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Fire's Effects on Wildlife Habitat— Symposium Proceedings

Missoula, Montana, March 21, 1984

FOREWORD

The symposium, "Fire's Effects on Wildlife Habitat," represents one of the closing ceremonies of the Fire Effects and Use Research and Development Program, conducted by the Intermountain Research Station from 1979 to 1984. One of the R&D program's most important goals had been to study the long-and short-term effects of fire on plant communities. We sought to thus enhance our understanding of fire's effects on vegetation, so fundamental to managing forests and rangelands for their many resources.

Judicious use of fire probably benefits wildlife more than any other resource. For eons, the wildlands and wildlife of the Northern Rockies and Intermountain West have been shaped by fire. Therefore no management tool is more appropriate than fire for manipulating wildlife habitat. Fire, unfortunately, produces various effects on wildlife habitat, depending on fuels, weather, and the site. Before we can use fire with great confidence, we must be able to evaluate these factors and predict the result.

Settlement by Europeans drastically curtailed fire's influence on wildlife habitat. Fire control, grazing, and settlements have all markedly reduced the number and size of fires in the American West. George Gruell's comparisons of early and recent photos illustrate the magnitude of changes in vegetation over the past century. The photos document that the early stages of plant succession, perhaps the optimum in wildlife habitat, were gradually replaced by even larger and more abundant conifers that provide comparatively poorer wildlife habitat. We have come to recognize that prescribed fire is the most effective and most economically feasible tool for rejuvenating vast expanses of deteriorating wildlife habitat.

Land managers have slowly and carefully begun to use prescribed fire to rejuvenate wildlife habitat. Nevertheless, they desperately need sound knowledge of fire's effects. The kind of fire that results and the influence of the season in which the burn is done are particularly important. The purpose of this symposium is to assemble some of this knowledge and make it available to others. We trust that the information herein will ultimately benefit wildlife and that the work reported will stimulate additional investigations. The future of wildlife depends upon intelligent maintenance of its habitat and in this endeavor fire will remain an important tool.

James E. Lotan and James K. Brown
Symposium Co-chairmen

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Compilers

JAMES E. LOTAN, Program Manager,
Intermountain Research Station,
Missoula, Mont.

JAMES K. BROWN, Project Leader,
Intermountain Research Station,
Missoula, Mont.

WILDLIFE AND FIRE RESEARCH: PAST, PRESENT, AND FUTURE

E. V. Komarek

INTRODUCTION

A keynote speaker has a unique advantage. Somewhat like a historian, he can look backward in time and also discuss the present. Unlike the historian, he may also point to the future. A keynote speaker also can ramble more or less all over the countryside. He doesn't have to have too much quantitative data and must be rather holistic in his approach.

According to the dictionary, a keynote address is supposed to present the essential issues of interest to the assembly. To fulfill that requirement, I will spend most of my time for what I see as the problems for the future, pointing out areas where research needs to be done--or continued and expanded--on the relationship of fire and wildfire.

THE PAST

Game management began on an empirical basis in the South at least by the early 1800's. At that time, scientific wildlife management began with the Cooperative Quail Study Investigation in the 1920's. Although the use of fire to attract game animals has been a practice well known to early peoples, including American Indians and our pioneer ancestors, this folk knowledge was overlooked in the attempt to preserve our Southeastern forests in the late 1920's and early 1930's.

The passage of the Clarke-McNary Act (1924), sponsored by the American Forestry Association, provided for Federal matching funds from the U.S. Forest Service and the development of State forest agencies in the South. These funds were earmarked only for fire fighting, <u>not</u> for fire prevention.

Bonninghausen pointed out:

> "in order to carry our the cooperative fire control agreements which the Florida Forest Service entered in to with private land owners at that time, it was necessary to stipulate the exclusion of fire, or funds would not be made available and the Florida Forest Service would be subject to criticism" (Bonninghausen 1962).

Thus, southern silviculture in practice became largely fire control. Along with the stimulus of Federal funds came the philosophy that all that was necessary for the original splendid forest to return was to prevent fire, exclude hogs, and leave ample seed trees; nature herself would restore longleaf pine to its primeval state.

During this period, however, there were roughly 1 million acres (40 500 ha) of southeastern pine and agricultural lands throughout the Coastal Plain devoted to quail hunting and winter recreational activities. These plantations had been burned regularly, mainly on an annual basis, for well over 50 years. Many of these plantations, ranging from 5,000 to 20,000 acres (2 000 to 8 000 ha), also had winter residences upon them; owners and their friends often came South for the 3 winter months. The area around Thomasville, GA, and Tallahassee, FL became the center for some of the earliest hunting. In addition to hunting owned land, these plantation owners also leased adjacent lands for hunting; within the lease was always a stipulation that after the end of the hunting season each year, usually on the last day of February, the properties would be burned in order to maintain the quail population.

With the Clarke-McNary Act, however, intensive efforts were made to stop all burning in the Coastal Plain of the Deep South. Instead of being blamed on timbermen, forest destruction was blamed on fire. The South was then subjected to a "crusade" by the American Forestry Association and the participating southern State forest services (Florida, Georgia, and Mississippi). It was called the Southern Forestry Education Project (1927-30).

> Teams of young men (were sent) into the South called "Dixie Crusaders" who spearheaded the assault on southern customs (on woods, range, game, and agricultural burning) as their truck caravans rolled through the piney woods broadcasting "with all the drama of the day" . . . . the crusaders traversed 300,000 miles, disseminating two million pieces of literature along the way. More than 5,200 motion picture programs and lectures were presented to three million people, one half of them children, with the USDA film "Trees of Righteousness" enjoying the most universal appeal. By 1923 the woods burner, sought out in his own lair, had been made to know the way of his transgression. "A great tide of indignation", the association asseverated, was sweeping out over the piney woods mobilizing sentiment against the woods burner (Schiff 1962).

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Author is at the Tall Timbers Research, Inc., Route 1, Box 678, Tallahassee, Fla.

A policy that totally excluded fire was successfully instituted in Florida and southern Georgia; by 1923 the formerly open pine lands in the Thomasville-Tallhassee region became brush-choked, and the quail population drastically decreased. This alarmed the plantation people, who agreed among themselves to finance a scientific investigation to determine why the quail population was declining. They established the Cooperative Quail Study Investigation (1923-28), headed by Herbert L. Stoddard. As early as 1925, in a preliminary report to the supporters of the Investigation, Stoddard pointed out that the absence of fire was the key to the shortage of the Bobwhite quail in this region. He finished his studies 4 years later and published his famous book, "The Bobwhite Quail: Its Habits, Preservation and Increase" (1931). Game management, or wildlife management as we now know it, had really begun. Stoddard was the first to demonstrate scientifically that wildlife was a crop of the land and that wildlife populations could be manipulated through land management practices. He pointed out fire may well be the most important single factor in determining what animal and vegetable life will thrive in many areas (Stoddard 1931).

The Cooperative Quail Study Investigation was succeeded by the Cooperative Quail Study Association, a consulting service that took the research Stoddard and others had conducted and applied it to management plans on more than 100 plantations, averaging about 10,000 acres (4 000 ha) each, scattered from North Carolina to Arkansas. Work was also conducted with several government agencies on the use of fire, but for political reasons most of these preferred not to publicize the fact that they were even interested in burning.

I worked with Stoddard in the Quail Association from 1931 to 1943. We found that on more than 75 percent of the hunting plantations we studied, fire exclusion was the principal factor in declining quail abundance. Other key factors were improper forestry operations and improper distribution of agriculture.

In 1945 my brother, Roy Komarek, and I were asked to manage Greenwood Plantation. The owner, John Hay Whitney, instructed us to "do something to benefit southern agriculture," to develop Greenwood's forests along the lines originally discussed by Stoddard, and to develop game and other resources along the lines recommended in the Cooperative Quail Study Association reports.

The property consists of 18,000 acres (7 300 ha) and is still under our management, so we have had ample opportunity to test our theories and ideas on the use of fire and the production of game animals like quail and many other wildlife species, including song birds. In 39 years of active administration and practical management, the ideas that Stoddard first advocated regarding fire and game management have proved sound.

Henry L. Beadel, owner of Tall Timbers Plantation, had been an original supporter of the Quail Investigation and a prime mover in the organization of the Cooperative Quail Study Association. In 1958 he founded, in cooperation with Stoddard, the Komareks, and many others, Tall Timbers Research, Inc., a foundation whose purpose is "a quest for ecological understanding."

The proper understanding of the place of fire in wildlife management was anchored in the Charter and in Mr. Beadel's will, which gave his 3,000-acre (1200 ha) plantation to the Foundation to be used for its research station.

Beginning in 1962, Tall Timbers Research, Inc., began sponsoring Fire Ecology Conferences, which promoted a better understanding of the use of fire and its many ramifications in nature. The conferences' proceedings brought international recognition to the Station for its pioneering efforts in this controversial field. Scientists and investigators in many disciplines (forestry, wildlife, agriculture, botany, zoology, geography, anthropology, and others) reported on their studies and ideas. More than 400 speakers from 22 countries throughout the world have taken part. Speakers have represented government agencies, private industry, and publicly and privately financed research institutions. There is no doubt that these meetings have done much to stimulate research in fire ecology (a term coined at the first conference, which has since become universally recognized) and the use and management of fire, particularly in wildlife and forestry practices.

The Clarke-McNary Act of 1924 had also spurred fire control and raised the possibility of total fire exclusion in the West, where its effects proved long-lasting. As recently as 1947, Schantz was asked to survey fire in the brushlands of California for the California Forestry Department. His report seldom referred to the possible beneficial use of fire for game habitat management but dealt largely on the destruction of game animals by massive wildfires in the State.

The 14th Tall Timbers Conference was held in 1976 at Missoula, Mont., and was sponsored jointly with the Intermountain Fire Research Council, an organization of Federal, State, and other foresters. The first paper presented was "From Fire Control to Fire Management: A Major Policy Change in the Forest Service." Since that conference many studies have been conducted in the West, on the use of fire in forestry practices as well as in wildlife habitat management. Public attitudes have changed to the point that now even commercial timber companies advertise that prescribed burning "sweeps the forest" of flammable debris.

THE PRESENT

In the past decade, the use of prescribed burning to manipulate wildlife habitat and for forestry and range practices has become commonplace in most parts of the United States, though the Northeast still lags somewhat. Prescribed burning is being used even there, however, on barrier islands and on certain lands devoted to range, forestry, wildlife, hunting, and recreation.

An example of public acceptance of controlled burning involves the helitorch, a 55-gallon (200 L) drum filled with jellied gasoline, equipped with an ignitor, and fastened beneath a helicopter. Fires can be ignited by dropping globs of burning jellied gasoline in spots throughout a forest; thousands of acres then burn properly and safely. The use of the helitorch was once considered spectacular and newsworthy, but in parts of the West and in the Southeast its use has become so commonplace it is now largely ignored by newspapers and television.

A great deal of research in fire ecology has focused only on certain facts of fire's relationship to wildlife habitat, which is concentrated, especially in the West, on large game animals. Innumerable studies have established that vegetation regenerated after burning--grass, brush, or even some trees--is always higher in protein, calcium, phosphorus, and other elements necessary for the good health of such animals. It is also widely recognized that such palatable material is absolutely essential for their well-being throughout the reproductive cycle--conception to birth--and during the milk-producing period.

The other emphasis in fire ecology in the last decade or so has been modifying the habitat for game species. Unfortunately, most of these studies investigate only the changes in plant communities and the resulting effects on the bird or mammal population being studied. The impression given is that habitat consists exclusively of cover and structure. The fact that the habitat must have food seems often to be overlooked; yet without the necessary food, any habitat, regardless of its structure and composition, will be of little value to most animals.

For example, over half the families of birds are species with precocial young, able to forage for themselves immediately after hatching. Every study made on any gallinaceous game bird, in the United States, as well as in other parts of the world, has shown that insects and other invertebrate material make up more than 80 percent of the normal diet of these precocious chicks during their first 2 to 3 weeks of life. Fledgling young that are raised in nests, (except for water birds that are fed fish) also are fed for a period of several weeks on nothing but insects or other invertebrates. Studies on related domestic species like chickens or more or less domesticated game birds have shown that a high-protein diet is also necessary in order for the female to lay a large number of healthy eggs. Furthermore, without a high-protein diet, the chicks that hatch will not be strong and may not live. A high-protein diet for song birds is just as necessary as it is for game birds and for the same reasons. Some of the most fruitful and valuable research in the coming decade could focus on the effect of fire on the invertebrate species that play such an important part in the food chain of so many of our wildlife species, particularly during the reproductive cycle.

THE FUTURE

The quality and value of research can be greatly influenced by the institution which produces it. There is real danger that the work of research institutions closely controlled by governmental, or even by commercial, interests will reflect official policy at best--and politics at worst--instead of objective information. The history of fire ecology and its relationship to the ecology of plants and animals as well as humans, shows the dangers of such a "controlled" situation. In his book "Fire and Water: Scientific Heresy in the Forest Service," Schiff (1962) pointed out the dangers and effects of government and academic dominances over fire ecology research during the second quarter of this century and beyond.

The reluctance of government-supported research to document the dangers of some pesticides points up the need for independent, privately financed, nongovernmental biological research organizations to serve the public by presenting impartially all the facts in this vital debate.

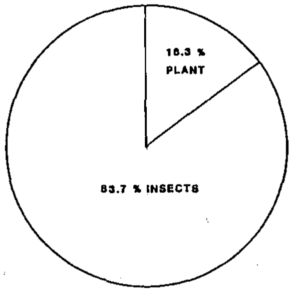
When the founders of Tall Timbers Research, Inc., set up that institution and stated its purpose, they recognized the necessity to develop public and scientific interest in fire ecology through long-term experiments, research, and demonstrations. This meant a research institution well structured and stable enough to guarantee experiment continuity and complete investigative freedom.

"A quest for ecological understanding," the Tall Timbers purpose, cannot be limited to game management alone, and the species studied cannot be only game species. Some of the most fruitful and valuable research in the coming decade could deal with information on the populations, composition, and abundance of such invertebrates as insects, spiders, snails, and earthworms, particularly as they relate to some of our endangered species of vertebrates.

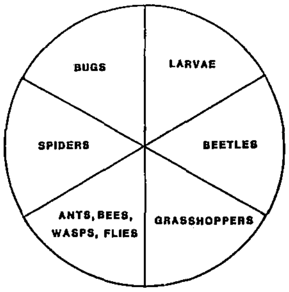
In the past decade or so, the Tall Timbers Research Station has realized the lack of information on the relationship of fire and various invertebrates and has conducted small, rather desultory, studies on the effect of fire on different invertebrates, including insects, spiders, earthworms, and snails. On the basis of this work more extensive studies of insects on the fire plots at Tall Timbers began in 1981.

In 1958, 84 half-acre (0.2 ha) plots were chosen at random all over the 3,000 acres (1 200 ha) of Tall Timbers Research Station on as many different soil types, topography, and conditions as possible. Since the Station's founding, these areas have been burned at specified intervals: annual, biennial, triennial, quadrennial, every 5th year, 7th year, 12th year, 25th year, 50th year, and so on. By design, some were not burned at all. Thus plots annually burned have been burned 25 times in the past 25 years; biennial plots have been burned 12 times; triennial burned 8 times, and so forth. Definitive studies on the insects on these plots began in 1982 and carried on intensively in 1983.

One of the reasons for this intensive study is that Stoddard (1931) had listed more species of insects and other invertebrates (over 400) as food for quail than other species of plants and seeds. All subsequent work on food habits on the Bobwhite quail seems to have focused on seeds and plants in spite of the fact that Stoddard showed that insects made up 82 percent or more of the diet of baby quail in the first 2 weeks of life (fig. 1).



TOTAL DIET



INSECTS CONSUMED

Figure 1.--Diet of Bobwhite quail during first two weeks of life based on research of Herbert L. Stoddard.

Studies in Britain have also shown the value of insect populations to partridge chicks by demonstrating that if insects are not available, the chicks starve to death. In 1970, Hurst also showed that on small quadrats on a burned right-of-way powerline in Mississippi, the diet of baby chicks was almost entirely insects.

In 1982 and in 1983, 1-day-old baby quail chicks were obtained from a propagating plant and fed a variety of insects as well as high-protein mash. It was quickly found that the baby chicks would eagerly go after grasshoppers that had been frozen and thawed out and that apparently they readily ate many species of grasshoppers and many species of miscellaneous insects. In 1983 these experiments were continued in much more detail; figure 2 shows the results. It was soon obvious that 1-day-old baby chicks when given a choice instinctively chose grasshoppers over miscellaneous insects or high-protein mash and that they thereby gained more weight when doing so.

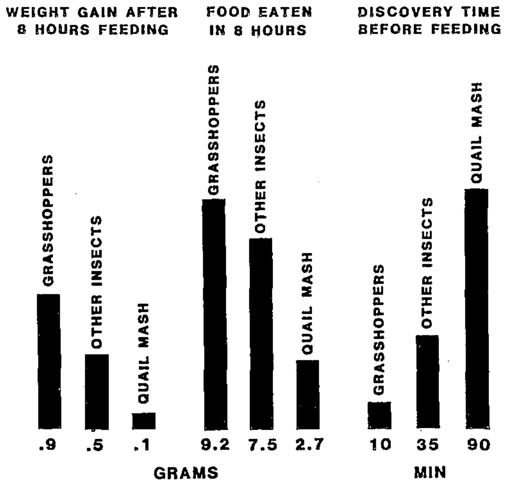


Figure 2.--Response of quail chicks to various foods. Weight and amount of food consumed in 10th of grams over 8-hour period. Discovery time is time elapsed before chicks began feeding.

While these experiments were going on, two quail propagating plants received the wrong mash from their supplier. Instead of a 27 percent protein mash, 20 percent protein mash had been substituted by error. Immediately after feeding with lower-protein mash, the laying hens' production dropped drastically, and eggs did not hatch properly, and the chicks produced were very weak and had a high mortality rate. One week after the mash was replaced by 27 percent protein mash, the quail hens began laying their normal complement of eggs. The eggs that were incubated hatched properly, and the chicks were strong. This demonstrated that the Bobwhite hen, as well as the chicks, requires a high-protein diet. Unfortunately, the average legume seeds on which many of us, including myself, had previously assumed were adequate to feed quail, are not high enough in protein, since they contain only about 20 percent protein.

Once these experiments showed us that quail chicks as well as adult quail apparently readily ate any kind of insect (though there seemed to be some preference for grasshoppers over miscellaneous invertebrates, including spiders), we began intensive, sweeping experiments on the Tall Timbers fire plots. For each collection, each plot was swept 200 times with a 10-inch butterfly net. We then sorted this collection into grasshoppers, miscellaneous insects, larvae, and spiders. Figure 3 shows that on the annually burned plots there were more Orthoptera in 1983, but less on the biennial plots, still less on the triennial plots, much less in the quadrennial plots, and on the unburned plots few or none at all. This demonstrated that the periodicity of fire plays a considerable part, not only in plant succession, but in insect succession and the kind and species that occur.

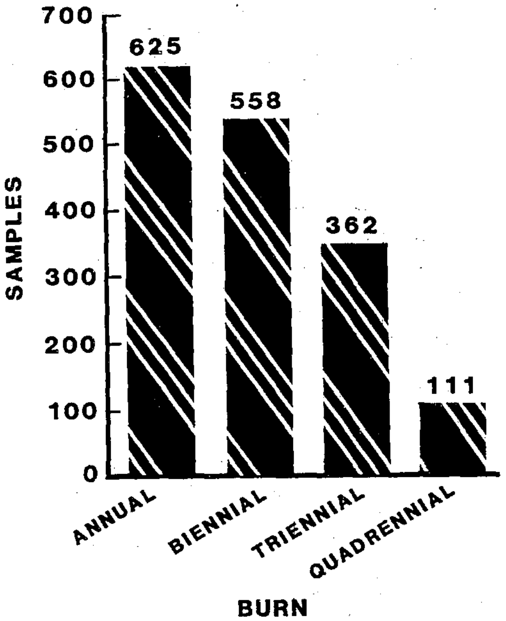


Figure 3.--Orthoptera collected on burned plots by burning frequency.

The grasshoppers in 1982 were identified but apparently only five or six species are abundant enough to play a big part in quail diets. As far as we can ascertain, however, quail showed no preference in species. Our study also shows that in 1983 the relationship of fire and Orthoptera for the month of July was the same as in 1982, in spite of the fact that in March 1983 all the plots (1, 2, 3, and 4), were burned. (The reason for this burning is that they have to be burned simultaneously every 12 years and 1983 was the 24th year of the burning schedule.) Even though these plots were burned in March 1983, they show the same trend in Orthoptera population as the collections made in 1982. What few studies had been made in insects and fire have unfortunately been made only on a 1-year basis, sometimes after a period of fire exclusion. Long-term studies using recurring periodicities of fire at varying frequencies, as occurs in nature, are needed. In the plots burned every 1, 2, 3, or 4 years, we have three major replications, however, because at the time we set up the plots we were afraid we might lose some, an additional three (X, Y, and Z). Future studies will include all six replications.

Snails

Through many years of burning on Birdsong, as well as in other parts of the world where the land had been burned regularly, my wife and I had often noted an abundance of snail shells. These were not new shells from snails that had been killed by the fire, but evidence that there was a high population of snails--in Africa, Asia, United States--that inhabited regularly burned grasslands. The species most frequently occurring on grasslands in the Thomasville-Tallahassee region are *Triodopsis albolabris* (Say), *T. hopetonosis*, and *Euglandina rosea*. Their abundance shows that these snails are as properly the inhabitants of a regularly burned grassland as are the bobwhite quail or other birds that live there. Even though fire may kill some of them, there is always enough of the population left to recuperate quickly. In 1976 a staff member, Dr. Virgina Vail, studied *Triodopsis albolabris* on an area that had been burned annually for 36 years under my direction. This was a mixed hardwood forest with a few scattered pines. The hardwoods consisted largely of black gum, sweet gum, hickory, and some magnolia and beech. She found that the snail had a remarkable behavior pattern, which allowed it to live in a fire-maintained environment, apparently laying its eggs in places usually protected from fire. Dr. Vail suggests that some of the young and adults take refuge in areas where the surface fire does not reach them (Vail 1978). Even though fires of some intensity do kill a number of snails, by the end of the fall after a late winter burn the population is about what it was before the fire. D. Gillon (1972) and Y. Gillon (1972) found the same egg-laying pattern with insects on the Ivory Coast. Populations of Orthoptera and Hemiptera were somewhat reduced and subject to heavier predation after burning, but after 6 to 9 months, the population was the same as it was before the fire occurred. These studies were made on land that had been burned annually for a great many years.

Salt Water Snails

In studies just initiated it has been found that certain of the salt water snails such as periwinkles (*Littorina*), the common marsh snail *Melampus*, and others apparently also are adapted to fires in salt water marshes. Although these are preliminary results, it does appear that many of these also have behavior patterns that protect them from fire. In one case it was observed with periwinkle (*Littorina irrorata*) that after a purposely set and exceedingly hot experimental fire in needle rush (*Juncus*), the periwinkle had dropped down to the surface of the mud flats, where it was relatively cool. The fire apparently did not kill any, for the next morning the periwinkles all had climbed up on the charred stubble of the vegetation; from a distance it looked like little white specks all over the burned marsh. Curiously enough, Hamilton (1977) found in laboratory studies that this species apparently preferred or went to darkened stalks. In laboratory experiments, where stalks ranged from rather light to dark, the periwinkle largely went to the dark. On the marsh burn, we had a field experiment that showed exactly the same thing. The next morning after the burn I was not able to find any dead periwinkles, however, 5 days later the population had diminished somewhat because the stubble was not high enough to keep the periwinkles out of the higher tides (the marsh was burned at low tide), which allowed heavy predation. Apparently with this species, predation is quite a problem, and they seek higher stalks to get away from salt water predators.

At a burn on the St. George Island State Park, also in a needle rush and cordgrass (*Spartina*) marsh, we found that *Melampus* and several other snails appeared to be much more abundant on burned marsh than on unburned marsh. Unfortunately, there seems to be scant literature dealing with the invertebrates of salt water marshes, particularly in needle rush, *Spartina*-type marshes. These marshes are a grassland, so it may be that some of the same principles apply as in burning upland grasslands, although we have an added factor here of high and low tides. Dealing with both fire and water complicates the matter considerably, however, we can state tentatively that fire does not seem to affect the *Juncus* marsh because these marshes have been burned in some areas over a considerable period for livestock range. On the St. Marks National Wildlife Refuge, *Spartina* marshes along the Gulf coast have been burned for many years to provide goose and duck food. There are many studies on the relationship of *Spartina* to fire but practically nothing that applies to the invertebrate life.

