th February, a report and map of Lt. Simpson, of the route from Fort Smith to Santa Fe; also, a report on the same subject from Captain R.B. Marcy, 5th Infantry. Washington, D.C.: 31st Congress, 1st Session, House of Representatives Executive Document 7 No. 45.
- Marcy, R. B. 1853. *Exploration of the Red River of Louisiana in the Year 1852*. Washington, D.C.: 32^d Congress, 2^d Session, Senate Executive Document no. 4.
- Marcy, R. B. 1854. Report of an expedition to the sources of the Brazos and Big Wichita rivers, during the summer of 1854. 34th Congress, 1st Session, Senate Ex. Doc. No. 60. 41 p.
- Mares, M. A.; Enders, F. A.; Kingsolver, J. M.; Neff, J. F.; Simpson, B. B. 1977. *Prosopis* as a niche component, pp. 123-149. In: *Mesquite, Its Biology in Two Desert Shrub Ecosystems*, B. B. Simpson (ed.), US/IBP Synthesis Series No. 4. Dowden, Hutchinson and Ross, Inc., Stroudsburg. 250 p.
- McComb, D. G. 1989. *Texas: A Modern History*. University of Texas Press, Austin. 197 p.
- McDonald, J. N. 1981. *North American Bison, Their Classification and Evolution*. Univ. of California Press, Berkeley. 316 p.
- McKelvey, S. D. 1955. *Botanical Exploration of the Trans-Mississippi West, 1790-1850*. Arnold Arboretum, Harvard University, Jamaica Plain, MA. 1144 p.
- Mead, W. R.; Brown, E. H. 1970. *The United States and Canada, A Regional Geography*. Hutchinson Educational, LTD, London. 368 p.

- Meko, D. M. 1995. Dendroclimatic evidence from the Great Plains of the United States, pp. 312-330. In: R. S. Bradley and P. D. Jones, eds., *Climate Since A.D. 1500*. Routledge, London. 706 p.
- Meyers, H. C. 2003. The mystery of Coronado's route from the Pecos River to the Llano Estacado, pp. 140-150. In: *The Coronado Expedition, From the Distance of 460 Years*. R. Flint and S. C. Flint (eds.), Univ. of New Mexico Press, Albuquerque. 338 p.
- Mooney, H. A.; Simpson, B. B.; Solbrig, O. T. 1977. Phenology, morphology, physiology, pp. 26-43. In: *Mesquite, Its Biology in Two Desert Shrub Ecosystems*, B. B. Simpson (ed.), US/IBP Synthesis Series No. 4. Dowden, Hutchinson and Ross, Inc., Stroudsburg. 250 p.
- Moorhead, M. L. (ed.). 1954. *Josiah Gregg, Commerce of the Prairies*. Univ. of Oklahoma Press, Norman. 469 p.
- Morris, J. M. 1997. *El Llano Estacado, Exploration and Imagination on the High Plains of Texas and New Mexico, 1536-1860*. Texas State Historical Association, Austin. 414 p.
- Muhs, D. R.; Holliday, V. T. 1995. Evidence of active dune sand on the Great Plains in the 19th century from accounts of early explorers. *Quaternary Res.* 43:198-208.
- Nall, G. L. 1972. The farmer's frontier in the Texas Panhandle. *Panhandle-Plains Historical Review*. XLV:1-20.
- NOAA. 1982. *Climatology of the United States*, No. 60, Climate of Texas. 46 p.
- Olson, D. W.; Olson, M. S.; Doescher, R. L.; Lambert, L. L.; Lemke, D. E.; Carl, A. M.; Johnson, R.; Smith, S. D.; Trede, K. H. 1997. Pinon pines and the route of Cabeza de Vaca. *Southwestern Historical Quarterly* 101:174-186
- Parker, W. B. 1854. Notes taken during the expedition commanded by Capt. R.B. Marcy, U.S.A., through unexplored Texas in the summer and fall of 1854. Texas State Historical Association, Austin. 242 p.
- Peacock, J. T.; McMillan, C. 1965. Ecotypic differentiation in *Prosopis* (mesquite). *Ecology* 46:35-51.
- Pike, A. 1832. Narrative of a journey in the prairie. In: J. E. Haley.
- Reeves, C. C., Jr. 1965. Pleistocene climate of the Llano Estacado. *J. Geol.* 73:181-189.
- Reeves, C. C., Jr. 1976. *Caliche: Origin, Classification, Morphology, and Uses*. Estacado Books, Lubbock, 233 p.
- Schmidly, D. J. 2002. *Texas Natural History, A Century of Change*. Texas Tech University Press, Lubbock, 534 p.
- Scifres, C. J.; Hahn, R. R. 1971. Response of honey mesquite seedlings to top removal. *J. Range Management* 24:396-398.
- Shantz, H. L.; Zon, R. 1924. *Atlas of the American Agriculture*. USDA, 29 p.
- Shantz, H. L. 1938. Plants as soil indicators, pp. 835-860. In: *Soils and Men, Yearbook of Agriculture, 1938*. USDA, 1232 p.
- Shelford, V. E. 1964. *The Ecology of North America*. Univ. of Illinois Press, Urbana, 610 p.
- Stahle, D. W.; Cook, E. R.; Cleaveland, M. K.; Therrell, M. D.; Meko, D. M.; Grissino-Mayer, H. D.; Watson, E.; Luckman, B. H. 2000. Tree-ring data document 16th century megadrought over North America. *EOS. Trans. Amer. Geophys. Union* 81:121, 125
- Stebbins, G. L. 1981. Coevolution of grasses and herbivores. *Ann. Missouri Bot. Gard.* 68:75-86.
- Taylor, A. J. 1997. Hispanic settlement of the Texas Panhandle-Plains, 1876-1884. *Panhandle-Plains Historical Review* LXX:36-58.
- Terrell, J. U. 1962. *Journey into Darkness*. Morrow, New York, 289 p.
- Thwaites, R. G. (ed.). 1966. From Part III of James's account of S. H. Long's Expedition, 1819-1820, in *Early Western Travels, 1748-1846*. Vol. XVI. A.M.S. Press, Inc., NY 291 p.
- Turner, R. M.; Webb, R. H.; Bowers, J. E.; Hastings, J. R. 2003. *The Changing Mile Revisited, An Ecological Study of Vegetation Change with Time in the Lower Mile of an Arid and Semiarid Region*. University of Arizona Press, Tucson. 334 p.
- Weaver, J. E.; Clements, F. E. 1938. *Plant Ecology*. McGraw-Hill Book Co., Inc. New York. 601 p.
- Weltzin, J.; Archer, S.; Heitschmidt, R. 1998. Defoliation and woody plant (*Prosopis glandulosa*) seedling establishment: potential vs. realized herbivory tolerance. *Plant Ecology* 187:127-135.
- Whipple, A. W. 1853. Reports of explorations and surveys to ascertain the most practicable and economical route for a railroad from the Mississippi river to the Pacific ocean. 33^d Congr., 2^d Session, Senate Ex. Doc. No. 78. 128 p.
- White, R. 1991. "It's your misfortune and none of my own": A new history of the American West. Univ. of Oklahoma Press, Norman.
- Winship, G. P. 1964. *The Coronado Expedition, 1540-1542*. The Rio Grande Press, Inc., Chicago, 403 p.
- Woodhouse, C. A.; Overpeck, J. T. 1998. 2000 years of drought variability in the central United States. *Bull. Amer. Meteorol. Soc.* 79:2693-2714.
- Wright, H. A.; Bailey, A. W. 1982. *Fire Ecology, United States and Southern Canada*. Wiley-Interscience, NY. 501 p.

The Author

¹Department of Range, Wildlife, and Fisheries Mgt., Texas Tech University, Lubbock, TX. david.wester@ttu.edu

Prescribed Fire to Restore Shrublands to Grasslands

Carlton M. Britton¹

David B. Wester¹

Brent J. Racher

Abstract: Prescribed burning to restore grasslands is more complicated than just setting a fire or, worse, letting a fire burn. We will examine how fire may be used to restore a more desirable landscape. First, any area that might be considered for prescribed fire should be thoroughly evaluated. Soils are paramount as they will indicate what we can expect from a given site. Then, we should study the plant community which originally existed on the site. Comparing the original plant community to the current plant community will help us construct a viable set of objectives. Second, we will determine how prescribed fire might be used in this restoration process. Should it be the first and only tool used or must it be preceded by some other tool, such as a mechanical or herbicidal treatment? Finally, we will consider a planning chart to organize the re-treatment scenario.

Introduction

Historically, periodic fire was the primary force in holding shrub populations at low densities on native grasslands west of the Mississippi River. Questions arise as to the timing and frequency of these fire events. Unfortunately, we will never know the exact nature of these events, as no recorders such as fire scarred trees are available to help us estimate what happened to grasslands in the past.

Frequency of fire occurrence in grasslands has usually been estimated in the range of once every 2 to 25 years. There is no normal or average fire return interval because the sequence of wet years and dry years impacts fuel loads and atmospheric condition conducive to fire spread. It would be a good guess to assume that widespread natural fires would dominate in dry years that followed one or more very wet year(s) (Wright and Bailey 1982). We believe that precipitation regimes and dry lightning storms produced the fire environments that shaped the western grasslands.

We would like to dispel the myth that summer fires are the most natural. If we take the human factor out of the equation, then the natural ignition source is lightning. Lightning can occur any month of the year throughout the western grasslands; thus, the condition of the fuel becomes paramount. Fuel moisture is the major predictor of when natural fires occurred. Except in drought years, this would narrow the most likely period from late winter to early spring just before green-up of grasses. Air temperature is the third most important factor in determining the natural fire period. During late winter and early spring, there are frequent warm days, and in summer, warm days are abundant. Lastly, humidity is a prominent factor. Relative humidity is commonly high in summer for most western grasslands. More importantly, absolute humidity is extremely high in summer compared to late winter and early spring. Absolute humidity is the factor that regulates dormant fine fuel moisture. In summary, we can say that a natural fire can occur in any month if the fine fuel is dry and lightning occurs.

Another myth that should be dispelled is that because summer fires were most common, they are the most natural and the most beneficial. We are aware of no data to support this myth in grasslands or shrublands. The opposite is supported by the literature (Wright and Bailey 1982). The more correct scenario would be to follow well-established rules of defoliation. After all, fire represents a severe defoliation with removal of herbaceous phytomass to near the soil surface. The accepted opinion is that in most western grasslands, herbaceous removal is least damaging in the winter dormant period and most damaging during the period of seed-set or mid summer (Holechek and others 2004). Sosebee and others (2004) emphasize this fact by stating "The most important deferment or rest period for grasses is post-reproduction to dormancy. For perennial, warm-season grasses in the southern Great Plains, this occurs from late summer to early autumn." This clearly illustrates that fire in this period would be damaging to the forage resource.

Using fire in plant communities that have not experienced their historic fire regime is equivalent to applying a natural tool to an unnatural situation. We have mismanaged our plant communities so that the fuel matrix has been radically changed. We currently operate on the two extremes. Either we have reduced the fuel to such an extent that a fire will not spread, or fuel has accumulated to such high loads that the resulting fire is catastrophic. By resource mismanagement we have eliminated any possibility of a natural fire. Thus, our object in fire management is to apply prescribed fire to meet well-thought-out objectives relating to healthy, balanced, and productive grassland communities. Restoring fire as an ecological force in native plant communities is a priority of all land managers. Determining how and when to burn to achieve the most natural effect requires planning based on sound ecological and historical evidence. Natural landscapes and their features—geologic, edaphic, and biotic—are the manifestations of factors that structure the world around us. An important corollary of this principle is that natural landscapes also are *indicators* of these factors, both historically

In: Sosebee, R.E.; Wester, D.B.; Britton, C.M.; McArthur, E.D.; Kitchen, S.G., comp. 2007. Proceedings: Shrubland dynamics—fire and water; 2004 August 10-12; Lubbock, TX. Proceedings RMRS-P-47. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 173 p.

and currently. For example, geological processes in the distant past produce the parent material from which soil is formed by edaphic processes. These processes form the abiotic arena in which biotic factors operate to assemble the communities characterizing every landscape.

This perspective provided the conceptual cornerstone of Frederick Clements' pioneering vision of the climax community: *the* climax community was considered to be *the* ultimate expression of *the* stable equilibrium between vegetation and its environment. Hans Jenny and Jack Major later formulated these ideas into "factors of soil development" and "factors of vegetation development," respectively, frameworks that have guided the thinking of several generations of ecologists.

With European settlement of the U.S., the pristine environment, supposedly the climax, was altered in far-reaching ways. It was only natural to view these changes as *reversible* consequences of disturbance. After nearly a century of land management experience, most observers are reconciled with the conclusion that many of these changes may not be reversible. This realization motivated the development of *multiple stable equilibria*, whose trajectories depend on the nature of the disturbance and the accidents of subsequent vegetational development.

Most interpretations of vegetation change have variously implicated land use changes (usually in the context of domestic herbivory), climate (both short-term weather fluctuations and long-term climatic trends), and fire history. Climate change is a *global* issue that may be beyond our control. Land use patterns are a *local* issue best decided in the private sector by responsible land owners. Fire history is a *regional* issue that lies within the domain of state and federal agencies charged with land management. In this paper, we focus on the importance of fire history in understanding today's landscapes.

Recreating fire history is difficult even with the best information. In the forest, decisions based on trees with cat-faced scars that document past fire are rife with errors. In grassland or pygmy forest, this task becomes virtually impossible. However, good descriptions of previous landscapes can be reasonably approximated with an understanding of the total resource complex.

Old photographs offer good approximations of previous landscapes. Numerous examples throughout the western U.S. have been published, and many more can be found in private collections through diligent searching. These photographs must be evaluated with care to understand the complete natural resource base. For example, figure 1 illustrates a view on the historic Three Block Ranch in south-central New Mexico. The top photograph was taken in 1905 from the western peak of the Twin Mountains looking west. Erwin Smith took this photograph with George Patullo in the foreground. The ridge in the background has a sparse stand of juniper with possibly a few small pinon trees. The bottom photograph shows the identical location as photographed in 1990. Vegetation on the ridge has changed dramatically with juniper density and size increasing over the interval between photographs. The question is which photograph illustrates the *appropriate* ecological state of this ridge? Contemporary wisdom will say the 1905



Figure 1. These photographs were taken from the same location looking westward from atop the Twin Mountains along the Cienega del Macho at the headquarters of the Three Block Ranch.

photograph. After all, this rangeland had been stocked with cattle for less than 25 years and, although altered, the period of time had been short enough that the negative impacts were not yet fully manifest. Fire was eliminated from this plant community, and thus, no pyric control on woody plants has operated for at least 85 years. This resulting landscape is not in balance with historic ecological forces that included recurrent fire. Our challenge is to restore these natural forces.

We suggest additional information be found to support the evidence seen in the photographs. The first and easiest place to seek excellent information is a soil survey. In this case, the Soil Survey of Lincoln County Area New Mexico. This ridge is mapped as a 14 Deama-Rock outcrop association, very steep (fig. 2).

The following description is provided:

This map unit is on hills and breaks. Slope is 15 to 50 percent. Areas are irregular in shape and are 1,000 to 5,000 acres in size. The native vegetation is mostly short and mid grasses. Elevation is 4,500 to 6,000 feet. The average annual precipitation is 12 to 16 inches, the average annual air temperature is 45 to 56 degrees F, and the average frost-free period is 150 to 190 days,

This unit is 60 percent Deama very cobbly loam, 15 to 50 percent slopes, and 20 percent Rock outcrop of

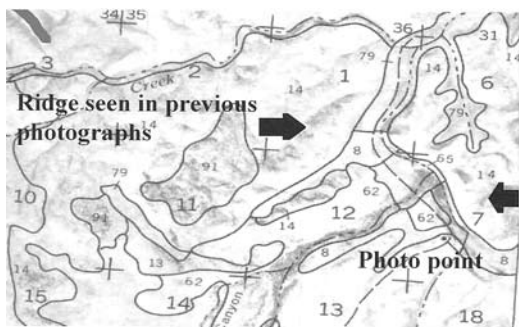


Figure 2. Section from Lincoln County Soil Survey showing the ridge illustrated in Figure 1 and the approximate location where the previous photographs were taken.

limestone. The Deama soil is on hills, and the Rock outcrop is on breaks.

Included in this unit are areas of other soils that may or may not be present in all mapped units. These areas are Harvey, Dixice, and Pena soils on hillsides and Pastura soils on summits. Included areas make up about 20 percent of the total acreage.

The Deama soil is very shallow to shallow and is well drained. It formed in material derived dominantly from limestone. Typically, the Deama soil is brown, very cobbly loam about 7 inches deep over limestone.

Permeability of the Deama soil is moderate. Effective rooting depth is 7 to 20 inches. Available water capacity is very low. Runoff is rapid, and the hazard of water erosion is high. The hazard of soil blowing is slight.

This unit is used for livestock grazing and wildlife habitat.

The potential plant community on this unit is mainly sideoats grama, New Mexico feathergrass, plains lovegrass, and little bluestem. This unit can support scattered oneseed juniper. As the plant community deteriorates, the desirable forage plants decrease and there is an increase in threeawn, curlyleaf muhly, and catclaw acacia, which normally occur in small amounts in the potential plant community. Grazing management should be designed to increase the productivity and reproduction of plains lovegrass, sideoats grama, and little bluestem. This unit is poorly suited to rangeland improvement practices such as fences, pipelines for providing stock water, water impoundments facilities, and mechanical brush management because of the shallow and very shallow depth to bedrock and steepness of slope.

The average annual production of air-dry vegetation on this unit ranges from 1,100 pounds per acre in favorable years to 300 pounds in unfavorable years.

This range site description provides abundant information. First, it describes the soils on the range site and several important characteristics of the soils. If we do not understand soils, we do not understand the very basic unit of ecological planning. Second, it gives us a brief description of the common vegetation we should expect on the site and the most common increasers that occur as the plant community moves away from the climax. Vegetation description is the second basic unit of ecological planning. The herbaceous production also gives us a good indication of potential yield for this range site. This information clearly agrees with what we see in the 1905 photograph as it describes the site with “scattered oneseed juniper,” not the dense juniper stand shown in the 1990 photograph.

Now that we have an initial impression of what this site should look like, we can expand and refine our view. Many sources of additional information are easily available. Surveyors’ notes can be especially useful. Diaries of early explorers and settlers may yield helpful information. Descriptive ecological research also can be valuable if one is careful to read and understand the sampling methodologies. Many times, the methodologies are not suitable to yield data that are useful. Old aerial photographs are especially useful as they illustrate changes in tree and shrub densities over time. Vast amounts of information are available to reconstruct our vision of past rangeland plant communities.

Reconstruction of past communities from historical sources (for example, old photos) and an understanding of current potential (for example, from soil survey descriptions) involve a number of interpretational issues that must be considered. For example, *suppose* that in the earlier photograph in figure 1, there was evidence of human habitation (an old ranch house, mining structure, or church). In this case, the absence of woody vegetation might then be only *apparent* if, in fact, woody vegetation was an important, harvested source of fuel. In this case, the presence of woody vegetation in the latter photograph in figure 1 might then be attributed to re-growth of woody plants that were, in fact, part of the historical community recorded in the earlier photograph and not woody plant invasion into a historical grassland because of the absence of fire.

Assuming that the *apparent* absence of woody vegetation in the earlier photograph in figure 1 is also a *real* absence, some investigators have attributed increases in woody shrubs throughout the Southwest to changes in climate. This interpretation may have merit, but it also is controversial, and resolution awaits additional research.

Once we understand the soils, plants, and ecology of an area, it is time to organize the planning chart for our fire treatment scenario. Our main objective is to ensure we have enough fine fuel (grass and forbs) to carry the fire and also accomplish our management goals. Redberry juniper at canopy covers of even less than 10 percent can greatly decrease fine fuel levels (Racher 2000). When juniper canopy cover reaches 30 percent, fine fuel is not continuous and a broadcast burn becomes extremely difficult and fire is not the first treatment. Therefore, we must resort to some

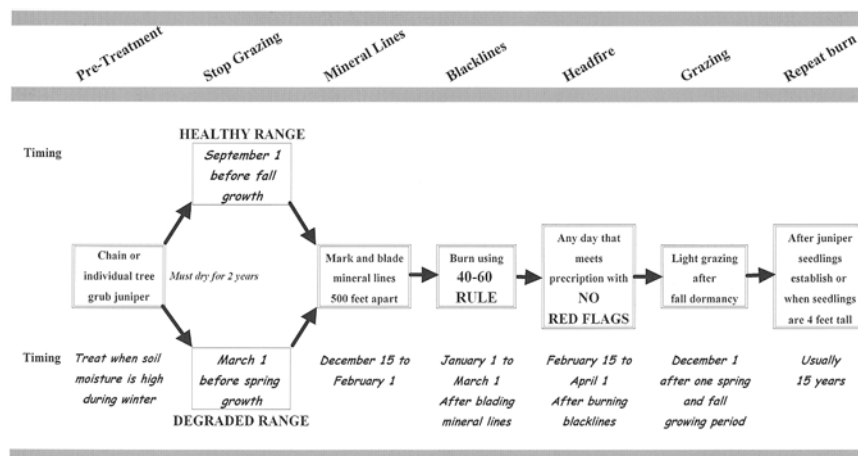


Figure 3. Planning Chart for a prescribed burn on lightly infested juniper rangeland in the Rolling Plains of Texas. Complex burn implies a volatile fuel involved in the fuel matrix.

mechanical treatment to reduce juniper canopy cover and increase fine fuel. On other rangeland communities herbicides may be effective in increasing fine fuel so fire can be returned to its natural role. The planning chart illustrated in figure 3 shows an initial mechanical treatment step. Next, we would have to allow the pasture to rest until sufficient herbaceous growth occurs to accumulate fine fuel. All these items must be flexible, as precipitation will exert a continuous and changing influence.

Weather conditions prior to the burn are very important. Excessive rainfall in the weeks before a prescribed burn can be either beneficial or disastrous. On the beneficial side, it is always desirable to have good soil moisture available so desirable plants can have an uninterrupted growth period after the fire. On the negative side, prolonged high moisture conditions will result in high juniper leaf moisture contents (Mitchell and Britton 1998). Leaf moisture concentrations above 70 percent reduce the ignition potential for the juniper canopy, and when the moisture concentration reaches 80 percent, canopy torching is nearly eliminated. Also, on clayey soils, precipitation can cause long intervals when road and firelines are impassible.

The reburn phase of the planning chart would also need to be flexible. If several above average precipitation years followed the burn, large numbers of juniper seed may germinate and establish. Fire should be applied sooner before either a high density of small plants reduces fine fuel load or the sprouting collar of redberry is buried and the plant becomes resistant to fire induced mortality.

Detailed planning and constructing a meaningful planning chart will help eliminate the wide variety of oversights that cause failure in prescribed burning. Attention to the interactions between environmental and plant responses will help increase the benefits of the prescribed burn.

The absence of fire in ecosystems that have historically burned must be an integral component in our understanding changes in plant communities. Considerable research has

yielded a thorough understanding of fire's role in natural plant communities (FEIS 2005). With our understanding of how we might reintroduce fire into natural plant community dynamics, we can begin proactive management to achieve desirable goals. Since fire has been absent from our rangeland plant communities for a great number of years, it may not magically take us to the point we envision. It is reasonable to believe that fire will take us closer to our vision, but it is contrary to ecological principles for it to immediately return us to the original condition. Patience must be the guiding factor in our quest to pursue more natural plant communities through the process of goals, objectives, and strategies.

Literature Cited

- FEIS. 2005. Fire effects information system. (Online) U.S.D.A., F.S., Mitchell, R. B.; Britton, C. M. 1998. Redberry juniper foliage moisture dynamics in the Texas Rolling Plains. Texas J. Agric. and Nat. Resc. 11:23-30
- Racher, B. J. 1998. Herbaceous production as influenced by juniper canopy cover in west Texas. M.S. Thesis. Texas Tech University. 190 p.
- Sprinkle, D. G. 1983. Soil Survey of Lincoln County Area, New Mexico. USDA Soil Conservation Service. 217 p.
- Sosebee, R. E.; Wester, D. B.; Villalobos, J. C.; Britton, C. M.; Wan, C.; Nofal, H. 2004. How grasses grow—How plant growth relates to grazing management. Second National Conf. Grazing Lands. GLCI. Dec. 2003. Nashville, TN.
- Wright, H. A.; Bailey, A. W. 1982. Fire ecology: United States and Southern Canada. John Wiley and Son, Wiley Interscience. 501 p.

The Authors

¹Professors, Department of Range, Wildlife and Fisheries Management, Texas Tech University, Lubbock, TX. carlton.britton@ttu.edu

Role of Summer Prescribed Fire to Manage Shrub-invaded Grasslands

Charles A. Taylor¹

Abstract: Prior to development of the livestock industry, both anthropogenic and natural disturbances (such as prescribed and wild fire) played key roles in shaping the different plant communities across Texas. Historically, fires occurred during all seasons of the year, but summer fires were probably more frequent due to dry conditions combined with increased lightning frequency during the summer. When fire was frequent, the upland or western divide region of the Edwards Plateau was typical of a savanna ecosystem. The purpose of this study was to determine the effects of summer and winter burning and no burning (controls) on vegetation. Woody and succulent vegetation species were highly vulnerable to both summer and winter fire. Herbaceous response was species dependent; however, overall grass production was greater under a summer burning regime compared to control and winter burn treatments. Summer burning is recognized and recommended for reclamation of rangeland vegetation under appropriate conditions and levels of supervision, experience, and training. Once reclaimed with one or two summer fires, management can shift to lower risk, cool-season burns for maintenance.

Introduction

When European explorers and settlers first came to the Edwards Plateau, they found a different landscape than what is present today—especially for the uplands and “divide” regions of the Edwards Plateau (Cory 1948; Smeins and others 1997). The landscape appeared open with stubby thickets of liveoak (*Quercus virginiana* Mill.) and shinoak (*Quercus* spp.) and an occasional larger liveoak. On the valleys, slopes, and shallow soils, the dominant grasses were little bluestem (*Schizachyrium scoparium* (Michx.) Nash), sideoats grama (*Bouteloua curtipendula* [Michx.] Torr.), Indian grass (*Sorghastrum nutans* L. Nash), cane bluestem (*Bothriochloa barbinodis* var. *barbinodis* Lag. Herter), Texas cupgrass (*Eriochloa sericea* [Scheele] Munro), common curlymesquite (*Hilaria belangeri* [Steud.] Nash), Texas wintergrass (*Stipa leucotricha* Trin. & Rupr.), and others. Warm season perennial forbs were also abundant with a diverse mixture of desirable woody shrubs. Kidneywood (*Eysenhardtia texana* Scheele), littleleaf leadtree (*Leucaena retusa* Benth. in Gray), Carolina buckthorn (*Phamus Caroliniana* Walt.), Texas mulberry (*Morus microphylla* Buchl.), white honeysuckle (*Lonicerna albiflora* T.&G.), Plum (*Prunus* spp.), bumelia (*Bumelia lanuginosa* [Michx.] Pers.), sumacs (*Rhus* spp.), etc., are just a few of the more desirable woody shrubs that were abundant.

With the development of the livestock industry, Edwards Plateau rangelands were fire-proofed due to excessive numbers of livestock and yearlong grazing that grazed out the tall and mid grasses. The more productive grasses were replaced with short grasses, which were more resistant to grazing and provided much less fuel for fires. Reduced fuel loads were also followed by fire suppression activities by early settlers. For example, in 1848, a state law was passed in Texas that made

it illegal to fire the prairies between July 1 and February 15. In 1884, another Texas law was passed that made setting fire to grass a felony. It was not until 1999 that a law was passed in Texas that unambiguously stated that a landowner had the right to conduct a prescribed burn on his or her own property.

The natural and man-made fires kept woody plants in check and allowed the higher successional grasses to dominate the landscape. It is well documented that prior to European settlement, both prescribed and wild fires were disturbances that played key roles in shaping the different plant communities across the United States (Baker 1992; Foster 1917). Historically, fires occurred during all months of the year (Higgins 1986; Komarek 1968), but summer fires were probably more frequent due to dry conditions combined with increased lightning frequency during the summer (Komarek 1968; Taylor 2001). With the reduced fire frequency, redberry juniper (*Juniper pinchotii*), Ashe juniper (*J. Ashei*), and prickly pear (*Opuntia* spp.) began to increase across the landscape.

The Insidious Invasion of Juniper

A common principle in vegetative ecology is given a certain set of circumstances (such as weather, soil, herbivory, fire, etc.), some plant species will be more competitive and dominate the landscape at the expense of other species. Natural competition is the concept that individuals of a species, which survive and reproduce better than other species, will have their genes proportionally represented in future populations to a greater extent because they leave more offspring. Nowhere can this be better demonstrated than with the increase of juniper species across the “divide” region of the Edwards Plateau.

At the time of European settlement, juniper species were not perceived as a problem and for various reasons. Firewood

In: Sosebee, R.E.; Wester, D.B.; Britton, C.M.; McArthur, E.D.; Kitchen, S.G., comp. 2007. Proceedings: Shrubland dynamics—fire and water; 2004 August 10-12; Lubbock, TX. Proceedings RMRS-P-47. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 173 p.

and building materials were important commodities to early settlers. For example, Ashe juniper was an important source of lumber for construction of houses, railroad ties, fences, pens, etc. for the early settlers (Smeins and others 1997). It still has commercial and ecological value today (Garriga and others 1997; Rollins and Armstrong 1997).

The increase in juniper density is slow at first and can go unnoticed for many years until it becomes a serious problem. In the early 1900s, juniper represented a small part of the plant composition on many areas of the Edwards Plateau. With the reduction in fire frequency and intensity, the process of juniper encroachment was initiated on many areas that had previously been grasslands. However, some areas, especially on the southeastern Edwards Plateau, are not as conducive to repeated fires because of the highly variable topography and fine fuel discontinuity (Smeins and others 1997). Therefore, it is probable that juniper was present in some local areas and occurred in association with rocky outcrops, canyon-lands, or along streams and rivers where fire frequency was low. A thorough review of the history of juniper in the Edwards Plateau is presented by Smeins and others (1997) and Ueckert (1997).

My concern is the encroachment of juniper on areas in the Edwards Plateau that were historically grasslands or savannas. Also, it is not the author's intent to suggest that all areas of juniper be removed from the Edwards Plateau. In fact, some juniper, even some deliberately located dense stands, may be desirable. However, for the sake of biodiversity, wildlife habitat, domestic livestock production, water availability, and management of volatile fuels, juniper has to be managed and fire should be a major part of an active integrated juniper management program.

Methods

Study Site

The data presented herein were collected from a replicated study from the Texas Agricultural Experiment Station located 45 km south of Sonora, Texas (31°N; 100°W). The landscape of the Sonora Station is rolling stony hill topography typical of the Edwards Plateau. Soils on the site are Tarrant stony clays and Tarrant silty clays of the Lithic Haplustolls family. The growing season associated with the Sonora Station is 240 days. Most of the precipitation results from intense, convective storms of short duration. The average precipitation (1919 to 2003) recorded at the station is 57.4 cm per year.

In 1993, six study sites of approximately 2.5 ha each were established from two adjacent pastures to measure the effects of seasonal fire on native perennial vegetation. Summer and winter burning treatments were established along with an unburned control with two replications per treatment. Each treatment was blocked within each of the two pastures. Sites were selected to represent similar woody plant cover and herbaceous composition. Dominant herbaceous plants included common curlymesquite, threeawn, sideoats grama, and Texas wintergrass. Dominant woody plants were live oak, ashe juniper, and redberry juniper.

Vegetation in all six sites was sampled for species composition and woody canopy cover in July, 1994. Data were collected from transect lines that are permanently marked. Various vegetation measurements were sampled that included percent composition based on frequency and line intercept. Standing crop of grasses was measured by hand clipping vegetation from 50 quadrats per replicate. Analysis of variance was conducted on standing crop data with the general linear model univariate analysis option of SPSS (SPSS 2001). Significance levels for the tests were set at $\alpha = 0.05$.

Two replicates were burned in August, 1994 (growing season treatment), two burned in February, 1995 (dormant season treatment) and two were left as unburned controls. The winter burn treatments were burned for a second time in February, 2000, and summer burned treatments in August, 2000. The emphasis of this study is to measure the long-term effects of repeated seasonal fire on the perennial vegetation community. These sites will continue to be periodically burned for at least 20 years or longer. Only the major species are discussed in this report. Livestock have not grazed these pastures since 1993, but white-tailed deer have access to the treatments.

Results and Discussion

In 1994, prior to implementation of the burn treatments, standing crop of grass was measured on all six treatment sites. Standing crop was not different among treatments and averaged 42 g/m² per treatment (fig. 1). The first burn had little impact among burn and control treatments. It was not until after the second burn that treatment differences were first measured. The reason for the increased grass production after two summer burns is due to the reduced liveoak canopy cover, and elimination of juniper growing under the oak canopies, and reduction in prickly pear (*Opuntia* sp.).

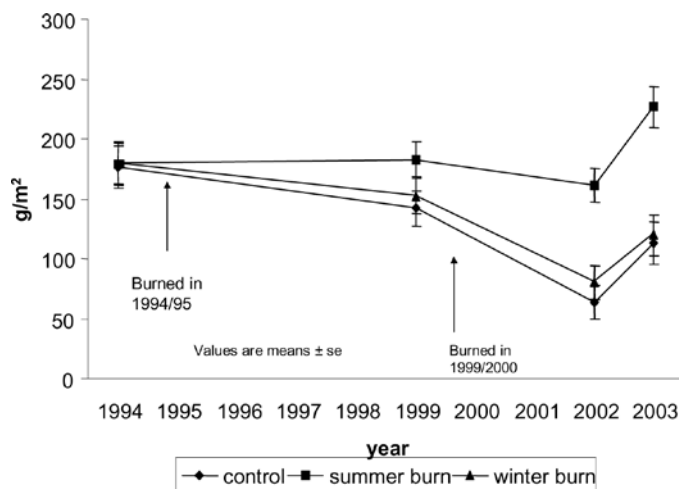


Figure 1. Standing crop of grass (g/m²) from control, winter, and summer burned pastures. Winter burned replicates were burned in February of 1995 and 2000 and the summer burned replicates were burned in August of 1994 and 2000.

Liveoak is an evergreen that is usually classified as moderately preferred by livestock and wildlife. Liveoak increases in the absence of fire and low browsing pressure, but does not generally have the potential to dominate a landscape like juniper. Liveoak tends to cluster in mottes on soils derived from Buda limestone, which is typical for pastures in the current research project.

Liveoak trees make good perch sites for robins (*Turdus migratorius*) and cedar wax wings (*Bombycilla cedrorum*). These two bird species, along with other animals that consume juniper berries, disperse the seeds over large areas, especially under the canopy of liveoak trees.

For example, after two burns, 100 percent of the oak mottes in the unburned control pastures had juniper compared to 67 and 8 percent for the winter and summer burned treatments, respectively. Juniper density was similar for all treatments prior to the implementation of the burning treatments (approximately 74 plants per ha in 1993). After two prescribed burns, average number of juniper plants per motte was larger for the control pastures compared to the summer and winter burn pastures—46, 4, and .1 plants, respectively.

Summer fire was more effective than winter fire at managing juniper in liveoak mottes and was also more damaging to the liveoak. Liveoak canopies were reduced 60 percent in the summer burned treatments and 20 percent in the winter burns treatment.

Juniper density was measured in June, 2001, and averaged 1,013, 100, and 25 plants per ha for the control, winter burned, and summer burned treatments, respectively. Recall, that both burn treatments had received two prescribed fires prior to the 2001 sampling period. Although juniper density was light at the beginning of the study, the trees were large and had the potential to produce large seed crops. Also, no livestock grazing/browsing has occurred since 1993. The rapid recruitment of juniper in the control treatments is a good example how quickly juniper density can increase in an area without any type of management (such as fire and/or use of goats).

Most ranchers in the Edwards Plateau attempt to manage prickly pear because of its competitive nature with herbaceous forages (Mayeux and Johnson 1989; Ueckert and others 1988). Prescribed burns conducted in the winter period reduced prickly pear density to about half of the control treatments (642 and 370 plants/ha, respectively), whereas summer fire reduced prickly pear to less than 4 percent of the controls (25 plants/ha).

Grass response

Common curly mesquite grass is an abundant warm-season perennial grass that has increased with the advent of excessive livestock grazing in the Edwards Plateau (Merrill and Young 1959). Under better management, or complete rest from grazing, common curly mesquite is replaced by higher successional grasses (Smeins and Merrill 1988).

In this study, frequency of common curly mesquite decreased from 60 percent in 1994 to 32 percent in 2003. Because the response of common curly mesquite was similar across all treatments, including the non-burned control

treatments, it appears that fire had little influence and indicates that this grass may be neutral to fire.

Sideoats grama, a climax warm season perennial grass, has two different growth forms for this region (rhizomatous type and bunch type). The rhizomatous type (underground stems) dominates the pastures in this study. These underground rhizomes are a major source of new tillers for the plants and would appear to be resistant to fire.

Averaged across all treatments, frequency of sideoats grama was the same in 2003 as in 1994 (19 vs. 20 percent, respectively). Frequency of sideoats grama was not affected by the fire effect ($P = 0.717$).

Texas wintergrass, a desirable cool season grass, responded differently than sideoats grama. Averaged across all treatments, frequency of Texas wintergrass increased from 1994 to 2003 (36 and 44 percent, respectively). Frequency of Texas wintergrass increased for all treatments over the course of the study and was not affected by either summer or winter fire.

Threeawn species (*Aristida* spp.) include both annual and perennial threeawns. Most threeawns are not considered as good forage, although Wright's threeawn provides early grazing prior to the green-up of the more productive grasses. Averaged across all treatments, threeawn frequency decreased from 1994 to 2003 (33 and 10 percent, respectively). For the summer burning treatments, threeawn frequency decreased from 30 to .3 percent ($P = 0.064$) from 1994 to 2003, respectively. Threeawn tends to accumulate dead leaves and stems, which may play a part in its response to hot fire.

Management Implications

These data illustrate the importance of a long-term, sustainable management program for juniper. Without fires, or when their severity is reduced because of low fuel, juniper can quickly invade and start to dominate a range site in a few years. Warm-season fires are more effective in killing juniper than cool-season fires. After two prescribed burns, it is the author's opinion that the summer burn treatments in this study would not have to be burned again for up to 30 years, possibly longer, to maintain their grassland dominance. The winter burn treatments, given their current juniper status, would need to be burned within 15 years to maintain their grassland dominance. Recruitment of new seedlings is occurring at an accelerated rate in the control treatments. Within a few years, juniper will start to dominate the control areas and significantly reduce the carrying capacity for both livestock and wildlife.

Because of this, landowners are facing a dilemma with predictable consequences. One option, to do nothing, has major negative ecological consequences. Without intervention with proper management, the ecological system is locked indefinitely into an unnatural juniper dominated woodland.

Literature Cited

Baker, W. L. 1992. Effects of settlement and fire suppression on landscape structure. *Ecology* 73:1879-1887.

- Cory, V. L. 1949. On some grasses, chiefly of the Edwards Plateau of Texas. *Field & Laboratory* 17:41-52.
- Foster, J. H. 1917. The spread of timbered areas in central Texas. *Journal of Forestry* 15:442-445.
- Garriga, M.; Thurow, A. P.; Thurow, T.; Conner, R.; Brandenberger, D. 1997. Commercial value of juniper on the Edwards Plateau, Texas. pp. 8.3-8.12. in C. A. Taylor, Jr., ed. *Proceedings, 1997 Juniper Symposium*. Texas A&M University Research & Extension Center Technical Report. 97-1. San Angelo, Texas.
- Higgins, K. F. 1986. Interpretation and compendium of historical fire accounts in the Northern Great Plains. U.S. Department of the Interior. Resource Publ. 161. USDI, Washington, DC.
- Komarek, E. V. 1968. Lightning and lightning fire as ecological forces. *Proc. Tall Timbers Fire Ecology Conference* 7:169-197.
- Mayeux, H. S., Jr.; Johnson, H. B. 1989. Absorption and translocation of picloram by Lindheimer pricklypear (*Opuntia lindheimeri*). *Weed Sci.* 37:161-166.
- Merrill, L. B.; Young, V. A. 1959. Response of curly mesquite to height and frequency of clipping. *Texas Agric. Exp. Sta. MP-33*.
- Rollins, D.; Armstrong, B. 1997. Cedar through the eyes of wildlife, pp. 4.23-4.31. in C. A. Taylor, Jr., ed. *Proceedings, 1997 Juniper Symposium*. Texas A&M University Research and Extension Center Tech Report 97-1. San Angelo, Texas.
- Smeins, F. E.; Merrill, L. B. 1988. Long-term change in a semiarid grassland, p. 101-114. In: B. Amos; Gehlbach, F. (eds). *Edwards Plateau vegetation: plant ecological studies in central Texas*. Baylor Univ., Press, Waco. 145 p.
- Smeins, F.; Fuhlendorf, S. Taylor, Jr, C. A. 1997. Environmental and land use changes: a long-term perspective. pp. 1.3-1.21, in C. A. Taylor, Jr., ed. *Proceedings, 1997 Juniper Symposium*. Texas A&M University Research and Extension Center Technical Report. 97-1. San Angelo, Texas.
- Taylor, C. A., Jr. 2001. Summer fire for the Western Region of the Edwards Plateau: A case study. *Texas Agricultural Experiment Station Technical Report* 01-2. Sonora, Texas.
- Ueckert, D. N.; Peterson, J. L.; Potter, R. L. ; Whipple, J. D.; Wagner, M. W. 1988. Managing pricklypear with herbicides and fire. *Texas Agric. Exp. Sta. Prog. Rep.* Pr-4570.
- Ueckert, D. N. 1997. Juniper control and management. pp. 5.23-5.34, in C.A. Taylor, Jr., ed. *Proceedings, 1997 Juniper Symposium*. Texas A&M University Research and Extension Center Technical Report. 97-1. San Angelo, Texas.

The Author

¹Professor and Research Station Superintendent, Texas Agricultural Experiment Station—Sonora, Sonora, TX. angora@sonoratx.net

Fire Session

Management of South Texas Shrublands with Prescribed Fire

C. Wayne Hanselka¹

D. Lynn Drawe²

D.C. Ruthven, III³

Introduction

The Rio Grande Plains (RGP) and Coastal Prairie (CP) of South Texas is the southernmost extension of the Great Plains Grasslands. Fire, along with other climatic variables, such as drought, presumably maintained mesquite (*Prosopis glandulosa* Torr.) savannas and interspersed grasslands of pre-European settlement South Texas. Frequency of fire appeared to be highly variable and ranged from 5 to 30 years (Wright and Bailey 1982). Following European settlement, the change from grassland to woodlands/shrublands was accelerated by introduction of livestock and fencing. Domestic animals served as ideal agents of seed dispersal for some species, notably mesquite. Removal of biomass by grazing also removed the fine fuel necessary to generate the intense, hot fires required to kill young woody plants. Where fuel was available to carry the fires, people worked to suppress them. Through time, woody plants gained a decided competitive edge over the grasses and forbs that had characterized the original grasslands, and the “brush country” was formed (Scifres and Hamilton 1993). Thus, suppression of fire, combined with heavy livestock grazing, led to the current thorn woodlands common throughout South Texas (Archer et al. 1988; Archer 1994).

Beginning in the mid-twentieth century, South Texas landowners began to convert thorn woodlands back to grasslands to enhance rangelands for livestock production. Treatments, such as root plowing and herbicides, were commonly used to achieve this goal. In recent years the size of individual landholdings has decreased and revenue from wildlife has

increased (Wilkins and others 2000). Brush management to enhance habitat has evolved into “brush sculpting” where brush is manipulated to increase edge, juxtaposition, and biodiversity. Mechanical, chemical, and prescribed fire treatments are used in this effort.

Fire provides an economical means of controlling woody species and maintaining the life of mechanical and chemical brush management treatments. Burning during late winter and early spring has been recommended for achieving many goals on South Texas rangelands (Scifres and Hamilton 1993), however, information on summer burning has been collected (Drawe and Kattner 1978; Ruthven and Synatzske 2003) and summer burning is now somewhat more acceptable.

Although fire has been used as a management tool for over a hundred years, the effects of fire on South Texas rangeland have not been studied until relatively recent times. In a thorough review of the literature, the earliest study mentioned by Vogl (1974) was that of Box and others (1967). However, since 1967, much work has since been conducted in the region. Certainly, a landmark publication that documents the state of the art of the use of prescribed fire in the region is Scifres and Hamilton’s (1993) book titled “Prescribed Burning for Brushland Management: The South Texas Example”.

Methods and Materials

Information in this paper was collected mainly from three South Texas locations (fig. 1). The Chaparral Wildlife Management Area, in the western RGP, is characterized by

In: Sosebee, R.E.; Wester, D.B.; Britton, C.M.; McArthur, E.D.; Kitchen, S.G., comp. 2007. Proceedings: Shrubland dynamics—fire and water; 2004 August 10-12; Lubbock, TX. Proceedings RMRS-P-47. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 173 p.

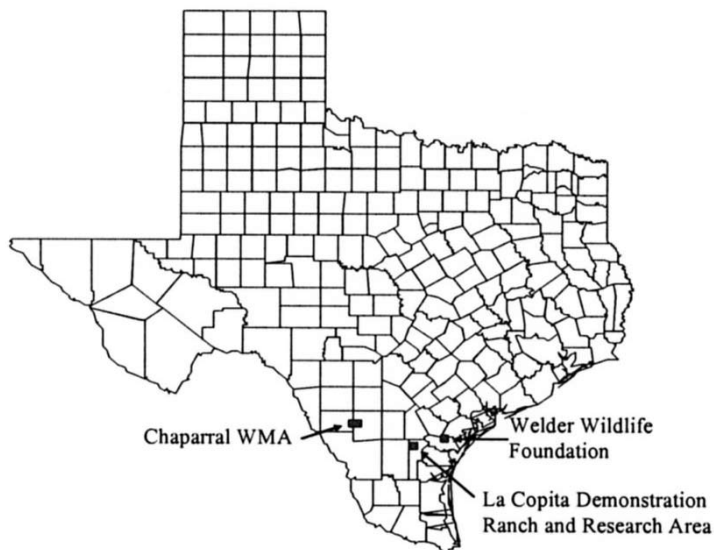


Figure 1. Location of study sites on the Rio Grande Plain and Coastal Prairie.

hot summers and mild winters. The growing season is 249 to 365 days, and precipitation patterns is bimodal with peaks occurring in late spring (May-June) and early fall (September-October). The 11-year (1989-2000) average precipitation amount is 54 cm. The second study area was on La Copita Demonstration Ranch and Research Area in the eastern RGP. Climate is subtropical with mild winters and hot summers. Mean annual temperature is 22.4 °C and the growing season is 289 days. Average annual rainfall is 68 cm, with maxima in May and September. The third area was the Rob and Bessie Welder Wildlife Foundation Refuge, located on the transitional zone between the CP and RGP. Average annual precipitation (1956-1985) is 906 mm.

Although generally considered historic grassland, South Texas today is a brush-grass complex; a grassland with brush of various densities covering almost all sites except the deep sands of the Nueces soils. Vegetation at all three locations is dominated by honey mesquite with various mixtures of broad-leaved evergreen and deciduous shrubs in its understory. Herbaceous vegetation between shrub clusters was composed of C4 grasses such as thin paspalum (*Paspalum setaceum*), knotroot bristlegrass (*Setaria geniculata*), Texas grama (*Bouteloua rigidisetia*), and hooded windmill grass (*Chloris cucullata*), which give way to grasses such as three-awns (*Aristida spp*), red grama (*Bouteloua trifida*), grassburs (*Cenchrus incertus*), and windmillgrass (*Chloris verticillata*) under prolonged, heavy grazing by cattle.

The major woody species in mixed brush communities are honey mesquite, black brush (*Acacia rigidula*), agarito (*Berberis trifoliolata*), brasil (*Condalia obovata*), Mexican persimmon (*Diospyros texana*) lime pricklyash (*Zanthoxylum fagara*), spiny hackberry (*Celtis pallida*), pricklypear (*Opuntia engelmannii*), and lotebrush (*Ziziphus obtusifolia*), among others. Huisache is also a component of these communities.

Management Implications

Historically, fires burned in the summer and early winter in the RGP and CP, and, currently, summer fires are more effective in suppressing woody plant growth than are cool season burns. Prescribed fire has been used successfully to suppress woody plants in the eastern RGP and CP, however, fire does not kill brush. Research indicates that fire does reduce brush cover (Box and others 1967; Dodd and Holtz 1972), and two or more burns are more effective in reducing brush than a single fire (Box and White 1969). Gordon and Scifres (1977) found that prescribed burning, particularly when combined with chemical or mechanical methods, was effective in restoring rangeland heavily infested with Macartney rose (*Rosa bracteata*). Rasmussen and others (1983) found that in a fire regime the cool season Texas wintergrass (*Stipa leucotricha*) increased with increasing huisache (*Acacia smallii*) canopy up to approximately 40 percent canopy coverage of the woody invader, but that total herbage production declined beyond 40 percent canopy. Therefore, to promote cool season plants, a certain amount of properly spaced woody cover maintained by prescribed fire may be desirable for both cattle and wildlife.

To suppress brush, the most effective burns are those used in combination with chemical or mechanical treatments. For example, huisache can be removed with chemical or mechanical means, but is only temporarily reduced solely by fire. So, fires reduce canopy cover and productivity of woody plants and enhance herbaceous growth. It can be used to increase the wildlife value of the habitat by causing resprouting of woody plants and by increasing forb growth. Fire also increases both chemical and mechanical defense mechanisms in certain woody species.

Since fire suppresses but does not kill most species of resprouting brush, this can be used to great benefit in wildlife habitat management. Top growth removal of brush by fire stimulates succulent regrowth for consumption by browsing wildlife, and it can create habitat diversity. Hot fires may be used in a patchwork design, alternated within burned areas. Cool fires, burned over a whole range interspersed with brush mottes, will burn around mottes and will leave portions of the range unburned thus creating greater diversity.

Timing of burning has a strong influence on the composition of the plant community following the fire and has profound effects on animal communities through effects on habitat. Plant species composition can be altered by timing of burning, thus the manager can create a plant community desirable for wildlife (Hansmire and others 1988). Late winter burning reduces forb populations and benefits grasses; whereas, early winter burning is followed by normal forb populations. In addition to reducing forbs, late winter burns may reduce the amount of other cool season plants, particularly Texas wintergrass.

Several studies have concentrated on the influence of repeated fires on both woody and herbaceous vegetation. More recently, summer prescribed fire has been implemented in an

attempt to suppress woody plant encroachment. An area was established on the Welder Wildlife Refuge in 1975 to assess the effects of repeated cool season fires on CP vegetation. A non-burned control was located adjacent to the burned block. The area was initially burned in the winter of 1974 and then was subsequently reburned in 1977 and 1980.

Repeated burning effectively suppressed woody vegetation. After the 1974 fire there was almost total top removal of woody species. The 1977 fire, which was extremely hot, burned through most of the smaller chaparral mottes. On the windward side of a motte the 1977 fire removed 100% of the cover. On the leeward side of a motte, depending upon wind speed during the fire, there were protected areas where some woody plants avoided topkill. In the larger mottes, i.e., those greater than 20 feet in diameter, woody plants survived in the center and on the leeward side of the motte. Fine fuel was essentially nonexistent within mottes. Only crown fires burned completely across a large motte. Whole mottes survived in the cooler 1980 burn, even some of the smaller mottes less than 20 feet in diameter. Individual woody plants between mottes were top-killed. Following the third burn, canopy cover was reduced from the original 40% to less than 2%. By the summer following the third burn, there appeared to be a reduction in the amount of cover of all woody species. However, one year after the burn, all species were growing vigorously. Weedy herbaceous vegetation was abundant in the mottes totally top killed by the fire.

Long periods between burns allow brush to regrow to its former height and density and possibly increase in density. A prescribed fire program to suppress brush in South Texas should be designed to be burned every 3 to 4 years. Otherwise, brush regrowth is so rapid that any greater time sequence between burns will allow the brush to grow to the point that fire can no longer be used as an effective tool for suppressing regrowth.

Fire is also an effective tool in removing excess mulch accumulations that occur during wet cycles under conservative grazing. On the Welder Refuge, fine fuel loads from 4,500 pounds per acre to 16,000 pounds per acre were burned (average 5,500 pounds per acre). Large amounts of fine fuel form a mat that may not be penetrated by light and actually acts to suppress plant growth. There is an increase in herbaceous production in the year following the initial burn, because more light penetrates to the soil surface and nutrients are released to the soil from decadent plants.

On the Chaparral Wildlife Management Area, rangeland was subjected to two winter prescribed burns and a winter burn followed by a summer fire. Prescribed burning can manage woody vegetation without dramatic reduction in woody plant diversity, which is common with many traditional mechanical treatments. However, percent woody plant cover was reduced by 50 percent and 41 percent on winter and winter-summer combination burned sites, respectively. Woody plant density declined by 29 percent and 23 percent on winter and winter-summer combination burned sites, respectively (Ruthven and others 2003). Density of guayacan (*Guajacum angustifolium*), wolfberry (*Lycium berlandieri*), and tasajillo (*Opuntia*

leptocaulis) was less on all burning treatments. Percent cover of spiny hackberry and density of pricklypear declined on winter burned sites. Inclusion of summer fire into the burning regime did not increase the decline in woody plants. Fire does create a post-fire environment, which results in the decline of many woody plant species. It is unclear to what degree other environmental factors, such as herbivory and competition between woody plants and among woody and herbaceous vegetation, may have interacted with fire to produce woody plant declines.

Combinations of winter and summer burns can effectively reduce the cover of honey mesquite, twisted acacia, Texas persimmon, lotebush, wolfberry, and tasajillo. Canopy cover of spiny hackberry and density of pricklypear decline following multiple winter burns. Soil moisture at the time of fire application may have a greater impact on woody vegetation response than season of burn.

Both summer and winter burning are effective at reducing honey mesquite cover, which may promote increases in herbaceous vegetation following fire. Summer burning following significant rainfall is effective in managing honey mesquite, while maintaining desirable woody species such as spiny hackberry. If reducing total woody plant cover is a management goal, burning during winter following periods of little or no rainfall is recommended.

Summer and winter prescribed fire produce similar responses from herbaceous vegetation (Ruthven and Synatzke 2002). Warm season annuals, such as croton (*Croton* spp.), were more prevalent on burned sites. However, increases in annuals did not persist into the second growing season following burning. Cool season annuals demonstrated little response to summer or winter burns. Perennials such as erect dayflower (*Commelina erecta*) and beach groundcherry (*Physalis cinerascens*) increase following summer and winter burns, whereas silky evolvulus (*Evolvulus alsinoides*) and hoary blackfoot (*Melampodium cinereum*) decrease following summer fires. Grass density decreased following summer fire; yet, productivity was similar among treated and nontreated sites one year post burn.

Initial burns on native RGP rangelands should be conducted on a 2-year interval until the desired structure of woody vegetation is achieved. Once desired goals are met, as stated earlier, maintenance burning on a 3- to 5-year frequency is adequate. Grazing strategies that allow for substantial deferment to produce adequate fuels to carry fire are critical to the successful application of fire on both CP and RGP rangelands. Other considerations to be taken into account are the highly unpredictable weather patterns in South Texas. Short-term periods of drought are common and rainfall can be highly variable between locations. Drought can severely impact production of fine fuels necessary to carry fire and may require flexibility in burning schedules. One should plan on burning as the opportunity arises since, if a critical burn is missed, conditions may not allow burning for several more years.

As stated earlier, fire may be integrated with other practices in brush management systems. An evenly-distributed, fine fuel load of 2,500 to 3,000 lb/acre is considered adequate

for an effective burn. However, rangelands supporting moderate to heavy brush cover are characterized by seriously reduced and patchy herbaceous cover (Scifres and others 1982, 1983), resulting in inadequate fine fuel load. Because of the dependence on an adequate load of evenly distributed fine fuel, burning of brushy South Texas rangelands usually is a treatment subsequent to an initial method that uniformly reduces the brush canopy and releases the fine fuel. Moreover, prescribed burning often increases the effective life of initial treatments and compensates for characteristic weaknesses of several of the methods. Because of this utility, fire-based Integrated Brush Management Systems (IBMS) can take maximum advantage of several methods, including fire, over a relatively long time period. (Scifres and others 1985).

Prescribed burning has been evaluated following applications of herbicide sprays and of pellets as broadcast or individual plant treatments. It has also been effectively used in conjunction with various mechanical methods for brush management as both herbicide and mechanical applications reduce brush canopies and release fine fuel for prescribed burning. Prescribed burning then suppresses surviving woody plants, removes rough forage plants, promotes legumes and other desirable forbs usually damaged by sprays, promotes uniform distribution of livestock grazing, expedites secondary succession and improves botanical composition of grass stands. South Texas mixed brush is characterized by all of the problems and potentials described above. In most cases, burning is impossible until the brush canopy is reduced and fine fuel is released.

In 1999, an IBMS was installed in a mixed brush community on La Copita Demonstration Ranch and Research area. An outline of the State of Texas was superimposed on a DOQQ map of a pasture and coordinates around the perimeter of the map were recorded. Using a backpack GPS unit these coordinates were located around a 35 acre parcel of rangeland and staked. A D-8 Caterpillar tracked tractor then pulled a "rolling chopper- aerator" around the perimeter before chopping the area within the perimeter.

As expected, brush regrowth after top removal was rapid. In September, 2002, the 35 acres was divided into several plots and a variety of herbicides and mixes of herbicides were applied to each. Efficacy varied dependent upon species and herbicides treatment but, overall, canopy was reduced by 90% the first year. By the second year plants/acre were reduced by 50%. In spite of being part of a grazing program air dried forage production in the fall of 2003 was 280 lbs/ac in the control—open pasture; 320 lbs/ac in the control—brushy pasture; and 1500–2800 lbs/ac. in the chopped and sprayed pasture

Brush regrowth of those species not killed by the herbicide treatments was rapid. In February, 2004, the "State of Texas" was burned with a prescribed fire. The fire further thinned the brush stand, the species mix of forbs and grasses was enhanced and wildlife, such as bobwhite quail and white-tailed deer, prefer this pasture to non-treated pastures. Measurements of cattle grazing also indicate a preference for this pasture.

Summary

In summary, fire affects vegetation by suppressing woody growth, removing excess buildup of litter, and stimulating herbage production. Fire will not kill the majority of South Texas woody plants because of their resprouting characteristics, although there is an indication that repeat burns may kill a small percentage of plants of certain species. Timing of burning is one of the most important factors to consider in planning a burn. Fire stimulates growth of forbs following the top removal of woody plants in dense mottes of brush.

Literature Cited

- Archer, S.; Scifres, C.; Bassham, C. R.; Maggio, R. 1988. Autogenic succession in a subtropical savanna: conversion of grassland to thorn woodland. *Ecol. Monogr.* 58:111-127.
- Archer, S. 1994. Woody plant encroachment into southwestern grasslands and savannas: rates, patterns and proximate causes, p. 13-68. In: M. Vavra et al. (eds.) *Ecological implications of livestock herbivory in the west*. Society for Range Management, Denver, Colo.
- Box, T. W.; Powell, J.; Drawe, D. L. 1967. Influence of fire on south Texas chaparral communities. *Ecology*. 48:955-961.
- Box, T. W.; White, R. S. 1969. Fall and winter burning of south Texas brush ranges. *J. Range Manage.* 22:373-376.
- Dodd, J. D.; Holtz, S. T. 1972. Integration of burning with mechanical manipulation of south Texas grassland. *Journal of Range Management*. 25:130-135.
- Drawe, D. L.; Kattner, K. R. 1978. Effect of burning and mowing on vegetation of Padre Island. *Southwestern Naturalist*. 23:273-278.
- Gordon, R. A.; Scifres, C. J. 1977. Burning for improvement of Macartney rose-infested Coastal Prairie. Bulletin B-1183, Texas Agricultural Experiment Station, College Station, TX.
- Hansmire, J. A.; Drawe, D. L.; Wester, D. B.; Britton, C. M. 1988. Effects of winter burns on forbs and grasses of the Texas Coastal Prairie. *Southwest. Nat.* 33:333-338.
- Rasmussen, G. A.; Scifres, C. J.; Drawe, D. L. 1983. Huisache growth, browse quality, and use following burning. *Journal of Range Management*. 36:337-342.
- Ruthven, D. C.; Braden, A. W.; Knutson, H. J.; Gallagher, J. F.; Synatzske, D. R. 2003. Woody vegetation response to various burning regimes in South Texas. *J. Range Manage.* 56:159-166.
- Ruthven, D. C.; Synatzske, D. R. 2002. Response of herbaceous vegetation to summer fire in the western South Texas Plains. *Tex. J. Sci.* 54:195-210.
- Scifres, C. J.; Hamilton, H. T. 1993. Prescribed burning for brushland management: the south Texas example. Texas A&M University Press, College Station, Tex. 246 p.
- Scifres, C. J.; Hamilton, H. T.; Conner, J. R.; Inglis, J. M.; Rasmussen, G. A.; Smith, R. P.; Stuth, J. W.; Welch, T. G. (eds.) 1985. *Integrated brush management Systems for South Texas: Development and implementation*. *Tex. Ag. Exp. Stat. B-1493*. 71 p.
- Scifres, C. J.; Mutz, J. L.; Drawe, D. L.; Whitson, R. E. 1983. Influence of mixed brush cover on grass production. *Weed Sci.* 31:1-4.
- Scifres, C. J.; Mutz, J. L.; Whitson, R. E.; Drawe, D. L. 1982. Interrelationships of huisache canopy cover with range forage on the coastal prairie. *J. Range Manage.* 35:558-562

- Vogl, R. J. 1974. Effects of fire on grasslands. Pages 139-194 in T. T. Kozlowski and C. E. Ahlgren, (Ed). Fire and ecosystems. Academic Press, New York, NY.
- Wilkins, N.; Brown, R. D.; Conner, R. J.; Engle, J.; Gilliland, C.; Hays, A.; Slack, R. D.; Steinbach, D. W. 2000. Fragmented lands: changing land ownership in Texas. Texas A&M Univ, Agr. Commun. Pub. MKT-3443, College Station, Tex.
- Wright, H. A.; Bailey, A. W. 1982. Fire Ecology. John Wiley and Sons, New York, N.Y. 501 p.

The Authors

¹ Texas Cooperative Extension. c-hanselka@tamu.edu

² Welder Wildlife Foundation.

³ Texas Parks and Wildlife Dept.

Hydrology, Erosion, Plant, and Soil Relationships after Rangeland Wildfire

Kenneth E. Spaeth¹

Frederick B. Pierson²

Peter R. Robichaud³

Corey A. Moffet⁴

Abstract: Wildfire is an important ecological process and management issue on western rangelands. Fire suppression activities in the past century have increased the number and severity of wildfires, resulting in increased soil erosion and decreased water quality. Many infiltration studies on rangeland have shown that litter and vegetation cover protect the soil and enhance infiltration. After fire, water repellency is typically found on the soil surface or a few centimeters below and is also common on unburned rangelands and dry soils conditions. However, the causal agents of water repellency are different for burned and unburned conditions. Rainfall simulation studies were conducted for 3 consecutive years immediately following a catastrophic wildfire in Denio, Nevada, in 1999. Study sites were chosen on north-facing hillslopes (35 to 40 percent slope) where the vegetation was dominated by mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*). The objective of this study was to use indirect gradient analysis on the 1999 data to evaluate and summarize pertinent relationships between vegetation, soil, topographic features, infiltration, runoff, sediment production, and microsite distinction (shrub coppice and interspace) on burned and unburned areas. The first ordination (strategy 1) used four infiltration parameters and the results were unexpected. In the multivariate context, higher infiltration trends were associated with the burned treatment compared to the unburned treatment. Water repellency on the burned sites was apparent at the soil surface; however, it appears that repellency was also a significant factor on the unburned area. Water repellency in the unburned treatment was likely caused by assorted litter buildup (up to 11,605 kg/ha) in > 80-year stands (sagebrush duff and grass in the shrub coppice areas and grass litter in the interspace). The second ordination (strategy 2) involved the same four infiltration parameters, but specifically used plots from the burned treatment. More runoff and sediment was associated with the burn shrub coppice plots; in contrast, higher infiltration capacity in the burned interspace. The third ordination (strategy 3) was based on plant canopy cover by species. Discrete taxa of native grasses, forbs, and shrubs were correlated with infiltration, runoff, and sediment loss on burned and unburned sites. On the unburned sites, water repellency and higher runoff was correlated with Sandberg bluegrass (*Poa secunda*), bluebunch wheatgrass (*Pseudoroegneria spicata*), and western aster (*Symphyotrichum ascendens*). Greater infiltration capacity was correlated with increasing cover of Idaho fescue (*Festuca idahoensis*) and mountain big sagebrush. Future analysis will evaluate conditions after the first years growing season and beyond.

Introduction

Fire suppression activities during the past century often increase the severity of wildfires resulting in increased soil erosion and decreased water quality (Pearson and others 2001, 2002). Increased runoff and erosion can lead to loss of soil productivity, flooding, and increased risk to human life and property. Many non-fire related infiltration studies on rangeland have shown that litter and vegetation cover protect the soil and enhance infiltration (Rauzi and others 1968; Blackburn and others 1986). Fire removes this protective covering, reduces soil surface organic matter, and exposes the soil to raindrop impact. After fire, soils can become water-repellent (hydrophobic) although this condition is also common on unburned rangelands (DeBano 1981) and dry soils conditions (Bond and Harris 1964ab; Rutin 1983; Jungerius and de Jong 1989). In the unburned setting, the

partially decomposed organic matter from brush species, when intermixed with the soil surface layer, can also produce a water-repellent situation (DeBano and Rice 1973; Pierson and others 2001).

The USDA-ARS Northwest Watershed Research Center (NWRC) has been investigating wildfire interactions with hydrologic processes on steep, coarse textured, sagebrush (*Artemisia*) dominated landscapes in Nevada and Idaho. The sagebrush-steppe is an extensive rangeland shrub type in North America and occupies about 42.5 million ha² in the 11 western states. The objectives of these studies are to quantify the impacts of wildfire on infiltration capacity, runoff, erosion, and soil surface characteristics and determine how long fire effects persist. The objective of this paper is to summarize interactions between vegetation, soil, topographic features, hydrologic parameters, and sediment production after a high intensity wildfire.

In: Sosebee, R.E.; Wester, D.B.; Britton, C.M.; McArthur, E.D.; Kitchen, S.G., comp. 2007. Proceedings: Shrubland dynamics—fire and water; 2004 August 10-12; Lubbock, TX. Proceedings RMRS-P-47. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 173 p.

Study Area

This ongoing study is approximately 24 kilometers southwest of Denio, Nevada, in the Pine Forest Range. The Denio Fire burned in late July 1999 and consumed approximately 34,400 ha. Mean elevation of the research area is 2,050 m, average annual precipitation of the study area is 350–400 mm. Study sites were located on north-facing hillslopes (35 to 40 percent slope). The soil is an Ola bouldery sandy loam which consists of moderately deep soils formed in residuum from granite on mountain sideslopes. The ecological site description is classified as a Granitic slope 14–16" P.Z., mountain big sagebrush/Idaho fescue/bluebunch wheatgrass (USDA-NRCS 1990). Other common subdominant grass species include Columbia needlegrass (*Achnatherum nelsonii*), bottlebrush squirrel-tail (*Elymus elymoides*), and Sandberg bluegrass. Associated shrubs on the site were common snowberry (*Symphoricarpos albus*) and green rabbitbrush (*Chrysothamnus viscidiflorus*). The major forb species were lodgepole lupine (*Lupinus parviflorus*), nettleleaf giant hyssop (*Agastache urticifolia*), longleaf hawksbeard (*Crepis acuminata*), small bluebells (*Mertensia longiflora*), indian paintbrush (*Castilleja* spp.), alpine lake prairie-dandelion (*Nothocalais alpestris*), Siskiyou Mountain ragwort (*Packera macounii*), arrowleaf balsamroot (*Balsamorhiza sagittata*), rosy pussytoes (*Antennaria rosea*), common yarrow (*Achillea millefolium*), western aster, and low scorpionweed (*Phacelia humilis*).

Methods

Rainfall simulator experiments were conducted in 1999 under antecedent surface soil moisture conditions. The study included two treatment effects: microsites (shrub coppice and interspace) with 20 plots (0.5 m²) and 10 plots each on the three burned and unburned areas. A greater number of sample plots were sampled on the burned sites in anticipation of greater variability in response variables compared to the control sites. Four portable oscillating-arm rainfall simulators (specifications described by Meyer and Harmon [1979]) were used to apply rainfall to each runoff plot for 60 minutes. A rainfall rate of 85 mm/hr, equal to the rainfall intensity of a 10-minute thunderstorm with a 10-year return period (Hanson and Pierson 2001), was applied to each runoff plot.

Plot frames were installed immediately after the fire in September 1999 and were left in place for subsequent rainfall simulation treatments. Rainfall was first applied starting 6 weeks following the fire before any natural rainfall events had occurred. All burned and unburned control plots were sampled within 10 days of the start of rainfall simulations. Runoff was routed through a collection tray at the bottom of each plot and collected at one- or two-minute intervals throughout the entire rainfall simulation. Runoff samples were analyzed for runoff volume and sediment concentration by weighing, drying at 105 °C, and re-weighing each sample. Infiltration capacity for

each time interval was calculated as the difference between measured rainfall and runoff.

Prior to the simulation runs, soil samples were collected adjacent to each runoff plot and analyzed for gravimetric soil moisture content. Following rainfall simulation, bulk density using the core method (Blake and Hartge 1986), organic carbon content using the ashing method (Nelson and Sommers 1982), and soil texture using the hydrometer method (Bouyoucos 1962) were determined from soil samples taken immediately adjacent to each plot. Vegetative canopy cover for each plant species, standing dead material, basal vegetative crowns, ground cover of cryptogams, woody and non-woody litter, rock, and bare ground were estimated ocularly to the nearest percent for each plot (Elzinga and others 2000). Some of the rarer species occupy < 1.0 percent canopy cover; therefore, we split the cover classes into finer units (0.05, 0.025, and 0.01 percent). To improve the estimation procedure, each 0.5 m² plot was divided into 4 segments (0.125 m²) and cover values were estimated using a nested frame for calibration, which contained representative areas of 50, 25, 15, 10, 5, 1, 0.05, 0.025, and 0.01 percent. Accuracy of the ocular method was evaluated from random plots by recording 500 points with a point cover frame. Corresponding percent differences between ocular and point cover measurements were not more than ± 2 percent.

The experimental design of this study is given in Pierson and others (2001). In this analysis, indirect gradient analysis using detrended correspondence analysis (DCA) (Hill and Gauch 1980) was used to evaluate plant, soil, site, and hydrology interactions following the wildfire. The following strategies were used: Strategy 1, because all the above ground vegetation including woody stems of shrub species were entirely consumed in the 1999 fire, a comparative ordination (main matrix) using four infiltration parameters was made of both the 1999 burn and unburned sites ($n = 90$). The infiltration parameters were: minimum infiltration rate (mm/hr)—the lowest average infiltration rate of all sample intervals from the respective rainfall simulation runs; final infiltration rate (mm/hr) is the average infiltration rate of the 58 to 60 min time interval; time to minimum infiltration (min) (equivalent to peak runoff); and cumulative infiltration (mm/hr) calculated as total amount of rainfall applied less cumulative runoff. Secondary matrix environmental variables were correlated with axis loadings from the infiltration data. The environmental variables used appear in Table 1. The axes in DCA are scaled in units of the average standard deviation (SD) of species turnover. A change of 50 percent occurs in about 1 SD. Strategy 2 was the same as 1, except that only burned plots were used ($n = 60$). The third strategy consisted of a DCA ordination using the 1999 unburned plant species canopy cover data as the main matrix, the secondary matrix data were the environmental factors ($n = 30$). The false discovery rate (FOR) (Benjamini and Hochberg 1995) was used to test for false positives in the correlation data between axis loadings and plant and environmental variables.

Table 1. Pearson correlations (strategies 1, 2, and 3) with the first two detrended correspondence analysis axes for Denio, Nevada, Mountain big sagebrush study sites (fire year, 1999).