Earthworms

In some earthworm studies at Tall Timbers and adjoining regions it has been found that the three commonest species--*Diplocardia mississipiensis*, *D. longa, and D. floridana*--all inhabit regularly burned open pine woodlands. There are also several other species found in these areas, from small earthworms only an inch or two (1.3 to 5 cm) long (some of which have yet to be described) to *D. longa*, which can be up to 18 inches to 2 feet (45 to 60 cm). The fact that these three species occur only in open fire-maintained pine lands is well known to many local people. On the Apalachicola National Forest, for example, many families make their living harvesting these worms. These people are called "grunters" because they put a staub in the ground and then vibrate it with another one, producing a grunting sound. This vibration brings the worms to the surface, and families can make a reasonably good living collecting them. The earthworms are then processed through sawdust for shipment, often by air, to fishing localities throughout the Southeast. In fact, the Apalachicola National Forest had numerous problems during an almost 20-year period of fire exclusion, because these "grunters" constantly burned holes in the forest in order to maintain the earthworms. Today the Apalachicola National Forest receives an appreciable amount of money every year for the right to collect these earthworms on the forest. The worms are valuable by-product of a slash pine, flatwoods type forest.

All three of these earthworm species occur at slightly different elevations. *Diplocardia floridana* is usually on the highest ground and can occur even on sandy ridges, particularly during exceptionally wet years; *D. longa* seems attracted to an intermediate area of hillocks throughout the flatwoods; and *D. mississipiensis* is in the lowest elevation, sometimes in areas that are wet a good part of the time. In the absence of fire, within 4 to 5 years (as in our plots at Tall Timbers) the grassland disappears and is replaced by hardwood and shrub species. These in turn shade the ground and cover it with their litter, eliminating the grassland, which also eliminates the earthworms. Thus the most abundant species in the flatwoods area of Florida and Georgia, adjacent Alabama and southern Mississippi, and possibly Louisiana, are earthworms that might be terms "fire earthworms," since they only occur in fire-maintained environments. Little detailed study about them has been published. Tall Timbers has done a number of earthworm studies, but most are unpublished.

These four brief examples show an entirely new field, literally untouched by fire ecologists. We know little about the invertebrates of fire-maintained grasslands. On insects there are few studies, and usually these are based on only 1 or 2 years of experiments. I cannot stress too strongly that with the invertebrates (particularly insects, spiders, earthworms, and snails) we are dealing with an important part of the food chain of at least half of the families of song birds and game birds in the United States and of many small mammals, amphibians, and reptiles. Few studies have focused on the recycling of the nutrients in fresh- and salt-water marshes and how these nutrients affect these invertebrates populations. In the past we have paid entirely too much attention to the effect of fire on the habitat as a whole, particularly cover or nesting areas, and not enough to what happens to components of those habitats that serve as food for the birds and mammals and other animal life during their critical periods of reproduction. Investigations of these aspects are greatly needed.

I cannot stress too strongly that almost any study made on fire and its relationship to the invertebrates will be a pioneer venture. Practically everything that an investigator finds will be new to science.

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POSTFIRE SUCCESSION OF AVIFAUNA IN THE OLYMPIC MOUNTAINS, WASHINGTON

Mark H. Huff, James K. Agee, and David A. Manuwal

ABSTRACT: The lower montane zone in the Olympic Mountains (Olympic National Park) was selected to study fire effects in west-slope western hemlock (*Tsuga heterophylla*)/Douglas-fir (*Pseudotsuga menziesii*) forests. Birds were examined along a postfire chronosequence: years 1 to 3, 19, 110, 181, and 515. The objectives of this research were to document the successional patterns of a moist temperate coniferous forest following large lightning fires and to determine the broad ecological effects of fire in these forests. Avifauna that commonly breed in disturbance or mature-type forests were present in postfire years 1 to 3. In year 1, the breeding density and diversity were similar to the nearby old-growth (preburn) forest. Breeding density and diversity decreased in years 2 and 3. The 19-year-old site maintained the highest number of species and second highest density throughout the study areas. Diversity and density were lower at the closed canopy forest, except in the old-growth forest (year 515), where the highest avian density was recorded.

INTRODUCTION

Knowledge of ecosystem processes is essential for the management of natural resources. Fires influence forest ecosystems by altering biotic and abiotic resources, which in turn influence the characteristics of biological succession. Many plant and animal communities are maintained by periodic disturbances, and fire is often the major factor in initiating landscape diversity.

The importance of fire in the long-lived forests of the Pacific Northwest is poorly understood. Regional fire history, plant and animal associations, and successional relationships need to be determined for most vegetation types. The western hemlock (*Tsuga heterophylla*)/Douglas-fir (*Pseudotsuga menziesii Franco var. menziesii*) vegetation zone, extensive on the west slope of the Olympic Mountains and primarily encompassed within Olympic National Park (fig. 1) was chosen as the study region. This research was designed to document the successional patterns of avian communities in a coniferous forest following large lightning fires and to determine the broad ecological effects of fire on bird populations in these forests. We hypothesized that patterns of avian density, species composition, and structure would change with stand age.

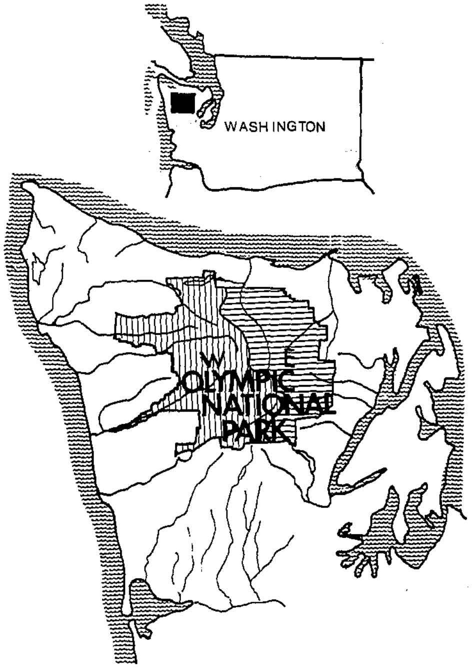

Figure 1.--Geographic location of Olympic National Park.

STUDY REGION

Climate

The Olympic Mountains are an isolated range of precipitous peaks situated on the Olympic Peninsula and in the northwest corner of Washington State (fig. 1). The montane forests that grow on the west side of the Olympic Mountains receive a mean annual precipitation

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Mark H. Huff is a post-doctoral research associate in fire ecology and wildlife science. James K. Agee is research biologist and associate professor, National Park Service Cooperative Park Studies Unit. David A. Manuwal is professor of forest zoology. Common address is College of Forest Resources, AR-10, University of Washington, Seattle, WA 98195.

between 225 and 450 cm. Winters are wet and mild. Below 1969 ft (600 m) winter precipitation is mostly rain. During the summer months the maritime air keeps the temperature cooler than in the interior regions of western Washington (Fonda 1974). Long summer droughts are possible since the air remains relatively dry during this period.

Fire

Since 1916, when fire records from Olympic National Park were first recorded, lightning fires have been responsible for most of the area burned in the Park. From 1916 to 1979 a total of 7,368 acres (2 984 ha) burned; 83 percent of this area was burned by lightning fires (Huff and Agee 1980; Pickford and others 1980). Little is known about the fire history of the Olympic Mountains before historical records began. In general, the forests of the eastern Olympic Mountains are younger than are those of the west side. It has been hypothesized that most of the eastern slope burned about 300 years ago (Henderson and Peter 1981). In the western Olympic Mountains, vast expanses of old-growth forests are found, generally exceeding 300 years of age. The more moist conditions on the west side have been an important factor regulating fire occurrence and have made these forests less prone to burn. Historically, the west-side fires have occurred infrequently and are small compared to fires in other coniferous ecosystems (Heinselman 1981).

Vegetation

Fonda and Bliss (1969) have identified five distinct montane forest communities for the northern and eastern Olympic Mountains, one of which, *T. heterophylla-P. menziesii*, is common throughout the lower montane forests of the western Olympic Mountains. The *T. heterophylla-P. menziesii* type is dominated by these two species, which comprise 80 to 90 percent of the total tree density and basal area (Agee and Huff 1980; Fonda and Bliss 1969). Western redcedar (*Thuja plicata*), widely distributed in this type, rarely comprises more than 10 percent of the total basal area or density. The shrub and herb layer is poorly developed. Mosses cover most of the forest floor, and only a few herbaceous species are present.

Avifauna

Information of forest bird communities of Olympic National Park is sparse. The information available consists only of a checklist of relative abundance for individual species adapted from Kitchin's 1949 field guide to the birds of the region. Recently, as this study was being initiated, Zarnowitz (1982) began a study that measured the effects of logging on bird populations in Olympic National Forest, an area bordering Olympic National Park. The emphasis was on cavity-nesting species; in addition, avian communities were sampled. A wide range of different-age sites from recent clearcuts to old-growth forests were sampled in western hemlock-Douglas-fir forests. The most common bird species were rufous hummingbird (*Selasporus rufus*), clearcut to year 50; chestnut-backed chickadee (*Parus rufescens*), year 30 to old-growth; western flycatcher (*Empidonax difficilis*), year 30 to old-growth; golden-crowned kinglet *(Regulus satrapa)*, year 30 to old-growth; and winter wren (*Troglodytes troglodytes*), all ages. In general, birds bred in a wide variety of different-age forests, and species diversity was highest in the uncut old-growth forests.

Response of avian communities to wildland conflagrations has not been studied in moist forests of the Pacific Northwest. Fire-related bird studies have been limited to the effects of prescribed burning (Hanson 1978) or population changes by game species (Doer and others 1970; Redfield and others 1970). Outside the Pacific Northwest, wildland fire-related studies on avian communities are also sparse, however, some general trends for western coniferous forests can be synthesized from the research to date (Bock and others 1978; Bock and Lynch 1970; Taylor 1969, 1976; Taylor and Barmore 1980). The first few years after a catastrophic fire, rapid changes in forest structure are evident: the opening of the canopy layer, rapid influx of herbs and shrubs, and the appearance of many standing dead trees. This is a sharp contrast to the structure of a preburn forest. As a consequence of fire, the density and diversity of timber drilling and ground/brush foraging species increase. Of the ground/brush foraging species, insect eaters are more numerous than seed eaters. The flycatching foraging guild shows only minor changes in species composition and density. Tree foliage feeders show sharp decreases (more than the timber foraging guild) in species richness and density following fire. With further forest seral development, the habitat structure changes; avian response is reflected in the reassortment of species adapted to the changes in food abundance and cover. Lowest diversity and density of birds occurs in the thick, closed-canopy forests. As the forest matures, density and number of species increase, yet the increase remains at a lower level than the precanopy stage of succession.

METHODS

Fire effects were documented using the chronosequence approach. This technique assumes that sites of different ages can form a chronological sequence if environmental factors are controlled carefully to ensure similarity among sites (Daubenmire 1968). A chronosequence study must be designed to reduce sampling variability. To accomplish this, the following assumptions were developed for the selection of sample areas:

1. Similar environmental characteristics, ecological stages at the time of disturbance, and disturbance intensity.

2. Stability of species and conditions affecting reestablishment. For the first assumption a set of sample criteria were established after extensive reconnaissance. Each study area was required to have similar (1) aspects (120 to 260 degrees), (2) elevation 1,312 to 2,132 ft (400 to 650 m), (3) slopes (40 to 70 percent), (4) habitat types (western hemlock-Douglas-fir overstory and swordfern ground cover) (Franklin and Dyrness 1973), (5) fire history (burned while in an old-growth seral stage and with extensive overstory mortality).

The second assumption assumes stability of species and climate. These variables are impossible to control; therefore, the role of climate and introduced species must be carefully considered when interpreting results.

Five study areas were chosen in the lower montane zone to represent different stages of postdisturbance stand development over 500 to 600 years (cf. Oliver 1981): stand initiation (Hoh Fire, years 1 to 3, and Queets Fire, year 19); stem exclusion (North Fork Fire, year 110); understory reinitiation (Mineral Creek Fire, year 181); and old-growth (Olympus Guard Fire, year ±515).

In each study area, one bird plot was established to census breeding avifauna. Each bird plot was relatively homogenous in vegetative composition and structure. Adverse terrain prevented the bird plots from being equal in size, but all plots were between 25 and 30 acres (10 to 12 ha).

The spot map method (Kendeigh 1944; Williams 1936), in which bird sightings and vocalizations are recorded on grid maps for each bird plot, was used as the census technique. Bird species, sex, nest site, directional movement, and breeding behavior (for example, song or aggressive interaction) were noted.

Censuses were conducted during the peak activity for most species--0515 to 1000 hours. Because of steep and dissected terrain, a bird plot census took 3 to 4.75 hours and one plot was completed per day. A census of each bird plot was taken eight times spread over the breeeding season (April 15 to July 4). A total of 80 censuses were made: 16 in 1979, 32 in 1980, and 32 in 1981.

Study areas by avian sample years

Study Area	Breeding Season 1979	1980	1981
Hoh Fire	x[1]	x	x
Queets Fire		x	
North Fork Fire			x
Mineral Creek Fire		x	x
Olympus Guard Fire	x	x	x

[1] Breeding season in which bird samples were taken.

RESULTS

Forty-eight bird species were recorded throughout the study areas. Only four species bred in all five study areas: winter wren, chestnut-backed chickadee, hairy woodpecker (*Picoides villosus*), and western flycatcher. The results of the avian community data are presented by study areas and community similarity.

Study Area

<u>Hoh Fire (years 1 to 3, 1979-81)</u>--Despite immediate and extensive tree mortality from the Hoh Fire, during the first 2 years as many bird species were breeding on the Hoh Fire plot as in the nearby (unburned) 515-year-old forest (see fig. 2). After year 2, the diversity dropped from 14 to 11 species. In years 1 to 3, avifauna that commonly breed in either disturbance or mature type-forests were present. Fewer mature forest species that were present after the fire bred in year 3; those missing included the golden-crowned kinglet, Steller's jay (*Cyanocitta stelleri*), and varied thrush (*Ixereus naevius*).

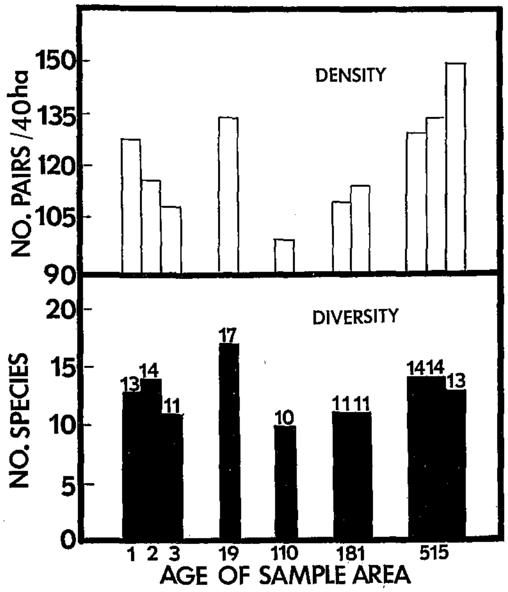

Figure 2.--Density and diversity of breeding birds by sample area.

The bird community at the Hoh Fire year 1 had more dominant species (a species with a breeding density exceeding 10 pairs/100 acres (40 ha)) than any other study area (table 1). These same species were dominant species in years 2 and 3, except the chestnut-backed chickadee, blue grouse (*Dendragapus obscurus*), and western flycatcher in year 3. Winter wrens were the most abundant species in all three breeding seasons (24.9, 29.9, and 44.8 pairs/100 acres [40 ha] respectively). In year 3, nearly three times as many winter wrens were present than the next most numerous species, the dark-eyed junco (*Junco hyemalis*).

Table 1.--Dominant breeding birds on the burn plots

Density dominance (>10 pairs/100 ac (40 ha))

HOH FIRE 1

1. Winter wren
2. Western flycatcher
3. Dark-eyed junco
4. Chestnut-backed chickadee
5. Blue grouse
6. Brown creeper

HOH FIRE 2

1. Winter wren (+)[1]
2. Dark-eyed junco (+)
3. Brown creeper (+)
4. Western flycatcher (-)[2]
5. American robin (±)[3]

HOH FIRE 3

1. Winter wren(+)
2. Dark-eyed junco (-)
3. American robin (+)
4. Brown creeper (-)

QUEETS FIRE 19

1. Dark-eyed junco (+)
2. Rufous hummingbird (+)
3. American robins (+)

NORTH FORK FIRE 110

1. Winter wren (+)
2. Golden-crowned kinglet (+)
3. Townsend's warbler (+)
4. Chestnut-backed chickadee (+)
5. Western flycatcher (+)

MINERAL CREEK FIRE 181

1. Western flycatcher (+)
2. Winter wren (±)
3. Chestnut-backed chickadee (+)
4. Golden-crowned kinglet (±)

OLYMPUS GUARD FIRE 515

1. Western flycatcher (+)
2. Winter wren (±)
3. Chestnut-backed chickadee (+)
4. Brown creeper (+)

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[1] Increase.
[2] Decrease.
[3] No change.

This was the highest breeding density of any species recorded during the study. In year 1, the breeding density of western flycatchers was 21.9 pairs/100 acres (40 ha), but they decreased 50 percent by year 2 and were scarcely observed in year 3 (2.0 pairs/100 acres (40 ha)). This species is a common bird of mature and old-growth forests; it was affected more negatively by habitat modifications from the fire than any other species.

Initially, the Hoh Fire did not alter the total density of birds but did affect species composition. The breeding densities of the old-growth (preburn) forest and Hoh Fire year 1 were virtually identical, at approximately 128 pairs/100 acres (40 ha). In year 2, the total density decreased 10 percent and another 7 percent in year 3. During this period, the bird density in the old-growth forest increased 4 and 17 percent, respectively.

Queets Fire (year 19, 1980).--This plot consisted of a dense to partially open cover of small trees, highly diverse herbs and shrubs, and ample, well-decayed snags in an open setting. This strikingly diverse habitat attracted the highest number of breeding (17) species, and the second highest total breeding density (134.3 pairs/100 acres (40 ha)), even though the fewest number of dominant species (3) were recorded at this study area (table 1). The dark-eyed junco had the highest density (28.4 pairs/100 acres (40 ha)), slightly more than the Hoh Fire population. Because young burns and large open spaces are rare within the western Olympic Mountains, the density of rufous hummingbirds on the 19-year-old plot was probably the highest anywhere on the west slope of Olympic National Park. At this site, hummingbirds were common for at least two reasons: the diversity of flowering herbs and shrubs (nectar feeding) and the open space which benefited their courtship behavior (large circular aerial displays). Winter wren, the most common bird in a montane sere, had lower densities at this stage of succession.

Woodpeckers were rarely observed during this study except on the Queets Fire plot, where four species were recorded: northern flicker (*Colaptes auatus*), pileated woodpecker (*Dryocopus pileatus*), yellow-bellied sapsucker (*Sphyrapicus varius*), and hairy woodpecker (*Picoides villosus*).

North Fork Fire (year 110, 1981).--The most depauperate bird community was observed in year 110. The lowest number of breeding species (10) and density (97.5 pairs/100 acres (40 ha)) were recorded (fig. 2). Certain characteristics of this study area may have made it less attractive to birds: (1) a high density of relatively uniform-size trees, (2) small snags, and (3) lack of diverse vertical structure (a one-layered canopy and poorly developed understory). For example, the 110-year-old site had the highest density of snags yet the lowest diversity and density of hole-nesting avifauna. The absence of certain unidentified food resources may be the most critical factor.

Despite the sparse understory, the winter wren, an understory species, was the numerical dominant (table 1). Only 33 percent of the total bird community regularly lived within the understory component, and the winter wren composed 80 percent of that. The other dominants were canopy dwellers: golden-crowned kinglet, Townsend's warbler (*Dendroica townsendi*), chestnut-backed chickadee, and western flycatcher. Over half of the total birds lived in the tree canopy. The townsend's warbler was the only species to attain its highest density in the 110-year-old forest.

Mineral Creek Fire (years 181 & 182, 1980-81).--Structurally, the 181-year-old plot was most similar to the 110-year-old site, but the trees were larger, understory more developed, and greater vertical structure existed in the canopy layer. Eleven species bred on this plot, one more than the 110-year-old site; however, the density was 15 percent higher (fig. 2). The same species as on the 110-year-old site (western flycatcher, winter wren, chestnut-backed chickadee, and golden-crowned kinglet) were numerically dominant, except for Townsend's warbler. At this stage of succession, the western flycatcher and winter wren were equally the most common species (2-year mean = 26.1 pairs/100 acres (40 ha)). In addition, most of the species that bred at lower densities (<10 pairs/100 acres (40 ha)) were present at both the 100- and 181-year-old sites.

Golden-crowned kinglets attained their highest density in the Mineral Creek study area; however, significant fluctuations were observed between breeding seasons. An eightfold increase in kinglet density was observed between 1980 and 1981. A smaller population explosion of golden-crowned kinglets was recorded on the 515-year-old plot during the same time period.

Olympus Guard Fire (± 515, 1979-81).--The 515-year-old site was used extensively by many breeding and transient species. The old-growth forest offers habitat heterogeneity, which was poorly developed in the 100- and 181-year-old sites. It included a wide diversity of tree sizes from small to large, a higher density of shrub cover, large snags and logs on the forest floor, and massive foliar biomass in canopy dominants.

At this stage of succession, western flycatcher, winter wren, and chestnut-backed chickadee, plus the brown creeper (*Certhia familiaris*) were numerically dominant. The western flycatcher bred at the highest density (3-year average = 36.5 pairs/100 acres (40 ha)), noticeably more than the next most common species, the winter wren (3-year average = 27.4 pairs/100 acres (40 ha)). Compared to the 110- and 181-year-old forests, more bird species reached their highest population level in the old-growth forest: western flycatcher, chestnut-backed chickadee, brown creeper, and varied thrush. In addition, total density of hole-nesting birds was maximized on the 515-year-old plot. The total density of birds increased each breeding season from 1979 to 1981; however, no species increased in population all three seasons. The 1981 census showed the highest density of birds recorded during the study 149.5 pairs/100 acres (40 ha)).

Community Similarity

Similarity of species composition between sample areas and breeding seasons was examined. Nearly all of the coefficient-of-community values were above 50 percent (see table 2), meaning that more similarity than dissimilarity existed. Of all the sample areas, the Queets Fire (19-year-old site) avifauna was the most dissimilar. Compared to the other study areas, the Queets Fire habitat was unique; it included many small trees in open and dense patches, a lush herbaceous and shrub component, and the lack of tree canopy. The avian community of the 19-year -old site most closely resembled the other open plot sampled at the Hoh Fire site. The bird community of the Hoh Fire 3 was more closely related to the Queets Fire avifauna than was Hoh Fire years 1 and 2. Hoh Fire years 1 and 2 resembled the avifauna of the old-growth (prefire) plot more than the 19-year-old burn.

Similarity was highest within the closed forests: North Fork (110), Mineral Creek (181), and Olympus Guard (515) study areas. Even though more than 300 years of seral development separated the Mineral Creek and Olympus Guard sites, the similarity of species was over 90 percent.

The similarity between sample years was 10 to 21 percent higher in the closed forest sites (Mineral Creek and Olympus Guard Fires) than the Hoh Fire plot (table 2). At both the Olympus Guard and Hoh Fire sites, however, the similarity was higher between successive breeding seasons (year 1 and year 2 or year 2 and year 3) than alternate breeding seasons (year 1 and year 3).

DISCUSSION

We hypothesized that bird populations would change significantly with respect to stand age (time since last burn). Because of the rapid shifts in species composition and density, the changes were more evident during the pioneer stages of succession. During the first few years after a fire there is an influx of new species (not commonly found in the old-growth forest) intermixed with most of the "old-growth" type species. The burned habitat goes through rapid physical and biological changes not characteristic of an old-growth forest; it is likely that the burned forest harbors relatively unstable food resources.

Table 2.--Matrix of coefficients of community[1] for breeding avifauna

Sample site year	HF 1 1979	HF 2 1980	HF 3 1981	QF 19 1980	NFF 110 1981	MCF 181 1980	MCF 182 1981	OGF ±515 1979	OGF ±515 1980
HF 1979									
HG 1980	81.5								
HF 1981	75.0	80.0							
QF 1980	60.0	64.5	64.3						
NFF 1981	60.9	58.3	47.6	37.0					
MCF 1980	66.7	64.0	54.5	37.0	76.2				
MCF 1981	66.7	80.0	54.5	50.0	76.2	90.0			
OGF 1979	66.7	71.4	56.0	51.6	75.0	80.0	80.0		
OGF 1980	66.7	78.4	56.0	51.6	66.7	80.0	80.0	92.6	
OGF 1981	69.2	81.5	58.3	53.3	69.6	83.3	91.7	88.9	96.3

[1] Percent similarity = $\frac{2c}{a+b}$ x 100 where c = number of species in common between study areas a and b; a = number of species in study area a; b = number of species in study area b.

Taylor and Barmore (1980) studied bird populations along a postfire vegetation sequence ranging from 1 to 304 years in Yellowstone and Grand Teton National Parks. They grouped birds in order of appearance and disappearance in the time sequence. More species were unique to the early stages (1 to 17 years) than to the later stages (111 to 304) years of succession. Forty-three percent of the birds in the early successional plots bred only on these plots; on the contrary, 7 percent of the late successional species bred only in the late successional plots. In comparing the bird populations in the Olympic Mountains, a somewhat similar trend was detected: 30 percent and 11 percent, respectively, but the percentage of early successional birds was noticeably higher in Yellowstone and Grand Teton National Parks. Because fires occur more frequently in this region of the Rocky Mountains (Romme 1982), more habitat is available for species that prefer recently disturbed over not recently disturbed habitats. This attracts more species that specialize in early seral stages, more so than the Olympic Mountains where fire-disturbed habitat is sparsely distributed.

Bock and Lynch (1970) censused bird populations in a *Pinus jeffreyi/Abies concolor* forest 6 to 8 years after a fire along with a mature forest (preburn) control plot. After 7 years elapsed, these plots were remeasured (year 15) (Bock and others 1978). The changes in bird species in the two sampling periods were far greater on the burn plot than in the mature forest. On the burn in year 8, the avian species more closely resembled those in the mature forest than those in the 15-year-old forest. The habitat structure by year 15 was so different from the preburn forest (control plot) that a distinct avian community had developed.

In the Olympic Mountains, as in the California plots, there is a high similarity between the bird species breeding in the early postfire plots (years 1 to 3) and the preburn forest (year 515), more so than the bird species breeding at year 19. Unlike the California plots, avian diversity was much lower in the early postfire plot compared with further successional development in year 19; however, since postfire revegetation is so slow in the Olympic Mountains, a 19-year-old forest may structurally resemble a considerably younger forest in California. If so, a longer period of high avian diversity can be expected with a slow reestablishment period in the Olympic Mountains. Once a full tree canopy develops in the Olympic Mountains, there are few changes in bird species composition. Even though a forest may develop over several centuries, the type of species breeding in these seres changes very little.

CONCLUSIONS

1. Relatively few bird species breed in the montane forests of the Olympic Mountains.
2. Because fire modifies the vegetation composition and structure, there are changes in density and species composition of the bird communities.
3. A unique avifauna bred on the younger burns; however, species that commonly breed in a preburn forest also breed in the very early postburn forest.
4. The highest diversity of birds occurs in the 19-year-old forest and the highest density in the old-growth forest.
5. The most common species in the montane forest sere are the winter wren (young and old sites) and western flycatcher (primarily 110-, 181-, and 515-year-old sites).
6. During the early stages of succession, populations of western flycatcher are negatively affected by fire more than other species.
7. Fire enhances the habitat resources for ground/brush-foraging species; increased diversity and density of this guild are observed in the first few years after fire.

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FIRE'S EFFECTS ON A SMALL BIRD POPULATION

L. Jack Lyon and John M. Marzluff

ABSTRACT: Changes in bird populations as a result of a 122 ha forest fire are evaluated. There is little evidence of any drastic effect on numbers of birds, species, or species diversity in the year of the fire or 2 years later.

INTRODUCTION

The influence of fire on small bird populations is most often visualized in the context of the Smokey Bear poster showing a female robin on the nest--and the obvious implication that the bird, and the eggs or young, will be burned to a crisp if someone is careless with matches. A somewhat more pragmatic view suggests that direct mortality, even in large forest fires, is a relatively unusual event (Vogl 1967; Phillips 1965; Stoddard 1963). Nevertheless, modification of important niches in the habitat might be as lethal as fire if the bird is unable to find other, equally suitable, places to feed and nest. Bendell (1974), for example, concluded that bird species that forage on the tree trunk and in the canopy may be eliminated from burned areas but that ground feeders may be attracted and benefited. Overall, his summary of 22 reported studies suggests remarkable stability, although the postfire avifauna might be slightly richer. There is also some possibility of a shift to larger birds (Bock and Lynch 1970; Martin 1960).

STUDY DESCRIPTION

Study Areas

As a part of an exploratory investigation of small bird habitat utilization on the Lolo National Forest in 1979, we selected 21 representative 5-ha study sites in the Lolo Creek drainage. Our locations included habitats varying from ponderosa pine (*Pinus ponderosa*) types at 1 052 m to Engelmann spruce (*Picea engelmannii*)-subalpine fir (*Abies lasiocarpa*) types at 1 628 m. Representative forest communities ranging from clearcuts to old-growth timber stands were selected. Results of the first year of study were reported by Marzluff and Lyon (1981, 1983). Field work was repeated in 1981 on the same areas by Lucia Settimi under a contract with the U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station.

On July 20, 1979, two of the study areas burned in a forest fire. The burned area was relatively small (122 ha), but the fire was intense, and it appeared to destroy all green vegetation at ground level and many of the tree tops. In this paper, we report the immediate response of birds to this drastic change in the environment and the apparent effect on bird populations 2 years later.

Of the 21 areas on which birds were counted, none were considered directly comparable to the two that burned. The Mill Creek upland site that burned (MCB) was located adjacent to another upland site with fewer trees but in a similar forest community. This area, Mill Creek unburned (MCU), was not disturbed in the fire. The Mill Creek riparian area (MCR), so designated because of its location on the first bench above the creek, was virtually unique; however, we had another area, about 14 km away, near the Lewis and Clark campground (LCC) that was also adjacent to a flowing stream. For comparative purposes in these analyses, we have included both burned and unburned areas, but it should be recognized that the four study sites are only comparable in that all are south of Lolo Creek on generally north aspects, all were unlogged until after the fire, and all are in a similar forest community mostly dominated by Douglas-fir. All areas were classified as Douglas-fir/*Physocarpus malvaceous* habitat types (Pfister and others 1977), although MCR and LCC both had some Engelmann spruce and several species of large shrubs that indicate a slightly more mesic condition than the two upland sites, MCB and MCU.

Field Methods

Bird censuses were taken in both years of study at about 2-week intervals in the period between June 15 and September 15. Working between a half hour before sunrise and noon, observers walked slowly along a transect 500 m in length and recorded all birds seen or heard within a belt approximately 100 m wide. A 3-minute pause at each of 20 permanently marked transect points allowed the observer to carefully scan the area for nonsinging or inactive birds.

Vegetation data were recorded in each of 20 circular plots, 5.6 m in radius (100 m^2), spaced at 25 m intervals along the transect. Data

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L. Jack Lyon is wildlife research biologist, Intermountain Research Station, Forest Service, U.S. Department of Agriculture, Missoula, Mont. John M. Marzluff's current address is Department of Biological Sciences, Northern Arizona University, Flagstaff, AZ 86001.

included categorical classifications for percentage cover (0 = 0%, 1 = <5%, 2 = 5-25%, 3 = 25-50%, 4 = 50-75%, and 5 = >75%) within each of six vertical intervals (0.0-0.5 m; 0.5-1.5 m; 1.5-2.5 m; 2.5-8.0 m; 8-25 m; and >25 m); number of live and dead stems in six diameter classes (0-2 cm, 2-5 cm, 5-10 cm, 10-25 cm, 25-50 cm, and >50 cm); live and dead basal area; counts of dead and down stems; slope; aspect; and elevation. Vegetation sampling was repeated in 1981 to detect any permanent changes in habitat structure. We are indebted to Kenneth Pitt for completing the 1981 sampling under the Volunteers in Service program of the U.S. Department of Agriculture, Forest Service.

Analyses

The test hypothesis of primary interest was whether numbers of birds or the bird community structure were significantly changed as a response to changes in the habitat. Initial examination of the data, however, revealed substantial changes in species composition during the 2-week observation cycles and a significant decline in numbers of birds observed in the second year of study. Thus, it became necessary to compare all analyses on the burned areas with similar analyses of comparable unburned areas in an attempt to recognize changes unrelated to the fire. Data were compiled and examined with variance analysis in matrixes using combinations of the following categories two at a time:

Season, N=6 (June, July A and B, August A and B, September)
Guild, N=8 (feeding guilds, see footnote, table 3)
Area, N=4 (two burned, two unburned).

In a few instances, it was possible to combine two selected categories with years in a three-way factorial analysis; however, this design was not considered statistically acceptable if it forced us to interpret first- or second-order interactions that were even slightly obscure. Thus, our analyses are broken up into a series of smaller analyses rather than the large factorial: Years X Areas X Seasons X Guilds.

Each variance analysis was replicated to test for differences in numbers of birds recorded, numbers of species recorded, and average weights of birds observed. We also examined changes in species composition of bird populations observed on each area by season and calculated the Shannon/Weiner diversity index (see Krebs 1972:506) for each replication in an Area X Season matrix.

STUDY RESULTS

Changes in Available Habitat

All study transects were evaluated in 1979 and again in 1981 to determine changes related to vegetation regrowth and/or salvage logging. Averages for cover category estimates, stem densities, and basal areas, 1979 and 1981, on four study areas are presented in table 1.

A common perception about the effects of fire in a coniferous forest is that the postfire community will consist of blackened stems with bare branches. In fact, unless a forest fire sweeps through the crowns, it is possible to kill the trees without even removing the needles. For some period after the fire, the ground surface may be blackened and bare, but the cover above ground level, and particularly above 1.5 m may not be perceptibly different than before the fire. As a general rule, needles scorched by ground fires will turn brown in the first 2 weeks, and in some cases the scorched trees may even recover.

Both burned areas in this study retained some cover at all levels following the fire. The most noticeable characteristics of the burned areas in mid-August 1979 were a broad layer of ash 2 to 5 cm deep, and a lack of green vegetation below 2.5 m, but there were small patches of unburned vegetation at ground level and considerable amounts of green canopy interspersed with the brown-needle cover above 2.5 cm. Three sample points on MCB remained unburned, and although the majority of tree boles were scorched on both transects, the crowns of some mature trees were still green 3 weeks after the fire. The immediate habitat change on MCR was somewhat greater than on MCB because the preburn community had an understory component of large shrubs. These lost all their foliage even though many of the stems were still present.

In the 18 months following the fire, the landowner completed a salvage logging operation in which the majority of the larger trees were removed. About the same basal area was removed from both areas, but MCB had fewer stems in the large-diameter classes, and as a result, the remaining forest stand in 1981 was similar to the undisturbed area MCU except for a greater basal area of snags. By contrast, the riparian burned area, MCR, was almost completely salvage logged. The removal of all stems over 15 cm resulted in a substantial loss of both tree cover and basal area. By 1981, however, the shrub understory had resprouted, and cover up to a height of about 1.5 m was only slightly less than that recorded before the fire.

In addition to structural changes in the habitat, we also noticed an immediate postfire increase in apparent numbers of a variety of insects that had not been commonly observed before the fire. Charles F. Tiernan, Forest Service entomologist, conducted a brief survey of the burned area for us, and reported intense insect activity involving at least four species of wood borers (genera *Buprestis, Monochamus, Neoclytus, and Agrilus*); ichneumonid females (parasites of wood borers); and predaceous flies of the families Therevidae and Asilidae. Attraction of insects to either the smoke or heat of forest fires has previously been reported (Evans 1971). On both of the burned study areas, we observed almost frenetic feeding activity among warblers and a few species of woodpeckers.

Table 1.--Cover category means, number of stems, basal area and snag basal area on four study areas in the Lolo Creek drainage, 1979 and 1981

	Mill Creek-Burned		Mill Creek-Unburned		Mill Creek-Riparian		Lewis & Clark Campground	
Area	1979	1981	1979	1981	1979	1981	1979	1981
Average cover[1]								
25 m+	0.10	0.05	0.05	0.05	0.25	0.00	0.00	0.00
8.0-25 m	0.95	0.75	0.80	0.80	1.35	0.05	1.85	1.85
2.5-8.0 m	2.15	1.40	0.95	0.95	1.80	0.15	2.10	2.10
1.5-2.5 m	1.20	1.25	0.85	1.00	2.25	0.50	1.45	1.45
0.5-1.5 m	1.55	1.50	1.55	1.55	3.15	2.10	1.85	1.85
0.0-0.5 m	4.95	5.00	5.00	5.00	5.00	4.90	4.90	4.90
Numbers of Stems/ 100 m^2								
50 cm+	0.05	0.00	0.05	0.00	0.15	0.00	0.00	0.00
25-50 cm	0.30	0.05	0.20	0.20	1.05	0.00	1.10	1.10
10-25 cm	3.90	0.90	1.25	1.50	2.40	0.10	5.45	5.50
5-10 cm	4.90	1.25	0.90	1.15	1.30	0.15	3.95	3.85
2-5 cm	3.45	0.65	1.00	1.30	0.70	0.10	1.95	1.50
<2 cm	2.85	0.20	2.10	2.15	1.20	0.00	0.65	0.50
Basal area, m^2/ha	3.27	0.48	0.94	1.06	2.94	0.01	4.35	4.27
Snag basal area, m^2/ha	0.29	1.32	0.09	0.14	0.38	0.57	0.46	0.42

[1] Cover categories scaled 0-5: 0 = 0, 1 = < 5%, 2 = 5%-25%, 3 = 25%-50%, 4 = 50%-75%, 5 = > 75%.

Changes in Bird Species and Numbers

In the initial analysis of variance, each study area was examined in a 6 X 8 matrix of Seasons X Guilds. This analysis did not prove to be informative. Almost without exception, there were significant differences among guilds and no differences among seasons. Throughout all observations on all study areas, the two guilds including insect feeders contained more birds and more species than all other guilds combined.

Analysis of the 4 X 6 matrices of Areas X Seasons was more revealing. In 1979, an average replicate produced observations of 36 birds of 10 species (table 2). In 1981, the overall means dropped to 20 birds and 8 species. Seasonal differences were significant only in 1979, but a consistency can be detected in both years. Immediately following the fire, in 1979, there was a significant depression in numbers of birds seen and a concurrent depression in the numbers of species. This depression occurred on both the burned and unburned areas, although it appeared to be slightly more severe in the burn. A similar depression was recorded 2 weeks earlier in 1981, and in both years, the depressed counts were followed by substantially increased counts as immature birds and family groups began to move about and flock before migration. Because the immediate postfire decline was slightly greater on burned areas, the increases also seem larger for the burn, but there is actually nothing in these data to indicate that the burn was anything more or less than a favorable transitory hunting opportunity. In 1981, the four species primarily involved in the apparent increases repeated similar patterns of increased abundance in late August, although actual numbers were somewhat subdued because of an overall decline in insectivorous birds. Numbers of chipping sparrows, yellow-rumped warblers, golden-crowned kinglets, and Townsend's warblers increased dramatically during this period.

Analysis of the 4 X 8 matrices of Areas X Guilds (table 3) confirmed the already-mentioned dominance of insect feeders in these bird populations. Overall, the numbers of birds and numbers of species that feed on insects in the foliage was significantly greater than the numbers and species of insect feeders on the ground, which, in turn, exceeded any other feeding guild.

Further examination of the numbers of birds recorded by guild reveals that, although maintaining numerical superiority, insect feeders suffered a disproportionate share of the decline in numbers of birds recorded between 1979 and 1981. Analysis of variance of the factorial design Years X Areas X Guild demonstrates a significantly greater decline in the two insect feeding guilds than in other guilds. Foliage insect feeders, in particular, declined to only a third of the numbers seen in 1979.

Several other high and low numbers in table 3 seem worthy of examination, although in no case were

Table 2.--Numbers of birds and numbers of species, Area X Season for 1979 and 1981

Area	Season						Area
	June	July A	B	Aug. A	B	Sept.	sum
1979			Numbers of Birds				
Mill Creek-Burned	36	33	42	14	61	29	215
Mill Creek-Unburned	34	31	51	23	81	43	263
Mill Creek-Riparian	28	45	46	9	62	29	219
Lewis & Clark Campground	23	28	26	18	56	16	167
Season sum	121	137	165	64	260	117	Mean=36
1981							
Mill Creek-Burned	30	30	24	26	17	18	145
Mill Creek-Unburned	27	29	18	43	16	5	138
Mill Creek-Riparian	19	15	10	31	2	18	95
Lewis & Clark Campground	16	23	6	11	33	9	98
Season sum	92	97	58	111	68	50	Mean=20
1979			Numbers of Species				
Mill Creek-Burned	9	9	9	6	10	7	50
Mill Creek-Unburned	14	9	15	11	13	14	76
Mill Creek-Riparian	14	14	12	3	13	10	66
Lewis & Clark Campground	7	9	9	7	9	6	47
Season Sum	44	41	45	27	45	37	Mean=10
1981							
Mill Creek-Burned	6	12	8	7	5	7	45
Mill Creek-Unburned	14	13	11	15	7	4	64
Mill Creek-Riparian	10	8	3	11	2	6	40
Lewis & Clark Campground	6	8	4	6	9	6	39
Season sum	36	41	26	39	23	23	Mean=8

Table 3.--Numbers of birds recorded, Year X Area X Guild[1]

Area	Feeding guild								Area sums
	GS	FS	GI	FI	AI	TD	TG	AO	
1979									
Mill Creek-Burned	6	23	83	78	3	7	15	0	215
Mill Creek-Unburned	14	29	59	108	6	7	38	2	263
Mill Creek-Riparian	8	33	37	115	17	3	6	0	219
Lewis & Clark Camp	5	6	28	112	4	0	12	0	167
Sums	33	91	207	413	30	17	71	2	864
1981									
Mill Creek-Burned	26	22	56	14	12	5	3	7	145
Mill Creek-Unburned	4	19	39	34	16	4	18	4	138
Mill Creek-Riparian	9	10	21	34	11	1	3	6	95
Lewis & Clark Camp	1	18	3	52	2	1	15	6	98
Sums	40	69	119	134	41	11	39	23	476
Guild Totals	73	160	326	547	71	28	110	25	

[1]	Guild	(representative species)
GS	Ground seed feeders	(dark-eyed junco)
FS	Foliage seed feeders	(pine siskin)
GI	Ground insect feeders	(chipping sparrow)
FI	Foliage insect feeders	(yellow-rumped warbler)
AI	Aerial insect feeders	(flycatchers)
TD	Timber drillers	(hairy woodpecker)
TG	Timber gleaners	(red-breasted nuthatch)
AO	All others	

the relationships found to be statistically significant. The high count for insect feeders on the ground (GI) on MCB in 1979, for example, traces to flocks of chipping sparrows seen both before and after the fire. The high count for timber gleaners on MCU traces to two flocks of mountain chickadees. These birds were recorded after the fire burned through the adjacent forest, and the observations might be interpreted to indicate that chickadees were attracted to the general area of the burn. It also seemed meaningful to us that the decline in numbers of timber gleaners from 1979 to 1981 seems to have been disproportionately larger on the two areas that were burned and that numbers of seed feeders on the ground (GS) on MCB was quite high in 1981. These observations appear to confirm Bendell's (1974) conclusion that species which forage on the tree trunk may be eliminated whereas ground feeders may be benefited. On the other hand, Bendell's conclusion that fire will eliminate bird species which forage in the canopy was not confirmed.

Changes in Average Weights of Birds

Analyses examining average weights of birds observed proved to be confusing and not particularly informative. With only one exception, there were no differences among areas or seasons, whereas differences among feeding guilds were always extremely high. These differences among guilds, however, were not consistent. In almost every analysis we found that significant differences were associated with the observation of a single bird. A ruffed grouse or a large hawk would produce statistical significance in any category, and even when these species were removed from the data, a single mourning dove, Steller's jay, or northern flicker would raise the average weight of birds in a guild to a significant level.

The only analysis in which weight differences could be interpreted in a meaningful context involved the seasonal movement of Clark's nutcrackers from higher elevations to the general elevation of Mill Creek in September. Arrival of the nutcrackers made average weights of birds in September significantly higher than in previous observation periods.

Changes in Bird Species Diversity

Shannon/Weiner diversity for 6 replications of field counts on 4 study areas ranged from $H = 1.2$ to 3.6 (mean = 2.7) in 1979 and from $H = 1.0$ to 3.6 (mean = 2.5) in 1981 (table 4). Analysis of variance revealed no significant differences among areas or seasons in either year of study, and we could detect no certain influence of the fire on bird species diversity. Examination of individual observation means, however, reveals that one or more H were outside the $P < 0.01$ confidence interval for the overall mean in both years. In 1979, $2.3 < H < 3.1$, and in 1981, $2.1 < H < 2.9$. Of the H outside these ranges, the most interesting is probably the low index for MCR in the first observation period after the burn. Only 9 birds of 3 species were observed, whereas 2 weeks later, the same area produced 62 birds of 13 species. Because this decline in diversity was not duplicated on the adjacent burned area, MCB, we can only speculate about the consistency of the influence of fire. These data supply no indication that burned areas had higher or lower diversities than unburned areas, but there is a strong implication for population instability on recently burned areas. In 1981, despite the passage of two growing seasons in which there was some vegetation recovery, the average change in H from one observation period to the next was more than twice as great on burned areas as on areas that remained unburned.

Table 4.--Shannon/Weiner diversity indices (H) for six replications on four study areas, 1979 and 1981

Area	June	July A	B	Aug. A	B	Sept.
1979						
Mill Creek-Burned	2.82	2.33	2.51	2.41	2.64	2.36
Mill Creek-Unburned	3.28	2.45	3.43	3.05	2.97	3.18
Mill Creek-Riparian	3.61	3.40	3.06	1.22	3.13	2.25
Lewis & Clark Campground	2.49	2.92	2.82	2.44	2.49	1.62
1981						
Mill Creek-Burned	1.87	3.12	2.65	2.47	1.89	2.68
Mill Creek-Unburned	3.63	3.37	3.09	3.44	2.42	1.92
Mill Creek-Riparian	2.97	2.87	1.16	3.09	1.00	1.97
Lewis & Clark Campground	2.31	2.49	1.79	2.37	2.77	2.42

This observation prompted us to develop an expression of the relative turnover rate in bird populations from one observation period to the next. The proportions presented in table 5 are calculated as the ratio of the number of species seen in one or the other of two observation periods, but not both, to the total number of species seen both observation periods. We were surprised to find that a turnover rate in excess of 50 percent was not unusual. On all four areas, in an average 2-week period, more than half of the species identified were replaced by other species. Despite this already existing high replacement, we found that turnover increased substantially following the fire in 1979, and it appears that the habitat changes on MCR were great enough to continue this high turnover rate into 1981. During the course of this study MCR was modified far more than MCB, and it appears that the removal of most of the cover above 1.5 m produced a less desirable small bird habitat.

Table 5.--Relative turnover rates in species composition from one observation period (season) to the next

Area	June	July		August	
		A	B	A	B
1979					
Mill Creek					
-Burned	0.800	0.615	0.636	0.667	0.786
-Unburned	0.722	0.588	0.471	0.400	0.773
-Riparian	0.444	0.471	0.846	0.857	0.722
Lewis & Clark Campground	0.667	0.364	0.364	0.545	0.750
1981					
Mill Creek					
-Burned	0.733	0.824	0.636	0.667	0.800
-Unburned	0.773	0.588	0.700	0.778	0.778
-Riparian	0.800	0.900	0.883	0.818	1.000
Lewis & Clark Campground	0.833	0.800	0.750	0.636	0.750

Observations and Field Notes

Throughout the compilation of these statistical tests we held in abeyance the recognition that some observations simply cannot be tested. The almost total dominance of these bird populations by insect feeders tends to obscure the fact that changes in some of the less abundant guilds or individual species may have been ecologically important even though the available data provide no potential for demonstrating statistical significance.

We were able to demonstrate that the number of birds observed increased significantly after the middle of August 1979 and further, that these large increases primarily involved insect feeders. We were unable to show that some species of insect feeders, notably MacGillivray's warbler, Swainson's thrush, and the warbling vireo, disappeared from the burned areas immediately after the fire.

The Swainson's thrush was not seen in either burned area in 1981, and we have presumed this to be an indication that too much canopy was removed to leave a desirable habitat. MacGillivray's warbler, on the other hand, returned to the same areas occupied in 1981 and repeated an identical disappearance pattern in late August. In 2 years, including data from all the other study areas in the Lolo Creek drainage, only one MacGillivray's warbler was recorded after the middle of August at an elevation below 1 250 m.