Variables	Strategy 1		Strategy 2		Strategy 3	
	Axis 1 (r)	Axis 2 (r)	Axis 1 (r)	Axis 2 (r)	Axis 1 (r)	Axis 2 (r)
Cumulative infiltration (mm)	-0.67	-0.53	-0.63	-0.55	-0.54	-0.19
Final infiltration rate (mm/hr)	-0.74	-0.45	-0.55	-0.55	-0.55	-0.12
Minimum infiltration (mm/hr)	-0.39	-0.80	-0.83	-0.14	-0.48	-0.31
Runoff/Rain ratio (mm mm)	0.69	0.54	0.66	0.53	0.55	0.18
Cumulative runoff (mm)	0.66	0.54	0.65	0.52	0.54	0.16
Time-to-runoff (min)	-0.04	-0.41	-0.38	0.18	-0.47	-0.34
Time-to-peak runoff (min)	0.47	0.24	0.31	0.40	-0.02	-0.40
Cumulative sediment (kg/ha)	0.15	0.45	0.50	0.31	0.46	0.17
Sediment/Runoff ratio (kg/ha mm)	-0.18	0.19	0.23	0.06	0.23	0.006
Water repellency index	0.83	-0.38	-0.83	0.50	0.66	-0.17
Antecedent moisture 0-2 cm (%)	0.38	-0.10	0.07	0.26	0.01	-0.06
Bulk Density 0-2 cm (g/cm ³)	-0.44	0.02	-0.08	-0.09	-0.09	-0.14
Bulk Density 2-4 cm (g/cm ³)	-0.55	0.02	-0.19	-0.39	-0.05	-0.007
Grass cover (%)	0.62	-0.08	-0.34	0.20	0.21	0.23
Forb cover (%)	0.13	-0.15	-0.11	0.02	-0.20	-0.21
Shrub cover (%)	0.19	-0.16	-0.24	0.06	-0.32	-0.67
Litter cover (%)	0.54	-0.13	0.16	0.13	0.09	-0.41
Sand 0-2 cm (%)	-0.48	0.10	-0.17	-0.31	0.17	-0.15
Silt 0-2 cm (%)	0.52	-0.08	0.18	0.32	-0.05	0.14
Clay 0-2 cm (%)	-0.12	-0.15	-0.01	0.007	-0.38	0.03
Rock (%)	-0.22	-0.08	-0.16	-0.14	.	.
Slope (%)	0.44	0.19	0.40	0.10	0.10	0.06
Aspect (degrees)	0.27	-0.10	-0.20	-0.44	-0.39	0.21
Microsite (Coppice, Interspace)	0.19	-0.38	-0.60	0.35	0.31	0.69
Microtopography	-0.35	-0.08	-0.20	-0.32	.	.
Treatment (burn, unburn)	0.52	-0.15	.	.	.	.

Results

Strategy 1

Figure 1 is an ordination diagram of 1999 infiltration parameters for the burned and unburned plots. Examination of the burn and unburned treatments shows definitive groupings between burned and unburned treatments along DCA axis 1. The angle and length of the centroid line shows the delineation and degree of correlation of the respective variables. Each line can be related to other variable lines to denote possible environmental gradients (groups of variables). Pearson correlation cutoff values in the ordination diagrams were set at $r = 0.50$. Table 1 shows correlation coefficients of environmental variables with the first two DCA infiltration axes.

There is a strong infiltration gradient along axis 1 (fig. 1). Final and cumulative infiltration were highly negatively correlated with axis 1. Cumulative infiltration and final infiltration rate decrease toward the right along axis 1; therefore, the burn treatment plots are associated with higher rates for these two variables (table 1). Water repellency as calculated in Pierson and others (2001), cumulative runoff, silt, litter, and runoff-rainfall ratio were positively correlated with axis 1 (table 1). These variables increase in magnitude from left to right. Pierson and others (2001) found that infiltration rate and capacity in water repellent soils after fire were reduced during the early stages of the infiltration curve. In the latter stages of the rainfall simulation, water repellency decreased with time.

The hydrophobic causative agents deteriorated resulting in gradual recovery of infiltration. Bulk density at 2- to 4-cm was negatively correlated with axis 1—higher values in the burned treatment.

An infiltration gradient also appears along axis 2, where minimum infiltration (the lowest average infiltration rate for all sample intervals) and cumulative infiltration are negatively correlated (table 1). In the lower left region, interspace microsite burn plots predominate. Although minimum infiltration is not significant between burned (45.2 mm/hr) and unburned treatments (45.9 mm/hr), it was significant between coppice (37.8 mm/hr) and interspace (53.6 mm/hr) microsites on the burned treatment (Pearson and others 2001). The complementary measurement to cumulative infiltration, cumulative runoff, were positively correlated. Also, the runoff-rainfall ratio was positively correlated with axis 2 (table 1).

Strategy 2

Strategy 2 was included in this paper so that microsites in the burned area could be compared. Figure 2 shows the 1999 burned plots and there were definitive groupings between the interspace and coppice microsites. For an in depth review of the hydrologic data, refer to Pierson and others (2001). Minimum infiltration, cumulative infiltration, final infiltration rate, and water repellency were negatively correlated with axis 1, and cumulative runoff was positive along axis 1. The interspace plots are predominantly on the left side of axis 1 where

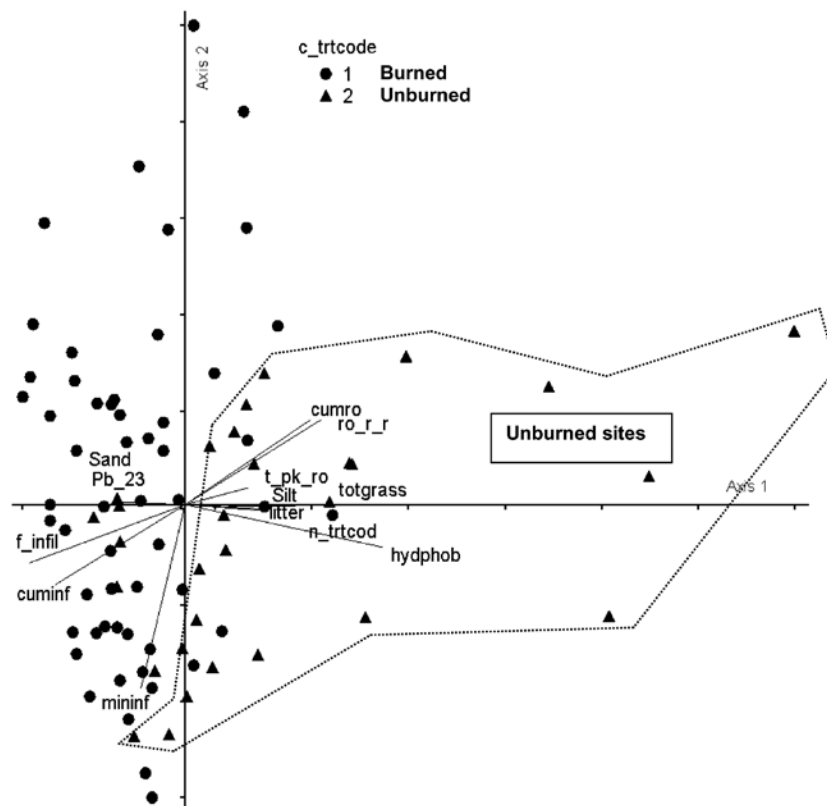


Figure 1. Detrended correspondence analysis of 1999 Denio wildfire hydrology data from all rainfall simulation plots (n=90). Plot points represent an ordination of four infiltration variables [minimum infiltration rate, final infiltration rate, cumulative infiltration rate, and time to minimum infiltration (equivalent to peak runoff)]. Secondary matrix correlations were the remaining variables listed in table 1. Pearson correlation coefficients cutoff values in the figure were set at $r = 0.5$. The dotted polygon represents the relative grouping of the unburned 1999 sites. The points outside the polygon are the 1999 burned plots. Correlated variables in diagram are: sand, Pb_23=bulk density at 2-4cm, f_infil=final infiltration rate, cuminf=cumulative infiltration, cumro=cumulative runoff, ro_r_r=runoff/rainfall ratio, t_pk_ro=time to peak runoff, silt, litter, totgrass=total grass cover of all species, hydphob=water repellency index, and n_trtcd=treatment (burned and unburned).

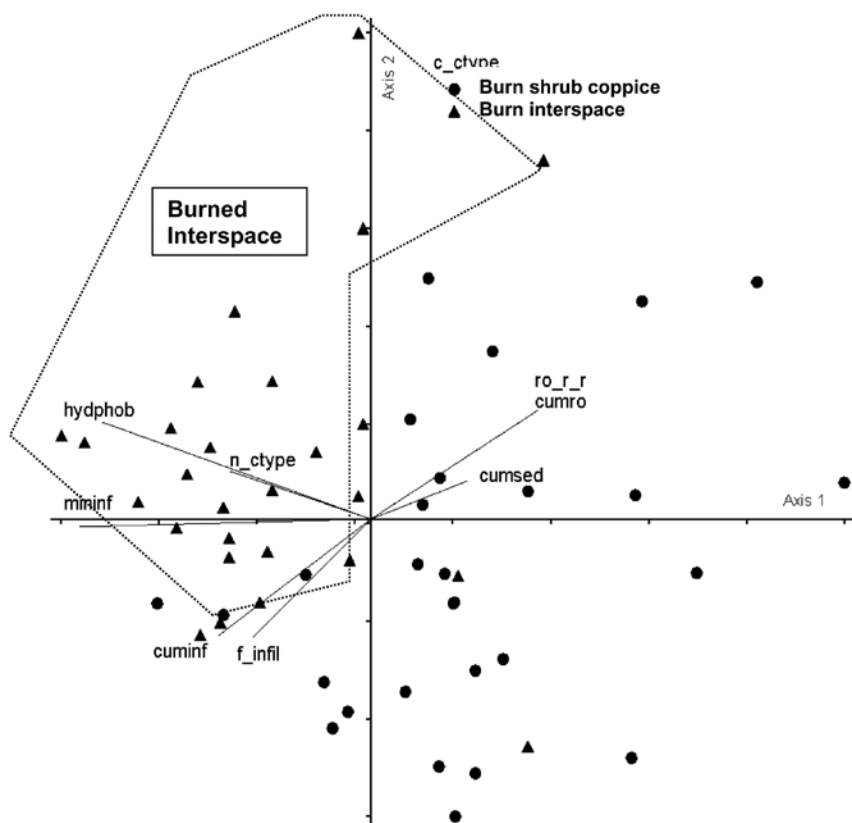


Figure 2. Detrended correspondence analysis of 1999 Denio wildfire hydrology data from rainfall simulation burned plots (n=60). Plot points represent an ordination of four infiltration variables [minimum infiltration rate, final infiltration rate, cumulative infiltration rate, and time to minimum infiltration (equivalent to peak runoff)]. Secondary matrix correlations were the variables listed in table 1. Pearson correlation coefficients cutoff values in the figure were set at $r = 0.5$. The dotted polygon represents the relative grouping of the burned interspace 1999 plots. The points outside the polygon are the 1999 burned shrub coppice plots. Correlated variables in diagram are: hydphob=water repellency index, mininf=minimum infiltration rate, cuminf=cumulative infiltration, f_infil=final infiltration rate, n_ctype=microsite cover type (interspace, coppice), ro_r_r=runoff/rainfall ratio, cumro=cumulative runoff, and cumsed=cumulative sediment.

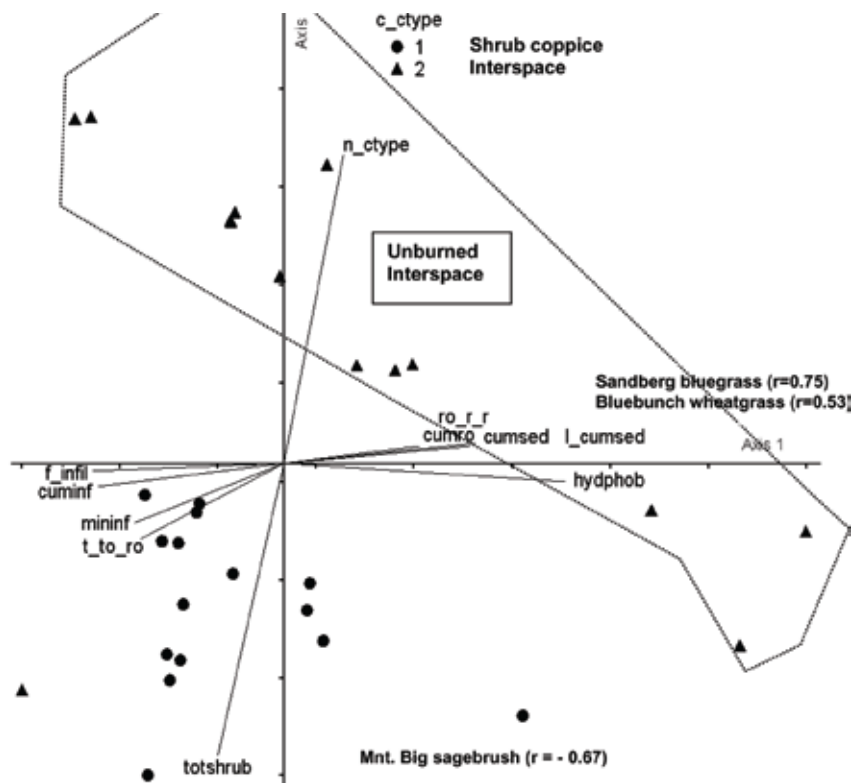


Figure 3. Detrended correspondence analysis of 1999 Denio wildfire hydrology data from rainfall simulation unburned plots (n=30). Plot points represent an ordination of plant canopy cover for all species. Secondary matrix correlations were the variables listed in table 1. Pearson correlation coefficients cutoff values in the figure were set at $r = 0.5$. The dotted polygon represents the relative grouping of the unburned interspace 1999 plots. The points outside the polygon are the 1999 unburned shrub coppice plots. Correlated variables in diagram are f_infil =final infiltration rate, $cuminf$ =cumulative infiltration, $mininf$ =minimum infiltration rate, t_to_ro =time-to-runoff, $totshrub$ =total shrub canopy cover, n_ctype =microsite cover type (interspace, coppice), ro_r_r =runoff/rainfall ratio, $cumro$ =cumulative runoff, $cumsed$ =cumulative sediment, l_cumsed =log of cumulative sediment, and $hydphob$ =water repellency index. Correlated plant species appear in the respective ordination quadrants.

average final infiltration, cumulative infiltration, minimum infiltration, and water repellency were higher compared to the shrub coppice to the right on axis 1. As Pierson and others (2001) mentioned, there was more fuel on the shrub coppice microsites which may have resulted in higher burn temperatures and a greater tendency for water repellent conditions. Fire vaporizes some organic compounds on the soil surface and distills the rest downward, concentrating the hydrophobic substances in the upper soil surface. On the right side of axis 1 where the coppice plots are grouped, cumulative sediment yield was higher coppice = 410 kg/ha; interspace = 210 kg/ha (fig. 2). The runoff-rainfall ratio was also higher for the burned shrub coppice area (0.37 mm/mm) compared to the burned interspace (0.30 mm/mm) (fig. 2).

Strategy 3

Figure 3 is an ordination of plant canopy cover data for all species in the unburned area. In figure 3, the unburned coppice and interspace microsites are definitively separated. The microsite groupings are unique with respect to plant species composition. Near plots have more similar plant species composition, far plots are more dissimilar. Along axis 1, final infiltration and cumulative infiltration are associated with the shrub coppice microsites. In contrast, cumulative runoff, runoff-rainfall ratio, water repellency, and cumulative sediment are higher in the unburned interspace.

In Pierson and others (2001), final infiltration rates were about equal between the burned (55.5 mm/hr) and the unburned coppice (55.9 mm/hr) plots. After an intense wildfire, we expected to see a difference in infiltration rates between the

coppice microsites; however, infiltration between burned and unburned coppice areas immediately after the fire was about the same. We propose that the litter buildup in the unburned treatment area was responsible. On the unburned plots, litter averaged 5 cm deep and averaged 7,275 kg/ha with a high value of 11,605 kg/ha. The litter, sagebrush duff, and grass on shrub coppice and senescent grass in the interspace apparently have water repellent properties. We observed this during the rainfall simulation experiments. In contrast to the coppice areas, final infiltration rate in the burned interspace (60.0 mm/hr) was significantly greater compared to the unburned interspace (40.4 mm/hr).

In figure 3, Sandberg bluegrass and bluebunch wheatgrass were positively correlated with axis 1 (> canopy cover), the zone of unburned interspace plots. Idaho fescue was negatively correlated with axis 1—where the unburned shrub coppice plots have higher Idaho fescue and Columbia needlegrass canopy cover. Regression analyses of the unburned data showed:

$$\text{Infiltration} = f(+ \text{Idaho fescue}, + \text{Columbia needlegrass}, + \text{mountain big sagebrush}),$$

$$\text{Runoff} = f(+ \text{Sandberg bluegrass}, + \text{bluebunch wheatgrass} + \text{western aster}),$$

$$\text{Cumulative sediment} = f(+ \text{Sandberg bluegrass}, + \text{western aster}),$$

where f = function of the following independent variables, + sign indicates positive association.

Spaeth and others (1996, 2003) proposed that plant species appear to have an impact on rangeland hydrology. Therefore,

we hypothesize that plant species (considering importance values such as cover, biomass, and root biomass) can affect hydrology.

Discussion

In Pierson and others (2001), we showed that wildfire can have a significant hydrologic impact on the hydrology of sagebrush dominated rangelands. In Pierson and others (2001) we hypothesized that during the burn year, average infiltration rates would be reduced on the burned compared to the unburned treatment because of soil water repellency caused by the hot fire. This hypothesis was rejected because rainfall simulation experiments shortly after the fire did not result in a significant effect on average infiltration between the burn and unburned treatments.

A second hypothesis was tested: infiltration rates will be different between microsites for burned and unburned treatments (based on previous work by Blackburn 1975, Pierson and others 1994). Infiltration rates were reduced on burned shrub coppices compared to burned interspace. Burned shrub coppice microsites were associated with very uniform fire induced water repellency with an average infiltration rate reduction of 28 percent. On unburned plots, infiltration rates were greater on the shrub coppice areas compared to interspace areas. Comparisons between burned and unburned treatments showed that infiltration rates were about the same on coppice microsites, but different between interspace areas. Infiltration was higher, and runoff lower, on the burned interspace compared to the unburned interspace. Pierson and others (2001) attributed this unexpected result to the dense mat of senescent grass (litter) on the soil surface. The water repellent litter in the interspace area intercepted the rainfall and initiated runoff before the water reached the mineral soil surface.

In this paper, we examined possible relationships between individual species composition and hydrology. In mountain big sagebrush vegetation, plant composition, and soil physical properties are different in microsite areas (shrub coppice, shrub dripline, and varying distances along the interspace). Idaho fescue, lupine, mountain big sagebrush, and snowberry are more prevalent in the coppice areas; whereas, Sandberg bluegrass, bluebunch wheatgrass, rosy pussytoes, common yarrow, and western aster occur mostly in the interspace areas. The presence or absence and magnitude of canopy cover of certain plant species seems to be associated with infiltration capacity, runoff, and sediment loss. This preliminary study showed certain plant species were associated with higher and lower infiltration and runoff. In figure 3, textural differences, antecedent moisture, bulk density, total grass cover, and total forb cover were not correlated with the infiltration gradient (unburned coppice to unburned interspace). However, Idaho fescue and Columbia needlegrass canopy cover were correlated with higher infiltration; whereas, Sandberg bluegrass and bluebunch wheatgrass were associated with higher runoff.

Future analysis will incorporate several more years of rainfall simulation experiments at Denio, Nevada to deter-

mine the impact of these plant species on hydrology in high elevation mountain big sagebrush vegetation. In addition to the Denio sites, the NWRC is conducting similar rainfall simulation experiments at sagebrush sites at Reynolds Creek Experimental Watershed in southwest Idaho.

References

- Benjamini, Y.; Hochberg, Y. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society Series. B* 57:289-300.
- Bond, R. D.; Harris, J. R. 1964a. The influence of the microflora on physical properties of soils. I. Effects associated with filamentous algae and fungi. *Australian Journal Soil Research* 2:111-122.
- Bond, R. D.; Harris, J. R. 1964b. The influence of the microflora on physical properties of soils. II. Field studies on water repellent sands. *Australian Journal Soil Research* 2:123-131.
- Blackburn, W. H.; Thurow, T. L.; Taylor, C. A. 1986. Soil erosion on rangeland. Symposium on the use of cover, soils, and weather data in rangeland monitoring, Orlando, Florida, February 12, 1986. *Texas Agr. Exp. Sta., TA-2119*: College Station.
- Blake, R. G.; Hartge, K. H. 1986. Bulk density. In: *Methods of Soil Analysis. Part I. Physical and Mineralogical Methods*, Klute A. (ed). *Agronomy Series #9, ASA, SSSA: Madison, Wisconsin*.
- Bouyoucos, G. J. 1962. Hydrometer method improved for making particle size analysis of soil. *Agronomy Journal* 54:464-465.
- DeBano, L. F. 1981. Water repellent soils: a state of the art. In: *USDA Forest Service General Technical Report PSW-46: Pacific Southwest Forest and Range Experiment Station: Berkeley, California*.
- DeBano, L. F.; Rice, R. M. 1973. Water-repellent soils: their implications in forestry. *Journal of Forestry* 71:220-223.
- Elzinga, C. L.; Salzer, D. W.; Willoghby, J. W. 2000. Measuring and Monitoring Plant Populations. *USDI-BLM Technical Reference 1730-1*. Denver, Colorado.
- Hanson, C. L.; Pierson, F. B. 2001. Characteristics of extreme precipitation and associated streamflow in the Reynolds Creek Experimental Watershed, Idaho. In: *Proceedings of the 12th Symposium on Global Climate Change: American Meteorological Society: Boston*.
- Hill, M. O.; Gauch, H. G. 1980. Detrended correspondence analysis, an improved ordination technique. *Vegetatio* 42:47-58.
- Jungerius, P. D.; de Jong, J. H. 1989. Variability of water repellence in the dunes along the Dutch coast. *Catena* 16:491-497.
- Meyer, L. D.; Harmon, W. C. 1979. Multiple-intensity rainfall simulator for erosion research on row sideslopes. *Transactions ASAE* 22 :100-103.
- Nelson, D. W.; Sommers, L. E. 1982. Total carbon, organic carbon, and organic matter. In: *Methods of Soil Analysis. Part 2. Chemical and Microbiological Properties. Second Edition*, Page AL (ed). *Agronomy Series #9, ASA, SSSA: Madison, Wisconsin*.
- Pierson, F. B.; Van Vactor, S. S.; Blackburn, W. H.; Wood, J. C. 1994. Incorporating small scale spatial variability into predictions of hydrologic response on sagebrush rangelands. *Soil Science Society of America Special Publication* 38:23-34.
- Pierson, F. B.; Carlson, D. H.; Spaeth, K. E. 2002. Impacts of wildfire on soil hydrologic properties of steep sagebrush-steppe rangeland. *International Journal of Wildland Fire* 11:145-151.
- Pierson, F. B.; Robichaud, P. R.; Spaeth, K. E. 2001. Spatial and temporal effects of wildfire on the hydrology of a steep rangeland watershed. *Hydrological processes* 15:2905-2916.

- Rauzi, F.; Fly, C. L.; Dyksterhuis, E. J. 1968. Water intake on midcontinental rangelands as influenced by soil and plant cover. USDA Tech. Bull. No. 1390.
- Rutin, J. 1983. Erosional processes on a coastal sand dune, DeBlink, Noordwijkerhout. Physical Geography and Soils Laboratory Publication 35. University of Amsterdam, The Netherlands.
- Spaeth, K. E.; Pierson, F. B.; Weltz, M. A.; Awang, J. B. 1996. Gradient analysis of infiltration and environmental variables related to rangeland vegetation. Transactions of the ASAE 39(1): 67-77.
- Spaeth, K. E.; Pierson, F. B.; Weltz, M. A.; Blackburn, W. H. 2003. Evaluation of USLE and RUSLE estimated soil loss on rangeland. J. Range Management. 56:234-246.
- USDA-NRCS. 1990. Rangeland ecological site description: Granitic Slope 14-16" P.Z. (023XY043NV) ARVA/FEID-AGSP. USDA-NRCS Technical Guide Section IIE, Reno, Nevada.

The Authors

- ¹Rangeland Hydrologist, USDA-NRCS, Ft. Worth, TX.
- ²Research Hydrologist, USDA-ARS, Northwest Watershed Research Center, Boise, ID.
- ³ Research Engineer, USDA-Forest Service, Rocky Mountain Research Station, Moscow, ID.
- ⁴Rangeland Scientist, USDA-ARS, Dubois, ID.

Using Relative Humidity to Predict Spotfire Probability on Prescribed Burns

John R. Weir¹

Abstract: Spotfires have and always will be a problem that burn bosses and fire crews will have to contend with on prescribed burns. Weather factors (temperature, wind speed and relative humidity) are the main variables burn bosses can use to predict and monitor prescribed fire behavior. At the Oklahoma State University Research Range, prescribed burns are conducted during different seasons of the year and in different fuel types all over the state of Oklahoma. Since 1996 records have been kept to track spotfires that occur on these prescribed burns. Most of these spotfires were due to firebrands caused by crowning eastern redcedar (*Juniperus virginiana*). Leaves from oak (*Quercus* spp.) trees or tallgrasses floating or blowing across the fireline and smoke or fire whirls were responsible for most of the other spotfires. When burn data were reviewed, one weather variable stood out as the main cause of spotfires, low relative humidity. Of the 99 burns conducted there were 21 spotfires. From the data, the probability of a spotfire occurring on any prescribed burn with the relative humidity between 20 and 80 percent was determined to be 21.2 percent or approximately one out of five burns. Looking at the 40 percent relative humidity threshold, there is a probability of 41.3 percent for a spotfire occurring below 40 percent and 3.8 percent above 40 percent. There also appears to be another threshold at less than 25 percent relative humidity. At this point, there is a 100 percent probability of a spotfire occurring. With this information burn bosses can determine spotfire potential when considering burn units or burn days. It can also assist them when considering crew size and equipment needed. Most of all, inexperienced burn bosses can use this to help reduce risk (liability) and increase safety for their crews.

Introduction

Spotfires have and always will be a problem that burn bosses and fire crews will have to contend with on prescribed burns. Spotfires can cause mental and physical stress on burn bosses and crews if they occur or not. If a spotfire does take place it can cause injury to personnel or even loss of life, as well as monetary damages and loss of public support for the prescribed burning program. From interviewing many private and public land managers in Oklahoma, spotfires or risk of escape (liability) is the main reason many of them do not conduct prescribed fires. Many of these land managers have the personnel and equipment needed to conduct prescribed fires, but lack the experience or knowledge to deal with spotfires. So any type of simple guideline or rule-of-thumb is always needed to assist these people with their prescribed fires.

Temperature, wind speed, and relative humidity are the most important weather factors that burn bosses can use to predict and monitor prescribed fire behavior. Bunting and Wright (1974) determined that danger from firebrands was lower if the ambient air temperature was below 60°F (15°C) when conducting prescribed burns. Burning above 40 percent relative humidity has been shown to slow rates of spread significantly (Lindenmuth and Davis 1973) and reduce danger from firebrands (Green 1977). Wind speeds of 8 mph (13 km/h) are needed to ignite and burn standing fuels (Britton and Wright 1971), but with winds over 20 mph (32 km/h) firebrands and other debris become problems (Wright and Bailey 1982). As

indicated from the research, there are several weather related thresholds that influence the occurrence of spotfires. So if spotfire causes can be narrowed down to one key weather factor, this will help burn bosses to focus on that single variable, possibly reducing the likelihood of spotfires.

Methods

At the Oklahoma State University Research Range (OSURR) prescribed burns are conducted during different seasons of the year and in different fuel types all over the state of Oklahoma. These burns are conducted in a wide variety of fuels: Tallgrass Prairie (NFES fuel models 1, 3), Postoak-Blackjack Oak (NFES fuel models 3, 8, 9), Eroded Mixed Prairie (NFES fuel models 1, 3), Sandsage Grassland (NFES fuel model 4), and Oak-Pine Forest (NFES fuel models 3, 8, 9, 11) (NFES fuel models from Anderson 1982). Since 1996, records have been kept to track spotfires that occur on these prescribed burns. For this study, a spotfire is considered any fire that occurs outside the burn unit no matter what size it is or what caused it. The size of a spotfire is relative to fuel loads outside of the burn unit, crew size, crew experience, equipment present, equipment dependability, firebreak type and size, and weather conditions. The spotfires during this study ranged in size from less than 1 ft² (.09-m²) to 120 acres (264 ha). Most of these spotfires were due to firebrands caused by crowning eastern redcedar (*Juniperus virginiana*), while leaves from

In: Sosebee, R.E.; Wester, D.B.; Britton, C.M.; McArthur, E.D.; Kitchen, S.G., comp. 2007. Proceedings: Shrubland dynamics—fire and water; 2004 August 10-12; Lubbock, TX. Proceedings RMRS-P-47. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 173 p.



Figure 1. Fire whirls and ignition by other volatile fuels can cause spotfires on prescribed burns. The probability of a spotfire occurring is considerably less when the burn is conducted when the relative humidity is over 40 percent.

oak (*Quercus* spp.) trees or tallgrasses floating or blowing across the fireline and smoke or fire whirls were responsible for most of the other spotfires (fig. 1).

When prescribed fires are conducted by the OSURR crew, weather is recorded on site before, during and after the burn. This weather data consists of dry bulb and wet bulb temperature, wind speed and direction, and relative humidity, which is calculated from the dry and wet bulb temperatures. Information is also recorded about spotfires, such as if one occurred and time it occurred.

Results and Conclusions

When the burn data was reviewed, one weather variable stood out as the main cause of spotfires – low relative humidity. Of the 99 burns conducted, there were 21 spotfires, with 19 of the spotfires occurring at or below 40 percent relative humidity (fig. 2). Research has shown that below 40 percent relative humidity fine fuels ignite and burn easily, while above 40 percent ignition slows (Britton and Wright 1971; Lindenmuth and Davis 1973; Green 1977). This research validates that the threshold value of 40 percent relative humidity is an excellent rule-of-thumb to follow when conducting prescribed burns. This does not mean that there should be no prescribed burns conducted below 40 percent relative humidity. There are many regions of the US and certain burn units that require low relative humidity to allow for the goals and objectives of that specific burn to be met. But it should be imprinted in the burn boss' mind that there is an excel-

lent probability for a spotfire to occur if the burn is conducted below 40 percent relative humidity. In the same instant burn bosses should be ready for spotfires on all prescribed burns no matter what the relative humidity values are. For example, we recorded one spotfire when the relative humidity was at 73 percent, which was caused by crowning eastern redcedar throwing firebrands across the firebreak into heavy fuels. This proves spotfires can occur at higher relative humidity values.

Since most spotfires occur at or below 40 percent relative humidity, then what is the probability of a spotfire occurring at the 40 percent threshold value or any other relative humidity value? This information would be important for burn bosses to know as they prepare for and conduct prescribed burns to help reduce the risk to personnel and property. The information from the 99 prescribed burns was used to develop a set of probabilities for a spotfire occurring at a certain relative humidity. To determine this probability the following formula was used (Steele and Torrie 1980):

$$P = \frac{\text{number of successes (spotfires)}}{\text{total number of events (successes + failures) (fires)}}$$

From the data collected at the OSURR, the probability of a spotfire occurring on any prescribed burn with the relative humidity is between 20 and 80 percent was determined to be 21.2 percent, so approximately one out of five burns could be a spotfire. The data was then tested for the probability of spotfires above and below the 40 percent relative humidity threshold. There was a 41.3 percent probability for a spotfire occurring when the relative humidity was below

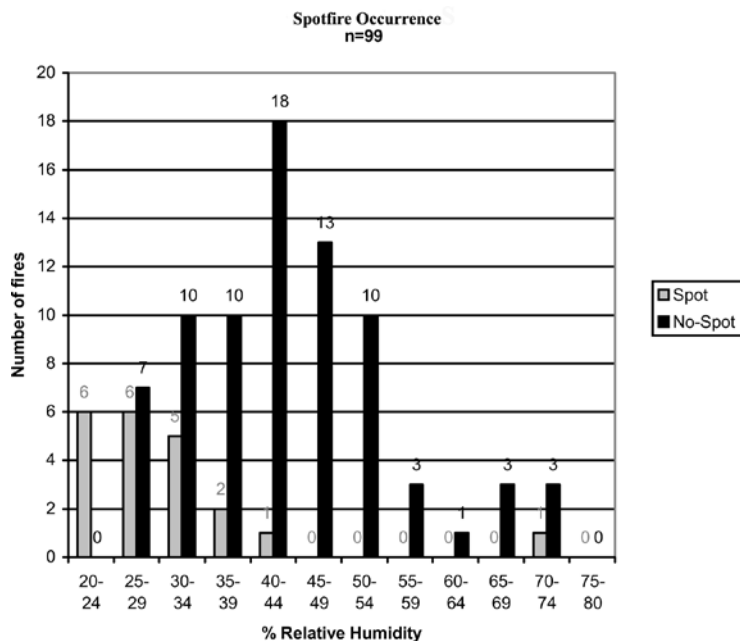


Figure 2. Of the 99 prescribed fires conducted from 1996 to 2002, 21 burns had spotfires. Only two spotfires occurred when relative humidity was greater than 40 percent.

40 percent and only a 3.8 percent probability when the relative humidity was above 40 percent. This is a large difference and the 40 percent threshold should be considered when inexperienced personnel are conducting prescribed burns or when heavy fuel loads are adjacent to the burn unit or if escape could bring possible public scrutiny or litigation. Again this is not condemning prescribed burning below 40 percent relative humidity.

If burns are conducted under 40 percent relative humidity, does the probability of spotfires change at lower relative humidity values? As figure 3 shows, there is a difference

in probability at each 5 percent drop in humidity below 40 percent. There also appears to be another threshold at less than 25 percent relative humidity. At this point, there is a 100 percent probability of a spotfire occurring. So below 25 percent relative humidity, burn bosses should be prepared for a spotfire. The spotfire probability drops to 46.2 percent in the 25 to 29 percent relative humidity range, which reduces spotfire risk over half with just a couple of percentage point increase in relative humidity. When the relative humidity is between 30 and 34 percent, only one out of three prescribed burns is likely to have a spotfire. So even within the range of 20 to 40 percent relative humidity there is a large difference in the probability of a spotfire occurring.

With this information, burn bosses can determine spotfire potential when considering burn units or burn days. It can also assist when considering crew size; equipment needed and possibly reduce anxiety when burning below 40 percent relative humidity. Most of all inexperienced burn bosses can use this to help reduce risk (liability) and increase safety for their crews. The main item to remember is to burn when conditions are safest for the crew and surrounding neighbors.

Literature Cited

- Anderson, H. E. 1982. Aids to determining fuel models for estimating fire behavior. USDA For. Serv. Gen. Tech. Rep. INT-122, 22 p. Intermt. For. and Range Exp. Stn., Ogden, Utah 84401.
- Britton, C. M.; Wright, H. A. 1971. Correlation of weather and fuel variables to mesquite damage by fire. J. of Range Manage. 23:136-141.
- Bunting, S. C.; Wright, H. A. 1974. Ignition capabilities of nonflaming firebrands. J. For. 72:646-649.
- Green, L. R. 1977. Fuel breaks and other fuel modification for wildland fire control. USDA Handbook No. 499. Washington, D.C.

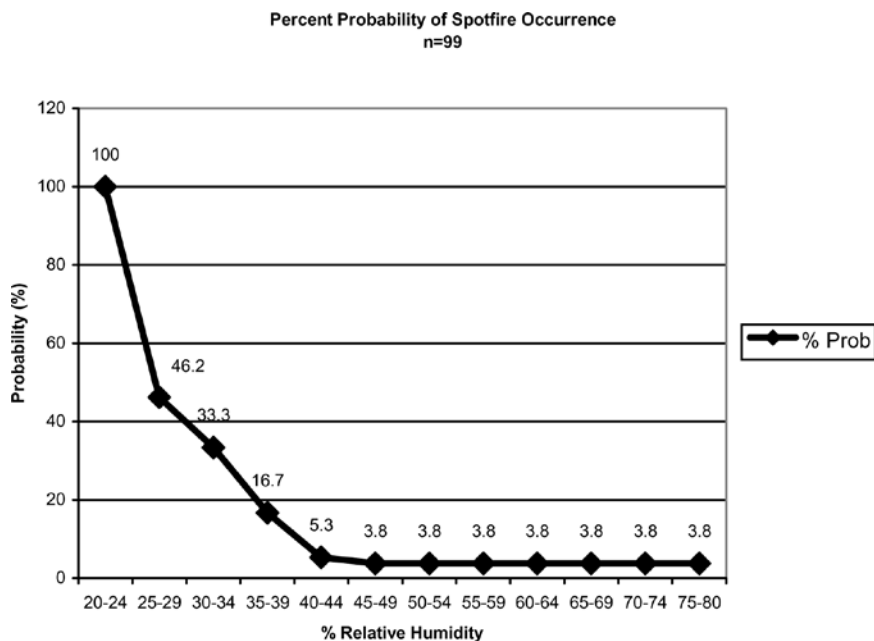


Figure 3. The percent probability of spotfires as a function of relative humidity determined from 99 prescribed fires conducted across Oklahoma from 1996 to 2002.

- Lindenmuth, A. W.; Davis, J. R. 1973. Predicting fire spread in Arizona oak chaparral. USDA For. Ser. Res. Paper RM-101. Rocky Mtn. For. and Range Exp. Stn. Fort Collins, CO.
- Steele, R. G. D.; Torrie, J. H. 1980. Principles and Procedures of Statistics. Second Edition. McGraw-Hill Book Company, New York, NY.
- Wright, H. A.; Bailey, A. W. 1982. Fire Ecology: United States and Southern Canada. John Wiley and Sons, New York, NY.

The Author

¹Research Station Superintendent, OSU Research Ranch, Oklahoma State University, Stillwater, OK. weir@agr.okstate.edu

Mesquite Cover Responses in Rotational Grazing/ Prescribed Fire Management Systems: Landscape Assessment Using Aerial Images

R. J. Ansley¹
W. E. Pinchak²
W. R. Teague³

Abstract: Prescribed fire is used to reduce rate of mesquite (*Prosopis glandulosa*) encroachment and dominance on grassland ecosystems, but is difficult to apply in continuous-grazed systems because of the difficulty in accumulating sufficient herbaceous biomass (that is, 'fine fuel') that is needed to fuel fire. We evaluated the potential of rotationally grazing cattle as a means to defer grazing to provide fine fuel burning. Mesquite cover changes from 1995 to 2000 were compared in four systems: continuous grazing, mesquite untreated (Cont.), 4 pasture/1 herd with fire (4:1F), 8 pasture/1 herd with fire (8:1F), and 4:1 with fire + herbicide (4:1F+H). There were two replicate systems per treatment, each 1,400-2,100 ha. The initial goal in the 4:1F and 8:1F systems was to burn 25 percent of the total area each year (1 pasture in 4:1F; 2 pastures in 8:1F). Fires were conducted in late winter. Mesquite cover was measured using digitized aerial images in 1995 (pre-treatment) and 2000. Droughts limited burning over this 5-year period to half the intended area of each system. Stocking rates, while adjusted in response to droughts, were maintained at similar levels in all systems. Net change in mesquite cover, scaled to account for soil types and pasture sizes in each system, was +34 percent, +15 percent, +5 percent, and -41 percent in the Cont., 4:1F, 8:1F, and 4:1F+H systems, respectively. Cattle performance was similar for all systems during the study period. Rotational grazing and fire systems slowed the rate of mesquite cover increase but did not reduce it. Fire was easier to apply in the 8:1F than the 4:1F system during drought because total area burned could be reduced to 1/8 instead of 1/4 of the system.

Introduction

Prescribed fire is an attractive option for reducing mesquite dominance on grasslands because it is less costly than other options and reduces the need for chemical and/or mechanical applications (Wright and Bailey 1982; Teague and others 1997; Ansley and Jacoby 1998). However, for fire to be an effective method for mesquite control, a grazing management strategy must be devised to accumulate the herbaceous biomass (otherwise called 'fine fuel') that fuels a fire. Moreover, because fire kills very few mesquite and only provides a 'top-killing' suppression effect at best (Ansley and others 1998; Ansley and Jacoby 1998), a management system must allow for frequent planned burning (at least every 8 to 10 years) to maintain sufficient suppression of mesquite regrowth.

It is difficult in continuous-grazed systems to accumulate sufficient herbaceous fine fuel to carry a fire of sufficient intensity to suppress woody vegetation. Prescribed burning may be more easily incorporated into systems using one-herd and multiple-paddocks (Scifres and Hamilton 1993). Using such management systems, we hypothesized that fire could be applied every 4 to 6 years and that the deferral period required to accumulate fuel could be 'internalized' within a management system by burning a small percentage of the system each year and rotating burning each year to different paddocks. Not

burning riparian vegetation and burning to create a savanna effect in selected areas on a site specific basis allowed for maintenance of wildlife habitat and biodiversity that did not impact livestock operations (Teague and others 1997).

Our objectives were to (1) evaluate the utility of rotational grazing and deferment as a means of facilitating use of prescribed fire for mesquite suppression through the accumulation of herbaceous fine fuel, and (2) determine system-level changes in mesquite cover in different rotational grazing and fire/herbicide management scenarios. Mesquite aerial cover was used as an indicator of level of mesquite dominance in the each system.

Methods

Site Description

The investigation was conducted in the Rolling Plains in north central Texas on a 14,400 ha portion of the W.T. Waggoner Estate termed the "Kite Camp." The climate is continental with an average 220 frost-free growing days. Mean annual precipitation is 648 mm, bimodally distributed with peaks in May and September. The mean annual temperature is 17°C and elevation ranges from 335 m to 396 m.

In: Sosebee, R.E.; Wester, D.B.; Britton, C.M.; McArthur, E.D.; Kitchen, S.G., comp. 2007. Proceedings: Shrubland dynamics—fire and water; 2004 August 10-12; Lubbock, TX. Proceedings RMRS-P-47. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 173 p.

Mesquite trees with aerial cover of 15 to 20 percent dominated the vegetation matrix. The herbaceous understory consisted of roughly an equal mixture of C_4 and C_3 perennial grasses. The major C_4 grasses are shortgrass buffalograss (*Buchloe dactyloides*), and mid-grasses sideoats grama (*Bouteloua curtipendula*), silver bluestem (*Bothriochloa saccharoides*), and meadow dropseed (*Sporobolus asper*). Mid-grass Texas wintergrass (*Nassella leucotricha*) and the annual grass, Japanese brome (*Bromus japonicus*), are the major C_3 grasses. Soils are variable on the Kite Camp with approximately 50 percent shallow clays (3 to 8 percent slopes), 40 percent moderately deep clay-loams (1 to 3 percent slopes), and 10 percent deep loamy bottomlands in riparian zones (0 to 1 percent slopes). The clay-loam areas are where mesquite size, density, and cover are greatest and pose the greatest problems for livestock management.

Mesquite Treatments

The experiment consisted of four treatments with two replicate pastures of 1,400 to 2,100 ha each per treatment. Initial treatments were (1) continuous grazing with no mesquite treatment, (2) a 4-pasture, 3-herd rotation where one pasture was burned each year (4:3F), (3) a 4-pasture, 1-herd rotation where one pasture was burned each year (4:1F), and (4) an 8-pasture, 1-herd rotation where two pastures were burned each year (8:1F). A total of 34 paddocks were involved in the study (2 in continuous, 8 in 4:3s, 8 in 4:1s, 16 in 8:1s). Area of paddocks within each system were not exactly the same but were roughly 25 percent of the total area in four pasture systems and 12.5 percent of the total area in eight pasture systems. Paddocks were fenced in 1995 and first burns were conducted in January-March 1996. Fires were applied as headfires that were burned into pre-burned blacklines (50 m wide) according to procedures outlined by Wright and Bailey (1982).

In the fire-based systems, the goal was to burn a different 25 percent of the area of each system each year. Burns were conducted in winter months (January to March) and were planned as high-intensity mesquite top-killing fires to maximize mesquite suppression. To accumulate herbaceous fuel on the 25 percent to be burned, cattle were rotationally grazed on the remaining 75 percent of each system for 4 to 6 months *without* a reduction in stocking rate determined for the entire system. Thus, costs of deferral were internalized. Fire was to be used when average or above-average precipitation resulted in sufficient fine fuel ($> 1,500 \text{ kg ha}^{-1}$) to suppress mesquite. During drought years deferred pastures were not burned but grazed as needed.

A severe spring drought following 1996 fires forced us to discontinue the 4:3 system and in 1998 these pastures were converted to 4:1 systems with herbicide as the method of mesquite control. These paddocks had an initial fire in one paddock in 1996 and herbicide aerial spray in the other paddocks in 1999 (0.28 kg/ha clopyralid+0.28 kg/ha triclopyr; see Ansley and others 2003). This treatment was designated as 4:1 fire+herbicide (4:1F+H). Herbicide spray was

concentrated on the clay loam soils where mesquite cover was greatest. Most of the mesquite on shallow soils was not sprayed because of light cover and density.

Livestock were managed in each pasture as a cow-calf operation (Hereford breed). Cattle stocking rates were maintained at similar levels in all systems throughout the study and were initially set at 7 ha per cow in 1995. Rates were reduced to 11 ha per cow in 1996 and 14 ha per cow by 2001 following several droughts.

Mesquite Cover Quantification

Color infrared (CIR) aerial images of Kite Camp (1:7,000) were taken in October 1995 and September 2000. Images were scanned and geo-referenced in Arcview GIS using ortho-quads available from the USGS (Ansley and others 2001). Green vegetation appears as varying shades of pink or red on CIR images. Normally, on late summer/early fall images, mesquite canopies appear as a bright pink color and the herbaceous understory is light gray. However, because of well-above average precipitation, herbaceous vegetation remained green throughout 1995 and it was not possible to use the automated color classification system within ArcView to digitally separate mesquite cover from understory vegetation because both vegetation types had similar shades of pink. We could visually discern individual mesquite canopies from the understory, however, because canopy margins cast a small shadow. Therefore, mesquite cover was quantified on the images using a variation of the line intercept technique (Canfield 1941). Two 1 ha (100 x 100 m) plots each were randomly located on clay loam and shallow soil types on images of each paddock of each system. Ten parallel computer generated lines, each scaled at 100 m length, were placed in each 1 ha plot and mesquite canopy intercept was measured manually along each line using the distance measure feature in Arcview (after Ansley and others 2003). Cover values from images were verified with field transects ($r^2 = 0.94$; $\hat{y} = 0.97x - 0.98$; $n = 12$). The same process was used for images taken in 2000, although color separation between mesquite canopies and understory was very good. Cover was determined on 1,360 separate 100 m transect lines (34 paddocks x two soil types/paddock x two 1-ha plots/soil type x 10 lines/plot); far more than would be possible using field measurements.

Plot-level changes in mesquite cover were scaled to the system (pasture) level for each system (4:1, 8:1, etc). Scale factors were percent area of each soil type (shallow or clay loam) in each paddock and percent area of each paddock relative to the total area of each system. Riparian areas were excluded from the analysis.

Statistical Analysis

Mesquite percent change values relative to pre-treatment levels were analyzed using a completely randomized design with treatment (Continuous, 4:1F, 8:1F and 4:1F+H) or paddock (1-4 or 1-8) as the main effect (two replicates per treatment or paddock) (SAS 1988). Percentage data were

arc-sine transformed prior to analysis. Means were separated using LSD ($P < 0.05$).

Results and Discussion

Precipitation and Fire History

The 1995 growing season (March-October) was much wetter than average, followed by an extremely dry period from November 1995 through June 1996 (fig. 1). Severe growing season droughts were experienced in 1996, 1998, and 2000. The years 1997 and 1999 had key periods during each growing season when precipitation was less than average and, with the exception of the July-August period in 1997, there was no 2-month period from 1996 through 2000 when precipitation during the growing season was much above average.

A burn ban due to drought during most of February-March 1996 limited burning to five of the eight paddocks that were scheduled to burn. One paddock in the remaining unburned pasture was burned in 1997 to equalize replicates so that one paddock had been burned in every system. Droughts in 1996 and 1998 reduced grass production, which limited the number of paddocks that were burned to 14 of the original 36 that were planned (table 1).

With the exception of the 1996 fires, droughts also limited the intensity of fires because of low herbaceous fine fuel amounts. In addition, intensity of the 1998 fires was limited because a wet and warm January-February 1998 increased C_3

grass growth and green tissue content in the fine fuel retarded combustion. Of the 14 fires conducted, 6 had high (60 to 90 percent), 4 had moderate (40 to 60 percent), and 4 had poor (10 to 40 percent) levels of mesquite top-kill (table 2). As expected, none of the fire treatments killed more than 2 percent of the mesquite and most plants re-sprouted from stem bases following top-killing fires. The herbicide treatments root-killed over 60 percent and top-killed nearly 100 percent of the mesquite plants. Herbicide results were viewed as typical for this mixture (Ansley and others 2003; Mitchell and others 2004). Detailed summaries of herbaceous vegetation responses and cattle performance are available elsewhere (Teague and others 2001a).

Mesquite Cover Changes Within Each Soil Type

In continuous-grazed, untreated systems, mesquite cover increased on clay loam soils from 22.3 to 35.6 percent from 1995 to 2000, an increase of 13.3 percentage units, or 2.7 percentage units per year. This is a slightly faster rate of cover increase than the 2.2 percentage unit per year rate that Ansley and others (2001) found over a 20-year period on a clay loam site near the current study area. On shallow soils in the continuous-grazed, untreated systems, mesquite cover increased from 5.8 to 6.9 percent from 1995 to 2000, or 0.2 percentage units per year. Mesquite cover was not high on shallow soils at study initiation and did not increase at a rate that was considered a management problem. However,

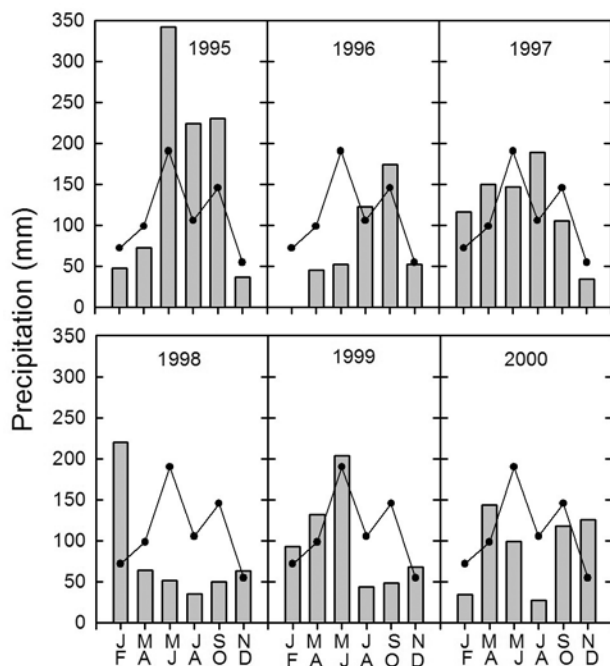


Figure 1. Bi-monthly precipitation at the research site from 1995-2000. Line indicates 30-yr average precipitation for each 2-month period.

Table 1. Planned burns vs. completed burns on the Kite Camp study, 1996-2000.

Burn dates	Paddocks planned to burn	Paddocks burned	Comments
Jan-March 1996	8	5	Burn ban Feb-March
Jan-March 1997	8	1	1996 drought - low fine fuel
Jan-March 1998	8	6	Feb - March very wet, green
Jan-March 1999	6	0	1998 drought - low fine fuel
Jan-March 2000	6	2	High <i>Opuntia</i> ; low fuel in one
1996 - 2000	36	14	

¹ Planned burns were reduced from eight to six in 1999 because two systems were changed from fire to herbicides as the means for mesquite control.

Table 2. Effectiveness of prescribed fires on mesquite topkill, Kite Camp.

Burn year	Good topkill 60 - 90 %	Moderate topkill 40 - 60 %	Poor topkill 20 - 40 %
1996	4	1	0
1997	0	1	0
1998	1	2	3
2000	1	0	1
1996-2000	6	4	4

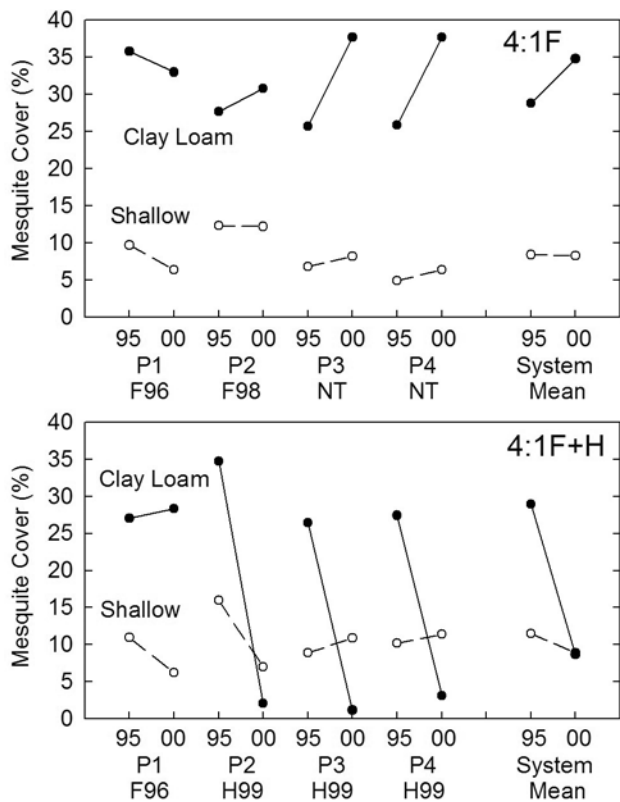


Figure 2. Mesquite cover from 1995 to 2000 within each paddock (P) and soil type (clay loam = solid; shallow = open) and the mean of all four paddocks in 4:1F (top) and 4:1F+H (bottom) systems (n = 2). F = fire, H = herbicide, NT = no treatment.

mesquite did attain a level of dominance on clay loam soils over the 5-year period of the study that was of considerable management concern. Ansley and others (2004) found on a clay loam site near the current study site that mesquite cover did not reduce C_4 midgrass production until it was greater than 25 percent. However, at that point C_4 midgrass production declined sharply to levels that were 25 percent of the maximum recorded values (50 g m^{-2} vs 200 g m^{-2}). Thus, an increase in mesquite cover on clay loam soils in the present study from 22 to 36 percent would be expected to reduce C_4 midgrass production to a much greater degree in 2000 than in 1995, assuming similar climatic conditions.

Increases in mesquite cover in untreated paddocks of the 4:1F systems followed a similar pattern as that of the continuous-grazed, untreated systems (fig. 2). In untreated paddocks 3 and 4, cover increased slightly on shallow soils and from about 26 percent to 38 percent on clay loam soils. Responses were similar on each soil type in untreated paddocks of the 8:1F systems (data not shown). Thus, the type of grazing pattern (continuous, 4:1 or 8:1) did not appear to affect the rate of mesquite cover increase on either soil type if mesquite was left untreated. Thus, rotational grazing alone (that is, without fire or some other mesquite treatment) did not increase the competitive ability of the herbaceous community to slow the rate of mesquite canopy growth, as measured by aerial cover.

In treated paddocks in each system, mesquite cover changes on each soil type varied considerably with treatment type

and/or intensity. In the 4:1F systems, paddocks 1 and 2 were burned in 1996 and 1998, respectively. The 1996 fire, which was very intense, initially reduced mesquite cover on clay loam soils from 36 percent to less than 10 percent (data not shown). However, by 2000, mesquite cover had increased due to mesquite regrowth to levels that were only slightly lower than in 1995 on both soil types (fig. 2). The 1998 fires were much less effective in top-killing mesquite than the 1996 fires. As a result, by 2000, mesquite cover had increased on clay loam soils to levels that were greater than the initial level of 27 percent. This was a slower rate of increase than what was found in the untreated paddocks 3 and 4, however. Clearly, the fires reduced the rate at which mesquite cover increased. Averaged over the four paddocks in the 4:1F systems, cover increased on clay loam soils from 29 to 35 percent and did not change on shallow soils (fig 2). Averaged over the eight paddocks in the 8:1F systems, cover increased on clay loam soils from 32 to 35 percent and did not change on shallow soils (data not shown in a figure).

In the 4:1F+H systems, the 1996 fire in paddock 1 of each replicate yielded a similar result as found for paddock 1 in the 4:1F systems (fig. 2). The other three paddocks were treated with herbicides in 1999 that reduced mesquite cover on clay loam soils to < 5 percent. Much of the mesquite that occurred on shallow soils was not sprayed because of light cover and density. When averaged over the four paddocks, mesquite cover in the 4:1F+H systems was reduced from 30 percent to 9 percent on clay loam soils and from 12 to 8 percent on shallow soils. These results agree with what other studies have found for this clopyralid+triclopyr treatment (Ansley and others 2003; Mitchell and others 2004). This treatment is not only effective at reducing mesquite cover but also reduces mesquite density (root-kill is usually 60 to 70 percent) and has a treatment life of > 20 years (Ansley and others 2004). However, typical cost for this treatment is \$25 per acre compared to \$2 to 3 for fire (Teague and others 2001b).

Scaling Mesquite Cover Responses Over Soil Types

Following scaling mesquite cover changes over both soil types in each paddock, the 1996 fires (paddock 1) were the only treatment in the 4:1F systems that reduced mesquite cover from 1995 to 2000 (fig. 3). Cover increased in the other three paddocks but at a slower rate in paddock 2 due to the 1998 fires. In contrast, the four paddocks that received prescribed fire in the 8:1F systems all yielded lower mesquite cover in 2000 than 1995. In this treatment, the most recent fires were in the year 2000 (paddock 4) just 8 months prior to the date of the 2000 CIR images. We were unable to burn in the 4:1F systems after 1998 because droughts prevented grazing deferral on 25 percent of the system. The remaining 75 percent of the system simply could not sustain the herd for any length of time even though stocking rates had been reduced for each system. We were able to burn one paddock in each of the 8:1 systems in 2000 because we could defer grazing in 1/8 of the area of each system and rotate the herd on the remaining 7/8 of the area.

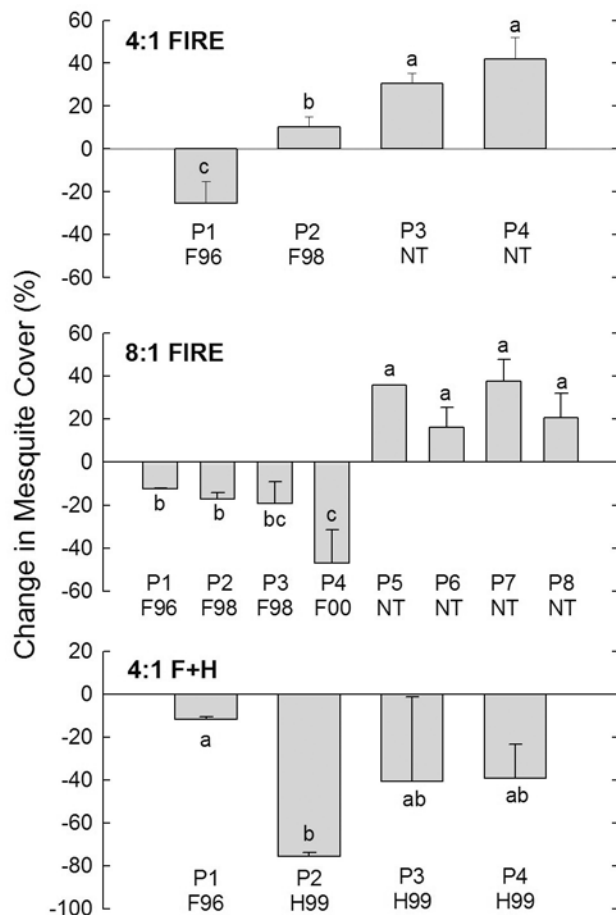


Figure 3. Percent change in mesquite cover from 1995 to 2000 within each paddock (P) in 4:1F, 8:1F, and 4:1F+H systems when scaled over both soil types. Error bars indicate ± 1 S. E. ($n = 2$). Means with similar letters are not significant at $P < 0.05$.

In the 4:1F+H systems, mesquite cover decreased from 1995 to 2000 in all four paddocks (fig. 3) due to the intense fire in 1996 (paddock 1) and the herbicide treatments in the other three paddocks. The reason mesquite cover reduction was greater in paddock 2 than paddocks 3 and 4 was because there was more clay loam soil in paddock 2 and therefore more area was sprayed. Paddocks 3 and 4 had a high percentage of shallow soils.

Scaling Mesquite Cover Changes Over Soils and Paddocks

Net change in mesquite cover, when scaled over soil type and area of each paddock within each system, was +34 percent, +15 percent, +5 percent, and -41 percent in the Continuous, 4:1F, 8:1F, and 4:1F+H systems, respectively (fig. 4). Mesquite cover was reduced only in the fire+herbicide system during the period of the study. However, the rate of system-level increases in mesquite cover were much lower in the 4:1F and 8:1F systems compared to the continuous grazed, untreated systems. In addition system-level increases in mesquite cover were slower in the 8:1F than the 4:1F systems.

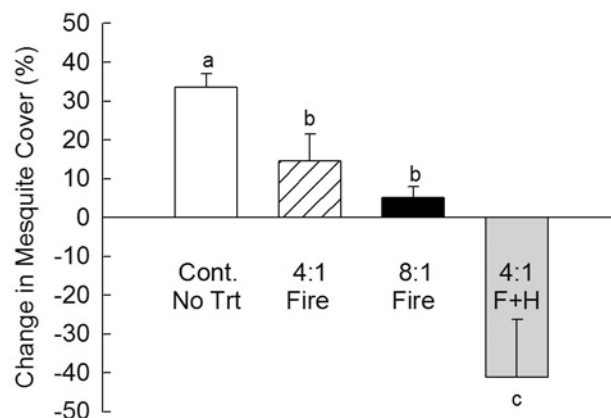


Figure 4. Percent change in mesquite cover from 1995 to 2000 within each management system when scaled over area per paddock in each system and area per soil type within each paddock. Error bars indicate ± 1 S. E. ($n = 2$). Means with similar letters are not significant at $P < 0.05$.

Conclusions

Rotational grazing and fire systems (4:1F and 8:1F) slowed the rate of increases in mesquite cover but did not reduce it within the time-frame of this study. Severe droughts in 1996, 1998, and 2000 limited burning to only 14 paddocks in 5 years compared to the original goal of 36. It should be noted, however, that, while we did not conduct the number of fires intended over the scheduled time frame, we were able to conduct more fires during these periods of severe drought than any ranch in the region. This was attributed to the utilization of rotational grazing systems. As a result, increases in system-level mesquite cover were lower in both fire-only systems compared to the untreated system.

System-level rate of mesquite cover increase was slower in the 8:1F than the 4:1F systems. We believe that one of the most significant discoveries in this study was that fire was easier to apply in the 8:1F than the 4:1F systems during droughts because the area deferred and burned could be reduced to 1/8 (that is, one paddock) instead of 1/4 of the total area of the system. Eight paddocks provided more flexibility for burning in drought years than did four paddock systems.

Mesquite cover was reduced to a much greater degree in the fire+herbicide systems than the two fire-only systems. We believe the fire-only systems would have been more effective at suppressing mesquite had precipitation been near average. One of the advantages of the herbicide option is that, unlike prescribed fire, it requires virtually no pre-planning and is not as dependent as is a fire plan on long-term weather patterns. However, typical cost for this treatment is \$25 per acre compared to \$2-3 for fire (Teague and others 2001b).

Acknowledgments

The authors wish to acknowledge Kelli Barnett and Betty Kramp who quantified mesquite cover on the aerial images.

David Jones, Betty Kramp, Gerral Schulz, Steve Dowhower, Tim Tunnell, Matt Angerer, Doug Tolleson, Bob Cross, and many others assisted with the prescribed fires. This research was funded by grants from USDA-NRI Managed Ecosystems, Dow AgroSciences, Indianapolis, IN, and the North Texas Brush Control Association, Albany, TX. The E. Paul and Helen Buck Waggoner Foundation, Vernon, TX, provided significant funding, land area, and cattle for the project and Waggoner Ranch personnel assisted with all phases of live-stock handling.

References

- Ansley, R. J.; Jones, D. L.; Tunnell, T. R.; Kramp, B. A.; Jacoby, P. W. 1998. Honey mesquite canopy responses to single winter fires: relation to fine fuel, weather and fire temperature. *International J. Wildland Fire*. 8: 241-252.
- Ansley, R. J.; Jacoby, P. W. 1998. Manipulation of fire intensity to achieve mesquite management goals in north Texas. Pages 195-204. In: Pruden, T. L.; Brennan, L. A. (eds). *Fire in Ecosystem Management: Shifting the Paradigm from Suppression to Prescription*. Tall Timbers Fire Ecology Conf. No. 20. Tall Timbers Research Station, Tallahassee, FL.
- Ansley, R. J.; 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.
- Ansley, R. J.; Kramp, B. A.; Jones, D. L. 2003. Converting mesquite thickets to savanna through foliage modification with clopyralid. *Journal of Range Management*. 56: 72-80.
- Ansley, R. J.; Teague, W. R.; Pinchak, W. E.; Kramp, B. A.; Jones, D. L. 2004. Long-term grass yields following chemical control of honey mesquite. *Journal of Range Management*. 57: 49-57.
- Archer, S.; Schimel, D. S.; Holland, E. A. 1995. Mechanisms of shrubland expansion: land use, climate or CO₂? *Climatic Change*. 29: 91-99.
- Bedunah, D. J.; Sosebee, R. E. 1984. Forage response of a mesquite-buffalograss community following range rehabilitation. *Journal of Range Management*. 37: 483-487.
- Blackburn, W. H.; Tueller, P. T. 1970. Pinyon and juniper invasion in black sagebrush communities in east-central Nevada. *Ecology*. 51: 841-848.
- Canfield, R. H. 1941. Application of line interception in sampling range vegetation. *Journal of Forest*. 39: 388-394.
- Carlson, D. H.; Thurow, T. L.; Knight, R. W.; Heitschmidt, R. K. 1991. Effect of honey mesquite on water balance of Texas Rolling Plains rangeland. *Journal of Range Management*. 43: 491-496.
- Dahl, B. E.; Sosebee, R. E.; Goen, J. P.; Brumley, C. S. 1978. Will mesquite control with 2,4,5-T enhance grass production. *Journal of Range Management*. 31:129-131.
- Koos, W. M.; Williams, J. C.; Dixon, M. L. 1962. Soil survey of Wilbarger County, Texas. USDA Soil Conservation Service, Soil Survey Series 1959 No. 18, Fort Worth, TX.
- Kramp, B. A.; Ansley, R. J.; Tunnell, T. R. 1998. Survival of mesquite seedlings emerging from cattle and wildlife feces in a semi-arid grassland. *The Southwestern Naturalist*. 43: 300-312.
- Mitchell, R.; Whisenant, S.; Sosebee, R. 2004. A paradigm shift. Chap. 6, pages 67-75. In: W. T. Hamilton and others (Editors), *Brush Management—Past, Present and Future*. Texas A&M University Press, College Station, TX.
- SAS. 1988. SAS/STAT User's Guide Version 6.03, SAS Inst., Inc., Cary, N.C.
- Scifres, C. J.; Hamilton, W. T. 1993. Prescribed burning for brushland management: The south Texas example. Texas A&M Press, College Station, Texas.
- Teague, R.; Borchert, R.; Ansley, J.; Pinchak, B.; Cox, J.; Foy, J.; McGrann, J. 1997. Sustainable management strategies for mesquite rangeland: the Waggoner Kite project. *Rangelands* 19: 4-8.
- Teague, W. R.; Ansley, R. J.; McGrann, J. M.; Pinchak, W. E. 2001a. Developing sustainable grazing management strategies for mesquite rangeland. Pages 493-502. In: *Proceedings: First National Conference on Grazing Lands—Heightening the Awareness of the Economic and Environmental benefits of Grazing Lands*, Las Vegas, Nevada, 5-8 Dec. 2000.
- Teague, W. R.; Ansley, R. J.; Kreuter, U. P.; Pinchak, W. E.; McGrann, J. M. 2001b. Economics of managing mesquite in north Texas: a sensitivity analysis. *J. Range Management* 54: 553-560.
- Wright, H. A.; Bailey, A. W. 1982. *Fire ecology—United States and southern Canada*. Wiley-Interscience, John Wiley & Sons, New York.

The Authors

¹ Professor of Rangeland Shrub and Fire Ecology, Texas Agricultural Experiment Station, Vernon, TX. r-ansley@tamu.edu

² Professor of Range Animal Nutrition, Texas Agricultural Experiment Station, Vernon, TX.

³ Professor of Rangeland Ecology, Texas Agricultural Experiment Station, Vernon, TX.

Modeling Erosion on Steep Sagebrush Rangeland Before and After Prescribed Fire

Corey A. Moffet¹

Frederick B. Pierson²

Kenneth E. Spaeth³

Abstract: Fire in sagebrush rangelands significantly alters canopy cover, ground cover, and soil properties that influence runoff and erosion processes. Runoff is generated more quickly and a larger volume of runoff is produced following prescribed fire. The result is increased risk of severe erosion and downstream flooding. The Water Erosion Prediction Project (WEPP), developed to model erosion on cropland, forest, and rangeland, is a tool that has the potential to model erosion and help managers address erosion and runoff risks following fire. WEPP views erosion as two processes: interrill and rill. Experimental results on a steep (35 to 50 percent slope) sagebrush site suggest that rill erosion is the dominant erosion process following fire and must be adequately understood so that models can provide reliable predictions. Evaluation of WEPP parameterization equations using data from steep burned sagebrush rangelands suggests that critical parameter estimation procedures within WEPP need improvement to include fire effects on infiltration and rill erosion processes. In particular, rill detachment estimates could be improved by modifying regression-estimated values of rill erodibility. In addition, the interactions of rill width and surface roughness on soil grain shear estimates may also need to be modified. In this paper we report the effects of prescribed fire on runoff and soil erosion and compare WEPP estimated erosion for several modeling options with measured erosion.

Introduction

Current trends in soil erosion modeling under various management scenarios consist of analyzing erosion in probabilistic terms to account for storm variability and provide accurate event-based erosion estimates (Elliott and others 2001). Under this paradigm, it is not sufficient if a model significantly underestimates large events or overestimates small events, but does well for long-term averages. The physically-based Water Erosion Prediction Project (WEPP) model (Flanagan and others 1995) is a model that has been used to provide event-level erosion estimates (Robichaud and others 2003).

Soto and Diaz-Fierros (1998) measured runoff and erosion from natural rainfall on burned and non-burned plots with similar vegetation, slopes, and soil textures on shrublands in northwest Spain over a 4-year period. Total runoff from the control was only 59 percent of that from the burned area during the 4 years of study. Measured erosion was significantly higher from the burned area than from the control during the first 2 years after fire.

Soto and Diaz-Fierros (1998) compared measured and WEPP estimated soil water content, runoff, and erosion on burned and non-burned sites. Their comparisons excluded events during May through September when the soil was dry and water repellent. They reported that WEPP did reasonably well at predicting runoff and erosion values, although they reported that on severely burned areas, erosion estimates were consistently underestimated. In one erosion measurement period (6 to 10 months post-burning), WEPP grossly

underestimated erosion for control and prescribed burn plots that they attribute to the fact that the erosion all occurred during one large rainfall event (50.3 mm) when water repellency was severe. Soto and Diaz-Fierros (1998, p. 268) concluded, “the model shows a clear tendency to underestimate erosion following severe burns.”

The objectives of this paper were to: (1) evaluate differences in runoff and erosion on a steep mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) community between burned and non-burned conditions; (2) test the capability of rangeland WEPP for estimating runoff and erosion for burned and non-burned conditions; and (3) suggest how improvements in rangeland WEPP might better represent fire impacts on rangelands.

WEPP

The WEPP model treats interrill and rill erosion as separate processes (Flanagan and others 1995). Interrill erosion is a function of soil interrill erodibility (K_i , adjusted for canopy and ground cover in the interrill area), effective rainfall intensity, interrill runoff rate, interrill sediment delivery ratio (computed as a function of random roughness), and runoff duration (Foster and others 1995; Foster 1982). Interrill erosion on undisturbed rangeland has been well studied and is typically low (Pierson and others 2001).

In WEPP, rill erosion is a function of rill detachment capacity, sediment load, transport capacity, rill width, runoff duration, and rill spacing. Rill detachment capacity is modeled

In: Sosebee, R.E.; Wester, D.B.; Britton, C.M.; McArthur, E.D.; Kitchen, S.G., comp. 2007. Proceedings: Shrubland dynamics—fire and water; 2004 August 10-12; Lubbock, TX. Proceedings RMRS-P-47. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 173 p.

as a function of excess soil shear stress (Foster and others 1995, Foster 1982):

$$D_{rc} = \begin{cases} K_r (\tau_{fe} - \tau_c); & \tau_{fe} > \tau_c \\ 0; & \tau_{fe} \leq \tau_c \end{cases} \quad [1]$$

where D_{rc} is the rill detachment capacity ($\text{kg m}^{-2} \text{s}^{-1}$), τ_{fe} is the soil shear stress due to rill flow at the end of the uniform slope (Pa), τ_c is the critical soil shear stress (Pa) that is required for detachment initiation, and K_r is the rill erodibility (s m^{-1}).