Observations made of the warbling vireo were inadequate to demonstrate whether the species responded to habitat change, is an early migrant, or simply reacted to a short-term, locally favorable feeding situation caused by the fire. In 1979, the number of vireos recorded on MCU increased after the fire. Numbers of several other species also increased on MCU at this time, and our initial impression was that MCU was receiving some spillover of birds displaced from the nearby burned areas. Too few vireos were observed in 1981 to determine whether the burned areas continued to be less acceptable than the adjacent unburned area, but we did determine that the vireos observed in 1979 were the only warbling vireos recorded after mid-August on any area in the Lolo Creek drainage in either year of study. This suggests a possibility that the specific foraging opportunity available in MCU following the fire enabled vireos to remain in the area longer than is usual for this species.

In a number of ways, the data describing small bird use of area MCU seem somewhat unusual. There is a general impression in our data of a very favorable small bird habitat. For both years of study, MCU averaged more birds, more species, and a higher ranking of the diversity index in comparisons with the other study areas. It is our impression, however, that this attraction for birds is somewhat greater than might normally have been expected in a plant community of this structure. The location of MCU, immediately adjacent to the two burned areas, has created a relatively unique combination of habitat diversity and edges that make this specific site and the surrounding area appear far more attractive and productive than it really is.

Our final observation from our field notes involves the several species of woodpeckers recorded during the study. Birds classed as timber drillers in 1979 increased from 5 before the fire to 12 after the fire. This difference, since it involved such a small number, was not significant even though 10 of 12 woodpeckers were recorded in the burned areas. In addition, it seemed important to us that these observations included the only northern three-toed woodpeckers seen in 1979 and that this species was seen only on a burned area in 1981.

SUMMARY AND CONCLUSIONS

In the data presented here, there was surprisingly little evidence that the Mill Creek fire of 1979 had any drastic effect on numbers of birds, numbers of species, or species diversity--either during the year of the fire or 2 years later. Considering only the data from the burned areas, it might have been concluded that an immediate postfire depression in bird numbers and a subsequent substantial increase were fire-associated phenomena. A majority of the bird species recorded were insect feeders, and one of the immediate changes in the burned area was a sudden increase in insects attacking the burned trees. Apparently, however, an increase in numbers of birds observed after the end of July is a predictable annual occurrence related to movement by family groups and flocking before migration.

One immediate physical effect of the fire was removal of much of the cover below 2.5 m and thinning of the canopy above that height. Salvage logging further reduced the canopy, especially above 2.5 m. These changes were potentially significant for a few species, but for small bird populations as a faunal group, the influence of the burn was relatively subtle and appeared to cause modifications in patterns of habitat use rather than any strong attraction or avoidance of the modified habitat. The Mill Creek fire, because it was small, and possibly because it was not a completely destructive burn, may actually have increased habitat diversity for the larger area including the unburned forest immediately adjacent to the burn. At the same time, this increased habitat diversity was accompanied by an increase in species turnover from one biweekly observation period to the next.

One of the more significant observations presented in this paper has little to do with the influence of fire. During the summer of 1980, western Montana was subjected to a fine-grain ash fall following the eruption of Mount St. Helens. There was some conjecture at the time about the influence this ash fall might have on insect populations and, potentially, on other fauna dependent on insect foods. We believe the available data indicate a very substantial influence of ash fall on nesting success by insect-eating small birds. We cannot report with certainty that 1980 was a poor year for nesting success by insectivorous birds in western Montana, but such an event would explain the decline in numbers of birds observed in 1981. Data from 19 unburned study areas represent a much larger evaluation base than the four study areas examined here, and we are evaluating those data for presentation in the future.

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FIRE, LOGGING, AND WHITE-TAILED DEER INTERRELATIONSHIPS IN THE SWAN VALLEY, NORTHWESTERN MONTANA

June D. Freedman and James R. Habeck

ABSTRACT: The historical importance of fire was investigated on the upper Swan Valley winter white-tailed deer range in northwestern Montana. The relatively recent impacts of logging on winter range quality were also included in these studies. Fire exclusion has led to successional development of once open-canopied mature seral forests, and the original fire-maintained vegetation mosaic became altered. Thirty years of timber harvesting treatments, including the clearcutting of large blocks of the winter range, has effectively interrupted the natural deer use patterns on this winter range.

INTRODUCTION

The white-tailed deer (*Odocoileus virginianus*) is an important big game species throughout much of western Montana, and its distribution is closely associated with the lower coniferous zone, characterized by Douglas-fir (*Pseudotsuga menziesii*), ponderosa pine (*Pinus ponderosa*), and western larch (*Larix occidentalis*) (Mackie and others 1979; Gruell 1983, in press). The Swan Valley, located north and east of Missoula, Mont. (fig. 1), is representative of this association of deer and conifer forest. Since the mid-1950's however, the upper Swan Valley has been the scene of major timber management activity (roading, cutting, plantation establishment). During the past three decades nearly 50 percent of the white-tailed deer's Swan Valley range has been logged. Timber harvesting has been directed primarily at mature seral forest types.

It is expected that within the next few decades there will be a complete conversion to harvesting of managed second-growth forests. Concurrent with this timber management activity has been the development of other parts of the deer range for rural or recreation subdivisions. In just the past 10 years, we have witnessed an increased public demand for wildlife habitat improvement, expansion of recreation opportunities, as well as safeguarding the valley's watershed values. These demands have led to conflicts among management groups.

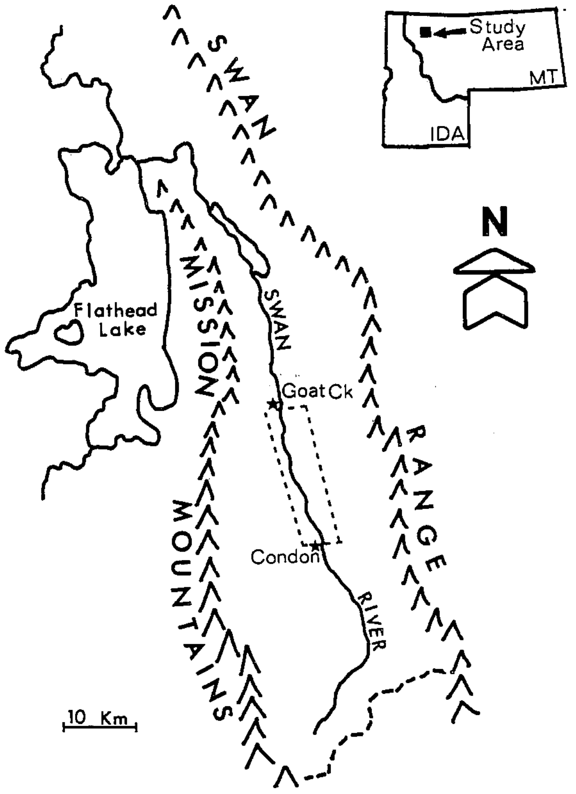

Figure 1.--Location of the upper Swan Valley white-tailed deer winter range in northwestern Montana. Dashed line outlines the approximate location. Southern Mission Mountains are depicted taller than those farther north.

Our contribution to this fire and wildlife symposium focuses upon the results of a recent investigation of the Swan Valley winter deer range (Freedman 1983). Understanding the historical role of fire in the Swan Valley winter deer range was an initial study objective, similar to the study undertaken by Hawkes (1983) in western Canada. Historical information about deer numbers and their distributions, we discovered, is nearly nonexistent. Early reports and assessments made by wildlife biologists suggest that white-tailed deer have been common residents on the upper Swan Valley landscape for a long time and were probably hunted annually by Indians for centuries before Europeans arrived. Deer numbers are believed to have peaked between 1900 and 1915 and again during the 1950's (Bergeson 1943; Weckwerth 1958).

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June Freedman is Plant Ecologist, Biology Dept., Idaho State University, Pocatello, Idaho, and James Habeck is Professor of Botany, University of Montana, Missoula, Mont.

Mundinger's recent (1982) field studies on this range encompassed deer distribution patterns, habitat and food use, and population dynamics. He found that winter deer use is concentrated within riparian forest types and that more dispersed use occurs within the upland forests. Mundinger determined that deer generally avoided the clearcuts and open-canopied young forests; he concluded that the white-tailed deer population in the Swan Valley is basically controlled by the amount of suitable winter deer habitat. His interpretations suggest that the deer are specifically adapted to and dependent upon the valley's mature, subclimax forest (late seral) and, furthermore, that a relatively stable deer population density is a consequence of that adaptation and dependency. Mundinger believes that the winter range in the valley has been reduced in quality and quantity due to the loss of thermal and concealment cover, to reductions in available winter forage, and to the spatial segmentation and isolation of the critical riparian winter habitats. Modern logging and widespread fire exclusion have altered the winter range, characterized by an overall change in habitat diversity.

Wildfire has been an important ecological influence in the Northern Rocky Mountains for thousands of years (Habeck and Mutch 1973; Arno 1980; Barrett and Arno 1982; Gruell 1983, in press). Early reports (especially Ayres 1900) and an abundance of field evidence indicate that wildfire was commonplace in the Swan Valley. Fire-scarred ponderosa pines, charcoal in the soil layers, and the occurrence of even-aged stands of lodgepole pine (*Pinus contorta*) on parts of the range attest to the past presence of fire; the relative scarcity of old-growth climax forests provides further insight into the influence of historic fire.

Before the introduction of effective fire suppression in western Montana in the 1930's, recurrent wildfires maintained much of the lower forest zones in a complex, mosaic pattern of developmental stages of succession. Gruell (in press) has provided a detailed photographic analysis of western vegetation types and has determined that fires did maintain mosaics of young and mature seral types; fires thinned the forests and produced gaps in the canopies. Fire's influence is likely to have been repetitive and predictable, leading to a degree of stability in range habitat components. We believe the best interpretation of the Swan Valley white-tailed deer population dynamics encompasses the view that long-term stability (steady state) in deer numbers is geared toward the effective exploitation of a relatively stable physical habitat maintained, in this case, by periodic fire disturbances. This important concept, developed by Loucks in 1970, is similar to the ideas expressed by Bormann and Likens (1979). Both view ecosystem stability as equivalent to a shifting mosaic steady state. Schoen and others (1982) and Wallmo and Schoen (1980) have translated these ecologic concepts into recommendations for timber and wildlife managers. It seems evident to us that a clear understanding of the Swan Valley's fire/forest interactions is essential for the correct interpretation of deer/habitat interrelationships. This understanding requires assessing the influence of modern fire suppression on the deer/timber harvest relationships.

Our objectives in the Swan Valley were to evaluate (1) the impacts of modern fire exclusion on winter range quality; (2) the role of recent timber harvesting on range conditions, including browse production and availability; and (3) the consequences of multiple land ownership on the vegetation comprising the winter range.

DESCRIPTION OF THE WINTER RANGE

The Swan Valley is located in northwestern Montana and extends from the Swan River-Clearwater River Divide north to Swan Lake (fig. 1). The valley is bounded to the west by the Mission Mountains and to the east by the Swan Mountains. The Swan Valley is about 40 mi (66 km) long and ranges from 6 to 10 mi (10 to 16 km) wide. Elevations on the valley floor range from 3,000 to 4,000 ft (909 to 1 212 m), whereas the adjacent mountain crests reach heights between 7,000 to 10,200 ft (2 121 to 3 090 m). White-tailed deer can be found throughout the upper valley area, but the winter range unit, as delineated in our study, is located between Condon and Goat Creek (fig. 1). The multiplicity of land ownerships on the winter range exists as alternate mile-square sections. Some land is federal forest (Flathead National Forest), Swan River State Forest, or Burlington Northern (Plum Creek Timber Co.), and the remainder consists of numerous private tracts.

During the Pleistocene the Swan Valley was completely filled with an ice layer; local mountain glaciers moved into the valley also (Antos and Habeck 1981; John 1970). This glaciation left behind a complex microtopography--wetlands mixed with upland terrain--that strongly influences forest community distribution patterns and, importantly, seasonal deer activity within the valley.

The Swan Valley receives about 30 inches (75 cm) of moisture annually; although in the geographic center of the valley, near Condon, a noticeable rainshadow is expressed due to the high Mission Mountains lying directly to the west of the winter range. The annual precipitation at Condon is not known, but July-August measurements are one-third less than stations located just to the north and south. Drier summers in the vicinity of Condon no doubt influenced wildfire behavior in the past.

During typical winters the snow accumulates to over 3 ft (1 m); snow cover is usually continuous on the winter range from mid-November to the end of March. January is the coldest month in the Swan Valley; average maximum/minimum temperatures at the nearest stations, at Swan Lake and Lindbergh Lake, are 31°/14° and 29°/11° F (-0.5°/-10°; -1.6°/-11.7°C, respectively. Midwinter thaws, accompanied by cold rains, commonly occur in January and February.

The Swan Valley is predominantly forested, with the exception of the wet meadows and riparian sites.

The winter range is composed of late-stage seral forests comprising several habitat types (h.t.) as classified by Pfister and others (1977). These are as follows:

1. *Picea/Clintonia uniflora* h.t. (PICEA/CLUN): This spruce type occupies the floodplain of the Swan River as well as occurring along the courses of tributary streams and on low terrain surrounding depressions and marshlands. On certain local sites the PICEA/CLUN type is replaced by the cedar type, *Thuja plicata/Clintonia uniflora* h.t. (THPL/CLUN), especially where frost is less severe.

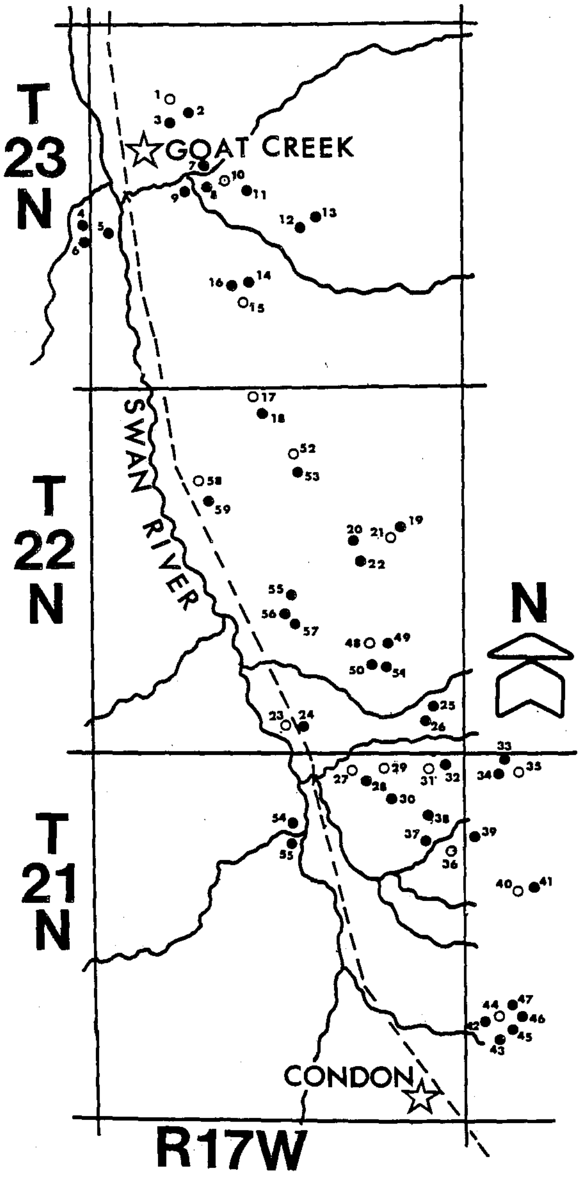

Figure 2.--Swan Valley winter range. Locations are shown of stand samples (solid dots) and stands employed in fire chronology (numbered open circles; see figure 3.)

2. *Abies grandis/Clintonia uniflora* h.t. (ABGR/CLUN): grand fir and subalpine fir types (*Abies lasiocarpa/Clintonia* h.t. [ABLA/CLUN]) occur on the better-drained bottomland terraces and on cool, moist upland sites and/or benches, such as frost pockets and lower north-facing slopes.

3. *Pseudotsuga menziesii/Symphoricarpos albus* h.t. (PSME/SYAL) and (*Pseudotsuga/Vaccinium caespitosum* h.t. (PSME/VACA): the Douglas-fir snowberry and Douglas-fir/dwarf huckleberry types are found on the warmer, well-drained upland slopes, with the former occupying the driest ridgeline sites.

Sapling and pole-sized Douglas-fir, in various combinations with ponderosa pine, western larch, and lodgepole pine, which collectively function as successional dominants, presently occupy the grand fir (ABGR), subalpine fir (ABLA), and Douglas-fir (PSME) habitat type sites. Past fires (Ayres 1900; Antos and Habeck 1981) prevented the expression of the potential climax forests on large portions of the valley's winter range. Wetland forest types and island-like upland forests burned less frequently and likely supported examples of older, later successional stages.

STUDY METHODS

After a reconnaissance of the main parts of the winter range, in an area defined as comprising about 35,200 acres (14 250 ha), a series of 59 stand samples were taken that represent a wide range of the site conditions, habitat types, and silvicultural treatments on the deer range (fig. 2). In each study area a one-tenth acre (about 375 m^2) plot (releve) was positioned to represent the average stand conditions. We employed the paired-stand approach and sampled an untreated or undisturbed stand adjacent to a silviculturally treated stand; both occupied similar physical settings. The field methods follow those described by Pfister and Arno (1980). Tree densities of each plot were recorded by diameter classes (2-inch [5-cm] intervals), and canopy coverages were also assigned to each tree species. Tree age classes were also measured through stem coring. Canopy coverage values were assigned each vascular ground layer plant by sampling twenty 20- by 50-cm quadrats in each releve; physical site features were also recorded. The 59 samples were used in the construction of a polar ordination (Bray and Curtis 1957).

Fire history data were collected from fire-scarred trees searched out in or near each of the sampled stands (fig. 3). The fire history methodology we followed has been described by Arno and Sneck (1977) and by Arno and Peterson (1983). Establishing stand ages by routine increment cores supplemented the fire dates determined from scars.

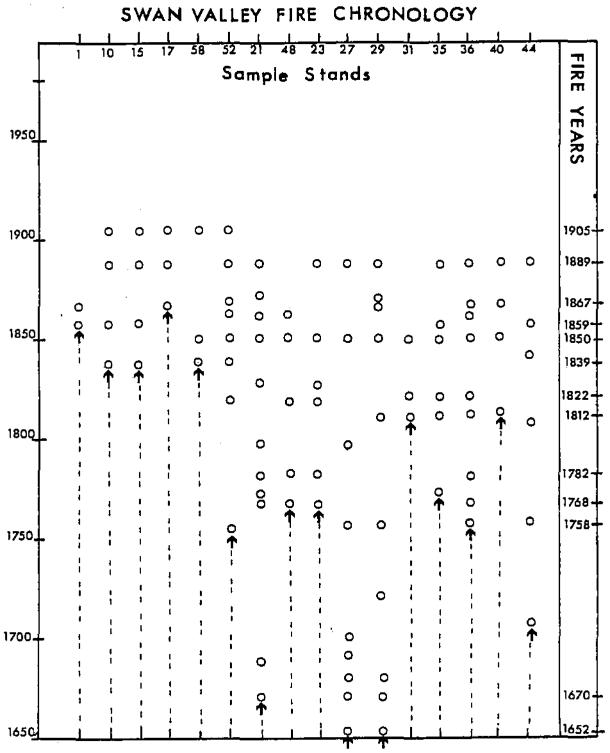

Figure 3.--Swan Valley fire chronology. Each open circle represents the adjusted mean fire-free interval for each stand. The arrow and dashed lines delineate the start of each stand's fire history. The stand arrangement, from left to right, represents a north-to-south geographic gradient (see fig. 2).

The majority of fire-scarred trees encountered were ponderosa pine. Some multiscarred lodgepole pines were also sampled, and their dates of establishment were also used in constructing the fire chronology.

The availability of 1934 aerial photos covering the winter range, as well as current ones, permitted us to analyze winter range changes over a 50-year period. The areas covered with uncut forests, logged/roaded areas, riparian, marsh-shrub, and recent human-made developments were mapped for both sets of photos, and changes in area were determined for each category.

The impact of fire exclusion over the past half century on the compositions of the uncut winter range forests was studied by a detailed diameter/age analysis in an intact PSME/VACA stand. A circular plot, 0.2 acres (0.07 ha), was employed, and the exact positions of all trees in this plot were mapped. Age-diameter relationships were established by coring. Graphical representations of the plot were prepared; a series of plot depictions was prepared, each of a different historical period between 1600 and 1982.

Lastly, the production levels and availabilities of the important winter deer woody browse species were determined, following methods described by Cole (1959) and Lonner (1977); percentage cover values, shrub heights, and degree of hedging were all measured. The distribution and intensity of winter deer use were estimated directly from a series of 1981-82 midwinter cross-country ski trips over the winter range.

RESULTS AND DISCUSSION

Fire History of the Swan Valley

Fortunately for our study a turn-of-the-century descriptive narrative exists, with photos, of this part of western Montana. H. B. Ayres (1900), an employee of the U.S. Geological Survey, was assigned to assess the Lewis and Clark Forest Reserve, which included the upper Swan Valley. He gives special attention to the occurrence of wildfires and their impacts on the timber of the valley. It is worthwhile to summarize some of Ayres' observations and interpretations:

1. At the time of his survey, about 1897, he noted that much of the Swan River Valley was "much burned" with fire-killed timber covering large parts of it. This must have been the results of fires in 1889, a date we have discovered is common in the valley's fire scar record.

2. Ponderosa pine was common in the upper Swan Valley, near Condon, and frequently exhibited fires scars, according to Ayres. We have witnessed this ourselves in the remnant, uncut portions of the winter range.

3. In the Swan Valley, trees, although scarred by fire, still remain abundant, especially in the tributary gulches. Moderate fires, Ayres says, overran the forests, but the treatment merely thinned the forests; tree seedlings are seldom over 10 ft. high.

4. In some forests influenced by light fires, tree restocking was so dense it practically formed a conifer "underbrush" layer. In general, Ayres says, underbrush is not dense except in some wetter lower Swan Valley.

5. Some tree cutting, at the time of Ayres' examination, was for cabin building by prospectors, hunters, trappers, and "squatters." Although lightning is given credit for ignitions, Ayres blames most on the carelessness of men, and here Ayres includes Indians. In 1889, 1,200 mi^2 (768,000 acres; 310 931 ha) was burned in the Forest Reserve.

6. Ayres states that fires in the area occurred at all levels of intensity. High-intensity fires occurred in 1889 as well as "forty" years earlier; he is referring to 1850, when the Swan Valley also experienced extensive wildfire. The more common light fires simply crept along the surface, thinning the forests, and causing scars ("defects").

7. The low-intensity fires killed lodgepole pines because they lack thick bark; the same fires, observed Ayres, encouraged western larch dominance. This relationship between lodgepole pine, western larch, and other conifers in the Swan Valley has been discussed by Antos and Habeck (1981) and Antos and Shearer (1980).

8. As of 1900, Ayres claims that 90 percent of the Swan Valley had been burned over in the preceding 100 years, but much of this fire was not of the high-intensity stand-replacement type, since the burned areas remained forested. Ponderosa pine remains as an overstory dominant, whereas invading red fir (PSME), larch (LAOC) and spruce (PICEA) are repeatedly killed by fire.

Upper Swan Valley Fire Chronology

We must compliment Ayres for being such a keen observer and interpreter of the early Swan Valley landscape. It helps us greatly in making modern evaluations of the past role of fire. The fire history data we collected were used to construct a master fire chronology (fig. 3) that spans the period between 1650 and the present. Technical assistance was provided by Stephen Arno and Andrew Wilson of the Northern Forest Fire Laboratory (Missoula, Mont.). The fire chronology developed follows the methodology recommended by Arno and Peterson (1983). The dates of major fires are shown in this chronology; each stand's fire-free intervals are identified separately by the open circles, but a composition chronology is also shown on the right-hand margin. The arrows and dashed lines identify the date when a given stand's fire history begins.

The fire-scarred trees in the vicinity of our sample plot were separately inspected and fire dates and intervals determined (see Romme 1982 for definitions of terms). Next an adjusted mean interval was derived; occasional missing scar recovery rings required such adjustments. The development of stand values (fire-free intervals) from two or more trees assumes that fires that are clearly identified on one tree can be counted as a fire event for the entire stand (Arno and Peterson 1983). On open mountain slopes, past fires could run through a stand and miss being registered on some of the trees. In the glaciated upper Swan Valley, the uneven terrain (mosaic of wetlands and uplands) makes it less likely that a given fire, in a typical year, could spread the same way. In years of severe drought all sites might be dry and fires could move unimpeded.

Our Swan Valley fire chronology is based on composite fire scar data that may possess some inherent problems due to the fire-spread differences stated above. Composite fire chronologies do shorten the fire-free intervals. Two ponderosa pine trees, for example, sampled in the vicinity of our plot 27 (fig. 2) comprise the data for this plot sample in the chronology (fig. 3). The fire intervals for each tree, individually, are 47 and 49 years, but since 1693 they have shared only two fire dates out of a possible six. The composite fire-fire interval is less than 30 years. Since the trees are not clumped, but in different microsites near the plot, they could have witnessed different regimes of fire.

The scars record 33 separate fires between 1652 and 1925; figure 3 indicates the major fire years. The pre-fire suppression era predates 1905 (effective exclusion came only after 1930, however) when ignitions were mostly by lightning and Indians (Ayres 1900; Barrett 1980; Davis 1980; Barrett and Arno 1982). After 1905 some organized fire exclusion was initiated; this was the beginning of altered fire frequencies and reduced burned acreage (Gruell in press).

Our fire history analysis indicates that the winter range was burned frequently; in the drier southern half of the range the intervals were shorter than on the more moist northern part. In figure 3 samples 1, 10, 15, 17, 58, and 52 are from the northern part of the range (fig. 2). Between 1758 and 1905 this portion of the range had fire-free intervals of about 30 years, and the presence of western larch and even-aged lodgepole pine suggests the fires here were of higher intensity. The remaining samples are from the southern end of the winter range, and these have a shorter interval of 17 years. It is the latter area that supported the open park-like ponderosa pine forests described and pictured by Ayres (1900). Our data at present do not clearly indicate that the dry habitat types (PSME/SYAL and PSME/VACA) burned more often than the more moist types (ABLA/CLUN, ABGR/CLUN, and PICEA/CLUN), but the geographic position of any of these types within the winter range was indeed important in their burning frequencies.

Other Winter Range Changes

Table 1 summarizes other changes that we were able to document by comparing the 1934 and 1981 aerial photos. Nearly 50 percent of the 35,200 acre (14 250 ha) winter deer range has been structurally modified by logging and attendant activities; much of the change recorded took place between 1955 and 1970, but it continues today. Riparian forests (PICEA/CLUN) and wetland marsh/shrub types have also been reduced in areas by at least 10 percent. The ecological value of these latter types as deer habitat exceeds the percentage of the area they represent. The checkerboard-appearing, alternate-section ownership pattern shows up clearly on the aerial photos. An intricate system of interconnecting access roads evolved to service the various ownerships, and such roading no doubt has also affected the quality of winter deer habitat.

Recent decades have also seen the successful establishment and expanded growth of conifers of all species on the upland forest sites that fires had maintained as savannas. Douglas-fir has been the primary beneficiary of the fire suppression. The historical changes within a single representative PSME/VACA h.t. forest are graphically displayed in figures 4 and 5. The earlier, fire-maintained, open-canopied ponderosa pine (fig. 4, pre-1900) stand rarely included Douglas-fir. In our 1982 census, however, Douglas-fir had gained a strong foothold (fig. 5) and was likely capable of replacing the pine with continued fire exclusion. The Douglas-fir, however, also represent ladder fuels that would remove the ponderosa pine if a fire entered this stand. Similar interpretations have been made by Dieterich (1983) for a mixed conifer forest in Arizona and by Gruell (in press) for other parts of the Northern Rocky Mountains.

Although the occurrence of fire on the winter range has not been completely eliminated, the majority of the fires occurring, from all causes, between 1940

Table 1.--Change in winter range habitat components in the Swan Valley between 1934 and 1981

Winter range Subunits[1]	Year	Acres	Percent of total range
I. Unlogged forests	1934	27,280	77.5
	1981	10,710	30.4
II. Logged forests	1934	40	0.1
	1981	17,360	49.3
III. Riparian/deciduous forests	1934	4,040	11.5
	1981	2,160	6.1
IV. Marshland/shrub types	1934	3,250	9.2
	1981	2,430	6.9
V. Roads, homesites, agriculture	1934	590	1.7
	1981	2,540	7.2
Totals (1981)		35,200	100.0

[1] The areas within each subunit were delineated from aerial photography.

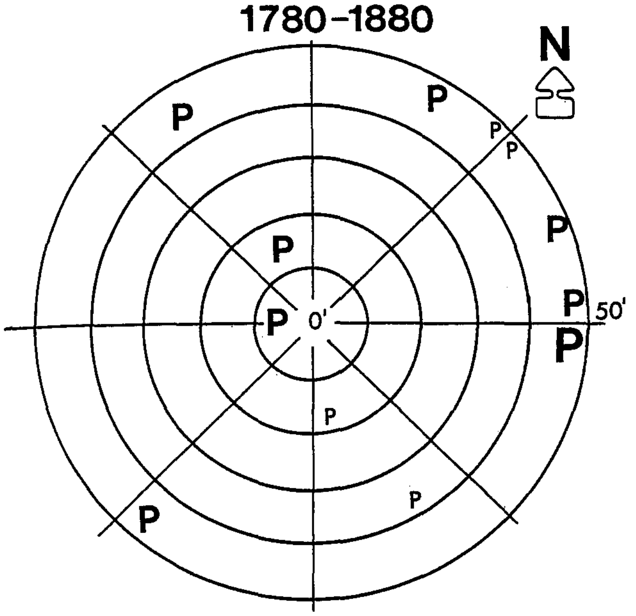

Figure 4.--Graphical analysis of a 0.2-acre (0.07-ha) plot in the Swan Valley winter range, as the site existed between 1780 and 1880. A *Pinus ponderosa* parklike forest was present. The largest P symbol indicates location of a 40-inch d.b.h. pine; the next smaller P's are trees between 20 and 30 inches d.b.h.; the smallest are pines 15 to 20 inches d.b.h.

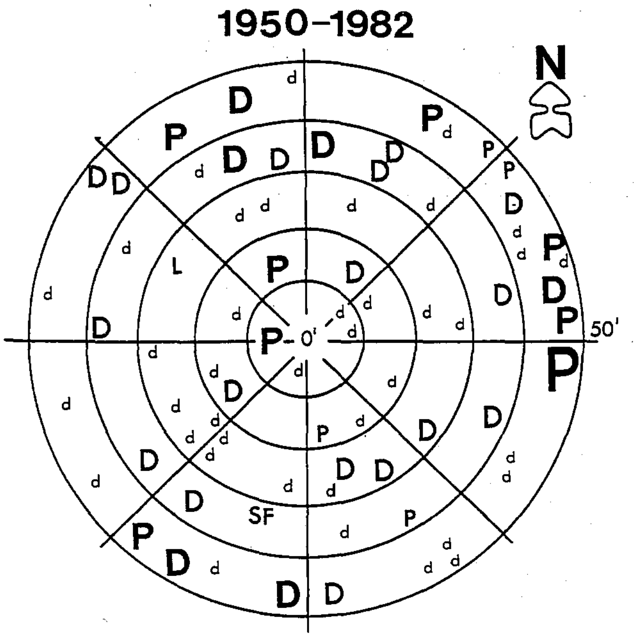

Figure 5.--Same plot as shown in fig. 4, but representing the 1950-1982 era. *Pseudotsuga menziesii* has become well established. The largest D's are Douglas-fir, 6-11 inches d.b.h.; the next smaller D's are 2-5 inches d.b.h.; the lower case d's are seedlings 0-2 inches d.b.h. The L is a 6-inch d.b.h. *Larix occidentalis*, and the SF is a 5-inch d.b.h. *Abies lasiocarpa*. Site is classified as a PSME/VACA h.t. (see text).

to the present have been controlled at Class A (less than 1 acre). The once open-canopied forests, especially those on the southern half of the range, now exhibit increased snow interception as well as increased thermal and hiding cover. They also reveal reduced production of important winter browse species. Fire exclusion and forest succession have altered the pattern of interspersion and diversity of critical deer habitat components. Presently the unlogged upland forests supply needed winter cover, whereas the riparian sites provide much of the essential browse. Many of these changes took place between 1930 and 1955 before large-scale logging was initiated.

Logging Impacts on the Winter Range

Beginning in the mid-1950's, logging entries and other human developments accelerated; these, in a sense, tended to bring about increased landscape diversity but did not replicate the original patterns. The present-day pattern effectively isolates the valuable surviving parts of the winter range from one another.

Large cutting units, ranging up to 1 mi^2 (640 acres; 259 ha) or more, have spatially isolated the riparian components and have generally reduced winter browse availability by removing canopies that previously prevented deep winter snow accumulations. Specific timber harvesting techniques directly influence winter deer movements as well as levels of winter browse utilization. The white-tailed deer prefer serally mature forests that are positioned near the riparian sites. Recent clearcut sites and newly established plantations (under 15 years) were discovered to be only lightly used, if at all, during the period of our study (table 2). The browse species are commonly abundant on most logged sites, but their availability is reduced due to deep snow cover. We estimate that 20 to 40 years of recovery may be needed before significant winter deer use can be expected on such sites. Depending upon site productivity, this is the time required for effective tree canopy to be established. The abundance (percentage cover) of most winter browse species changes on logged sites, but the degree of change depends upon the type of silvicultural system employed. Table 3 compares browse species occurrences in our untreated stands to those in paired treated stands. The data for each species listed must be checked for these interpretations. Some increase following any period of logging, and others respond differently to complete versus partial canopy removal. Table 4 provides data on herbs and grasses in the untreated and treated plots. Many native species show reductions after disturbance, whereas exotics become more common in the logged areas.

Ordination Analysis

Further interpretation of the Swan Valley winter range data was facilitated by the construction of a polar ordination (fig. 6). Much of the compositional variability existing among the 59 samples is

Table 2.--Analysis of Swan Valley winter range[1]

Topographic positions		Upland sites						Riparian sites		
Moisture categories		Dry types (PSME/VACA,PSEM/SYAL)			Mesic types (ABLA/CLUN,ABGR/CLUN)			Mesohydric types (PICEA/CLUN,THPL/CLUN)		
Seral classification		Sapling	Pole	Mature	Sapling	Pole	Mature	Sapling	Pole	Mature
Treated										
A. Logged & burned (clearcut, plantation, seed tree)	Canopy cover	Low	Med	High^{2}	Low	Med	High^{2}	Low	Med	High^{2}
	Browse	High	Med	Low^{2}	High	Med	Med^{2}	High	High	Med^{2}
	Deer use	Low	Med	Med^{2}	Low	Med	High^{2}	Low	Med	High^{2}
B. Logged only (selective)	Canopy cover		Med^{2}	High^{2}		Med	High^{2}		Med	High^{2}
	Browse		Low^{2}	Low^{2}		Med	Low^{2}		Med	Med^{2}
	Deer use		Low^{2}	Med^{2}		Med	Med^{2}		Med	High^{2}
C. Burned only	Canopy cover	Low^{2}	Med	High	Low^{2}	Med	High	Low^{2}	Med	High
	Browse	High^{2}	Low	Low	High^{2}	Low	Med	High^{2}	High	Med
	Deer use	Low^{2}	Low	Med	Low^{2}	Low	High	Low^{2}	High	Extreme
Untreated										
Mature, old growth	Canopy cover			High			High			High
	Browse			Low			Med			Med
	Deer use			Med			High			Extreme

[1] Average canopy cover of tree species (qualitative assessment from coverage class midpoints) average browse (qualitative assessment from availability and productivity of prominent browse species), and overall deer use are summarized according to seral classification and treatment category.

[2] Estimates (not from actual sampling).

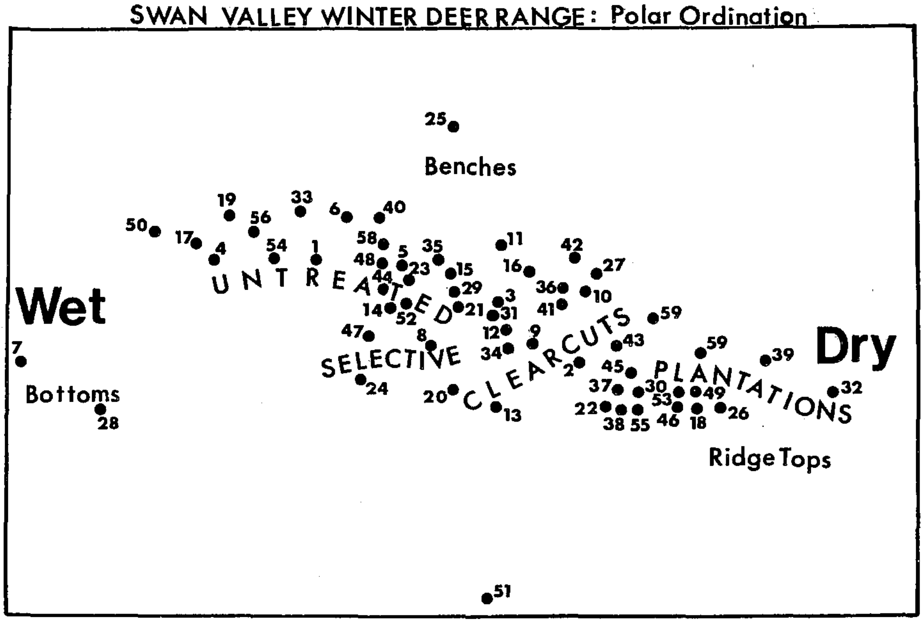

Figure 6.--Polar ordination of the samples taken on the Swan Valley winter deer range. Numbers refer to samples of untreated and treated sites. See text for further explanation.

Table 3.--Average canopy cover of major winter range shrub species in the Swan Valley[1]

Species	Percentage cover				
	Untreated (n = 31)	Silviculturally treated			
		Clearcut (n-8)	Plantation (n = 11)	Seed tree (n = 4)	Selection (n = 3)
Shrubs:					
Acer glabrum	27	36	15	38	9
Alnus sinuata	63	15	37	--	--
Amelanchier alnifolia	26	39	38	34	9
Ceanothus velutinus	9	20	24	24	--
Holodiscus discolor	8	15	10	--	3
Juniperus communis	6	t[2]	3	15	--
Lonicera cilosa	3	t[2]	t[2]	t[2]	3
Lonicera utahensis	8	6	--	--	--
Pachistima myrsinites	2	3	--	--	5
Rosa gymnocarpa	16	18	12	3	5
Cornus stolonifera	26	--	--	--	15
Rubus ideaus	2	15	12	3	--
Rubus parviflorus	13	15	3	18	15
Salix spp.	8	24	10	15	3
Shepherida canadensis	22	15	38	15	--
Spiraea betulifolia	10	3	3	6	9
Symphoricarpos albus	30	18	38	30	63
Vaccinium caespitosum	12	12	3	10	3
Vaccinium globulare	11	--	--	15	--
Subshrubs:					
Arctostaphylos uva-ursi	23	22	42	50	30
Berberis repens	5	9	3	10	3
Linnaea borealis	16	12	3	10	13

[1] Data are provided for untreated stands and various logged and/or planted stands of occurrence.

[2] t = trace percent cover.

displayed within this two-dimensional figure. With this ordination, we have identified several interacting ecological gradients within the winter range: site moisture, topographic position, and silvicultural treatment (fig. 6). Topography and site moisture are closely linked and stem from the past influence of glaciation. The untreated (uncut) stands occupy the left half of the ordination; the wettest forest type, PICEA/CLUN, occurs on the extreme left, whereas the drier, untreated PSME/VACA stands occupy the central part, with other mesic types in between. Any of the past-silvicultural treatments applied to these stands (clearcut), selection, (plantation) induced compositional alterations, and these changes cause an ordinational shift of the stands to the right, with the clearcut/plantations occupying the extreme right side of the stand ordering.

The ordination approach allows us to evaluate the degree of community change induced by logging in the various forest habitat types that compose the valley's winter deer range. The moist forest types studied, PICEA/CLUN, ABGR/CLUN and THPL/CLUN, are compositionally altered to a greater degree than are the drier, upland forest types, such as PSME/VACA and PSME/SYAL. That is, the percentage of compositional dissimilarity between the paired PICEA/CLUN samples (about 70 percent) is greater than between the stand pairs taken from PSME/VACA sites (about 50 percent dissimilar). The cutover moist forests become very brushy, with shrub species residing in low amounts in the untreated stands achieving much higher cover values after canopy removal and other shrubs species entering and becoming well established after the logging treatments. These phytosociological differences were determined from detailed interpretations of the untreated and treated stand pairs within the polar ordination.

Classification of Treated Stands

We developed a classification for the silvicultural treated stands located on the winter deer range. A combination of current cover dominants and successional recovery stage was used to arrive at four different community/structural classes (table 5).

Table 4.--Comparison of forb and graminoid responses in untreated (n = 31) and treated (n = 28) plot pairs sampled on the Swan Valley winter range[1]

Species	Untreated Plots		Treated Plots	
	Presence	Cover	Presence	Cover
	Percent			
Forbs:				
Achillea millefolium	9	2	27	t
Actaea rubra	33	2	12	3
Aralia nudicaulis	15	12	12	19
Arnica latifolia	42	3	19	2
Aster conspicuous	39	1	19	2
Athyrium filix-femina	6	20	-	-
Clintonia uniflora	73	4	46	2
Cornus canadensis	33	4	12	10
Fragaria vesca	76	5	85	4
Galium triflorum	52	6	23	1
Lupinus sericeus	39	2	12	2
Melilotus officinalis	3	t	12	14
Smilacina racemosa	30	4	8	1
Smilacina stellata	42	4	35	2
Streptopus amplexifolius	42	6	12	2
Thalictrum occidentale	55	5	23	1
Trifolium repens	3	3	12	14
Viola orbiculata	45	2	31	2
Xerophyllum tenax	6	t	4	3
Grasses:				
Bromus vulgaris	36	2	46	3
Calamagrostis rubescens	88	18	96	17
Carex geyeri	79	3	92	8
Festuca occidentalis	48	2	62	12

[1] Percentage presence and average percentage cover, based on plots of occurrence, are given t = trace.

Table 5.--Community-structural classification for the silviculturally treated study areas in the Swan Valley winter range[1]

Community/structural category	Treatment type	Associated tree species[2]	Canopy coverage	Browse levels	Winter deer use
Ponderosa pine/sapling	Plantation Clearcut	PICO,PSME, LAOC ABLA, PICEA, ABGR	Low	High	Low
Ponderosa pine/pole	Plantation	PICO, PSEM, LAOC	Medium	Medium	Medium
Douglas-fir/pole	Selection	LAOC, PIPO, PICEA ABGR	Medium	Medium	Medium
Lodgepole pine-larch/ sapling	Clearcut Seed tree	PIPO, PSME, ABLA, PICEA	Low	High	Low
Lodgepole pine-larch/ pole	Clearcut Seed tree	PSME, PIPO, ABGR, ABLA	Low	High	Low

[1] Dominant tree and seral stage are employed in establishing the classes. Levels of canopy cover are based on estimated cover classes; browse assessments are based on field assessments of average availability and productivity; and deer use is based on qualitative assessments taken in winter months and direct field observations.

[2] Listed in order of descending dominance: PICO = *Pinus contorta*; PSME = *Pseudotsuga menziesii*; LAOC = *Larix occidentalis*; ABLA = *Abies lasiocarpa*; ABGR = *Abies grandis*; PICEA = *Picea spp.*

1. The ponderosa pine/sapling type is common on sites that were either clearcut or left for natural regeneration or clearcut and established as plantations. This category often exhibits light winter deer use. We recorded lodgepole pine, Douglas-fir, and western larch, as well as the climax species in these young forest types.

2. The ponderosa pine/pole type includes stands that do receive moderate levels of winter deer use; overstory canopy is sufficient to provide cover, and browse is available. Established ponderosa pine plantations often include other seral conifers that have invaded.

3. The Douglas-fir/pole types that have been selectively logged support moderate levels of winter deer use.

4. Lodgepole pine/larch/sapling-pole types are derived from stands that were either clearcut or seed-tree cut. These types are dominated jointly by lodgepole pine and western larch, but Douglas-fir, ponderosa pine, and each site's climax species (spruce, grand fir, subalpine fir) are often present in varying amounts. Winter deer use was low in the lodgepole and larch types; browse is adequate, but insufficient cover exists.

SUMMARY AND CONCLUSIONS

The upper Swan Valley winter deer range in western Montana, before modern fire suppression and other intrusions by Euroamericans, consisted of a complex mosaic of successional stages representing a fairly wide assortment of vegetation types. The vegetation mosaic provided both summer and winter habitat requirements, but we can only speculate on the details of the original fire-induced forest diversity and the numbers of white-tailed deer it supported. The winter range, furthermore, is set upon a landscape that exhibits a diverse microtopography developed by Pleistocene glaciation. We believe that this intricate pattern of diversity was critical to the maintenance of the historical deer populations in this valley.

Our studies suggest that frequent low-intensity fires, before 1930, maintained open savanna-like ponderosa pine stands (mature seral), with forb-graminoid understories, on the southern half of the winter range. At the same time, longer interval fire rotations affected the northern third, producing a greater proportion of western larch dominance as well as even-aged lodgepole pine cover types. Although sufficient snow intercept cover (thermal/hiding cover) might have been present during these presuppression times, tall browse species may not have been consistently represented in these fire-maintained ecosystems. And these plants likely remained in low abundance and low availability until the turn of this century. We are in agreement with Wallmo and Schoen (1980) that ecologists need to practice greater care in interpreting deer-fire vegetation relationships and be site-specific when interpretations are made.

We also believe the 50+ years of fire exclusion, the multiple land ownerships that fragmented the winter range, and the timber harvesting regimes combined to alter white-tailed deer numbers and distributions. Deer numbers likely increased to levels during the fire suppression era (post-1930) exceeding the number present before these landscape changes (that is, browse increased and canopies remained intact). And, as succession continued toward climax, forest development and structural attributes advanced or "succeeded" beyond the ecological optimum for the deer. Before the singular impact of fire suppression could be witnessed and assessed by ecologists, however, the winter range was subjected to the logging entries we have described in this report.

Concerning the modern complexities associated with multiple land ownership and diverse management philosophies, it would be unrealistic to think of managing the upper Swan Valley deer range as a natural area with pristine qualities. Carefully planned, integrated, and implemented silvicultural treatments, however, could closely mimic known natural processes, resulting in a more productive habitat for a relatively stable white-tailed deer population. The white-tailed deer in this part of Montana have adapted themselves to present-day habitat components, best described as a "cultivated" landscape. However, future numbers of deer sustained on this range, maintained as a part of an ecologic steady state, will depend on the timing, type, and intensity of timber harvests, postlogging site treatments, and how we employ our improved understanding of the role of fire, and its absence, in the successional process. None of this will be possible without coordination of future development policies of the multiple land owners.

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BIGHORN SHEEP AND FIRE: SEVEN CASE HISTORIES

James M. Peek, Dennis A. Demarchi, Raymond A. Demarchi, and Donald E. Stucker

ABSTRACT: Responses of seven bighorn sheep populations and habitats to prescribed fire and wildfire in southern British Columbia, Idaho, and Glacier National Park ranged from no influence to increase; interacting factors such as lungworm infection, livestock grazing, and reduction in forage overrode potential benefits of subsequent increases in production and nutritive content of forages. A list of factors to be considered before prescribed fire is used in bighorn habitats is provided.

INTRODUCTION

The purpose of this paper is to summarize investigations of responses of vegetation and bighorn sheep *(Ovis canadensis nelsoni, O. C. californiana)* to wildfire and prescribed burns in British Columbia, Idaho, and Montana. Historical records compiled by Stelfox (1971) and Smith (1954) suggest that, in addition to other habitats, bighorn originally occurred in areas where fires were frequent. Perhaps because of the sensitivity of this species to human influences, direct or indirect (as through livestock grazing), and their frequent association with climax bunchgrass winter range, the prevailing management for bighorn habitat has been to exclude livestock and minimize human activity. In the last decade, a few investigations into fire-bighorn-habitat relationships have occurred, motivated primarily by the low population levels which continued to persist in some areas even after adequate protection of habitat and populations was achieved. Additionally, habitat manipulation to improve forage sources using prescribed fire was becoming more widely recognized as an acceptable practice. Finally, areas of prime bighorn habitat where wildfire was common were being incorporated into wilderness, and a knowledge of bighorn response to fire was needed if fire was to be restored to the ecosystem.

Seven areas have been investigated in the British Columbia-Idaho-Montana region and are reviewed here: Wigwam Flats and the Bull, Chilcotin, and Ashnola River areas in British Columbia; East Fork and Middle Fork Salmon River areas in Idaho; and Glacier National Park, Mont. Each represents a case study comprising different habitats, responses, and implications for management and further research.