The values for K_r and τ_c are WEPP input parameters. In rangeland WEPP, these parameters are determined based on soil properties and do not vary with management, but τ_{fe} is a function of ground cover and soil surface characteristics, slope, and rill flow characteristics:

$$\tau_{fe} = \gamma R_h \sin(\tan^{-1}(S)) \left(\frac{f_s}{f_t} \right) \quad [2]$$

where γ is the specific weight of water (N m^{-3}), R_h is the hydraulic radius of the rill flow (m), S is the slope of the energy gradient (assumed equal to the soil surface slope, fraction m/m), f_s is the Darcy-Weisbach roughness coefficient due to soil grains (assumed to be 1.11), and f_t is the total Darcy-Weisbach roughness coefficient due to soil grains, ground cover (litter, rock, plant bases, and cryptogams), and random roughness. The Darcy-Weisbach roughness coefficient used in rangeland WEPP is empirically estimated from ground cover and random roughness parameters.

The rill hydraulic radius (R_h) is the ratio of flow cross-sectional area ($A = wd$) to wetted perimeter ($P = 2d + w$), both are functions of width (w) and depth (d). In WEPP, rills are assumed of rectangular shape with width a function of rill discharge rate (q , $\text{m}^3 \text{s}^{-1}$):

$$w = 1.13q^{0.303}. \quad [3]$$

Given the rill discharge rate, slope, width, and Darcy-Weisbach roughness coefficient, depth is computed by WEPP.

For a given storm, infiltration and therefore runoff volume are affected by the effective hydraulic conductivity (K_e) and the matric potential gradient across the wetting front, but not f_t . Peak discharge, q_{peak} (and therefore q), and runoff duration, t_{RO} , however, are sensitive to f_t . As f_t increases, q_{peak} decreases and t_{RO} increases.

For a given discharge rate the excess soil grain shear stress computed by WEPP is a function of only one factor affected by management—the Darcy-Weisbach roughness coefficient. In the current version of WEPP any effect of management on estimated rill erosion must be expressed through differences in runoff and Darcy-Weisbach roughness coefficients among the management scenarios.

Material and Methods

The study area is located in the Reynolds Creek Experimental Watershed in southwest Idaho near the divide

between Reynolds Creek and Dobson Creek watersheds ($43^\circ 6' 30'' \text{ N}$; $116^\circ 46' 50'' \text{ W}$). The elevation of the research site is about 1,750 m and mean annual precipitation is approximately 549 mm.

The vegetation was a typical mountain big sagebrush community with subdominant shrubs of rabbitbrush (*Chrysothamnus viscidiflorus*), antelope bitterbrush (*Purshia tridentata*), and widely scattered juniper (*Juniperus occidentalis*), and dominant grasses were bluebunch wheatgrass (*Pseudoroegneria spicata*) and Idaho fescue (*Festuca idahoensis*). The soils are mapped Kanlee-Ola-Quicksilver association, 3 to 50 percent slopes. All plots in the study are on the deeper Kanlee and Ola series. The slopes of the study area are 35 to 50 percent with an east facing aspect on granite bedrock hillslopes. Soil textures are coarse sandy loam in the surface 30 cm and loam or coarse sandy loam in the subsoil that extends beyond 100-cm depth. Rock fragment (>2 mm diameter) content in the surface layer is about 5 to 15 percent and ranges between 5 and 50 percent in the subsoil. Soil water content during all phases of this research was low (approximately 0.03 kg kg^{-1}).

Sixteen rectangular plots (6.5 m long by 5 m wide) were selected within a narrow elevation band near the top of the hillslope prior to prescribed fire. Eight plots each were assigned to the non-burned and burned treatments. Plots in the non-burned treatment were characterized (canopy and ground cover, slope, and random roughness) and rainfall simulations were performed in August and early September. The prescribed fire was ignited in late September and a head fire burned the study area. The burned plots were characterized and simulated rainfall was applied in October.

Rainfall was applied on two plots each day with a Colorado State University (CSU) type rainfall simulator (Holland 1969) at a rate of 61 mm hr^{-1} for 1 hr; however, observed application rates differed from the design due to mechanical difficulties and wind. The observed range was 45.3 to 76.1 mm. Several samples of rainfall that fell directly in the runoff collection trough were collected during the first several minutes of each simulation. Timed samples (500 ml to 1,000 ml) were collected approximately every minute. The mass of sediment and volume of water collected in each sample was determined in the laboratory. The mean trough catch that would have been collected during the sample time was subtracted from each sample volume.

Vegetation cover, ground cover, slope, and surface random roughness were sampled in each large plot prior to the rainfall simulations with 100 evenly-spaced point samples recorded along six horizontal transects (0.5, 1.5, 2.5, 3.5, 4.5, and 5.5 m from the upslope end of a plot). At each point the relative elevation of the ground surface (measured to the nearest mm), the ground cover class and the canopy cover class (if present) were recorded. Vegetation and litter mass were determined by harvesting all standing plant material by functional group and collecting litter from 30 small (1 m^2) plots nearby. The vegetation and litter samples were oven-dried and weighed.

Three parameterization schemes were used to explore the WEPP rill erosion estimation capabilities. The first scheme

(Option A) used readily available data; infiltration and erosion parameters were computed by WEPP from soil and cover data. The next scheme (Option B) used optimized effective hydraulic conductivity (K_e) values to match total runoff on a plot by plot basis. Option C used the (K_e) values from Option B, and optimized rill erodibility (K_r) values and 0.0001 for critical shear (τ_c).

In all scenarios, the soil data were those available in the 1995 WEPP soils database. Initial saturation was always adjusted to 25 percent and K_e and K_r were adjusted as described above. The management data were written to run WEPP for rangelands in event mode using measured canopy cover, ground cover (litter, plant base, cryptogam, and rock), and random roughness to parameterize the initial condition section for each plot. Precipitation data were based on the measured simulated rainfall on each plot. Pattern parameters were assumed to be the same on all plots (duration of 1 hr, peak intensity of 1.01 times the mean intensity, and time to peak intensity at 20 percent of the simulation duration).

One-way analysis of variance was used to test the significance of treatment effects on response variables. Since only two treatment levels were studied, a significant F-test indicated that the means were different. Welch's *t*-test was used within each treatment to compare WEPP estimated responses with measured responses.

Results and Discussion

Plot and Simulation Characteristics

Total precipitation applied and plot slope were similar for burned and non-burned treatments (table 1). On burned plots, almost no standing material remained except occasional bitterbrush shrub skeletons (sagebrush was consumed to within 5 cm of the soil surface). Average canopy cover of the shrub skeletons was 0.2 percent.

The burn treatment significantly reduced total litter, plant basal cover, and canopy cover (table 1). Litter cover outside the plant canopy (ashy unconsumed litter and wood) was not different between the burned and non-burned treatments even though the fire reduced total litter cover. This was because the total area outside the canopy significantly increased following the fire. Random roughness was significantly less in burned than in non-burned treatment plots (table 1). This was most likely due to much of the root crowns and litter under shrubs being consumed during the fire. The burned treatment plots had greater rock cover compared to the non-burned treatment plots (table 1). However, a 0.5 percent increase in rock cover in burned plots probably had little or no effect on hillslope hydrologic or erosion responses.

Mass of litter and vegetation were reduced by fire (table 1). Litter accumulation, including dung, and wood accounted for nearly 45 percent of the total mass of above ground organic matter. Litter in non-burned treatment plots was not uniformly distributed on the ground, but rather occurred as a thick almost continuous layer under canopies and patchy thin

Table 1. Comparison of site and simulation characteristics between burned and non-burned treatments. Means for a characteristic followed by the same letter are not significantly different.

Characteristic	Units	Burned	Non-burned
Precipitation	mm	59.1 a	61.4 a
Slope	%	41.6 a	40.8 a
Random roughness	mm	10.8 b	21.1 a
Ground Cover ^a			
Litter below canopy	%	0.1 b	49.6 a
Rock below canopy	%	0.0 a	0.1 a
Basal cover below canopy	%	0.0 b	1.3 a
Litter outside canopy	%	23.3 a	24.7 a
Rock outside canopy	%	1.0 a	0.3 b
Basal cover outside canopy	%	0.0 b	0.6 a
Canopy cover	%	0.2 b	57.0 a
Litter total	%	23.4 b	74.3 a
Rock total	%	1.0 a	0.5 b
Basal cover total	%	0.0 b	1.9 a
Bare ground total	%	75.6 a	24.3 b
Ground litter	kg ha ⁻¹	808 ^b	9517
Vegetation	kg ha ⁻¹	— ^c	12125

^a The sum of litter, rock, and basal cover below canopy and outside canopy and total bare ground is equal to 100.

^b Burned treatment litter samples were collected in the spring and early summer following the fire.

^c Burned treatments vegetation samples were not collected.

accumulations outside canopies. The litter mass in burned treatment plots was 8 percent of that in non-burned plots, but total litter cover on the burned treatment was 31 percent of that on the non-burned treatment. The effect of fire on litter cover reduction was less than its effect on litter mass/volume reduction.

Measured Large Plot Runoff and Erosion

Fire significantly increased total runoff volume from burned plots (16.6 mm) compared to non-burned plots (3.1 mm, fig. 1). All burned plots yielded runoff, whereas three of the eight non-burned plots yielded no runoff. This is consistent with findings from Soto and Diaz-Fierros (1998) who found that wet-season runoff doubled in the first year after fire.

Areas burned by fire generated runoff more quickly than non-burned areas. The mean time to initiation of runoff for burned and non-burned plots was 3.3 min and 7.1 min, respectively (excluding the three non-burned plots with no runoff). Peak runoff rates from burned treatment plots were about three times higher than the non-burned treatment plots (all non-burned plots) and about two times greater than the five non-burned treatment plots with measurable runoff (fig. 1). Regardless of treatment, runoff rates peaked 10 to 20 minutes into the simulated rainfall event and diminished with time thereafter (fig. 1). The decrease in runoff rate with time during the simulation, for both burned and non-burned treatment plots, indicates that the soil in both treatments may have had significant water repellent soil properties. Pierson and others (2001) found significant water repellency in both burned and non-burned plots for similar sites during late summer and early

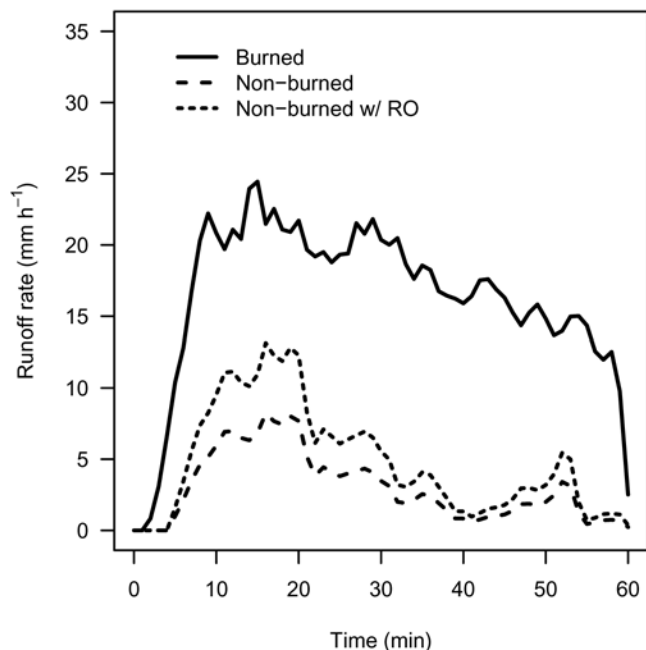


Figure 1. Mean hydrographs for 60-minute simulated rainfalls on burned and non-burned plots ($n = 8$). Three non-burned plots yielded no runoff and the mean hydrograph for the five plots that did generate runoff is also shown (dotted line).

fall when the soils were dry. Soto and Diaz-Fierros (1998) reported that runoff to precipitation ratios for natural rainfall on control and burned plots were significantly greater during periods of high water repellency.

The effect of burning on total soil erosion was also significant ($\alpha = 0.05$, fig. 2). Sediment yield for burned plots was significantly greater (10.7 Mg ha^{-1}) than non-burned plots (0.1 Mg ha^{-1}). Erosion rates in both burned and non-burned treatments were greatest during the first 7 to 20 minutes of the simulated rainfall event and steadily decreased thereafter (fig. 2). Soto and Diaz-Fierros (1998) reported that erosion was higher in burned compared to control plots the first 2 years post fire. In one erosion measurement period, when almost all erosion occurred from one 50.3 mm storm on dry water repellent soils, erosion was 6.6 times greater from burned plots than from control plots (Soto and Diaz-Fierros 1998).

WEPP Estimated Runoff and Erosion

Using WEPP estimated infiltration and erosion parameters (Option A), model predicted runoff was significantly greater than measure runoff regardless of treatment (fig. 3). Predicted runoff was nearly 10 times greater than measured runoff in the non-burned treatment and nearly double in the burned. Burning caused a large increase in measured runoff while model predicted runoff was similar between treatments (fig. 3). This indicates a lack of model sensitivity to burning.

Model predicted erosion was significantly less than measured in burned treatments and significantly greater than measured in non-burned treatments. Predicted erosion was 24 percent less than measured in the burned treatment, but 2.6

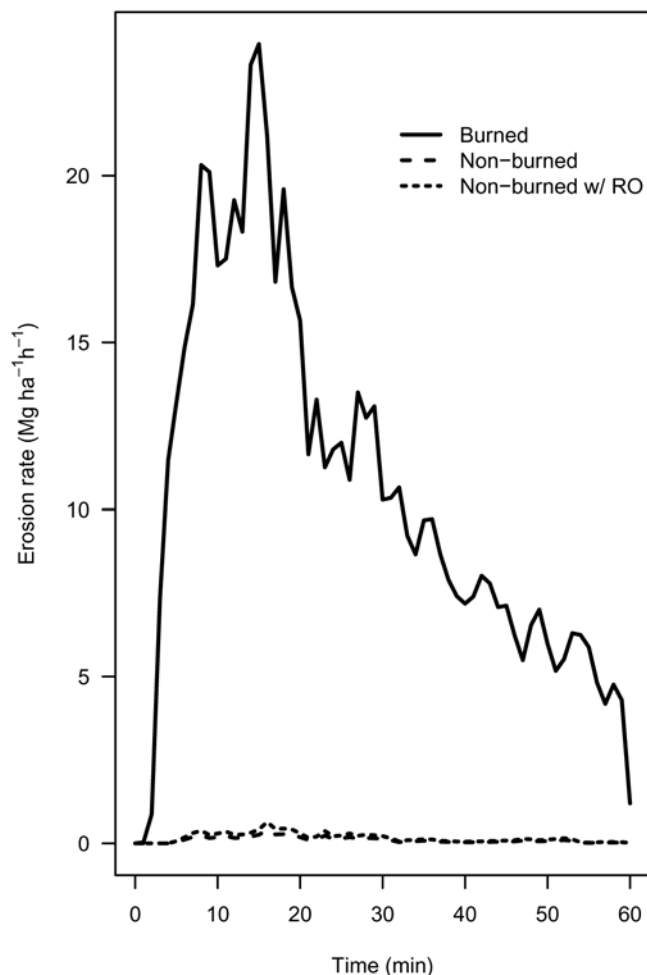


Figure 2. Mean sediment yield for 60-minute simulated rainfalls on burned and non-burned plots ($n = 8$). Three non-burned plots yielded no runoff or sediment and the mean sediment yield response for the five plots that did generate runoff is also shown (dotted line).

times greater in the non-burned. However, model estimates of erosion showed some degree of sensitivity to burning (fig. 4). Interpretation of this sensitivity is complicated by errors in runoff prediction. Because runoff drives the rill erosion process, treatment induced trends in predicted erosion cannot be effectively evaluated.

To correct errors in model predicted runoff (Option B) we used optimized effective hydraulic conductivity (K_e) for each plot which ranged from 6.7 to 32.3 mm h^{-1} for burned and 26.3 to 77.9 for non-burned. These values are two to four times greater than WEPP estimated K_e values used in Option A (table 2). Using optimized K_e values, runoff matched measured runoff within 0.2 mm on all plots (fig. 3).

Using optimized K_e and WEPP estimated erosion parameters (Option B), predicted erosion was 13 percent of measured erosion for the burned treatment and statistically similar for the non-burned treatment (fig. 4). WEPP adequately estimated low erosion for the non-burned condition and showed an increase in erosion due to fire. However, the predicted increase was only 1.3 Mg ha^{-1} compared to a 10.6 Mg ha^{-1} measured

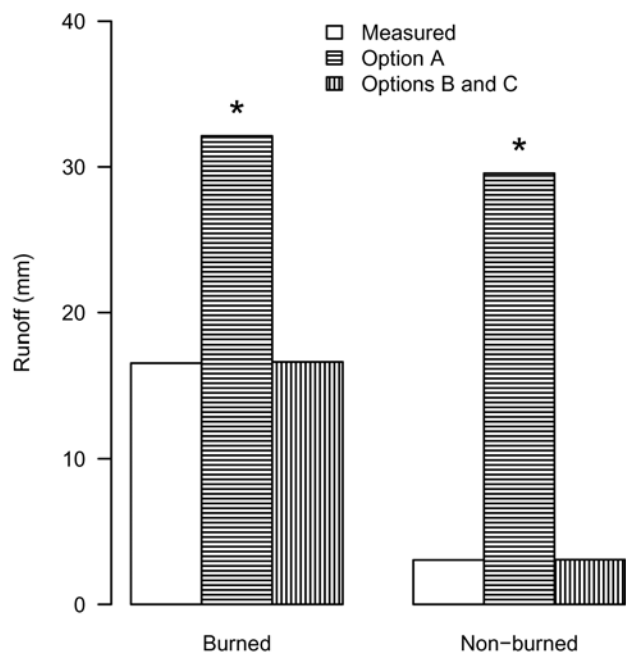


Figure 3. Mean measured and WEPP estimated total runoff for three parameterization options. WEPP estimated values within a treatment that are marked above the bar with an asterisk are significantly different ($\alpha = 0.05$) from the mean measured value.

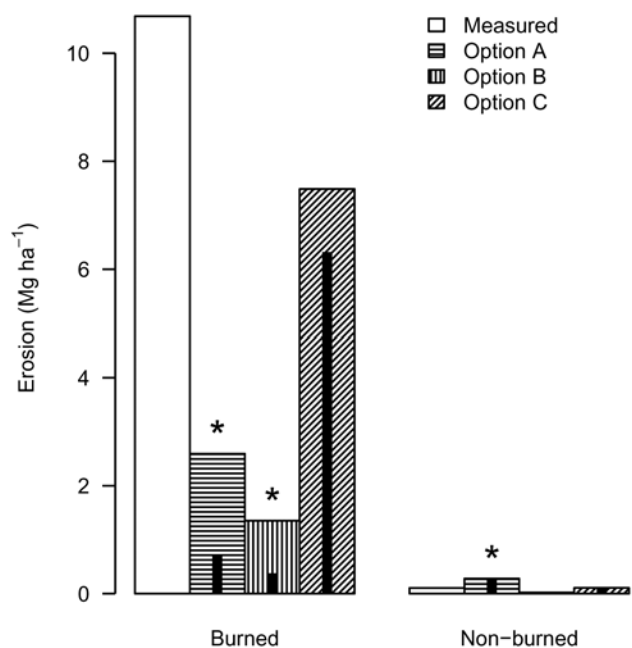


Figure 4. Mean measured and WEPP estimated erosion for three parameterization options. Solid vertical line in the center of each bar is the mean WEPP estimated rill erosion. WEPP estimated erosion values within a treatment that are marked above the bar with an asterisk are significantly different ($\alpha = 0.05$) from the mean measured value.

Table 2. Mean WEPP estimated and optimized runoff and erosion parameters for burned and non-burned treatments.

Parameter	Units	Burned	Non-burned
WEPP estimated			
K_e	mm h ⁻¹	8.97	11.31
K_r	s m ⁻¹ × 10 ³	0.629	0.629
τ_c	Pa	0.939	0.939
$K_{i,adj}^a$	kg s m ⁻⁴ × 10 ⁻⁶	0.3470	0.0001
Optimized values			
K_e	mm h ⁻¹	20.66	44.79
K_r	s m ⁻¹ × 10 ³	67.290	1.132 ^b
τ_c	Pa	0.0001	0.0001

^a Adjusted interrill erodibility.

^b Mean of the five non-burned plots with runoff.

increase. The increase in WEPP estimated erosion due to fire was predominately due to an increase in interrill erosion (fig. 4). Pierson and others (2003) found that for similar sites rill erosion dominated total sediment yield compared to interrill erosion. Therefore, it was assumed the majority of error in WEPP estimated erosion under Option B was due to error in estimated rill erodibility (K_r) and perhaps critical shear (τ_c) parameters.

Optimized K_r values were greater than WEPP estimated values regardless of treatment (table 2). When we optimized K_r values (Option C), WEPP estimated and measured erosion converged (within 0.02 Mg ha⁻¹) in only three of the eight burned plots. The K_r values for these plots ranged from 0.00373 to 0.02470 s m⁻¹ compared to the model estimated value of 0.00063 s m⁻¹. The remaining five burned plots had such high measured erosion values that WEPP under-predicted erosion even using the highest allowable value for K_r (0.09999). On all eight non-burned plots (only five of which produced runoff), good agreement was achieved with optimized K_r values (fig. 4). Optimized K_r values for the non-burned plots ranged from 0.00037 to 0.00296 s m⁻¹ compared with a model estimated value of 0.00063 s m⁻¹ (table 2) that did not vary between burned and non-burned conditions.

Prescribed fire increased K_r values by nearly two orders of magnitude (table 2). It seems reasonable that loss of surface soil organic matter by fire (Soto and Diaz-Fierros 1998) could result in increased rill erodibility. Fire consumes organic matter that binds soil particles together making them more difficult to detach (Pierson and others 2001). Currently, WEPP has no mechanism to incorporate this effect. This paper shows that appropriate adjustments to K_r could provide improved erosion predictions. However, adjustments in WEPP parameter estimation procedures for Darcy-Weisbach roughness coefficients, rill width, and rill depth may also aid in improving rill erosion predictions following fire. Future work will explore these options.

Summary

Runoff and erosion from high intensity storms on steep sagebrush rangeland were greatly increased immediately after prescribed burning. Runoff was generated more rapidly and in larger volume from burned areas compared to non-burned areas. Soil erosion increased 100 times following the prescribed fire. The rangeland WEPP model significantly underestimated soil erosion after fire. The model was unable to achieve agreement with measured erosion values even using optimized infiltration (K_e) and rill erosion parameters (K_r and τ_c). The WEPP model does not currently provide sufficient mechanisms to adequately model the impacts of fire on soil erosion. Improvements are needed in estimated adjustments to K_e and K_r to account for changes in surface cover and organic matter decreases following burning. In addition, adjustments to other factors such as the hydraulic radius and Darcy-Weisbach roughness coefficients need to also be considered.

Literature Cited

- Elliot, W. J.; Robichaud, P. R.; Hall, D. E.; Cuhaciyan, C. O.; Pierson, F. B.; Wohlgemuth, P. M. 2001. A probabilistic approach to modeling erosion for spatially-varied conditions. American Society of Agricultural Engineers Annual Meeting, Sacramento, CA. July 2001. Paper No. 01-8006. 16 p.
- Flanagan, D. C.; Ascough II, J. C.; Nicks, A. D.; Nearing, M. A.; Laflen, J. M. 1995. Chapter 1. Overview of the WEPP erosion prediction model. In: D. C. Flanagan and M. A. Nearing, editors. USDA-water erosion prediction project: Technical documentation. USDA-ARS National Soil Erosion Research Laboratory, NSERL Report No. 10, West Lafayette, IN.
- Foster, G. R. 1982. Modeling the erosion process. In: C. T. Haan; Johnson, H. P.; Brakensiek, D. L. (Eds). Hydrologic modeling of small watersheds. ASAE Monograph No. 5, Saint Joseph, MI.
- Foster, G. R.; Flanagan, D. C.; Nearing, M. A.; Lane, L. J.; Risse, L. M.; Finkler, S. C. 1995. Chapter 11. Hillslope erosion component. In: D. C. Flanagan; Nearing, M. A., editors. USDA-water erosion prediction project: Technical documentation. USDA-ARS National Soil Erosion Research Laboratory, NSERL Report No. 10, West Lafayette, IN.
- Holland, M. E. 1969. Colorado State University experimental rainfall-runoff facility, design and testing of rainfall system. Colorado State University experiment station, CER 69-70 MEH 21.
- Pierson, F. B.; Robichaud, P. R.; Spaeth, K. E. 2001. Spatial and temporal effects of wildfire on the hydrology of a steep rangeland watershed. *Hydrological Processes* 15:2905-2916.
- Pierson, F. B.; Robichaud, P. R.; Spaeth, K. E.; Moffet, C. A. 2003. Impacts of fire on hydrology and erosion in steep mountain big sagebrush communities. p. 625-630. In: Renard, K. G.; McElroy, S. A.; Gburek, W. J.; Canfield, H. E.; Scott, R. L., (eds.) First Interagency Conference on Research in the Watersheds, October 27-30, 2003. U.S. Department of Agriculture, Agricultural Research Service.
- Robichaud, P. R.; Elliot, W. J.; Hall, D. E.; Pierson, F. B.; Moffet, C. A. 2004. Erosion risk management tool (ERMiT). Available at: <http://forest.moscowfs1.wsu.edu/cgi-bin/fswepp/ermit/ermit.pl>, United States Department of Agriculture, Forest Service, Rocky Mountain Research Station, Moscow, ID.
- Soto, B.; Diaz-Fierros, F. 1998. Runoff and soil erosion from areas of burnt scrub: comparison of experimental results with those predicted by the WEPP model. *Catena* 31:257-270.

The Authors

- ¹ Rangeland Scientist, USDA-ARS, Dubois, ID. cmoffet@pw.ars.usda.gov
- ² Research Hydrologist, USDA-ARS, Northwest Watershed Research Center, Boise, ID.
- ³ Rangeland Hydrologist, USDA-NRCS, Ft. Worth, TX.

Water and Ecophysiology Session

Germination Responses to Temperature in Three *Caragana* Species in Loess-gully Region, China

Zhao Xiaoying¹
Ren Jizhou²

Abstract: The leguminous *Caragana* species are important components of vegetation in the semi-arid Loess-gully region, China. These shrub species are important for maintaining the dynamics and function of the ecosystem in the region. They are potential plant resources for restoration of degraded ecosystems. The germination responses to temperatures in two indigenous and one exotic *Caragana* species were studied under controlled conditions in the laboratory. Treatments were nine temperature regimes (constant temperatures of 5, 10, 15, 20, 25, and 30°C and three alternating day/night temperature regimes of 10/5, 25/15, and 30/20°C). Germination response to temperature was different for the three species. For *C. intermedia*, the temperature range for germination was 5 to 30 °C and germination rate was quick. Percentage germination was low at all temperature regimes for *C. licentiana*. Germination was inhibited at 30°C for *C. opulens* and at 5°C for *C. licentiana*. The average incubation period needed for seeds to germinate was longer for *C. licentiana* than for the others. Alternating day/night temperature had no significant effect on germination in the three species. Hard-coat seeds existed at different percentages in this plant subfamily. Rate of hard-coat seeds was 5.14 percent for *C. licentiana* and 0.79 percent for *C. intermedia*, but *C. opulens* had no hard-coat seeds. Germination responses to temperature in the three species are related to their ecological distribution and habitat. The different germination patterns in the species imply different life cycles. The germination strategies for *C. licentiana* and *C. opulens* mean that these two endemic species include potential value as good candidates for restoration of degraded land in the semi-arid Loess-gully region, China.

Introduction

Semi-arid gully-hill region covers a great many acres of China. In this region, vegetation degradation and severe soil erosion are obstacles to the sustainable development in the region. Vegetation rehabilitation is essential for ecological restoration in the region and sustainable development. Selection and use of species adaptation to the local environment are directly related to succession of vegetation rehabilitation and efficiency of water and soil protection.

In the region, water is the limiting factor for the development of the vegetation. Plants have to take maximum advantage of the scarce and irregular rainfall, which varies between 380 mm annually distributed over a rainy period of 3 months (June-September). The most common vegetation in these regions is desert steppe, but the most common plant in south-sloping land is *Caragana licentiana*. Precipitation

varies from year to year in these regions and droughts can last up to 5 years. Under these conditions, plants species have become adapted to tolerate, evade, and escape drought and have developed germination, establishment, growth, and reproduction strategies that allow for the perpetuation of the species in these conditions. The subfamily *Caragana* Febr. includes major leguminous shrubs in the semi-arid region of China. There are 62 species in China (Liu 1987) and 15 species in Loess Plateau region (BINC 1992). *Caragana* species are key components of vegetation in the loess-gully region (Wu Zhengyi 1995). These species are examples of plants that have successfully colonized these semi-arid loess-gully zones and they are important for maintaining the dynamic and function of the ecosystem. They are also important for restoration of degraded ecosystems. In particular, some indigenous *Caragana* species have potential value for vegetation establishment, but they have attracted little attention from restoration ecologists and researchers. Lack of knowledge on their pattern of seed

In: Sosebee, R.E.; Wester, D.B.; Britton, C.M.; McArthur, E.D.; Kitchen, S.G., comp. 2007. Proceedings: Shrubland dynamics—fire and water; 2004 August 10-12; Lubbock, TX. Proceedings RMRS-P-47. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 173 p.

germination and life cycle is a major factor restricting their use in ecological restoration.

The three *Caragana* species are of particular importance because they are drought resistant and two of them are endemic. *Caragana licentiana* Hand-Mazz is a species found in the Dingxi, Lanzhou, and Yongdeng regions in Gansu Province, China. It is drought resistant and carries on the active phases of its life cycle when soil moisture is abundant. It can survive and grow well in extreme habitats in the region. *Caragana opulens* Kom is distributed in some regions of the Loess Plateau. *Caragana intermedia* Kuang has been planted on Gansu Loess Plateau to prevent soil erosion, but it is difficult to regenerate by seed in this region for population expansion.

Seed germination of mimosa and acacia species, leguminous shrubs, has been reported by several authors (Orozco-Almanza 2003; Abulfatih 1995). Studies on temperature range of seed germination of *C. intermedia* and *C. korshinskii* were reported by BINC (1992). But studies on germination patterns of others *Caragana* species have not been carried out, especially regarding comparative studies of seed germination in this species.

This study was carried out to answer the following questions: What is the effect of temperature on the seed germination of the three species? What are the germination patterns of each species and the implications of its restoration? Are the seeds dormant after dispersal? Are there differences in dormancy among the three species? Are there any moisture or temperature mediated mechanisms preventing germination under unfavourable conditions?

Species and Methods

Seed Collection

Seeds of *C. licentiana* and *C. opulens*, endemic to Dingxi County, were collected from the species of the genus *Caragana* growing in natural communities in the Dingxi County Gansu province (35°44' 14.9"N, 104°24' 17.2"E) in June 2002 and seeds of *C. intermedia* were collected from the species in semi-artificial communities in the county in July 2002. Seeds were stored in a laboratory in Dingxi County without heat or air condition. Seeds that had been attacked by insects were excluded from the test. Dingxi County is considered a typical representation of gully-hill region in Loess Plateau, China. The plant communities are dominated by *Stipa ungeana* Trin, *Stipa breviflora* Griseb, *Ajanía fruticulosa* Ledeb, and *Artemisia frigida* Willd. Average annual precipitation and temperature (over 10 years) in the region were 380 millimeters and 6.3°C.

Germination under Laboratory Conditions

Trials were carried out in May 2003. Treatments were nine temperature regimes: six constant temperatures of 5, 10, 15, 20, 25, and 30°C and three alternating day/night

temperature regimes of 10/5, 25/15, and 30/20°C. For each thermal treatment, 200 seeds of each species were divided into four replicates of 50 seeds each. Each replicate was placed in a 9 cm Petri dish (in diameter) on 1 percent 20 ml water agar and incubated in a germination chamber at each temperature. The seeds were inspected every day and were considered to be germinated when the radical penetrated the seed coat and reached about 1mm in length (Teketay 1996). Germinated seeds were removed after counting. Trials were run until no more seeds germinated for 5 days. Percent germination was calculated as the number of seeds germinated divided by the number of viable seeds. Dead seeds were excluded. Hard-coat seeds were counted.

Statistical Analysis

The results of the germination experiment were analyzed for statistical significance with a general linear model analysis of variance (ANOVA) from the SPSS package for personal computer (version 11.0, SPSS Inc.). Percent germination data were arcsine-square-root transformed prior to analysis. Arcsine-transformed means and standard errors were back transformed for graphic presentation. Multiple comparisons of means were made with Tukey tests. A significance level of $\alpha = 0.05$ was used for all statistical analyses.

Results

Germination Response

Seed germination of the three *Caragana* species, tested in the laboratory on a constant and alternating temperature gradient bar, showed three patterns of response to temperature. The pattern of seed germination for *C. intermedia* was germination over a broad range of temperatures between 5°C and 30°C. The pattern for *C. licentiana* was cold-evading germination between 10°C and 30°C. The pattern for *C. opulens* was heat-evading germination between 5°C and 25°C. The seeds of each species germinated within a specific temperature range (table 1, fig.1).

C. intermedia and *C. opulens* showed a very high percentage of germination at their respective optimum temperatures (100 percent and 99. percent ± 1 percent). The percent germination for *C. licentiana* was lower at its optimum temperatures (89.0 percent ± 2.5) than the other two species. The effect of alternating day/night temperature on germination in the three species was not significant.

Germination Process

The average incubation period needed for seeds to germinate was longer for *C. licentiana* than for the other species (fig. 2). Seeds began germination after 4 days at 25°C and total percent germination reached 25.5 percent ± 6.3 after 8 days. Few seeds germinated each day for *C. licentiana*. Germination rate was very quick for *C. intermedia* and

Table 1. Seed germination percentage of three *Caragana* species at constant and alternate temperatures.

Temperature (°C)	Species		
	<i>C. licentiana</i>	<i>C. opulens</i>	<i>C. intermedia</i>
5	0a ¹	78.5 ± 1.3a	7.0 ± 1.3 a
10	8.7 ± 4.2 a	100 b	66.8 ± 3.9 b
15	64.8 ± 11.7 b	100 b	98.0 ± 0.9 c
20	81.5 ± 2.4 c	100 b	99.0 ± 1.0 c
25	89.0 ± 2.5 c	100 b	99.0 ± 1.0 c
30	65.0 ± 7.7 b	0 d	98.5 ± 1.0 c
0 / 5 ²	1.0 ± 0.6 a	97.9 ± 0.8 c	11.5 ± 4.7 a
25 / 15	90.3 ± 1.9 c	100 b	99.5 ± 0.6 c
30 / 20	93.2 ± 4.0 c	100 b	99.5 ± 0.5 c

¹ Percentage germination with same letter are not significant at $P < 0.05$.

² 10h in light and then transfer 14h in dark.

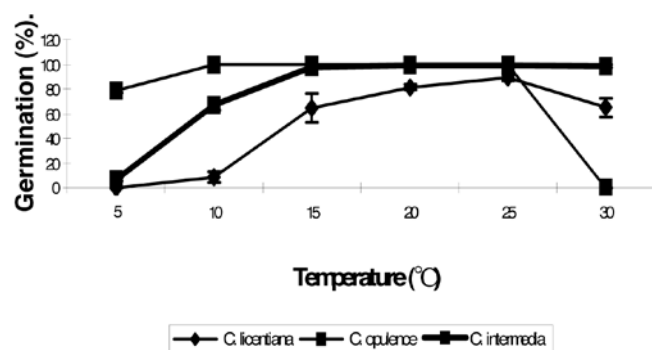


Figure 1. Percent seed germination at constant temperatures in three *Caragana* species after 20 days of incubation.

C. opulens (fig. 3). *C. opulens* seeds began germination after 3 days at optimum temperature and total percent germination reached 67.6 percent ± 6.6 after 4 days. *C. intermedia* seeds began germinating after 2 days and total percent germination reached 70.9 percent ± 1.3.

Hard-Coat Seeds

No hard-coat seeds were found for *C. opulens* in the germination trial. The rate of hard-coat seeds was 0.79 percent for *C. intermedia* and 5.14 percent for *C. licentiana*.

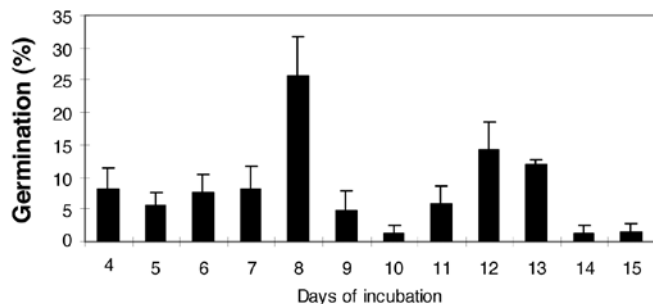


Figure 2. Percent germination of *C. licentiana* after different time periods of incubation at 25°C.

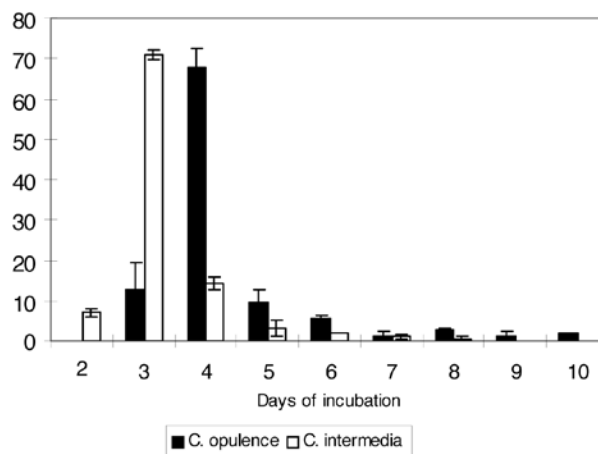


Figure 3. Percent germination of *C. opulens* and *C. intermedia* after different time periods of incubation at 25°C.

Discussion

Plants are generally in areas with temperatures that are appropriate for their germination and growth (Krebs 1978; Bewley and Black 1994). This is true for leguminous shrubs (Orozco-Almanza, 2003), as well as others species (Baskin and Baskin 1971; Linington 1979; Probert 1985; Abulfatih 1995). Differences in the temperature requirement for seed germination in the three species reflected the distribution and habitat of the species. The place of origin for *C. intermedia* is sandy desert (Liu 1987) where temperature in the growing season is high and temperature fluctuations are great. These conditions determine the wide range of temperature within which *C. intermedia* can germinate.

C. opulens is distributed in some regions of higher altitude in the Loess Plateau (Liu 1987). It grows in the northwest sloping habitat of the Dingxi County. Therefore, germination was inhibited at 30°C for this species and germination percentage at 5°C still reached 78.5 percent ± 1.3. *C. licentiana* grows mainly in southeast sloping habitat and seeds can not germinate at 5°C.

Germination over a wide range of temperatures has important practical implications in the Loess Plateau, where different temperature conditions prevail as a result of the topography of the region. Furthermore, seeds can artificially propagate the species in regions with different temperature conditions. Such characteristics make these species good candidates for restoration in semi-arid region of Loess Plateau, China.

Speed of seed germination presents a strategy for species survival and development in habitats where precipitation is unpredictable such as in semi-arid regions (Guterman 1993; Wang 1998). Only a fraction of *C. licentiana* seeds germinated every day under adequate moisture that could decrease seedling mortality rate following a drought. This germination strategy coincides with the desert plants *Agriphllum wquarrosom* (Wang 1998). Seed-coat imposed dormancy is a delaying mechanism that prevents germination under conditions that might prove to be unsuitable for establishment, thereby separating germination in both time and

space (Charper 1995). A small percentage (5.14 percent) of hard-coat seeds did not germinate under unfavorable conditions and have a lower percentage of predation. This allows them to persist in unpredictable environments, and may be another strategy that adapts the species to the habitat. This strategy suggested that *C. licentiana* might have a potential value in rehabilitation of degraded sloping land, especially dry southeastern sloping land.

A majority of seeds germinate and a fraction do not germinate in suitable conditions for *C. intermedia*. This germination response may ensure that a majority of seeds germinate in the suitable season to increase seedling survive rate in its original sandy habitat. But in the gully-hill loess habitat of Dingxi County, this germination behavior increases the risk of seedling mortality in a following drought. This may be one of reasons that little seedlings of *C. intermedia* were found in an artificial community in Dingxi County. Seeds almost synchronously germinated in favorable conditions for *C. opulens*. This may increase seedling survival rate in suitable conditions and decrease seeds predation by rodents.

Conclusions

Seeds of three *Caragana* species can germinate in different ranges of temperatures in the laboratory. This is directly related to their distribution and habitats. Speed of seed germination in the species is different and this may be a strategy that ensures the species persist in specific habitats. Seeds in the three species were dormant at different percentages and this has important ecological significance. These germination strategies mean *C. licentiana* and *C. opulens*, the endemic species, have potential value as good candidates for revegetation of different habitat in Loess Plateau region.

Acknowledgments

The NKBRF Project G2000D18602 and the project "Light for Western China" of Chinese Academy of Sciences supported this work. We are grateful to Wang Yan-rong for providing experiment equipment and Li Yan-mei, Zhang Jian-quan for assistance with germination trial. An earlier draft was improved by the comments of Ms. Margaret Cargill and Mr. Liu Zhi-ming.

References

- Abulfatih, H. A. 1995. Seed germination in acacia species and their relation to altitudinal gradient in south-western Saudi Arabia. *Journal of Arid Environments* 31: 171-178.
- Baskin, C. C.; Baskin, J. M. 1998. *Seeds: Ecology, Biogeography and Evolution of Dormancy and Germination*. Academic Press, San Diego, 666 p.
- The Botany Institute of Northwest China. (BINC) 1992. *Flora in Loess Plateau*. Tomus II. Forest Press.
- Grime, J. P. 2001. *Plant strategies, vegetation processes, and ecosystem properties*. Chichester: John Wiley and Sons.
- Gutterman, Y. 1993. *Seed germination in desert plants*. Berlin: Springer.
- Huang, Zhen-ying; Gutterman, Y.; Zheng-hai, H. 2001. Seed germination in *Artemisia sphaerocephala* II. The influence of environmental factors. *Acta Phytocologica Sinica* 25(2): 240-246.
- Liu, Ying-xing. 1987. *Flora in desertis deipublicae populorum sinarum*: Tomus II. Beijing: Science Press.
- National Quality Technology Bureau. 2001. *Rules for forage seed testing*. Standards Press of China.
- Orozco-Almanza, M. S.; León-Garíca, L. P.; Grether, R. 2003. Germination of four species of the genus *Mimosa* (leguminosae) in a semi-arid zone of Central Mexico. *Journal of Arid Environments* 55: 75-92.
- Proberts, R. J. 2000. The role of temperature in germination ecophysiology. In: M. Fenner (Editor), *Seeds: The ecology of regeneration in Plant Communities*. C. A. B. International, Wallingford, pp. 285-325.
- Probert, R. J.; Smith, R. D.; Berch, P. 1985. Germination responses to light and alternating temperatures in European populations of *Dactylis glomerata* L. I. Variability in relation to origin. *New Phytologist* 99: 305-316.
- Teketay, D. 1996. Germination ecology of twelve indigenous and eight exotic multipurpose leguminous species from Ethiopia. *Forest Ecology and Management* 80:209-223.
- Van Rheede, van; Oudtshoorn K.; van Rooyen, M. W. 1999. *Dispersal biology of desert plants*. Berlin: Springer-Verlag.
- Wang, Zong-ling; Xu, Yu-qing; Wang, Gang. 1998. Germination strategies of annual sandy plants under limited precipitation. *Journal of Lanzhou University (Natural Sciences)* 34(2): 98-103.
- Wang, Zong-ling; Wang, G.; Liu, X. M. 1998. Germination strategy of the temperate sandy desert annual chenopod *Agriophyllum squarrosum*. *Journal of Arid Environments* 40: 69-76.
- Wu, Zheng-yi. 1995. *China Vegetation*. Science Press.

The Authors

- ¹ College of Life Sciences and Chemistry, Xinjiang Normal University, Urumqi, 830054, China. xyzhao63@hotmail.com
- ² College of Pastoral Agriculture Science and Technology, Lanzhou University, Lanzhou 730000, China.

Saltcedar Control and Water Salvage on the Pecos River, Texas, 1999 to 2003

Charles R. Hart¹

Larry D. White²

Alyson McDonald¹

Zhuping Sheng³

Abstract: A large scale ecosystem restoration program was initiated in 1997 on the Pecos River in western Texas. Saltcedar (*Tamarix* spp.), a non-native invasive tree, had created a near monoculture along the banks of the river by replacing most native vegetation. Local irrigation districts, private landowners, federal and state agencies, and private industry worked together to formulate and implement a restoration plan, with a goal of reducing the effects of saltcedar and restoring the native ecosystem of the river. An initial management phase utilizing state-of-the-art aerial application of herbicide began in 1999 and continued through 2003. Initial mortality of saltcedar averaged 85 to 90 percent. Monitoring efforts were initiated at the onset of the project to include evaluating the effects of saltcedar control on salinity of the river water, efficiency of water delivery down the river as an irrigation water source, and estimates of water salvage. To date, no effect on salinity can be measured and irrigation delivery was suspended 2002 through 2003 due to drought conditions. Water salvage estimates show a significant reduction in system water loss after saltcedar treatment. However, a flow increase in the river is not yet evident. Monitoring efforts will continue in subsequent years.

Introduction

The Pecos River Ecosystem Project was proposed in 1997 by the Red Bluff Water and Power Control District to address saltcedar issues along the Pecos River. Initial objectives of the project were to increase efficiency of water delivery in the river to irrigation districts within the Red Bluff District and improve the quality of the water by decreasing the salinity. After 4 years of herbicide application on saltcedar, the project has emerged as the first step to what could be important to the overall statewide plan for water conservation along Texas' rivers by managing saltcedar infestations. Success of the Pecos River Ecosystem Project can be attributed mainly to its cooperative effort and organization. Numerous agencies, organizations, and companies, such as Upper Pecos Soil and Water Conservation District; Texas Cooperative Extension; Texas Department of Agriculture; USDA Natural Resources Conservation Service; Red Bluff Water and Power Control District; Irrigation Districts in Loving, Reeves, Ward, and Pecos Counties; US Environmental Protection Agency; Pecos River Compact Commission; International Boundary and Water Commission; BASF Co.; North Star Helicopters Inc.; and local landowners, were involved in the organizational efforts early in the project development.

Saltcedar (*Tamarix* spp.) is an introduced phreatophyte in western North America estimated to occupy well over 600,000 ha of waterways (Robinson 1965; Kunzmann and others 1988). It is a vigorous invader of riparian zones and sub-irrigated pastures. The plant was introduced into the United States as an ornamental in the early 1800s. In the early 1900s,

government agencies and private landowners began planting saltcedar to control stream bank erosion along such rivers as the Pecos River in New Mexico and Texas (Everitt 1998). The plant has spread down river in Texas and occurs along the river south of Interstate 10 to the confluence with the Rio Grande. Mature plants can reach heights of 6 to 9 m and densities of 700 to 1,000 plants/ha in this region. More recently, saltcedar has become a noxious plant not only along rivers and their tributaries, but also along irrigation ditch banks, low-lying areas that receive extra runoff accumulation, and areas with high water tables.

Saltcedar occupies a near continuous buffer along both banks of the Pecos River from Red Bluff Dam southward for the entire area (approx. 289 river km) of the Red Bluff Irrigation District. This region of Texas is characterized by a semi-arid, desert environment receiving 152.5 to 203.2 mm of average annual rainfall. This is one of the important reasons for controlling saltcedar, which is to conserve water, especially for the semi-arid area experiencing drought most, if not all of the time. The width of the saltcedar band varies from 7.6 to 152.5 m with an average of 45.8 m on each river bank. Within this stretch of river, saltcedar occupies about 7.5 to 10 ha per river kilometer. Additionally, the Pecos River in Texas is a meandering stream with a ratio of river kilometers to air kilometers of about 3 to 1. Another primary concern of the project was to apply the herbicide with minimal contact of off-target vegetation. This situation created a real challenge for aerial application of herbicides. This paper describes the Pecos River saltcedar control program in Texas and its preliminary results.

In: Sosebee, R.E.; Wester, D.B.; Britton, C.M.; McArthur, E.D.; Kitchen, S.G., comp. 2007. Proceedings: Shrubland dynamics—fire and water; 2004 August 10-12; Lubbock, TX. Proceedings RMRS-P-47. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 173 p.

Methods and Procedures

The first step undertaken by the planning group was to develop a section 24(C) special use label to use Arsenal™ herbicide on saltcedar within rangeland and aquatic areas in Texas. The label was prepared by the Pesticide Division of the Texas Department of Agriculture and approved for use in 1999. The project was designed with two major phases, saltcedar treatment phase and debris removal and follow-up management phase. Also of major concern to the project group was the revegetation of the river banks with native plants to complete the ecosystem restoration. Once the label and funding were secured, the project was ready to begin the first phase of herbicide treatments. The Upper Pecos Soil and Water Conservation District Board of Directors were selected to administer the project.

During the initial meetings to begin planning the process of saltcedar removal, several major concerns emerged. First, the treatment method selected should provide a high rate of saltcedar mortality while minimizing the detrimental effects on existing native vegetation. Second, this should be accomplished in the most economical way possible. And finally, soil loss from stream banks should be minimized as much as possible. Another daunting task was to obtain permission from private landowners to treat saltcedar along the river, as much of the land is in private ownership. A “spray easement” was developed and used as a contract between the Project and private landowners, allowing access for treatment and follow-up management for a 10-year period. To date, over 800 easements have been signed by private landowners, with a rejection rate of less than 1 percent. Bids were solicited from aerial applicators in late summer 1999 with the project ultimately being awarded to North Star Helicopters from Jasper, Texas. With funding, landowner permission, and applicator contract in hand by August 1999, initial treatments could begin in September.

The ecohydrological study was conducted after the application of herbicide to assess impacts of saltcedar control in terms of water quality and water quantity. To quantify water flow between surface water and ground water, surface water flow release and diversions were monitored and groundwater level diurnal fluctuations were monitored at both treated and untreated sites. The latter were used to estimate the water losses by evapotranspiration and water salvage potential from the saltcedar control. Details for each component are described in this paper.

Herbicide Applications

Applications of 1.12 kg a.i./ha of Arsenal™ herbicide were made by helicopter, applied with a specially-designed boom that produced large droplets and high total spray volume. The helicopter had the advantage of being able to fly at slower air speeds compared to fixed-wing aircraft, which made the sharp turns of the river much easier to navigate. The helicopter application also provided for much higher precision of application by utilizing specialized nozzle and boom technology.

The herbicide was applied in a total spray volume of 140 L per hectare with a 1000 to 1500 μ droplet. Less than 0.5 percent of the droplets were “driftable” fines ($< 200\mu$). The boom was also sectioned into 3 to 4.5 m sections for an overall width of 13.5 m. Combinations of the boom could be turned on to allow for a 4.5, 9, or 13.5 m swath width. This further reduced the amount of herbicide that came in contact with off-target vegetation. Another advantage of the helicopter over fixed-wing aircraft was its ability to land on loader trucks that were positioned near the river and eliminated the need of ferrying to and from a landing strip.

Helicopters were equipped with GPS navigational equipment to aid in application. The use of on-board GPS allowed for near elimination of skips between spray swaths and allowed pilots to easily return to the point where they finished spraying the previous spray load. The system was also connected into the sprayers flow control system so that rate of flow through the boom was varied to precisely match ground speed, eliminating the need to maintain a constant ground speed. After completion of treatments, GPS log files were downloaded to a computer to produce maps of the treated area and make calculations about the area treated.

Percent mortality of saltcedar plants was estimated after a minimum of 2 years post-treatment. Counts were conducted at multiple locations to determine percent mortality of saltcedar by counting live and dead plants along belt transects on both sides of the river. If any green plant tissue was evident on a plant, it was recorded as live. Plants were counted within a 2.5-m wide belt transect until 100 plants were recorded as live or dead. A minimum of four transects were conducted at each sample location, two on each side of the river.

Measuring Water Quantity/Flow

Water quantity is monitored through release and delivery data from Red Bluff Water and Power Control District. Water released from Red Bluff Reservoir and delivered to seven local irrigation districts along the Pecos River is recorded daily during the irrigation season in ac-ft. Release and delivery data is obtained from weirs located at point of release from Red Bluff Reservoir and at each irrigation turnout point on the river. Historical release and delivery data have also been provided by the Red Bluff Water and Power Control District, with pre-treatment averaged from 1988 through 1999 to establish a comparative baseline. Flow data is obtained from United States Geological Survey (USGS) Gauging Station 13257 located at Girvin, Texas. This gauging station is located at the southern end of the Red Bluff Water and Power Control District boundary. Water released from Red Bluff Reservoir that is not delivered to upper districts is captured at Imperial Reservoir, located upstream from the USGS gauging station.

Estimating Water Salvage

Water loss resulted from evapotranspiration within saltcedar stands and water salvage from saltcedar control is estimated by monitoring groundwater diurnal fluctuations within saltcedar

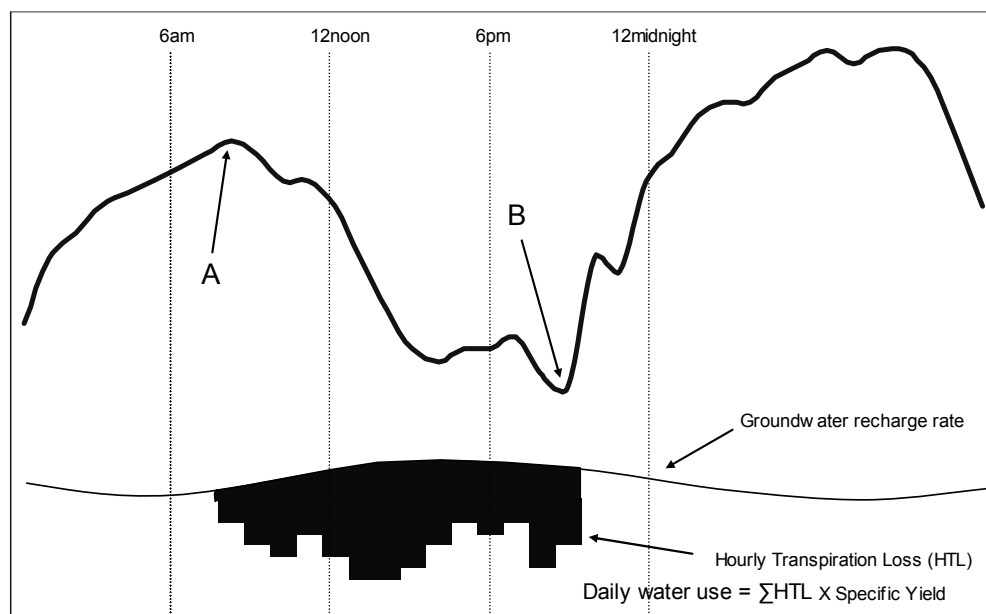


Figure 1. Conceptual illustration showing diurnal fluctuation in groundwater and representation of drawdown-recharge method for calculation of water loss.

sites. Shallow groundwater monitoring wells were installed at a study site located on the Pecos River near Mentone, Texas, to provide data on the fluctuation of the groundwater table. A description of methods used to construct monitoring wells is provided in Hays (2003). Water level loggers (Global Water Instrumentation, Inc. Model WL14X) were used to measure hourly water levels in the wells and the river. The sensor on the WL14X is a submersible pressure transducer that is amplified and temperature and barometric pressure compensated with an accuracy of 0.2 percent. Logger models used in this study had a reported accuracy of 0.0091 m and were calibrated prior to being placed in the wells. Additionally, wells were cleaned and flushed annually to remove silt and root accumulation. Loggers were programmed to record water level every hour.

A drawdown-recharge method (fig. 1) of calculation was used to estimate water loss from hourly measurements that produced diurnal fluctuations in the water table. This method assumes little evapotranspiration occurs during the nighttime (21:00 to 08:00 hours) and that the period from the low point of the water table during daylight hours to the nighttime high can be used to calculate a recharge rate for the drawdown period. This method requires a drawdown and recharge diurnal cycle; hence, days when the water table rapidly rises or falls through out the diurnal cycle were excluded from the calculations. More information on the procedures and calculations used are found in Hays (2003).

A paired-plot design was used, with four monitoring wells and a river monitor at each of two plots. Each plot was monitored for an entire growing season (December 1999 through September 2001). The relationship between wells across plots was established through simple linear regression and reported by Hays (2003). In September 2001, one plot was treated with Arsenal™ herbicide and the saltcedar killed. When sufficient data are available, water loss on untreated plots will be used to predict that on untreated plots, and a comparison made between predicted and actual. To date, this calculation has

not been performed due to low water releases for the latest 2 years.

Results and Discussion

Based on field observation and data analysis over the last 3 years, the following preliminary results were obtained for herbicide application, water quality, water losses by evapotranspiration, and water salvage potential by saltcedar control. Additional research is also recommended to gain a better understanding of the impacts of saltcedar control and quantifying volume and fate of water salvage by saltcedar control.

Herbicide Applications

The project was funded in 1999 and 2000 by Red Bluff Water and Power Control District and irrigation districts along the Pecos River. Approximately 106 river kilometers or about 544 hectares of saltcedar were treated with an actual spray cost of \$253,555.

During 2001, \$1 million was allocated to the Pecos River Ecosystem Project by the State of Texas through the Texas Department of Agriculture. Eight percent (8 percent) of these funds were used for project administration and monitoring with the remaining 92 percent used for saltcedar treatments in 2001 and 2002. Third year (2001) applications treated approximately 92 river kilometers or 583 hectares of saltcedar at a cost of \$263,000. From 1999 through 2001, 1127 hectares of saltcedar were treated at a total cost of \$515,635.

Fourth-year applications were completed in September 2002. Approximately 1,444 ha were treated including segments of the river between Red Bluff and Grandfalls, Texas, that were not sprayed during the previous years, from the New Mexico/Texas state line to Red Bluff Reservoir (including areas around the lake) and 8 kilometers of Salt Creek, a major tributary of

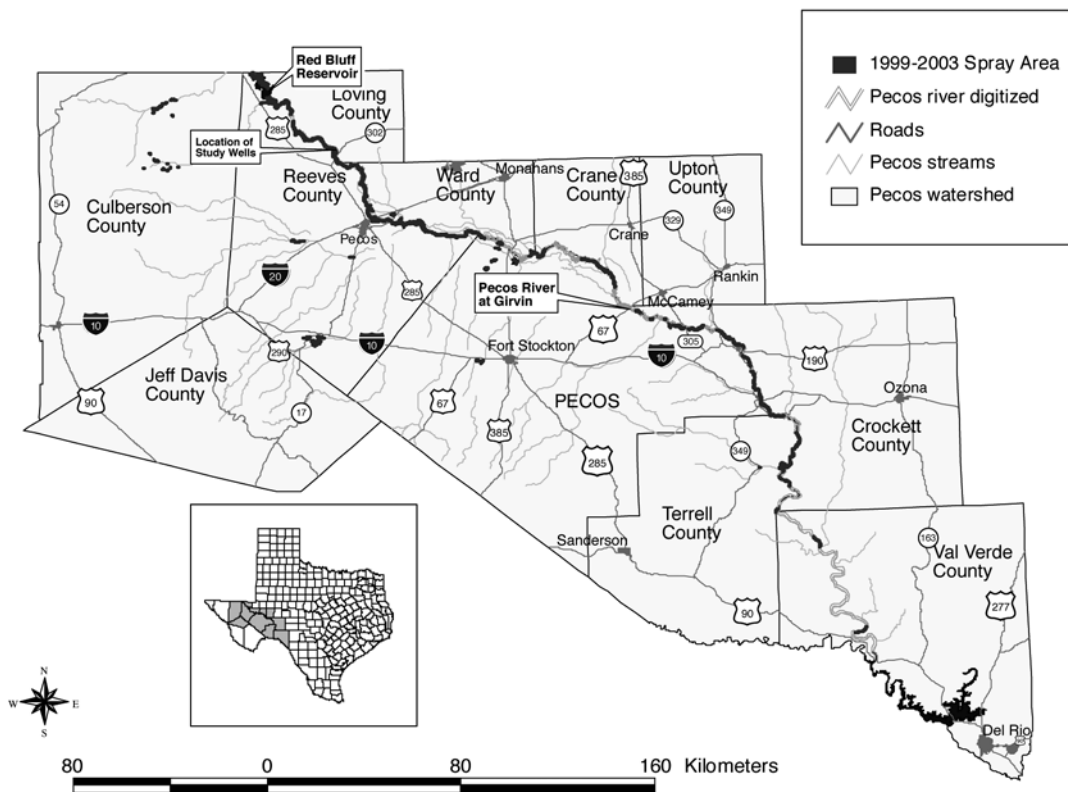


Figure 2. Areas of the Pecos River Basin treated for saltcedar control during 1999-2003.

the Pecos River in Reeves County. About \$660,000 was spent during the 2002 spray season.

Applications in 2003 were funded through a joint effort of the USDA-NRCS Environmental Quality Incentives Program (EQIP) and Texas State Soil and Water Conservation Board Brush Control Program. EQIP is a private landowner based program for cost share of environmental practices. This program provided 75 percent of the saltcedar treatment costs to the landowner. The Texas State Soil and Water Conservation Board provided the remaining 25 percent of the cost through the Texas Brush Control Program. During 2003, approximately 1,510 hectares of saltcedar were treated within the Pecos Basin Watershed in Culberson, Reeves, Ward, Crane, Pecos, Crockett, Terrell, and Val Verde counties. Of this area treated, approximately 122 kilometers or 1,080 ha were along the main river channel. The remaining hectares were treated along tributaries and springs within the basin. Treatment cost during 2003 was \$518.70/ha for a total of \$783,300.

To summarize, from 1999 through 2003, 320 kilometers of the Pecos River and various tributaries and springs within the basin have been treated for saltcedar control in Texas (fig. 2). Approximately \$1.9 million was spent to treat 4,081 ha. Debris removal and follow-up management continues to be a priority to complete the project and this phase is currently being planned.

Percent mortality estimates were made during the summer of 2002 at six sites along the river treated in 1999 and 2000. Average estimated mortality within a site ranged from a low of 84 percent to a high of 90.7 percent after herbicide applications. Across all sample sites, saltcedar mortality averaged

87.5 $\pm$ 0.1 percent 2 years after treatment. These results are very close to other studies (Duncan and McDaniel 1998).

Water Quantity/Flow

One priority was to determine if a relationship existed between water released at Red Bluff Reservoir and the amount of flow measured at Girvin. A coefficient of determination was calculated on flow (cfs) measured at Girvin and the volume of water (cfs) released from Red Bluff Reservoir, where $r^2 = 0.15$ ($P < 0.05$). A low correlation provides evidence that release from Red Bluff Reservoir is at best only weakly related to flow through the USGS station at Girvin (Clayton 2002).

After it was determined that losses occurring between release and delivery were not highly correlated to the flow at Girvin, only release and delivery data were analyzed and the Girvin data were not utilized in the analysis. It was observed that during certain time periods within a delivery year, percent loss changed considerably (fig. 3). This pattern precipitated dividing the irrigation delivery year into three categories, initial release and delivery (first month), release and delivery during the growing season, and later release and delivery (later irrigation season). Initial releases did not occur during the same month each year but varied between March and April. Delivery months were then numbered consecutively from the first month of release each year. The three categories allowed for a characterization of changes in percent loss occurring during the delivery year.

A monthly average was calculated for each of the three delivery categories (table 1). The first month releases

Average Monthly Release and Percent Loss for the Pecos River 1988-1999

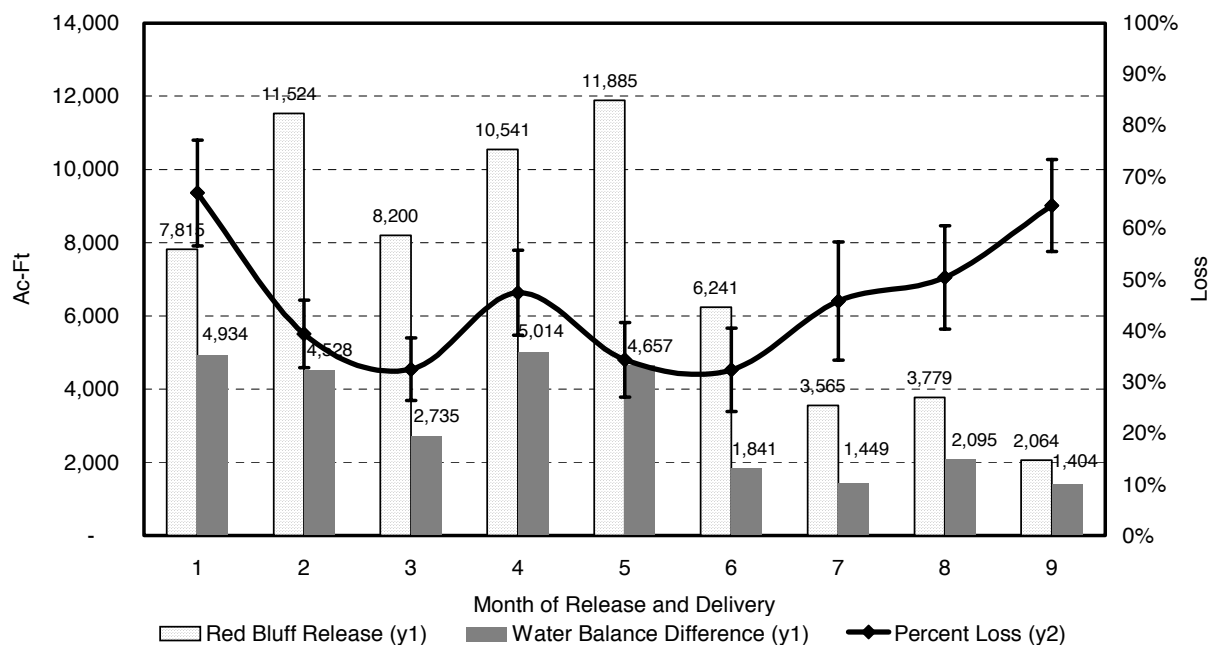


Figure 3. Average monthly release, delivery, and percent loss of Pecos River irrigation water during consecutive delivery months from 1988 through 1999, with standard deviations of percent loss illustrated.

averaged 7,862 ac-ft with a delivery of 2,927 ac-ft and resulted in an average percent loss of 68 percent. Monthly releases increased during the growing season to an average of 11,015 ac-ft, but losses decreased to 39 percent. Average release for the late season showed to be the lowest, 3,534 ac-ft, with a loss of 43 percent. It is obvious that much of the release during the first month is used to “re-charge” the banks that were naturally “drained” during the non-irrigation winter months. This initial loss can account for a significant amount of the water lost during the irrigation delivery year.

An average pattern of release and percent loss was also determined for each month from 1988 through 1999 during the period of a delivery year. The highest average loss occurred during the first month (67 percent) of release. Percent loss decreased during the second month of release, and for the next 5 months of release, the loss ranged from 32 percent to 47 percent. However, when the amount of

water released begins to decrease in month 7, the percent loss begins to increase (46 percent) and by month 9, the loss increased to 64 percent.

Ultimately, this release and delivery data from pre-treatment years will be compared to post-treatment years to determine if control of saltcedar decreases the loss of water during the irrigation period thereby increasing the delivery efficiency. Only a small portion of the Red Bluff District had been treated during 2000-2001 delivery years. During the 2002 and 2003 delivery season, no water was released from Red Bluff Reservoir for delivery to irrigation districts. As irrigation delivery resumes, comparisons of pre-treatment to post-treatment will be made.

Estimating Water Salvage

Shallow groundwater wells have been monitored during the 2001 through 2003 growing seasons. Total water loss is calculated for each of the two plots for each year monitored. During the 2001 growing season, irrigation water was released as normal from Red Bluff Reservoir, but no irrigation water was released during the 2002 and 2003 seasons.

Due to the lack of river flow during the 2002 and 2003 growing seasons, several of the wells were dry during the year; hence, only the wells closest to the river are reported at this time. Herbicide treatment was applied to plot A at the end of the 2001 growing season. Nearly 90 percent control of all vegetation was observed at this plot after the 2002

Table 1. Average monthly release, delivery, and percent loss for three release and delivery periods for the Pecos River from 1988 to 1999.

Average monthly (acre-feet)			
Delivery period	Release	Delivery	Percent loss
First month	7,862	2,927	68%
Growing season	11,105	6,648	39%
Late season	3,534	2,074	43%

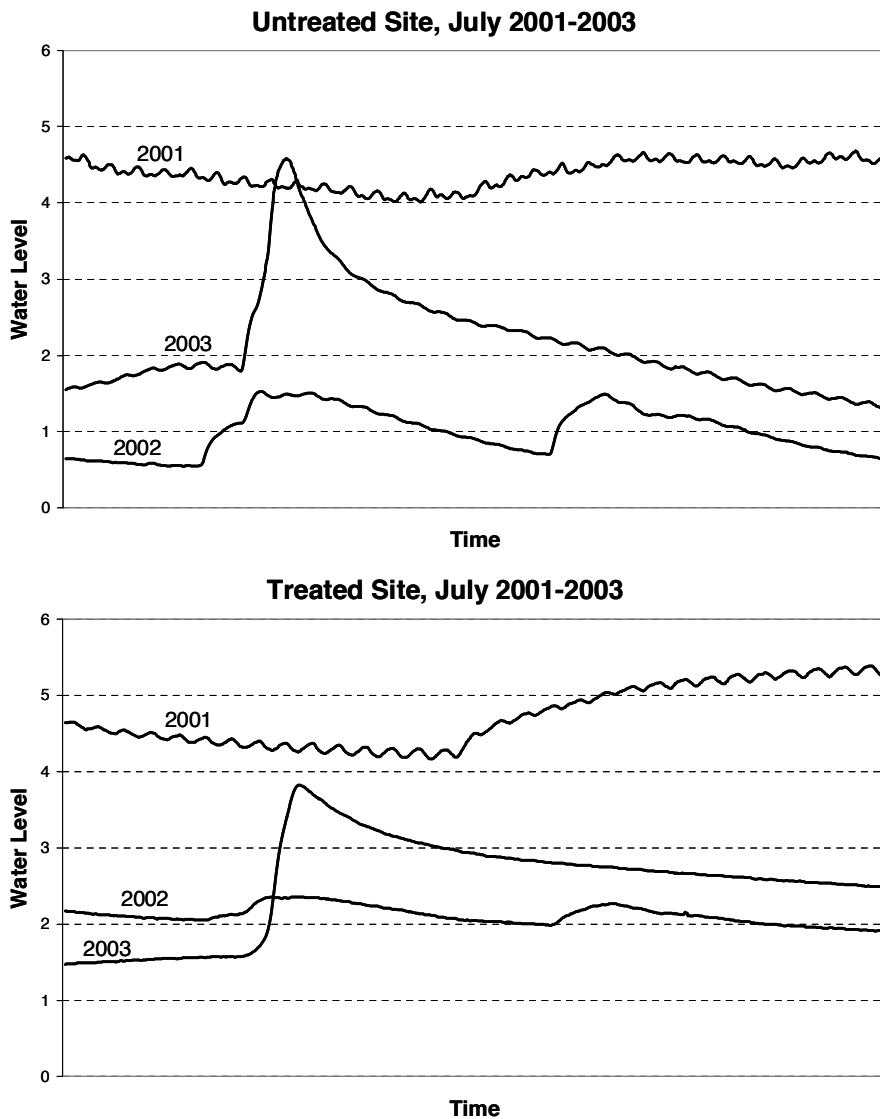


Figure 4. Shallow groundwater levels at sites A1 (Treated) and B1 (Untreated) during the month of July for the 2001 through 2003 growing seasons. Saltcedar on the treated site was killed after the 2001 growing season. Note the absence of diurnal fluctuations on the treated site during the 2002 and 2003 growing season.

growing season. Figure 4 shows the diurnal fluctuations in the groundwater table during July of each of the years for well locations A1 (treated plot) and B1 (untreated plot). Note that at well location B1, the diurnal fluctuations are evident for all 3 years. However, at well location A1, the diurnal fluctuations disappear during the 2002 and 2003 growing season. This is attributed to the fact that the saltcedar was killed on this plot after the 2001 growing season. Total water loss per year was calculated at 1.37 m at well location B1 and 0.95 m at well location A1 for the 2001 growing season (fig. 5). Water loss at well location B1 dropped due to drought to 0.89 and 1.0 m, respectively for 2002 and 2003. Water loss at well location A1 was reduced to 0.11 and 0.07 m, respectively for 2002 and 2003, after saltcedar treatment.

Total water loss was greatly reduced following saltcedar control, although actual amount of salvage cannot yet be calculated. In addition, native plants take over some of the area where the saltcedar has been treated, which will further complicate the estimate of water salvage and its fate. Research will continue to document actual water loss and estimate amount and fate of salvaged water. Additional, updated

information on the project can be obtained from the Internet at the following web site: <http://pecosbasin.tamu.edu>

Conclusions

In summary, saltcedar control using the herbicide application described was successful with an average of 85 to 90 percent apparent mortality of saltcedar 2 years after treatment. With long-term monitoring, treatment life of the control strategies should be further evaluated and follow-up management alternatives explored.

Preliminary results indicate that there is a great potential for water salvage by saltcedar control even though no fixed values were obtained for amount of water salvage, nor is the fate of the salvaged water identified. It is recommended that additional studies on surface water and shallow ground water interaction be conducted to have a better understanding of the fate of the potentially salvaged water. Additional study is also recommended to explore and validate the methodology for assessment of water salvage.

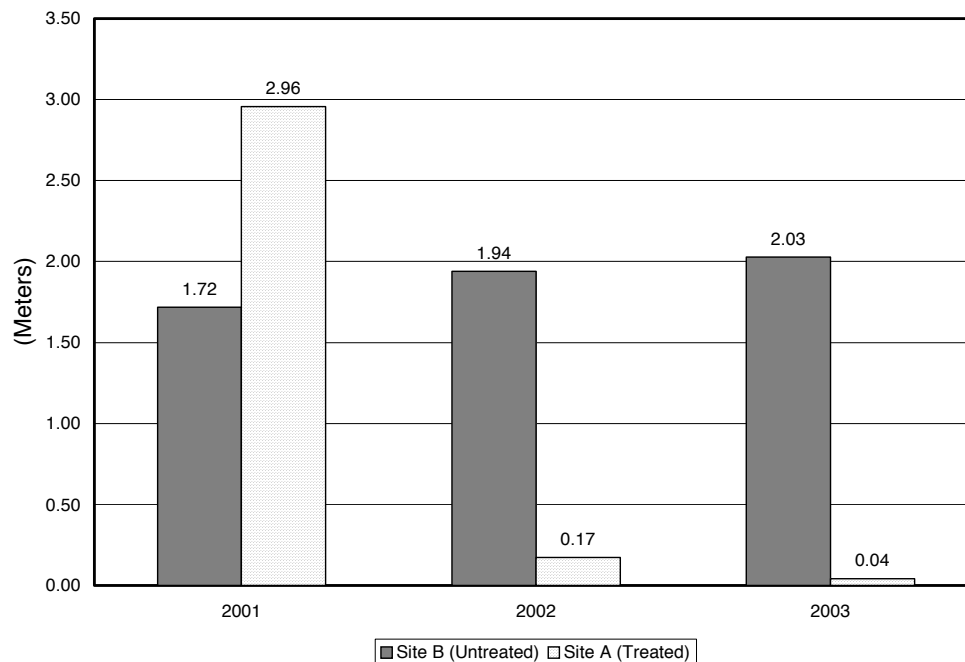


Figure 5. Total annual ground-water loss from Site A (Treated) and Site B (Untreated) for three growing seasons. Site A saltcedar was treated after 2001 growing season and shows dramatic decrease in water loss. Site B remains untreated through 2003.

This paper presents preliminary results of an ongoing project. Besides above-mentioned recommendations, the authors also identified several other related issues that should be addressed in future studies. One of the factors that affect assessment of the water salvage is the drought in the region. To overcome such an effect, long-term monitoring is recommended to gain a better understanding of the fate of salvaged water during the wet period. The second factor is re-vegetation or taking-over of the riparian zone by native plants, which could use some of the water salvaged by saltcedar control. Therefore, how much water is needed by native plants should be considered in estimate of long-term water salvage.

Acknowledgments

Research and monitoring efforts on the Pecos River Ecosystem Project were funded by a grant from the Texas Department of Agriculture and by the Rio Grande Basin Initiative administered by the Texas Water Resources Institute of the Texas A&M University System Agriculture Program with funds provided through a grant from Cooperative State Research, Education, and Extension Service, U.S. Department of Agriculture, under Agreement No. 2001-45049-01149.

Literature Cited

Clayton, L. 2002. Saltcedar Management Strategies and Effects on Water Quality and Quantity of the Pecos River. Texas A&M University, Masters Thesis. 86 p.

Duncan, K. W.; McDaniel, K. C. 1998. Saltcedar (*Tamarix* spp.) management with Imazapyr. Weed Technology. Vol.12, Issue 2:337-334.

Everitt, Benjamin L. 1998. Chronology of the spread of tamarisk in the central Rio Grande. Wetlands. 18(4):658-668.

Hays, K. B. 2003. Water Use by saltcedar (*Tamarix* sp.) and associated vegetation on the Canadian, Colorado and Pecos Rivers in Texas. Texas A&M University, Masters Thesis. 115 p.

Kunzmann, M. R.; Johnson, R. R.; Bennett, P. S. Technical coordinators. 1988. Tamarisk control in southwestern United States; 1987 September 2-3; Tucson, AZ. Special Report No. 9. Tucson, AZ: National Park Service, Cooperative National Park Resources Studies Unit, School of Renewable Natural Resources: 141 p.

Robinson, T. W. 1965. Introduction, spread, and areal extent of saltcedar (*Tamarisk*) in the western states. U.S. Geol. Serv. Prof. Paper 491-A. 12 p.

The Authors

¹Texas Cooperative Extension, Fort Stockton, TX.
cr-hart@tamu.edu

²Retired, Texas Cooperative Extension, College Station, TX.

³Texas Agricultural Experiment Station, El Paso, TX.

Mesquite Root Distribution and Water Use Efficiency in Response to Long-term Soil Moisture Manipulations

R. J. Ansley¹

T. W. Boutton²

P. W. Jacoby³

Abstract: This study quantified honey mesquite (*Prosopis glandulosa*) root growth and water use efficiency following chronic soil drought or wetness on a clay loam site in north Texas. Root systems of mature trees were containerized with barriers inserted into the soil. Soil moisture within containers was manipulated with irrigation (Irrigated) or rain sheltering (Rainout). Other treatments included containerized precipitation-only (Control) and non-containerized precipitation-only (Natural) with three trees per treatment. After four years of treatment, soil cores to 2.7 m depth were obtained beneath each tree canopy. Mesquite and grass roots were extracted, separated into size classes, and weighed. Root length density (m m^{-3}) was quantified for mesquite roots. Averaged over the entire sample depth, Irrigated trees doubled root length density of small (< 2 mm diam.) roots compared to Control trees (232 vs 105 m m^{-3}). Below 90 cm depth, root length density of large (2 to 10 mm diameter) roots was five times greater in Rainout (36 m m^{-3}) than Control trees (7 m m^{-3}). Over all depths, root biomass was greatest in Rainout trees and root:shoot (biomass) ratio was three times greater in Rainout than Control or Irrigated trees. Mesquite leaf carbon isotope ratio ($\delta^{13}\text{C}$) was lower (more negative) in Irrigated trees than other treatments, suggesting these trees had lower water use efficiency. Leaf $\delta^{13}\text{C}$ was not different between Rainout and Control trees. Mesquite adapted to chronic wet or drought cycles through increased root growth but patterns of distribution differed as Irrigated trees emphasized growth of small roots throughout the profile and Rainout trees grew large roots into deeper soil layers.

Introduction

Encroachment of woody plants into arid and semi-arid grasslands has occurred on a world-wide scale (van Vegten 1983; Smeins 1983; Ansley and others 2001; Archer and others 2001). Causal factors include reduced fire frequency, livestock overgrazing, increased seed distribution via livestock consumption and fecal deposition, and possibly increased CO_2 levels that favors growth of C_3 shrubs over C_4 grasses (Archer and others 1995; Kramp and others 1998). Success of woody plants is also attributed to an ability to grow deeper roots than grasses and thus better withstand droughts (Hinckley and others 1983; Hesla and others 1985; Gibbons and Lenz 2001).

In the southern Great Plains and southwestern USA, adaptation of honey mesquite (*Prosopis glandulosa* Torr.) to a variety of environments may be related to a plasticity of root system distribution (Gile and others 1997). When available, mesquite will exploit sources of deep water by growing a taproot (Phillips 1963; Mooney and others 1977; Nilsen and others 1981). Mesquite can also persist on sites that have little or no ground water by growing lengthy shallow lateral roots (Heitschmidt and others 1988; Ansley and others 1990). Mesquite in north Texas have been termed “facultative

phreatophytes” that function as phreatophytes if unlimited water is available, but are capable of surviving on sites with limited soil water (Wan and Sosebee 1991).

Few studies have observed the influence of extended droughts or wet periods on water relations and rooting behavior of woody perennials such as mesquite, yet prolonged climatic trends may confer competitive advantage to woody perennials such as mesquite and contribute significantly to their encroachment on grasslands (Kummerow 1980; Ansley and others 1992; Archer and others 1995). Our objective was to determine the effect of chronic drought or wetness on distribution and quantity of mesquite roots. A second objective was to quantify the isotopic carbon signature of mesquite foliage as an indicator of water use efficiency response to extended droughts or wet periods. We hypothesized that (1) mesquite exposed to chronic drought would grow deeper roots in search of other water sources and (2) mesquite exposed to chronic wetness would emphasize root growth in shallow layers and possibly sacrifice some deeper roots. Finally, because the site where we were conducting the study had little or no available soil moisture below about 2 m depth (from Ansley and others 1990, 1992), we hypothesized that trees exposed to chronic drought would eventually die.

In: Sosebee, R.E.; Wester, D.B.; Britton, C.M.; McArthur, E.D.; Kitchen, S.G., comp. 2007. Proceedings: Shrubland dynamics—fire and water; 2004 August 10-12; Lubbock, TX. Proceedings RMRS-P-47. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 173 p.

Materials and Methods

Site Description and Treatments

The study was conducted within a dense stand of mature mesquite trees in the northern Rolling Plains ecological area of Texas, south of Vernon (33°52'N, 99°17'W; elevation 368 m). Average annual precipitation is 665 mm. Primary grass species are Texas wintergrass (*Nassella leucotricha*) and buffalograss (*Buchloe dactyloides*). Soils are Typic Paleustolls of the Deandale and Kamay series (Koos and others 1962). Both series have clay loam surfaces underlain by a sandstone and shale parent material beginning at 1 m depth. Soil moisture measurements to 8 m depth indicated that there was little available moisture below 2 m depth.

Twelve multi-stemmed mesquite (3.5 ± 0.3 m height; 5.1 ± 0.2 cm diameter, 6.1 ± 0.7 basal stems) were selected for the study on the basis of uniform canopy size. All trees occurred within a 1.3 ha area. During December 1985 through February 1986, aerial portions of neighboring woody vegetation occurring within 20 m of each experimental tree were removed and remaining stumps killed with diesel oil. A 0.5 m wide and 2.5 m deep trench was dug and a sheet metal and plastic barrier was placed vertically around each of nine trees before re-filling the trench (Ansley and others 1988). Each barrier wall was hexagon shaped with each point of the hexagon 4.1 m from tree center. Trees with root barriers were called "containerized" trees, although bottoms of the containers were unsealed; however, soils were dry below 2 m depth. Surface area and soil volume within each container was 42.4 m² and 106 m³ (2.5 m x 42.4 m²), respectively. Each container wall extended 10 cm above ground to prevent flooding onto the container surface. The three non-containerized trees were termed Natural trees.

Three containerized trees, termed Control trees, had no manipulations other than the root container. Control and Natural trees received rainfall only. Three containerized trees, termed Irrigated trees, received precipitation plus periodic irrigation at about 35 mm each month during the growing season. The irrigation system was supplied via underground polyvinyl chloride (PVC) tubing connected to a 23,000 L tank and electric pump powered by a generator. Water from a municipally approved drinking system was supplied to the tank. Three other containerized trees, termed Rainout trees, received a reduced soil moisture level after installation of a "sub-canopy" rain shelter beneath the foliage of each tree that prevented water from falling on the surface of the container but allowed foliage to be exposed to sunlight. Rain shelters consisted of a wood frame suspended 1 m above ground that was covered with wire netting and glasshouse grade 6-mil plastic (Jacoby and others 1988). The frame and covering were built around the base stems of each tree and extended beyond the root container edge with a slight slope away from tree center. The shelters did not exclude stem flow. Plastic sheets were applied to shelters 29 May 1986. Shelters remained in place from May 1986 through July 1989, except for an eight month period from September 1986 to April 1987 for repairs.

Irrigation treatments were also discontinued at the end of July 1989.

Measurements

Four 5-cm diameter aluminum tubes were installed within each root container to 2.2 m depth at 2 m laterally from tree center for soil moisture measurement. Volumetric soil moisture was measured every two weeks and at 30 cm increments to 180 cm depth during each growing season (April-September) using a neutron probe (Greacen 1981). Measurements were calibrated to field-collected samples.

For root measurements, three 10-cm diameter soil cores were taken to 270-m depth near the drip line of each tree during the fall 1989 to spring 1990 using a soil coring device (Giddings Inc., Ft. Collins, CO). Each core was divided into 10-cm segments from 0 to 90 cm, and 30-cm segments from 90 to 270 cm. Soil was separated from all roots in each segment with a hydro-pneumatic elutriation system (Smucker and others 1982). Mesquite roots were separated from roots of other species using a dissecting scope and were divided into two size classes, small (0 to 2 mm diameter) and large (2 to 10 mm diameter). Total root length within each soil segment and root size class was quantified using an automated image analyzer (Harris and Campbell 1989). Values for root length were expressed as root length density (RLD; m root length m⁻³ of soil) (Bohm 1979). Following RLD determination root samples were oven dried and weighed.

Leaf samples were collected from each tree at two week intervals during the 1988 and 1989 growing seasons. Samples were oven dried and ground and isotopic carbon ratio ($\delta^{13}\text{C}$), percent N and percent C was determined using methods described by Boutton (1991). Leaf samples were also collected in late August and September 1989, one month following termination of irrigation July 1989 to determine the effect of dry down within root containers following chronic wetness on leaf $\delta^{13}\text{C}$.

Canopy height of each tree was measured each year. Canopy biomass in each treatment was estimated from a height-to-mass relationship determined by harvesting over 20 trees (height range: 2-5 m) near the study site as part of another study (Ansley, unpublished data). Root:shoot (R:S) ratios were calculated for containerized trees using these derived canopy mass values and root mass data that were scaled to the volume of the root containers.

Statistical Analysis

Root length density and root mass data were analyzed within each root size and soil depth segment using a one-way ANOVA with treatment (Irrigated, Rainout, Control, Natural) as the main effect (three replicates per treatment) (SAS 1988). Non-normal data were square-root transformed prior to analysis. Means were separated using LSD ($P < 0.05$). Soil moisture values were pooled over all depths and sample dates within each year prior to analysis and analyzed with a

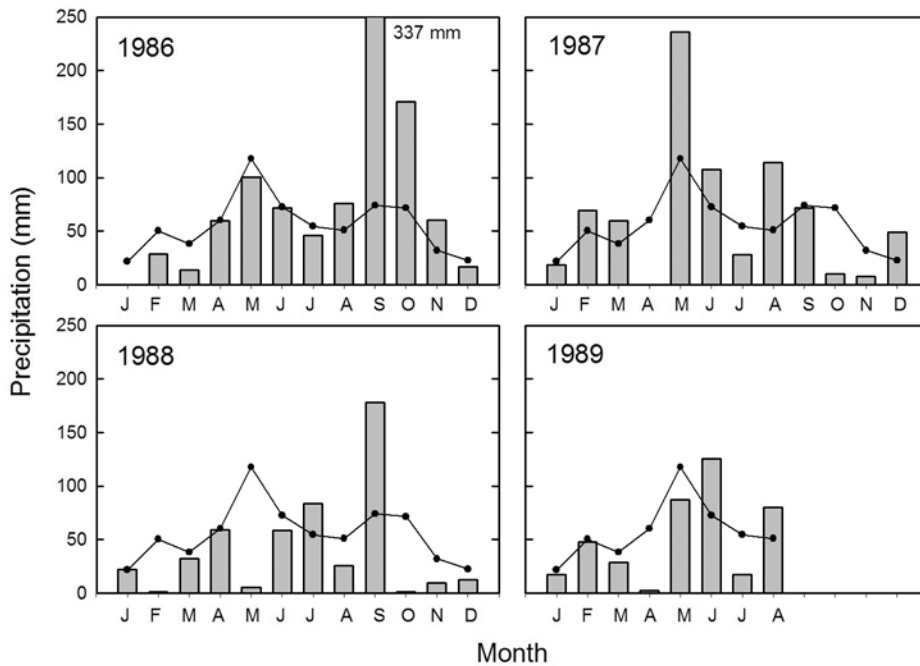


Figure 1. Monthly precipitation at the research site from 1986 until August 1989. Line indicates 30-yr average precipitation for each month.

two-way repeated measures GLM with treatment and year as main effects.

Results

Precipitation and Soil Moisture

Precipitation was near average for every month in 1986 except for extremely high amounts in September and October (fig. 1). Precipitation was above normal in 1987, below normal in 1988 and slightly below normal in 1989 prior to termination of soil manipulations in July 1989.

For the duration of the study (June 1986 through July 1989), total incoming water (precipitation or irrigation) was 2,438, 2,629, 3,455, and 1,021 mm for Natural, Control, Irrigated, and Rainout trees, respectively (table 1). Average annual incoming moisture was 1,037 mm (41 in.) for Irrigated and

306 mm (12 in.) for Rainout trees with Control and natural trees near the normal 665 mm (26 in.). Small differences in incoming water between Control and Natural trees were the result of periodic irrigations of Control and/or Rainout trees as part of other studies (Ansley and others 1992). The largest influx of water to Rainout trees occurred from September 1986 to April 1987 when rain shelters were removed for repairs and rainfall was well above normal.

At study initiation, all containerized trees had similar soil moisture when averaged over all depths (fig. 2). Soil moisture was greatest in Irrigated and lowest in Rainout treatments throughout the study. Soil moisture in the Control treatment was between Irrigated and Rainout trees. Abundant rainfall during the fall of 1986 and the 1987 growing season increased soil moisture substantially in the Irrigated and Control treatments in 1987. Soil moisture also increased slightly in the Rainout treatment due to removal of shelters from September 1986 to April 1987. Soil moisture near Natural trees was

Table 1. Incoming water for each treatment during the 40-month period from 29 May 1986 through 05 September 1989. NA = Natural, CT = Control, IR = Irrigated, RO = Rainout.

Interval	Precip. (mm)		Irrigation (mm) ¹			Precip.+ Irrigation (mm)			
	NA	CT	IR	CT ²	RO ²	NA	CT	IR	RO
	IR	RO							
29 May 86 to 31 Aug 86	193	0	283	73	73	193	266	476	73
01 Sep 86 to 30 Apr 87	731	731	0	0	99	731	731	731	830
01 May 87 to 31 Aug 87	485	0	325	92	92	485	577	810	92
01 Sep 87 to 30 Apr 88	253	0	0	0	0	253	253	253	0
01 May 88 to 05 Sep 89	776	0	409	26	26	776	802	1185	26
Totals (mm)	2438	731	1017	191	290	2438	2629	3455	1021
Average per year (mm)						732	788	1037	306

¹ Irrigation values are precipitation equivalent in mm over the surface area of each root container.

² CT and RO trees were irrigated occasionally FROM 1986 to 1988 as part of other study objectives not specific to this paper.

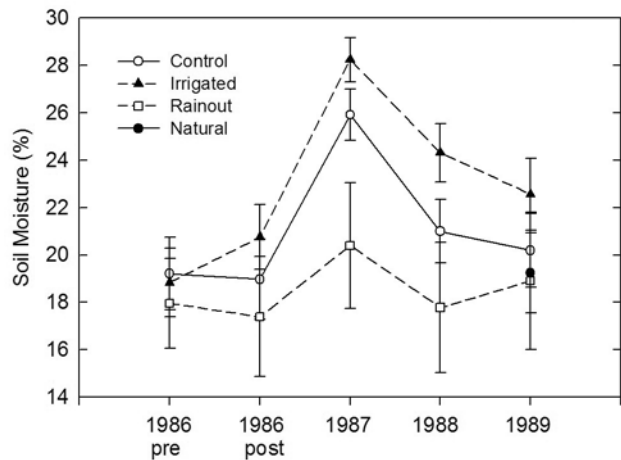


Figure 2. Soil moisture when averaged over all depths and dates in each growing season. Vertical bars indicate ± 1 S. E. ($n = 3$). Data for NA treatment were not available, 1986-88.

not measured until 1989 and was similar to the Rainout and Control treatments.

Grass cover was > 50 percent in all treatments at study initiation and remained at 50 to 80 percent in Natural, Control, and Irrigated treatments throughout the study. Grass cover declined in the Rainout treatment such that, by 1989, most of the area beneath the rain shelters was bare ground.

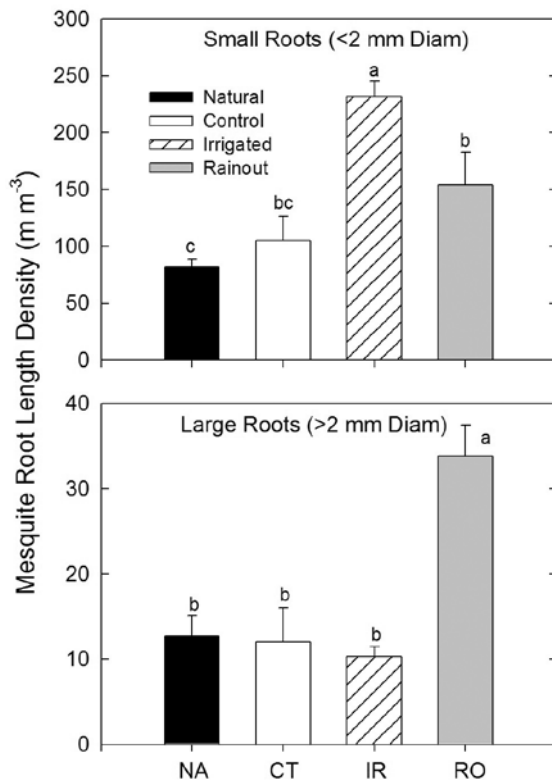


Figure 3. Root length density of small and large mesquite roots averaged over all soil depth segments (0-270 cm depth). Error bars indicate ± 1 S. E. ($n = 3$). Means with similar letters are not significant at $P < 0.05$.

Root Growth and Distribution

Mesquite root length density (RLD) of small (< 0.2 mm diameter) roots, when averaged over all soil segments (0 to 270 cm depth), was significantly greater in Irrigated trees than Natural or Control trees, with Rainout tree RLD intermediate trees in the other treatments (fig. 3). Mesquite RLD of large roots (> 0.2 mm diameter) was significantly greater in Rainout trees than in all other treatments when averaged over all soil segments. Large root RLD was similar among Natural, Control, and Irrigated trees.

Small root RLD, when averaged within 10 soil segments, was greater in Irrigated trees than Control or Natural trees in half of the soil segments (fig. 4). Most of these differences occurred within 30 to 180 cm depths. Small root RLD of Rainout trees fell between that of Irrigated and Control trees in most segments. At 0 to 10 cm, small root RLD showed a trend of being greater in Rainout and Irrigated than Control or Natural trees, but this was not significant at the 5 percent significance level.

Distribution of large root RLD was similar in Natural, Control, and Irrigated trees with greatest values between 30 to 90 cm and a sharp decline below 60 or 90 cm depth (fig. 4). In contrast, large root RLD of Rainout trees was three to eight

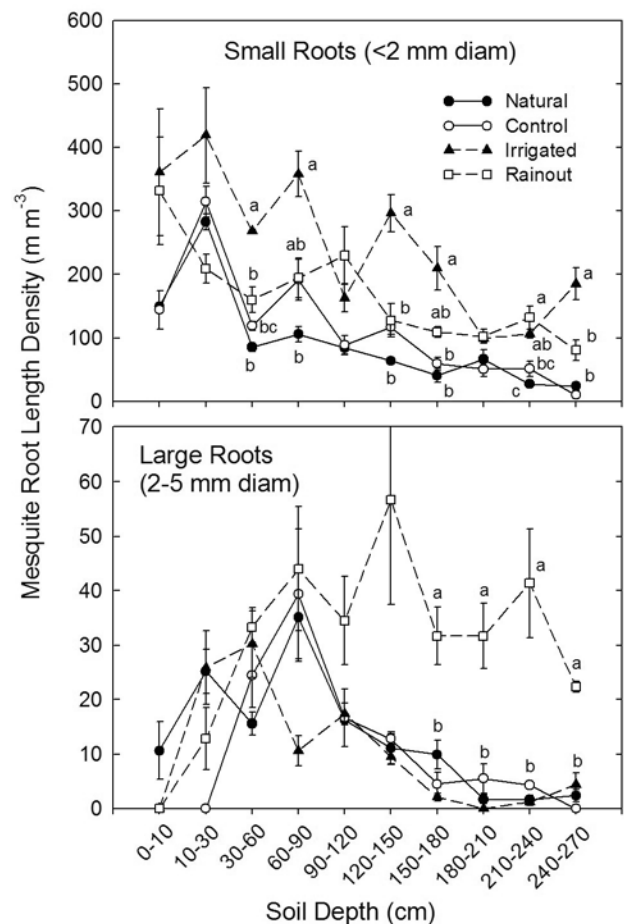


Figure 4. Root length density of small and large mesquite roots within 10 soil depth segments. Error bars indicate ± 0.5 S. E. ($n = 3$). Means with similar letters are not significant at $P < 0.05$.

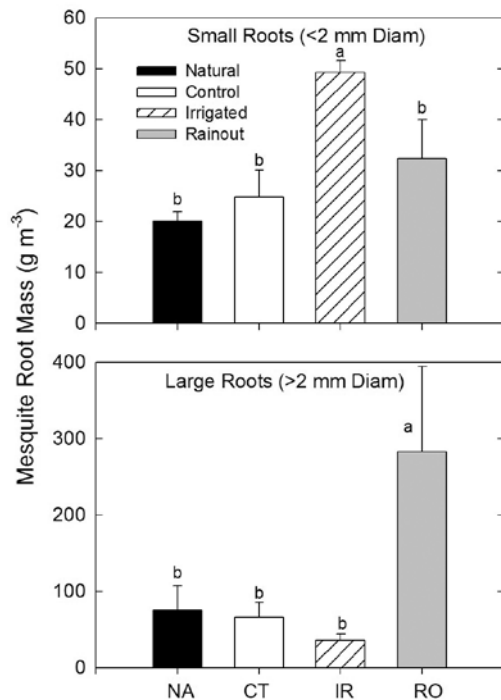


Figure 5. Root mass of small and large mesquite roots averaged over all soil depth segments (0-270 cm depth). Error bars indicate ± 1 S. E. ($n = 3$). Means with similar letters are not significant at $P < 0.05$.

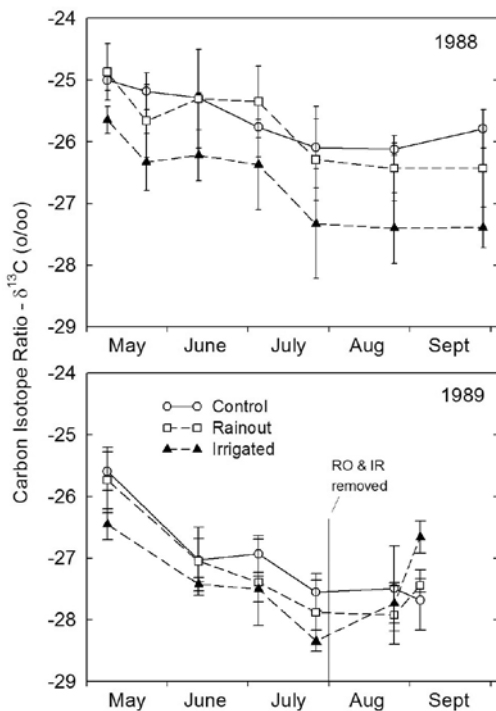


Figure 6. Carbon isotope ratios of mesquite leaf tissue in each treatment during 1988 and 1989. Error bars indicate ± 1 S. E. ($n = 3$).

times greater than the other treatments in segments below 90 cm. Averaging the six segments below 90 cm depth, RLD of large roots was 36.4, 7.3, 7.1, and 5.8 m m^{-3} in Rainout, Control, Natural, and Irrigated trees, respectively.

Irrigated trees exhibited greater small root mass than trees in the other treatments when averaged over all soil segments (fig. 5). Rainout trees exhibited greater large root mass than trees in other treatments but variability was high. Large root mass was similar in Control, Natural, and Irrigated trees.

Carbon Isotope Ratios and Canopy Growth

Leaf $\delta^{13}\text{C}$ declined in all treatments during each growing season (fig. 6). Irrigated trees tended to have lower $\delta^{13}\text{C}$ values than other treatments throughout 1988 and 1989, although differences between treatments were greater in 1988. After rain sheltering and irrigation treatments were discontinued at the end of July 1989, $\delta^{13}\text{C}$ increased sharply in Irrigated trees. Leaf C/N ratio was slightly lower in Irrigated trees (14.6 ± 0.3) than Control (15.4 ± 0.6) or Rainout (15.2 ± 0.5) trees throughout 1988, the result of a combination of slightly higher N and lower C in these trees than in the other treatments. There were no differences in leaf N, C, or C/N ratios between treatments in 1989.

Mesquite canopy height increased in all treatments by 0.5 m over the course of the study to about 4 m, with no difference between treatments (table 2). The root:shoot ratio was 0.3 for Control and Irrigated trees and 1.2 for Rainout trees.

Discussion

Survival of mesquite after 4 years of nearly continuous rain-sheltering reinforces the suggestion by Gile and others (1997) and other studies that root system plasticity affords this species a competitive advantage during extended droughts. When moisture was not manipulated (Natural and Control treatments), most mesquite roots were concentrated at 10 to 90 cm soil depth (fig. 4). Grass roots in these treatments were concentrated in the upper 10 cm (data not shown). Thus, grass and mesquite root systems were distributed in the classic “two-layer” pattern proposed by Walter (1954) and Walker and Noy Meir (1982) in which grasses occupy the upper soil layer and woody plant roots occur beneath the grass roots.

Exposed to chronic soil drought, Rainout mesquite explored deeper soil layers by investing energy into growth of larger “feeder” roots from which smaller roots extended. Caldwell (1976) emphasized that continued root extension into regions of soil in which the plant already has a well-established root system is a means for evading drought. Other studies have shown there can be considerable space between roots of woody plants (Chew and Chew 1965; Ludwig 1977), including mesquite (Heitschmidt and others 1988), that may be exploited during droughts.

We hypothesized that rain-sheltered mesquite would eventually die within a few years because the study site had little or no soil moisture below 2 m depth. Because the root containers

Table 2. Root mass (g m⁻³), root mass within each container, canopy height, projected canopy biomass, and root:shoot biomass ratios for containerized trees at study end, 1989.

Treatment	Root mass (g m ⁻³) ¹	Root mass/cont. (kg)	Canopy height (m)	Canopy biomass (kg) ²	Root:shoot ratio
Control	90.5	9.6	4.10	28.4	0.33
Irrigated	85.0	9.0	4.00	26.6	0.34
Rainout	315.3	33.4	4.13	28.9	1.15

¹ Data in left column taken from figure 5 (small + large roots).

² Canopy biomass (leaf + wood) was estimated via height-to-mass relationship derived from 23 harvested trees.

Mass (y) to height (x) relationship was: $\hat{y} = 0.99 - 4.76x + 2.79x^2$; $r^2 = 0.76$.

prevented trees from growing extensive lateral roots that are critical to the water use patterns of mesquite on this site (Ansley and others 1990), we assumed that the combination of the root container and rain sheltering would result in tree mortality. However, mesquite not only survived 4 years of nearly continuous drought, but exhibited an aggressive strategy of increased root growth and continued canopy growth. Canopy growth was maintained levels similar to other less stressed treatments possibly because Rainout mesquite found new sources of soil moisture through increased root growth. In contrast, the grass understory in the Rainout treatment ultimately disappeared. These results imply that mesquite responses during drought were manifest through *increased* physiological activity and growth rather than by simply surviving drought at some reduced metabolic level.

Response to Prolonged Soil Wetness

One reason not often emphasized for the success of mesquite may be the ability to exploit wet periods through increased root growth. Irrigated mesquite in this study increased growth of small roots to a much greater degree than did trees in other treatments. This increase in small root growth was not concentrated in upper soil layers as we originally hypothesized; rather, it occurred throughout the profile. These smaller roots would theoretically be more efficient at absorbing soil moisture than would larger roots. High concentrations of fine roots would allow exploitation of frequent soil wettings. However, this did not translate into greater canopy height or biomass in this treatment. Perhaps Irrigated trees increased foliage density that we did not measure. Ansley and others (1998) found a similar response when intraspecific competition was removed from mesquite.

Lower carbon isotope ratio in Irrigated trees suggests a lower water use efficiency (WUE) in this treatment (Ehleringer 1988). In indirect support of this conclusion, the rapid increase in leaf $\delta^{13}\text{C}$ in this treatment in the latter part of the 1989 growing season when irrigation was terminated suggests leaf $\delta^{13}\text{C}$ values were closely linked to soil moisture conditions. We assume trees in this treatment, with their larger network of small roots, rapidly absorbed any excess soil moisture in the root containers following termination of irrigation and became sufficiently moisture stressed that it affected leaf isotopic ratio.

The lack of a difference in leaf $\delta^{13}\text{C}$ values between Rainout and Control trees suggests that Rainout trees were able to capture sufficient soil moisture through increased growth of large and small roots at least during the period of the study. Had the study continued, Rainout trees may have experienced sufficient moisture stress to have affected leaf water use efficiency and carbon isotope ratios.

Root:Shoot Ratios

The root:shoot (R:S) biomass ratios estimated for mesquite imply that mesquite adjusted root system mass to maintain a consistent canopy mass in response to soil drought. However, the increase in growth of small roots in Irrigated trees did not affect total root mass enough to change R:S ratio compared to the Control.

The R:S ratios estimated in this study were likely lower than actual R:S ratios because soil cores were obtained closer to the canopy dripline of each tree than directly beneath the center of the canopy where there was likely greater root mass per unit soil volume. The R:S ratio was not calculated for Natural trees because the root system in this treatment was not contained and roots were likely very extensive (Ludwig 1977; Heitschmidt and others 1988).

Summary and Implications

Root adaptation to prolonged climatic and edaphic changes is an important element for survival of adult mesquite. This study demonstrated that mesquite accelerated root growth during periods of drought and wetness and that major adjustments to root system architecture occurred within a few years. These results imply that mesquite has a natural competitive advantage during both wet and dry cycles. This inherent capability, coupled with any management practice, such as livestock grazing, that confers even a slight advantage to this species over other species during atypical climatic cycles will likely accelerate the process of ecosystem domination by mesquite. The tendency of managers to increase grazing during wet periods to "make up" for grazing losses during droughts will likely enhance the natural competitive advantage mesquite possesses via root system adaptation.

Acknowledgments

The authors wish to acknowledge Keith Lawrence, Cecil Meadors (deceased), and Bertha Trevino for assisting in the field and laboratory. This research was funded in part by a grant from University Lands-Surface Interests, Univ. of Texas System, Midland, TX. The research site was provided by the E. Paul and Helen Buck Waggoner Foundation, Vernon, TX.

References

- Ansley, R. J.; Jacoby, P. W.; Lawrence, B. K. 1988. Root containerization for physiological studies of shrubs and trees on rangeland. *Journal of Range Management*. 41: 90-91.
- Ansley, R. J.; Jacoby, P. W.; Cuomo, G. J. 1990. Water relations of honey mesquite following severing of lateral roots: Influence of location and amount of subsurface water. *Journal of Range Management*. 43: 436-442.
- Ansley, R. J.; Jacoby, P. W.; Meadors, C. H.; Lawrence, B. K. 1992. Soil and leaf water relations of differentially moisture-stressed honey mesquite (*Prosopis glandulosa* Torr.). *Journal of Arid Environments*. 22: 147-159.
- Ansley, R. J.; Trevino, B. A.; Jacoby, P. W. 1998. Intraspecific competition in honey mesquite: leaf and whole plant responses. *Journal of Range Management*. 51: 345-352.
- Ansley, R. J.; 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.; Schimel, D. S.; Holland E. A. 1995. Mechanisms of shrubland expansion: land use, climate or CO₂? *Climatic Change*. 29: 91-99.
- Archer, S. R.; Boutton, T. W.; Hibbard, K. 2001. Trees in grasslands: biogeochemical consequences of woody plant expansion. Pages 115-137. In: Schulze, E. -D.; Harrison, S. P.; Heimann, M.; Holland, E. A.; Lloyd, J.; Prentice, I. C.; Schimel, D. (editors) *Global Biogeochemical Cycles in the Climate System*, Academic Press, San Diego.
- Bohm, W. 1979. *Methods of studying root systems*. Springer-Verlag, Berlin.
- Boutton, T. W. 1991. Stable carbon isotope ratios of natural materials. 1. Sample preparation and mass spectrometer analysis. Pages 155-171. In: Coleman, D. C.; Fry, B. (editors), *Carbon Isotope Techniques*, Academic Press, New York.
- Caldwell, M. M. 1976. Root extension and water absorption. Pages 63-85. In: Lange, O. L.; Kappen, L.; Schulze, E.-D. (editors), *Water and Plant Life—Ecological Studies Vol. 19*, Springer-Verlag, Berlin.
- Chew, R. M.; Chew, A. E. 1965. The primary productivity of a desert shrub (*Larrea tridentata*) community. *Ecological Monographs*. 35: 355-375.
- Ehleringer, J. R. 1988. Carbon isotope ratios and physiological processes in aridland plants. Pages 41-54. In: Rundel, P. W.; Ehleringer, J. R.; Nagy, K. A. (editors), *Stable Isotopes in Ecological Research—Ecological Studies Vol. 68*, Springer-Verlag, New York.
- Gibbons, R. P.; Lenz, J. M. 2001. Root systems of some Chihuahuan desert plants. *Journal of Arid Environments*. 49: 221-263.
- Gile, L. H.; Gibbons, R. P.; Lenz, J. M. 1997. The near-ubiquitous pedogenic world of mesquite roots in an arid basin floor. *Journal of Arid Environments*. 35: 39-58.
- Greacen, E. L. 1981. *Soil water assessment*. CSIRO, Adelaide, Aust.
- Harris, G. A.; Campbell, G. S. 1989. Automated quantification of roots using a simple image analyzer. *Agronomy Journal*. 81: 935-938.
- Heitschmidt, R. K.; Ansley, R. J.; Dowhower, S. L.; Jacoby, P. W.; Price, D. L. 1988. Some observations from the excavation of mesquite root systems. *Journal of Range Management*. 41: 227-231.
- Hesla, B. I.; Tieszen, L. L.; Boutton, T. W. 1985. Seasonal water relations of savanna shrubs and grasses in Kenya, East Africa. *Journal of Arid Environments*. 8: 15-31.
- Hinckley, T. M.; Duhme, F.; Hinckley, A. R.; Richter, H. 1983. Drought relations of shrub species: assessment of the mechanisms of drought resistance. *Oecologia*. 59: 344-350.
- Jacoby, P. W.; Ansley, R. J.; Lawrence, B. K. 1988. Design of rain shelters for studying water relations of rangeland shrubs. *Journal of Range Management*. 41: 83-85.
- Koos, W. M.; Williams, J. C.; Dixon, M. L. 1962. *Soil survey of Wilbarger County, Texas*. USDA Soil Conservation Service, Soil Survey Series 1959 No. 18, Fort Worth, TX.
- Kramp, B. A.; Ansley, R. J.; Tunnell, T. R. 1998. Survival of mesquite seedlings emerging from cattle and wildlife feces in a semi-arid grassland. *The Southwestern Naturalist*. 43: 300-312.
- Kummerow, J. 1980. Adaptation of roots in water-stressed native vegetation. Pages 57-74. In: Turner, N. C.; Kramer, P. J., (editors), *Adaptation of Plants to Water and High Temperature Stress*. John Wiley and Sons, New York.
- Ludwig, J. A. 1977. Distributional adaptations of root systems in desert environments. Pages 85-91. In: J. K. Marshall (editor), *The Belowground Ecosystem: A Synthesis of Plant-Associated Processes*. Range Science Dept, Colorado State Univ. Series No 26, Fort Collins, CO.
- Mooney, H. A.; Simpson, B. B.; Solbrig, O. T. 1977. Phenology, morphology, physiology. Pages 26-41 In: B. B. Simpson (editor), *Mesquite—Its Biology in Two Desert Ecosystems*. US/IBP Synthesis Series No 4. Dowden, Hutchinson and Ross Inc, Stroudsburg, Penn.
- Nilsen, E. T.; Sharifi, M. R.; Rundel, P. W. 1981. Summer water relations of the desert phreatophyte *Prosopis glandulosa* in the Sonoran desert of southern California. *Oecologia*. 50: 271-276.
- Phillips, W. S. 1963. Depth of roots in soil. *Ecology*. 44: 424.
- SAS 1988. *SAS/STAT User's Guide Version 6.03*, SAS Inst., Inc., Cary, N.C.
- Smeins, F. E. 1983. Origin of the brush problem—a geographical and ecological perspective of contemporary distributions. Pages 5-16 In: K. McDaniel (editor), *Proceedings—Brush Management Symposium*. Texas Tech University Press, Lubbock.
- Smucker, A. J. M.; McBurney, S. L.; Srivastava, A. K. 1982. Quantitative separation of roots from compacted soil profiles by the hydropneumatic elutriation system. *Agronomy Journal*. 74: 500-503.
- van Vegten, J. A. 1983. Thornbrush invasion in a savanna ecosystem in eastern Botswana. *Vegetatio*. 56: 3-7.
- Walter, H. 1954. Die Verbuschung, eine Erscheinung der subtropischen Savannengebiete, und ihre ökologischen Ursachen. *Vegetatio*. 5/6: 6-10.
- Walker, B. H.; Noy-Meir, I. 1982. Aspects of the stability and resilience of savanna ecosystems. Pages 556-590 In: Huntley, B. J.; Walker, B. H., (editors). *Ecology of Tropical Savannas*. Springer-Verlag, Berlin.

Wan, C.; Sosebee, R. E. 1991. Water relations and transpiration of honey mesquite on 2 sites in west Texas. *Journal of Range Management*. 44: 156-160.

The Authors

¹ Professor of Rangeland Ecology, Texas Agricultural Experiment Station, Vernon, TX. r-ansley@tamu.edu

² Professor of Rangeland Ecology, Dept. Ecosystem Science and Management, Texas A&M Univ., College Station, TX.

³ Associate Dean, College of Agriculture, Washington State University, Pullman, WA.

Response of Seedlings of Two Hypogeal Brush Species to CO₂ Enrichment

Charles R. Tischler¹

Justin D. Derner²

H. Wayne Polley³

Hyrum B. Johnson⁴

Abstract: Previous work has demonstrated that epigeal woody invasive plants (with expanding, photosynthetic cotyledons), such as honey mesquite (*Prosopis glandulosa* L.), respond positively to elevated atmospheric CO₂ concentrations in as little as 3 days after emergence. No research has addressed the behavior of larger seeded, hypogeal invasive plants (common in south Texas) exposed to elevated CO₂. We studied two such species, guajillo (*Acacia berlandieri* Benth.) and cat claw acacia (*Acacia greggii* Gray var. *wrightii* [G. Benth.] D. Isley), to quantify growth stimulation at a doubled concentration of CO₂. Seedlings were grown in glasshouses in 1.5 m tubes at Temple, TX, in the late summer of 2000. Only seeds within a narrow range of masses were selected for each species, to reduce effects of seed mass on seedling size. Plants were harvested 15 days after emergence. Leaf area, shoot weight, leaf weight, root weight, and depth of root penetration were determined for each plant. Both species exhibited marked root length at sampling, with mean values of about 75 and 90 cm for guajillo and cat claw acacia, respectively. For both species, all parameters demonstrated a positive numerical response to elevated CO₂, although no differences were statistically significant. The lack of statistical verification of the observed differences was likely caused by the great deal of variability observed within both species. For example, values for specific parameters varied by as much as a factor of six within a species and CO₂ treatment. These results suggest that seedling growth responses to elevated CO₂ may be smaller in hypogeal than in co-occurring epigeal species.

Introduction

Several studies have demonstrated that seedlings of C₃ species demonstrate significant positive growth responses to elevated CO₂ concentrations relatively soon after emergence. For example, Tischler and others (2000) found that for five herbaceous species, significant responses to doubled ambient CO₂ concentration were observed by 3 days after emergence. In another study utilizing woody species, significant responses were observed by one week after emergence (Tischler and others 2003). All species utilized in these studies were epigeal—that is, the cotyledons were elevated above soil level by elongation of the hypocotyl. Furthermore, in all species utilized in these studies, the cotyledons expanded and quickly became photosynthetically active.

Another grouping of dicots is termed “hypogeal.” In these species, the cotyledons remain at planting depth (or often, in nature, on the soil surface), as the epicotyl elongates to elevate the growing point above the soil surface. In this grouping of plants, the cotyledons serve only a storage function and do not contribute to the photosynthetic activity of the plant. Numerous surveys indicate that hypogeal species have a considerably greater seed mass than epigeal species (for example, see Ng 1985; Bazzaz and Pickett 1980).

Total reproductive output represents a balance between seed size and seed number (Smith and Fretwell 1974). For a species to allocate a larger proportion of resources to a smaller number of seeds, hypogeal germination morphology (and

greater seed mass) must confer an advantage to the seedling. One advantage is resistance to clipping. Adventitious buds in the axles of the cotyledons are at or below soil level in hypogeal seedlings, so these seedlings readily survive clipping at soil level. In epigeal species, clipping at soil level severs the hypocotyl and cotyledons, and thus removes meristematic tissue. Another advantage of hypogeal germination (and the concomitant abundance of seed reserves) is an innate ability to survive stresses, such as low light levels, in the seedling stage (Ganade and Westoby 1999). A tradeoff of hypogeal germination morphology may be depressed seedling relative growth rate (Maranon and Grubb 1993; Stebbins 1976a, b). Indeed, the literature indicates that seedling growth rates are slower in hypogeal than epigeal species. This fact prompted us to question if the rapid growth response to elevated CO₂ observed in epigeal species might be delayed or less dramatic in hypogeal species. If so, CO₂ enrichment might actually be a disadvantage for hypogeal species in competitive situations where growth rate is important, and thus results from one functional type could not be extrapolated to the other type when assessing potential effects of increasing atmospheric CO₂ concentrations on ecosystem dynamics. The two hypogeal species we chose to study were guajillo (*Acacia berlandieri* Benth) and cat claw acacia (*Acacia greggii* Gray var. *wrightii* [G. Benth.] D. Isely). Guajillo is a significant brush species in south Texas, from west of Corpus Christi to Uvalde. Guajillo thrives on chalky limestone (caliche) outcroppings, where it is the predominant species, as well as on deeper soils where it is

In: Sosebee, R.E.; Wester, D.B.; Britton, C.M.; McArthur, E.D.; Kitchen, S.G., comp. 2007. Proceedings: Shrubland dynamics—fire and water; 2004 August 10-12; Lubbock, TX. Proceedings RMRS-P-47. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 173 p.

one component of a mixed brush community. Cat claw (called Wright acacia in the older literature) is also one component of mixed brush stands in south Texas.

Materials and Methods

Seeds of guajillo were harvested from shrubs near Beeville, TX, in June of 1999. Cat Claw Acacia seeds were harvested from trees near Pearsall, TX, in 1998. Both groups of seeds were stored in a seed vault. Because there is considerable variability in seed mass in these species, we weighed individual seeds and selected those within a relatively narrow band of seed masses. For guajillo, this was from 0.42 to 0.58 g, whereas values for cat claw acacia ranged from 0.16 to 0.24 g. Obtaining uniform guajillo seed is especially difficult because as seed mature, they are rapidly parasitized by weevils of the genus *Bruchid*. Seeds which appear normal often already have damage to the embryo, which becomes obvious only after the seedling emerges.

Seeds were planted at a 2 cm depth in 1.5 m pvc tubes (5-cm diameter) containing Pedernales Fine Sandy loam soil wetted with tenth strength Hoagland's solution. Two seeds were planted per tube. In cases when both seed germinated, the weaker of the two seedlings was destroyed. Seeds were planted on August 1, 2001. Four groups of tubes of each species were assigned to four separate greenhouses, two maintained at ambient CO₂ concentration and two maintained at 700 ppm CO₂. Periodic monitoring of light levels indicated that irradiance was very similar among greenhouses. As is common in August in central Texas, days were sunny with only occasional scattered clouds, analogous to conditions encountered by Tischler and others (2003) in a prior experiment with woody epigeal seedlings. Plants were monitored for insect infestation, but none was observed. However, several guajillo plants were attacked by fungus. These plants were discarded.

Seedlings were watered as needed to maintain soil near drip capacity with one-tenth strength Hoagland's solution for the duration of the experiment. At 15 days after emergence, the culture tubes were removed from the greenhouse and carefully split so that roots could be washed from the soil media. Leaf area was determined with a photoelectric leaf area meter, and root lengths were measured with a meter stick and recorded. Plants were divided into leaves, root, and stem (remnants of the seedcoat and hypogeal cotyledons were discarded), dried at 70 C for 24 hours, and weighed.

The growth period of 15 days was selected based on earlier experimentation, which indicated that no responses to elevated CO₂ were observed in these species at earlier harvest dates.

Results

Data presented in tables 1 and 2 indicate no significant effect of elevated CO₂ by day 15 on any plant parameter for either species, although values were numerically higher in elevated CO₂ for all parameters except root length for guajillo. These results, although not unexpected, are in stark contrast

Table 1—Plant parameters of 15-day-old Guajillo seedlings.

Parameter	CO ₂ Concentration (ppm)		
	365 (n = 8)	700 (n =12)	P
Leaf area (cm ²)	37.6	43.7	0.4777
Rooting depth (cm)	77.9	75.9	0.4760
Stem wt (mg)	32.9	43.7	0.0814
Root wt (mg)*	151.2	173.7	0.3498
Leaf wt (mg)	178.2	246.7	0.2290
Total biomass (mg)	362.3	464.2	0.1978

*Remnants of seed coat and hypogeal cotyledons not included in mass.

Table 2—Plant parameters of 15-day-old Cat Claw Acacia seedlings grown at two CO₂ concentrations.

Parameter	CO ₂ Concentration (ppm)		
	360 (n = 13)	700 (n = 14)	P
Leaf area (cm ²)	22.1	26.1	0.3498
Rooting depth (cm)	90.2	92.2	0.7322
Stem wt (mg)	27.4	33.1	0.1805
Root wt (mg)*	98.7	117.39	0.0954
Leaf wt (mg)	122.9	156.0	0.1789
Total biomass (mg)	249.0	306.5	0.1172

*Remnants of seed coat and hypogeal cotyledons not included in mass.

with data we previously presented for epigeal herbaceous and woody species (Tischler and others 2000, 2003), where significant positive effects of CO₂ were observed between 1 and 3 days after emergence.

The root lengths of the two species were somewhat greater than would have been expected, based on behavior of mesquite (*Prosopis glandulosa* L.) in other experiments. The fact that root lengths were greater for the smaller-seeded catclaw was also unexpected.

Discussion

Several features of these data sets merit further consideration. First, total biomass of the guajillo seedlings, 362 and 464 mg, respectively, for ambient and elevated CO₂, was still less than the 420 to 580 mg range of the seed used in the experiment. Of course, a portion of the seed mass was contributed by the inert seed coat, but at very best, at 15 days the seedlings were barely more massive than the starting seed. The same general trends were true for cat claw acacia (249 and 307 mg for seedlings at ambient and elevated CO₂, with an initial seed mass of 160 to 240 mg). A second significant feature of the data sets is the somewhat amazing root length of the seedlings (approximately 75 cm for guajillo; greater than 90 cm for cat claw acacia).

In work with epigeal woody species at ambient and elevated CO₂, Tischler and others (2003) observed significant effects of elevated CO₂ on total biomass for mesquite at day

3, and for parkinsonia (*Parkinsonia aculeata* L.), honey locust (*Gleditsia triacanthos* L.), and huisache (*Acacia farnesiana* (L.) Willd.) at day 8. These experiments were conducted in an earlier year (1996) in the same greenhouse, with all aspects of plant culture being the same, except for the fact that seed were planted about August 26, as compared to August 1 in this study. Thus, seedlings in this study experienced slightly longer day length than those in the 1996 study. Obviously, it is hazardous to compare seedlings grown in two separate experiments, but given the similarity of the experimental system, it is clear that the hypogeal species' response was much less than would have been expected from woody epigeal species.

Another interesting observation relates to root lengths. Admittedly, the root lengths we measured were longer than would be expected in a shallow soil or caliche outcropping. However, the fact that roots penetrated $\frac{3}{4}$ to almost one meter with no major increase in seedling dry weight suggests that these two hypogeal species may reach a developmental stage that could be described as "established" with only minimal carbon input from photosynthetic activity. This observation argues against any significant role for elevated CO₂ in improving seedling establishment or seedling competitive ability of guajillo and cat claw acacia, in stark contrast to observations of corresponding epigeal species. Thus, blanket predictions about effects of elevated CO₂ on ecosystem processes, especially seedling recruitment, must be tempered with an understanding of how seedling morphology can modify these responses.

References

Bazzaz, F. A.; Pickett, S. T. A. 1980. Physiological ecology of tropical succession: A comparative review. *Annual Review of Ecology and Systematics* 11:287-310.
 Ganade, G.; Westoby, M. 1999. Seed mass and the evolution of early-seedling etiolation. *American Naturalist* 154:469-480.

Maranon, T.; Grubb, P. G. 1993. Physiological basis and ecological significance of the seed size and relative growth rate relationship in Mediterranean annuals. *Functional Ecology* 7:591-599.
 Ng, F. S. P. 1985. Strategies of establishment in Malayan forest trees. *Tropical Trees as Living Systems* (eds P. B. Tomlinson and M. H. Zimmermann), pp. 129-162. Cambridge University Press, Cambridge.
 Smith, C. C.; Fretwell, S. D. 1974. The optimal balance between size and number of offspring. *American Naturalist* 108:499-506.
 Stebbins, G. L. 1976a. 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.
 Stebbins, G. L. 1976b. Seed and seedling ecology in annual legumes. II. Stem growth, seed production and mechanisms for transport. *Oecologia Plantarum* 11:333-344.
 Tischler, C. R.; Polley, H. W.; Johnson, H. B.; Pennington, R. E. 2000. Seedling response to elevated CO₂ in five epigeal species. *International Journal of Plant Science* 161:779-783.
 Tischler, C. R.; Derner, J. D.; Polley, H. W.; Johnson, H. B. 2004. Responses of seedlings of five woody species to carbon dioxide enrichment. 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. 216 p.

The Authors

- ¹ Plant Physiologist, USDA-ARS Grassland, Soil & Water Research Laboratory, Temple, TX. ctischler@spa.ars.usda.gov
- ² Research Leader, USDA-ARS Grassland, Soil & Water Research Laboratory, Temple, TX.
- ³ Ecologist, USDA-ARS Grassland, Soil & Water Research Laboratory, Temple, TX.
- ⁴ Range Scientist, USDA-ARS, High Plains Grasslands Research Station, Cheyenne, WY.

Shrub Biomass Production Following Simulated Herbivory: A Test of the Compensatory Growth Hypothesis

Terri B. Teaschner¹
Timothy E. Fulbright²

Abstract: The objective of this experiment was to test the hypotheses that 1) simulated herbivory stimulates increased biomass production in spiny hackberry (*Celtis pallida*), but decreases biomass production in blackbrush acacia (*Acacia rigidula*) compared to unbrowsed plants and 2) thorn density and length increase in blackbrush acacia to a greater extent than in spiny hackberry in response to tissue removal. Blackbrush acacia shrubs defoliated repeatedly at the 75 percent level produced about 66 percent more biomass than control shrubs, while shrubs receiving 100 percent repeat defoliation treatments produced double the biomass as control shrubs ($p < 0.05$), suggesting overcompensation. Spiny hackberry repeat defoliated shrub biomass production was double control shrub production at 25 percent treatment levels and 81 percent higher in repeat defoliated shrubs at 50 percent defoliation levels relative to control shrubs ($p < 0.05$). Biomass production during the third and fourth defoliation events was 90 percent lower than ($p < 0.05$) biomass removed in the initial defoliation. New twig and thorn production occurred only in 2003, but only in blackbrush acacia. These results suggest that spiny hackberry, a highly palatable shrub, is negatively impacted at high defoliation intensity, while the less palatable shrub, blackbrush acacia, responds to intense defoliation with increased biomass production.

Introduction

Compensation, over-compensation, and under-compensation were the three original plant responses to biomass removal by herbivores (McNaughton 1983). Production of mechanical and chemical defenses has been characterized as an induced response to biomass loss (Rhoner and Ward 1997). Increased thorn length and density may retard browsing (Cooper and Owen-Smith 1986). Our goal is to determine plant response to various levels of simulated herbivory in two important south Texas shrubs.

Spiny hackberry (*Celtis pallida*) and blackbrush acacia (*Acacia rigidula*) are important browse species for wildlife in southern Texas (Graham 1982, Varner and Blankenship 1987). Many wildlife species utilize spiny hackberry and blackbrush acacia during dry periods when other available forage has been exhausted (Varner and Blankenship 1987).

Spiny hackberry has spines, but no chemical defensive mechanisms against herbivory have been documented and the shrub appears to respond to removal of tissue with compensatory growth (Asah and others 1987, Schindler 2000). After top growth removal, new spiny hackberry shoots and tissue are often higher in nutritive value than previous tissues (Asah and others 1987, Schindler and others 2004). Blackbrush acacia is more heavily defended with thorns and chemical compounds (Clement and others 1998, Schindler and others 2003). Previous studies have suggested that thorn length and density increase on thorn scrub vegetation following mechanical brush clearing (Schindler and others 2004). It is therefore important to understand how these two important browse plants respond to biomass removal by herbivores.

We hypothesize that 1) simulated herbivory stimulates increased biomass production in spiny hackberry but decreases biomass production in blackbrush acacia compared to unbrowsed plants and 2) thorn density and length increase in blackbrush acacia to a greater extent than in spiny hackberry in response to tissue removal.

Materials and Methods

Study Site

Research was conducted on the Jack R. and Loris J. Welhausen Experimental Station in Webb County, about 56 km northeast of Laredo, Texas (27°40'57N, 98°56'51W), at an elevation of about 137 m. The surface layer soil at the site is a sandy clay loam with 0 to 3 percent slopes, with a caliche layer underlying the soil at depths of 1 to 5 m (Soil Conservation Service 1985). Precipitation, as recorded in Laredo (1947-2003), averages about 50 cm a year but varied during the 2 years of this study (fig. 1) and deviated from long term averages (National Climate Data Center 2004, Asheville, NC). Maximum temperatures above 35°C occur from June to August and the lowest temperatures, around 8°C, usually occur December to January (National Climate Data Center). Vegetation at the study site is a mixed shrub community with little grass cover (Varner and Blankenship 1987). Cattle and wildlife both are present on the ranch under a continuous grazing system. However, little use was observed by cattle or wildlife of the selected study site area. The area has been mechanically cleared of brush in the past, but sufficient time

In: Sosebee, R.E.; Wester, D.B.; Britton, C.M.; McArthur, E.D.; Kitchen, S.G., comp. 2007. Proceedings: Shrubland dynamics—fire and water; 2004 August 10-12; Lubbock, TX. Proceedings RMRS-P-47. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 173 p.

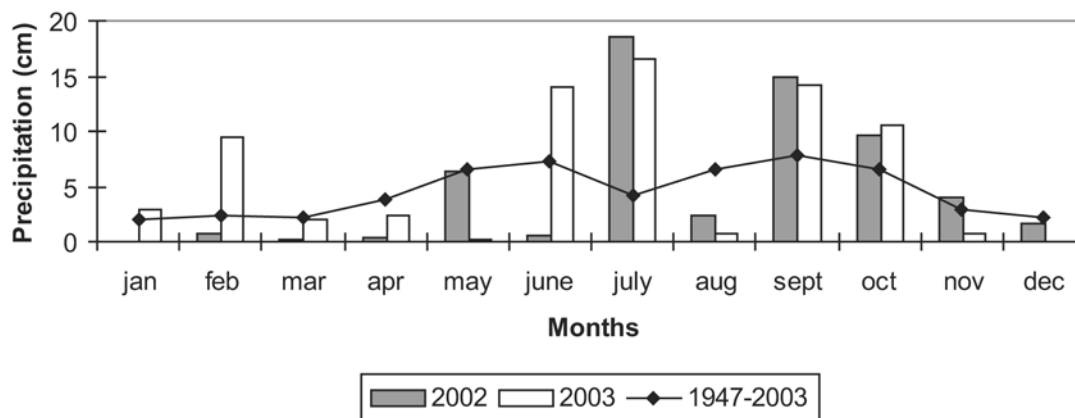


Figure 1. Precipitation by month as recorded in Laredo (1947-2003) and the Welhausen Research Station (2002, 2003), Webb County, TX.

has elapsed for vegetation to recover and form a mature shrub community. A representative area was selected in May 2002 and an enclosure about 60 x 80 m surrounded by a 1.2 m tall welded wire fence was established to prevent wildlife and livestock browsing on shrubs. Chicken wire with a 2.5 cm diameter mesh was used along the bottom 0.6 m of the fence to retard small mammals. A CM20 Campbell Scientific Weather Station located on the Welhausen Research Station < ½ km from the study site provided local hourly and daily weather conditions (Campbell Scientific Inc., Logan, UT).

Methods

A randomized, complete-block design was used in this experiment. Five blocks per species were used, with each treatment randomly assigned to a selected shrub in the block ($n = 5$). Twenty-five plants of each species, blackbrush acacia and spiny hackberry, were randomly selected in May 2002 from plants within the enclosure. Plants had a similar number of basal stems and were 1.5 to 2 m tall, which is considered the upper limit white-tailed deer (*Odocoileus virginianus*) browse. Plants of each species were randomly chosen and were assigned to one of five defoliation treatments on a randomly selected stem: 0 percent, 25 percent, 50 percent, 75 percent, and 100 percent. The 0 percent defoliation was the control group and was defoliated at the end of the experiment in October. For the 2003 field season, additional controls were added for harvest at the second and third defoliations to add a finer degree of resolution for temporal variations that might influence biomass production, such as tropical storms or insect defoliation. Shrubs were initially defoliated in late June and repeat removal of regrowth biomass was conducted at 6 week intervals until late October, resulting in one initial and three repeat defoliation periods for each year. Leaf tissue and new twig material was removed by hand, placed on dry ice, weighed, freeze dried for 48 hours, and then reweighed. Thorn length and density was measured on new season twig growth at the initial defoliation and then only on regrowth twig biomass at each repeat defoliation period. Leaf and

twig biomass production, thorn length, and thorn density were analyzed separately by species using ANOVA and Proc Mixed commands in SAS version 8 (SAS Institute 1999). Independent variables consisted of defoliation intensity, clipping treatment (control or treated), and defoliation event. Dependent variables were biomass production, thorn length, and thorn density.

Results

Blackbrush acacia

There were no significant ($p > 0.05$) differences between years for blackbrush acacia biomass production. Total biomass production by repeat defoliated blackbrush acacia shrubs subjected to 25 percent and 50 percent defoliation did not differ ($p > 0.06$) from control shrubs (fig. 2). Blackbrush acacia shrubs subjected to 75 percent and 100 percent tissue removal produced more ($p < 0.01$) biomass, double the control production for 100 percent removal, than associated

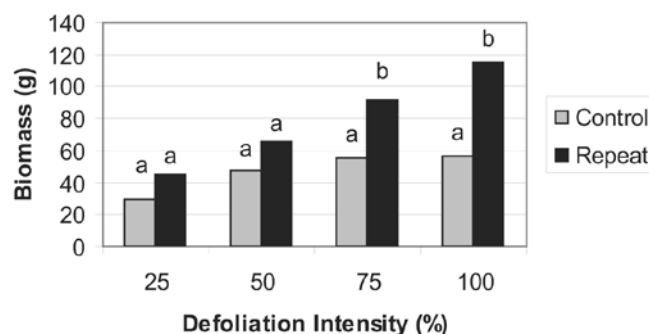


Figure 2. Mean of total blackbrush acacia biomass summed across defoliation events for each treatment, no difference between 2002 and 2003. Control plants were harvested only at end of growing season in October; repeat is sum of all biomass removed. Means within a defoliation intensity with a different letter are different ($p < 0.05$) at that defoliation level. Research conducted in 2002 and 2003 at Welhausen Research Station, Webb County, Texas.

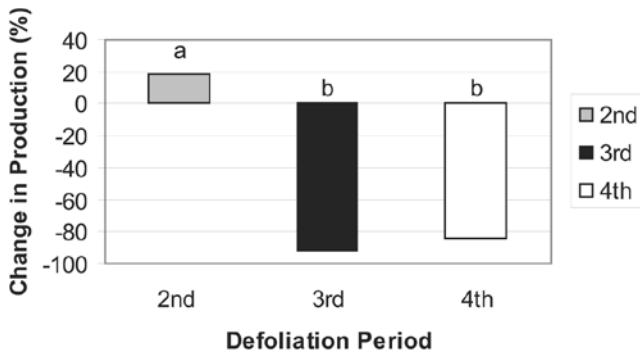


Figure 3. Change (percent) of blackbrush acacia biomass production as a percent of the original biomass removed. Years and treatment are not different. Means across defoliation periods with a different letter are different ($p < 0.05$). Research conducted in 2002 and 2003 at Welhausen Research Station, Webb County, Texas.

non-defoliated control shrubs. We reject our hypothesis that simulated herbivory decreases biomass production in blackbrush acacia because shrubs defoliated at 25 percent and 50 percent produced biomass amounts similar to control shrubs and shrubs defoliated at 75 percent and 100 percent levels overcompensated or produced more biomass than control shrubs.

The change (percent) in blackbrush acacia regrowth biomass compared to initial biomass removed demonstrated overcompensation during the second defoliation period, but a decrease or under-compensation during the third and fourth defoliation events (fig. 3). There was no difference ($p > 0.05$) in defoliation intensity (percent removed) or year for each of the three repeat defoliation periods. Biomass removed at the second defoliation was about 20 percent more than was originally removed. Biomass production 12 and 18 weeks post defoliation demonstrated an 80 percent reduction in biomass production compared to initial biomass amounts removed.

Blackbrush acacia did not produce new twig growth after defoliation events in 2002. We hypothesize the drought of 2001, coupled with low rainfall in early 2002, was partially responsible for this. In 2003, twig and thorn production occurred in treated and control blackbrush acacia shrubs, except during the third defoliation period when treated plants did not produce any twigs or thorns (figs. 4 and 5). Thorns on repeat defoliated plants were twice as long as thorns on control shrubs at the second defoliation event and were three times longer on treated plants at the final defoliation event than control shrubs ($p < 0.02$, fig. 4). Thorn density in treated plants was greater (0.76 thorns/cm) than control plants (0.57 thorns/cm) ($p < 0.02$). This appears to support our hypothesis that defoliation increased thorn density and length in treated shrubs.

Spiny Hackberry

There was no significant difference ($p > 0.05$) between years for spiny hackberry biomass production. Spiny hackberry shrubs exhibited the opposite compensation pattern than

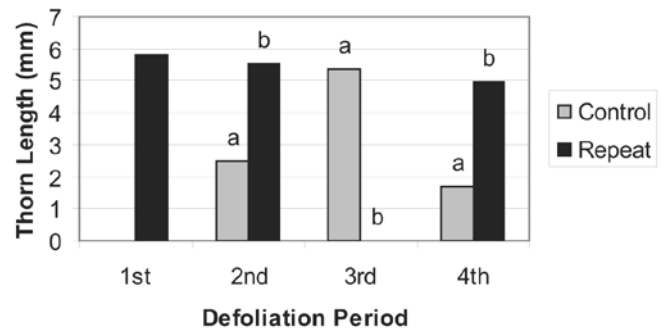


Figure 4. 2003 Blackbrush acacia thorn length. No thorn production in 2002. No repeat thorn production at 3rd defoliation period. Means within a defoliation period with a different letter are different ($p < 0.02$). Research conducted in 2002 and 2003 at Welhausen Research Station, Webb County, Texas.

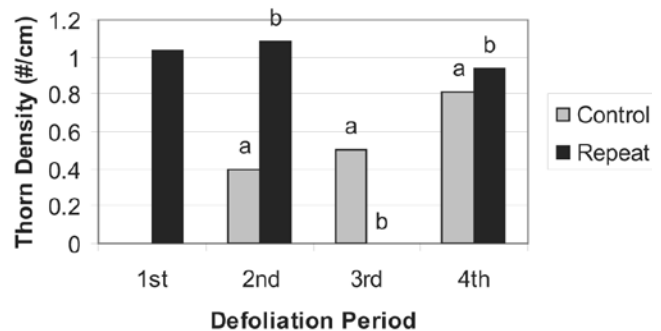


Figure 5. 2003 Blackbrush acacia thorn density (number of thorns per cm). No repeat thorn production at 3rd defoliation period. Means within a defoliation period with a different letter are different ($p < 0.02$). Research conducted in 2002 and 2003 at Welhausen Research Station, Webb County, Texas.

blackbrush acacia. Spiny hackberry shrubs repeatedly defoliated at 25 percent produced almost double ($p < 0.01$) the amount of biomass as control shrubs (fig. 6). Biomass production in shrubs subjected to repeat defoliation at 50 percent produced approximately 81 percent more ($p < 0.01$) biomass production than associated controls (fig. 6). However, there was no difference ($p > 0.09$) in biomass production in repeatedly defoliated and control shrubs defoliated at 75 percent and 100 percent levels (fig. 6). This suggests that spiny hackberry shrubs compensated for tissue removal at higher defoliation intensities and over-compensated for biomass loss at lower defoliation intensities, a partial validation of our hypothesis that simulated herbivory stimulates increased biomass production in spiny hackberry compared to non-defoliated controls.

The change (percent) of spiny hackberry regrowth biomass compared to biomass removed in the initial defoliation was higher in 2002 compared to 2003 (fig. 7). In 2002, repeatedly defoliated shrubs produced more biomass at the second defoliation than was originally removed, but less biomass was produced relative to the original biomass following the second and third defoliation events. In 2003, biomass production following defoliation never exceeded the biomass that was originally removed, resulting in under-compensation by the plant.

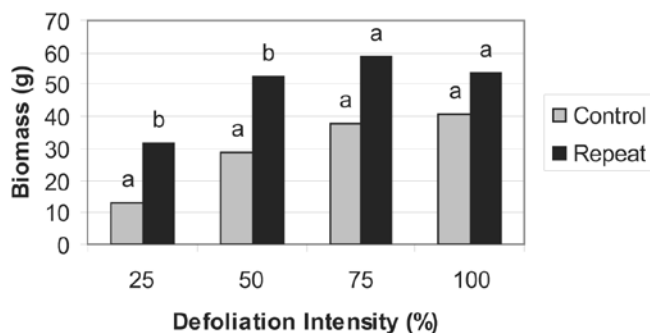


Figure 6. Mean of total spiny hackberry biomass production summed across defoliation events for each treatment, no difference between 2002 and 2003. Control plants were harvested only at end of growing season in October; repeat is sum of all biomass removed. Means within a defoliation intensity with a different letter are different ($p < 0.05$) at that defoliation level. Research conducted in 2002 and 2003 at Welhausen Research Station, Webb County, Texas.

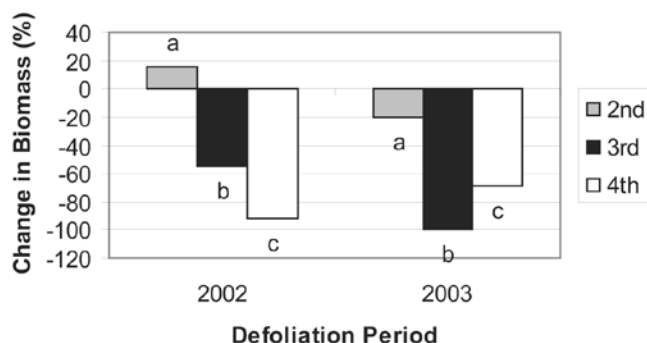


Figure 7. Change (percent) of spiny hackberry biomass production as a percent of the original biomass removed. Treatments not different; means across defoliation periods with a different letter are different ($p < 0.05$). Research conducted in 2002 and 2003 at Welhausen Research Station, Webb County, Texas.

Repeatedly defoliated spiny hackberry shrubs did not produce new twig browse or thorns following defoliation in 2002. In 2003, spiny hackberry produced new twigs, but no thorn production occurred in repeatedly defoliated shrubs. Many possible reasons exist for the lack of twig browse production in spiny hackberry. During summer 2001, leaf drop was observed in spiny hackberry. In 2002, spiny hackberry had delayed leaf bud until late May, almost 2 months past normal leaf bud as reported by Everitt and Drawe (1993). We hypothesize the drought of 2001 coupled with low early rainfall in 2002, was partially responsible for the lack of twig and thorn production.