ASHNOLA RIVER-EWART CREEK, BRITISH COLUMBIA

Description of Area

The prime California bighorn (*Ovis canadensis californiana*) winter range habitat in the Similkameen River valley has been preempted by orchards, alfalfa fields, livestock grazing, and human settlement. The bighorn winter ranges in the Ashnola River valley can be considered as refuges for a historically much larger population. Two populations exist in the Ashnola: one on the grasslands above Ewart Creek and one on the grasslands of Crater Mountain.

The Ashnola valley is dominated by steep relief, with deeply entrenched valleys. The grasslands are topographically controlled, and few potential grassland sites exist. The existing winter ranges above Ewart Creek are a mixture of bunchgrass communities dominated by *Agropyron spicatum, Festuca idahoensis, Koeleria micrantha, Poa pratensis, or Festuca scabrella.* This area would be considered a high mountain winter range area.

Areas adjacent to the grasslands are dense forests of *Pseudotsuga menziesii, Pinus contorta, or Picea engelmanii*, depending on elevation. Six major fires have occurred in the valley in the past 140 years. The most recent, in the late 1920's, occurred during a period of extreme drought (Harcombe and Kowall 1983).

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J. M. Peek is professor, Department of Fisheries and Wildlife, University of Idaho, Moscow, Idaho; R. A. Demarchi is Regional Wildlife Biologist, British Columbia Fish and Wildlife Branch, Cranbrook, British Columbia; D. A. Demarchi is wildlife biologist, British Columbia, Surveys and Resource Mapping Branch, Victoria, British Columbia; D. E. Stucker is conservation officer, Idaho Department of Fish and Game, Elk City, Idaho.

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There is only minor encroachment of forests onto grassland soils; the boundary between grassland soils and those associated with forests is distinct, following almost exactly the present tree margins. Present grasslands have remained stable for several centuries (Harcombe and Kowall 1983).

Burning Management Program

The bunchgrass communities have been heavily grazed by domestic livestock (cattle, sheep, and horses) in the past and by bighorn sheep and mule deer (*Odocoileus hemionus*) (Blood 1961; Demarchi 1965). Any effects of fires on the grasslands have been greatly masked because of heavy grazing.

The British Columbia Fish and Wildlife Branch regional office at Penticton suggests that the Ewart Creek herd of bighorn sheep would benefit if nine designated areas were burned (Hankins 1962); however, it is doubtful that burning any of those nine areas would increase forage productivity on winter ranges or that burning would create new winter ranges or enlarge existing ones. In addition, burning existing grasslands would cause a net nutrient loss due to the poor cation exchange capacities of these soils (Harcombe and Kowall 1983).

Burning the immature forests and scrublands adjacent to the winter ranges could provide migration avenues from winter ranges to summer ranges, with some potential spring and fall use ranges being created. Several sparsely forested sites are now used as migration corridors, and it is doubtful that additional corridors are necessary.

Bighorn Response

A closed bighorn hunting season from 1909 to 1955 (except for 1947), a predator control program from 1952 to 1955, and the removal of domestic sheep from the summer ranges produced no immediate observable increase in the bighorn numbers (Blood 1961). Bighorn numbers did increase, however, by two to two and one-half times in the mid-1960's. Cattle were removed from the main Ewart Creek bighorn winter ranges in 1968; as yet the bighorn numbers have not increased over those of the mid-1960's.

Few plant species changed so as to affect grasslands composition in the period 1960 to 1972, although almost all sites visited were in a better condition class in 1972 than in 1960 or 1963. Bighorn sheep distribution and use patterns had changed after the cattle were removed, and one consequence was that some sites had a lower condition class after the cattle were removed than under heavy cattle grazing. In total, though, the winter ranges were in better condition 4 years after the cattle were removed than while they were still grazing this area.

BULL RIVER, BRITISH COLUMBIA

Description of Area

The Bull River Rocky Mountain bighorn (*Ovis canadensis canadensis*) winter range is located on the glacier terraces and cutbanks of the north side of the Bull River in the Rocky Mountain Trench. This winter range was logged in the 1920's; in July 1931, two large fires burned the logging debris and remaining forests. Once the tree canopy was removed, the high evapotranspiration rate and calcareousness of the limestone-derived soils were able to retard any tree encroachment on to the newly established shrub-grasslands.

Subsequent to the removal of the forest canopy, feral horse numbers increased until an active program by the British Columbia Forest Service was initiated to remove them from all public lands in the East Kootenay. Domestic sheep were permitted on crown range in the 1940's and 1950's but were replaced by cattle. Mule deer, white-tailed deer (*Odocoileus virginianus*), and bighorn sheep numbers increased subsequent to the forest canopy removal and then declined rapidly in the early 1960's during a period of deep snow winters, probably as a result of forage shortages due to too many ungulates on the range.

Burning Management Program

The Bull River winter range was subjected to several decades of overgrazing by domestic and wild ungulates; this caused severe livestock-wildlife interest conflicts. In 1974 this winter range was included in a coordinated wildlife-livestock management plan that allowed for the buildup of forage carryover, control of livestock distribution by herding and drift fences, and the implementation of a controlled burning program.

On April 15 and 16, 1975, the British Columbia Fish and Wildlife Branch and the B.C. Forest Service burned approximately 600 ac (243 ha) of shrub/grass vegetation on moraine, alluvial fans, and lower mountain slopes. On April 5 and 6, 1976, they burned approximately 540 ac (218 ha) of shrub/grass vegetation on glacial terraces and escarpments. The primary vegetation community before these burns was seral shrub-grassland dominated by *Purshia tridentata, Amelanchier alnifolia, Rosa woodsii, Arctostaphylos uva-ursi, Poa pratensis, Poa compressa, Bromus tectorum, Stipa occidentalis, and Antennaria rosea.*

The burning reduced the *P. tridentata* canopy and increased the grass and forb component of the stand. The control of cattle grazing allowed reestablishment of *A. spicatum, F. scabrella,* and *F. idahoensis*.

Population Response

Rocky Mountain bighorn response to the 1931 fires was not documented. An adjacent bighorn population, on the Wildhorse River bighorn winter range that exists on a series of rocky outcrops and escarpments in a dense *P. menziesii/Pinus ponderosa* forest, has about 50 animals. The Bull River area would probably have had the same stand structure before logging in the 1920's as the Wildhorse River has now and was approximately the same size, so there would have been habitat for 40 to 60 animals. By 1964, in spite of the heavy livestock, elk (*Cervus elaphus*), mule deer, and white-tailed deer grazing, there were 250 to 300 bighorn on this winter range. A severe die-off occurred in the winter of 1964-65, affecting all age classes of bighorn; only about 10 animals survived. By 1981 the bighorn population had recovered to about 50 animals.

The bighorn responded to the original logging and forest fire that eliminated the forest canopy by increasing fivefold to sixfold. Animals that had survived a severe die-off caused by overgrazing and deep snows in 1964-65 were able to rebuild the population to 50 from less than 10 once the range condition had been improved by proper livestock distribution and a prescribed burning program. The Bull River bighorn herd appears to have resisted the pneumonia-lungworm epidemic which decimated adjacent herds in the 1981-82 and 1982-83 winters.

CHILCOTIN RIVER-JUNCTION WILDLIFE MANAGEMENT AREA, BRITISH COLUMBIA

Description of Area

The California bighorn (*Ovis canadensis californiana*) that occur along the river breaks of the lower Chilcotin River and breaks off the lower Chilcotin River and adjacent Fraser River (designated as the Junction Wildlife Management Area) are nonmigratory. They exist year-round on dry, low-elevation grasslands, which are composed of few plant species. The climax communities are dominated by *A. spicatum, K. micrantha,* and *Artemisia frigida*, whereas seral stands reflecting intense grazing pressure are dominated by *Stipa comata, K. micrantha, A. frigida, and A. rosea* (Demarchi and Mitchell 1973). Some stands of *A. tridentata and A. spicatum* exist at low elevations above the Fraser and Chilcotin Rivers. Some *P. menziesii* forests occur on strong east- and northward-facing slopes, although on the bighorn range few such sites exist.

This area is composed of deep lacustrine silts over deeper fluvial deposits; the rivers are deeply incised and have long grassland slopes interspersed with exposed silt or rock. The Fraser River flows around this land unit, and the Chilcotin, which takes the full force of southerly winds, flows southeasterly into the Fraser River valley.

The grasslands do not show any evidence of being burned; such sign probably has been obliterated by the intense livestock grazing that occurred on this range from the late 1800's to 1973. Adjacent forests are often immature, and the large matriarchal *P. menziesii* show evidence of multiple fire scars--on an adjacent range, Strang and Parminter (1980) suggest that the last large forest fire in the region was before 1926, and that the lack of subsequent fires was due to the removal of litter by grazing.

Burning Management Program

The British Columbia Fish and Wildlife Branch regional office at Williams Lake developed a management plan for the Junction Wildlife Management Area. They recommended prescribed burning as a tool to reduce or retard encroachment of brush or coniferous species. Prescribed burning was also to be used to rejuvenate the soil and increase grass production (Mitchell and Prediger 1974). Several sites were burned before spring green-up in the period 1975-81. Each area was completely burned.

In 1970 a drift fence was constructed to restrict livestock movement on the main bighorn range, and in 1973 cattle were removed from this area. For several decades before 1973, this area was used to winter-over several hundred steers.

Burning of the *A. tridentata* stands killed off all the *A. tridentata* and most of the *A. frigida. Agropyron spicatum* was not affected, and *S. comata* increased on some sites.

Burning of previously overgrazed sites that had been dominated by *S. comata, A. frigida, and C. album* resulted in stands that became dominated by dense swards of *S. comata.*

Bighorn Population Response

Bighorn populations in this range have fluctuated; however, most of that information has been lost with time. The area was closed to bighorn hunting from 1918 to 1975. In the 1930's a local rancher complained that placer miners were decimating the bighorns. In 1954, 250 bighorn were counted, and in 1961, the year of the first helicopter survey, 401 animals were observed. Deep snow and extreme cold in the months of December 1968 and January 1969 triggered a decline and in March 1969 only 231 animals were counted (Demarchi and Mitchell 1973). By February 1981 there were over 600 bighorn on this range (Mitchell 1981).

The reduction of cattle grazing from 1969 to 1973 and the full removal of cattle from this range since 1973 have undoubtedly been the major reasons for the improved forage carryover and species composition changes that have been observed in the period 1968 to 1983. The spring burning program, however, may have hampered the recovery of the overgrazed grasslands. These grassland soils have low cation exchange capacities, so it is doubtful burning will help achieve the management objective of releasing soil nutrients for further plant growth (Dick 1980). Any increase in bighorn numbers can be attributed to the termination of abusive livestock grazing, which has subsequently increased forage carryover and improved range conditions.

The burning program does not seem to have had any negative impacts on the bighorn. In fact, they are probably less likely to be discouraged from traversing the narrow bands of forests where the canopy has been opened. There is, however, no forest encroachment onto areas that are considered potential winter range habitat or that are critical habitats because these sites are essentially permanent grasslands. The burning of the *A. tridentata* stands may have removed some cover that could be used as hiding cover, thermal cover (from intense summer heat), a snow interceptor, and a possible forage source.

WIGWAM FLATS, BRITISH COLUMBIA

Description of Area

The Wigwam Flats Rocky Mountain bighorn (*Ovis canadensis canadensis*) winter range is located on a large glacial terrace, steep rocky outcrops, and fluvial deposits north of the Wigwam River and east of the Elk River in the Rocky Mountain Trench. This unit was not logged before the large fire that burned across it in July 1931. Once the tree canopy was removed, the high evapotranspiration rate combined with the calcareousness of the limestone-derived soils was able to retard any tree encroachment onto the newly established shrub-grasslands.

Several attempts were made to homestead this range unit, and it was grazed with domestic sheep, horses, and cattle until the mid-1950's. From 1954 to the early 1970's only a few domestic horses grazed this unit. In 1929 the area was designated as a Hunting Closed Area, and a hunting ban was placed on all members of the deer family (but not on bighorn sheep). The numbers of elk and mule deer increased to form large herds until the fall of 1965, when the hunting restrictions were removed. Bighorn sheep numbers had increased until the early 1960's, when a die-off reduced their numbers to about 200 or 250, or one-half the former population.

Burning Management Program

This winter range has not been grazed by cattle for several decades; the primary use of the forage resource is for elk, bighorn sheep, and mule deer. The British Columbia Fish and Wildlife Branch has burned some of the seral shrub-grass communities in order to stimulate resprouting of shrubs to benefit the elk and mule deer. Bighorn habitat has been burned in the process. This burning, conducted before spring green-up, has produced positive responses in the vegetation. In most sites only the standing litter was removed; at other sites, the shrub growth has been retarded, allowing *A. spicatum* and *F. scabrella* to dominate.

Population Response

Rocky Mountain bighorn response to the 1931 fire is not documented. Judging from the small bighorn populations that occur in adjacent forested habitats and other similar areas, the Wigwam Flats bighorn herd before 1931 was probably less than 200. By 1964, in spite of the homesteading attempts and the heavy elk and mule deer grazing, bighorns numbered about 450 to 500.

An all-age die-off occurred in the winter of 1963-64 and was followed by low lamb production. The population declined to about 200 or 250. With the opening of the range to the hunting of elk and deer, their numbers were severely reduced and the condition of the range improved. By 1970 there were 300 to 350 bighorn on this range, and by 1977 the number had reached 450 to 500. In the winter of 1981-82, however, another die-off and subsequent lamb crop failure occurred, and the bighorn numbers were reduced to 125.

Elimination of the forest canopy through burning has improved the conditions for bighorn sheep on this range. As there is very little forest encroachment on the bighorn winter range at present, fire is not needed to increase winter range habitat for bighorns. There is sufficient bighorn, elk, and mule deer grazing to prevent the forage species from becoming rank. Burning of the seral shrub-grasslands at this time will not further enhance this range for bighorn; however, burning of adjacent areas would be desirable to expand mule deer and elk winter ranges in order to reduce competition with bighorns.

EAST FORK SALMON RIVER, IDAHO

Description of Area

The bighorn winter range on the East Fork of the Salmon River is about 21,200 ac (8 582 ha) of sagebrush-grassland communities and is dominated by *A. tridentata wyomingensis, A. spicatum, F. idahensis, and Poa sandbergi* (Lauer and Peek 1976). This area receives approximately 7 in (18 cm) annual rainfall and is thus among the drier winter ranges occupied by bighorn in this region. The area is high, ranging from about 5,700 to about 8,000 ft (1 744 to 2 438 m) elevation, and is representative of bighorn winter ranges along the Salmon River south of Salmon, Idaho.

Vegetation Response and Utilization

Seven study sites 0.12 to 1.1 acres (0.05 to 0.45 ha) were burned in September 1974 using hand-held propane torches and flares (Peek and others 1979). Each area was completely burned, with unburned stubble height on bluebunch wheatgrass being less than 0.1 in (0.25 cm), and all Wyoming big sagebrush plants burned to ground level. No fall regrowth occurred after burning. Bluebunch wheatgrass declined in production the first year after the fire, then increased the following 2 years. No change in basal diameters of this species after burning were noted. Other grasses were not affected.

Perennial forbs were not affected, except for an increase in production the second year following burning. This was likely related to precipitation patterns. *Lupinus spp.*, and *Crepus acuminata* were the major forbs. Big sagebrush seedlings appeared two growing seasons after the fire.

Heavy utilization by bighorn sheep using these burned areas occurred the following two winters after the fire, with over 66 percent of the plants grazed. Utilization was consistently higher on burned sites than on adjacent unburned sites for 4 years after the fire.

The Bureau of Land Management (BLM) developed a habitat improvement plan for this winter range after these experimental burns suggested that vegetation could be made more palatable to bighorn sheep by using prescribed fire. Drainage heads on this winter range, which are preferred bighorn sheep sites, have received most attention. To date, an estimated 15 to 20 percent or 346 acres (140 ha) of these drainage heads have been treated (Smith 1983). BLM is continuing this program of burning.

Bighorn Sheep Population Response

The bighorn sheep population was estimated at less than 50 animals by Idaho Department of Fish and Game from 1960 to 1970. After this date, the population started to increase, until in 1983, 132 individuals were present (Hickey 1983).

Bighorn sheep populations have thus gone through three fluctuations, ranging from fewer than 50 individuals to over 100 individuals in the 1920 to 1983 period in this area. Causes of these fluctuations are unknown, but the lungworm-pneumonia infection is implicated in the two early crashes (Lauer and Peek 1976). The impetus for the current population increase is not clear. Cattle were removed from critical winter range, and trespass livestock were blocked from access by fencing in 1975, but the degree to which domestic livestock competed for forage with bighorn sheep appeared low, especially on the higher, more rugged areas preferred by bighorn sheep. Human exploitation was consistently low over the period and again would not have been a likely factor influencing sheep population. The burning project conducted by BLM may have been substantial enough to affect bighorn sheep populations, along with the series of milder winters experienced in the region since 1976. At least the burning program must be considered to either have had no effect or a positive effect on this population--certainly not a negative effect. The ultimate test will be if no major die-off occurs again or, if one does, the population crashes to a low which is higher than the previous two lows.

MIDDLE FORK SALMON RIVER, IDAHO

Description of Area

The Middle Fork Salmon River bighorn sheep populations occupy extremely rugged and steep winter ranges dominated by bunchgrass and shrub communities. Sparse stands of *P. ponderosa and P. menziesii* occur in some areas. *A. spicatum and F. idahoensis* are common grasses, and *Balsamorhiza hookeri* is a common forb. Stands of *Cercocarpus ledifolius* occur on the more exposed and rocky sites. The winter ranges extend from 3,280 to 4,920 ft (1 000 to 1 500 m) elevation, whereas summer ranges extend to 9,840 ft (3 000 m) (Smith 1954). Average precipitation is about 12 in (30 cm) annually, with temperatures over 86° F (30° C) in July and August, and less than -2° F (-30° C) in winter having been recorded.

The Ship Island Fire of August 1979 burned 11,000 acres (1 635 ha) from the riverbank to the heads of drainages, encompassing the entire range occupied by one band of bighorn sheep. The area represents typical bighorn sheep habitat for the drainage. The fire was extremely hot.

Vegetation Response

Grasses, including *A. spicatum, Calamagrostis rubescens, and Poa spp.*, were depressed in production, clump diameter, and canopy coverage the year following the burn. *Poa spp. and Bromus tectorum* increased in production the second growing season after the fire.

C. ledifolius was completely burned, with no resprouting or seedling establishment evident for three growing seasons following the fire. *Salix scouleriana and Ceanothus velutinus* seedlings were abundant at higher elevations in *P. menziesii* habitat types the second growing season after the fire. *Glossopetalon nevadense* was determined to be a resprouter and was browsed at approximately twice the level on burned sites as on unburned sites.

The major effects of this fire were a dramatic reduction in forage the winter following the fire and elimination of *C. ledifolius*, an important forage species for these bighorn sheep (Smith 1954).

Bighorn Sheep Population Response

The bighorn sheep population on the Ship Island Burn and immediately adjacent drainages was estimated at approximately 90 animals before the fire (Hickey 1983). Variation in the number following the fire was attributable to weather conditions during the count and differences in winter severity, rather than actual changes in population size. Population parameters of bighorn sheep occupying the Ship Island Burn are similar to those of bighorn sheep immediately across the river and unaffected by the burn.

Bighorn sheep did prefer to graze on areas which had been burned after vegetation had regrown; however, no major shifts in distribution were apparent, and thus the only discernible response by bighorn sheep was local shifts in habitat use, initially a shift away from burned areas, and then a shift onto the new vegetation.

GLACIER NATIONAL PARK, MONTANA

Description of Area

The bighorn sheep winter range of 420 acres (170 ha) in the Swiftcurrent Valley, the major winter range for bighorn sheep in Glacier National Park, was almost completely burned in 1936 (Riggs 1977). This area is a mixture of climax bunchgrass communities dominated by *A. spicatum, F. idahoensis, F. scabrella, and Amelanchier alnifolia*, and seral vegetation of subalpine fir habitat types (Pfister and others 1977). The seral communities important to bighorn occurred on microsites of concave relief which would retain windblown snow in winter; these comprised 26 percent of the winter range. *Carex geyeri, Spiraea betulifolia, and Calamagrostis rubescens* were common species in these seral stands. Succession toward conifers after the 1936 fire was very slow on this area because of the severe climate of high winds and rapid freezing-thawing conditions in winter. Very little conifer regeneration was apparent 40 years after the fire, illustrating the severity of the climate on these sites. This area would be considered a high mountain winter range with vegetation representative of the eastern Rocky Mountain slopes at 4,600 to 6,900 ft. (1 400 to 2 100 m) elevation in this region.

Vegetation Response and Habitat Use Patterns

Climax bunchgrass communities occupied 74 percent of the winter range that Riggs (1977) described. His investigations of composition and characteristics of these communities revealed little, if any, effect attributable to the burning 40 years afterward. Nevertheless the seral communities previously described did persist over that period of time and likely will continue to be recognizable in the near future. These seral communities were preferred foraging areas for bighorn sheep when they were snow free in winter. Since succession to conifer vegetation would likely reduce the forage on these sites, and bighorn sheep generally favor nonconiferous vegetation, the tentative conclusion is that the fire added winter range to this area for bighorn sheep.

Population Response

Bighorn sheep population response to the 1936 fire was not well documented, but available records were summarized by Riggs (1977). Population estimates in the 1925-83 period ranged from 40 to 134, with a history of artificial winter feeding, horse grazing on the winter range, and periodic die-offs due to pneumonia among the bighorn sheep. Following the 1936 fire, the population suffered substantial mortality due to lungworm (*Protostrongylus stilesi*)-pneumonia interactive infection and disease. The winter feeding program, which concentrated the bighorn sheep and may have aggravated the die-off, was discontinued after that winter, and the population increased from 30 in 1939, to 40 in 1951, 82 in 1967, and 115 in 1975. Whereas the earlier estimates occurred in winter, the 1975 estimate was taken in May and may reflect better observing conditions and/or a spring influx of bighorn sheep onto this winter range coincident with spring green-up.

Responses of bighorn sheep populations to this burn were obscured by the artificial feeding, grazing, and disease-parasite interactions; however, population estimates before the burn ranged from 40 to 134 and, after the burn, 30 to 115. On this basis, the conclusion is that no appreciable response to vegetation change attributable to this fire occurred.

It is noteworthy that no die-offs due to the lungworm-pneumonia complex have been observed in this area since the winter following the burn. This does not mean that die-offs have not occurred or will not in the future or that the additional range provided by the fire is related. It does however, bring up the possibility that the population, which appears to have been at the same level before and after the fire, may not be as concentrated on habitats now as before. If so, this postulated broader dispersal pattern of sheep across this winter range may be related to the absence of a die-off since the fire and thus is a relationship worthy of further investigation.

DISCUSSION

The areas considered here encompass the broad range of habitats occupied by bighorn sheep in this region. Some were forested sites that were changed to shrub/grass ranges by wildfires in the early part of the century. Other sites were native grasslands or shrub-steppe that may have burned periodically. Plant succession following burning varied extensively, from rapid restoration of preburn conditions to extremely slow changes where conifer cover was removed. A variety of responses in vegetation and bighorn sheep were evident. The British Columbia experience illustrated that once the initial bighorn sheep range is created, additional burning may not benefit bighorn sheep if subsequent livestock grazing is intensive enough to affect forage species used by bighorn sheep. The lungworm-pneumonia complex, if prevalent, may limit capabilities of bighorn sheep to respond to increases in forage quantity and/or quality resulting from burning. In areas of high fire frequency where plant responses are short-lived, the bighorn sheep response may also be short-lived or nonexistent.

Positive results from burning these areas range from changes in bighorn sheep distribution (which may have reduced the effects of lungworm infection), to stabilization of populations, to increases. In all cases, however, definite proof that burning was responsible is lacking because we are unable to isolate the effect of the fire from other potential limiting factors. The increase of bighorn sheep in the East Fork Salmon River area may be the exception, since the only factor that appeared to have changed over the period that was considered to be affecting the sheep population was the prescribed burning program.

At least four important factors can be considered to potentially limit these populations, including lungworm; poor range conditions due to past livestock use; low range productivity (due to drought, lack of grazing, or poor soils); and competition with other big game. All of these may be predisposed by severe weather. Additionally, predation is a possible limiting mechanism.