Conclusions

The shrubs in this experiment demonstrated compensatory and over-compensatory biomass growth at different intensities of defoliation. In contrast to our original hypothesis, blackbrush acacia responded with overcompensation at high levels of tissue defoliation and compensation at lower levels. Spiny

hackberry demonstrated over-compensation at low defoliation levels but not at high defoliation levels where compensation occurred. Repeat defoliation resulted in under-compensation in biomass production. This suggests that if defoliation occurs frequently, these shrub species may continue to under-compensate, possibly resulting in shrub death (Forbes and others 1995). Lack of precipitation appears to intensify the influence of tissue removal.

Implications

The summer months in southern Texas, May to August, are characterized by high temperatures and low rainfall. Late summer, the third and fourth defoliation periods, are normally the driest in southern Texas. The low biomass production during this study may reflect the combined influence of increased number of defoliations (frequency) and drought. The third defoliation of spiny hackberry in 2003 had a 99 percent reduction in biomass production (fig. 7) and during the 6 weeks before the third defoliation in <6 mm of precipitation was received. Forbes and others (1995) reported similar results concerning lack of biomass production and stem death following repeat defoliations of guajillo (*Acacia berlandieri*), another common south Texas shrub, during a period of low precipitation. Our results indicate that biomass removal and shrub response may be dependent upon the species of shrub, the intensity of biomass removal, the frequency of removal, and the amount of precipitation received.

Acknowledgments

This research would not have been possible without help from various sources. Field crews including M. Asher, E. Dacy, H. McIntyre, and T. Neubauer. Funding and support provided by Caesar Kleberg Wildlife Research Institute and the Jack R. and Loris J. Welhausen Experimental Station.

Literature Cited

- Asah, H. A.; Fulbright, T. E.; Land, M. L. 1987. Effects of simulated browsing on spiny hackberry after top removal. *Texas Journal of Agriculture and Natural Resources*. 1:16-18.
- Clement, B. A.; Goff, C. M.; Forbes, T. D. A. 1998. Toxic amines and alkaloids from *Acacia rigidula*. *Phytochemistry*. 49:1377-1380.
- Cooper, S. M.; Owen-Smith, N. 1986. Effects of plant spinescence on large mammalian herbivores. *Oecologia*. 68:446-455.
- Everitt, J. H.; Drawe, D. L. 1993. *Trees, shrubs, and cacti of south Texas*. Lubbock, TX: Texas Tech University Press. 213 p.
- Forbes, T. D. A.; Pemberton, I. J.; Smith, G. R.; Hensarling, C. M. 1995. Seasonal variation of two phenolic amines in *Acacia berlandieri*. *Journal of Arid Environments*. 30:403-415.
- Graham, M. W. 1982. *Diets of white-tailed deer and nilgai antelope in South Texas*. Kingsville: Texas A&M University-Kingsville. 122 p. Thesis.
- McNaughton, S. J. 1983. Compensatory plant growth as a response to herbivory. *Oikos*. 40:329-326.

- Rohner, C.; Ward, D. 1997. Chemical and mechanical defense against herbivory in two sympatric species of desert *Acacia*. *Journal of Vegetation Science*. 8:717-726.
- SAS Institute. 1999. SAS/STAT user's guide, version 8. Cary, NC: SAS Institute Inc. 3089 p.
- Schindler, J. 2000. Role of spinescence and secondary compounds in white-tailed deer preference of shrubs in burned and mowed areas in South Texas. Kingsville: Texas A&M University-Kingsville. 171 p. Thesis.
- Schindler, J. R.; Fulbright, T. E.; Forbes, T. D. A. 2003. Influence of thorns and tannins on white-tailed deer browsing after mowing. *Journal of Arid Environments*. 55:361-377.
- Schindler, J. R.; Fulbright, T. E.; Forbes, T. D. A. 2004. Shrub regrowth, antiherbivore defenses, and nutritional value following fire. *Journal of Range Management*. 57:178-186.
- Soil Conservation Service. 1985. Soil survey of Webb County, Texas. Temple, TX: U.S. Department of Agriculture, Soil Conservation Service.
- Varner, L. W.; Blankenship, L. H. 1987. Southern Texas Shrubs—nutritive value and utilization by herbivores. In: Provenza, F. D.; Flinders, J. T.; McArthur, E. D., comps. *Proceedings—symposium on plant herbivore interactions*; 1985 August 7-9; Snowbird, UT. Gen. Tech. Rep. INT-222. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 108-112.

The Authors

¹Graduate Student, Caesar Kleberg Wildlife Research Institute, Texas A&M University-Kingsville, Kingsville, TX.

²Meadow's Professor, Caesar Kleberg Wildlife Research Institute, Texas A&M University-Kingsville, Kingsville, TX.
kftf00@tamuk.edu

Soil Responses to Human Recreational Activities in a Blackbrush (*Coleogyne ramosissima* Torr.) Shrubland

Simon A. Lei¹

Abstract: Soil responses to human trampling, biking, and off-road motor vehicle traffic were quantitatively investigated in a blackbrush (*Coleogyne ramosissima* Torr.) shrubland in Kyle Canyon of the Spring Mountains in southern Nevada. Soil compaction, bulk density, and temperature increased significantly, while soil moisture, organic matter, and percent pore space (macropore) decreased in disturbed (compacted) areas compared to adjacent undisturbed areas. Among disturbed soils, motor vehicle trails and parking lots had a significantly greater compaction, higher bulk density, and a lower percent pore space compared to human hiking/biking trails. Water infiltration and area of water spread (surface water runoff) were an interactive function of disturbance type and landform (terrace and slope). When examining disturbance type and landform factors independently, significant differences were detected in all of the measured soil moisture characteristics. Results of this study revealed that soil compaction led to increased soil bulk density and surface-water runoff, along with decreased macropore and water infiltration into the soil in Kyle Canyon of southern Nevada.

Introduction

Kyle Canyon of the Spring Mountains is a popular recreational area for nature-loving tourists and local residents in southern Nevada (Lei 2004). Due to rapid population growth and use of off-road motor vehicles in recent years, there has been a considerable increase in anthropogenic (recreational) activities, and the landscape disturbance has become increasingly noticeable (Davidson and Fox 1974). A complex network of roads and trails, including human foot, bicycle, and motor vehicle traffic is evident to casual observers and appears to have a long-term adverse effect on soil properties in blackbrush (*Coleogyne ramosissima* Torr.) shrubland (Lei 2003).

Human activities in Kyle Canyon include hiking and biking (bicycles and mountain bikes), while off-road vehicle activities include both motor vehicle trails and parking lots. These recreational activities are disturbance agents that cause soil disturbance through disruption and compaction of surface soil (Lei 2004). If disturbed areas were compared to adjacent undisturbed areas, an increase in the bulk density or degree of compaction of the soil in disturbed areas would be expected in the Mojave Desert of southern California (Davidson and Fox 1974). The greatest soil disturbance occurs in “pit areas” where motor vehicles are parked at the beginning of human hiking trails (Davidson and Fox 1974).

Human trampling, biking, and off-road motor vehicle traffic adversely affect soil properties by compacting the soil (Wilshire and Nakata 1976). Soil compaction can promote water (fluvial) erosion at the original site (Nakata and others 1976) and can reduce soil porosity, infiltration capacity, and hydraulic resistance to overland flow (Iverson and others

1981). Fluvial erosion can cause “head cutting” as erosion channels progress into adjacent areas.

Severely compacted soils reduce porosity, which in turn decreases water infiltration into the soil in southern Nevada (Marble 1985). Compaction through animal, human, or vehicle traffic can increase soil bulk density due to applied pressure or loading (Iverson and others 1981). Bulk density, which increases with compaction, is mainly a function of amount of void and the density of soil minerals. The degree of compaction can influence soil erosion dynamics and soil moisture status (Marble 1985). Webb and Wilshire (1980) suggest that severely compacted soils may require at least a century for natural recovery in southern Nevada.

Soil compaction studies have been documented in blackbrush (*Coleogyne ramosissima* Torr.) shrubland in southern Nevada (Lei 2003, 2004). Nevertheless, soil responses to various types of compaction and landforms in blackbrush shrublands remain poorly understood. From casual observations, extensive recreational activities removed the vegetation in trails and parking lots, leaving more soil exposed and making it highly susceptible to soil erosion than adjacent undisturbed areas. Two hypotheses were formulated prior to data collection. First, soil properties would be different between disturbed (compacted) and adjacent undisturbed (reference) areas, as well as between motor vehicle-compacted and human-trampled soils. Second, there would be interactive effects of disturbance type and landform on selected soil moisture characteristics. Interactions of disturbance type and landform may yield a greater effect than examining disturbance type or landform alone. These two hypotheses were tested by a combination of field and laboratory measurements

In: Sosebee, R.E.; Wester, D.B.; Britton, C.M.; McArthur, E.D.; Kitchen, S.G., comp. 2007. Proceedings: Shrubland dynamics—fire and water; 2004 August 10-12; Lubbock, TX. Proceedings RMRS-P-47. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 173 p.

of soil properties and soil moisture variables with appropriate statistical analyses.

Methods

Study Site

Southern Nevada, within the Basin and Range geological province, is a region characterized by annual weather extremes and a sparse vegetation cover (Brittingham and Walker 2000). The majority of annual precipitation occurs between October and April as frontal systems, with the remainder precipitation occurring in the summer as convectional thunderstorms (Smith and others 1995). Summer rains occur as brief, intense, and localized events that are highly variable in both time and space. Prolonged mountain thunderstorms in summer seasons can cause flash flooding in canyons and nearby washes. Winter rainfalls, on the contrary, are mild and widespread, and can last up to several days.

Field studies were conducted during fall 2000 in Kyle Canyon (36°01'N, 115°09'W), which is located on the eastern slope of the Spring Mountains. The blackbrush shrubland, ranging from 1,250 to 1,600 m in elevation, is dominated by a closely-spaced matrix of blackbrush shrubs with a scattered distribution of other shrub species. Common associated woody species that occur in this zone include Joshua tree (*Yucca brevifolia*), Nevada ephedra (*Ephedra nevadensis*), spiny menodora (*Menodora spinescens*), turpentine bush (*Thamnosma montana*), and Anderson lycium (*Lycium andersonii*). The herbaceous species present are mostly members of the Asteraceae, Brassicaceae, Fabaceae, and Poaceae families.

The terrain is exposed to abundant solid rocks on the soil surface. Bajadas, rocky slopes, and alluvial fans are dissected by numerous dry wash (intermittent) channels. Soil are calcareous, poorly developed (without distinct soil horizons), and composed primarily of weathered granite and limestone bedrock. Multiple caliche layers are found in the subsoil. Organic decomposition and soil formation are slow due to the arid nature of the region.

Field Design and Sampling

Three anthropogenic disturbance areas—human hiking/biking trails, motor vehicle trails, and parking lots—were selected, and were completely interspersed within a single area in Kyle Canyon. Within each type of disturbance, 60 soil samples from three transects were randomly selected, and were excavated 10 cm in diameter to depth of 15 cm. Soil samples among three transects in each type of disturbance were pooled. Intervals within each transect were randomly chosen to avoid biased sampling. Adjacent reference soils were sampled, with no clear evidence of compaction or other types of soil disturbance. Because of the close proximity among the 3 disturbance areas, the same set of reference soils was paired with soil samples in each type of disturbance. Soil

samples were sieved through a 2-mm mesh to remove surface litter, plant roots, and rocks > 2 mm in diameter. All tests were performed on < 2mm soils oven-dried at 65°C for 72 h. Soil samples were measured for bulk density, percent pore space, gravimetric moisture, organic matter, and pH.

Fresh soil cores of known volume were carefully removed from the field and were oven-dried at 65°C until they reached a constant mass. Soil bulk density was obtained by dividing mass by volume. Soil compaction was measured in the field using a penetrometer, which was inserted into the soil after removing stony surface pavements. The penetrometer readings were taken at the point where the cone base reached the soil surface (point depth = 3.8 cm). Average pore space (macropore) was determined using the equation: pore space (%) = $100 - (D_b/D_p * 100)$, where D_b is bulk density of the soil and D_p is average particle density, usually about 2.65 g cc⁻¹ (Hausenbuiller 1972; Davidson and Fox 1974). Soil moisture content was determined gravimetrically by computing differences between fresh and oven-dried mass. Soil temperature readings were recorded in the field at 15 cm below the soil surface using a metallic soil thermometer. Soil organic matter was acquired by mass loss on ignition at 550°C for 4 h. Soil pH was determined by preparing a paste consisting of a ratio of 1:1 dry soil:distilled water mixture and by measuring with an electrode pH meter.

Soil sampling was also stratified by landform, which was classified into terrace and slope. Within each type of landform, 60 plots were randomly selected to determine each of the six soil moisture variables. Water infiltration rates were measured by using PVC pipes, 5.5 cm in diameter and 9.5 cm tall. These pipes were open at both ends and were gently tamped into the compacted and reference soils to a depth of 2 cm to prevent leakage, and then 50 mL of water was poured into the pipes. Time taken for the water to soak into the soil was recorded with a stop-watch.

Exactly 1.5 L of water, acting as an 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 aboveground. Total delivery time was 1 min for the water to be dispensed on the soil surface, simulating precipitation at a cloudburst level (Brotherson and Rushford 1983). A sudden heavy precipitation is significant due to its impact on surface-water runoff and fluvial erosion. Depth of water penetration (water movement through the soil) was measured once the water had disappeared completely into the soil surface.

Surface-water runoff was measured by recording the downslope and across-slope spread of water that was artificially rained onto study sites (Brotherson and Rushford 1983). The area of water spread (surface-water runoff) was computed using the formula for the area of an ellipse (πab), where a and b are radii of the ellipse (Larson and others 1994). Since surface-water runoff was not a perfect elliptical shape, measured areas were likely to be an overestimation.

Soil movement was assessed by estimating the amount of soil moved through fluvial erosion during a measured (simulated) rain. The following index was used: 1 = no appreciable movement; 2 = moderate movement, up to 10 percent of the

soil volume displaced; and 3 = heavy movement, between 10 percent and 20 percent of the soil volume displaced (Brotherson and Rushforth 1983).

Statistical Analyses

One-way analysis of variance (ANOVA; Analytical Software 1994), followed by Tukey's multiple comparison test was used to compare differences in soil properties and to compare site means when a significant disturbance effect was detected, respectively. Two-way ANOVA (Analytical Software 1994) was computed on soil moisture status, with disturbance type (control, human hiking/biking trail, motor vehicle trail and parking lot) and landform (terrace and slope) as main effects. Statistical significance was tested at $P \leq 0.05$.

Results

Soil compaction, bulk density, and soil temperature were significantly greater ($P \leq 0.001$; table 1) in disturbed areas compared to adjacent undisturbed areas. Gravimetric soil moisture, organic matter, and macropore were significantly lower ($P \leq 0.001$; table 1) in disturbed than undisturbed areas. Among disturbed areas, motor vehicle-compacted (trails and parking lots) soils had a significantly greater compaction, higher bulk density, and lower macropore compared to hiking/biking soils ($P \leq 0.01$; table 1). In general, parking lots were more compacted, but differences were not statistically significant ($P > 0.05$) when compared to motor vehicle trails. Nevertheless, soil pH did not differ significantly ($P > 0.05$; table 1) between compacted and non-compacted soils.

In evaluating soil moisture status, significant differences were detected between disturbance type and all of the measured soil moisture characteristics, as well as between landform and all moisture characteristics ($P \leq 0.05$; tables 2 and 3). Motor vehicle-compacted soils had a significantly lower water infiltration and water movement through the soil and had a significantly greater downslope and across-slope water spread, and surface-water runoff than human-trampled/biking soils, which in turn differed significantly from adjacent

reference soils ($P \leq 0.01$; tables 2 and 3). Between the two types of motor vehicle-compacted soils, water infiltration was significantly lower, while downslope and across-slope water spread, surface-water runoff, and fluvial erosion were significantly greater on parking lots than on motor vehicle trails ($P \leq 0.05$; tables 2 and 3).

Between the two types of landform, water infiltration and water movement through the soil increased, while downslope and across-slope water spread, as well as surface-water runoff decreased significantly at terrace than at slope sites ($P \leq 0.05$; tables 2 and 3). Moreover, significant interactions ($P \leq 0.01$; table 3) were detected between disturbance type and landform for water infiltration and area of water spread (surface-water runoff).

Discussion

Concentrated use of human hiking/biking trails, along with off-road use of all-terrain motor vehicles, severely compacted soils and triggered a chain of events that significantly altered a number of soil properties in the blackbrush shrubland in Kyle Canyon of southern Nevada. With greater compaction from off-road motor vehicles, soil particles were pressed closer together and the bulk density was increased significantly. Soil compaction has been defined as the physical packing together of soil particles by instantaneous forces exerted at the soil surface (Lei 2004). Soil compaction occurs when the weight of humans, bikes, and motor vehicles pushes the soil particles together, thus substantially reducing the size of macropores (Smith and Smith 2001).

In this study, a combination of increased soil compaction, bulk density, and decreased macropore significantly reduced soil moisture content, water infiltration, and water movement through the soil in disturbed compared to adjacent undisturbed areas. Such combination also reduces soil permeability, resulting in a significantly greater surface-water runoff and fluvial erosion in compacted than non-compacted (reference) soils. The increase in bulk density of disturbed soils, along with the resulting decrease in macropore, probably decreases the amount of water that the soil can hold and the rate at which

Table 1. Soil properties (n = 60 per characteristic per disturbance type) of disturbed (human hiking/biking trails, motor vehicle trails, and parking lots) and adjacent undisturbed (reference) areas in the blackbrush shrubland. Pore space, moisture content, and organic matter are expressed in percentages. Soil temperatures were measured at 15-cm depth. Mean values in rows followed by different letters are significantly different at $P \leq 0.05$ using one-way ANOVA and post-hoc Tukey multiple comparison test.

	Disturbance type			
	Reference	Hiking/biking	Motor vehicle trail	Parking
Compaction (kg cm^{-2})	5.9 a	6.6 b	7.0 c	7.2 c
Bulk density (g cm^{-3})	1.28 a	1.42 b	1.51 c	1.53 c
Pore space (%)	51.7 a	46.4 b	43.0 c	42.3 c
Moisture (%)	2.91 a	1.02 b	0.70 c	0.61 c
Temperature ($^{\circ}\text{C}$)	24.7 a	27.1 ab	28.7 b	28.8 b
Organic matter (%)	2.45 a	0.81 b	0.30 c	0.20 c
pH	7.7 a	7.6 a	7.6 a	7.6 a

Table 2. Soil moisture characteristics (n = 60 per treatment per characteristic) of disturbed (human hiking/ biking trails, motor vehicle trails, and parking lots) and adjacent undisturbed areas in the blackbrush shrubland.

	Disturbance type			
	Reference	Hiking/biking	Motor vehicle trail	Parking
Infiltration (sec.)				
Terrace	182.3	365.9	420.8	432.1
Slope	210.2	408.6	492.7	498.5
Depth of water Penetration (cm)				
Terrace	3.8	3.2	2.3	2.4
Slope	3.3	2.5	1.7	1.8
Downslope spread (cm)				
Terrace	77.2	129.4	179.8	188.1
Slope	89.8	162.4	213.1	224.9
Across slope spread (cm)				
Terrace	60.1	127.2	164.9	189.5
Slope	75.4	157.7	215.4	227.8
Area of spread (cm ²)				
Terrace	3642.2	11996.5	23274.5	25518.3
Slope	5315.2	17504.5	35627.4	36299.1
Soil movement				
Terrace	1.2	1.3	1.3	1.4
Slope	1.3	1.4	1.4	1.5

Table 3. Results of two-way ANOVA showing effects of disturbance type, landform, and their interactions on various soil moisture characteristics. df = 1 for landform; df = 3 for disturbance type and for disturbance type * landform combination.

	Disturbance type		Geomorphic surface		Disturbance type x geomorphic surface	
	F	P	F	P	F	P
Water infiltration	2567.69	<0.0001	447.27	<0.0001	637.88	<0.0001
Depth of water penetration	302.55	<0.0001	213.16	<0.0001	1.21	0.3417
Downslope water spread	218.84	<0.0001	47.07	<0.0001	2.61	0.0911
Across slope water spread	139.10	<0.0001	51.88	<0.0001	0.59	0.6385
Area of water spread	207.70	<0.0001	64.07	<0.0001	5.77	0.0092
Soil movement	3.67	0.0385	5.51	0.0342	0.34	0.7146

water can flow through the soil (Yang and DeJong 1971). The increase in bulk density also reduces the permeability of the soil so that surface-water runoff is greater (Kubota and Williams 1967). Consequently, there is a substantial reduction of water stored in the soil and water available for plant growth in the Mojave Desert of southern California (Davidson and Fox 1974).

On severely compacted soils, water is trapped at the soil surface rather than reaching deeper into the subsoil. With less moisture content in subsoil due to compaction, temperatures of subsoil were expected to be higher in this study. Soil moisture content and temperature are inversely related; drier soils tend to be warmer than moist soils. Moisture tends to increase the specific heat of the soil. When soils are drier because of reduced water infiltration and depth of water penetration, the specific heat of the soil would be lower, so that the same insolation rate would cause higher soil temperatures. There would be less evaporation from the soil surface, so that the cooling caused by the latent heat of evaporation would be less. In this

study, the lack of shading contributed to increased soil temperature due to the removal of vegetation and plant litter.

Moreover, moisture-holding capacity was also affected by organic matter content of the soil. Organic matter decreases bulk density of the soil because it is lighter (less dense) than a corresponding volume of mineral soil (Barbour and others 1999). In this study, severely disturbed areas, such as motor vehicle trails and parking lots, were completely devoid of vegetation, organic litter, and debris because of the change in soil properties and because the vegetation was crushed or smashed. Severely compacted soils through extensive recreational activities resembled pavement, thus unable to retain moisture and develop new organic layer to sustain any plant growth.

Intensity of disturbance and size of pit area depend on number of motor vehicles parked, duration of parking, as well as number of times people return during the year and from year to year in the Mojave Desert of southern California (Davidson and Fox 1974). Anthropogenic activities including hiking, biking, and off-road motor vehicle traffic all

contributed to soil compaction, although the degree of compaction and disturbance varied significantly in this study. Water infiltrability and surface-water runoff were an interactive function of disturbance type and landform. The greatest surface-water runoff and the least water infiltrability occurred on motor vehicle-compacted soils at slope sites than human hiking/biking trails at terrace sites in this study.

Because summer monsoonal thunderstorms are highly localized and intense in southern Nevada, much of the rainfall cannot be absorbed by the soil, so that the excess running water rapidly flows across the compacted soil surface during and shortly after major storm events, resulting in fluvial erosion. With increased surface-water runoff and decreased water infiltration, shallower penetrations of water into compacted soils occur at slope than at terrace sites. Substantially greater surface-water runoff and fluvial erosion would be expected on compacted soils at slope sites compared to non-compacted soils at terrace sites if cloudbursts occurred with longer duration, higher frequency, and greater intensity (Lei 2000).

Ecological Implications

A combination of active hiking and biking trails, as well as off-road motor vehicle driving and parking have caused significant soil property changes in the blackbrush shrubland in Kyle Canyon of southern Nevada. Soil compaction, which adversely impacts various soil attributes, is an aspect of land degradation. From a distance, a complex network of roads and trails is evident. Anthropogenic disturbances, such as human foot, bicycle, and motor vehicular traffic can scuff away the protective organic layer, halting the development of a new organic layer on the soil surface. Impact of raindrops increases on compacted soils as organic litter and debris are removed. Both terrace and slope sites are vulnerable to catastrophic fluvial erosion during and shortly after major storm events. Despite growing evidence that hiking, biking, and relentless motor vehicle use is very damaging to fragile desert soils, the public continues to use Kyle Canyon and other areas of the Mojave Desert for recreational activities.

Acknowledgments

The author gratefully acknowledge Steven Lei, David Valenzuela, and Shevaun Valenzuela for valuable field and laboratory assistance. Steven Lei assisted with statistical analyses. Critical review provided by David Charlet greatly improved the manuscript. Department of Biology at the Community College of Southern Nevada (CCSN) provided logistical support.

Literature Cited

Analytical Software. 1994. Statistix 4.1, an interactive statistical program for microcomputers. St. Paul, MN: Analytical Software. 329 p.

- Barbour, M. G.; Burk, J. H.; Pitts, W. D. 1999. Terrestrial Plant Ecology, 3rd edition. Menlo Park, CA: The Benjamin/Cumming Publishing Company, Inc.
- Brittingham, S.; Walker, L. R. 2000. Facilitation of *Yucca brevifolia* recruitment by Mojave Desert shrubs. Western North American Naturalist. 60: 374-383.
- 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.
- Davidson, E.; Fox, M. 1974. Effects of off-road motorcycle activity on Mojave Desert vegetation and soil. Madrono. 22: 381-390.
- Hausenbuiller, R. L. 1972. Soil science: principles and practices. Dubuque, IA: William C. Brown Company Publishers. 504 p.
- Iverson, R. M.; Hinkley, B. S.; Webb, R. M.; Hallet, B. 1981. Physical effects of vehicular disturbances on arid landscapes. Science. 212: 915-917.
- Kubota, T.; Williams, R. J. 1967. The effects of changes in soil compaction and porosity on germination, establishment, and yield of barley and globe beet. Journal of Agricultural Science. 68: 227-233.
- Larson, R. E.; Hostetler, R. H.; Edwards, B. H. 1994. Calculus. 5th edition. Lexington, MA: D.C., Heath and Company. 1256 p.
- Lei, S. A. 2000. Ecological impacts of seed harvester ants on soil attributes in a *Larrea*-dominated shrubland. Western North American Naturalist. 60: 439-444.
- Lei, S. A. 2003. Soil compaction and moisture status from large mammal trampling in a blackbrush (*Coleogyne ramosissima*) shrubland. Southern California Academy of Sciences. 102: 119-129.
- Lei, S. A. 2004. Soil Compaction from human trampling, biking and off-road motor vehicle activity in a blackbrush (*Coleogyne ramosissima*) shrubland. Western North American Naturalist. 64: 125-130.
- Marble, J. R. 1985. Techniques of revegetation and reclamation of land damaged by off-road vehicles in the Lake Mead Recreational Area. Las Vegas, NV: Cooperative National Park Resources Studies Unit, University of Nevada, Las Vegas. 71 p.
- Nakata, J. K.; Wilshire, H. G.; Barnes, G. G. 1976. Origin of Mojave Desert dust plumes photographed from space. Geology. 4: 644-648.
- Smith, S. D.; Herr, C. A.; Leary, K. L.; Piorkowski, J. M. 1995. Soil-plant water relations in a Mojave Desert mixed shrub community: a comparison of three geomorphic surfaces. Journal of Arid Environments. 29: 339-351.
- Smith, R. L.; Smith, T. M. 2001. Ecology and field biology, 6th edition. San Francisco, CA: The Benjamin/Cummings Publishing Company, Inc. 771 p.
- Webb, R. H.; Wilshire, H. G. 1980. Recovery of soils and vegetation in a Mojave Desert ghost town, Nevada, U.S.A. Journal of Arid Environments. 3: 291-303.
- Wilshire, H. G.; Nakata, J. K. 1976. Off-road vehicle effects on California's Mojave Desert. California Geology. 29: 123-132.
- Yang, S. J.; DeJong, E. 1971. The effect of soil water potential and bulk density on water uptake patterns and resistance to flow of water in wheat plants. Canadian Journal of Soil Science. 51: 211-220.

The Author

¹Statistics and Research Methods Instructor, Department of Educational Psychology, University of Nevada, Las Vegas, NV. liesa@unlv.nevada.edu

Influence of Shrubs on Soil Chemical Properties in Alxa Desert Steppe, China

Hua Fu¹; Shifang Pei¹

Yaming Chen²

Changgui Wan³

Abstract: Alxa desert steppe is one of severely the degraded rangelands in the Northwest China. Shrubs, as the dominant life form in the desert steppe, play an important role in protecting this region from further desertification. Chemical properties of three soil layers (0 to 10, 10 to 20 and 20 to 30 cm) at three locations (the clump center [A], in the periphery of shrub canopies [B], and the inter-shrub space [C], at least one m away from the edge of shrub canopies) were investigated in two prominent shrub communities (*Zygophyllum xanthoxylum*, *Ammopiptanthus mongolicus*) in Alxa desert steppe. The results showed that: (1) soils in three layers at the clump center exhibited significantly higher contents of organic carbon (SOC), total N, total P, and lower pH value compared to the inter-shrub space. Soils in the 0 to 10-cm and 10 to 20-cm depths under periphery of shrub canopy showed significantly higher contents of SOC and total N, and slight, but significantly lower, pH value compared to the same soil layers in the inter-shrub space. However, there was no significant difference in total P in three soil layers between shrub periphery and inter-shrub space; (2) the soil enrichment ratios of SOC, total N, and total P at clump center were significantly higher, while ratio for pH significantly lower compared to the shrub periphery; and (3) SOC and total P contents at all locations around *Z. xanthoxylum* were higher, while total N and pH values lower compared to soils around *A. mongolicus*. The enrichment ratios of SOC, total N, and total P at the same location were not significantly different between *Z. xanthoxylum* and *A. mongolicus*. The litter-fall seems to influence the soil chemical properties at clump center, shrub periphery, and inter-shrub open space, resulting in “fertile island” under shrub canopies. This study shows that shrubs play a vital role in accumulating SOC and nutrients and maintaining soil fertility in Alxa desert steppe.

Introduction

Alxa desert steppe is one of the severely degraded rangelands in the arid and semiarid areas in the northwestern China. Grazing has been the most common management practice in this region. In recent decades, this region has become one of the major sources of sandstorms in the northwestern China (Wang and others 2004) due to overgrazing and population growth (Fu and Chen 2003). Overgrazing may induce dramatic changes in vegetation composition and in soil nutrient cycling in native rangelands (Fu and Chen 2003). The degree of rangeland degradation can be measured by declines in soil fertility (Fang and Peng 1997).

Zygophyllum xanthoxylum and *Ammopiptanthus mongolicus*, the two dominant shrub species belonging to the family of *Zygophyllaceae* and *Leguminosae*, respectively, are widely distributed in the Alxa desert steppe as the main forage species for camels, sheep, and goats (Cheng and Zhang 2001). These shrubs play an important role in protecting this area from wind erosion (Charley and West 1975; Garner and Steinberger 1989). These shrubs may also affect the distribution and biochemical cycle of soil nutrients (Halvorson and others 1995), resulting in the formation of islands of fertility around shrubs (Schlesinger 1996).

The development of islands of fertility may be important strategies and mechanisms for shrubs to use and recycle soil

nutrients effectively. Thus, shrubs are important for maintaining the stability of arid ecosystems (Martinez-Meza and Whitford 1996). Information about shrub-soil interaction and shrub-induced soil chemical changes is vital for a better understanding of the ecological processes in Alxa desert steppe. The objective of this study was to investigate the effects of two prominent shrub species on soil nutrient accumulation and distribution. The study attempted to quantify the magnitudes of element enrichment in SOC, total N, and total P under shrub canopy as compared to the inter-shrub space and to test if there are any differences in enrichment ratios in SOC, total N, and total P between the two shrub communities.

Materials and Methods

Study Site

The study was conducted in a desert steppe of Alxa (105°35′ E, 39°08′ N; elevation 1360m), western Inner Mongolia, China. The climate is arid with mean annual precipitation of 105 mm and nearly 70 percent of rainfall occurs between July and September. Mean annual evaporation capacity is 3,000 to 4,100 mm. Mean annual temperature is about 8°C. Mean annual wind velocity ranges from 3.44 to 4.74 ms⁻¹. The brown desert soil in this region is highly

In: Sosebee, R.E.; Wester, D.B.; Britton, C.M.; McArthur, E.D.; Kitchen, S.G., comp. 2007. Proceedings: Shrubland dynamics—fire and water; 2004 August 10-12; Lubbock, TX. Proceedings RMRS-P-47. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 173 p.

Table 1. Morphological traits of shrubs (n = 6).

Item	Family	Height cm	Crown diameter cm	Biomass of shrub g	Height of mound cm
<i>Z. xanthoxylum</i>	Zygophyllaceae, shrub	59~87.5	129~202.5	221.63~594.06	19~25
<i>A. monglicus</i>	Leguminosae, shrub	61.05~84	178~280.5	425.35~862.99	31~60

susceptible to wind erosion due to its coarse texture and loose structure characteristics according to the Alxa soil classification system (Plan Committee of Alxa League 1991).

Sampling

Z. xanthoxylum and *A. monglicus* are two dominant woody shrub species in the study area. In August of 2003, six individuals of *Z. xanthoxylum* and *A. monglicus*, respectively, were randomly selected and the morphological traits of the plants were measured (table 1). Soil samples were taken from three depths (0 to 10 cm, 10 to 20 cm, 20 to 30 cm) in each of the three locations around an individual shrub plant. The three locations were: center of the shrub clump (A), under the periphery of the shrub canopy (B), and the inter-shrub space (at least one meter away from the edge of shrub canopy) (C). For each individual plant, four soil samples each at one direction were taken and the samples were then mixed for lab analysis.

Laboratory Analyses

Soil samples were air-dried, sieved to pass a 2-mm screen to remove plant materials and other debris, and analyzed for pH (1:1 distilled water). The samples were ground and then sieved to pass a 0.5-mm screen and analyzed for organic carbon (oxidization with potassium dichromate in presence of H_2SO_4 , heated at 180°C for 5 minutes), total nitrogen (Kjeldahl method), and total phosphorus (by spectrophotometer after NaOH digestion) (Institute of Soil Sciences, Chinese Academy of Sciences 1978).

Data Analyses

The enrichment ratio (E) was used to evaluate the spatial pattern of soil element distribution (Wezel and others 2000), where $E_A = A/C$, $E_B = B/C$. The more E differs from 1, the more soil elements in A or B deviate from C. $E > 1$ means a higher concentration for the elements analyzed in either A or B than in C. An E value less than 1 for pH value means a more acid soil environment in either A or B than in C.

Data were analyzed using SPSS 11 package for significance at $P \leq 0.05$. Significant differences in mean soil properties analyzed in the three locations and in the three depths in the same sampling location were determined by analyzing replicate means (n = 6) with a one-way analysis variance (ANOVA) and least significance difference tests (LSD). The figures of results showed as means $\pm$ S.E.

Results

General Trends in Soil Chemical Properties Around Shrubs

The following data are averages around the two shrub communities. SOC, total N, and total P generally showed a declining trend from the canopy center to the inter-shrub space in the 0 to 10-cm, 10 to 20-cm, and 20 to 30-cm soil profiles, respectively (table 2, fig. 1). SOC and total N were significantly higher in 0 to 10-cm and 10 to 20-cm soil layers under periphery of the shrub canopy compared to the adjacent inter-shrub open space. The means of SOC and total N in 0 to 10-cm soils under the canopy periphery increased by 58 and 60 percent respectively, and total P was not significantly different ($P = 0.345$), but pH values decreased 0.30 units ($P < 0.05$) compared to the inter-shrub space. SOC, total N, and total P in 0 to 10-cm soils in the clump center were higher by 164 percent, 117 percent, and 19 percent respectively, but pH values lower by 0.70 units ($P < 0.05$) than in soils in the inter-shrub space. SOC, total N, and total P in 10 to 20-cm soil layers at the clump center increased by 103 percent, 96 percent, and 20 percent respectively, while pH decreased 0.40 units ($P < 0.05$) compared to the inter-shrub space. There were significant differences in SOC and total N in 20 to 30-cm soil layers between clump center and the inter-shrub space. However, SOC, total N, and total P in 20 to 30-cm soil layers between canopy periphery and the inter-shrub space were not different.

The enrichment ratios of soil organic C, total N, and total P at the clump center were significantly higher, while pH values significantly lower than the canopy periphery with exception of total P at 10 to 20-cm soil layers. Our data showed that contents and enrichment ratios of SOC and total N decreased with the increase of depth.

Soil Chemical Properties as Related to Shrub Species

Soil chemical properties were somewhat related to shrub species (fig. 1). SOC and total P in the topsoil layers under the canopy around *Z. xanthoxylum* were higher, while total N and pH value lower than those around *A. monglicus*. The enrichment ratios of SOC, total N, and total P at the same soil depths were not significantly different between *Z. xanthoxylum* and *A. monglicus* (table 3).

Table 2. Soil chemical properties and enrichment ratios for two shrub communities (E_A and E_B , $n = 6$). A: clump center, B: canopy periphery, C: inter-shrub space.

Depth	Variable	Unit	Location	Value	Enrichment ratio		t-test ¹
				Mean $\pm$ S. E.	E_A (A/C)	E_B (B/C)	P
0-10 cm	Organic C	g kg ⁻¹	A	4.834 $\pm$ 0.27a			
			B	2.893 $\pm$ 0.21b			
			C	1.831 $\pm$ 0.12c	2.74	1.64	<0.001
	Total N	g kg ⁻¹	A	0.496 $\pm$ 0.01a			
			B	0.366 $\pm$ 0.02b			
			C	0.228 $\pm$ 0.01c	2.20	1.63	<0.001
	Total P	mg·kg ⁻¹	A	0.266 $\pm$ 0.01a			
			B	0.243 $\pm$ 0.01ab			
			C	0.223 $\pm$ 0.02b	1.21	1.10	0.009
10-20 cm	Organic C	g kg ⁻¹	A	8.68 $\pm$ 0.10a			
			B	9.08 $\pm$ 0.08b			
			C	9.38 $\pm$ 0.04c	0.93	0.97	<0.001
	Total N	g kg ⁻¹	A	3.338 $\pm$ 0.17a			
			B	2.262 $\pm$ 0.12b			
			C	1.727 $\pm$ 0.13c	2.03	1.30	0.002
	Total P	mg·kg ⁻¹	A	0.397 $\pm$ 0.02a			
			B	0.285 $\pm$ 0.02b			
			C	0.202 $\pm$ 0.01c	1.96	1.43	<0.001
20-30 cm	Organic C	g kg ⁻¹	A	0.246 $\pm$ 0.01a			
			B	0.228 $\pm$ 0.01a			
			C	0.209 $\pm$ 0.01a	1.20	1.09	0.132
	Total N	g kg ⁻¹	A	8.99 $\pm$ 0.08a			
			B	9.25 $\pm$ 0.05b			
			C	9.42 $\pm$ 0.06b	0.95	0.99	0.001
	Total P	mg·kg ⁻¹	A	2.749 $\pm$ 0.23a			
			B	1.808 $\pm$ 0.07b			
			C	1.660 $\pm$ 0.10b	1.67	1.11	0.002
	Organic C	g kg ⁻¹	A	0.338 $\pm$ 0.01a			
			B	0.259 $\pm$ 0.01b			
			C	0.184 $\pm$ 0.01b	1.85	1.40	<0.001
	Total N	g kg ⁻¹	A	0.228 $\pm$ 0.01a			
			B	0.214 $\pm$ 0.01a			
			C	0.202 $\pm$ 0.01a	1.14	1.06	0.028
	Total P	mg·kg ⁻¹	A	9.02 $\pm$ 0.11a			
			B	9.26 $\pm$ 0.03b	0.96	0.99	0.050
			C	9.39 $\pm$ 0.04b			

¹ t-test for paired samples for enrichment ratios.

Means followed by the same letters are not different at $P = 0.05$ level.

Correlation Between Organic C, Total N, and Total P at the Various Locations

Contents of elements were linearly correlated between clump center and canopy periphery (table 4). The highest values of coefficient r were found between A and B for SOC ($r = 0.705^{**}$), total N ($r = 0.851^{**}$), and total P ($r = 0.974^{**}$). The correlation coefficients between canopy periphery (B) and clump center (A) were higher than between canopy periphery and the inter-shrub space (C). No significant correlations were observed between total N and SOC in inter-shrub space, nor were there significant correlations between total N and total P in A, B, and C.

Discussion

The concentrations of nutrients in soils under shrub canopies tend to be greater than in the shrub interspace, thus forming “islands of fertility.” This phenomenon has been well documented in arid and semiarid ecosystems (Garner and Steinberger 1989; Schlesinger and others 1990; Halvorson and others 1995; Whitford and others 1997; Wezel and others 2000; Su and others 2004). The increased spatial heterogeneity of soil resources may be a useful indicator of desertification in arid and semi-arid ecosystems (Schlesinger and others 1990). Our results show that fertile islands become relatively stable features in this landscape. In these

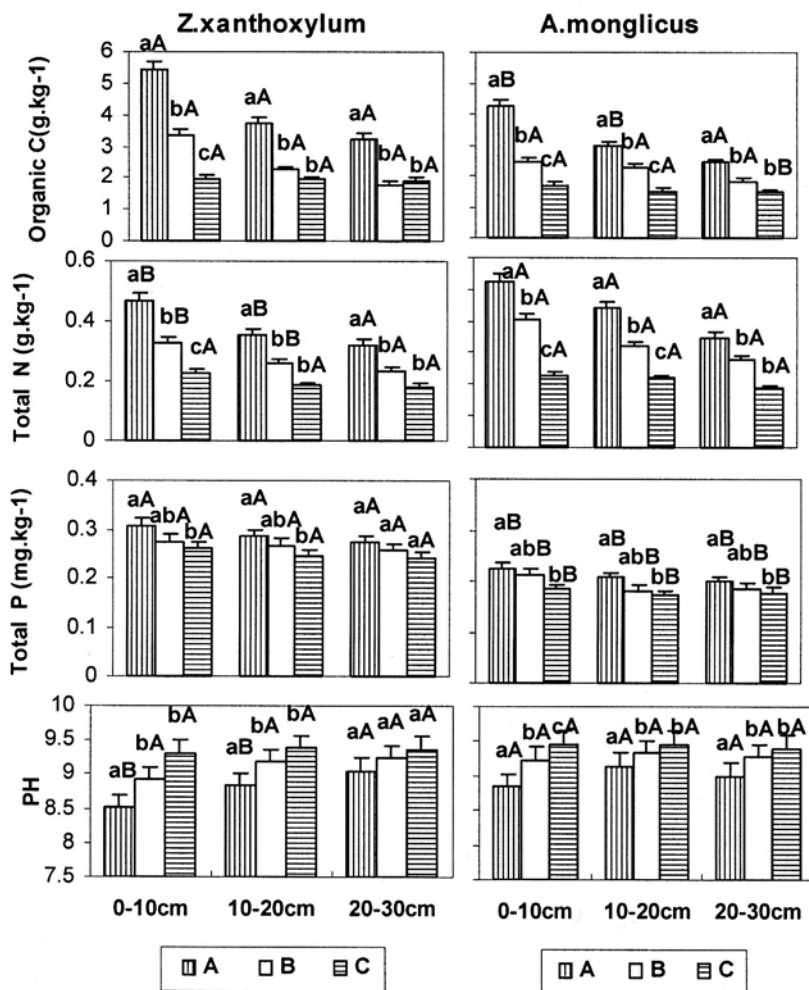


Figure 1. Soil chemical properties as related to shrub species in Alxa desert steppe. A: in the center of clump, B: under shrub canopies, C: the inter-shrub space. Means at the same soil depth within a species not followed by the same lowercase letters differ ($P < 0.05$, LSD multiple range tests). Means at the same location and same soil depth not followed by the same uppercase letters differ (between species difference, $P < 0.05$, t -tests).

Table 3. Enrichment ratios of soil nutrients for two shrub species in Alxa desert steppe.

		<i>Z. xanthoxylum</i>			<i>A. mongolicus</i>			t-test for E	
Variable	Depth	E _A A/C	E _B B/C	t-test ^{1/} P value	E _A A/C	E _B B/C	t-test ^{1/} <i>p</i>	P value (between species) (E _A) (E _B)	
Organic C									
	0-10 cm	2.81a	1.77a	0.001	2.66a	1.51a	0.010	0.609	0.495
	10-20 cm	2.02b	1.18b	0.002	2.03ab	1.44a	0.095	0.954	0.030
	20-30 cm	1.68b	0.93b	0.001	1.66b	1.24a	0.097	0.779	0.018
Total N									
	0-10 cm	2.12a	1.49a	0.001	2.29a	1.77a	0.001	0.528	0.302
	10-20 cm	1.90a	1.37a	0.018	2.01b	1.51b	0.001	0.573	0.602
	20-30 cm	1.81a	1.30a	0.001	1.87b	1.47b	0.001	0.872	0.212
Total P									
	0-10 cm	1.19a	1.05a	0.043	1.23a	1.15a	0.147	0.686	0.088
	10-20 cm	1.18a	1.10a	0.006	1.23a	1.08a	0.266	0.704	0.788
	20-30 cm	1.15a	1.08a	0.330	1.13a	1.05a	0.005	0.561	0.435
pH									
	0-10 cm	0.92a	0.96a	0.018	0.94a	0.98a	0.002	0.828	0.742
	10-20 cm	0.94ab	0.98ab	0.001	0.97b	0.99b	0.064	0.118	0.069
	20-30 cm	0.97b	0.99b	0.207	0.96b	0.99b	0.097	0.181	0.723

A: clump center, B: canopy periphery, C: inter-shrub space.

^{1/} t-test for paired samples of enrichment ratios. Means under each category within a column not followed by the same letters are different at $p = 0.05$.

Table 4. Pearson linear correlation coefficients (r) between SOC, total N, and total P in soils of the different locations (n =36).

Variable	Sampling location	Organic C			Total N			Total P	
		A	B	C	A	B	C	A	B
Organic C	B	0.705**							
	C	0.418*	0.419**						
Total N	A	0.632**	0.552**	0.235					
	B	0.431**	0.448**	0.166	0.851**				
Total P	C	0.237	0.293	-0.177	0.743**	0.738**			
	A	0.781**	0.517**	0.564**	0.197	0.027	-0.158		
	B	0.634**	0.437**	0.562**	0.162	0.002	-0.132	0.974**	
	C	0.610**	0.513**	0.643**	0.160	0.016	-0.114	0.956**	0.999**

ecosystems, shrubs protect topsoil from wind erosion and effectively trap wind-blown materials and litters from unprotected areas. Microtopographic mounds ranging from 19- to 60-cm height were observed around shrub crowns (table 1). This suggests that topsoil material mainly accumulated under shrub canopies. Such mounds create a landscape that alternates between mounds and inter-shrub open space. The mound itself is a soil forming process (Rostagno and others 1991), because it creates patches with higher concentrations of soil resources.

Higher concentrations of total N and total P were linked to the higher concentration of SOC under shrub canopies because SOC is the most important factor in the storage of nutrients in infertile soils (table 4, Wezel and others 2000). It is evident from our data that shrubs exert great impacts on nutrient redistribution, with a significant accumulation of growth-limiting nutrients such as total N and total P under the shrub canopies. This effect was particularly evident in the 0 to 10-cm and 10 to 20-cm soil layers.

Higher concentration and enrichment ratios of SOC were found in soils under *Z. xanthoxylum* and higher content and enrichment ratios of total N were found under *A. mongolicus*. This may relate to the fact that *A. mongolicus* is a legume that has root nodules to fix nitrogen, thus producing a higher concentration of total N in the soil around the shrub (Cheng and Zhang 2001).

Nutrient enrichment at the clump center was more pronounced than at the shrub periphery (fig. 1, table 2). This is because there is much greater litter-fall at the clump center than some distance away from the center. In addition, shrub plants tend to have more roots at the clump center than near the canopy periphery. A larger amount of organic substrates, such as exudates, secretions, sloughed cells, and mucilage may be released from roots and deposited in the rooting zone at the clump center (Lynch and Whipps 1990; Petersen and Bottger 1991) leading to higher enrichment ratios.

No significant statistical differences in E_A and E_B between the two shrub species were found, which may suggest that two species were both capable of altering nutrient redistribution in the soil. The capacity to accumulate soil nutrients under their canopies is similar regardless of whether the shrub is leguminous or not.

Acknowledgments

This research was supported by the National Natural Science Foundation of China (90102011, 30371023).

References

- Charley, J. L.; West, N. E. 1975. Plant-induced soil chemical patterns in some shrub-dominated semi-desert ecosystems of Utah. *Journal of Ecology*. 63: 945-963.
- Cheng, S. H.; Zhang, H.; and others (eds.). 2001. *Plant Root System in Northwest China*. Jilin University Press, P. 341-343 (in Chinese).
- Fang, W.; Peng, S. L. 1997. Development of species diversity in the restoration process of establishing a tropical man-made forest ecosystem in China. *Forest Ecology and Management*. 99: 185-196.
- Fu, H.; Chen, Y. M. 2003. Change of vegetation and soil environment of desert grassland in the early period of restoration in Alxa, Inner Mongolia. *Journal of Desert Research*. 23(6): 661-664 (in Chinese with English abstract).
- Garner, W.; Steinberger, Y. 1989. A proposed mechanism for the formation of 'fertile islands' in the desert ecosystem. *Journal of Arid Environments*. 16: 257-262.
- Halvorson, J. J.; Smith, J. L.; Bolton, H. 1995. Defining resource islands using multiple variables and geostatistics. *Soil Science Society of America Journal*. 59: 1476-1487.
- Institute of Soil Sciences, Chinese Academy of Sciences (ISSCAS), 1978. *Physical and chemical analysis methods of soils*. Shanghai, Shanghai Science Technology Press, P. 7-86 (in Chinese).
- Lynch, J. M.; Whipps, J. M. 1990. Substrate flow in the rhizosphere. *Plant and Soil*. 129: 1-10.
- Martinez-Meza, E.; Whitford, W. G. 1996. Stemflow, throughfall and channelization of stemflow by roots in three Chihuahuan desert shrubs. *Journal of Arid Environments*. 32: 271-287.
- Petersen, W.; Bottger, M. 1991. Contribution of organic acids to the acidification of the rhizosphere of maize seedlings. *Plant and Soil*. 132: 159-163.
- Plan Committee of Alxa League. 1991. *Terrestrial resources of Alxa league*. Inner-Mongolia People Press, P. 31-34 (in Chinese).
- Rosagno, C. M.; Valle, H. F.; Videla, L. 1991. The influence of shrubs on some Chemical and physical properties of an aridic soil in north-eastern Patagonia, Argentina. *Journal of Arid Environments*. 20: 179-188.

- Schlesinger, W. H.; Raikes, J. A.; Hartley, A. F.; Cross, A. F. 1996. On the spatial pattern of soil nutrients in desert ecosystems. *Ecology*. 77: 364- 374.
- Schlesinger, W. H.; Reynolds, J. F.; Cunningham, G. L.; Huenneke, L. F.; Jarrell, W. M.; Virginia, R. A. 1990. Biological feedbacks in global desertification. *Science*. 247: 1043-1048.
- Su, Y. Z.; Zhao, H. L.; Lin, Y. L.; Cui, J. Y. 2004. Influencing mechanisms of several shrubs on soil chemical properties in semiarid Horqin sandy land, China. *Arid Land Research and Management*. 18: 1-13.
- Wang X. M.; Dong, Z. B.; Zhang, J. W.; Liu, L. C. 2004. Modern dust storms in China: an overview. *Journal of Arid Environments*. 58: 559-574.
- Wezel, A.; Rajot, J. L.; Herbrig, C. 2000. Influence of shrubs on soil characteristics and their function in sahelian agro-ecosystems in semi-arid Niger. *Journal of Arid Environments*. 44: 383-398.
- 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.

The Authors

- ¹ College of Pastoral Agricultural Science and Technology, Lanzhou University, Key Laboratory of Grassland Agro-Ecosystem Ministry of Agriculture, PR China. fuhua@lzu.edu.cn
- ² College of Life Sciences, Lanzhou University, PR China.
- ³ Department of Range, Wildlife, and Fisheries Mgt., Texas Tech University.

Fungal Genomes that Influence Basic Physiological Processes of Black Grama and Fourwing Saltbush in Arid Southwestern Rangelands

J.R. Barrow¹
M. Lucero²
P. Osuna-Avila²
I. Reyes-Vera³
R.E. Aaltonen⁴

Abstract: Symbiotic fungi confer multiple benefits such as enhanced photosynthetic rates and drought tolerance in host plants. Shrubs and grasses of southwestern deserts are colonized by symbiotic fungi that cannot be removed by conventional sterilization methods. These fungi were extensively studied in *Bouteloua eriopoda* (Torr.) Torr. and *Atriplex canescens* (Pursh) Nutt. over a wide range of locations and environmental conditions. Fungi were intrinsically integrated with cells, tissues, and regenerated plant cultures. These composite plant-fungus organisms are comprised of more than one fungal species. Fungal association with photosynthetic cells and accumulation of lipids provide evidence for carbon management. Fungal biofilms that coat cells, tissues, roots, and leaves suggests protection of plants from direct exposure to stressed environments. Associations with vascular tissues suggests a role in resource transport. Association with stomata indicates an influence in gas exchange, photosynthesis, and evapo-transpiration. Transfer of fungal endophytes from native plants to non-host plants resulted in substantial modifications in root, shoot morphology and biomass, chlorophyll content, and fruiting. Host plants are modified by fungi at the genetic, cellular, and physiological level and positively enhance ecological fitness.

Introduction

Fungi are unable to synthesize organic carbon, therefore they either assimilate exogenous organic carbon as saprophytes or they form associations with photosynthetic organisms. Lichens provide the simplest symbiotic model where fungi form associations with photosynthetic microorganisms. Evidence supporting similar symbioses between fungi and higher plants is increasingly overwhelming. Fungi reside in healthy tissues of every native plant examined to date and range from destructive pathogens to mutualists that profoundly affect ecological fitness (Arnold and others 2000). Some endophytic fungi occupy the apoplast of leaves, stems, and reproductive organs of many grasses (Clay 1990; Schulz and others 2002). Mycorrhizal fungi colonize roots of most plant species and have significant, well documented ecological roles in the nutrition and survival of host plants in natural ecosystems (Smith and Read 1997). Apparent saprophytic fungi also colonize roots with symptomless endophytic or biotrophic phases in their life cycles that are not obvious to casual observers (Parbery 1996). Most fungal associations are localized, while a few inhabit the entire apoplast and are vertically transmitted by seed (Clay and Schardl 2002). Not surprisingly, fungal endophytes confer multiple benefits to their host, such as enhanced tolerance to disease, drought, herbivory, and heavy metals and enhanced nutrient uptake and photosynthetic efficiency (Arnold 2003; Clay 1990; Ruiz-Lozano 2003; Obledo and others 2003).

Recent attention has been given to a diverse group of ascomycetous fungi designated as dark septate endophytes (DSE). These fungi have been detected microscopically by their inter- and intracellular, darkly pigmented (melanized) septate hyphae and microsclerotia in the root cortex (Barrow and Aaltonen, 2001; Jumpponen 2001). They are found extensively in cold, nutrient-stressed environments where AM fungi do not proliferate (Kohn and Stasovski 1990). A higher incidence of DSE than AM fungi was found in *Carex* sp. in subarctic alpine regions (Haselwandter and Read 1982; Ruotsalainen and others 2002). Non-staining hyaline hyphal extensions from stained or melanized structures were reported by Barrow and Aaltonen (2001), Haselwandter and Read (1982), Newsham (1999), and Yu and others (2001) revealing morphological variability. DSE are the primary fungal associates of dominant native grasses and shrubs in the northern Chihuahuan Desert (Barrow and others 1997).

Barrow and Aaltonen (2001) and Barrow (2003) evaluated *Bouteloua eriopoda* Torr. (BOER) and *Atriplex canescens* (Pursh) Nutt. (ATCA), important forage shrub and grass species of the northern Chihuahuan Desert. Histochemical staining revealed greater colonization of atypical forms of DSE than previously observed using conventional methods. Osuna-Avila and Barrow (2004) regenerated plants from embryonic shoot meristem cells of naturally produced BOER seed and found fungal endophytes to be intrinsically integrated in regenerated plants (Barrow and others 2004).

In this study, naturally colonized roots and leaves of native *Bouteloua eriopoda* Torr. and *Atriplex canescens* (Pursh) Nutt.

In: Sosebee, R.E.; Wester, D.B.; Britton, C.M.; McArthur, E.D.; Kitchen, S.G., comp. 2007. Proceedings: Shrubland dynamics—fire and water; 2004 August 10-12; Lubbock, TX. Proceedings RMRS-P-47. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 173 p.

plants are compared with cell cultures, germinating seedlings, and micro-propagated plants of both species using scanning electron microscopy (SEM) and light microscopy with dual-staining methodology. Endophytic fungal endophytes were transferred from BOER and ATCA to non-host plants.

Materials and Methods

Tissue Samples

Root and leaf samples of native and micro-propagated plants and germinating seedlings of BOER and ATCA were analyzed in this study. Roots were sampled every two weeks, from 2001 to the present from native populations of ATCA and BOER on the USDA Agricultural Research Service's Jornada Experimental Range in southern New Mexico. Soil moisture in the chronically dry collection sites are generally less than 3 percent. Significant precipitation events are intense, localized rain showers during the summer monsoons that saturate the soil for only brief periods. Sampling times included a wide range of seasonal, physiological, and climatic conditions. Uniform expression of fungal structures was consistent within the population at each sampling period. Leaves from native plants were sampled over all seasons and included different physiological stages ranging from actively growing to drought induced dormant plants.

Tissue Preparation and Staining

Staining and mounting methods were modified by Barrow and Aaltonen (2001) and Barrow (2003) for optimal fungal expression. Tissues were dual stained with trypan blue (TB), which targets fungal chitin, and sudan IV (SIV), which targets lipid bodies found previously to stain lipids attached to fungal structures (Barrow and Aaltonen 2001; Barrow 2003). Samples were analyzed with a Zeiss Axiophot microscope with both conventional and differential interference contrast optics at 1000x. Images were captured with a high resolution digital camera and processed using auto-montage 3-D software by Syncroscopy™ to give a focused image.

Tissue Preparation by Liquid Nitrogen

Roots and leaves from native and propagated plants and germinated seedlings were also placed in liquid nitrogen and dried at 100°C. Tissues were then ground with a mortar and pestle and suspended in a centrifuge vial in 10 ml of 2.5 percent KOH and micro-waved for 1.5 min prior to centrifugation at 3000 rpm until a stable pellet formed. The supernatant was removed by pipette and the pellet was re-suspended in 10 ml dH₂O and centrifuged again. The pellet was re-suspended in 10 ml HCL and micro-waved for 1.5 min. The vial was filled with dH₂O and the cell pellet was harvested again by centrifugation. Next, the cell pellets were suspended in 5ml trypan blue and 5 ml sudan IV and micro-waved for 2 min. The vial was rinsed with dH₂O and centrifuged, and the supernatant was again removed by pipette.

Stained ground material was suspended in a drop of mounting medium on a slide and sealed with a cover slip and microscopically examined. This procedure resulted in tissues fractured in all possible planes permitting analysis of single layers of cells at 1000x magnification. Power settings, time, and sample size must be adjusted to prevent over heating in the microwave.

Scanning Electron Microscopy

Fresh leaves and roots of native and propagated plants were sampled from the field and from micro-propagated plants and placed in moist plastic bags and analyzed within 1h by placing them in a vacuum chamber of a biological scanning electron microscope.

Micro-Propagated BOER Plants

Seeds were manually harvested from native BOER plants; caryopses were separated from florets and surface disinfested and germinated. Embryonic shoots were excised from roots and plated on an auxin supplemented medium to induce callus from meristematic shoot cells. Plants were regenerated via somatic embryogenesis from callus cells after transferring to an auxin-free medium (Osuna and Barrow 2004).

Micro-Propagated ATCA Plants

Seeds of four-wing saltbush, *Atriplex canescens*, were surface disinfested by soaking them in 95 percent ethanol for 1 minute, followed by 2.6 percent sodium hypochlorite (50 percent dilution of commercial liquid bleach) for 7 minutes. Seeds were rinsed three times in sterile distilled water then were placed on hormone-free, modified White's media (White 1934) for germination. Germinated seedlings of *Atriplex canescens* were used to initiate shoot cultures by transferring them to shoot proliferation media consisting of standard Murashige and Skoog (MS) basal salts (Murashige and Skoog 1962) supplemented with 11.42 μ M Indole-3-Acetic Acid (IAA) and 18.58 μ M 6-Furfurylaminopurine (Kinetin). Vitamins were supplemented according to the L2 formulation of Phillips and Collins (1979), 30 g l⁻¹ sucrose, and solidified with 0.8 percent agar. The pH of the medium was adjusted to 5.8 $\pm$ 0.05 prior to autoclaving at 121°C at 125 kPa for 35 minutes. Cultures were grown in 100 x 25 mm polystyrene petri dishes and sealed with Parafilm®. They were subcultured to fresh media every 4 weeks. This protocol represents the standard control media.

Shoots were originally vitrified and were reverted to normal by transferring to shoot proliferation media with the following modifications. Ammonium-free MS (NH₄NO₃ excluded from the original major salts composition) was supplemented with 4.40 g/L of casein hydrolysate to provide an amount of total nitrogen content comparable with the standard MS formulation. Standard MS basal salts served as the control. Vitamin supplements were added according to the L2 formulation by Phillips and Collins (1979) plus 30 g l⁻¹ sucrose. All experimental

media treatments were solidified with 5.0 g/L of Agargel® (Sigma Chemical Co., St Louis MO, USA), a blend of agar and phytagel documented to control vitrification (Pasqualetto and others, 1986). Growth regulator composition consisted of 24.61 μM 6-(γ - γ -Dimethylallylamino) purine (2iP). The pH of the medium was adjusted to 5.8 ± 0.05 prior to autoclaving at 121°C at 125 kPa for 35 minutes and dispensed in polycarbonate Magenta® GA7 vessels (Magenta Corp., Chicago, IL., USA). Culture boxes were closed with either standard Magenta® GA7 vessel covers or vented lids with a 10 mm polypropylene membrane (0.22 μm pore size) Magenta® (Magenta Corp. Chicago, USA). All cultures were incubated at $28 \pm 1^\circ\text{C}$ under continuous fluorescent light (14–18 $\mu\text{mol}^{-2} \text{s}^{-1}$). Normal shoots were removed from culture boxes and subcultured on the reversion medium.

Normal shoots of three nodes or longer were rooted by culturing on White's media culture (White, 1934) supplemented with 2.46 μM of indolebutyric acid (IBA), 30 g/l of sucrose, and solidified with 2.5 g/L of Phytigel® (Sigma Chemical Co., St Louis MO., USA). Pure phytagel facilitated easy visual evaluation of root initials. The pH was adjusted to 5.5 ± 0.05 prior to autoclaving at 121°C at 125 kPa for 35 min and dispensed in 107 x 107 x 96 mm high LifeGuard® polycarbonate culture boxes closed with vented lids with an opening of 22 mm and a 0.3 μm pore size (Osmotek Ltd, Israel).

Fungal Transfer

Fungi were transferred from BOER and ATCA by placing germinating disinfested tomato seed in contact with callus cultures of both species. Tomato plants with fungi were compared with control plants without fungi under greenhouse conditions.

Ribosomal DNA Analysis

Polymerase chain reactions (PCRs) targeting ribosomal DNA (rDNA) and internal spacer regions (ITS) developed for identification of fungi (White, 1990) were applied to tomato DNA isolated from leaves of control, BOER- and ATCA-inoculated plants. Electrophoresis of PCR products was used to identify products that differed between treatment groups.

Some of the fungal endophytes present in BOER and ATCA inoculated plants have been previously characterized by sequence analysis of cloned PCR products and/or by isolation and morphological identification (Barrow and others 2004; Lucero and others 2004). The ATCA callus used to inoculate tomato was known to contain *Aspegillus ustus*, *Pennicillium olsoni*, and *Bipolaris spicifera*. The BOER callus was also associated with *A. ustus*. In addition, BOER callus contained *Engyodontium album* and an uncharacterized, teliospore-producing fungus (Lucero and others 2004). Mention of trade names or commercial products in this publication is solely for the purpose of providing specific information and does not imply recommendation or endorsement by the U.S. Department of Agriculture.

Results and Discussion

Symbiotic fungal presence was verified in plant tissues by light and electron microscopy and DNA sequence analysis. Fungi were found to be intrinsically integrated with all cells tissues and organs of native and aseptically regenerated BOER and ATCA plants. Significant associations with specific cell types and potential functions are presented here. A key observation was the consistent association of fungal tissue, as indicated by positive staining with TB (fig. 1, sf), with all root meristem and daughter cells. The transmission of fungi to daughter cells explains how fungi become associated with all host plant cells. Such an association has significant implications regarding how the host plant may perform at the genetic, physiological, and ecological levels. Internal fungal structures were morphologically variable; many differed from classically recognized structures and escape detection using conventional analytical methods.

Fungi were previously found to be non-destructively associated with xylem and sieve elements of the vascular cylinder, cortical, and epidermis of native BOER and ATCA roots with external hyphal extensions into the soil (Barrow and Aaltonen 2001; Barrow 2003). Such associations suggest the potential enhancement of resource transport in the vascular cylinder by fungal symbionts. Historically, axenically cultured plants have been considered microbe free (Borkowska 2002). However, tissue cultured BOER and ATCA plants were found to have intrinsically associated fungi that were found to be continuous from embryonic shoot meristem cells, to callus and to regenerated BOER plants (Barrow and others 2004). SEM analysis of callus tissue induced from embryonic BOER cells (fig. 2) reveals hyphae (h) enmeshed within the biofilm (bf) that completely encapsulates the axenically cultured callus tissue. This is consistent with observations of Pirttila and others (2002), who also found fungal biofilms on the surface of *Pinus* tissue cultures. Embryos were induced within the callus (Barrow and others 2004). SEM analysis of embryonic roots of developing plantlets (fig. 3) shows a tightly woven hyphal mass (hn) enmeshed within a biofilm (bf). Symbiotic fungal endophytes are shown here to totally encapsulate cells, callus, and roots and prevent their direct exposure to the external environment. Similar fungal layers have been observed to completely cover all root and leaf surfaces of native plants in the field.

Native plants in the northern Chihuahuan are chronically exposed to extreme nutrient and soil water deficits (soil moisture < 3 percent) for long periods, as well as high temperatures, dry atmospheric conditions, and high light intensity. Fungi, as well as other microbes, synthesize exo-polysaccharides that attach to their cell surfaces (Sutherland 1998). Biofilms constitute a protective mode for the microbe (Costerton and others 1999). They have unique characteristics that may be valuable contributions to host plants in an arid ecosystem. They hydrate rapidly on contact with water and assist in the attachment to substrates or to host plants. Biofilms protect against invasions from pathogens and changes in the physico-chemical environment and allow microbes to survive in hostile

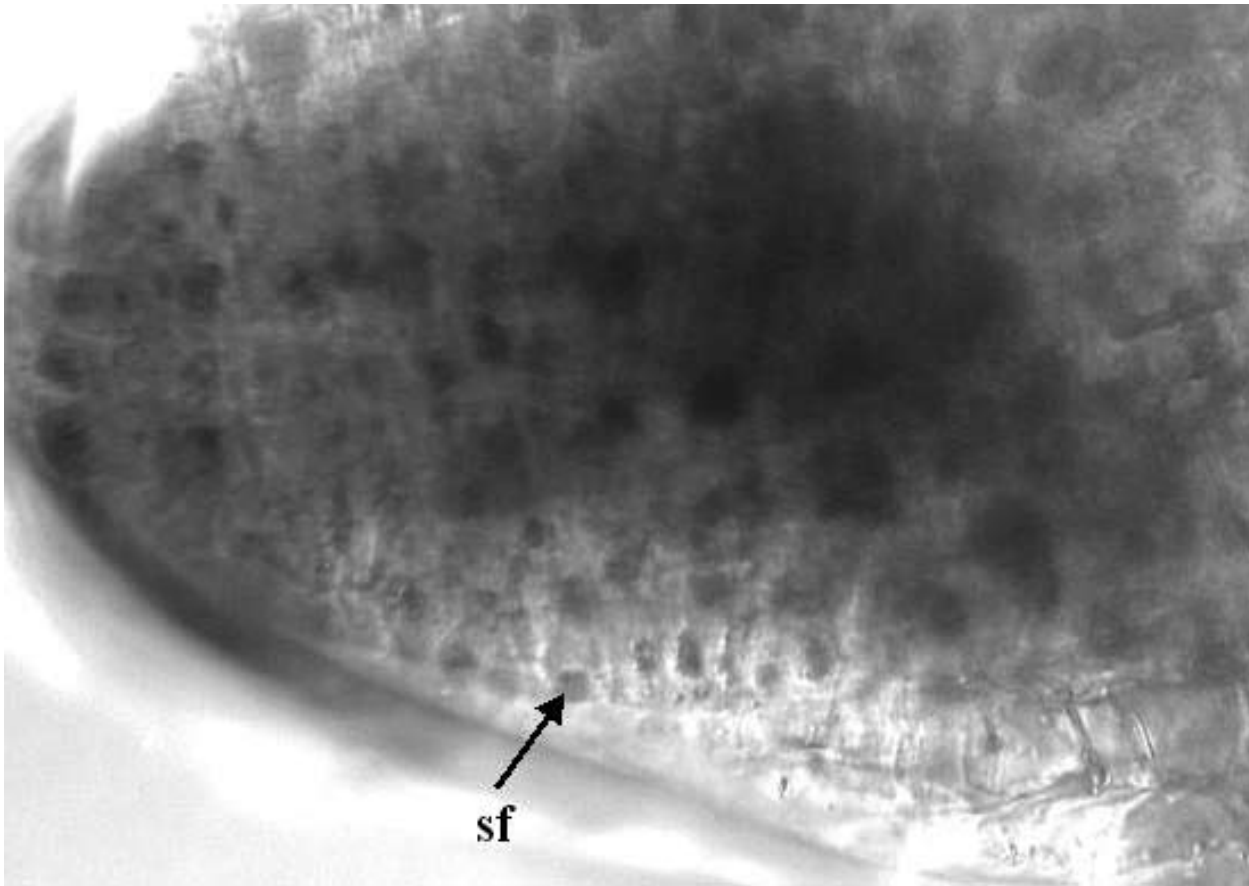


Figure 1. Meristematic cells of a lateral root initial of *Bouteloua eriopoda* seedling. Trypan blue stained fungus associated with all cells (sf).

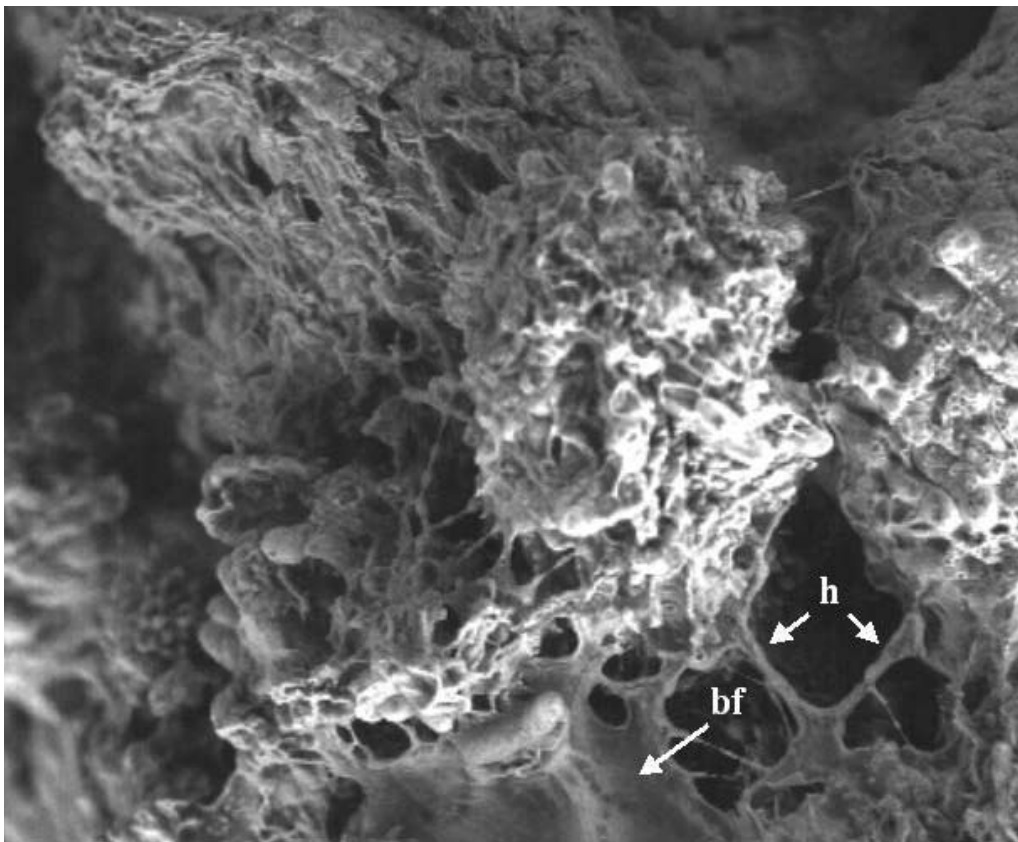


Figure 2. An SEM image of *Bouteloua eriopoda* callus tissue encapsulated with fungal hyphae (h) enmeshed within a biofilm (bf).