These case histories illustrate that prescribed fire will not necessarily increase bighorn sheep populations and may have a negative effect. The benefits of increasing forage production may be outweighed by other limiting factors. Nevertheless, there is evidence that use of prescribed fire reduces incidence of lungworm infections, and this should be evaluated further in populations with a history of chronic lungworm problems. There is also evidence that prescribed fire, used in conjunction with controlled grazing plans, may benefit bighorn sheep. In areas of high fire frequency where fire management policies will allow fires to burn, the effect on bighorn sheep should be minimal.

Prescribed fire is a useful tool in managing bighorn sheep habitat if a proper plan which identifies objectives and considers the limiting factors is developed, and the burning follows the prescription.

Fire can negatively affect bighorn sheep habitat when range condition is poor and forage species cannot respond, when nonresprouting species which provide important forage for bighorn sheep are eliminated, or when too much area is burned and inadequate forage remains until the next growing season. Another potential negative response is observed when other species, especially elk, are attracted to prescribed fires intended to benefit bighorn sheep. When fires produce these negative results, bighorn sheep then become more vulnerable to the other limiting factors. Therefore, a well-thought-out plan must be developed before fire is considered for use on bighorn sheep range. Plans must consider the following:

1. Condition of plants. Plants to be favored should be in robust condition to respond most satisfactorily to burning. This also means that timing of the burn and intensity of the burn must be considered.

2. Plant response. Are species that burn intended to resprout, reseed, or increase in productivity from unburned residual growth? Areas where nonresprouting species occur and which serve as forage at critical times should be given special attention. If objectives are to rejuvenate deteriorated stands, fire may still be considered a part of the treatment. If nonresprouting stands are productive, then efforts to restrict fire from these areas may be needed.

3. Adjacent conifers. The possibility of creating more open range that is favored by bighorn sheep exists if conifer stands, or tall shrub fields, occur next to currently used range. Bighorn sheep may colonize adjacent habitats as rapidly as commonly associated big game species like elk or mule deer.

4. Limiting factors. Factors that may limit bighorn sheep populations should be identified, and the effect of burning habitats on these limiting factors should be evaluated. Care should be taken since limiting factors are interactive.

    a. Lungworm. Lungworm infections can possibly be altered by reducing bighorn sheep concentrations; however, if burns are small and concentrate bighorn sheep, results could be negative. If burns disperse populations, the effects could be positive.

    b. Competitive. Burns may attract elk or deer to the ranges used by bighorn sheep, which may result in competition for forage.

5. Bighorn sheep response. Changes in distribution patterns may be a sufficient goal if the objective is to reduce lungworm infection. If population maintenance or increase is the goal, then larger burns will be needed. Provision for adequate forage remaining after the fire needs to be considered.

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RANGE BURNING, STONE'S SHEEP, AND

THE LEAKY BUCKET

Dale R. Seip and Fred L. Bunnell

ABSTRACT: Stone's sheep (*Ovis dalli stonei*) in northern British Columbia used subalpine, burned ranges at certain times of the year. In the spring, burned ranges did not appear to provide more nutritious forage or a greater intake rate for sheep than did unburned ranges despite much greater herbage production on burned slopes. The abundant forage on burned ranges did provide superior winter range when available; however, most burns were unavailable to sheep in a severe winter due to deep snow accumulation. Therefore, although burned ranges produced much more forage than unburned ranges, this forage generally was not available at the time of the year when forage was limiting.

INTRODUCTION

Stone's sheep (*Ovis dalli stonei*) and elk (*Cervus canadensis*) in northern British Columbia often use subalpine grassland slopes that occur in areas where the spruce forest has been burned by natural or human-caused fires. This observation has led to a widespread burning program directed toward improving wildlife habitat by creating more subalpine grasslands. The value of such a program; however, is based on an assumed relationship between habitat use and need. The same assumption is the basis of a wide range of other wildlife-habitat management programs. In this paper we examine the validity of the assumption using examples from our research on range burning and Stone's sheep.

The law of limiting factors states that if an organism is dependent on several environmental factors, the one closest to the minimal requirement for survival will be the limiting factor (Blackman 1905). The analogy of a leaky bucket with a series of holes in the sides demonstrates this concept. In this case, the lowest hole will determine the water level and plugging the uppermost holes will have no effect until the lowest hole is plugged. Similarly, increasing some necessary environmental factor for an organism will not be effective if some other factor is limiting. Although this principle does not always strictly apply because some factors may have synergistic effects with the limiting factor, the general principle remains valid. Thus an increase in a particular habitat type will not benefit a wildlife population if that habitat is not limiting, even if the animals extensively use the habitat. Our objective was to determine if range burning eliminated or alleviated a limiting factor and thereby benefited Stone's sheep populations.

STUDY AREA AND METHODS

The study was conducted in the northern Rocky Mountains in the vicinity of Toad River, B.C. (59°N, 125°W). We studied about 100 Stone's sheep living in an area about 350 mi^2 (900 km^2) of which about 75 mi^2 had been burned regularly at an average interval of about 9 years for the past 80 years (fire history analysis by J. Parminter). These animals were compared to a population of 125 to 150 sheep in another area about 300 mi^2 (780 km^2) that had not experienced fires for at least 125 years except for one small 2-mi^2 (5 km^2) burn that occurred 3 years before the study. During the study, about 20 to 30 percent of the burned slopes were reburned each spring by local residents attempting to increase forage production.

Herbage quantity was measured by clipping all the plant material in 2.7 ft^2 (0.25 m^2) plots and sorting the material into live graminoids, live forbs, and dead vegetation. This material was air dried, weighed, and the value multiplied by a correction factor of 0.92 to convert it to oven-dry weight (Seip 1983). Tiller length of grasses was measured from the ground to the tip of the longest leaf of randomly selected tillers. Forage samples were analysed for crude protein and acid detergent fiber (ADF). Fecal samples were collected and analysed for crude protein and lungworm larvae (*Protostrongulus spp.*). Lungworm counts were conducted by Dr. W. Samuel, Department of Zoology, University of Alberta. The other laboratory analyses were done by the Wildlife Habitat Laboratory, Washington State University, Pullman, Wash.

Foraging time was determined during dawn to dusk observations during which the behavior of each sheep was recorded at 5-minute intervals. Biting

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Dale R. Seip is a post-doctoral researcher and Fred L. Bunnell is a professor of wildlife ecology, in the faculty of forestry, University of British Columbia, Vancouver, British Columbia.

rate was determined by counting the number of bites taken by adult ewes during repeated 1- to 2-minute foraging periods. The study area and methods are described in detail in Seip (1983).

RESULTS AND DISCUSSION

Stone's sheep on the burned range extensively used fire-induced subalpine grasslands in the spring and to a lesser degree in the fall. These grasslands were dominated by ryegrass (*Elymus innovatus*) and mixed forbs. In winter, some sheep used burned slopes, but most sheep used windswept alpine ridges because deep snow prevented the use of most burned, subalpine slopes. Do Stone's sheep benefit from being able to use subalpine grasslands created by range burning? That is, are burned ranges a limiting resource?

Spring Range

Sheep without access to burns in spring used natural subalpine clearings such as rockslides and avalanche chutes instead. These natural clearings were dominated by bearberry (*Arctostaphylos uva-ursi*) cover and supported only sparse grass production. Graminoid production on burned ranges was about six times greater than production on natural, subalpine clearings in May (table 1). Stone's sheep fed primarily on grasses during the spring (Seip 1983); however, one cannot simply conclude that because sheep eat grass the range with greater grass production was superior.

The quantity of forage can be limiting if: 1) the total production is inadequate to meet the needs of the population or, 2) the forage distribution is too sparse to allow the animals to obtain an adequate intake rate of high-quality forage.

Spring ranges showed no evidence of heavy grazing pressure. The grass production on both burned and unburned ranges greatly exceeded the requirements of the sheep using these ranges. Alternatively, the sparse forage on unburned spring ranges potentially could have been inadequate to provide an adequate intake rate. Intake rate of sheep is primarily determined by the bite size that they can obtain and is independent of grass tiller density (Allden and Whittaker 1970). Bite size is primarily determined by the grass tiller length. The grass tiller length on unburned spring ranges was the same as on burned ranges (table 1). The lower grass biomass on unburned ranges was the result of a much lower tiller density; therefore sheep probably were able to obtain the same bite size on both ranges. The biting rate was also the same on both range types (table 1) despite the difference in tiller density. Thus, it appeared that the same intake rate could be attained on both range types. This conclusion was supported by the observation that the daily foraging time of the sheep was the same on both range types (table 1). If the sheep on unburned range had a lower intake rate, they would be expected to compensate by increasing their foraging time (Allden and Whittaker 1970; Arnold 1975).

Forage quality (crude protein, ADF) did not differ between burned ranges and natural subalpine clearings (table 1). The quality of food eaten by the sheep, as indicated by fecal protein levels, was also similar between range types in May (table 1), although it began to increase about 7 days earlier on burned range (Seip 1983). Food habits of the sheep were almost identical on the

Table 1.--Comparison of range characteristics and foraging behavior of Stone's sheep on burned and unburned ranges in northern British Columbia during mid-May

Item	Burned subalpine grassland	Natural subalpine clearings
Graminoid biomas	107 lb/acre (120 kg/ha)	17.8 lb/acre (20 kg/ha)
Tiller length	3.9 in (10.0 cm)	4.0 in (10.2 cm)
Tiller density	150 tillers/yd^2	25 tillers/yd^2
Graminoid quality		
Crude protein (%)	18.4	18.5
ADF (%)	28.6	26.1
Percent fecal protein (X±SE)	13.7±0.36	13.4±0.76
Percentage of daylight spent foraging		
Ewes	61-64	63
Rams	49-58	57
Bites/minute (X±SE)	34.2±1.5	34.8±2.6

different spring range types (Seip 1983). Horn growth of yearling rams was significantly greater on burned ranges (Elliot 1978; Seip 1983), but it was not clear if this was a function of superior spring range. Overall, it appeared that burned ranges were not superior to unburned ranges in spring because the forage available on unburned ranges was just as nutritious and forage quantity was not limiting the intake rate. Providing more spring forage by range burning would be like plugging up holes too high in the leaky bucket.

Summer Range

In the summer, Stone's sheep used high alpine ranges where forage quality was superior to that available on subalpine ranges (Seip 1983) and so the availability of subalpine, burned ranges was of no consequence at this time of the year.

Winter Range

When winter arrived, most sheep used windswept alpine ridges, but some sheep used fire-induced, subalpine grasslands. It was necessary to determine whether winter ranges were a limiting factor. Under conditions of high snowfall, Stone's sheep became restricted to small areas of the total range. Sheep did not use areas where the snow depth exceeded 12 inches (30 cm). Grazing pressure in these areas was heavy, and essentially all of the available forage was consumed on both alpine and burned, subalpine winter ranges. Less than 0.03 oz/yd^2 (1 g/m^2) remained in those areas of low snowfall that were heavily used in a severe winter. Burned, subalpine winter range produced much more forage than did the alpine range; this meant more food per sheep was available on the burned, subalpine winter range (table 2). The greater forage production on subalpine range was reflected by higher lamb production following the severe winter and lower lungworm larvae (*Protostrongulus spp.*) counts than for sheep wintering in the alpine (table 2). Therefore, winter forage appeared to be a limiting factor.

Even in areas with extensive burned slopes and abundant herbage production, however, most of the range was unavailable when the slopes became covered in deep snow. Thus it was not burned slopes that were limiting but windswept slopes that provided "available" winter forage. Creating more burned range, which is not available in severe winters, would be of no use. At present there are extensive areas of burned grassland that produced large amounts of forage, but usually these areas were unavailable in winter and most of the sheep were forced to retreat to windswept alpine peaks. Burning programs to enhance Stone's sheep range should be directed toward burning areas that will be windswept and remain snow-free in severe winters. Unfortunately, such areas appear to be rare. In the extensive subalpine areas that had previously been burned, few areas were used by Stone's sheep in winter. It may not be possible to increase the area of Stone's sheep winter ranges much beyond that already provided by windswept alpine areas.

A similar situation may be occurring with elk in the area. Elk used burned, subalpine slopes for most of the year, and the population has increased in response to the burning program. For most of the year, forage was superabundant on the ranges used by elk; however, in the severe winter during the study most of the range was also unavailable to elk due to deep snow. In this situation it is unlikely that more burning in the area would benefit elk despite the fact that burning initially created habitat for elk. In fact, too much burning could be detrimental because elk may need forested areas for cover or to provide browse in winter. Other studies have found that elk feed heavily on browse when grasses become unavailable due to snow (Janz 1983; Singer 1979).

CONCLUSIONS

The observation that animals use a particular habitat type does not necessarily mean that the animals need that habitat. The population will not necessarily increase if availability of that habitat is increased or decline if the habitat is

Table 2.--Herbage production, lamb production, and lungworm counts on two different winter ranges during a severe winter

Item	Burned subalpine	Alpine
Herbage production	984 lb/acre (1,100 kg/ha)	<90 lb/acre (100 kg/ha)
Forage availability (kg/sheep)	206	<100
Lambs/100 ewes produced the following spring	35	26
Lungworm larvae/g feces[1]	38	417

[1] *Protostrongylus spp.*

reduced. Rather, one must determine if the habitat type is a limiting factor. There are two criteria, either of which would justify the conclusion that a range is limiting:

1. The resources provided by that habitat are reduced in a density-dependent fashion by competition between the animals, resulting in negative feedback on the population.

Alternatively, even if the resources in a certain habitat type are not reduced by competition, animals that have access to that habitat type may be better off than animals that do not have access to that habitat type. In this situation, one must demonstrate that:

2. Animals with access to the different habitat type are in better condition and/or have a higher population growth rate than animals without access to that habitat.

In this case, once the animals do have access to the superior habitat type, providing more of that habitat type will not be beneficial until the resources become limited by density-dependent competition.

In the case of Stone's sheep, winter forage was progressively reduced by density-dependent competition resulting in reduced productivity and poorer physical condition, thus satisfying the first criterion. Providing more available winter range should benefit Stone's sheep. That task is made difficult, however, by the fact that available winter range is largely a function of snow accumulation, which is difficult to manipulate.

In spring, there was no evidence that the forage on either burned or unburned ranges was significantly reduced by grazing; thus the first limiting factor criterion was not satisfied. Alternatively, if burned ranges provided superior nutrition compared to unburned ranges, sheep populations could potentially benefit from access to burned ranges, thus satisfying the second criterion. Burned ranges, however, did not appear to provide superior nutrition because intake rate and forage quality were similar on both range types. Even if burned ranges were superior to unburned ranges in spring, even small burns would be adequate to meet the requirements of the animals because of the high forage production on burned slopes. Widespread burning would be superfluous once the animals had access to burns. More burning would be justified only when the resources became limited by density-dependent competition.

Overall, the value of range burning to enhance Stone's sheep range was limited because it did not appear to provide superior spring range and, although winter range was limited, most burned, subalpine ranges were not available in severe winters due to snow.

A final consideration is that habitat which currently does not meet the criteria for being a limiting resource may become limiting in the future under different environmental conditions or under conditions in which some other limiting factor is plugged up and the population level increases to a new hole in the bucket.

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FIRE ECOLOGY OF ANTELOPE BITTERBRUSH IN THE NORTHERN ROCKY MOUNTAINS

Stephen C. Bunting, Leon F. Neuenschwander,
and George E. Gruell

ABSTRACT: Frequency of resprouting and number of newly established seedlings of antelope bitterbrush were sampled on sites burned by prescribed burns and wildfires 3 to 10 years previously to determine the effect of habitat type, growth form, and season of the burn on bitterbrush. Significant differences in resprouting response occurred among the growth forms, season of burning, and habitat type. Seedling establishment was also markedly influenced by growth form, season of burning, and habitat type. Results of this study document the short-term effects of fire on bitterbrush populations in the Northern Rocky Mountains.

INTRODUCTION

Antelope bitterbrush (*Purshia tridentata*) is widely distributed on vast areas of western North America. It is a major component in the diet of big game animals in many areas (Guinta and others 1973; Kufeld and others 1978) and may be used seasonally by domestic livestock (Cook 1954; Julander 1955). Because bitterbrush is important as a forage species, it is a major consideration when planning management practices on range vegetation.

Reviews of bitterbrush literature have been written by Basile (1967) and Clark and Britton (1979). Literature regarding the effects of fire has also been summarized in recent publications (Martin and Driver 1983; Rice 1983); however, the reported response of bitterbrush to fire varies considerably. Hormay (1943) and Billings (1952) stated that bitterbrush sprouted rarely and was nearly eradicated by fire in California and the Great Basin. Others have reported low sprouting potential for the species (Nord 1965; Daubenmire 1970; Sherman and Chilcote 1972). In eastern Idaho, the resprouting ability has varied from moderate (Blaisdell 1953) to high (Pechanec and others 1965).

The variation in resprouting is due to a number of factors. The growth form of bitterbrush ranges from low decumbent individuals to upright columnar forms (Nord 1965) and has been reported to be related to resprouting potential. Decumbent forms have been reported to resprout more readily than the columnar forms (Wright and others 1978; Clark and others 1982). The season of the fire may also affect the ability of plants to resprout. Most research indicates that sprouting is greatest on spring fires and least on summer burns. Sprouting response of bitterbrush burned in the fall is intermediate (Blaisdell and Mueggler 1956; Clark and others 1982; Murray 1983). The effect of season of burning may be confounded with several other factors. Soil moisture is often highest in the spring and lowest in the summer. Clark and others (1982), however, could not show a significant effect of soil moisture by artificially watering bitterbrush plants before burning. The carbohydrate recharge pattern may also be a factor. Carbohydrate levels are lowest in midsummer after seed set and do not recover until late summer (Menke and Trlica 1981). Late summer corresponds to the time when bitterbrush is most susceptible to fire.

Fire severity varies seasonally and may affect resprouting ability. In most regions, low-severity fires often occur during late winter and spring. Highest severity fires would likely occur during the summer period. Studies have shown an inverse relationship between resprouting and fire severity (Blaisdell 1950, 1953; Blaisdell and Mueggler 1956; Murray 1983). Driscoll (1963), however, found little correlation with fire severity and indicated that the soil surface texture was a more important factor in central Oregon.

Murray (1983) concluded that bitterbrush annual production on burned sagebrush grass ranges in eastern Idaho was less than on unburned areas after 30 years; however, bitterbrush studies in forested communities have found increased production after fire even though plant density may decrease (Edgerton and others 1975; Stuth and Winward 1976).

Seedlings are the primary mechanism involved in the development of a new stand of bitterbrush following fire (Daubenmire and Daubenmire 1968; West 1968), and seedling establishment has been as variable following fire as resprouting. Blaisdell (1950) reported that seedling establishment varied inversely with fire intensity (severity). Sherman and Chilcote (1972) stated that rodent caches were important sources of seed reproduction and that rodents preferred to cache seeds in areas where the duff and litter were removed. Driver and others (1980) reported better reproduction from seed in

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Authors are Associate Professor of Range Resources; Associate Professor of Forest Resources, College of Forestry, Wildlife and Range Sciences, University of Idaho, Moscow, and Research Wildlife Biologist, Intermountain Research Station, Forest Service, U.S. Department of Agriculture, Missoula, Mont.

forested areas with the most severe fires. Some of this variation may depend on the microclimatic conditions of the site. In the more xeric sagebrush-grassland sites, adequate microsites for seedlings may be present following a low-severity fire. The remaining vegetation may be important to modify the microclimate; however, in more mesic forested sites, a more severe fire may open up the dense vegetation and provide suitable microsites for seedling establishment. Dealy (1970) and Hubbard (1956) found the release from competition by other plants a major factor in the establishment of bitterbrush seedlings. Ferguson and Medin (1983) found few bitterbrush seedlings on an area protected from livestock grazing and fire.

Production of bitterbrush seed varies annually, and good seed crops occur infrequently (Giunta and others 1978). Rodents are important in the dissemination and planting of seeds, and a high proportion of seedlings results from germination of seeds in unutilized rodent caches (Hormay 1943; Nord 1965; West 1968; Sherman and Chilcote 1972). Rodents transport seeds up to 1,000 ft (305 m) (Nord 1965) and are important in the movement of the relatively large bitterbrush seed away from parent plants. Rodents, however, may also reduce bitterbrush reproduction by consuming large quantities of the annual seed crop and by eating developing seedlings (Hubbard and McKeever 1961).

METHODS

This study was conducted in the Northern Rocky Mountains, primarily in Idaho and Montana. Within this region 56 prescribed burn and wildfire sites were located (fig. 1). These represent variation that occurs in habitat type, season of fire, growth form, and fire severity. Only burned sites between 3 and 10 years old were sampled. A minimum of 3 years was chosen because many plants that initially resprout following a fire die in succeeding years (Clark and others 1982). We believe that those individuals that lived for 3 years had a high probability of survival. The upper limit was chosen because our experience has shown that after 10 years the skeletons of the burned bitterbrush plants begin to decompose, thus making it difficult to establish the prefire density. Also, after 10 years, the sprouts become reproductively mature and begin to contribute to the seed source on the burn. Consequently, it would become increasingly difficult to determine the immediate postfire density of seedlings.

On each burn, one sample site was randomly selected from those where the prefire density of mature bitterbrush was estimated to exceed 200/acre (500/ha). Five 6.56- by 164-ft (2- by 50-m) belt transects were located by using a random numbers table. The density of dead, resprouting, and unburned plants on site at the time of the fire was recorded. Seedling density was also recorded for each transect. Additional data collected included habitat type, bitterbrush growth form, season of fire, elevation, slope, aspect, soil texture, and parent material. Where prefire density was less than 200 bitterbrush per acre, a plotless method was used to determine resprouting potential. Four random groups of 25 plants were located. Individuals were identified as dead or alive. Resprouting was estimated from this sample regardless of how much area was required to locate the 25 plants. An estimate of seedling density was not made on these sample sites.

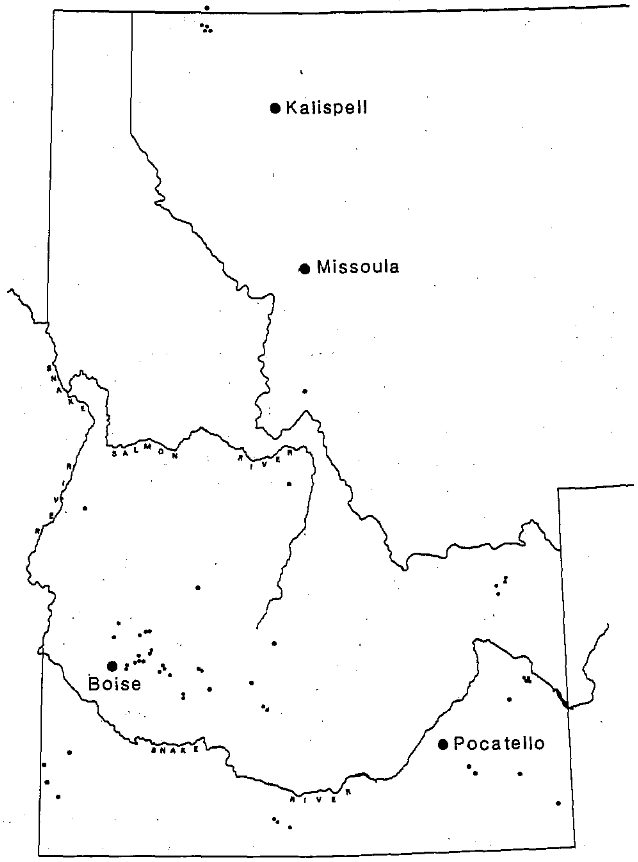

Figure 1.--Location of areas burned by prescribed burns or wildfires in the Northern Rocky Mountains which were sampled for bitterbrush resprouting frequency and establishment of seedlings.

The classification of habitat types follows Pfister and others (1977), Mueggler and Stewart (1980), Steele and others (1981), and Hironaka and others (1983), depending on the vegetation and area. A habitat type classification system for Utah juniper (*Juniperus osteosperma*) and western juniper (*J. occidentalis*) has not been developed for this region. These sample sites were classified only by the species of juniper present.

The other exception concerns a type of vegetation that has not been separately described. This vegetation has been included within the *Artemisia tridentata* ssp. *vaseyana-Symphoricarpos oreophilus/Festuca idahoensis* habitat type by Hironaka and others (1983) and will be referred to as "mountain shrub" in this paper. It is slightly more mesic than the typical *A. tridentata* ssp. *vaseyana-S. oreophilus/F. idahoensis* vegetation. It is characterized by the presence of one or more of the following shrubs: Saskatoon serviceberry (*Amelanchier alnifolia*), snowbrush ceanothus (*Ceanothus velutinus*), bitter cherry (*Prunus emarginata*), quaking aspen (*Populus tremuloides*), and squaw currant (*Ribes cereum*). Our experience indicated that this vegetation responds differently to fire than that included in the drier end of the habitat type as described by Hironaka and others (1983); it was, therefore, separated.