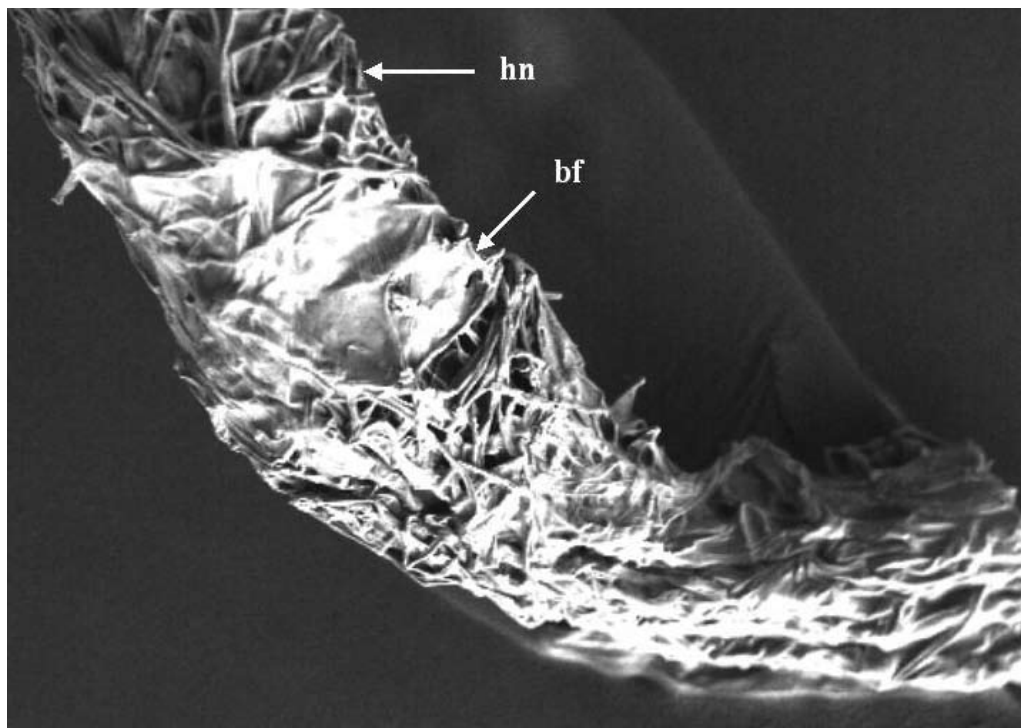


Figure 3. An SEM image of an embryonic root developing from a regenerated *Bouteloua eriopoda* plantlet that is encapsulated with a dense hyphal network (hn) and fungal biofilm (bf).

environments (Costerton and others 1999; Krembs and others 2002; Wotton 2004). Consistent with findings of Deckert and others (2001), we also observed that external hyphae on root and leaf surfaces that were embedded within a mucilaginous (polysaccharide) matrix. The fungus with a protective biofilm, makes fungi an attractive cohort for native plants that enables them to function under extreme stress. This barrier would be expected to confer multiple benefits to host plants, protecting plant surfaces from dry soil and atmospheric conditions, temperature extremes, intense light, salinity, absorption of heavy metals, or infection by pathogens.

Also significant was the association of symbiotic fungi with photosynthetic cells and the stomatal complex. Fungal associations with all photosynthetic cells of native and regenerated plants of BOER and ATCA were observed. Figure 4 shows stained fungal structures (sf) associated with photosynthetic bundle sheath cells (bs) and mesophyll cells (mp) of BOER. Note that the fungi assume the shape of the respective cells. The interpretation of extensive observations is that fungal tissue adheres to the outer plasmalemma of most cells and is transmitted to new cells at division. Positively stained fungal structures (fig. 5, sf) were also observed associated with bundle sheath cells of native and regenerated ATCA plants. The xylem vessels (st) also stained positively for fungal tissue. Fungi bind with and assume the shape of the lignified xylem vessels. Fungal association with photosynthetic cells suggests a potential site where these biotrophic endophytes may access carbon from the host plant. The quantity of exo-polysaccharides produced by these fungi for protective biofilms suggests considerable carbon expenditure for protection of the hybrid plant-fungus organism. Associations with xylem vessels suggest a role of active water transport by fungi and enhancement of drought tolerance.

Fungal association with cells of the stomatal complex with both native and regenerated plants further confirmed their distribution to all cells and tissues and their existence as a composite plant-fungus symbiota. Figure 6 shows stained fungal tissue (stf) associated with guard cells of stomata (st) in a regenerated ATCA plant. Similar fungal staining was consistently observed in cells of the stomatal complex of native and regenerated BOER plants (fig. 7). The staining pattern in BOER, was a consistent staining of the terminal ends of guard cells (gc), while in ATCA, staining of the entire guard cells was observed (fig. 6). Staining was also regularly observed in the subsidiary cells (sc) of the stomatal complex. Colonization of stomata of these native plants suggests that these endophytes influence stomatal regulation and evapotranspiration. Minimizing water loss in arid ecosystems would enhance drought tolerance. A suggested fungal role may be to maximize gas exchange and photosynthetic efficiency, while reducing water loss by transpiration.

Unexpected, was the intrinsic association of endophytic fungi with cell cultures, calluses, and axenically cultured plants, previously expected to be microbe free (Barrow and Osuna-Avila 2004; Borkowska 2002). Also of interest, was that these fungi did not grow on the carbon-mineral rich culture medium as long as the plant tissues were healthy. However, after the eventual death of plants, *A. ustus*, *Crinipellis* and *Engyodontium album* were isolated and grew well on the culture medium. This suggested an obligate affinity of these species to healthy living tissue compared to their saprophytic potential on artificial medium after plant health is impaired.

Attempts to completely separate BOER and ATCA cell cultures from fungi have not been successful. Therefore, in order to observe the effects that BOER- and ATCA-associated fungi might have on their prospective host plant, callus

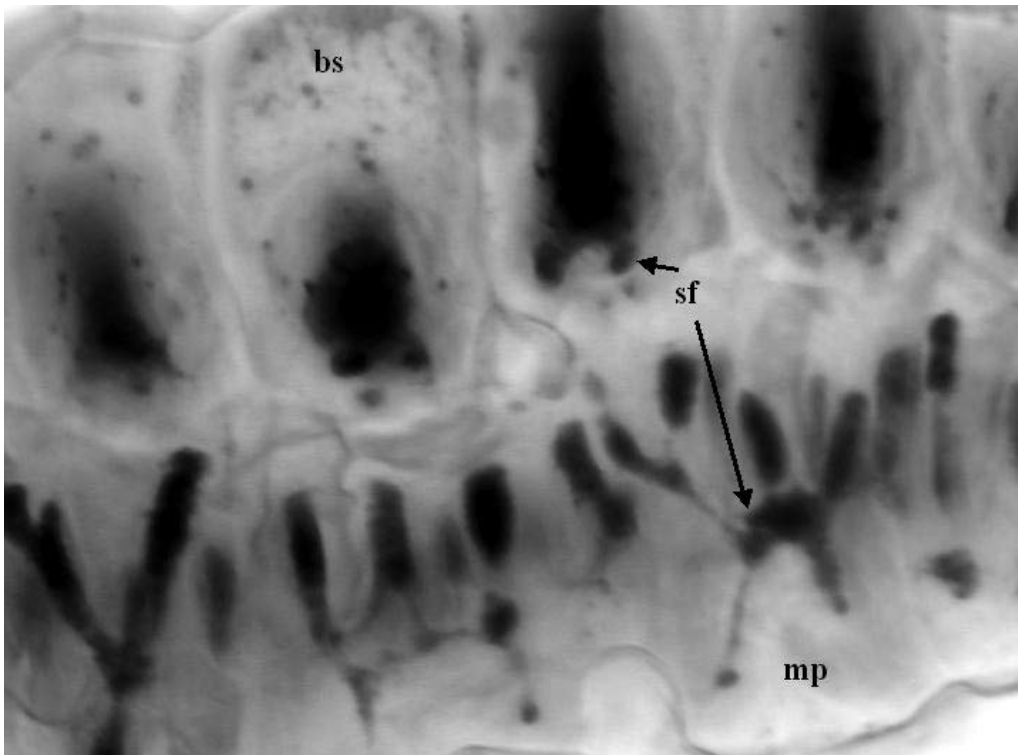


Figure 4. Trypan blue stained fungal tissue (sf) within photosynthetic mesophyll cells (mp) and bundle sheath cells (bs) of native *Bouteloua eriopoda*.

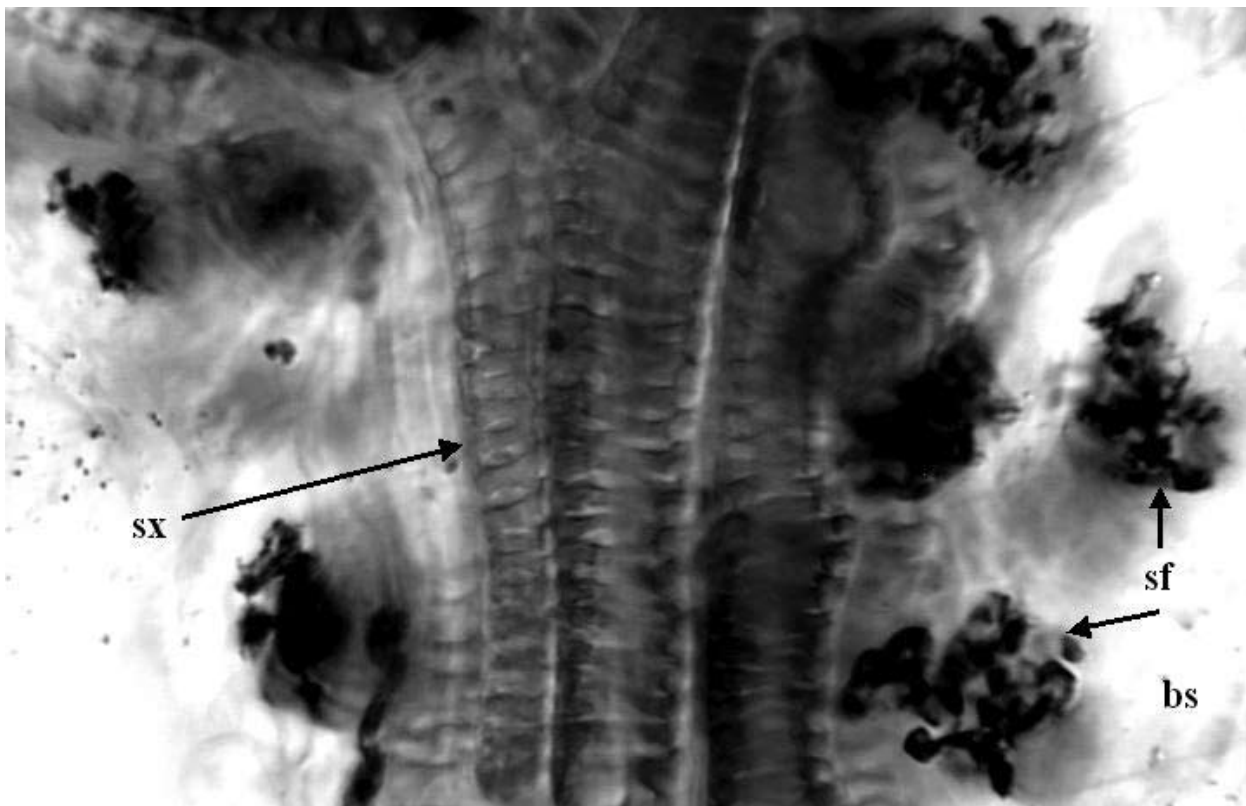


Figure 5. Trypan blue stained fungal tissue (sf) in photosynthetic bundle sheath (bs) cells in leaves of regenerated *Atriplex canescens* leaves. Lignified xylem vessels (sx) also stain positively for fungal tissue.

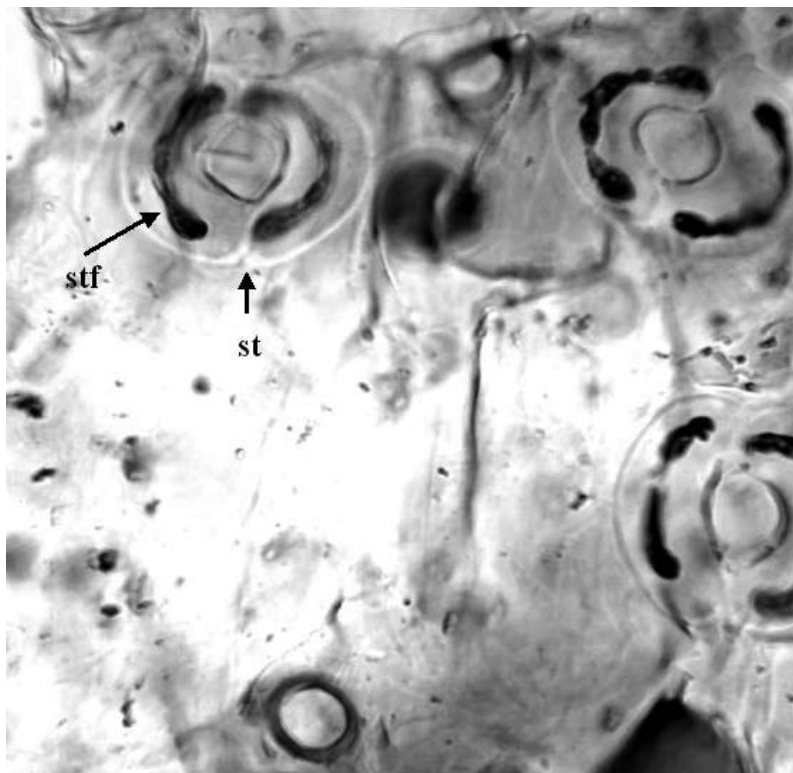


Figure 6. Trypan blue stained fungal tissue (stf) within guard cells of the stomata (st) in leaves of regenerated *Atriplex canescens* plantlets.

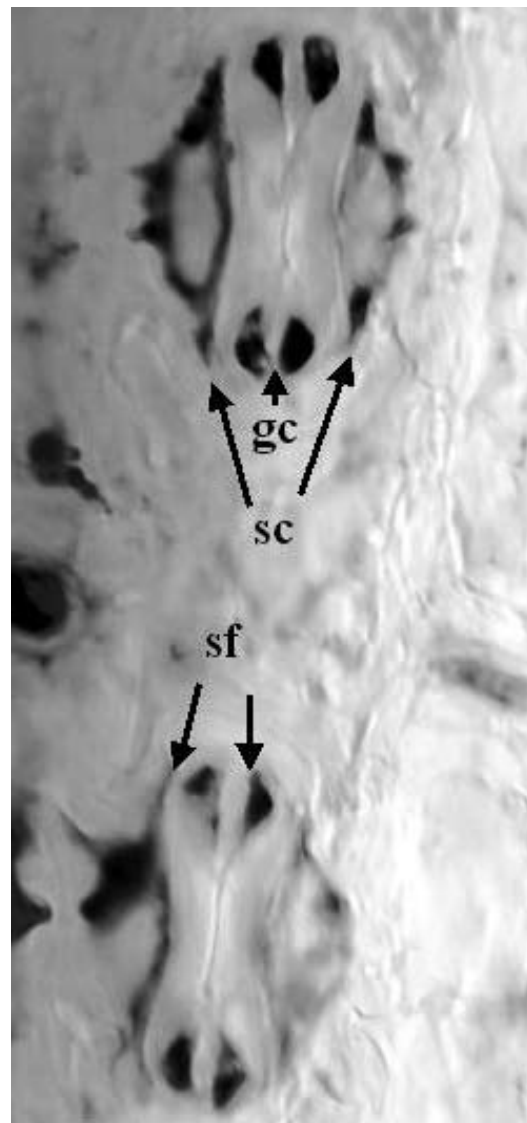


Figure 7. Trypan blue stained fungal tissue (sf) associated with terminal ends of guard cells (gc) and subsidiary cells (sc) of the stomatal complex of native *Bouteloua eriopoda* leaves.

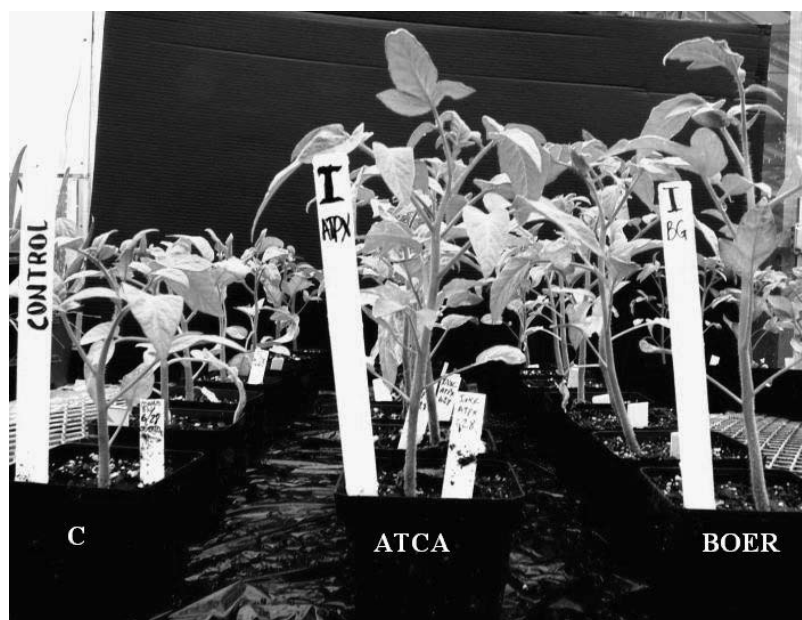


Figure 8. Control tomato plants, var. Bradley (without fungi). Fungi transferred to plants from *Atriplex canescens* (ATCA) callus. Fungi transferred to plants from *Bouteloua eriopoda* (BOER) callus.



Figure 9. PCR products obtained from amplification of rDNA from control tomato plants, var. Bradley (without fungi), and from tomato plants (var. Bradley) inoculated with *Atriplex canescens* (ATCA) callus or *Bouteloua eriopoda* (BOER) callus. Left to right: Lane 1-Molecular Weight Marker, Lane 2- Control tomato, Lane 3- Tomato inoculated with BOER callus, Lane 4- Tomato inoculated with ATCA callus.

from cell cultures was used to inoculate tomato seedling. Evidence for their transfer was a three- to five- fold increase in root and shoot biomass. Figure 8 compares standard tomato variety, Bradley, control plants (c) to plants with fungi transferred from ATCA callus, and to plants with fungi transferred from BOER callus. Transferred fungi immediately take up residence in the apoplastic spaces of the non-host tomato. Substantial increase in shoot biomass is observed with earlier and larger fruit production. Fungi increased root biomass from three to five times. Differences in responses were observed, suggesting that different fungi may have been transferred with ATCA and BOER callus.

When the primers NS1 and NS4 were used with defined protocols (White 1990), a band was seen in both BOER and ATCA treated samples that was absent from the control (fig. 9). Curiously, this band has not been seen in PCR products that have been amplified from endophytes such as the putative rust, the *Crinipellis* and the *Aspergillus ustus* (Lucero and others, submitted), which have previously been characterized in ATCA and BOER cultures. This suggests yet another fungal endophyte resides in these cell cultures. If the different effects observed in the BOER- and ATCA-inoculated treatment groups are indeed due to different fungi, then sequence analysis should produce a different sequence for each of the bands shown in figure 9. The intrinsic integration of symbiotic fungi with all cells and tissues suggests that fungi modify plant behavior at genetic, cellular, physiological, and ecological levels and that fungal genes contribute multiple benefits to the host plant. It is unlikely that plants bearing such large fungal populations would continue to thrive under any environment unless the fungi contributed benefits to the host plant in exchange for substantial quantities of organic carbon they consume.

The simplicity with which fungi can be transferred to new hosts, combined with the benefits conferred on plants by fungi, raises interesting possibilities for native and crop plant improvement. Continued research in the identification and characterization of fungal endophytes promises to yield a complex assortment of species that may serve as tools for plant improvement. Clearly, microbial diversity in our arid rangelands has been a largely overlooked and underutilized resource.

References

- Arnold, A. E.; Mehia, L. C.; Kyllö, D.; Rojas, E. I.; Maynard, Z.; Robbins, N.; Herre, E. A. 2003. Fungal endophytes limit pathogen damage in a tropical tree. *Proceedings National Academy Science* 100: 15649-15654.
- Arnold, A.; Maynard, Z.; Gilbert, G. S.; Coley, P. D.; Kursar, T. A. 2000. Are tropical fungal endophytes hyperdiverse? *Ecology Letters* 3: 267-274.
- 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.
- 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. 2003. Atypical morphology of dark septate fungal root endophytes of *Bouteloua* in southwestern USA rangelands. *Mycorrhiza* 13: 239-247.
- Barrow, J. R.; Osuna-Avila, P.; Reyes-Vera, I. 2004. Fungal endophytes intrinsically associated with micropropagated plants regenerated from native *Bouteloua Eriopoda* Torr. and *Atriplex canescens* (Pursh) NUTT. In *Vitro-Cellular Developmental Biology—Plant (In Press)*.
- Borkowska, B. 2002. Growth and photosynthetic activity of micropropagated strawberry plants inoculated with endomycorrhizal fungi (AMF) and growing under drought stress. *Acta Physiologiae Plantarum* 24: 365-370.
- Clay, K. 1990. Fungal endophytes of grasses. *Annual review of Ecology and Systematics* 21: 275-297.
- Clay, K.; Schardl, C. 2002. Evolutionary origins of ecological consequences of endophyte symbiosis with grasses. *The American Naturalist* 160: s99-s127.
- Costerton, J. W.; Stewart, P. S.; Greenberg, E. P. 1999. Bacterial biofilms: A common cause of persistent infections. *Science* 284: 1318-1322.
- Deckert, R. J.; Melville, L. H.; Peterson, R. L. 2001. Epistomatal chambers in the needles of *Pinus strobus* L. (eastern white pine) function as microhabitat for specialized fungi. *International Journal of Plant Sciences* 162: 181-189.
- Haselwandter, K.; Read, D. J. 1982. The significance of a root-fungus association in two *Carex* species of high-alpine plant communities. *Oecologia* 53: 352-354.
- Jumpponen, A. 2001. Dark septate endophytes: Are they mycorrhizal? *Mycorrhiza* 11: 207-211.
- Kohn, L.; Stasovski, I. 1990. The mycorrhizal status of plants at Alexandra Fiord, Ellensmere Island, Canada, a high Arctic site. *Mycologia* 82: 23-35.
- Krembs, C.; Eicken, H.; Junge, K.; Deming, J. W. 2002. High concentrations of exopolymeric substances in Arctic winter sea ice;

- implications for the polar ocean carbon cycle and cryoprotection of diatoms. *Deep-Sea Research* 49: 2163-2181.
- Lucero, M. L.; Barrow, J. R.; Osuna, P.; Reyes, I. 2004. Plant-fungal interactions: Large scale impacts from microscale processes. *Journal of Arid Environments* (Submitted).
- Murashige, T.; Skoog, F. 1962. A revised medium for rapid growth and bioassays with tobacco tissue cultures. *Physiologia Plantarum* 15: 473-497.
- Newsham, K. K. 1999. *Phialophora graminicola*, a dark septate fungus, is a beneficial associate of the grass *Vulpia ciliata* ssp. *ambigua*. *New Phytologist* 144: 517-524.
- Obledo, E. N.; Barragan-Barragan, L. B.; Gutierrez-Gonzalez, P.; Ramirez-Hernandez, B. C.; Rameriz, J. J.; Rodriguez-Garay, B. 2003. Increased photosynthetic efficiency generated by fungal symbiosis in *Agave victoria-reginae*. *Plant Cell, Tissue and Organ Culture* 74: 237-241.
- Osuna, P.; Barrow, J. R. 2004. Regeneration of black grama (*Bouteloua eriopoda* Torr.) via somatic embryogenesis. *In Vitro-Cellular Developmental Biology—Plant* 40: 299-302.
- Parbery, D. G. 1996. Trophism and the ecology of fungi associated with plants. *Biological Review* 71: 473-527.
- Pasqualetto, P. L.; Zimmerman, R. H.; Fordham, I. 1986. Gelling agent and growth regulator effects on shoot vitrification of 'Gala' apple *in vitro*. *Journal of American Society of Horticulture Science* 111(6): 976-980.
- Pirttila, A. M.; Laukkanen, H.; Hohtola, A. 2002. Chitinase production in pine callus (*Pinus sylvestris* L.): a defense reaction against endophytes? *Planta* 214: 848-852.
- Phillips, G. C.; Collins, G. B. 1979. *In vitro* tissue culture of selected legumes and plant regeneration of red clover. *Crop Science* 19: 59-64.
- Ruiz-Lozano, J. M. 2003. Arbuscular mycorrhizal symbiosis and alleviation of osmotic stress. *New perspectives for molecular studies. Mycorrhizae* 13: 309-317.
- Ruotsalainen, A. L.; Vare, H.; Vestberg, M. 2002. Seasonality of root fungal colonization in low-alpine herbs. *Mycorrhiza* 12: 29-36.
- Schulz, B.; Boyle, C.; Draeger, S.; Rommert, A.; Krohn, K. 2002. Endophytic fungi: a source of biologically active secondary metabolites. *Mycological Research* 106 (9): 996-1004.
- Smith, S. E.; Read, D. J. 1997. *Mycorrhizal Symbiosis*. Second Edition, Academic Press, San Diego, London 59-60.
- Sutherland, I. W. 1998. Novel and established applications of microbial polysaccharides. *Trends in Biotechnology* 16: 41-46.
- White, T. J.; Bruns, T.; Lee, S.; Taylor, J. W. 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics in PCR protocols: a Guide to Methods and Applications. Edited by: Innis, M. A., Gelfand, D. H. Sninsky, J. J. and White, T. J. Academic Press. Inc. New York. Pp. 315-322.
- White, P. R. 1934. Potentially unlimited growth of excised tomato root tips in a liquid medium. *Plant Physiology* 9: 585-600.
- Wotton, R. S. 2004. The ubiquity and many roles of exopolymers (EPS) in aquatic systems. *Scientia Marina* 68: 13-21.
- Yu, T.; Nassuth, A.; Petersen, R. L. 2001. Characterization of the interaction between the dark septate fungus *Phialocephala fortinii* and *Asparagus officinalis* roots. *Canadian Journal of Microbiology* 47: 741-753.

The Authors

¹Research Scientist, USDA-ARS-Jornada Experimental Range, Las Cruces, NM. jbarrow@nmsu.edu

²Postdoctoral Associate, USDA-ARS-Jornada Experimental Range, Las Cruces, NM.

³Graduate Assistant, USDA-ARS-Jornada Experimental Range, Las Cruces, NM.

⁴Research Associate, USDA-ARS-Jornada Experimental Range, Las Cruces, NM.

Ecology and Population Biology Session

Estimating Aboveground Biomass of Mariola (*Parthenium incanum*) from Plant Dimensions

Carlos Villalobos¹

Abstract: The distribution and abundance of plant biomass in space and time are important properties of rangeland ecosystem. Land managers and researchers require reliable shrub weight estimates to evaluate site productivity, food abundance, treatment effects, and stocking rates. Rapid, nondestructive methods are needed to estimate shrub biomass in semi-arid ecosystems. Shrub height and crown diameter are useful non-destructive measures of shrub size. Mariola (*Parthenium incanum*) is an important shrub that is widely distributed in the Chihuahuan and Sonoran deserts. Mariola is found from the southwest United States to the central part of Mexico. Regression analyses were used to examine the relationships between aboveground biomass and four plant measurements (shrub height, longest canopy width, shortest canopy width, and crown volume) from 45 plants. All variables were related to aerial biomass; R values varied from 0.73 to 0.98. Regression equations developed for mariola compared favorably to equations in similar species in desert environments, suggesting that results might be applicable to other desert regions for rapid and accurate estimation of shrub biomass.

Introduction

The Chihuahuan desert is the largest of the three creosote-bush-dominated deserts in North America. The Chihuahuan desert covers 450,000 to 629,000 km² (Henrickson and Straw 1976; Morafka 1977; Dinerstein and others 2000) in eastern Chihuahua, western Coahuila, San Luis, Potosi, southern Nuevo Leon, northeast Zacatecas, eastern Durango, southwest Texas, and southern New Mexico, as well as smaller but equally distinctive areas in southeast Arizona and northeast Sonora (Brown 1982). Chihuahuan desert grasslands contain a varied flora of herbaceous, suffrutescent, and woody species. Vegetation pattern is spatially diverse across the landscape and is influenced by highly variable patterns of precipitation and subtle changes in edaphic factors as well as natural and anthropogenic disturbance regimes (Buffington and Herbel 1965). Creosotebush, (*Larrea tridentata*), is a prominent element of the Chihuahuan Desert, often covering large areas. Other common shrubs include catclaw (*Mimosa biuncifera*), mesquite (*Prosopis glandulosa*), mariola (*Parthenium incanum*), fourwing saltbush (*Atriplex canescens*), tarbush (*Flourensia cernua*), javelinabush (*Condalia ericoides*),

goldeneye (*Viguiera cordifolia*), and ocotillo (*Fouquieria splendens*). Among these shrubs, fourwing saltbush (*Atriplex canescens*) and mariola (*Parthenium incanum*) are important components of the diet of grazing animals.

Maynez and others (1984) evaluated the nutritional value of mariola by collecting samples during 1 year in a monthly period. They found the highest crude protein (CP) values during September (20.3 percent) and April (18.3 percent). The lowest CP contents were measured during the months of October (11.7 percent), November (12.6 percent), and January (13.6 percent). The highest percentages of mariola in vitro organic matter digestibility (IVOMD) were determined during the months of September and April – 65.5 and 63.5 percent, respectively. In contrast, the lowest IVOMD values were found in November with an average of 54.1 percent.

Mariola is one of the most important components of the diet of grazing animals on a desert shrublands. Marquez and others (1984) used esophageal fistulated steers to determine dietary botanical composition. The most important plants were mariola buddleja (*Buddleja scordiodes*) and oreganillo (*Aloysia wrightii*). Mariola constituted about 31 percent of their diet for grazing steers. Villalobos and others (1984) working in the same vegetation type estimated that on

In: Sosebee, R.E.; Wester, D.B.; Britton, C.M.; McArthur, E.D.; Kitchen, S.G., comp. 2007. Proceedings: Shrubland dynamics—fire and water; 2004 August 10-12; Lubbock, TX. Proceedings RMRS-P-47. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 173 p.

average, 18 percent the diet with esophageal goats was made up of mariola.

The distribution and abundance of plant biomass in space and time are important properties of rangeland ecosystem. Researchers and natural resources managers require reliable estimates of shrub weights to assess site productivity, food abundance, treatment effects, and stocking rates. The accurate measurement of vegetative biomass by traditional clipping and weighing is a time-consuming and labor-intensive process. As a result, indirect methods are needed to rapidly determine shrub aerial biomass. Considerable research has gone into estimating the biomass of individual shrub species (Tucker 1980; Murray and Jacobson 1982; Frandsen 1983; Navar and others, 2002). However, established techniques, such as harvesting, are slow and expensive. Shrub height and crown diameter are useful non-destructive measures of shrub growth, but precise direct estimates of yields of aerial biomass require destructive methods that are unsatisfactory in studies on perennial shrubs.

Uresk and others (1977) estimated that clipping big sagebrush (*Artemisia tridentata*) phytomass was 120 times more expensive than using dimension analysis. Using the weight estimate technique (Pechanec and Pickford 1937) requires a considerable training and clipping to check estimates. A technique that is rapid, relatively accurate, and requires little training is desirable. Tufts (1919) found a high correlation between trunk circumference and weight of the top of fruit trees. Since this early beginning, many others including Kittredge (1944), Attiwill (1962), Baskerville (1965), and Brown (1978) have used combinations of trunk diameter, total height, live crown length, ratios of live crown length to total height, and crown widths to estimate tree biomass. In most cases, very useful predictive relationships were developed from these simple measurements. Similarly, biomass estimates of various shrub species and plant fractions have been developed using stem diameters (Telfer 1969; Brown 1976), crown diameter axes (Rittenhouse and Sneva 1977), crown volume (Chew and Chew 1965; Lyon 1968; Mack 1971; Burk and Dick-Peddie 1973; Ludwig and others 1975; Rittenhouse and Sneva 1977; Wakimoto and Menke 1978), crown cover (Ludwig and others 1975), and height x circumference (Harniss and Murray 1976) as independent variables.

A large number of variables can be used to predict biomass. However, variables that express the size of the crown or the volume appear to be most useful. The objective of this study was to examine the relationships between aboveground biomass and four plant measurements (shrub height, longest canopy width, shortest canopy width, and crown volume) recorded in the field.

Materials and Methods

This study was conducted on a private ranch 50 km east of Chihuahua city (28° 46' N, 65° 50' W) at elevation of 1,150 m. The climate of the region is semi-arid and warm. The average annual precipitation is 250 mm, with about 65 percent occurring between July and September. The

vegetation is characterized by perennial, drought resistant woody species adapted to conserve water in drought periods; perennial grasses; and various types of annual species. Dominant shrubs are creosotebush, mariola, tarbush mesquite, saltbush, and yucca (*Yucca* spp.). The study site received moderate continuous grazing all year by domestic livestock.

Four morphological variables were used to estimate aboveground biomass: plant height, longest canopy width, shortest canopy width, and crown volume. Mariola volume was computed as if the plant was the upper half of a spheroid in shape with the formula: canopy volume = $\pi (4/3) a^2 b$, where a is the average of the longest and shortest radii, and b is plant height (Ludwig and others 1975). Plant morphological measurements were recorded in the field on 45 randomly selected plants in December. A single estimate of biomass during December was considered an adequate basis to estimate shrub production because current year shoots and leaves remain attached to the plant and are easily identifiable. We did not consider diameter increases of branches but only their elongation; thus, our data may have a bias towards underestimation.

After recording morphological measurements, shrubs were clipped at ground level with all aboveground parts including branches, stems, and leaves collected. All plants were dried at 60°C to a constant mass and weighed to the nearest 0.01g. Plants chosen for this analysis represent the range of sizes encountered in the region based on experience with field work that occurred in conjunction with this study involving botanical composition of the diet of grazing animals at the same site. All plants collected were judged to be in good condition at the time of harvest and were collected from similar range sites.

Regression analyses were used to examine the relationships between aboveground biomass and four field measurements shrub height, longest canopy width, shortest canopy width, and crown volume from 45 plants.

Results and Discussion

The range in the height, longest canopy width, shortest canopy width, and crown volume of the shrubs was 17 to 77.0 cm (mean 42.82 cm, standard deviation [SD] 16.06 cm); 18 to 132 cm (mean 61.29, SD 29.48 cm); 16 to 124 cm (mean 52.51 cm, SD 25.41 cm); and volume, 0.3845 to 0.9939 cm³, respectively. Time spent clipping and harvesting each plant, averaged 20 to 30 minutes. In contrast, taking all the measurements averaged 4 to 6 minutes/plant.

All independent variables were highly correlated with shrub biomass. In general, the relationship among the variables, height, longest canopy width, and shortest canopy width, showed an exponential relationship. In contrast, crown volume indicated a linear relationship. The linear regression modeling results showed that different plant attributes predict plant biomass with a high coefficient of correlation (table 1).

Analyzing each independent variable individually showed that plant volume had the highest correlation with biomass ($r = 0.97$). Rittenhouse and Sneva (1976) and Bryan and

Table 1. Coefficients of determination for predicting total aboveground biomass of mariola (*Parthenium incanum* (n = 45).

Variables		Coefficients		Statistics			
Dependent	Independent	β_0	β_1	P > F	r ²	S _{xy}	n
Biomass	Height	-412.1	14.23	0.00	.730	0.31	45
Biomass	Longest canopy width	-317.7	8.406	0.00	.859	0.51	45
Biomass	Shortest canopy width	-313.5	9.73	0.00	.855	0.60	45
Biomass	Volume	-13.55	.0012	0.00	.965	0.87	45

Kothmann (1979) found similar results between aboveground biomass and volume. Longest canopy width ($r = 0.86$), shortest canopy width ($r = 0.74$), and height ($r = 0.73$) also were individually significantly related to biomass. Other studies on desert shrubs have demonstrated strong relationship between biomass and morphological measurements. Felker and others (1982) showed that the dry matter weight of *Prosopis* was highly correlated ($r^2 = 0.99$) with stem diameter. Sosa and Perez (1983) and Sosa and Baez (1985) mentioned that height was the best predictor of biomass for *Mimosa biuncifera* and *Menodora scabra*. However, height had the lowest correlation with the biomass in the current study. This may be related to differences among species in individual growth form and in response to site resources. Rittenhouse and Sneva (1977) also noted useful results in estimating big sagebrush biomass with one variable. Longest canopy width was successfully used to estimate biomass of mariola. Therefore, using at least one these variables, biomass can be estimated. However, Cook (1960) suggested using two or more plant measurements to a single measurement.

Although the statistical analysis in this study indicates strong relationships between plant attributes and biomass, caution should be used in estimating mariola biomass for seasons other than the season used in this study. The time of year when biomass prediction equations were developed for mariola can influence the magnitude of the equations parameters. Plant measurements have potential for predicting mariola production in the Chihuahuan and the Sonoran desert, mainly due to mariola definite growing pattern. Using prediction equations to estimate mariola biomass saves time and is not a destructive procedure.

Literature Cited

- Attiwill, P. M. 1962. Estimating branch dry weight and leaf area from measurements of branch girth in Eucalyptus. *Forest Sci.* 8: 132-141.
- Baskerville, G. L. 1965. Estimation of dry weight of tree components and total standing crop in conifer stands. *Ecology* 46: 867-869.
- Brown, J. K. 1976. Estimating shrub biomass from basal stem diameters. *Canad. J. Forest Res.* 6: 153-155.
- Brown, J. K. 1978. Weight and density of crowns of Rocky Mountain conifers. USDA-Forest Service Res. Pap. INT-197. 56 p.
- Burk, J. H.; Dick-Peddie, W. A. 1973. Comparative production of *Larrea divaricata* Cav. on three geomorphic surfaces in southern New Mexico. *Ecology* 54: 1094-1102.
- Buffington, L. C.; Herbel, C. H. 1965. Vegetational changes on a semi desert grassland range from 1858 to 1963. *Ecological Monographs* 35: 139-164.
- Bryant, F. C.; Kothmann, M. M. 1979. Variability in predicting edible browse weights. *J. Range Manage.* 32: 144-146.
- Chew, R. M.; Chew, A. E. 1965. The primary productivity of a desert shrub *Larrea tridentata* community. *Ecol. Monog.* 35: 355-375.
- Correll, D. S.; Johnston, M. C. 1970. Manual of the vascular plants of Texas. Texas Research Foundation. Renner Texas. 1881 p.
- Cook, C. W. 1960. The use of multiple regression and correlation in biological investigations. *Ecol.* 41: 556-560.
- Dinerstein, E.; Olson, D.; Atchley, J.; Loucks, C.; Contreras-Balderas, S.; Abell, R.; Inigo, E.; Enkerlin, E.; Williams, C. E.; Castilleja, G. 2000. Ecoregion-based conservation of the Chihuahuan Desert: a biological assessment. World Wildlife Fund, Commission National para el Conocimiento y Uso de la Biodiversidad (CONBIO), The Nature Conservancy, PRONATURA Noreste, and Instituto Tecnológico y de Estudios Superiores de Monterrey (ITESM), Washington, D.C.
- Felker, P.; Clark, P. R.; Osborn, L. F.; Cannell, G. H. 1982. Biomass estimation in young stand of mesquite (*Prosopis* spp.), ironwood (*Olneya tesota*), palo verde (*Cercidium floridum*), and *Parkinsonia aculeata*, and leucaena (*Leucaena leucocephala*). *J. Range Manage.* 35 (1): 87-89.
- Harniss, R. O.; Murray, R. B. 1976. Reducing bias in dry leaf weight estimates of big sagebrush. *J. Range Manage.* 29: 430-432.
- Henrickson, J.; Straw, R. M. 1976. A gazetteer of the Chihuahuan Desert region: a supplement to the Chihuahuan Desert flora. California State University, Los Angeles.
- Kittredge, J. 1944. The estimation of the amount of foliage of trees and stands. *J. Forest.* 42: 905-912.
- Ludwig, J. A.; Reynolds, J. F.; Whitson, P. D. 1975. Size-biomass relationships of several Chihuahuan desert shrubs. *Amer. Midl. Natur.* 94: 451-461.
- Lyon, L. J. 1968. Estimating twig production of serviceberry from crown volumes. *J. Wildlife Manage.* 32: 115-119.
- Mack, R. N. 1971. Mineral cycling in *Artemisia tridentata*. Ph.D. Diss. Washington State Univ., Pullman.
- Marquez, J.; Villalobos, J. C.; Vela, M. P.; Chavez, A.; Melgoza, G.; Chavez A.; Fierro, S. Y. L. C. 1984. Composicion Botanica y Valor Nutricional de la dieta de Bovinos Pastoreando en un matorral Inerme Parvifolio de Gobernadora (*Larrea tridentata*) en la Region Oriental del Estado de Chihuahua. X Congreso Nacional de Buiatria. AMMM-BPR. A.C. Acapulco Gro. 10-23 p.
- Maynez, M. L.; Garcia, A.; Chavez, A. 1984. Valor nutricional de las especies forrajeras a través del año en un matorral de gobernadora (*Larrea tridentata*) en: Contenido y Fluctuación de Nutrientes de las especies forrajeras consumidas por el Ganado

- en los Agostaderos de Chihuahua (ed. por A. Chacez S.). Bol. Pastizales. RELC-INIP-SARH. Vol. XV-1. 40 p.
- Morafka, D. J. 1977. A biogeographical analysis of the Chihuahuan Desert through its herpetofauna. Dr. W. Junk, The Hague, Netherlands.
- Pechanec, J. F.; Pickford, G. D. 1937. A weight estimate method for determination of range or pasture production. J. Amer. Soc. Agron. 29: 894-904.
- Rittenhouse, L. R.; Sneva, F. A. 1977. A technique for estimating big sagebrush production. J. Range Manage. 30: 68-70.
- Sosa, C. M.; Perez A. G. 1983. Evaluación de la biomasa de la *Mimosa biuncifera* en la región central del estado de Chihuahua. Producción Animal en Zonas Áridas y Semiáridas. Vol 3 No. 1 p 25.
- Sosa, C. M.; Baez, A. D. 1985. Evaluación de la biomasa de la *Menodora sabra* en la región desértica del estado de Chihuahua. Producción Animal en Zonas Áridas y Semiáridas. Vol 4 No. 3 p 27.
- Telfer, E. S. 1969. Weight-diameter relationships for 22 woody plant species. Canad. J. Bot. 47:1851-1855.
- Tufts, W. P. 1919. Pruning of deciduous fruit trees. Calif. Agric. Exp. Sta. Bull. No. 313.
- Uresk, D. W.; Gilbert, R. O; Richard, W. H. 1977. Sampling big sagebrush for phytomass. J. Range Manage. 30: 311-314.
- Villalobos, J. C.; Marquez, J.; Vela, M. P.; Chavez, A. G.; Melgoza, G. Chavez A.; Fierro, S. Y. L. C. 1984. Composicion Botanica y Valor Nutricional de la dieta de Caprinos Pastoreando en un matorral Inerme Parvifolio de Gobernadora (*Larrea tridentata*) en la Region Oriental del Estado de Chihuahua. X Congreso Nacional de Buiatria. AMMM-BPR. A.C. Acapulco Gro.
- Wakimoto, R. H.; Menke, J. W. 1978. Measuring chaparral fuels. Calif. Agric. October 15-16.

The Author

¹ Associate Professor, Department of Range, Wildlife, and Fisheries Management, Texas Tech University, Lubbock, TX. c.villalobos@ttu.edu

Shrub Establishment in the Presence of Cheatgrass: The Effect of Soil Microorganisms

Rosemary L. Pendleton¹

Burton K. Pendleton¹

Steven D. Warren²

Jeffrey R. Johansen³

Larry L. St. Clair⁴

Abstract: Invasive annual grasses, such as cheatgrass (*Bromus tectorum*), create changes in soil microorganism communities and severely limit shrub establishment, a situation that is of considerable importance to land managers. We examined the effects of biological crust-forming algae and arbuscular mycorrhizal fungi on growth and survival of *Ephedra viridis* (EPVI), *Coleogyne ramosissima* (CORA), *Artemisia filifolia* (ARFI), *Chrysothamnus nauseosus* ssp. *hololeucus* (CHNA), and *Artemisia nova* (ARNO), with and without competition from cheatgrass, in a controlled laboratory pot experiment. Shrub survival declined as soil fertility increased. Few shrubs were able to survive in competition with cheatgrass in fertilized growth medium. Under low nutrient conditions, the addition of mycorrhizal inoculum intensified competition with cheatgrass, reducing shrub shoot biomass over that of the control treatment in all species except ARFI. However, shoot growth of cheatgrass in the mycorrhizal treatment was reduced to an even greater extent in all cases except when grown with ARNO. Algal inoculation increased shrub survival and appeared to beneficially affect the growth of ARFI and EPVI at the expense of cheatgrass. Our findings suggest that soil microorganisms can, to some extent, improve shrub establishment in the presence of cheatgrass.

Introduction

Restoring disturbed rangelands infested with invasive annual grasses is a complex and difficult process. Once established, invasive annual grasses, such as cheatgrass (*Bromus tectorum*), create changes in soil moisture regimes, decomposition cycles, nutrient availability, and soil microorganism communities, as well as changes in fire frequency and frequency of native plant recruitment (Whisenant 1990; Belnap and Phillips 2001; Norton and others 2004). Competition from cheatgrass for limiting soil resources severely reduces shrub establishment (Stevens and Monsen 2004). Reversing these changes and reestablishing a functional native plant community is a difficult and often unsuccessful process. The role that soil organisms might play in such restoration efforts has yet to be explored.

Biological soil crusts of arid and semiarid lands contribute to a variety of ecological functions, including soil stabilization, nitrogen (N) fixation, nutrient availability, and vascular plant establishment (Belnap and others 2001). Considerable evidence also indicates that mycorrhizal fungi play an important role in plant uptake of N, including atmospheric N fixed by soil crust organisms, as well as that of more immobile elements such as phosphorus (Ibijbjen and others 1996; Hawkes 2003).

This study examines the effects of mass-produced, crust-forming soil algae and arbuscular mycorrhizal fungi on growth and survival of shrub seedlings grown with and without competition from cheatgrass under controlled greenhouse conditions. The ultimate goal of this research is to provide information on microorganism interactions that will aid revegetation efforts of disturbed arid lands.

Methods

Seeds of five shrub species—*Ephedra viridis* (EPVI), *Coleogyne ramosissima* (CORA), *Artemisia filifolia* (ARFI), *Chrysothamnus nauseosus* ssp. *hololeucus* (CHNA), and *Artemisia nova* (ARNO), representing both cold and mixed desert communities—were obtained from native populations in Utah. Cheatgrass (BRTE) seed was collected from the Whiterocks area in northern Utah.

Algal inoculum of the genus *Schizothrix* was produced in concentrated slurry form, pelletized, dried, and ground to a powder according to the procedures described in Buttars and others (1998). Mycorrhizal inoculum was produced from soil collected from beneath shrubs growing near Toquerville, UT. Shrubs growing at this location included *Coleogyne ramosissima*, *Artemisia filifolia*, *Artemisia tridentata*, and one species of *Ephedra*. We assumed that spores collected from this site, which had many of the same genera as were used in our experiment, would provide a compatible source of mycorrhizal inoculum. Spores were extracted from the soil by wet-sieving and decanting, followed by sucrose centrifugation (Daniels and Skipper 1982; Walker and others 1982). Freshly extracted spores were suspended in water and added to pots using a pipette. Replicate aliquots were decanted onto filter paper and spore counts made. Non-mycorrhizal treatments received an equal volume of killed (autoclaved) spore suspension combined with microbial-containing washings that had passed a 25-micron sieve.

One-liter Durapots (Hummert Int.) were filled with a steam-sterilized bank sand that had a pH of 8.3, conductivity of 0.58 mmhos/cm, and plant-available nutrient concentrations of 4.96, 2.48, and 41.6 ppm nitrate-N, phosphorus,

In: Sosebee, R.E.; Wester, D.B.; Britton, C.M.; McArthur, E.D.; Kitchen, S.G., comp. 2007. Proceedings: Shrubland dynamics—fire and water; 2004 August 10-12; Lubbock, TX. Proceedings RMRS-P-47. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 173 p.

and potassium, respectively. Following steaming, approximately one-third of the sand was amended using Osmocote 17-7-12 NPK (5 oz per cubic foot) formulated for 12 to 14 months continuous fertilization to produce a medium soil fertility level. The low fertility level had no additional fertilizer added.

Plants were grown using one of four inoculation treatments: algal crust inoculum applied to the soil surface at a rate of 100 g/m²; arbuscular mycorrhizal inoculum consisting of 50 to 100 spores added to pots at a depth of 1 to 2 inches; dual inoculation; and a non-inoculated control. Seeds of CORA and EPVI were pre-germinated on moistened filter paper before planting. All other shrub species were seeded into a sterile, sand-filled flat then transplanted to the treatment pots following emergence of the first true leaves. Half of the low fertility treatment pots were subsequently planted with one seed of BRTE. BRTE was not planted in the medium fertility pots because previous trials found that few shrubs could survive competition with BRTE in fertilized soils. Ten pots were used for each fertility/treatment/competition combination for a total of 120 pots per species.

Plants were grown for 5 months in a greenhouse that had been cleaned, sprayed with a biocide, and equipped with new evaporative cooling pads. Additional lighting was provided for 12 hours per day using mercury vapor lamps. Pots were randomized within the greenhouse bench using a computer-generated randomization procedure and watered as needed using a hose with a fine spray head. Shrub planting/transplanting was carried out from late November to mid-December 1996. Harvesting was accomplished throughout May. At harvest, shoots were excised at ground level, dried at 65°C, and weighed. Roots were washed free of sand, dried, and weighed.

Statistical analyses were accomplished using SAS version 6.11 for the personal computer (SAS Institute Inc. 1989). Survival data were analyzed using a logistic regression procedure. Growth effects were analyzed separately for each shrub species using the GLM procedure, with mycorrhizal inoculation, algal inoculation, and either soil fertility or competition with cheatgrass as main effects. These analyses were further subdivided depending on significance of the interaction terms. Treatment effects were also examined using GLM by first coding the four inoculation treatment combinations 1 to 4. Mean separations were determined using Tukey and GT2 procedures.

Results

The initial model used in the logistic regression for shrub survival included soil fertility level, shrub species, mycorrhizal inoculation, and algal inoculation, along with all two-way interactions. Stepwise elimination resulted in a final model containing soil fertility ($P = 0.0001$), shrub species ($P = 0.0001$), and algal inoculation ($P = 0.0014$) as significant effects in predicting shrub survival. There was no significant mycorrhizal effect for shrub survival. Survival of the two

sagebrush species (ARFI and ARNO) was high (> 95 percent at both soil fertility levels). Survival of the other three shrub species was reduced at the medium fertility level (35 percent for CORA, 53 percent for CHNA and EPVI). Algal inoculation increased shrub survival from 95 percent to 99 percent at low fertility and from 62 percent to 72 percent at medium fertility. Algal inoculation has consistently increased plant survival in our other greenhouse experiments (R. Pendleton, data on file, Rocky Mountain Research Station, Albuquerque, NM). Whether this effect is due to the presence of the algae themselves (possible precluding colonization by facultative pathogens) or to the alginic carrier is not known.

Soil fertility level significantly affected root and shoot biomass of all shrubs ($P \leq 0.0138$), except EPVI. Fertilization increased shoot biomass of the faster growing species (ARFI, ARNO, and CHNA) 20- to 40-fold (fig. 1a). CORA also responded to a lesser degree, increasing shoot growth five-fold. Soil fertility significantly altered root/shoot ratios of all shrub species ($P < 0.0001$) indicating proportionately less investment in root biomass at higher soil nutrient levels (fig. 1b). All species invested more actual biomass in roots than shoots at low fertility, but at medium fertility, the reverse was true.

Statistical differences in growth of individual species due to inoculation treatment were few and varied with soil fertility level. However, a comprehensive examination at growth results by fertility level allows some meaningful generalizations to be made. At medium fertility, the faster growing ARFI, ARNO, and CHNA produced the greatest shoot and total growth with no microorganism additions (significantly so for ARNO and CHNA; fig. 2a). Shoot growth of CORA grown at medium fertility was suppressed in the algal inoculation treatment ($P = 0.0299$), whereas EPVI grew best in the presence of the algae ($P = 0.0133$). Under low nutrient conditions, only CORA showed a significant difference with inoculation treatment, producing the greatest shoot growth in the mycorrhizal treatment (fig. 2b). However, in no case did control plants exhibit the greatest growth at low soil fertility, and most shrub species appeared to respond positively to one or more inoculation treatments: ARNO and CORA to mycorrhizal inoculum, CHNA and EPVI to the algal inoculum.

Competition with BRTE significantly affected all aspects of shrub growth ($P \leq 0.0033$), reducing biomass production of both roots (data not shown) and shoots (fig. 3). The effect of inoculation treatment on competitive interactions differed among shrubs. ARFI showed no significant treatment differences in shoot growth whether grown alone or in competition with BRTE (fig. 2b, 4a). It is interesting to note, however, that when ARFI and BRTE were grown together, the control treatment had the least average ARFI biomass and the most BRTE biomass (fig. 4). The mycorrhizal treatment averaged a 30 percent higher shoot biomass of ARFI over that of control plants, whereas shoot biomass of BRTE in the mycorrhizal treatment was 8 percent lower than that of control plants.

CHNA likewise showed no significant treatment differences at low fertility, either with or without competition from BRTE. BRTE, however, showed a significant treatment effect

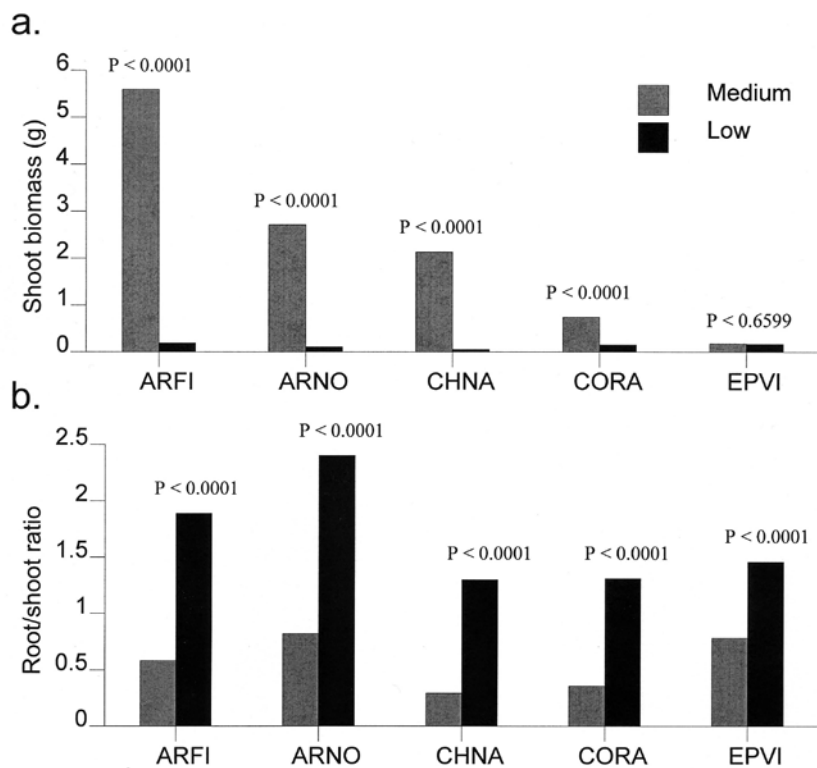


Figure 1. Effect of soil fertility level on (a) shoot biomass and (b) root/shoot ratio of five Intermountain shrub species. Shrub species are indicated by four letter codes. See text for an explanation of codes.

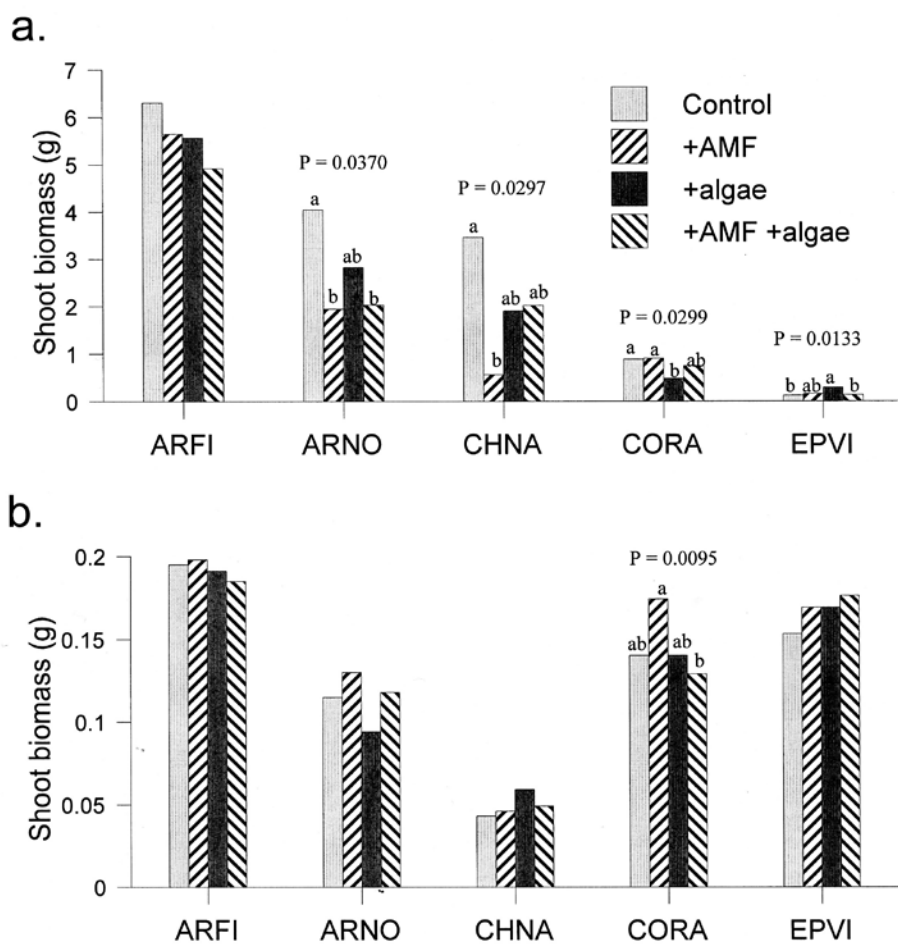


Figure 2. Effect of inoculation treatment on shoot growth of five Intermountain shrub species growing at (a) medium and (b) low soil fertility. Letters denote significant differences at $P < 0.05$ using the Tukey test for multiple comparisons.

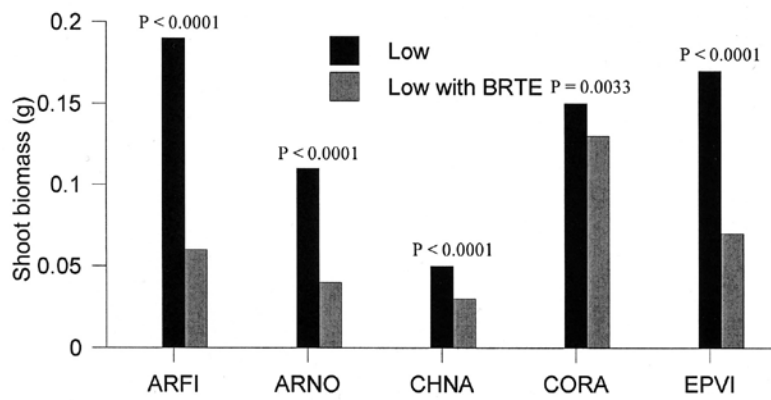


Figure 3. Effect of competition with cheatgrass on shoot biomass of five Intermountain shrub species. P values indicate level of significance when comparing shrubs grown alone versus those grown in competition with cheatgrass.

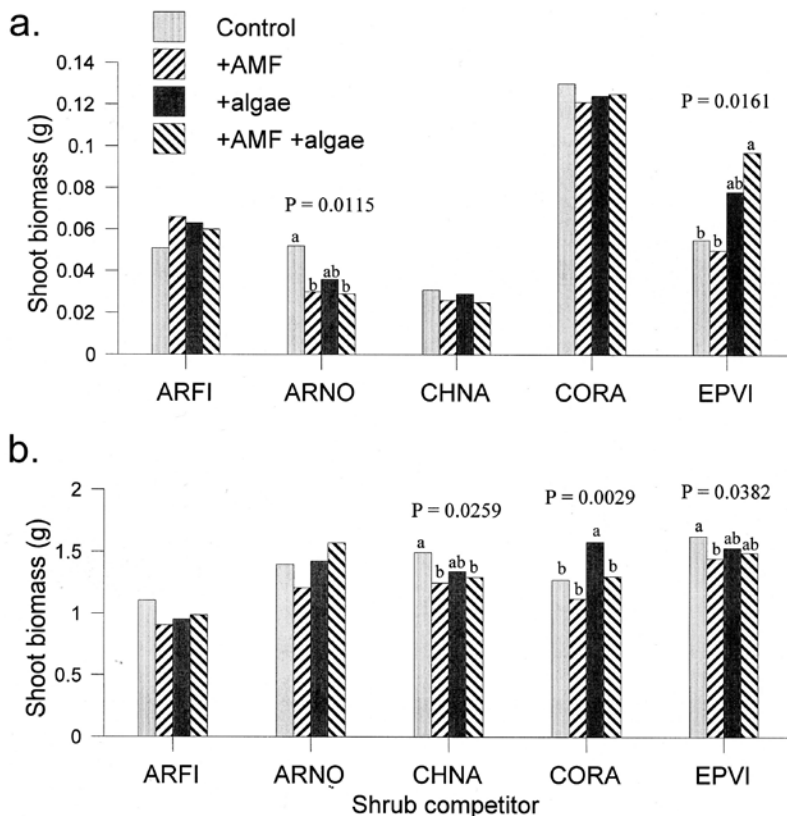


Figure 4. Shoot biomass of (a) shrubs and (b) cheatgrass grown together in a low fertility soil. Letters denote significant differences at $P < 0.05$ using the Tukey test for multiple comparisons.

for mycorrhizal inoculation ($P = 0.0259$). Shoot biomass of BRTE was reduced 17 percent (fig. 4) and root biomass was reduced 22 percent in the presence of mycorrhizae (root data not shown).

When grown alone at low soil fertility, CORA grew best in the presence of mycorrhizae (fig. 2b.). This difference disappeared when grown in competition with BRTE (fig. 4a). Shoot biomass of mycorrhizal CORA plants growing with BRTE averaged 7 percent lower (nonsignificant) than that of controls. Above-ground biomass of BRTE, however, was significantly affected by inoculation treatment. Shoot growth of BRTE was reduced by 12 percent in the presence of mycorrhizae ($P = 0.0112$), but increased 24 percent in the presence of the algal inoculum ($P = 0.0046$).

In the absence of competition, EPVI showed a slight, though not significant, increase in shoot growth in response to algal inoculation (fig. 2b). When grown with BRTE, algal inoculation made a much greater difference in EPVI shoot growth ($P = 0.0161$). The two algal treatments averaged a 58 percent increase in EPVI shoot growth (fig. 4a) and a 75 percent increase in root growth (data not shown) over that of control plants. Mycorrhizae alone did not affect shoot growth of the shrub, but significantly decreased shoot biomass of BRTE ($P = 0.0382$; fig. 4b).

ARNO also showed a small, though not significant, increase in shoot growth in response to mycorrhizal inoculation when growing alone at low soil fertility (fig. 2b). In competition with BRTE, however, control treatment shrubs produced the

greatest shoot growth ($P = 0.0115$; fig. 4a). Growth of BRTE was not significantly affected by treatment (fig. 4b). It therefore appears that, for ARNO, soil microorganisms did not provide a benefit for shrubs growing in competition with BRTE.

Discussion

Associations with arbuscular mycorrhizal fungi have been reported for many aridland plant species, including many shrubs (for example, see Bethlenfalvay and others 1984; Lindsey 1984). Benefits to the plant include enhanced uptake of minerals, improved water relations, and reduced susceptibility to pathogens (Miller and Jastrow 1994; Newsham and others 1995; Mathur and Vyas 2000). The presence or absence of mycorrhizal fungi can also affect plant community composition and diversity (Grime and others 1987; van der Heijden and others 1998; Hartnett and Wilson 1999). The role that mycorrhizal fungi might play in regulating competitive interactions between native vegetation and exotic annual grasses, such as cheatgrass, is not well understood. In monoculture, cheatgrass shows no positive response to mycorrhizal fungi, although colonization levels can be quite high (Allen 1984; Benjamin and Allen 1987; Schwab and Loomis 1987). Goodwin (1992) hypothesized that competition between native and exotic grasses would be little changed by mycorrhizal fungi. Experiments between cheatgrass and shrubs, however, had not previously been done.

Biological soil crusts have been shown to improve growth and establishment of many aridland plant species, including CORA (Harper and Pendleton 1993; Belnap and others 2003; Pendleton and others 2004). Unfortunately, manipulative studies looking at effects of soil crusts on interspecific competition have not been done. Larsen (1995) reported that density of cheatgrass was lower on intact crusts as compared to uncrusted soils, whereas density of native *Stipa* was unaffected. Biological crust-forming organisms interact with a variety of other organisms, including small invertebrates, rhizobia, and mycorrhizal fungi (Harper and Pendleton 1993; Belnap 2003). Furthermore, mycorrhizae may enhance a plant's ability to utilize nitrogen fixed by crust-forming cyanobacteria and lichens (Ibijbjen and others 1996; Hawkes 2003). These studies suggest that soil microorganisms may be important regulators of competition in arid shrubland ecosystems.

In this experiment, the addition of mycorrhizae appeared to intensify competition between shrub seedlings and cheatgrass. At low fertility, shrubs with mycorrhizal additions were equal to or slightly larger than controls. When grown with cheatgrass, however, mycorrhizal treatment shrubs tended to be smaller than control plants for all shrub species except ARFI. However, in four of five cases, shoot growth of cheatgrass growing with shrubs was reduced to a greater extent, suggesting that the presence of mycorrhizae may positively affect the shrub's ability to compete with cheatgrass.

Results for the algal inoculation were mixed. Algal inoculation increased growth of EPVI (and possibly ARFI) grown in competition with cheatgrass. In contrast, the algal inoculum appeared to benefit cheatgrass when grown in competition with ARNO and CORA. Competition for soil nutrients likely occurs between algae and vascular plants during initial crust formation. Results may have been different had the crust been allowed to establish for a period, or if mature crusts had been used.

The finding that soil microorganisms may affect survival, growth, and competitive interactions of native shrubs with exotic annuals, such as cheatgrass, is of considerable importance to current land management practices. Shrubs comprise the dominant form of plant life throughout much of the western United States and are important components of many other vegetation types. Shrubs contribute to vegetation structure, biodiversity, and provide food and shelter to a variety of wildlife. Reestablishing shrub cover is a priority for many management plans; however, seedling establishment in the presence of annual grasses is unlikely to succeed without some kind of weed control (Stevens and Monsen 2004). Our results indicate that soil microorganisms, including crust-forming algae and arbuscular mycorrhizal fungi, may enhance seedling establishment in the presence of cheatgrass. Additional field studies are warranted.

Literature Cited

- Allen, E. B. 1984. The role of mycorrhizae in mined land diversity. In: Munshower, F. F.; Fisher, S. E., Jr., eds. Third biennial symposium on surface coal mine reclamation on the Great Plains. Bozeman, MT: Montana State University: 273-295.
- Belnap, J. 2003. Microbes and microfauna associated with biological soil crusts. In: Baldwin, I. T.; Caldwell, M. M.; Heldmaier, G.; Lange, O. L.; Mooney, H. A.; Schulze, E. -D.; Sommer, U., eds. Biological soil crusts: structure, function, and management, 2nd edition, Ecological Studies 150. Berlin: Springer: 167-174.
- Belnap, J.; Prasse, R.; Harper, K. T. 2003. Influence of biological soil crusts on soil environments and vascular plants. In: Baldwin, I. T.; Caldwell, M. M.; Heldmaier, G.; Lange, O. L.; Mooney, H. A.; Schulze, E. D.; Sommer, U., eds. Biological soil crusts: structure, function, and management, 2nd edition, Ecological Studies 150. Berlin: Springer: 281-300.
- 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 130-2. Denver, CO: National Science and Technology Center, Bureau of Land management. 110 p.
- Belnap, J.; Phillips, S. L. 2001. Soil biota in an ungrazed grassland: response to annual grass (*Bromus tectorum*) invasion. Ecological Applications 11: 1261-1275.
- Benjamin, P. K.; Allen, E. B. 1987. The influence of VA mycorrhizal fungi on competition between plants of different successional stages in sagebrush grassland. In: Sylvia, D. M.; Hung, L. L.; Graham, J. H., eds. Mycorrhizae in the next decade, practical applications and research priorities. Gainesville, FL: University of Florida, Institute of Food and Agricultural Sciences: 144.

- Bethlenfalvay, G. J.; Dakessian, S.; Pacovsky, R. S. 1984. Mycorrhizae in a southern California desert: ecological implications. *Canadian Journal of Botany* 62: 519-524.
- 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.
- Daniels, B. A.; Skipper, H. D. 1982. Methods for the recovery and quantitative estimation of propagules from soil. In: Schenck, N. C., ed. *Methods and principles of mycorrhizal research*. St. Paul, MN: American Phytopathological Society: 29-36.
- Goodwin, J. 1992. The role of mycorrhizal fungi in competitive interactions among native bunchgrasses and alien weeds: a review and synthesis. *Northwest Science* 66: 251-260.
- Grime, J. P.; MacKey, J. M.; Hillier, S. H.; Read, D. J. 1987. Floristic diversity in a model system using experimental microcosms. *Nature* 328: 420-422.
- 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.
- Hartnett, D. C.; Wilson, G. W. T. 1999. Mycorrhizae influence plant community structure and diversity in tallgrass prairie. *Ecology* 80: 1187-1195.
- Hawkes, C. V. 2003. Nitrogen cycling mediated by biological soil crusts and arbuscular mycorrhizal fungi. *Ecology* 84(6): 1553-1562.
- Ibibi, J.; Uriquiaga, S.; Ismaili, M.; Alves, B. J. R.; Boddey, R. M. 1996. Effect of arbuscular mycorrhizas on uptake of nitrogen by *Brachiaria arrecta* and *Sorghum vulgare* from soils labeled for several years with ¹⁵N. *New Phytologist* 134: 353-360.
- Larsen, K. D. 1995. Effects of microbiotic crusts on the germination and establishment of three range grasses. Masters Thesis. Boise, ID: Boise State University.
- Lindsey, D. L. 1984. The role of vesicular-arbuscular mycorrhizae in shrub establishment. In: Williams, Stephen E.; Allen, Michael F., eds. *VA mycorrhizae and reclamation of arid and semi-arid lands*. Scientific Report Number SA1261: proceedings; 1982 August 17-19; Dubois, WY. Laramie, WY: Wyoming Agricultural Experiment Station, University of Wyoming: 53-68.
- Mathur, N.; Vyas, A. 2000. Influence of arbuscular mycorrhizae on biomass production, nutrient uptake and physiological changes in *Ziziphus mauritiana* Lam. under water stress. *Journal of Arid Environments* 45: 191-195.
- Miller, R. M.; Jastrow, J. D. 1994. The application of VA mycorrhizae to ecosystem restoration and reclamation. In: Allen, M. F., ed. *Mycorrhizal functioning: an integrative plant-fungal process*. New York: Chapman and Hall: 438-467.
- Newsham, K. K.; Fitter, A. H.; Watkinson, A. R. 1995. Multi-functionality and biodiversity in arbuscular mycorrhizas. *Trends in Ecology and Evolution* 10: 407-411.
- Norton, J. B.; Monaco, T. A.; Norton, J. M.; Johnson, D. A.; Jones, T. A. 2004. Soil morphology and organic matter dynamics under cheatgrass and sagebrush-steppe plant communities. *Journal of Arid Environments* 57: 445-466.
- Pendleton, R. L.; Pendleton, B. K.; Howard, G. L.; Warren, S. D. 2004. Growth and nutrient content of herbaceous seedlings associated with biological soil crusts. *Arid Land Research and Management* 17: 271-281.
- SAS Institute Inc. 1989. *SAS/STAT User's Guide*, Vol. 2, version 6, fourth ed. Cary, N.C.: SAS Institute Inc. 1686 p.
- Schwab, S. M.; Loomis, P. A. 1987. VAM effects on growth of grasses in monocultures and mixtures. In: Sylvia, D. M.; Hung, L. L.; Graham, J. H., eds. *Proceedings of the 7th North American conference on mycorrhizae*, Gainesville, FL: University of Florida, Institute of Food and Agricultural Sciences: 7.
- Stevens, R.; Monsen, S. B. 2004. Guidelines for restoration and rehabilitation of principal plant communities. In: Monsen, S. B.; Stevens, R.; Shaw, N. L., comps. *Restoring western ranges and wildlands*. Gen. Tech. Rep. RMRS-GTR-136-vol-1. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 199-294.
- van der Heijden, M. G. A.; Klironomos, J. N.; Ursic, M.; Moutoglis, P.; Strietwolf-Engel, R.; Boller T.; Wiekman, A.; Sanders, I. R. 1998. Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. *Nature* 396: 69-72.
- Walker, C.; Mize, C. W.; McNabb, H. S., Jr. 1982. Populations of endogonaceous fungi at two locations in central Iowa. *Canadian Journal of Botany* 60: 2518-2529.
- 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., eds. *Proceedings: 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.

The Authors

- ¹Research Ecologists, USDA Forest Service, Rocky Mountain Research Station, Albuquerque, NM. rpendleton@fs.fed.us
- ²Research Scientist, Center for Environmental Management of Military Lands, Colorado State University, Fort Collins, CO.
- ³Professor, Department of Biology, John Carroll University, University Heights, OH.
- ⁴Professor, Department of Integrative Biology and Curator of Lichens, M.L. Bean Museum, Brigham Young University, Provo, UT.

Differences in Volatile Profiles Between Populations of *Ceratoides lanata* var. *subspinoso* (Rydb.) J.T. Howell

Mary Lucero¹

Rick Estell²

Dean Anderson²

Ed Fredrickson²

Marta Remmenga³

Abstract: *Ceratoides lanata* (Rydb.) J.T. Howell, common winterfat, is valued for its nutrient content and palatability to livestock; however, the subspecies *Ceratoides lanata* var. *subspinoso* (Rydb.) J.T. Howell, ('subspinoso') is considered unpalatable. Curiously, observations of 'subspinoso' revealed several populations in central New Mexico that were heavily grazed. Volatile terpene profiles are associated with differences in palatability in many plant species. To determine whether differences in volatile profiles between 'subspinoso' populations would correlate with apparent differences in palatability, plants from 13 populations of 'subspinoso' were collected. Volatile analysis of shoot samples identified 33 compounds. Limonene, myrcene, and 3-carene were the most abundant volatiles in all populations, comprising 81 percent and 85 percent of the volatiles detected in heavily grazed and ungrazed plants, respectively.

Compounds present in at least half of either the heavily grazed or ungrazed plants were subjected to a stepwise discriminate analysis of relative quantities. The analysis identified a subset of 14 chromatographic peaks (myrcene, 3-hexenol, 3-carene, AR-curcumen, limonene, n-hexanol, p-cymene, a mixture thought to contain alpha-pinene, alpha-thujene, and tricyclene, a mixture thought to contain n-decanal, and five unknowns), which may distinguish between palatable and unpalatable phenotypes. When a discriminate rule based on these chemicals was applied to chemical data from individual plants at all sites, none of the plants were misclassified. The possibility that these varied oil profiles may be used to distinguish palatable from unpalatable phenotypes is discussed.

Introduction

Ceratoides lanata var. *lanata* (winterfat) is a widespread chenopod on western rangelands. The plant is valued for its nutrient content, grazing and drought tolerance, palatability to large herbivores, and ability to rapidly establish on disturbed soils (Stevens and others 1977). The subspecies *C. lanata* var. *subspinoso* ('subspinoso'), native to the southwestern U.S. and northern Mexico, is reputedly unpalatable to livestock (Gibbens 1999; Ueckert 2000). Although no controlled studies directly evaluating the palatability of 'subspinoso' have been found, its reputation for unpalatability has been indirectly supported in a high density stocking study at the Jornada Experimental Range in Southern New Mexico (Anderson 1990). In the study, cattle, sheep, and goats in mixed paddocks were more likely to consume tarbush (*Flourensia cernua* DC than 'subspinoso' (table 1). Tarbush is generally described as unpalatable, and has been used as a model "unpalatable" plant for studies evaluating diet selection by livestock (Estell and others 1994, 1996, 1998).

Curiously, observations of heavily grazed 'subspinoso' north of the Chihuahuan Desert suggest that some phenotypes of 'subspinoso' are palatable. Availability of palatable and unpalatable phenotypes could make *C. lanata* var. *subspinoso* a useful seed source for plant breeders seeking drought tolerant varieties and an interesting model plant for

identification of secondary compounds influencing diet selection. Here we report the identification of 33 volatile compounds extracted from 'subspinoso' using solid-phase microextraction. Relative amounts of these compounds were examined in 106 plants from 13 populations. These compounds were subjected to a stepwise discriminate analysis in order to test the hypotheses that differences in volatile composition could be used to distinguish between heavily grazed and ungrazed populations of 'subspinoso.'

Materials and Methods

'Subspinoso' was collected from 12 sites in New Mexico. The GPS coordinates for these sites, as determined using a Garmin GPS 12 personal navigator, are listed in table 2. Additional samples were provided by Darrell Ueckert from the Texas Agricultural Experiment Station in San Angelo. Each site was characterized as either "heavily grazed" or "ungrazed" (table 2). The populations from Carrizozo, Magdalena, Willard, Dusty, and Winston were all collected from populations that extended into pastures stocked with cattle. Plants inside the stocked pastures had been grazed to less than 20 cm.

Populations from two sites on the NMSU-Corona ranch were in pastures from which livestock grazing had been limited. One site was an official grazing exclosure. However,

In: Sosebee, R.E.; Wester, D.B.; Britton, C.M.; McArthur, E.D.; Kitchen, S.G., comp. 2007. Proceedings: Shrubland dynamics—fire and water; 2004 August 10-12; Lubbock, TX. Proceedings RMRS-P-47. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 173 p.

Table 1. Summary of bite-count data resulting from high density feeding trials with cattle, sheep, and goats (Anderson, 1990). Initial forage composition was determined, then fixed numbers of livestock were placed in paddocks under continuous observation. The number of bites taken from each species of plant was recorded. Data reflecting "subspinoso" (*Ceratoides lanata* var. *subspinoso* [Rydb.] J.T. Howell) and tarbush (*Flourensia cernua* DC [comp.]) selection are shown here.

Paddock	1		2		
	Plant species	% composition	% of bites	% composition	% of bites
	'subspinoso'	4.5	1.6	1.1	0.2
	tarbush	30.8	42.4	37.3	50

Table 2. Site locations, usage classification (heavily grazed or ungrazed, with "ungrazed" defined as populations that exhibited no clear evidence of grazing by livestock) of *Ceratoides lanata* var. *subspinoso* (Rydb.) J.T. Howell, ('subspinoso').

Site	Latitude	Longitude	Elevation (m)	Sampling date	Number of plants	Usage classification
Corona Range and Livestock Research Center	34°16.710'	105°23.612'	1,905	8/3/2000	10	grazed
Corona Range and Livestock Research Center	34°16.481'	105°19.862'	1,864	8/3/2000	10	grazed
Magdalena	33°51.515'	107°19.511'	1,912	8/10/2000	10	grazed
Willard	34°22.992'	105°42.985'	1,972	8/3/2000	10	grazed
Dusty	33°57.297'	107°39.869'	2,273	9/29/2000	10	grazed
Winston	33°21.107'	107°33.382'	1,838	9/29/2000	10	grazed
Chihuahuan Desert Rangeland Research Reserve	32°35.236'	106° 55.703'	1,341	7/27/2000	8	ungrazed
Chihuahuan Desert Rangeland Research Reserve	32°33.823'	106° 54.269'	1,341	7/27/2000	2	ungrazed
Jornada Experimental Range	32°43.295'	106°46.187'	1,352	7/25/2000	8	ungrazed
Jornada Experimental Range	32°31.142'	106°44.630'	1,325	7/7/2000	1	ungrazed
Jornada Experimental Range				7/30/2000		
Jornada Experimental Range	32°31.933'	106°41.773'	1,344	8/9/2000	7	ungrazed

plants on opposite sides of the fences to both pastures were accessible to sheep, and had been heavily grazed. Researchers working at the ranch stated that the winterfat populations were typically utilized by sheep, especially in the winter and early spring, when other forage was limited.

The samples from San Angelo were classified as unpalatable to cattle, sheep, and goats (Ueckert 2000). 'Subspinoso' populations from the Jornada Experimental Range, historically identified as common winterfat, have all been classified as unpalatable. One of these sites was previously utilized for the high density feeding study illustrated in table 1.

Two more populations were collected from the Chihuahuan Desert Rangeland Research Reserve near Las Cruces, NM. These populations were unusual in that they were small, both in number of plants (less than twenty plants each) and in size (less than 30 cm/plant). Observations of plants in the field revealed some evidence of light grazing. Approximately 5 percent of the shoots had been removed. The sharp edges remaining on removed shoots suggested grazing was by rabbits rather than livestock. We classified both these populations as "ungrazed."

All samples were collected in the fall of 2000 after flowering. Samples consisted of 10 ten cm leaders from each plant (table 2). When possible, 10 plants were sampled at each site. The year 2000 had little summer rainfall, and at some sites fewer than 10 plants had flowered. Samples were placed under dry ice upon harvesting. After transport, samples were

stored at -20°C prior to volatile extraction. Taxonomic classification was verified at the Range Science Herbarium at New Mexico State University and voucher specimens were deposited there.

Preparation for Solid Phase Microextraction (SPME) analysis consisted of grinding all leaders from a single plant to a coarse powder under liquid nitrogen. SPME was performed by placing 0.2 g (fresh weight) of ground plant tissue into 4 mL glass screw-cap vials. Vials were sealed with pre-baked aluminum foil and ethanol-washed Viton septa, then equilibrated for 3.5 h at 50°C. SPME fibers (100 uM PDMS, Supelco, Bellefonte, PA) were exposed to vial headspace at a depth of 1 cm for 20 min using a manual fiber holder (also from Supelco). The fiber was injected into a Varian model 3400 GC with a DB-5 column (30 m x 0.25 mm fused silica capillary column, film thickness 0.25 µm) coupled to a Finnigan ion trap mass spectrometer (EI, 70 eV) and desorbed for 3 min. Blank injections followed each sample to verify the absence of residual compounds on the SPME fiber.

GC/MS analysis was performed using Helium at approximately 1 mL/min as a carrier gas. Injector and transfer line temperatures were set at 220°C and 260°C, respectively. The initial column temperature was 60°C and a linear temperature increase of 3°C/min was programmed into each run. Duplicate extractions of each sample were examined. Compounds were identified by comparing mass spectra and retention indices

with literature data (Adams 1995, 2001) or with authentic standards.

Relative amounts of each compound detected were defined based on relative peak heights. [Total Ion Chromatogram (TIC) peak height]/[TIC peak height of 4 ng 3-carene] X 100. Compounds with relative heights greater than 0.01 detected in at least half of either the heavily grazed or ungrazed plants were subjected to a stepwise discriminate analysis of relative heights against palatability. The resulting discriminate rule was then applied individually to each plant sampled.

Results

A total of 62 unique volatiles were detected in SPME samples from winterfat. Those that comprised greater than 0.01 percent of the chromatographic peak area in at least 50 percent of the plants from either the grazed or the ungrazed

populations are presented in table 3. Amounts shown represent either the relative peak height (RH), which was calculated as the peak height relative to the height of 4 ng of the monoterpene standard 3-carene, or the percent height, which represents the percent of the chromatogram comprised of that particular peak. Derived, rather than actual values were necessary because analytical grade standards were not available for all of the compounds found in winterfat.

Of the 33 volatiles listed in table 3, fourteen were positively identified by matching spectra and retention indices to library values. Several compounds consistently gave non-gaussian peaks and spectra that varied at points across the peaks. These are identified in the table with question marks indicating that the peaks detected were probably co eluting with unknown compounds.

Limonene was the dominant peak in all samples, comprising nearly 50 percent of the SPME-extractable fraction. Curiously, seven plants from the site at Carrizozo also

Table 3. Compounds found in at least 50 percent of either the heavily grazed or ungrazed 'subspinoso' populations. Values represent the mean peak height relative to the height of 4 ng 3-carene (Mean RH), the standard deviation of the Mean RH, the mean peak height expressed as a percent of the total chromatogram (Mean pH), and the standard deviation of the Mean pH. Compounds whose spectra did not match anything in available reference libraries were designated as CELA (*Ceratoides lanata*), followed by the retention time at which they eluted from the DB-5 column. Retention index values indicated with an asterisk (*) were determined by extrapolation, since they eluted prior to the retention time of the earliest hydrocarbon standard. Compounds with identification followed by "_mix?" were not spectrally pure and probably contained two or more chemicals.

Retention time	Compound ID	Heavily grazed shrubs				Ungrazed shrubs			
		Mean RH	Std RH	Mean PH	Std PH	Mean RH	Std RH	Mean RH	Std PH
597*	CELA1.482	0.01	0.01	0.39	0.35	0.01	0.01	0.32	0.22
639*	CELA1.62	0.10	0.13	1.85	1.32	0.08	0.11	1.42	1.57
669*	CELA1.756	0.00	0.01	0.28	0.22	0.01	0.01	0.26	0.22
693*	CELA1.884	0.05	0.03	1.05	0.63	0.05	0.04	1.30	1.14
716	CELA1.977	0.01	0.01	0.28	0.17	0.01	0.01	0.28	0.22
782	CELA2.508_mix?	0.00	0.01	0.19	0.08	0.00	0.00	0.16	0.11
806	CELA2.806	0.02	0.02	0.44	0.33	0.02	0.03	0.42	0.32
861	(Z)-3-hexenol	0.09	0.10	1.66	1.14	0.03	0.06	0.83	1.29
872	n-hexanol	0.02	0.03	0.48	0.36	0.01	0.02	0.22	0.15
931	pinene-thujene mix?	0.03	0.04	0.99	0.60	0.02	0.04	0.74	0.48
940	CELA5.25	0.03	0.03	1.06	0.41	0.03	0.03	0.91	0.33
977	sabinene_mix?	0.06	0.05	1.10	0.54	0.06	0.04	0.96	0.23
981	6-methyl-5-hepten-2-one	0.02	0.02	0.46	0.41	0.01	0.01	0.24	0.07
988	CELA6.6	0.01	0.01	0.22	0.09	0.01	0.03	0.26	0.18
992	myrcene	0.87	0.66	16.12	2.37	0.89	0.54	16.13	1.47
1012	CELA7.38	0.01	0.01	0.20	0.11	0.01	0.01	0.20	0.09
1013	3-carene	0.89	0.69	16.56	2.15	1.05	0.56	19.33	2.03
1027	p-cymene	0.03	0.02	0.55	0.47	0.02	0.02	0.31	0.08
1032	limonene	2.47	1.65	48.78	5.29	2.59	1.26	49.60	5.24
1043	1,8-cineole	0.01	0.01	0.31	0.34	0.00	0.00	0.16	0.08
1074	CELA9.38	0.03	0.02	0.67	0.49	0.01	0.01	0.19	0.09
1085	artemisia alcohol	0.01	0.02	0.26	0.15	0.02	0.02	0.45	0.33
1106	n-nonanal_mix?	0.01	0.03	0.70	1.17	0.02	0.04	1.40	1.35
1107	CELA10.71	0.05	0.04	1.29	1.05	0.08	0.07	1.68	1.13
1170	CELA13.2	0.01	0.01	0.34	0.63	0.00	0.00	0.15	0.09
1206	n-decanal_mix?	0.01	0.01	0.22	0.13	0.01	0.01	0.18	0.09
1220	CELA15.47	0.01	0.01	0.19	0.09	0.00	0.01	0.12	0.03
1419	beta-caryophyllene	0.02	0.04	0.78	1.38	0.02	0.03	0.66	0.57
1438	CELA24.6	0.00	0.01	0.18	0.08	0.02	0.03	0.78	0.66
1458	alpha-humulene	0.01	0.01	0.23	0.13	0.01	0.02	0.33	0.17
1485	germacreneD	0.01	0.02	0.38	0.33	0.02	0.03	0.39	0.32
1486	AR-curcumen	0.01	0.02	0.34	0.26	0.03	0.03	0.55	0.50
1512	(E)-beta-ionone	0.01	0.02	0.38	0.37	0.01	0.01	0.31	0.22

contained relatively large peaks of a compound thought to be sylvestrene. The retention times of limonene and sylvestrene vary only by 2s, and the only significant difference in their mass spectra is that limonene has a strong 93 peak with a base peak of 67, whereas sylvestrene has a strong 67 peak with a base peak of 93. Because of the difficulties in separating limonene, a major component, from this putative sylvestrene peak (PSP), the decision was made to report calculated peak heights rather than areas. This would reduce the potential for inaccurate calculation of limonene quantities when PSP was present. Unfortunately, the point for the maximum height of PSP always fell underneath the shoulder of the limonene peak, therefore, relative amounts of PSP are not reported.

Two other major peaks, myrcene and 3-carene, were present in every sample analyzed. The combination of myrcene, 3-carene, and limonene peaks resulted in a distinct chromatographic fingerprint, also seen in common winterfat (not shown), which may be unique to *Ceratoides*.

Stepwise multivariate analysis of the compounds identified in table 3 identified a subset of 14 chromatographic peaks that best distinguished between grazed and ungrazed populations. The subset included myrcene, 3-hexenol, 3-carene, AR-curcumen, limonene, n-hexanol, p-cymene, a mixture thought to contain alpha-pinene, alpha-thujene, and tricyclene, a mixture thought to contain n-decanal, as well as five unknowns (table 3). When a discriminate rule based on these chemicals was applied to chemical data from individual plants at all sites, none of the plants were misclassified.

Discussion

The three major compounds present in all volatile profiles observed were limonene, myrcene, and 3-carene. These three compounds are ubiquitous monoterpenes found in many of the plants we have previously analyzed and often serve as precursors to biosynthesis of other terpenoids. Although the large percentages of limonene, an industrially important compound, seem attractive, the overall yield of oil in 'subspinosus' was low. Attempts to harvest and quantify oil by steam distillation resulted in less than 5 uL oil per gram dry weight of leaf tissue, approximately half of which was limonene. Therefore, even though limonene is abundant relative to other volatiles, it is not likely that purification for industrial use would be cost effective due to the low yield per gram of plant tissue.

Fifteen of the 33 peaks listed in table 3 could not be identified, even though 14 of these were spectrally pure. This abundance of previously undescribed compounds is not surprising in natural products analysis due to the remarkable diversity of plant volatiles.

The identification of 14 compounds that distinguished grazed from ungrazed populations in this preliminary study may be seen as a starting point for additional research. Although some of the observed differences are undoubtedly due to differences in environment and grazing intensity at the various sites, it is encouraging to note that some of the compounds identified, namely limonene, myrcene, p-cymene,

and alpha-pinene have also been associated with differences in livestock herbivory in tarbush [*Flourensia cernua* DC] (Estell and others 1996). Curiously, subsequent studies in which individual terpenes associated with low herbivory in tarbush were applied to alfalfa pellets in sheep feeding trials demonstrated only minimal reductions in herbivory (Estell and others 2002). It is possible that the mixture, rather than the individual compounds, is necessary for antiherbivory effects. If this is the case, a benefit of multivariate techniques is the ability to narrow down the possible combinations of compounds, permitting identification of groups of compounds, rather than individuals, which may act in conjunction to create an effect. Tests in which the compounds, combined in proportions defined in discriminate rules following multivariate analysis, need to be carried out.

Perhaps the most significant findings in this preliminary data include the abundance of *Ceratoides lanata* var. *subspinosus* (Rydb.) J.T. Howell in New Mexico, where it had not been previously described, and the observation that in some populations, 'subspinosus' showed evidence of heavy grazing. *C. lanata* has long been considered a desirable species on grazed lands and considerable effort has been devoted to development of germplasm suitable for revegetation in various environments. The availability of large and phenotypically diverse populations of 'subspinosus' may be useful in the development of germplasm for use in arid environments.

References

- Adams, R. P. 1995. Identification of essential oil components by gas chromatography/mass spectroscopy. Carol Stream, Illinois, Allured Publishing Corporation.
- Adams, R. P. 2001. Identification of essential oil components by gas chromatography/quadrupole mass spectroscopy. Carol Stream, Illinois, Allured Publishing Corporation.
- Anderson, D. A. 1990. Unpublished Data. Research Animal Scientist, USDA-ARS Jornada Experimental Range, Las Cruces, NM.
- Estell, R.; Fredrickson, E.; Anderson, D. M.; Havstad, K.; Remmenga, M. D. 2002. Effects of four mono- and sesquiterpenes on the consumption of alfalfa pellets by sheep. *Journal of Animal Science*. 80(12): 3301-3306.
- Estell, R. E.; Fredrickson, E. L.; Anderson, D. M.; Havstad, K. M.; Remmenga, M. D. 1996. Tarbush leaf surface terpene profile in relation to mammalian herbivory. In: Barrow, J. R., McArthur, E. D.; Sosebee, R. E.; Tausch, R. J., compilers. *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. 237-241.
- Estell, R. E.; Fredrickson, E.; Anderson, D. M.; Havstad, K.; Remmenga, M. D. 1998. Relationship of tarbush leaf surface terpene profile with livestock herbivory. *Journal of Chemical Ecology*. 24(1): 1-11.
- Estell, R. E.; Fredrickson, E.; Anderson, D. M.; Mueller, W. F.; Remmenga, M. D. 1994. Relationship of tarbush leaf surface secondary chemistry to livestock herbivory. *Journal of Range Management*. 47(6): 424-428.
- Gibbens, R. 1999. Personal communication. Range Scientist, USDA-ARS Jornada Experimental Range, Las Cruces, NM.

- Stevens, R.; Giunta, B. C.; Jorgensen, K. R.; Plummer, A. P. 1977. Winterfat (*Ceratoides lanata*). Publication 77-2. Salt Lake City, UT: Utah Division of Wildlife Resources. 41 p.
- Ueckert, D. 2000. Personal communication. Regent Fellow and Professor, Range Improvement Rangeland Ecology and Management, Texas A & M University San Angelo Research and Extension Center, San Angelo, TX.

The Authors

¹Postdoctoral associate, USDA-ARS-Jornada Experimental Range, Las Cruces, NM. malucero@nmsu.edu

²Research scientists, USDA-ARS-Jornada Experimental Range, Las Cruces, NM.

³Associate professor, Department of Economics and International Business, New Mexico State University, Las Cruces, NM.

Emergence and Growth of Four Winterfat Accessions in the Presence of the Exotic Annual Cheatgrass

Ann L. Hild¹

Jennifer M. Muscha²

Nancy L. Shaw³

Abstract: Winterfat (*Krascheninnikovia lanata* [Pursh] A. D. J. Meeuse & Smit; synonym: *Ceratoides lanata* [Pursh] J. T. Howell) is a desired shrub species and an integral component of salt desert shrublands in the Intermountain West. On the Snake River Birds of Prey National Conservation Area in southwestern Idaho, extensive loss of winterfat-dominated communities has been linked to altered fire regimes associated with cheatgrass (*Bromus tectorum* L.) invasions. Post-fire revegetation efforts are often hampered by the quick emergence of cheatgrass seedlings with autumn or spring moisture. We compare the establishment of four winterfat populations (Birds of Prey; northeastern New Mexico; Northern Cold Desert Select Germplasm; and Open Range Tested Germplasm) with and without cheatgrass competition. Seed of each accession was planted in 15 cm diameter pots containing four densities of cheatgrass (0, 2, 4, and 8 plants per pot) in a greenhouse. Plant measurements were made 4, 5, 7, 9, 11, 13, 15, 17, 19, and 21 weeks after planting. Measurements included winterfat survival, height and two canopy diameters, and cheatgrass height and number of leaves and culms per plant. Initial establishment was greatest for the New Mexico winterfat source at all cheatgrass levels. Growth of this source exceeded the others in the absence of cheatgrass. However, the presence of cheatgrass depressed growth of all sources by at least 90 percent. Establishment of winterfat on cheatgrass infested rangelands necessitates seeding on sites where cheatgrass densities are low or reduced by site preparation procedures.

Introduction

Widely distributed across the interior western United States, winterfat (*Krascheninnikovia lanata* [Pursh] A. D. J. Meeuse & Smit; synonym: *Ceratoides lanata* [Pursh] J. T. Howell) (U.S. Department of Agriculture, Natural Resources Conservation Service 2004) is an important subshrub on millions of acres of salt desert shrublands, often occurring as a landscape-dominating species. Although it is most common in valley bottoms and foothills, it is found on sites ranging from the Lower Sonoran and Mojave Deserts to mountain ridges above 3,050 m in Utah to mixed-grass prairies of the Midwest (Carey 1995; Stevens and others 1977). A highly variable species morphologically, dwarf forms of winterfat are common on desert floors, salty soils, and high mountain ridges, while larger, more woody forms, grow on alluvial fans, foothills, and mesas in the southern portion of the species' range (McArthur and Monsen 2004).

On the Snake River Birds of Prey National Conservation Area (listed hereafter as 'Birds of Prey') located southwest of Boise, Idaho, extensive loss of winterfat-dominated communities has been linked to shortened fire intervals associated with the advance of the annual exotic invasive, cheatgrass (*Bromus tectorum* L.). Winterfat communities at Birds of Prey are especially important for supporting high Townsend ground squirrel (*Spermophilus townsendii* Bachman) densities that provide a prey base for nesting raptor species (Nydegger and Smith 1986; Van Horne and others 1998).

Efforts to reestablish winterfat in the Birds of Prey following wildfires are often hampered by the lack of local seed supplies and the reportedly poor establishment of the indigenous seed source, particularly with competition from cheatgrass. Winterfat seeding efforts may be hampered by the rapid germination and root growth of cheatgrass seedlings with spring or autumn precipitation that allows them to compete successfully for available resources (Harris 1967, 1977; Harris and Goebel 1976). Concerns for reestablishing and maintaining the local winterfat population on the Birds of Prey make it essential that we understand the impact of cheatgrass competition on its germination and establishment. The purpose of this study was to compare germination and seedling growth of four native winterfat seed collections with cheatgrass competition.

Methods

The winterfat seed sources were: (1) Birds of Prey; (2) northeastern New Mexico; (3) Northern Cold Desert Selected Germplasm; and (4) Open Range Tested Germplasm. All seed was harvested in fall 2003.

The Birds of Prey seed was a composite of three local wildland collections made at the Birds of Prey National Conservation Area on the Lower Snake River Plain south of Boise, Idaho. The area ranges from 850 to 1,000 m in elevation and is characterized by dry, hot summers and mild

In: Sosebee, R.E.; Wester, D.B.; Britton, C.M.; McArthur, E.D.; Kitchen, S.G., comp. 2007. Proceedings: Shrubland dynamics—fire and water; 2004 August 10-12; Lubbock, TX. Proceedings RMRS-P-47. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 173 p.

winters. Annual precipitation in Boise averages 306 mm (U.S. Department of the Interior, U.S. Geological Survey, Biological Resource Division 1996). The dwarf, spreading growth form of this seed source averages about 0.2 m in height (Nydegger and Smith 1986) and is typical of populations found in association with other salt desert species such as shadscale (*Atriplex confertifolia* [Torr. & Frem.] S. Wats.), squirreltail (*Elymus elymoides* [Raf.] Swezey), and cheatgrass.

New Mexico seed was collected from native stands near Mora in northeastern New Mexico's Colfax County. The growth form is large, upright, and woody. Plants commonly grow on rocky foothills and valleys in association with ponderosa pine (*Pinus ponderosa* P. & C. Lawson) and pinyon-juniper (*Pinus* L.-*Juniperus* L.) communities at elevations from 1,500 to 2,000 m (Stevens and others 1977). This morphological variant has sometimes been given the subspecific or variety epithet *subspinosa* (see Booth 2005 for discussion). Annual precipitation in Colfax County ranges from 380 mm at lower elevations and increases to 400 mm in higher foothills (U.S. Department of Agriculture, Soil Conservation Service and Forest Service 1982). Northern Cold Desert Winterfat Selected Germplasm (NCD) was released by the U.S. Department of Agriculture, Natural Resources Conservation Service, Aberdeen Plant Materials Center in 2001 (St. John and Blaker 2004). A composite of four eastern and southern Utah and one western Colorado population, it was selected for cold, drought, and alkalinity tolerance. Plants have an upright growth habit, growing to 0.9 m in height. The germplasm is recommended for Intermountain sites receiving 180 to 400 mm of annual precipitation (U.S. Department of Agriculture, Natural Resources Conservation Service 2002). The seed used in this study was produced in a seed orchard.

The Open Range Tested Germplasm Winterfat is a composite of three accessions from eastern and south-central Montana and south-central Wyoming, selected for their seedling vigor and forage and seed production. Plants are spreading and 0.3 to 0.75 m tall. Recommended area of use includes the northern Great Plains, northern Intermountain area, and the Snake River Plain (Majerus and Holzworth 2003). Open Range seed was harvested from a nursery planting.

Cheatgrass seed and soil for greenhouse competition studies were collected from the Birds of Prey National Conservation Area in summer 2003. Soil texture was a silty clay loam, organic matter averaged 1.5 percent, and pH was 7.8. Potting soil was prepared by first sieving the field soil to remove large rocks and pieces of organic material. A soil mix of two parts of field soil to one part vermiculite by volume was prepared to insure water infiltration into the pots. All seed was allowed to afterripen for 12 weeks prior to study initiation to enhance germination (Springfield 1972) and then cleaned to remove debris and small utricles. For each source of winterfat, 12 pots, each 15 cm in diameter, were prepared for each block. Four winterfat seeds were centered in each pot. On the same date, cheatgrass seeds were placed around the perimeter of three pots for each source to obtain one of four densities: 0, 2, 4, or 8 seedlings per pot. Three pots containing no winterfat were also planted at each grass density to document cheatgrass

growth without winterfat present. Seeds were covered with a 0.5 cm layer of washed masonry sand to insure good seed-to-soil contact and to prevent seed movement during watering.

Because we hand selected large seed for both cheatgrass and winterfat (Springfield 1973) to optimize germination success, we had little problem in obtaining the desired densities. Excess seedlings of either species were thinned as necessary to obtain target densities by clipping seedlings at the plant base. However, at the time of seeding, we did start germination of both winterfat and cheatgrass seeds in additional identical pots to serve as replacement plants in case seeds in treatment pots did not germinate. In two cases, we transplanted winterfat seedlings into the study pots within the first 2 weeks of the study because winterfat seeds did not germinate in the center of treated pots. We did no additional transplanting or thinning after the second week.

Pots within each block were randomized on greenhouse benches and re-randomized weekly. Soils were thoroughly wetted at the time of planting. Pots were rewatered every 2 days for the first 2 weeks after seeding. For the remainder of the treatment period, pots were allowed to dry until cheatgrass plants in the four plants/pot treatments showed evidence of temporary wilt, when all treatments were again watered with equal amounts (200 ml) of water using a graduated cylinder. Temperatures in the greenhouse ranged from 20°C at night to 37°C during the day; day length averaged 12 hours.

Plantings were replicated on five dates (blocks) in 2003. We documented winterfat and cheatgrass seedling growth for 21 weeks following seeding (at 4, 5, 7, 9, 11, 13, 15, 17, 19, and 21 weeks). On each evaluation date, winterfat seedling survival, height, and two perpendicular canopy diameter measurements were recorded for determination of plant size (canopy volume). Cheatgrass seedling height and number of leaves and culms per plant were recorded on the two consecutive days prior to the winterfat measurements. At 21 weeks, we harvested plants, washed roots, and separated plants into above-ground and below-ground biomass for measurements of leaf and root area with a leaf area meter. Samples were oven-dried at 60°C for 48 hours and weighed.

Data were analyzed using ANOVA appropriate to a factorial arrangement in a randomized complete block design using sampling dates as repeated measures. Because winterfat seedling size was much smaller in the presence of cheatgrass plants than when grown without cheatgrass competition, we also compared the four winterfat seed sources to each other when grown only with three densities of cheatgrass (excluding the 0 cheatgrass treatment). Least significant difference (LSD) mean separations were evaluated at the 0.05 alpha level in SAS (SAS 2002).

Results and Discussion

Two-thirds of winterfat mortality occurred in the first 5 weeks after planting. After 21 weeks, survival of winterfat varied significantly among sources and was greatest for the northern New Mexico collection (98.3 percent) followed

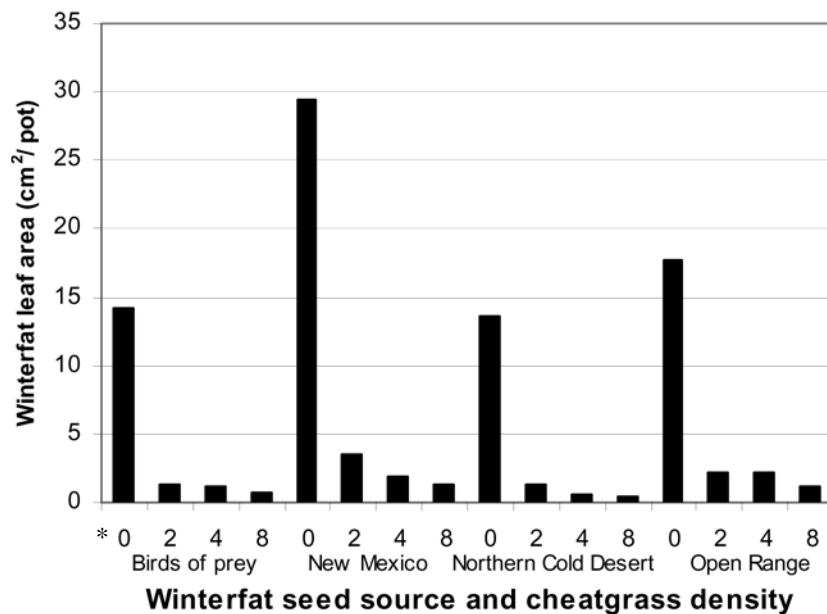


Figure 1. Winterfat seedling leaf area by seed source and cheatgrass density per pot (2, 4, or 8 seedlings) after 21 weeks of growth in a greenhouse.

*Number of cheatgrass seedlings per pot.

by the Open Range (79.7 percent) and Birds of Prey (78.7 percent) sources, with survival of the Northern Cold Desert seed source lowest (56.7 percent) when averaged across all four cheatgrass competition levels.

Winterfat leaf area was greatly reduced by the presence of cheatgrass at any density (fig. 1) and total biomass followed the same trend (data not shown). Leaf area of winterfat from New Mexico (2.23 cm²/plant) and Open Range (1.87 cm²/plant) sources were significantly greater than the Birds of Prey (1.09 cm²/plant) and Northern Cold Desert (0.71 cm²/plant) sources when grown without cheatgrass. Similar trends were noted for total winterfat biomass (data not shown). During weeks 11 through 21, New Mexico plants produced greater canopy volume (fig. 2 a-d) than other sources only in the absence of cheatgrass competition. The same differences were significant for winterfat leaf area (data not shown).

Growth of cheatgrass (biomass and leaf area) was not different among the 2, 4, and 8 plants/pot cheatgrass densities, but did differ among the winterfat seed sources (figs. 3 and 4) grown with cheatgrass. Cheatgrass biomass was reduced by 46 percent when grown with the Northern Cold Desert seed source and leaf area was reduced by 35 percent when grown with the Northern Cold Desert or Birds of Prey seed sources relative to the New Mexico source.

Our results indicate that initial emergence and survival of the larger-statured New Mexico source with or without cheatgrass competition, and 21-week growth (leaf area and biomass) of this source in the absence of cheatgrass competition, were greater than for any of the remaining sources. Booth (2005) commented that several authors (Booth 1992; Moyer and Lang 1976; Springfield 1968) have found differences in seed quality and seedling vigor among other accessions and suggested that these may result as adaptive responses to stressful environments. However, in the presence of

cheatgrass at any competition level, growth of all four sources was reduced by at least 90 percent. Consequently, winterfat at the seedling stage appears vulnerable to cheatgrass competition, even when the annual occurs at the lowest densities tested. However, it should be noted that as cheatgrass production did not vary among the cheatgrass densities, all of our treatments appear to have provided similar levels of competition (in terms of cheatgrass biomass present within a 7.5 cm radius of the winterfat seedling). Repeating the experiment using the same cheatgrass densities, but larger pots, might reveal whether there is a differential in competitive ability of the four winterfat sources at lower competition levels.

Both the Northern Cold Desert and Birds of Prey sources reduced cheatgrass production, while the more rapidly growing New Mexico source had no effect on cheatgrass growth. Although cheatgrass is generally considered to be a strong competitor with seedlings of other species, Francis and Pyke (1996) found that seedlings of 'Hycres' crested wheatgrass (*Agropyron desertorum* x *cristatum*), but not those of 'Nordan' crested wheatgrass (*Agropyron desertorum*), significantly reduced growth of cheatgrass seedlings. Identification of the mechanism responsible for differential suppression of cheatgrass growth by the winterfat seed sources included in this study would aid in understanding the dynamics of competitive interactions between cheatgrass and winterfat.

Although this research was conducted under greenhouse conditions, the results clearly indicate that sites where cheatgrass densities are high following wildfires are likely to be problematic for winterfat establishment regardless of the seed source planted.

Reduction of cheatgrass densities to low levels or seeding only in areas where competition is expected to be minimal is essential to permit emergence and growth of winterfat seedlings.

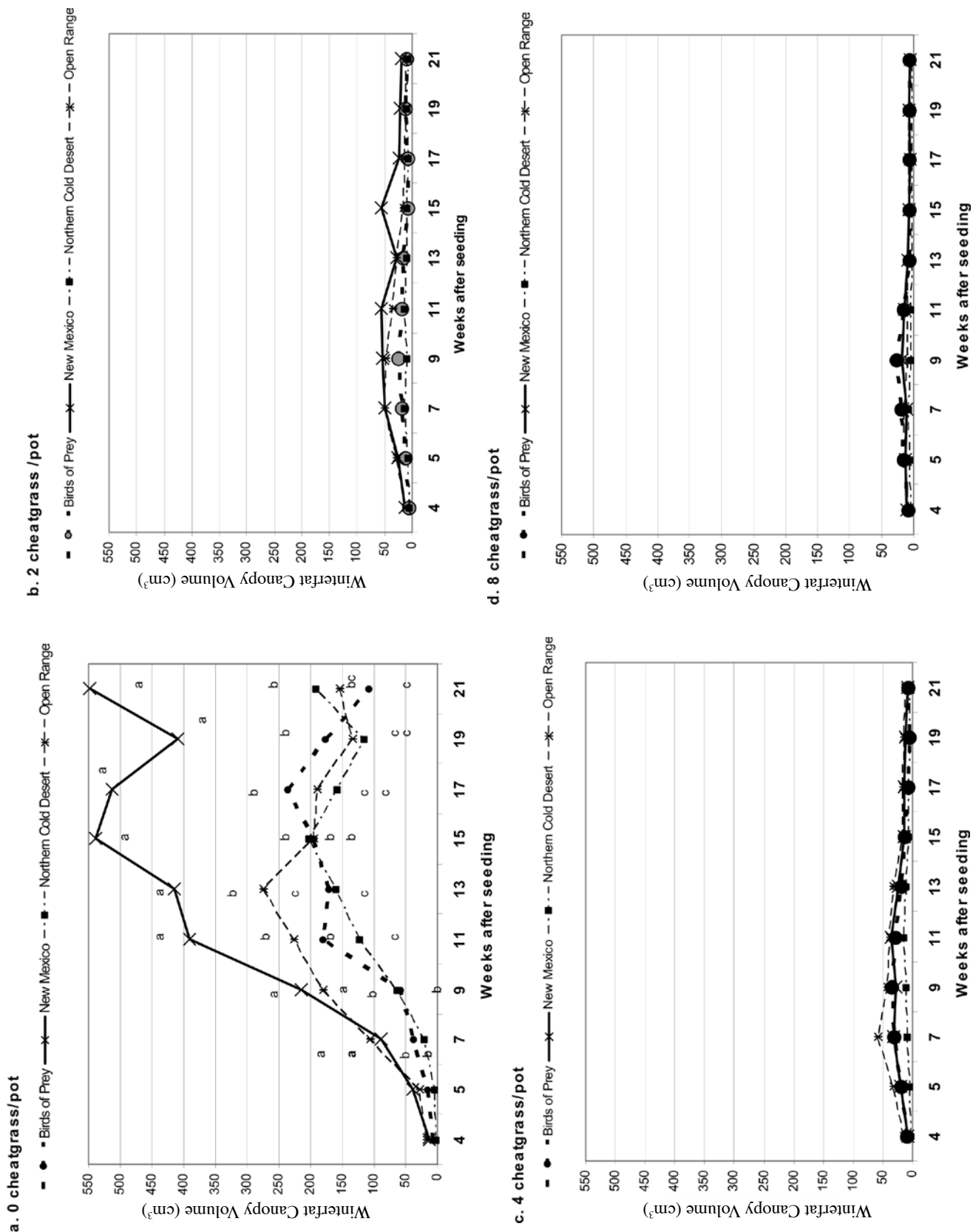


Figure 2. Canopy volume of winterfat seed sources in response to cheatgrass competition level during the 21-week period following seeding. Cheatgrass density: (a) 0 plants/pot; (b) 2 plants/pot; (c) 4 plants/pot; and (d) 8 plants/pot.

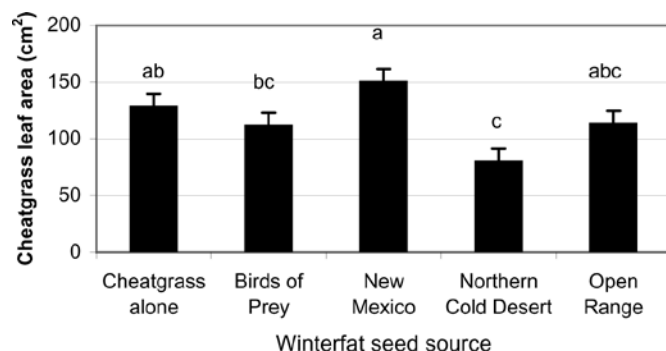


Figure 4. Cheatgrass leaf area (cm²) when planted at three densities (2, 4, or 8 seedlings per pot) alone or in the presence of winterfat seed sources.

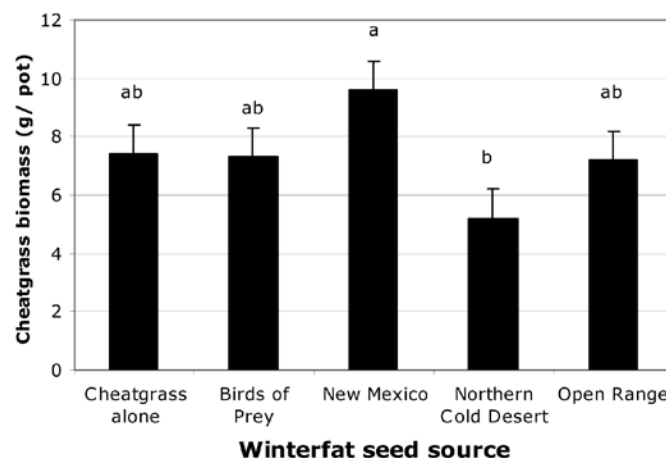


Figure 3. Cheatgrass biomass production (g) when planted at three densities (2, 4, or 8 seedlings per pot) alone or in the presence of winterfat seed sources.

References

- Booth, D. T. 2002. Seedbed ecology of winterfat: imbibition temperature affects post-germination growth. *Journal of Range Management*. 45: 159-164.
- Booth, D. T. 2005. *Krascheninnikovia lanata* (Pursh) A. D. J. Meeuse & Smit. In: Bonner, F. T.; Nisley, R. G., eds. *Woody Plant Seed Manual*. Washington, DC: U.S. Department of Agriculture, Forest Service. Online. Available: <http://nsl.fs.fed.us/wpsm/>
- Carey, J. H. 1995. *Krascheninnikovia lanata*. In: *Fire Effects Information System*. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). : <http://www.fs.fed.us/database/feis>
- Francis, M.; Pyke, D. A. 1996. Crested wheatgrass-cheatgrass seedling competition using a mixed-density design. *Journal of Range Management*. 49:432-438.
- Harris, G. A. 1967. Some competitive relationships between *Agropyron spicatum* and *Bromus tectorum*. *Ecological Monographs*. 37: 89-111.
- Harris, G. A. 1977. Root phenology as a factor of competition among grass seedlings. *Journal of Range Management*. 30: 172-177.
- Harris, G. A.; Goebel, C. J. 1976. Factors in plant competition in seeding Pacific Northwest ranges. *Agric. Exp. Sta. Bull.* 820. Pullman, WA: Washington State University.
- Majerus, M.; Holzworth, L. 2003. Open Range Tested Class Germplasm Winterfat: a conservation plant for Montana and Wyoming. Bridger, MT: U.S. Department of Agriculture, Natural Resources Conservation Service: 4 leaves. Brochure.
- McArthur, E. D.; Monsen, S. B. 2004. Ch. 20. Chenopod shrubs. In: Monsen, S. B.; Stevens, R.; Shaw, N. L., comps. 2004. *Restoring western ranges and wildlands*. Gen. Tech. Rep. RMRS-GTR-136-vol-2. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 467-492.
- Moyer, J. L.; Lang, R. L. 1976. Variable germination response to temperature for different sources of winterfat seed. *Journal of Range Management*. 29: 320-321.
- Nydegger, N. C.; Smith, G. W. 1986. Prey populations in relation to *Artemisia* vegetation types in southwestern Idaho. 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, Intermountain Research Station: 152-156.
- SAS. 2002. *Jmp Statistical Discovery Software*. SAS Institute Inc., Cary, NC.
- Springfield, H. W. 1972. Winterfat seeds undergo after-ripening. *Journal of Range Management*. 25: 479-480.
- Springfield, H. W. 1968. Germination of winterfat seeds under different moisture stresses and temperatures. *Journal of Range Management*. 21: 314-316.
- Springfield, H. W. 1973. Larger seeds of winterfat germinate better. *Journal of Range Management*. 26: 153-154.
- St. John, L.; Blaker, P. 2004. New native plant releases from the USDA-NRCS, Aberdeen, ID, Plant Materials Center. In: Hild, A. L.; Shaw, N. L.; Meyer, S. E.; Booth, D. T.; McArthur, E. D., comps. *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: 138-139.
- Stevens, R.; Giunta, B. C.; Jorgensen, K. R.; Plummer, A. P. 1977. *Winterfat (Ceratoides lanata)*. Pub. 77-2. Salt Lake City: Utah State Division of Wildlife Resources. 41 p.
- U.S. Department of Agriculture, Natural Resources Conservation Service. 2002. Northern Cold Desert Winterfat Selected Class Germplasm. Fact Sheet. Aberdeen, ID: U.S. Department of Agriculture, Natural Resources Conservation Service, Aberdeen Plant Materials Center. USDA, NRCS. 2004. The PLANTS Database, Version 3.5 (<http://plants.usda.gov>). National Plant Data Center, Baton Rouge, LA 70874-4490 USA.
- U.S. Department of Agriculture, Soil Conservation Service and U.S. Department of Agriculture, Forest Service. 1982. *Soil Survey of Colfax County New Mexico*. Washington, DC: U.S. Department of Agriculture, Soil Conservation Service and U.S. Department of Agriculture, Forest Service. 187 p.
- U.S. Department of the Interior, U.S. Geological Survey, Biological Resources Division. 1996. Effects of military training and fire in the Snake River Birds of Prey National Conservation Area. BLM/IDARNG Res. Proj. Final Rep. Boise, ID: U.S. Department of the Interior, U.S. Geological Survey, Biological Resources Division, Snake River Field Station. 130 p.
- Van Horne, B.; Schooley, R. L.; Sharpe, P. B. 1998. Influence of habitat, sex, age and drought on the diet of Townsend's ground squirrels. *Journal of Mammalogy*. 79: 521-537.

The Authors

¹ Associate Professor, University of Wyoming, Department of Renewable Resources, Laramie, WY. AnnHild@uwyo.edu

² Rangeland Scientist III, U.S. Department of Agriculture, Agricultural Research Service, Fort Keogh Livestock and Range Research Center, Miles City, MT.

³ Research Botanist, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Boise, ID.

Seed Germination Biology of Intermountain Populations of Fourwing Saltbush (*Atriplex canescens*: Chenopodiaceae)

Susan E. Meyer¹

Stephanie L. Carlson²

Abstract: Fourwing saltbush (*Atriplex canescens*) is a widely distributed shrub of semiarid western North America. We studied viability and germinability of fourwing saltbush seeds over 10 years for collections from 23 Intermountain populations. Fruit fill averaged 53 percent, and 96 percent of filled fruits contained viable seeds even after 6 years of laboratory storage. Seed collections were generally dormant to some degree at harvest and lost dormancy via two processes, moist chilling and after-ripening in dry storage. Prolonged chilling (24 wks) substituted for dry after-ripening, resulted in germination percentages similar to those obtained without chilling after 2 years of storage. Collections from warm desert habitats were generally least dormant, while collections from pinyon-juniper and mountain brush habitats were highly dormant. But these trends were not very strong. Seeds of the diploid population from Jericho Dunes were essentially nondormant at harvest, while those from a population near Page, Arizona, were essentially completely dormant. Unchilled seeds did not germinate to any degree until tested after 10 years of storage. Patterns of dormancy loss suggest that this species is opportunistic and generally able to establish in response to either winter or summer precipitation. In addition, its seeds probably form persistent seed banks in the field.

Introduction

Fourwing saltbush (*Atriplex canescens*) is one of the shrub species most widely seeded for reclamation, revegetation, and habitat improvement throughout the semiarid western United States (McArthur and Monsen 2004). It has proven to be relatively easy to establish from direct seeding, even on harsh disturbances, and it provides valuable forage for all classes of livestock as well as wild ungulates. Its seeds are easily collected in large quantities and readily cleaned and planted with commercial equipment. Perhaps because of this ease of use, the species has received relatively little study in terms of germination and establishment ecology (reviewed in Meyer on line). The classic work of Springfield (1970) remains the most detailed study of fourwing saltbush germination biology to date. He worked primarily with southwestern collections from summer rainfall areas and perhaps for this reason, recognized the role of dry after-ripening, but not moist chilling, in alleviating seed dormancy.

Fourwing saltbush is a fall to early winter ripening species, with fruits maturing earlier at higher elevations and later at lower elevations. The fruits often over-winter on the plants and are thus unavailable for germination the first spring after production. Whether they germinate soon after dispersal in spring, in response to summer rains, in response to winter chilling, or in later years depends on post-dispersal dormancy status and its interaction with the local environment.

In this study, our goal was to examine variation in the dormancy status of freshly harvested fourwing saltbush seed collections to determine the relative impact of moist chilling and dry after-ripening on dormancy status and to relate any differences in primary dormancy and patterns of dormancy

loss to habitat at the site of seed origin. We also wanted to look for differences in initial viability and in patterns of viability loss among seed collections. Our collections were made in the primarily winter precipitation regions of the Great Basin, Snake River Plains, Uinta Basin, Colorado Plateau, and Mojave Desert (table 1).

Methods

Seed collections were made in the fall of 1988. A total of 27 collections were made, but four collections were subsequently dropped from the study because of very low fruit fill (< 20 percent). Seed collections were obtained from four states and from the full range of habitat types where fourwing saltbush occurs (table 1). Fruits of each collection were de-winged on a rubbing board and cleaned by screening and fanning prior to the initiation of experiments. As a rough estimate of initial viability, we performed a cut test on 200 randomly selected fruits from each lot.

Experiments with seeds designated as recently harvested were begun in January of 1989, within 3 to 8 weeks of the harvest date, depending on individual collection dates. For each treatment, eight replications of 25 fruits were included. For each replication, fruits were placed in 100 mm plastic Petri dishes between two blue germination blotters (Anchor Paper, St. Paul MN) and moistened with tap water initially and as needed during the course of the experiment. The treatments were: no chilling, 4 weeks of chilling, and 24 weeks of chilling. Chilling took place in the dark (in boxes) in a walk-in cold room at 2°C, while post-chilling incubation, also in the dark, was carried out for 4 wks at 15°C. Germination was

In: Sosebee, R.E.; Wester, D.B.; Britton, C.M.; McArthur, E.D.; Kitchen, S.G., comp. 2007. Proceedings: Shrubland dynamics—fire and water; 2004 August 10-12; Lubbock, TX. Proceedings RMRS-P-47. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 173 p.

Table 1. Collection locations and habitat types for 23 *Atriplex canescens* seed collections included in the study. Collection locations are approximate.

Collection location	State	Habitat type
Littlefield	Arizona	Creosote bush shrubland
Glendale	Nevada	Creosote bush shrubland
Kingman	Arizona	Creosote bush shrubland
Snow's Canyon	Utah	Blackbrush shrubland
Santa Clara	Utah	Blackbrush shrubland
Page	Arizona	Blackbrush shrubland
Torrey	Utah	Salt desert shrubland
Caineville	Utah	Salt desert shrubland
Roosevelt	Utah	Salt desert shrubland
Nampa	Idaho	Sagebrush steppe
Jordan Valley	Idaho	Sagebrush steppe
Niagra Springs	Idaho	Sagebrush steppe
Burley	Idaho	Sagebrush steppe
Ephraim	Utah	Sagebrush steppe
Wales	Utah	Sagebrush steppe
Elberta	Utah	Sagebrush steppe
Jericho Dunes	Utah	Sagebrush steppe
Cedar Canyon	Utah	Pinyon-juniper/mountain brush
Beaver Canyon	Utah	Pinyon-juniper/mountain brush
Starvation	Utah	Pinyon-juniper/mountain brush
Gay Mine	Idaho	Pinyon-juniper/mountain brush
Book Cliffs	Utah	Pinyon-juniper/mountain brush
Winnemucca	Nevada	Pinyon-juniper/mountain brush

recorded weekly in the 24-wk chilling treatment and during post-chilling incubation for all treatments. Seeds were considered germinated when the radicle visibly protruded from the tip of the fruit. At the end of the incubation period, remaining fruits in each dish were subjected to a cut test to determine their viability. Germination proportion for each treatment and replication was calculated based on the total number of viable seeds in the dish.

Fruits of each of the 23 collections were stored unsealed under laboratory conditions (20 to 22°C, ca. 30 to 35 percent relative humidity) for 10 years following the initial germination experiment. Germination tests were carried out after 1, 2, 6, and 10 years of storage. The experiments at 1 and 2 years were similar in design to those for recently harvested seeds, except that 4 replications of 50 seeds were included for each treatment and collection. After 6 years, the 23 collections were subjected to the no chilling treatment only. At the end of the incubation treatment, these seeds were evaluated for viability using tetrazolium chloride in addition to a simple cut test, that is, fruits whose seeds appeared filled were stained to determine seed viability. After 10 years, four replications of 25 seeds for each collection were subjected to the no chilling and 4-week chilling treatments. These seeds were not subjected to a post-incubation cut test. We used initial viability values in the calculation of germination percentages for the 10-year data.

We analyzed our data using analysis of covariance for completely randomized

designs with seed collection as the class variable and seed age (storage period) and chilling duration as continuous variables. Two analyses were performed. The first was a complete factorial using the data for recently harvested, 1-year-old, and 2-year-old seeds. These were the experiments that included all three chilling durations. The second analysis was for the no chilling treatment only and included data for recently harvested seeds and seeds 1, 2, 6, and 10 years old. This approach gave two balanced designs. We did not analyze the 4-wk chilling data for the 10-year-old seeds beyond calculation of means and standard errors because it became apparent that the effects of dormancy loss and vigor loss were confounded in this treatment. Germination proportions were arcsine-transformed to improve homogeneity of variance prior to analysis.

Simple *t*-tests were used to compare means obtained from different measures of viability, that is, initial cut test, post-germination cut tests at 1 and 6 years, and tetrazolium viability evaluation at 6 years.

Principal components analysis (PCA) was performed using germination percentages from each of the 12 treatment combinations for each of the 23 seed collections as variables. The goal was to detect groups of collections with similar germination responses and to examine whether these groups could be interpreted ecologically. Because all the variables were in the same units, we performed PCA on the non-standardized correlation matrix. Scores from the first two principal components were plotted for each collection, and eigenvector loadings on these two principal components were used in the interpretation of the resulting scattergram.

Results

Viability Evaluation

Initial viability as estimated by fruit fill varied from 35 to 75 percent across collections, with a mean of 52.3 percent (table 2). This value was closely matched by the viability estimate based on germinated seeds plus filled seeds remaining from experiments with recently harvested seeds (52.0 percent mean). Viability percentages based on post-germination cut tests from the experiment with 6-year-old seeds were similar (54.3 percent mean). More importantly, the viability percentage based on tetrazolium staining at 6 years was also very close

Table 2. Mean percentage of viable seeds for 23 *Atriplex canescens* collections included in the study, as determined by initial cut test to determine fruit fill, post-germination cut tests on recently harvested and 6-year-old fruits, and post-germination tetrazolium staining for 6-year-old fruits.

Viability measure	Viability percentage		
	Mean	Standard error	Range
Initial fill estimate	52.3	2.25	35-75
Post-test fill estimate - recently harvested seeds	52.0	2.73	27-72
Post-test fill estimate - 6-year-old seeds	54.3	2.81	31-74
Tetrazolium viability - 6 year old seeds	52.0	2.69	30-72
Tetrazolium viability as percentage of filled fruits	95.8		

to these values (52 percent). The four viability estimates are not significantly different from each other. This means that the cut test is an excellent estimate of viability for fourwing saltbush seeds from 1 to 6 years of age, and that seeds in this study did not lose any significant viability overall during this period. Tetrazolium viability at 6 years averaged 96 percent of viability estimated by cut test.

Viability at 10 years was not explicitly measured, but decreases in germination percentage relative to the 6-year data suggest that seeds of some lots were beginning to lose vigor. This interpretation is supported by the fact that in many of these collections, a 4-wk chilling treatment actually resulted in a substantial decline in germination percentage relative to the no chilling treatment. This effect was rarely seen in earlier experiments.

Germination Experiments

Both moist chilling and dry after-ripening resulted in increases in germination percentage overall (fig. 1). In the factorial experiment with seeds up to 2 years old, both chilling and seed age main effects were highly significant, as was their

interaction (table 3). Longer chilling periods were especially effective in breaking the dormancy of recently harvested collections. After a year in storage, germination in both the no chill and 4-wk chill treatments increased substantially, while the increase in response to 24-wk chilling was smaller. After an additional year in storage, there was little further change in response to no chill and 4-wk chill treatments, while the response to a 24-wk chill increased.

There was also a significant increase in the fraction of seeds that could germinate without chilling as the storage period increased (seed age main effect highly significant; table 4). After 6 years of storage, germination of unchilled seeds was almost as high as the germination percentage after 24 weeks of chilling for 2-year-old seeds (fig. 1). These results show that chilling can be an important mechanism of dormancy removal for recently dispersed seeds, but that dry after-ripening will eventually render most of these seeds germinable without chilling. Chilling thus serves as a substitute for dry after-ripening in recently dispersed seeds. The net effect of these processes is to ensure a nondormant seed fraction available for germination in response to both winter and summer germination-triggering precipitation events. It also ensures

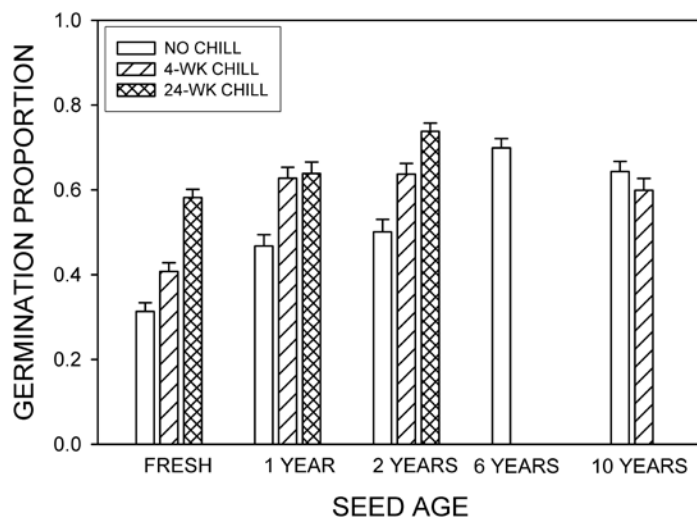


Figure 1. Mean germination proportions (averaged across 23 collections of *Atriplex canescens*) for 12 combinations of seed age and chilling duration. For each treatment combination, seeds were incubated for 4 weeks at 15°C following the seed storage and chilling treatments. Germination data are expressed as proportion of viable seeds. Standard error bars are shown for each mean.

Table 3. Analysis of covariance based on a completely randomized design for germination experiments with 23 collections of *Atriplex canescens* in which seeds of each collection were tested when recently harvested and after 1 and 2 years of laboratory storage. For each seed age, three chilling durations were included: no chilling, 4 weeks of chilling, and 24 weeks of chilling.

Source of Variance	d.f.	Mean square	F-value	P-value
Seed collection	22	1.4679	33.23	<0.0001
Seed age	1	9.3949	212.70	<0.0001
Chilling duration	1	10.7489	243.36	<0.0001
Seed collection x seed age	22	0.1943	4.40	<0.0001
Seed collection x chilling duration	22	0.3031	6.86	<0.0001
Seed age x chilling duration	1	0.5075	11.49	0.0007
Seed collection x seed age x chilling duration	22	0.0831	1.88	0.0083
Error	1012	0.0442		

Seeds were incubated at 15°C for 4 weeks after each treatment sequence, and germination proportion was scored as a fraction of viable seeds. Data were arcsine transformed for analysis. Seed age and chilling duration are treated as continuous independent variables in the analysis, while seed collection is considered a class variable.

Table 4. Analysis of covariance based on a completely randomized design for germination experiments with 23 collections of *Atriplex canescens* in which seeds were tested when recently harvested and after 1, 2, 6, and 10 years of storage. Seeds were incubated for 4 weeks at 15°C.

Source of Variance	d.f.	Mean square	F-value	P-value
Seed collection	22	0.7771	24.39	<0.0001
Seed age	1	8.6748	272.31	<0.0001
Seed collection x seed age	22	0.0969	3.04	<0.0001
Error	506	0.0319		

Germination data are based on viable seed proportion determined at the end of each test with one exception. For the 10-year data, germination is based on the proportion of fruits initially viable as determined by an *a priori* cut test on recently harvested seeds. Data were arcsine transformed for analysis. Seed age was treated as a continuous independent variable in the analysis, while seed collection was considered a class variable.

that not all seeds in a cohort will germinate in response to the same triggering event. Instead, germination may be spread across seasons and probably even across years.

The trend toward increasing germination percentages with increasing seed age did not hold for the 10-year data. Instead, percentages dropped slightly, and there was a trend for decreased germination after chilling. These effects are probably an indication of decreasing seed viability and vigor in 10-year-old lots.

There was tremendous variation among seed collections in terms of dormancy status at harvest and response to dormancy breaking treatments (highly significant seed collection main effects and interactions; tables 3, 4). We chose to group the collections in terms of their habitat of origin, then look for common patterns that could be interpreted ecologically. Such patterns were only sometimes in evidence, but examining collection responses by habitat enabled us to extract some meaningful generalizations from this complex data set.

Fourwing saltbush seed collections made in warm desert creosote bush (*Larrea tridentata*) habitats were relatively nondormant at harvest (51 to 77 percent without chilling; fig. 2). They generally changed very little in dry storage over 2 years, but after 6 years achieved germination from 76 to 95 percent without chilling. They showed little viability loss after 10 years.

Fourwing saltbush seed collections made in warm desert fringe blackbrush (*Coleogyne ramosissima*) habitats were extremely variable in their germination responses (fig. 3). They were generally more dormant at harvest than collections from creosote bush habitats, but showed sharply contrasting responses to chilling. The Santa Clara collection achieved germination of 86 percent after chilling when recently harvested, while at the other extreme the collection from Page, Arizona, germinated to only 4 percent when recently harvested regardless of chilling regime. The Page collection did not acquire any substantial ability to germinate without chilling until after 10 years of storage, and by that time was losing vigor, as indicated by the precipitous drop in germination after a 4-wk chill. The other two collections behaved more like collections from the creosote bush habitat, with generally small and inconsistent change in dormancy status and chilling responsiveness over the first 2 years, then a jump

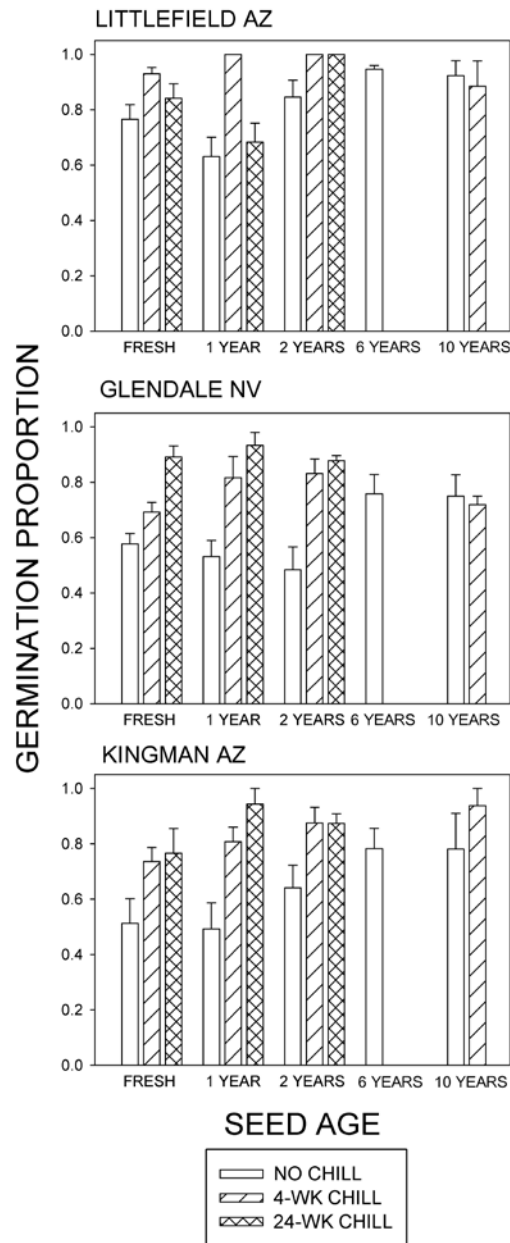


Figure 2. Germination proportions for three *Atriplex canescens* seed collections from the creosote bush shrubland habitat type following 12 combinations of seed age and chilling duration. For each treatment combination, seeds were incubated for 4 weeks at 15°C following the seed storage and chilling treatments. Germination data are expressed as proportion of viable seeds. Standard error bars are shown for each mean.

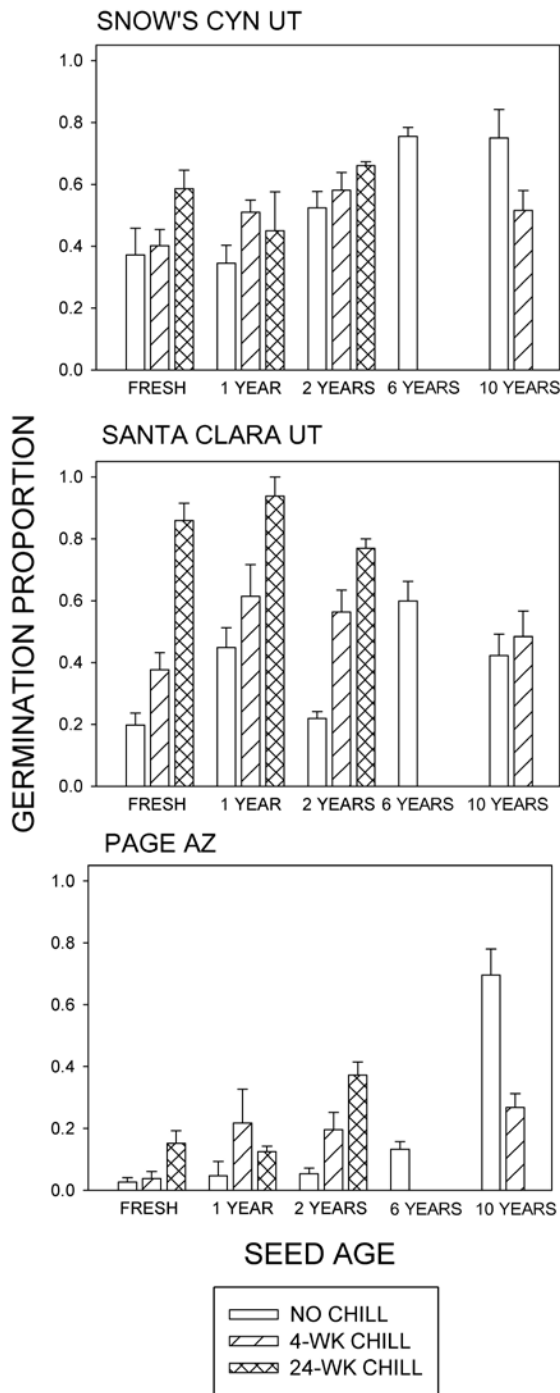


Figure 3. Germination proportions for three *Atriplex canescens* seed collections from the blackbrush shrubland habitat type following 12 combinations of seed age and chilling duration. For each treatment combination, seeds were incubated for 4 weeks at 15°C following the seed storage and chilling treatments. Germination data are expressed as proportion of viable seeds. Standard error bars are shown for each mean.

at 6 years in the fraction able to germinate without chilling. Both these collections showed signs of decreasing viability after 10 years.

Fourwing saltbush collections made in salt desert habitats were generally more dormant at harvest than those from warm desert habitats (15 to 36 percent germination without chilling)

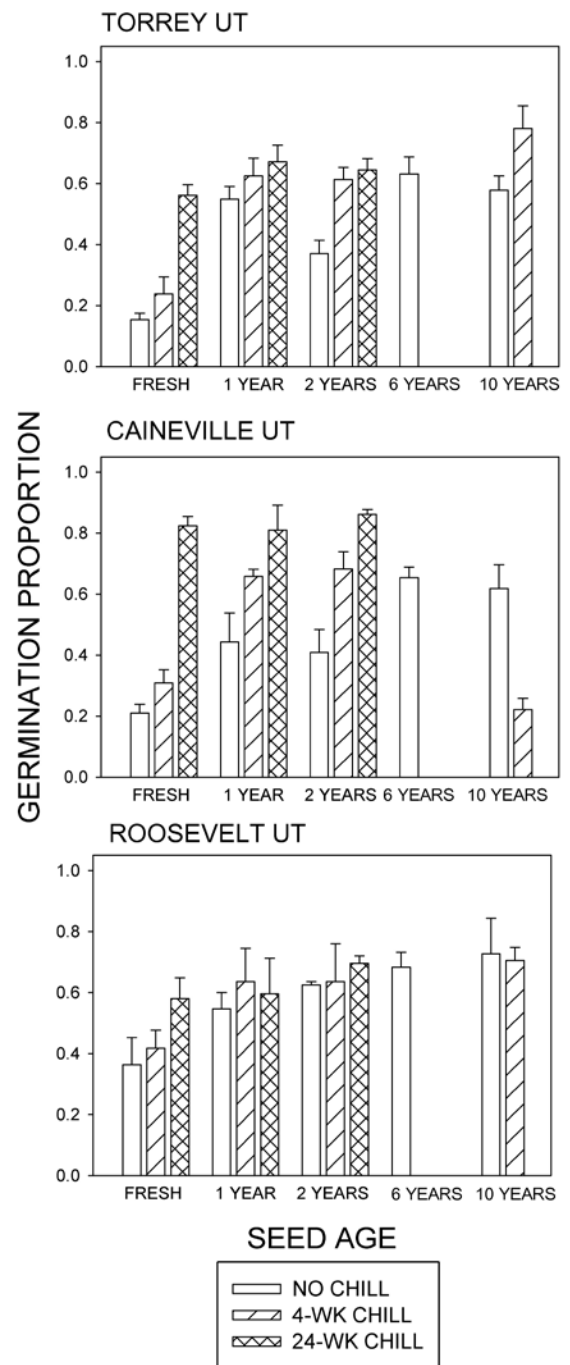


Figure 4. Germination proportions for three *Atriplex canescens* seed collections from the salt desert shrubland habitat type following 12 combinations of seed age and chilling duration. For each treatment combination, seeds were incubated for 4 weeks at 15°C following the seed storage and chilling treatments. Germination data are expressed as proportion of viable seeds. Standard error bars are shown for each mean.

and were not very responsive to short chilling (fig. 4). They varied in their response to long chilling; the Caineville collection was most responsive and the Roosevelt collection the least. Dormancy generally decreased in dry storage through 6 years, but maximum germination percentages without chilling were only moderate (63 to 68 percent) and chilling of

short duration, as would be expected in this habitat, did little to increase total germination beyond these values.

Fourwing saltbush probably achieves its greatest abundance in sagebrush steppe habitats in the Intermountain West, a fact reflected in the larger number of collections we made in this habitat (table 1). Seven of the eight collections in this group followed a similar pattern (fig. 5). Their seeds were moderately dormant at harvest (16 to 50 percent germination without chilling) and lost dormancy steadily and usually quickly in dry storage (38 to 92 percent germination after 2 years). They were generally not very responsive to short chilling when recently harvested and showed variable response to long chilling. The eighth collection included in the sagebrush steppe group, from Jericho Dunes, was actually from a sand dune habitat embedded within the sagebrush type, and is also unusual in being diploid (Stutz and others 1975). It was the least dormant collection in the study, with germination from 85 to 100 percent regardless of seed age or chilling treatment (fig. 5).

Fourwing saltbush collections from foothill woodland or mountain brush habitats were uniformly dormant when recently harvested (germination without chilling 3 to 11 percent). The fraction germinable without chilling increased steadily through time but never achieved high values (54 to 62 percent). Seeds were moderately chilling-responsive when recently harvested (21 to 45 percent maximum germination after chilling). The fraction to germinate in response to chilling generally showed incremental increase through time over the first 2 years (fig. 6).

Principal Components Analysis

The first principal component from PCA accounted for 77 percent of the total variance, and the eigenvector loadings for all 12 variables were positive and of similar magnitude. PC1 basically represents a scale of increasing overall germinability (decreasing dormancy), with the most dormant collection (Page) at the left hand extreme and the least dormant collection (Jericho Dunes) at the right hand extreme (fig. 7). In fact, scores on PC1 are highly correlated with mean germination percentages (averaged across 12 treatments), with an r -value of 0.982 (d.f.=21, $p<0.0001$). The high eigenvalue (77 percent) for PC1 reflects the fact that the germination variables tend to be correlated, sometimes highly correlated.

Other than the two anomalous collections (Page and Jericho Dunes), collections from different habitats form a reasonably orderly progression along PC1, with the more dormant foothill collections grouped to the left, the less dormant creosote bush shrubland collections grouped to the right, and the intermediate sagebrush steppe, salt desert shrubland, and blackbrush shrubland collections in the middle (fig. 7).

PC2 accounts for only an additional 9 percent of the total variance, so scores on this PC are less important for interpretation than scores on PC1. They do have a clear interpretation, however. The eigenvector loadings for PC2 are all either near zero or negative, except for the loadings for the three 24-week chilling response variables, which are all positive and

large. This can be interpreted to mean that collections with high scores on PC2 responded more to 24-week chilling than collections with low scores. All six foothill collections were intermediate in this respect, and form a tight group on the graph (fig. 7). The remaining collections did not show any clear relationship to habitat in terms of their scores on PC2. For example, Snow's Canyon and Santa Clara, both from blackbrush shrubland, had similar germination percentages overall and similar scores on PC1. But they differed widely on PC2, because Santa Clara seeds tended to respond positively to 24 week chilling, while Snow's Canyon seeds did not (fig. 3).

Discussion

We can safely conclude that both moist chilling and dry after-ripening play important roles in seed dormancy regulation for Intermountain populations of fourwing saltbush. Chilling is especially important as a mechanism of dormancy removal for recently dispersed seeds, but most seeds eventually become nondormant through the process of dry after-ripening.

Levels of primary dormancy and patterns of change in dormancy status as a function of both chilling and dry after-ripening varied dramatically among collections. With the notable exception of the collections from Page and Jericho Dunes, there was a general pattern of increasing primary dormancy and decreasing maximum germination percentages in the progression from warm desert to foothill habitats. Most collections from creosote bush dominated sites seemed to be composed of a sizeable fraction able to germinate at the first opportunity and a smaller fraction that became germinable after short chilling or short-term after-ripening. Seed bank carry-over across years seems unlikely in this group, except that in this dry environment, wet conditions that last long enough to trigger germination of non-dormant seeds may not be encountered in any given year. Particularly in a heterogeneous seed bed, many seeds may find themselves in microenvironments that dry very rapidly at germination-conducive temperatures. A 4-week period of moist chilling may be equally unlikely. Thus the seeds may not need elaborate dormancy protections in order for a fraction to persist across years.

At the other end of the spectrum, collections from foothill pinyon-juniper and mountain brush habitats were highly dormant at dispersal and achieved relatively low germination percentages even after prolonged chilling. Chilling continued to be incrementally effective as a dormancy-breaking treatment even in seeds stored 2 years. This response pattern would tend to limit emergence to the spring in these cold winter environments, where the winter chilling period lasts much longer than 4 weeks and occasionally even as long as 24 weeks, and where frost risk to fall-emerging seedlings is high. Seed bank carryover across years is assured in these environments by virtue of the fact that there is always a chilling non-responsive fraction, even after a very long chilling period.

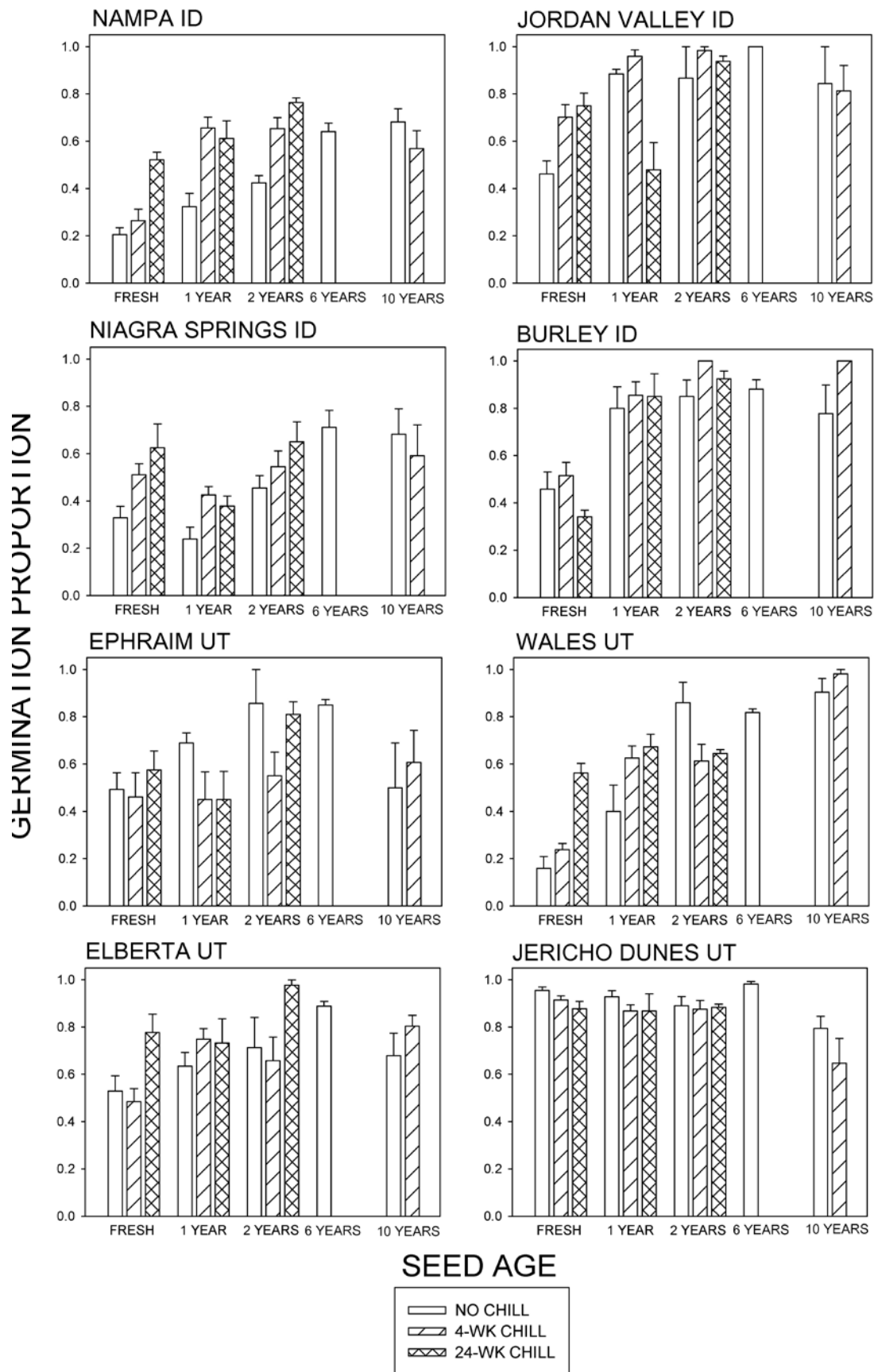


Figure 5. Germination proportions for eight *Atriplex canescens* seed collections from the sagebrush steppe habitat type following 12 combinations of seed age and chilling duration. For each treatment combination, seeds were incubated for 4 weeks at 15°C following the seed storage and chilling treatments. Germination data are expressed as proportion of viable seeds. Standard error bars are shown for each mean.

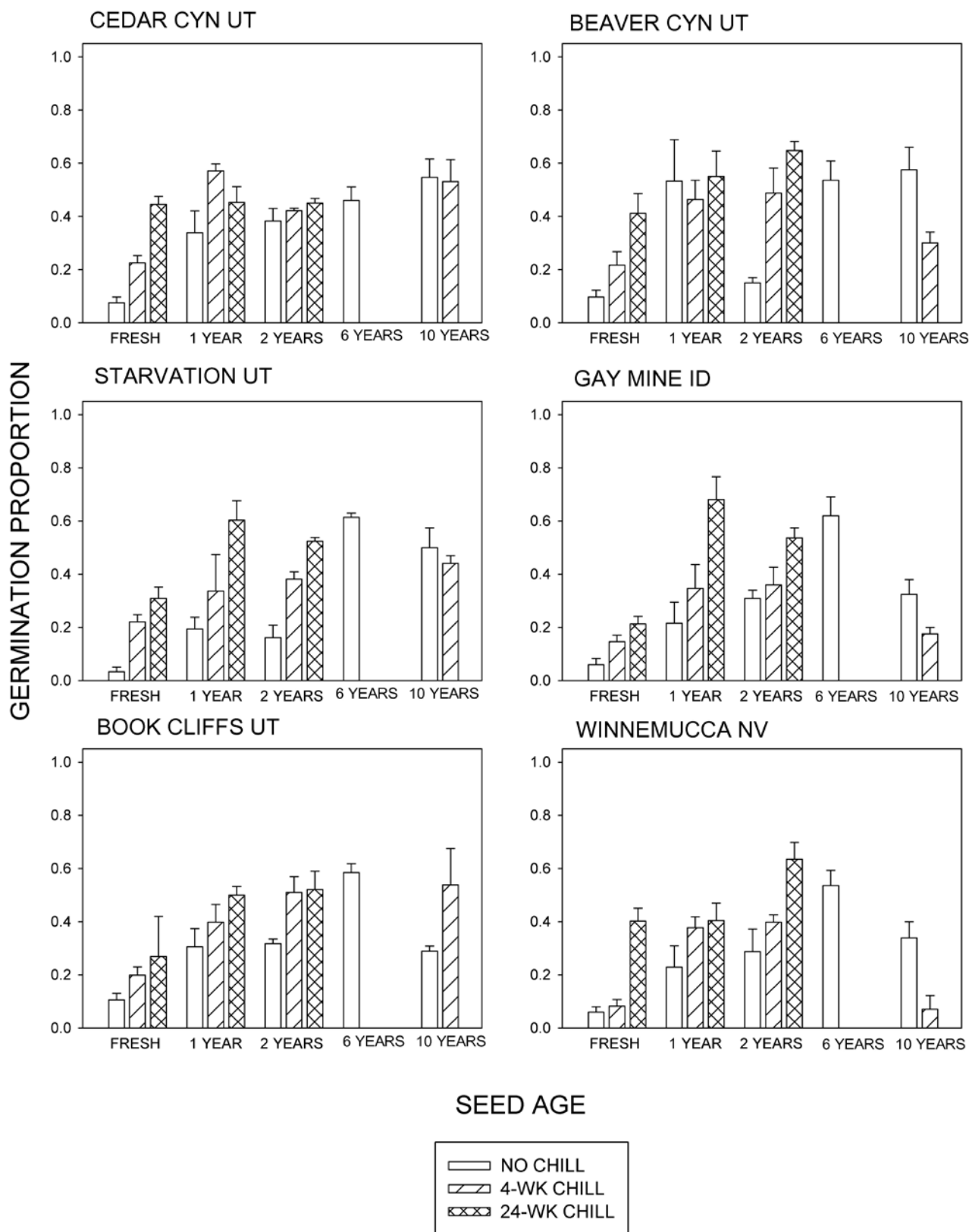


Figure 6. Germination proportions for six *Atriplex canescens* seed collections from the pinyon-juniper woodland/mountain brush habitat type following 12 combinations of seed age and chilling duration. For each treatment combination, seeds were incubated for 4 weeks at 15°C following the seed storage and chilling treatments. Germination data are expressed as proportion of viable seeds. Standard error bars are shown for each mean.

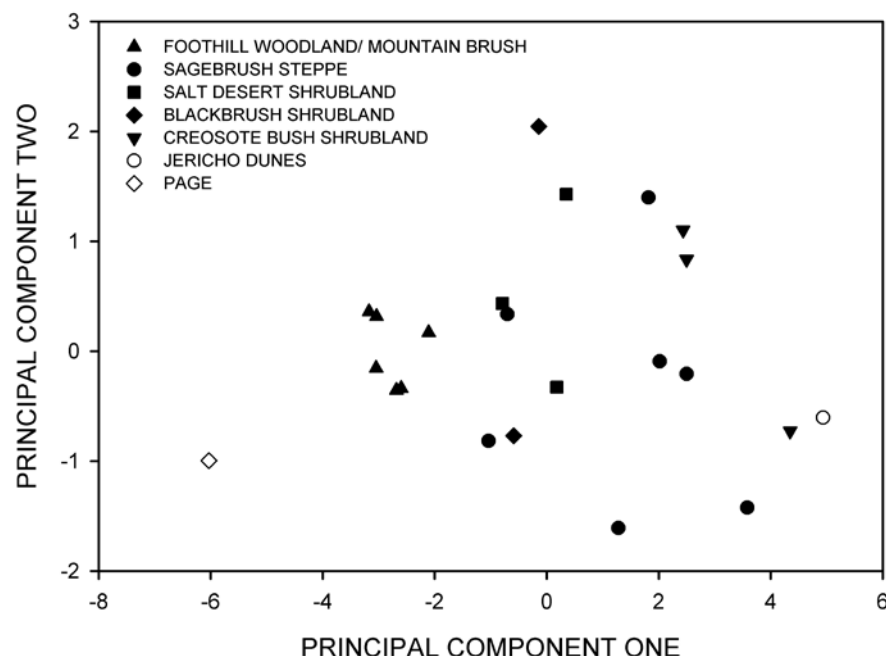


Figure 7. Principal components analysis based on *Atriplex canescens* seed germination data. Scores on the first two principal components for each of the 23 populations were used to create the plot. These two principal components accounted for 86 percent of the total variance. Symbols correspond to plant communities where the seed collections were made. Two unfilled (white) symbols correspond to populations with anomalous germination responses (see text for explanation).

Germination patterns for the numerous collections from intermediate blackbrush shrubland, salt desert shrubland and sagebrush steppe habitats were much more variable and difficult to generalize. The seeds tended to be intermediate between the warm desert and foothill groups in primary dormancy, to lose dormancy fairly rapidly in dry storage, and to reach intermediate to high final germination percentages under test conditions. An explicit ecological interpretation of these results would require much more detailed knowledge of the climate at particular collection sites, as well as additional experiments under a broader array of test conditions.

Because of the large number of collections in our study, we were limited in terms of the number of treatments we could apply, so that extrapolation of our laboratory results to the field must be done cautiously. Seeds under field conditions experience a changing temperature and moisture environment. For example, the rate at which seeds dry after-ripened in our experiment is only an index of the after-ripening speed under one uniform condition. While this index is useful in making comparisons among collections, it is almost certain that temperature will have a strong positive effect on after-ripening rate in fourwing saltbush, as it does in the related species shadscale (*Atriplex confertifolia*; Garvin and Meyer 2003). Similarly, temperature and moisture conditions during chilling are not uniform under field conditions, and this variation, as well as time spent either above or below effective stratification temperatures, undoubtedly has an effect on the pattern of change in dormancy status. This limits our ability to interpret our results in the absence of a field study to corroborate our laboratory findings. However, we were able to successfully predict germination timing and seed bank carryover for shadscale seed collections from contrasting habitats placed under field conditions, using results of experiments similar to those described here (Meyer and others 1998). The predictions were verified in a field seed retrieval experiment, an approach that

would be the logical next step in understanding dormancy loss and germination phenology in fourwing saltbush.

Acknowledgments

We gratefully acknowledge the able technical assistance of Scott Walker in the early stages of this study. Thanks also to Steven Monsen, Stan Kitchen, Richard Stevens, Dale Turnipseed, and Mike Pellant for providing seed collections. This research was supported in part by a CSREES Rangelands Special Grant.

References

- Garvin, S. C.; Meyer, S. E. 2003. Multiple mechanisms of seed dormancy regulation in shadscale (*Atriplex confertifolia*: Chenopodiaceae). *Canadian Journal of Botany* 81: 301-310.
- McArthur, E. D.; Monsen, S. B. 2004. Chenopod shrubs. p. 467-492. In: Monsen, S. B.; Stevens, R.; Shaw, N. L. (comps.). *Restoring Western Ranges and Wildlands*, Vol. 2. RMRS-GTR-136. USDA Forest Service, Rocky Mountain Research Station, Ft. Collins, Colorado.
- Meyer, S. E.; Carlson, S. L.; Garvin, S. C. 1998. Seed germination regulation and field seed bank carryover in shadscale (*Atriplex confertifolia*: Chenopodiaceae). *Journal of Arid Environments*. 38: 255-267.
- Meyer, S. E. *Atriplex*. In: *Woody Plant Seed Manual*. Published online at ntsl.fs.fed.us/wpsm/
- Springfield, H. W. 1970. Germination and establishment of fourwing saltbush in the southwest. Research Paper RM-55. USDA Forest Service, Rocky Mountain Research Station, Ft. Collins, Colorado. 48 p.
- Stutz, H. C.; Melby, J. M.; Livingston, G. K. 1975. Evolutionary studies of *Atriplex*: a relic gigas diploid population of *Atriplex canescens*. *American Journal of Botany*. 62: 236-245.

The Authors

¹Research Ecologist, USDA Forest Service, Rocky Mountain
Research Station, Shrub Sciences Laboratory, Provo, UT.
smeyer@fs.fed.us

²Biological Technician, USDA Forest Service, Rocky Mountain
Research Station, Shrub Sciences Laboratory, Provo, UT.

Efficacy of Exclosures in Conserving Local Shrub Biodiversity in Xeric Sandy Grassland, Inner Mongolia, China

Feng-Rui Li¹

Zhi-Yu Zhou²

Li-Ya Zhao¹

Zhi-Gang Huang¹

Ling-Fen Kang¹

Abstract: This study investigated the abundance and frequency of occurrence of all shrub species present in the standing vegetation at four sites, including a 5-year exclosure (protected grassland) and three adjacent unprotected grazing sites that had been subjected to different levels of degradation (light, moderate and severe), in xeric sandy grassland of Inner Mongolia for three growing seasons. Shrub species abundance, richness, and diversity in the exclosure were compared with three unprotected sites to determine the efficacy of exclosure on shrub biodiversity conservation. Using the data set, the responses of individual shrub species to level of grassland degradation were also examined by means of detrended correspondence analysis (DCA). Individual shrub species responded differently to degradation level. From individual species responses we identified three main response types. The first type is represented by *Artemisia holodendren* showing a positive response to degradation level. The second type is represented by *Lespedeza davurica*, *Hedysarum fruticosum*, and *Caragana microphylla* indicating a negative response to degradation level. The third type included *Ceratoides arborescens* and *Artemisia frigida* following a different response pattern from the first two response types. Exclosure effects varied remarkably with different shrub species. The results suggest that it is generally necessary to apply an exclosure to the severely degraded grassland while light to moderate grazing disturbance is helpful for the maintenance of shrub species diversity. These findings are important for understanding how grassland degradation affected the population demography of shrub species and for developing appropriate management strategies for conservation of degraded shrub vegetation.

Introduction

Grasslands in the arid, semi-arid and dry semi-humid regions of northern China are becoming increasingly degraded or lost due to anthropogenic influences (Li 1997; Chen 1998; Chen and Wang 2000), such as overgrazing, over-cultivation (conversion of grassland to farmland), extensive firewood collection, and excessive groundwater withdrawal or surface water use for agricultural purposes. This is particularly true for those ecologically fragile ecosystems with a low resilience, such as the xeric sandy steppe grassland in the Horqin Sandy Land of Inner Mongolia (Liu and others 1996). The total area of the Horqin sandy steppe is approximately 518×10^4 ha, which constitutes an important part in Inner Mongolia's pasture resources (Jiang and others 2003). Due to human activities, however, almost 80 percent of the Horqin sandy steppes suffered from desertification (a form of land degradation resulting primarily from wind erosion activity after destruction of vegetation by overgrazing), of which about one third was severely desertified (Zhu and Chen 1994; Wang 2000). Thus, the Horqin Sandy Land has been identified as one of the worst examples of desertification in northern China (Wang and others 2003). The ecological consequences

of unchecked desertification in this region are a substantial loss of the region's specific floristic biodiversity, as well as a range of negative environmental and socio-economic impacts (Chang and Wu 1997; Jiang and others 2003). For example, once the vegetation in sandy grasslands has been destroyed by overgrazing or other human activities, they become less stable and highly erodible during the dry and windy seasons (Li and others 2003a), which are most likely to become new sources of sand and dust that could contribute to sand-dust storms that occur frequently in the arid and semi-arid regions of the northern China (Xuan and others 2000).

Shrubs are an important component in degraded sandy grassland vegetation. Previous studies have shown that some of shrub species such as *Artemisia holodendren* is a pioneer sand-stabilizing plant and plays a key role in maintaining the stability of natural sandy grassland ecosystems (Liu and others 1996; Li and others 2002; Zhang and others 2004). Moreover, some of shrub species, such as *Artemisia frigida*, are commonly known as an indicator species. Its presence or absence in the grassland has been used for establishing whether grassland is degraded (Zhao and Zhou 1999; Li and others 2002). In the last decade, a number of experiments have been carried out in laboratory and experimental garden

In: Sosebee, R.E.; Wester, D.B.; Britton, C.M.; McArthur, E.D.; Kitchen, S.G., comp. 2007. Proceedings: Shrubland dynamics—fire and water; 2004 August 10-12; Lubbock, TX. Proceedings RMRS-P-47. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 173 p.

plots to explore the ecological and physiological adaptation mechanisms of several shrub species, such as *A. halodendron*, *A. frigida*, *Caragana microphylla*, and *Salix gordejvii*, to the harsh environmental conditions of sandy grassland ecosystems characterized by frequent drought, high temperature, and sand burial (Wang and Zhou 1999; Zhou 1999; Zhou and others 1999; Ren and others 2001; Zhou and Zhao 2002). However, few studies have examined the efficacy of short-term enclosure (grazing exclusion) in conserving local shrub species diversity and the response of individual shrub species to level of grassland degradation.

To address this deficiency, we carried out an experiment in the Horqin sandy grassland to examine how degradation level affects shrub species abundance, richness, and diversity and to assess the efficacy of short-term enclosure. The objectives of this study were to: (i) determine changes in the abundance, richness, and diversity of shrub species present in the established vegetation and (ii) determine the specific efficacy of a 5-year enclosure on the restoration of degraded shrub vegetation and the maintenance of shrub species diversity. Here, two specific hypotheses we posed were as follows: (1) Individual shrub species respond differently to degradation level due to their distinct life-history and plant morphological attributes. Some species will be advantaged by the local disturbances associated with moderate to heavy grazing, and will thus show trends of increasing abundance with increasing disturbance intensity (degradation level) and consequently occur more frequently in grasslands under moderate to severe degradation. Some species will be disadvantaged and will thus show patterns of decreasing abundance with increasing degradation level, and consequently disappear or occur less frequently in grasslands under moderate and severe degradation and (2) The effect of enclosure on the conservation of shrub biodiversity varies with different shrub species.

Materials and Methods

Site Description

The study site is located in Naiman county (42°55' N, 120°44' E; altitude c. 360 m a.s.l.) in the eastern part of Inner Mongolia, China, about 500 km northeast of Beijing (Li and others 2003b). Naiman is in the southwestern part of the Horqin Sandy Land, which represents the most desertification-threatened area in northern China (Jiang and others 2003). General landscape in this area is characterized by sand dunes alternating with gently undulating lowland areas. The soils are sandy, light yellow, and loose in structure (Zhu and Chen 1994). The main soil type is classified as an Arenosols in WRB (ISSS, ISRIC and FAO 1998). The climate is temperate, semi-arid and continental, receiving 360 mm annual mean rainfall, with 75 percent of the annual rainfall falling in the June–September period. The annual mean potential evaporation is 1,935 mm, and the annual mean temperature is 6.5°C.

The original vegetation of this area was an open, sparse forest steppe (Liu and others 1996). Due to human activities, however, woody species (mainly elm *Ulmus* spp.) have almost disappeared and most of the grass cover is gone (Andrén and others 1994). Degraded sandy grasslands are generally classified into three main forms: fixed or stabilized (light degradation), semi-fixed or semi-stabilized (moderate degradation), and mobile or least stabilized (severe degradation), representing a realistic range of historically grazing impacts. Over space, these differently degraded grassland patches occur in a complex mosaic (Zhao and others 2003).

Vegetation Survey Design and Sampling

A field survey of the abundance and frequency of occurrence of all shrub species present in the established vegetation was conducted in four sites, including a demonstration enclosure (protected grassland) and three adjacent communal grazing sites that were selected over an area of 3×3 km. The enclosure was established in an open and level grassland area of about 10 ha in April 1997. The grassland had been subjected to severe degradation due to a history of heavy grazing by livestock prior to fencing the enclosure. Three adjacent communal grazing sites differed in degree of vegetation degradation in terms of vegetation cover, species richness, and composition. According to the classification criteria of desertification degree of Zhu and Chen (1994), one of the three sites was identified as light degradation (LDG, lightly degraded grassland), another as moderate degradation (MDG, moderately degraded grassland), and the third one as severe degradation (SDG, severely degraded grassland). Thus, these three sites constitute a gradient of degradation in sandy grasslands. LDG was situated on a typical fixed sand dune area (two separated fixed dunes were selected for sampling). MDG was situated on a typical semi-fixed sand dune area (two separated semi-fixed dunes were selected for sampling). SDG was located on a typical mobile sand dune area (two separated mobile dunes were selected for sampling). Three unprotected grazing sites were at least 1 km apart from one another while their distances from the enclosure were 1.5 to 2 km apart.

A hundred and eighty plots (2 × 2 m) were randomly selected along five parallel transects (each 25 m apart) in the enclosure and 120 plots were randomly selected in each of the three unprotected grazing sites to investigate species composition and density of each shrub species present in each plot in the last week of August at the time of peak biomass production and species diversity. For each site, richness of the shrub species was assessed by the total number of shrub species per site and the mean number of shrub species m⁻². Abundance of each shrub species was assessed by its number of established plants m⁻² and its frequency of occurrence that was calculated as the percentage of the number of plots occupied by a species relative to the total number of plots per site. The sampling of the standing vegetation was repeated for three consecutive growing seasons (2002–2004).

Data Analysis

One-way analysis of variance (ANOVA) was used to test for differences in shrub vegetation parameters between sites. Significant differences between sites were compared using LSD tests. Data for species richness (measured as the mean number of shrub species m⁻²) and abundance (measured as the number of established plants m⁻²) were log-transformed to normalize the distributions. To detect any general patterns in species abundance relationships with sites, we undertook detrended correspondence analysis (DCA) based on the species abundance (density and frequency) data for the four sites. Shannon-Wiener diversity index (H' ; Magurran 1988) and Pielou's evenness index (J ; Pielou 1975) were used to analyse changes in shrub species diversity and evenness across sites. H' and J were calculated by the following formula:

$$H' = -\sum P_i \ln P_i$$

$$J = H' / \ln S$$

where P_i is the abundance of the i th species that was measured as the importance value (IV) of the i th species in the shrub community containing S species. IV was calculated as $IV = (D_r + F_r)/200$, where D_r is the relative abundance that is calculated as the percentage of the observed abundance of a species relative to the cumulative abundance for all species occurring in the shrub community; F_r is the relative frequency that is calculated as the percentage of the observed frequency of a species relative to the cumulative frequency for all species occurring in the shrub community. Data were pooled from the 3 years in the analyses because the interest in this study is to determine differences in shrub vegetation between sites rather than to determine inter-annual variability in shrub vegetation within sites.

Results

A total of six shrub species were recorded in the established vegetation of the four sites sampled and biological characteristics of these shrub species are shown in table 1. Degradation level had significant effects on the abundance, richness, and diversity of shrub species in the established vegetation. The total number of shrub species per site was much lower in grassland under severe degradation than in other three sites that were similar in this variable (fig. 1a). There were striking differences in the mean number of shrub species m⁻² among sites ($F_{3,1616} = 142.14$, $P < 0.0001$), with the lightly degraded grassland having a significantly higher mean number of shrub species m⁻² than other sites. At the same time, the mean number of shrub species m⁻² was also significantly higher in the moderately degraded grassland than in both the protected and severely degraded grasslands and in the protected grassland than in the severely degraded grassland (fig. 1b). Almost the same patterns were observed when comparing the shrub species diversity and evenness index values between sites (fig. 1c, d).

Total shrub abundance was significantly higher in the lightly degraded grassland than in other sites, because of high densities of established *Lespedeza davurica* and *Hedysarum fruticosum* plants at this site (table 2). Total shrub abundance was also significantly higher in the moderately degraded grassland than in the protected and severely degraded grasslands, because of high density of established *Artemisia halodendron* plants at this site, and in the protected grassland than in the severely degraded grassland (table 2).

Detrended correspondence analysis (DCA) showed tight associations between shrub species and particular sites (fig. 2). Of the six shrub species occurred at the study site, *Ceratoides arborescens* and *Artemisia frigida* were restricted to the

Table 1. Main biological characteristics of shrub species recorded at the study sites.

	Family	Life form	Growth form	Root growth form	Ecological type of water	Palatability
<i>Artemisia halodendron</i> Turcz. ex Bess.	Compositae	Hemicrypto-geophyte	Limb	Rhizome	Mesoxerophyte	Less palatable
<i>Artemisia frigida</i> Willd.	Compositae	Chamaephyte	Stolon	Taproot	Xerophyte	Palatable
<i>Lespedeza davurica</i> (Laxm.) Schindl.	Leguminosae	Chamaephyte	Limb	Taproot	Mesoxerophyte	Palatable
<i>Hedysarum fruticosum</i> Pall.	Leguminosae	Hemicryptophyte	Limb	Taproot	Mesoxerophyte	Palatable
<i>Caragana microphylla</i> Lam.	Leguminosae	Chamaephyte	Limb	Taproot	Mesoxerophyte	Palatable
<i>Ceratoides arborescens</i> (Losinsk.) Tsien et Ma	Chenopodiaceae	Chamaephyte	Turb	Taproot	Xerophyte	Less palatable

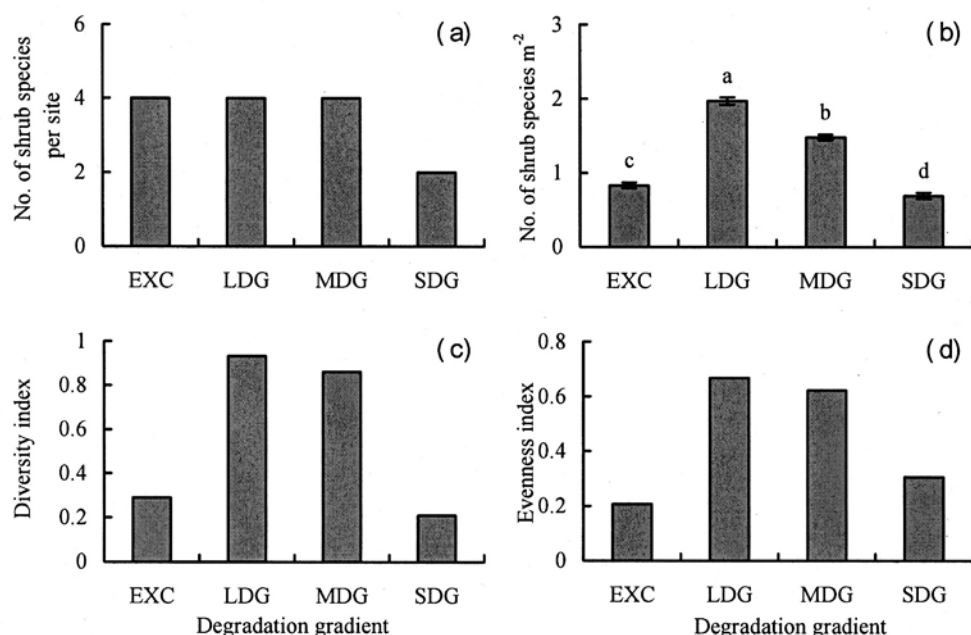


Figure 1. Changes in (a) total number of shrub species per site, (b) mean number of shrub species m^{-2} , (c) shrub diversity index and (d) shrub evenness index in the established vegetation of the four sites along the degradation gradient. EXC = exclosure (protected grassland). LDG = lightly degraded grassland. MDG = moderately degraded grassland. SDG = severely degraded grassland. Means with different letters indicate significant differences at $P < 0.05$ between the four sites (ANOVA followed by LSD tests).

Table 2. Mean ($\pm$ SE) density of established plants m^{-2} (% frequency) of shrub species present in the established vegetation of the four sites along the degradation gradient. EXC = exclosure (protected grassland), LDG = lightly degraded grassland, MDG = moderately degraded grassland, and SDG = severely degraded grassland. Means with different letters within each species indicate significant differences between the four sites (ANOVA followed by LSD tests). * $P < 0.05$, ** $P < 0.01$, *** $P < 0.0001$ and ns = not significant.

	EXC	LDG	MDG	SDG	$F_{(3, 1616)}$
<i>Artemisia halodendron</i>	$0.003 \pm 0.001c$ (1)	$0.50 \pm 0.16b$ (26)	$1.62 \pm 0.09a$ (91)	$0.60 \pm 0.07b$ (62)	53.45***
<i>Artemisia frigida</i>	$0.01 \pm 0.004a$ (1)	$0.00 \pm 0.00b$ (0)	$0.00 \pm 0.00b$ (0)	$0.00 \pm 0.00b$ (0)	2.01ns
<i>Lespedeza davurica</i>	$1.71 \pm 0.28b$ (75)	$11.60 \pm 1.22a$ (91)	$0.82 \pm 0.19bc$ (41)	$0.013 \pm 0.003c$ (6)	91.82***
<i>Hedysarum fruticosum</i>	$0.00 \pm 0.00b$ (0)	$1.13 \pm 0.18a$ (67)	$0.05 \pm 0.01b$ (9)	$0.00 \pm 0.00b$ (0)	52.63***
<i>Caragana microphylla</i>	$0.00 \pm 0.00a$ (0)	$0.07 \pm 0.05a$ (13)	$0.02 \pm 0.004a$ (5)	$0.00 \pm 0.00a$ (0)	2.08ns
<i>Ceratoides arborescens</i>	$0.05 \pm 0.02a$ (6)	$0.00 \pm 0.00b$ (0)	$0.00 \pm 0.00b$ (0)	$0.00 \pm 0.00b$ (0)	5.69**
Total shrub abundance	$1.77 \pm 0.27c$	$13.30 \pm 1.29a$	$2.51 \pm 0.20b$	$0.61 \pm 0.06d$	99.61***

exclosure, whereas *A. halodendron* occurred more frequently in grasslands under moderate and severe degradation (fig. 2a and table 2). Moreover, *L. davurica* and *Caragana microphylla* were far more frequent in occurrence in the lightly degraded grassland, although the former was present in all four sites (fig. 2a and table 2). Similar patterns were observed when performing DCA using the species abundance data for the four sites (fig. 2b and table 2).

Discussion

Effects of Degradation Level

This study indicates that degradation level strongly affected shrub plant diversity and abundance of individual species in the xeric sandy grasslands. This is consistent with observations from other studies to have demonstrated that overgrazing

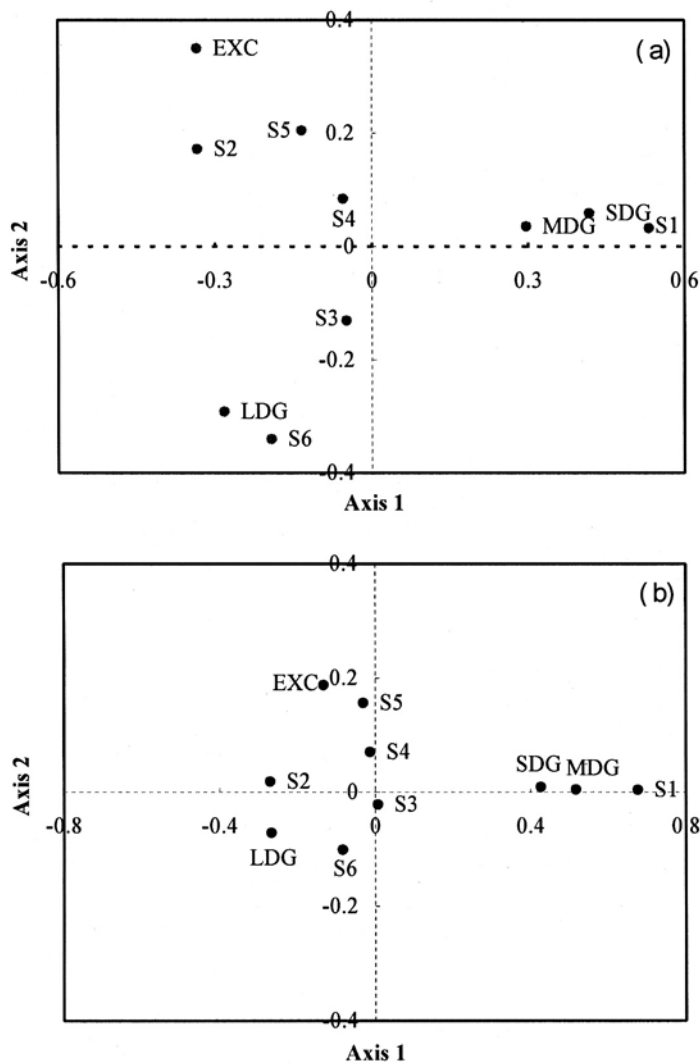


Figure 2. Derended correspondence analysis based on (a) frequency and (b) abundance of shrub species present in the established vegetation of the four sites along the degradation gradient. EXC = exclosure (protected grassland), LDG = lightly degraded grassland, MDG = moderately degraded grassland, and SDG = severely degraded grassland. S1 = *Artemisia halodendron*, S2 = *Lespedeza davurica*, S3 = *Hedysarum fruticosum*, S4 = *Ceratoides arborescens*, S5 = *Artemisia frigida*, and S6 = *Caragana microphylla*.

by herbivores generally has negative impacts on recruitment and regeneration of many species in most plant communities (Tiver and Andrew 1997; Li and others 2002; Landsberg and others 2003; Zhao and others 2004). However, the influence of degradation level varied with different shrub species, providing evidence supporting the hypothesis we originally posed, that is, different shrub species are likely to have had different responses to level of grassland degradation. From the responses of individual shrub species, we were able to identify three definite response types relating to degradation level. The first type is represented by *A. halodendron* showing a positive response to degradation level. Its number of established plants m^{-2} and its frequency of occurrence in the vegetation increased with increasing degradation level, and maximum

abundance and frequency were noted in the moderately degraded grassland. This indicates that moderate grazing disturbance favors the survival and growth of this species. This is in line with the study of Chao and others (1999) on the distribution of *A. halodendron* population in differently degraded grassland types, reporting that abundance of *A. halodendron* plants was highest on moderately degraded semi-fixed sand dunes, intermediate on severely degraded mobile sand dunes, and lowest on lightly degraded fixed sand dunes. In contrast, some shrub species such as *L. davurica*, *H. fruticosum* and *C. microphylla* belonged to the second type demonstrating a negative response to degradation level. Their number of established plants and their frequency of occurrence in the vegetation decreased dramatically with increasing degradation level, and peak abundance and frequency occurred in the lightly degraded grassland. This suggests that these three shrub species appear to be adapted to survive under light grazing pressure. *C. arborescens* and *A. frigida* belonged to the third type exhibiting a different response pattern from the first two response types. Both species had disappeared from the three unprotected sites and occurred only in the protected grassland (exclosure), again suggesting that they are very sensitive to grazing disturbances. Previous studies have shown that the survival and growth of *A. frigida* was strongly affected by defoliation due to its low grazing tolerance, and light to moderate grazing is likely to result in extinction of this species (Li and others 2002). Therefore, presence or absence of *A. frigida* in the community is usually used as an indicator for establishing whether grassland is overgrazed (Zhao and Zhou 1999). The observed differences in response patterns of individual shrub species to degradation level resulted most probably from the differences in their life-history and plant morphological traits, which in turn led to the differences in their ecological adaptation abilities to grazing disturbances. Many studies have shown that life history and plant morphology are important attributes in determining the responses of plant species to grazing intensity (Noy-Meir and others 1989; McIntyre and others 1995; Lavorel and others 1997). In the present study, for example, an explanation for high grazing tolerance of *A. halodendron* is its massive perennating buds on rhizomes that are buried near the soil surface (Li and Zhang 1991). Further, persistence of *A. halodendron* may also be associated with its superior capacity to produce offspring through vegetative propagation under the condition of sand burial (Chao and others 1999). This is because vegetative propagation of *A. halodendron* can take place only when its shoots are partially buried by moving sand, as the buried shoots can form roots from their nodes under favorable moisture conditions and consequently become new ramets (Chao 2000). The grasslands under moderate and severe degradation are generally characterized by a highly erodible environment (Li and others 2003a), providing greater opportunities for *A. halodendron* shoots to be buried by moving sand and thus encouraging its vegetative propagation. In contrast, both the protected and lightly degraded grassland are characterized by a significantly less erodible environment, providing less chance for *A. halodendron* shoots to be buried by moving sand and thus limiting *A. halodendron*'s vegetative

propagation. For that reason, it is not surprising why *A. halodendron* had significantly higher abundance and frequency in grasslands under moderate and severe degradation in comparison with the protected and lightly degraded grasslands.

Analysis of the associations between shrub species and sites sampled also provided further evidence for supporting the hypothesis above. In these analyses, we found that most of the shrub species were closely associated with particular sites relating to different degrees of degradation. Of the six shrub species recorded in the study site, *A. halodendron* and *L. davurica* occurred in all four sites but the former had the highest frequency in the moderately degraded grassland and the latter had the highest frequency in the lightly degraded grassland. *H. fruticosum* and *C. microphylla* were restricted to the lightly and moderately degraded grasslands and *C. arbore-scens* and *A. frigida* occurred only in the enclosure.

Role of Enclosure Management

Our results indicate that the short-term (5 years) enclosure resulted in an increase in shrub plant diversity through conserving species that decreased or disappeared under intense grazing conditions. However, enclosure effects were found to vary remarkably with the community parameter considered (for example, shrub species richness, species diversity, or shrub density of buried seeds). For example, the total number of shrub species per site was only higher in the enclosure than in the severely degraded grassland but no differences were found between the enclosure and both the lightly and moderately degraded grasslands. Nonetheless, the mean number of shrub species m⁻² and shrub species diversity index in the enclosure were consistently higher than in the severely degraded grassland but were significantly lower as compared with the lightly and moderately degraded grasslands. These results suggest that enclosure practice is generally necessary to the severely degraded grassland while light to moderate grazing disturbance is helpful for the maintenance of shrub species diversity. This agrees with findings of a 5-year grazing experiment conducted in a sandy grassland in the Horqin Sandy Land (Zhao and others 2004), reporting that light grazing favors vegetation restoration and community stability of the deteriorated grassland. Li and Wang (1999) and Li and Li (2000) also reported that light grazing is helpful in maintaining plant species diversity and standing crop biomass production in sandy grasslands of Inner Mongolia.

The effect of enclosure also changed with shrub species. The short-term enclosure only resulted in an increase of *L. davurica* abundance as compared with the moderately and severely degraded grasslands and re-colonization of *C. arbore-scens* and *A. frigida* that had disappeared from the unprotected grassland. However, enclosure had less impact on abundances of established *H. fruticosum* and *C. microphylla* plants. This species-specific response to enclosure may reflect a major difference in that the short-term enclosure may create a new biotic and abiotic environment by allowing only certain species to establish and survive but preventing recruitment of

other species. Further information on the mechanism how the survival and growth of individual shrub species is affected by interactive effects of a set of biotic and abiotic factors is needed to guide the management for conservation of degraded shrub plants in the studied sandy grassland ecosystem.

Acknowledgments

We gratefully acknowledge the Naiman Desertification Research Station in Chinese Academy of Sciences for permission to work on its experimental grasslands. This work was supported financially by the International Partnership Project (CXTD-Z2005-2-4), the National Natural Science Foundation of China (39730100 and 90102011), and the Innovation Research Project from the Cold and Arid Regions Environmental and Engineering Research Institute, Chinese Academy of Sciences (2004121).

References

- Andrén, O.; Zhao, X. Y.; Liu, X. M. 1994. Climate and litter decomposition in Naiman, Inner Mongolia, China. *Ambio*. 23: 222-224.
- Chang, X. L.; Wu, J. G. 1997. Species diversity changes during desertification in Horqin Sandy Land. *Chin. J. Appl. Ecol.* 8: 151-156. (In Chinese with English abstract).
- Chao, L. M.; Piao, S. J.; Zhi, R. N.; Song, M. H. 1999. The distribution patterns of *Artemisia halodendron* populations under different types of sandy grassland. *Journal of Desert Research*. 19: 45-48. (In Chinese with English abstract)
- Chao, L. M. 2000. The dynamics of *Artemisia halodendron* populations in different types of sandy land in Inner Mongolia. M.S. thesis, the University of Inner Mongolia, China. (In Chinese with English abstract)
- Chen, Z. Z. 1998. Degradation of natural grassland ecosystems and its control in China. Beijing, China Science & Technology Press, 86-89 p.
- Chen, Z. Z.; Wang, S. P. 2000. Typical grassland ecosystems in China. Beijing, Science Press, 1-9 p.
- ISSS, ISRIC, and FAO. 1998. World Reference Base for Soil Resources, World Soil Resources Reports 84, FAO, Rome.
- Jiang, D. M.; Liu, Z. M.; Cao, C. Y.; Kou, Z. W.; Wang, R. N. (eds) 2003. Desertification and ecological restoration of the Horqin Sandy Land in Inner Mongolia. Beijing, China Environmental Science Press, 63-142 p. (In Chinese)
- Landsberg, J.; O'Connor, T.; Freudenberger, D. 1999. The impacts of livestock grazing on biodiversity in natural ecosystems. In *Nutritional Ecology of Herbivores*. In: Jung, H. J.; Fahey, G. C., eds. American Society of Animal Science, Savoy, IL. 752-777 p.
- Li, B. 1997. Grassland degradation and its control strategies in North China. *Agricultural Science in China*. 30: 1-9. (In Chinese with English abstract)
- Li, F. R.; Zhao, A. F.; Zhou, H. Y.; Zhang, T. H.; Zhao, X. 2002. Effects of simulated grazing on growth and persistence of *Artemisia frigida* in a semiarid sandy rangeland. *Grass and Forage Science*. 57: 239-246.
- Li, F. R.; Zhang, H.; Zhang, T. H.; Shirato, Y. 2003a. Variations of sand transportation rates in sandy grasslands along a desertification gradient in northern China. *Catena*. 53: 255-272.

- Li, F. R.; Zhang, H.; Zhao, L.Y.; Shirato, Y.; Wang, X. Z. 2003b. Pedoecological effects of a sand-fixing poplar (*Populus simonii* Carr.) forest in a desertified sandy land of Inner Mongolia, China. *Plant and Soil*. 256: 431-442.
- Li, J.; Zhang, X. F. 1991. A preliminary study of growth traits of *Artemisia halodendron*. *Journal of Desert Research*. 11: 50-58. (In Chinese with English abstract)
- Li, Y. H.; Wang, S. P. 1999. Responses of plant and plant community to different stocking rates. *J. China Grassland*. 3: 11-19. (In Chinese with English abstract)
- Li, W. L.; Li, Z. Z. 2000. The degradation mechanism of desert grassland and the counter-measures for continued utilization of pastures. *J. Lanzhou Univ*. 36: 161-169. (In Chinese with English abstract).
- Liu, X. M.; Zhao, H. L.; Zhao, A. F. (eds.) 1996. *Wind-Sandy Environment and Vegetation in the Horqin Sandy Land, China*. Science Press, Beijing (In Chinese).
- Lovorel, S.; McIntyre, S.; Landsberg, J.; Forbes, T. D. A. 1997. Plant functional classifications: from general groups to specific groups based on responses to disturbance. *Trends in Ecology and Evolution*. 12: 474-477.
- Magurran, J. 1988. *Ecological Diversity and Its Measurement*. New Jersey, Princeton University Press.
- McIntyre, S.; Lavorel, S.; Tremont, R. M. 1995. Plant life-history attributes: their relationship to disturbance response in herbaceous vegetation. *Journal of Ecology*. 83: 31-44.
- Noy-Meir, I.; Gutman, M.; Kaplan, Y. 1989. Responses of Mediterranean grassland plants to grazing and protection. *Journal of Ecology*. 77: 290-310.
- Pielou, E. C. 1975. *Ecological Diversity*. New York, John Wiley & Sons Inc.
- Ren, A. Z.; Gao, Y. B.; Wang, J. L. 2001. Root distribution and canopy structure of *Salix gordejewii* in different sandy land habitats. *Acta Ecologica Sinica*. 3: 399-404. (In Chinese with English abstract)
- Tiver, F.; Andrew, M. H. 1997. Relative effects of herbivory by sheep, rabbits, goats and kangaroos on recruitment and regeneration of shrubs and trees in eastern South Australia. *Journal of Applied Ecology*. 34: 903-914.
- Wang, H. O.; Zhou, R. L. 1999. Physiological changes in *Artemisia frigida* and *Artemisia halodendron* under high temperature stresses. *Journal of Desert Research*. 19: 55-58. (In Chinese with English abstract).
- Wang, T. 2000. Land use and sandy desertification in North China. *J. Desert Res*. 20: 103-113. (In Chinese).
- Wang, T.; Wu, W.; Xue, X.; Zhang, W. M.; Han, Z. W.; Sun, Q. W. 2003. Temporal and spatial evolution of desertification land in northern China. *Chinese Journal of Desert Research*. 20: 230-235. (in Chinese with English abstract)
- Xuan, J.; Liu, G. L.; Du, K. 2000. Dust emission inventory in northern China. *Atmosph. Environ*. 34: 4565-4570. (In Chinese with English abstract)
- Zhang, T. H.; Zhao, H. L.; Li, S. G.; Li, F. R.; Shirato, Y.; Toshiya, O.; Taniyama, I. 2004. A comparison of different measures for stabilizing moving sand dunes in the Horqin Sandy Land of Inner Mongolia, China. *Journal of Arid Environments*. 58: 202-213.
- Zhao, A. F.; Zhou, H. Y. 1999. A preliminary study on grazing tolerance of *Artemisia frigida* population. *Chinese Journal of Desert Research*. 19: 65-68. (In Chinese with English abstract)
- Zhao, H. L.; Li, S. G.; Zhang, T. H.; Ohkuro, T.; Zhou, R. L. 2004. Sheep gain and species diversity: in sandy grassland, Inner Mongolia. *Journal of Range Management*. 57: 187-190.
- Zhao, L. Y.; Li, F. R.; Wang, X. Z. 2003. Characteristics of soil seed bank and standing vegetation changes in sandy grasslands along a desertification gradient. *Acta Ecologica Sinica*. 23: 1745-1756. (In Chinese with English abstract)
- Zhou, H. Y. 1999. Responses and variations of *Artemisia frigida* and *Artemisia halodendron* to water stress in Horqin Sandy Land, Inner Mongolia. *J. China Grassland*. 6: 13-17. (In Chinese with English abstract)
- Zhou, H. Y.; Zhao, A. F. 2002. Ecophysiological characteristics and their competition mechanism of the two dominant shrubs *Artemisia frigida* and *Artemisia halodendron* in Horqin Sandy Land. *Acta Ecologica Sinica*. 6: 894-900.
- Zhou, R. L.; Sun, G. J.; Wang, H. O. 1999. Changes in osmotic regulation substances as affected by drought and high temperature stresses in several shrub species in sandy land environment. *Journal of Desert Research*. 19: 18-22. (In Chinese with English abstract)
- Zhu, Z. D.; Chen, G. T. 1994. *The Sandy Desertification in China*. Beijing, Science Press, 250-268 p. (In Chinese)

The Authors

¹ Key Laboratory of Desert and Desertification, the Cold and Arid Regions Environmental and Engineering Research Institute, Chinese Academy of Sciences, Lanzhou 730000, China. lfengrui@vip.163.com

² Pastoral Agriculture Science and Technology. Lanzhou University, Lanzhou 730000, China.

Intraspecific Variation in Leaf Anatomy of Blackbrush (*Coleogyne ramosissima* Torr.)

Simon A. Lei¹

Abstract: Differences in anatomical characteristics of blackbrush (*Coleogyne ramosissima* Torr.) leaves were quantitatively investigated along an elevational gradient in Lee Canyon of the Spring Mountains in southern Nevada. Three elevational sites were selected: a lower blackbrush ecotone, a nearly monospecific stand in the middle of the gradient, and an upper blackbrush ecotone. Stomatal density was significantly greater and palisade parenchyma was significantly shorter in the lower ecotone compared to the upper ecotone. Vessel diameters and areas were significantly smaller, while vessel density was higher with increasing aridity. Blackbrush shrubs exhibited upper and lower elevational ecotypes at the anatomical level in Lee Canyon of southern Nevada.

Introduction

The blackbrush (*Coleogyne ramosissima* Torr.) vegetation type occurs at the bioregional transition between the Mojave and Great Basin Deserts from California through Nevada, Arizona, and Utah (Bowns 1973; Brooks and Matchett 2003). In the Mojave Desert, blackbrush occupies mid-elevations, with creosote bush-white bursage (*Larrea tridentata*-*Ambrosia dumosa*) vegetation zones below and pinyon-juniper (*Pinus monophylla*-*Juniperus osteosperma*) zones above (Bradley and Deacon 1967; Lei 1995; Lei and Walker 1997a, b). Blackbrush often forms nearly monospecific stands, which can comprise 90 to 95 percent of the total plant cover (Shreve 1942; Brooks and Matchett 2003).

Blackbrush generally grows less than 1 m in height in southern Nevada. Blackbrush has relatively small, ashy gray leaves from 5 to 15 mm long that turn black when wet (Bowns 1973). Terminal branches of blackbrush often die back several centimeters from the tip and become spinescent, allowing lateral growth to form intricate branches, resulting in a dense, rounded shrub (Provenza and Urness 1981). Blackbrush leaves are simple, sessile, and are semi-deciduous during many drought periods.

Blackbrush leaves possess some of the characteristics of xerophytic leaves that are typically small with reduced cell size, thick cuticle and blades, cylindrical, well-developed palisade mesophyll, and dense adaxial pubescence (Rundel and Gibson 1996). Such leaf design is generally interpreted as a response to arid habitats with water deficits and poor soil nutrients (Beadle 1966; Rundel and Gibson 1996). However, blackbrush leaves also share some of the features of typical sclerophyllous leaves. Plants, such as blackbrush, having revolute leaf margins and hypostomatic leaves with hypodermis are common occurrence in some sclerophyllous scrub (chaparral) communities of the Mediterranean-type climate or cool and high elevation xerophytic plant communities (Gibson

1996). Blackbrush does not occur in low Mojavean valleys in southern Nevada.

Previous studies by Bowns (1973), Bowns and West (1976), Callison and Brotherson (1985), Jeffries and Klopatek (1987), Provenza (1978), Lei (1995, 1997c, 1999, 2001, 2003), Lei and Walker (1997a and 1997b), Pendleton and Pendleton (1995), Brooks and Matchett (2003), and others have increased our understanding on various aspects of the biology and ecology of blackbrush. However, previous research studies did not examine ecotypic variation in blackbrush leaf anatomy as elevation changes. The objective of this study was to quantify ecotypic variation of anatomical characteristics in blackbrush leaves along an elevational gradient in a southern Nevada blackbrush shrubland.

Methods

Field and Laboratory Studies

Field studies were conducted in Lee Canyon (36°04' N, 115°16' W) of the Spring Mountains in southern Nevada. Lee Canyon is located approximately 70 km northwest of Las Vegas, Nevada. Within a climax blackbrush shrubland, three elevational sites were chosen: a lower ecotone (1,400 m), a nearly monospecific blackbrush stand (1,625 m), and an upper ecotone (1,750 m). Common woody plants present at the lower blackbrush ecotone included creosote bush and white bursage, while at the upper blackbrush ecotone, woody associates included big sagebrush (*Artemisia tridentata*) and Utah juniper. Common herbaceous plants contained members of the Asteraceae, Brassicaceae, Fabaceae, and Poaceae families.

Southern Nevada has an arid continental desert climate with hot, dry summers and cool, wet winters (table 1). Although most precipitation occurs during winter and summer seasons,

In: Sosebee, R.E.; Wester, D.B.; Britton, C.M.; McArthur, E.D.; Kitchen, S.G., comp. 2007. Proceedings: Shrubland dynamics—fire and water; 2004 August 10-12; Lubbock, TX. Proceedings RMRS-P-47. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 173 p.

Table 1. Mean monthly precipitation and mean monthly maximum and minimum air temperature in the Las Vegas Valley. The climatological data (National Weather Service) were obtained collectively from multiple long-term weather stations in Las Vegas of southern Nevada.

	Temperature (C)		Precipitation (mm)
	High	Low	
January	14.4	1.1	12.7
February	17.0	23.9	11.4
March	20.6	6.7	10.2
April	25.6	10.6	5.1
May	31.1	15.6	5.1
June	37.7	20.6	5.1
July	41.1	23.3	11.4
August	39.4	23.3	14.0
September	35.0	18.9	7.6
October	27.8	12.2	6.4
November	19.4	6.1	11.4
December	14.4	1.1	7.6

the total amount of annual precipitation varies considerably from year to year. Summer monsoonal rainfall and storms generally occur from July through early September, and primarily come from the Gulf of California. Summer storms, brief, episodic, and locally intense, are variable in both time and space. Winter rainfall, on the contrary, tends to be mild and widespread, and come from the Pacific Ocean. Winter rainfalls may last up to several days. Snow is frequent in upper blackbrush ecotones at relatively high elevations on desert mountain slopes. Southern Nevada is an area of temperature extremes, ranging from a mean minimum January temperature of 1.1°C to a mean July maximum of 41.1°C (Climatological Data, Las Vegas) (table 1). In general, precipitation is positively correlated, and air temperature is negatively correlated with elevation (Rowlands and others 1977; Lei 1997b).

Blackbrush leaves were collected for anatomical observations in a Community College of Southern Nevada (CCSN) biology laboratory. Fifteen (15) different plants were randomly selected in each of the three elevational sites. Within each blackbrush, a stratified random selection method was used, with two leaves being systematically collected—one from the upper canopy and one from the lower canopy. Within each layer of canopy, leaves were collected in all cardinal directions to avoid biased sampling. A thin coat of clear nail polish

was applied to the abaxial leaf surfaces, followed by the aid of an optical microscope (400X) to determine relative stomatal density and dimensions (length and width). Tiny, thin pieces of leaf tissues were sliced using two sharp razor blades that were compressed tightly. This optical microscope, with an ocular micrometer installed in the eyepiece, was also used to quantify vessel diameter and area, as well as to determine relative tissue thickness that were seen in the microscopic field. Vessel areas were computed using the standard circle formula (πr^2). A microprojector was used to enlarge the transection so that stomatal and vessel characteristics could be quantified.

Statistical Analyses

One-way analysis of variance (ANOVA; Analytical Software 1994) were performed to detect elevational ecotype variation in anatomical characteristics of blackbrush leaves. Tukey and Scheffe multiple mean comparison tests (Analytical Software 1994) were conducted to compare means when a significant elevation effect was detected. Mean values were presented with standard errors, and statistical significance was determined at $P \leq 0.05$.

Results and Discussion

Blackbrush leaves are hypostomatic. Stomates were deeply sunken in the abaxial epidermis only, and were connected to large substomatal chambers. Anatomical observations revealed that stomatal density of blackbrush decreased significantly ($P < 0.05$; table 1) with ascending elevation. Stomatal densities are greater in desert plants compared to mesophytic ecotypes (Gibson 1996). My results concur with Gibson's (1996) study since low elevational site had significantly greater stomatal densities per mm^2 when compared to high elevational site. Characteristic stomatal densities of geographically widespread species are 100 or more stomates per mm^2 (Mauseth 1988), which also corresponds with my data. Nevertheless, stomatal size (length and width) of blackbrush leaves did not differ significantly among the three elevational sites ($P > 0.05$; table 2), indicating that stomatal dimension was similar irrespective of elevational changes.

At the lower ecotone, vessel diameter and area of blackbrush leaves increased, whereas vessel density decreased significantly along a gradient of ascending elevation ($P \leq 0.05$; table 3). Vessels in desert shrubs would become shorter,

Table 2. Mean ($\pm$ se) stomatal density and dimension of blackbrush leaves along an elevational gradient in southern Nevada. Adaxial stomata are absent in blackbrush.

	Lower ecotone	Nearly pure stand	Upper ecotone
Stomatal density (stomates mm^{-1})	90.3 $\pm$ 13.2 a ¹	86.4 $\pm$ 12.6 ab	80.6 $\pm$ 10.7 b
Stomatal length (μm)	10.8 $\pm$ 0.7 a	11.0 $\pm$ 0.8 a	11.8 $\pm$ 1.1 a
Stomatal width (μm)	5.4 $\pm$ 0.3 a	5.6 $\pm$ 0.2 a	5.9 $\pm$ 0.2 a

¹ Means within a leaf character followed by the same letter are not significantly different ($P > 0.05$; $n = 30$).

Table 3. Mean ($\pm$ se) vessel characteristics of blackbrush leaves along an elevational gradient in southern Nevada.

	Lower ecotone	Nearly pure stand	Upper ecotone
Vessel diameter (μm)	5.1 $\pm$ 1.7 a	6.0 $\pm$ 1.6 ab	6.9 $\pm$ 1.2 b
Vessel area (μm^2)	20.4 $\pm$ 0.7 a	28.3 $\pm$ 0.8 b	37.4 $\pm$ 1.1 c
Vessel density (vessels mm^{-2})	98.6 $\pm$ 5.9 a	91.4 $\pm$ 5.5 b	86.1 $\pm$ 4.4 c

¹ Means within a leaf character followed by the same letter are not significantly different ($P > 0.05$; $n = 30$).

narrower, and more numerous with increasing aridity. This phenomenon also occurs in creosote bush, saltbush (*Atriplex hymenelytra*), and big sagebrush in Death Valley of southern California (Culp 1986). As predicted, conductive tissues in desert shrubs respond to greater water stress in lower than higher elevations (Culp 1986). Moreover, the range of vessel diameters is also of interest. Carlquist (1977) stated that foliar modifications can strongly affect a plant's response to its environment. Leaves exert a strong degree of control over water relations within big sagebrush (Sculth 1983) and blackbrush populations. Nevertheless, no comparative data are available since variations in vessel area and diameter of blackbrush leaves have not been measured quantitatively.

Vessel density increased significantly ($P \leq 0.05$; table 2) with decreasing elevation. The density of leaf vessels is known to increase with increasing aridity (Fahn 1982). The density of vessels is fewer at the higher elevations compared to the lower sites in southern Nevada (Culp 1986).

Below a uniseriate hypodermis, the palisade parenchyma was readily distinguished from the spongy parenchyma in this study. The palisade parenchyma consisted of continuously elongated (column-like) cells, mainly in the direction perpendicular to the leaf surface. The bifacial (abaxial) palisade parenchyma was significantly shorter ($P \leq 0.05$; table 4) with increasing aridity. The mean thickness of palisade parenchyma ranged from 165.9 μm in the lower ecotone to 176.8 μm in the upper ecotone. No comparative data are available since variations in palisade parenchyma of blackbrush have not been measured quantitatively. Palisade parenchyma in creosote bush was also shown to increase in length with increasing aridity in Death Valley of southern California (Culp 1986).

Water availability during a growth period is an important factor affecting cell elongation. Cells imbibe water and exert turgor pressure on the primary cell wall. Therefore, the more water available to the cell, the longer it is likely to grow (Culp 1986). This possible explanation for differential cell

elongation along the elevational gradient may be results of the greater amount of water available at higher elevations in southern California (Culp 1986). Shorter palisade cells allow space for an increase in vessel numbers without significantly increasing in leaf size (Culp 1986).

Other leaf anatomical structures did not differ significantly ($P > 0.05$; table 4), indicating that tissue thicknesses were similar irrespective of elevational changes. These structures included length (thickness) of total lamina, upper and lower epidermis, hypodermis, and spongy parenchyma.

Ecological Implications and Future Directions

Although blackbrush growing at various elevations looked similar in general appearance, plants exhibited significant differences in certain anatomical structures as elevation changes in Lee Canyon of southern Nevada. Discovering upper and lower elevational ecotypes within the same species reveal the usefulness of plant anatomy in detecting fine-tuned variation. However, one must realize that ecotypic variation in blackbrush leaves is not strictly a function of elevation. A number of environmental attributes vary with changing elevation. Air and soil temperatures increase, whereas precipitation and soil moisture decrease with descending elevation. Such variation in environmental attributes would cause anatomical changes observed in blackbrush leaves. The extent to which my results are representative of blackbrush occurring at other sites is not completely known. However, this study suggested that blackbrush leaves were anatomically adaptable to habitat changes in the Spring Mountains of southern Nevada.

Blackbrush also exhibits upper and lower elevational ecotypes at the seed germination (Lei 1997c) and imbibition levels (Lei 2007). Blackbrush shrublands are a dominant

Table 4. Mean ($\pm$ se) tissue thickness (μm) (excluding cuticles and intercellular spaces) of blackbrush leaves along an elevational gradient in southern Nevada. Adaxial stomata are absent in blackbrush.

	Lower ecotone	Nearly pure stand	Upper ecotone
Lamina	374.9 $\pm$ 13.2 a	376.2 $\pm$ 6.8 a	380.8 $\pm$ 5.6 a
Upper epidermis	16.4 $\pm$ 1.8 a	15.9 $\pm$ 2.5 a	15.8 $\pm$ 2.9 a
Lower epidermis	14.1 $\pm$ 1.2 a	14.1 $\pm$ 1.4 a	13.7 $\pm$ 1.5 a
Hypodermis	34.0 $\pm$ 3.1 a	33.1 $\pm$ 2.6 a	32.8 $\pm$ 1.9 a
Palisade parenchyma	165.9 $\pm$ 7.9 a	169.7 $\pm$ 7.3 ab	176.8 $\pm$ 8.2 b
Spongy parenchyma	140.5 $\pm$ 7.2 a	141.5 $\pm$ 8.9 a	141.7 $\pm$ 6.5 a

¹ Means within a leaf character followed by the same letter are not significantly different ($P > 0.05$; $n = 30$).

vegetation type in the Mojave Desert. Despite significant publications and contributions in the past, the biology of blackbrush are still not completely known and should deserve further investigations to improve our understanding on various aspects of blackbrush shrubs.

Acknowledgments

I gratefully acknowledge Steven Lei, David Valenzuela, and Shevaun Valenzuela for collecting fresh blackbrush leaves in the field and for meticulously observing anatomical structures in the laboratory. I also sincerely appreciate David Charlet for critically reviewing an earlier version of this manuscript. The Department of Biology at the Community College of Southern Nevada (CCSN) provided logistical support.

Literature Cited

- Analytical Software. 1994. Statistix 4.1, an interactive statistical program for microcomputers. St. Paul, MN: Analytical Software 329 p.
- Beadle, N. C. W. 1966. Soil phosphate and its role in molding the Australian flora and vegetation, with special reference to xeromorphy and sclerophylly. *Ecology* 47: 992-1007.
- Bowns, J. E. 1973. An autecological study of blackbrush (*Coleogyne ramosissima* Torr.) in southwestern Utah. Logan, UT: Department of Range Science, Utah State University. 115 p.
- Bowns, J. E.; West, N. E. 1976. Blackbrush (*Coleogyne ramosissima* Torr.) on southwestern Utah rangelands. Utah Agriculture Experimental Station Research Report 27: 1-27.
- Bradley, W. G.; Deacon, J. E. 1967. The biotic communities of southern Nevada. Nevada State Museum. Anthropological Papers. 13: 202-295.
- Brooks, M. L.; Matchett, J. R. 2003. Plant community patterns in unburned and burned blackbrush (*Coleogyne ramosissima* Torr.) shrublands in the Mojave Desert. *Western North American Naturalist*. 63: 283-298.
- Callison, J.; Brotherson, J. D. 1985. Habitat relationships of blackbrush community (*Coleogyne ramosissima*) of southwestern Utah. *Great Basin Naturalist*. 45: 321-326.
- Culp, M. G. 1986. Anatomical and morphological adaptations of plants to aridity in Death Valley National Monument. Las Vegas, NV: University of Nevada, Las Vegas. 65 p.
- Gibson, A. C. 1996. Structure-Function Relations of Warm Desert Plants. Berlin, Germany: Springer-Verlag. 215 p.
- Jeffries, D. L.; Klopatek, J. M. 1987. Effects of grazing on vegetation of the blackbrush association. *Journal of Range Management*. 40: 390-392.
- Lei, S. A. 1995. A gradient analysis of *Coleogyne* communities in Southern Nevada. Master's thesis. Las Vegas, NV: University of Nevada, Las Vegas. 117 p.
- 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.
- Lei, S. A. 1997. Variation in germination response to temperature and water availability in blackbrush (*Coleogyne ramosissima*) and its ecological significance. *Great Basin Naturalist*. 57: 172-177.
- Lei, S. A. 1999. Postfire woody vegetation recovery and soil properties in blackbrush (*Coleogyne ramosissima* Torr.) shrubland ecotones. *Arizona-Nevada Academy of Sciences*. 32: 105-115.
- Lei, S. A. 2001. Postfire seed bank and soil conditions in a blackbrush (*Coleogyne ramosissima* Torr.) shrubland. *Southern California Academy of Sciences*. 100: 14-22.
- Lei, S. A. 2007. Intraspecific variation in seed imbibition of blackbrush (*Coleogyne ramosissima*: Rosaceae). *Madroño*. 54: 27-29.
- Lei, S. A. 2003. Environmental attributes correlating with density of blackbrush (*Coleogyne ramosissima*) shrubs in the Spring Mountains of southern Nevada. *Western North American Naturalist*. 63: 391-399.
- Mauseth, J. D. 1988. Plant Anatomy. Menlo Park, CA: The Benjamin/Cummings Publishing Company, Inc. 560 p.
- Pendleton, B. K.; Pendleton, R. L. 1998. Pollination biology of *Coleogyne ramosissima* (Rosaceae). *The Southwestern Naturalist*. 43: 376-380.
- Provenza, F. 1978. Getting the most out of Blackbrush. *Utah Science*. 39: 144-146.
- 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, NY: John Wiley and Sons. 1002 p.
- Rundel, P. W.; Gibson, A. C. 1996. Ecological communities and processes in a Mojave Desert Ecosystem: Rock Valley, Nevada. Cambridge, MA: Cambridge University Press. 369 p.
- Shreve, F. 1942. The desert vegetation of North America. *Botanical Review*. 8: 195-246.

The Author

¹ Statistics and Research Methods Instructor, Department of Educational Psychology, University of Nevada, Las Vegas, NV. leisa@unlv.nevada.edu

Publishing Services Staff

Managing Editor • Lane Eskew

Page Composition & Printing • Nancy Chadwick

Editorial Assistant • Loa Collins

Contract Editor • Kristi Coughlin

Page Composition & Printing • Connie Lemos

Distribution • Richard Schneider

Online Publications & Graphics • Suzy Stephens



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 the 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	Reno, Nevada
Fort Collins, Colorado*	Albuquerque, New Mexico
Boise, Idaho	Rapid City, South Dakota
Moscow, Idaho	Logan, Utah
Bozeman, Montana	Ogden, Utah
Missoula, Montana	Provo, Utah

*Station Headquarters, Natural Resources Research Center, 2150 Centre Avenue, Building A, Fort Collins, CO 80526.

The U.S. Department of Agriculture (USDA) prohibits discrimination in all its programs and activities on the basis of race, color, national origin, age, disability, and where applicable, sex, marital status, familial status, parental status, religion, sexual orientation, genetic information, political beliefs, reprisal, or because all or part of an individual's income is derived from any public assistance program. (Not all prohibited bases apply to all programs.) Persons with disabilities who require alternative means for communication of program information (Braille, large print, audiotape, etc.) should contact USDA's TARGET Center at (202) 720-2600 (voice and TDD). To file a complaint of discrimination, write to USDA, Director, Office of Civil Rights, 1400 Independence Avenue, S.W., Washington, DC 20250-9410, or call (800) 795-3272 (voice) or (202) 720-6382 (TDD). USDA is an equal opportunity provider and employer.