Bitterbrush does not occur as distinctly different growth forms over the entire region. Variation within the species is continuous between populations which are decumbent and multiple stemmed to those which are upright (columnar) and single stemmed. The latter may exceed 9.6 ft (3 m) in height. Growth form variation was separated into three classes. The decumbent form included those low-growing multiple-stemmed individuals (less than 3.28 ft (1 m) tall) which commonly reproduce by layering. Subcolumnar individuals included those which did not layer, were usually between 2.5 and 4.9 ft (75 to 150 cm) tall, and multiple stemmed. The columnar form included plants that were usually greater than 3.28 ft (1 m) tall, did not layer, and had few to a single main stem. Mature, unburned plants in the general vicinity were used to make this distinction. When more than one form occurred on a site, the dominant form was recorded.

The season and year of the fire were obtained from land management agency records. Fires were located that had occurred in various seasons and habitat types in order to balance the design of the study as much as possible.

One-way analysis of variance (ANOVA) and Duncan's Multiple Range Test were used to test the data for significant differences. More complex ANOVA could not be used due to the unbalanced nature of the data.

RESULTS AND DISCUSSION

Habitat type-form-season of fire combination was found impossible to completely balance. The three forms of bitterbrush do not occur within every habitat type sampled. In general, there is an elevation-moisture gradient associated with form. The decumbent form is found at the higher elevations and on more mesic sites. The columnar form occurs primarily at the lower elevations and on more xeric sites. The subcolumnar form was intermediate in regard to both variables. In some instances pure stands of two different forms may be found close to each other, depending upon the site. Thus, large differences in elevations were not always necessary to cause a change in form.

In addition, different habitat types were not likely to be burned in all seasons due to differences in fuel conditions. The decumbent form occurs in communities that are not frequently burned by wildfires. Prescribed fire, however, is more likely to be utilized in these communities at the present time. With the columnar form, the reverse is true. They are likely to be burned by wildfire and only rarely burned with prescribed fires. Prescribed fires were usually ignited in the spring and fall, and wildfires occurred primarily in the summer and fall.

The habitat types were grouped into five major categories of conifer, mountain shrub, mountain big sagebrush, basin big sagebrush, and juniper (table 1). Bitterbrush responded similarly to fire in habitat types or communities within each group.

Resprouting

The decumbent form of bitterbrush resprouted more frequently than the other two forms (table 2), whereas the subcolumnar form resprouted on the average two times as frequently as the columnar form. The difference, however, was not significant. Columnar and subcolumnar forms resprout from a mass of dormant buds at ground level or from a callus of meristematic tissue above the ground level as described by Blaisdell and Mueggler (1956). The decumbent forms resprout from the central bud mass and from bud masses that form at the points where the branches layer. It was observed that when fire killed the above-ground connecting branches, the separate resprouting bud masses may no longer be interconnected. These individual bud masses may be over 3.28 ft (1 m) from the parent bud mass.

Resprouting frequencies of bitterbrush on sites burned in the spring- and fall-burned sites averaged 55 and 42 percent, respectively, but were not significantly different (table 3). Resprouting was less frequent on the summer-burned sites and averaged 21 percent. Summer fire may be more destructive to bitterbrush because burns occur during a period of lowest carbohydrate reserves (Menke and Trlica 1981), and summer is also when the most severe fires occur.

The highest resprouting potential of the five habitat groups was found to be in the mountain shrub and the conifer groups, with 60 and 49 percent of the plants surviving, respectively (table 4). The bitterbrush populations in these groups are composed primarily of decumbent plants. The mountain big sagebrush group is also dominated by the decumbent form, but resprouting was significantly lower than in the first two habitat groups. The habitat types in this group are slightly more xeric than those in the mountain shrub or conifer groups. Basin big sagebrush and juniper habitat groups had the lowest resprouting potential. These groups were dominated by columnar and subcolumnar forms of bitterbrush.

Seedling Establishment

Seedling establishment rates appeared to be most affected by moisture gradient (tables 2, 3, and 4). Postfire seedling densities were greater on the more mesic habitat types such as the conifer group. Seedling density was greatest on areas burned in

Table 1.--List of habitat types and other communities included within the analysis groups used in this study

Community or habitat type group	Habitat types and communities included within group	Reference
Conifer	*Pseudotsuga menziesii/ Symphoricarpos albus* ht	Pfister and others 1977
	Pseudotsuga menziesii/ Symphoricarpos oreophilus ht	Pfister and others 1977 Steele and others 1981
	Pinus ponderosa/Purshia tridentata ht	Pfister and others 1977 Steele and others 1981
Mountain shrub	*Artemisia tridentata* ssp. *vaseyana-Symphoricarpos oreophilus/Festuca idahoensis* (mesic phase) ht	Adapted from Hironaka and others 1983
Mountain big sagebrush	*Artemisia tridentata* ssp. *vaseyana-Symphoricarpos oreophilus/Festuca idahoensis* (dry phase) ht	Hironaka and others 1983
	Artemsia tridentata ssp. *vaseyana/Festuca idahoensis* ht	Hironaka and others 1983 Mueggler and Stewart 1980
Basin big sagebrush	*Artemisia tridentata* ssp. *vaseyana f. "xericensis"*[1] *Agropyron spicatum* ht	Hironaka and others 1983
	Artemisia tridentata ssp. *tridentata/Agropyron spicatum*	Hironaka and others 1983 Mueggler and Stewart 1980
Juniper	Includes all communities in which *Purshia tridentata* occurs with *Juniperus osteosperma* or *J. occidentalis*. At this date these habitat types have not been described for the region sampled.	

[1] Currently this taxon of *Artemisia* has not been officially established by taxonomists, but has been referred to by Winward and Tisdale (1977).

late winter or spring and least on areas burned in the summer (table 3). The rate of seedling establishment closely corresponds to resprouting potential. In general, the greater the ability to resprout, the greater the likelihood of seedling establishment. A notable exception is the conifer group. Although its average resprouting potential was slightly less than that of the mountain shrub, average seedling density was two times greater for the conifer group (table 4).

The lowest seedling density was found in the juniper group (table 4). We do not know why the rate is so low. Both the juniper and basin big sagebrush groups are usually dominated by the columnar form. Cheatgrass (*Bromus tectorum*), which competes with bitterbrush seedlings for soil moisture, was usually less prevalent within the juniper vegetation than in basin big sagebrush. Slow regeneration of bitterbrush on juniper sites probably involves more than plant competition. Precipitation in the

Table 2.--Percentage bitterbrush resprouting and seedling density 3 to 10 years after fire as affected by bitterbrush growth form in the Northern Rocky Mountains.

Growth form	Resprouting Mean[1]	n[2]	Seedling density Mean[1]	n[2]
	Percent		No./acre (No./ha)	
Decumbent	57a	28	189 (467)a	26
Subcolumnar	18b	12	87 (209)a	11
Columnar	7b	16	29 (71)a	9

[1] Values within a column followed by the same letter are not significantly different ($P \leq 0.05$) as determined by Duncan's Multiple Range Test.

[2] n is the sample size and varies within a growth form between resprouting and seedling density because density could not be sampled on all sites.

Table 3.--Percentage bitterbrush resprouting and seedling density 3 to 10 years after fire as affected by season of the fire

Fire season	Resprouting Mean[1]	n[2]	Seedling density Mean[1]	n[2]
	Percent		No./acre (No./ha)	
Late winter-spring	55a	10	266 (658)a	9
Fall	42a	19	136 (335)ab	16
Summer	21b	27	73 (181)b	21

[1] Values within a column followed by the same letter are not significantly different ($P \leq 0.05$) as determined by Duncan's Multiple Range Test.

[2] n is the sample size and varies within a season between resprouting and seedling density because density could not be sampled on all sites.

juniper types at least equals that of the basin big sagebrush group, so this probably is not a factor. Precipitation is low, however, in both types. The prefire density of bitterbrush was also approximately equal. It has been observed that seed production by bitterbrush on sites occupied by juniper is reduced as the juniper begins to dominate the site. This reduction would deplete seed reserves in the soil. This phenomenon has not been observed on sites occupied by sagebrush (Monsen 1984). Ferguson (1972) found soil moisture and surface temperature to be important in seedling establishment. In general, the juniper sites were more productive, cooler in summer, and not subject to as variable temperatures during the winter as the basin big sagebrush sites. It may be that large rodent populations remove seeds and girdle seedlings. The relationship of prefire and postfire rodent populations between the two groups is not known. Other research has shown that rodents have a significant impact on bitterbrush establishment from seed (Hubbard and McKeever 1961). On one burned site in this study, 25 seedlings were permanently marked with stakes. Close inspection of the burned area during the third year revealed that no seedlings had survived even through they were numerous the first 2 years after the fire. Browsing by rodents or rabbits was determined to have been the cause. This indicates the impact that rodents may have on bitterbrush regeneration.

Soil stability may be a factor in seedling establishment. Grazing by livestock after fire on unstable granitic soils near Horseshoe Bend, Idaho, had displaced substantial amounts of soil on the 56 percent slopes. The density of seedlings on this site was 145 per acre (360 per ha), which was the greatest of the sites dominated by the columnar form. The majority of seedlings were single plants, which indicated that they were not from rodent seed caches. This suggests that seed burial was a factor in seedling establishment.

Fall is believed to be the best time for prescribed burning if seedling establishment is a major consideration (Monsen and Christensen 1975). Fall burns occur after the current year's seed has fallen from the plants and the seed availability is maximized. This study, however, found two times as

Table 4.--Percent bitterbrush resprouting and seedling density 3 to 10 years after fire as affected by major habitat type groups or communities in the Northern Rocky Mountains

Community or habitat type group	Resprouting Mean[1]	n[2]	Seedling density Mean[1]	n[2]
	Percent		No./acre (No./ha)	
Mountain shrub	60a	12	107 (264)ab	11
Conifer	49a	15	260 (643)a	14
Mountain big sagebrush	28b	11	94 (231)ab	10
Basin big sagebrush	11bc	10	54 (133)b	6
Juniper	6c	8	6 (16)b	5

[1] Values within a column followed by the same letter are not significantly different ($P \leq 0.05$) as determined by Duncan's Multiple Range Test.

[2] n is the sample size and varies within a season between resprouting and seedling density because seedling density could not be sampled on all sites.

many seedlings on spring burns than fall burns, although the difference was not significant (table 3). It seems that fire severity and environmental conditions after the burn may be more important in seedling establishment than the number of seeds present.

Changes in Density Following Fire

When considering the short-term effects of fire on bitterbrush populations, overall changes in density may be more important than either mortality or seedling establishment. Changes in density are presented by habitat group in table 5. The smallest decrease in average density occurred in the conifer habitat group. Although the mountain shrub group had the greatest average number of resprouts (table 4), the higher seedling establishment in the conifer group more than compensated for this difference. The conifer group with density increases on 4 of 14 sites was also the only group in which density increased after fire. One site had 57 percent more bitterbrush plants after a fire than before it was burned.

The greatest decrease in bitterbrush density following fire occurred in the juniper group, which has low resprouting combined with low seedling establishment. The average decrease in this group was 91 percent. This poor response makes the management of bitterbrush difficult in the juniper communities because bitterbrush is poorly adapted to fire. It is probably fire dependent, however, in many of the communities in the Northern Rocky Mountains. It has been our observation that without fire or some other disturbance that removes the juniper, bitterbrush will eventually be replaced by the developing juniper stand. Similar results have been reported by Young and Evans (1981) for California.

Table 5.--Change in density of bitterbrush following fire by habitat type group or community averaged across season and growth form in the Northern Rocky Mountains

Community habitat type group	Change in density[1]	Standard deviation	Range Minimum	Range Maximum
	---------------percent---------------			
Conifer	-11	±36.9	- 62	+57
Mountain shrub	-30	±28.2	- 87	0
Mountain big sagebrush	-55	±30.6	-100	0
Basin big sagebrush	-68	±10.4	- 79	-54
Juniper	-91	±11.2	-100	-73

[1] Density change includes resprouting and seedling establishment 3 to 10 years after fire occurred minus mortality.

MANAGEMENT IMPLICATIONS

It is a common belief among land managers that prescribed burning has no role in the management of bitterbrush. This conclusion is based on the premise that bitterbrush is fire sensitive and needs protection. This study and others have shown that although variation in response to fire occurs due to growth form, habitat type, season of the fire, and other factors, some bitterbrush mortality should be expected in almost all situations. Seedling establishment also varies, but seldom compensates for the mortality in those areas where bitterbrush is not well adapted to fire in the short term (less than 10 years). Many prescribed fires in communities where bitterbrush is a component of the vegetation are currently conducted for objectives other than bitterbrush management. These objectives include sagebrush (*Artemisia* spp.) control, increased herbaceous production, or slash disposal. In these instances, prescribed burns may be conducted in a manner that minimizes the loss of bitterbrush or may be canceled because the bitterbrush losses are judged to be unacceptable. This and other research enable the manager to predict the short-term effects of fire on bitterbrush. The question then remains as to what, if any, is the role of prescribed burning in bitterbrush management.

In the Northern Rocky Mountain area, bitterbrush occurs as a component of many forested and nonforested habitat types. It may be present at the seral or climax stage or throughout the entire successional sequence. Even in those communities where it is a part of the climax vegetation, it may act as a pioneer species. Given a seed source, it is often one of the first species to reoccupy a disturbed site such as a roadcut (Nord 1965). Bitterbrush has also been shown to increase after other disturbances such as logging (Stuth and Winward 1976; Edgerton 1983) and fire (Sherman and Chilcote 1972; Driver and others 1980; Martin 1983). Consequently, it is important to realize the successional status of bitterbrush within the particular community and that these communities are dynamic, not static, even at the climax stage.

Our study and others have shown wide differences in the response of bitterbrush to fire; these differences depend upon several variables. These findings demonstrate that it may be ecologically sound to use fire in bitterbrush management. The level of fire use, however, varies with the situation.

The role of prescribed burning in the management of bitterbrush within the mesic forested communities, such as Douglas-fir (*Pseudotsuga menziesii*), is that of maintaining a subclimax community type. Peek and others (1978) found that bitterbrush was declining in a seral ponderosa pine (*Pinus ponderosa*) stand that had been protected from grazing and fire. The site was a Douglas-fir/snowberry (*Symphoricarpos albus*) habitat type. They stated that if the vegetation proceeded to the climax composition, bitterbrush would disappear from the community. This decline is now occurring within many bitterbrush stands in the Northern Rocky Mountain region.

Our data support the use of prescribed fire to regenerate bitterbrush in seral ponderosa pine stands. There are opportunities to either underburn or selectively log and burn in conifer types for bitterbrush improvement. Application of spring or fall prescribed fire would allow a rather high rate of resprouting of bitterbrush which are primarily decumbent. Establishment of many bitterbrush seedlings can be expected. This conclusion is similar to that drawn by Driver (1983) for ponderosa pine.

Bitterbrush is a climax component of the ponderosa pine/bitterbrush habitat type. Even in these communities, productivity and density will decline without periodic disturbance. Initially, bitterbrush increased on these areas as a result of fire protection (Leopold 1950; Weaver 1957; Johnson and Smathers 1974). With continued protection, however, many populations have become decadent. Sherman and Chilcote (1972) found that bitterbrush declined in density from 25 to 100 years following a fire. It has also been shown that productivity of individual plants greater than 70 years old declines (McConnell and Smith 1977). Fire suppression may reduce reproduction by reducing the available microsites for rodents to cache seeds since they prefer microsites with thin layers of litter (Sherman and Chilcote 1972). The establishment of bitterbrush seedlings on undisturbed sites is probably also regulated by competition. Any factor reducing competition enhances seedling survival. Litter accumulation also changes soil characteristics (Zinke 1962) which may influence seedling establishment.

The response of bitterbrush within the western juniper and pinyon-juniper communities is much different than the response in the more mesic forest types. In these communities, bitterbrush usually develops the columnar growth form, which is least adapted to fire. Our data indicated the lowest resprouting potential and number of established seedlings of bitterbrush in the juniper communities of those habitat types studied. It may seem logical then to restrict the use of fire in these communities in order to maintain the stands of bitterbrush; however, unless fire is permitted periodically into these areas the juniper will increase in density and invade adjacent sagebrush/grassland vegetation (Burkhardt and Tisdale 1976). Increasing dominance of juniper in a community decreases the understory shrub and herbaceous species. Consequently, with continued protection from fire the bitterbrush in these communities will be replaced by other species. Young and Evans (1981) found vigorous bitterbrush only in open stands of juniper. They suggested that these were probably areas that had previously burned and were being reinvaded by juniper. In dense juniper stands, the bitterbrush was dead or had very low vigor. It appears that even though bitterbrush is not well adapted to fire in these communities, it depends upon fire to maintain a lower successional stage than climax juniper.

Periodic fire will be necessary to maintain bitterbrush in juniper communities. The fire-free interval will need to be sufficiently long to allow the bitterbrush to redevelop. If the interval is too long, the reinvading juniper will eliminate the bitterbrush seed source. The development of a new bitterbrush stand will require more time because the seeds will have to be transported onto the burn from other areas. Dense juniper stands do not readily burn due to the lack of fine fuels; however, when they do burn the fires are usually severe. High-severity fires will also reduce the number of surviving plants. This situation is becoming common in many juniper communities at this time.

The role of prescribed fire in the management of bitterbrush in nonforested habitat types is less clear than that in the forested communities. Since these types are not occupied by trees, the decline in bitterbrush density and vigor is not as readily apparent even after long periods of fire absence. There is some evidence, however, that fire or other disturbance may be necessary to establish new bitterbrush plants in these communities. McConnell and Smith (1977) found that the productivity of bitterbrush was correlated to age regardless of browsing intensity. Annual production increased to a maximum at 60 to 70 years of age and then declined. In Idaho, it was found that deer browsing was not a significant factor in vegetation change over a 23-year period. Bitterbrush annual production and density decreased while canopy coverage increased (Ferguson and Medin 1983).

Bitterbrush associated with mountain big sagebrush is usually well adapted to fire. The bitterbrush present usually are of the decumbent form or, rarely, subcolumnar. Resprouting frequency averaged 45 percent in the nonforested communities where mountain big sagebrush was present. Prescribed fire is frequently used in these communities for sagebrush control. Coverage of mountain big sagebrush is among the greatest found in *Artemisia* types and may exceed 40 percent. Fire is an effective means to stimulate production of these communities. Initially, the herbaceous component is enhanced. Nearly all shrubs, including bitterbrush and mountain big sagebrush, establish more rapidly from resprouts or seed than many other sagebrush communities. Consequently, the productivity of the shrub component is also enhanced in the long term by periodic fire in many situations. Spring fires give the best results in this vegetation, but spring prescribed burning may be limited in some areas due to the climate. Most shrubs, including bitterbrush, also respond well to low-severity fall prescribed fires, however.

Bitterbrush in the basin big sagebrush and "species X" (*Artemisia vaseyana* f. "*xericensis*") (Winward and Tisdale 1977) communities are more seriously damaged by fire than those associated with mountain big sagebrush. They are usually columnar or subcolumnar forms which resprout poorly and do not readily establish from seed. Many of these communities are also heavily invaded by cheatgrass. This has altered the plant competition relationships, particularly at the bitterbrush seedling stage.

Cheatgrass, an exotic, has also altered the fire relationships in these areas by changing fuel distribution and amount. Since the invasion of cheatgrass, fires in these communities are likely more continuous than previously. The fire-free interval of fires in cheatgrass dominated areas is shorter. Cheatgrass responds favorably to fire, and fuels can return to sufficient levels to carry another fire within 1 to 2 years.

The role of fire in these communities before settlement is not known. It has been suggested that because the recovery of bitterbrush may take 30 years, the fire frequency would have been about 50 years for bitterbrush to exist (Wright and Bailey 1982). It has also been suggested that the fire interval was short and that many of the shrubs were not present in the densities we observe today (Gruell in preparation). This may have been the case with bitterbrush in the "species X" communities, which are often productive sites on moderate to steep slopes. They burn frequently today as a result of lightning and human-caused fires. Even though cheatgrass has increased the fire potential, it is probable that frequent Indian- and lightning-caused fires held bitterbrush to low levels in this community in presettlement times.

The current fire frequency combined with the poor adaptation of bitterbrush to fire in "species X" communities makes continued maintenance of bitterbrush difficult without artificial planting as suggested by Ferguson and Medin (1983). Another possibility is the development of a more fire-adapted cultivar of bitterbrush or the introduction of a resprouting browse species into these areas.

We conclude that although bitterbrush density usually decreases initially following fire, the continued productivity and dominance in a community of bitterbrush is disturbance-dependent. In many instances, continued protection from fire will result in low rates of reproduction and declining productivity. Proper application of prescribed fire may be used to maintain vigorous bitterbrush stands on a long-term basis. As managers we must not be so concerned with short-term effects that we lose sight of the future needs of the species and those animals that are dependent upon it.

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INFLUENCE OF FIRE ON CURLLEAF MOUNTAIN-MAHOGANY IN THE INTERMOUNTAIN WEST

G. Gruell, S. Bunting, and L. Neuenschwander

ABSTRACT: Comprehensive sampling of curlleaf mountain-mahogany (*Cercocarpus ledifolius*) on 41 sites in five States allowed an assessment of postfire population dynamics, differences in regeneration patterns, and critical events in stand regeneration. Historical accounts of fire, fire history studies, and early photographs provided historical perspective and contributed to interpretations.

The combined quantitative and historical evidence strongly suggests that before European settlement, fire significantly influenced mahogany in the Northern Rockies by restricting its development. A reduction of fire periodicity and size following Euroamerican settlement apparently allowed mahogany seedlings to regenerate far in excess of former levels. The absence of fire for long periods has resulted in great variation in structure of mahogany stands. Many stands are in a declining condition because the absence of fire has allowed them to reach advanced stages of succession. In some areas, closure of mahogany crowns, excessive litter accumulation, and competition from other vegetation are inhibiting regeneration. In other areas, young vigorous mahogany predominate. These wide differences in stand conditions suggest different management strategies. Many mahogany communities would respond positively to fire, whereas others would not. Management implications are given.

INTRODUCTION

Curlleaf mountain-mahogany, hereafter referred to as mahogany, is an important forage and cover plant on many game ranges in the Northern Rocky Mountains. Various questions about proper management of mahogany ecosystems have surfaced in recent years because of incomplete knowledge of regeneration potential. A primary question involves the role of fire. Mahogany grows in regions where fire has been a common ecological disturbance; however, there has been little research on the effects of fire on long-term mahogany production. To determine whether prescribed fire has a place in future management strategies, it is important to understand the past role of fire in representative mahogany types.

To understand the role of fire in managing mahogany, we conducted comprehensive sampling of mahogany stands on a wide range of sites in Idaho, Montana, and adjacent portions of Nevada, Utah, and Wyoming that were representative of stands in the Intermountain West. In this region mahogany is present in over 20 forested or nonforested habitat types (Henderson and others unpubl.; Hironaka and others 1983; Mueggler and Stewart 1980; Pfister and others 1977; Steele and others 1981). In the forested communities, mahogany may be potential climax or seral, but in the nonforested communities where it occurs, mahogany is potential climax. We assessed the postfire population dynamics, differences in regeneration patterns, and critical events in mahogany regeneration.

Quantitative data gathered at 41 locations (fig. 1) were complemented by fire history studies, fire occurrence records, historical literature, and comparison of historical photographs with recent photographs taken in mahogany types. Study findings allowed us to make implications for fire management, including use of prescribed fire in mahogany types.

PAST RESEARCH

Mahogany is widely distributed throughout semiarid regions of the Intermountain West from eastern California to southwestern Montana and north-entral Wyoming (Little 1976). Growth forms vary rom low shrubs to plants that may reach 30 ft 9 m) in height on productive sites. Older plants ay exceed 300 years in age.

hogany is a highly palatable forage for mule deer (*Odocoileus hemionus*) (Smith 1952), and it is a preferred browse (Kufeld and others 1973). Stands in many regions have grown above the reach of big game and are no longer a source of forage. These stands are, however, a valuable seed source and important hiding cover (Dealy 1971). Heavy winter utilization has been widely reported (Deitz

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G. Gruell is a research wildlife biologist with the Intermountain Research Station, Forest Service, U.S. Department of Agriculture, Missoula, Mont.

S. Bunting and L. Neuenschwander are associate professor of Range Resources and associate professor of Forest Resources, College of Forestry, Wildlife, and Range Sciences, University of Idaho, Moscow, Idaho.

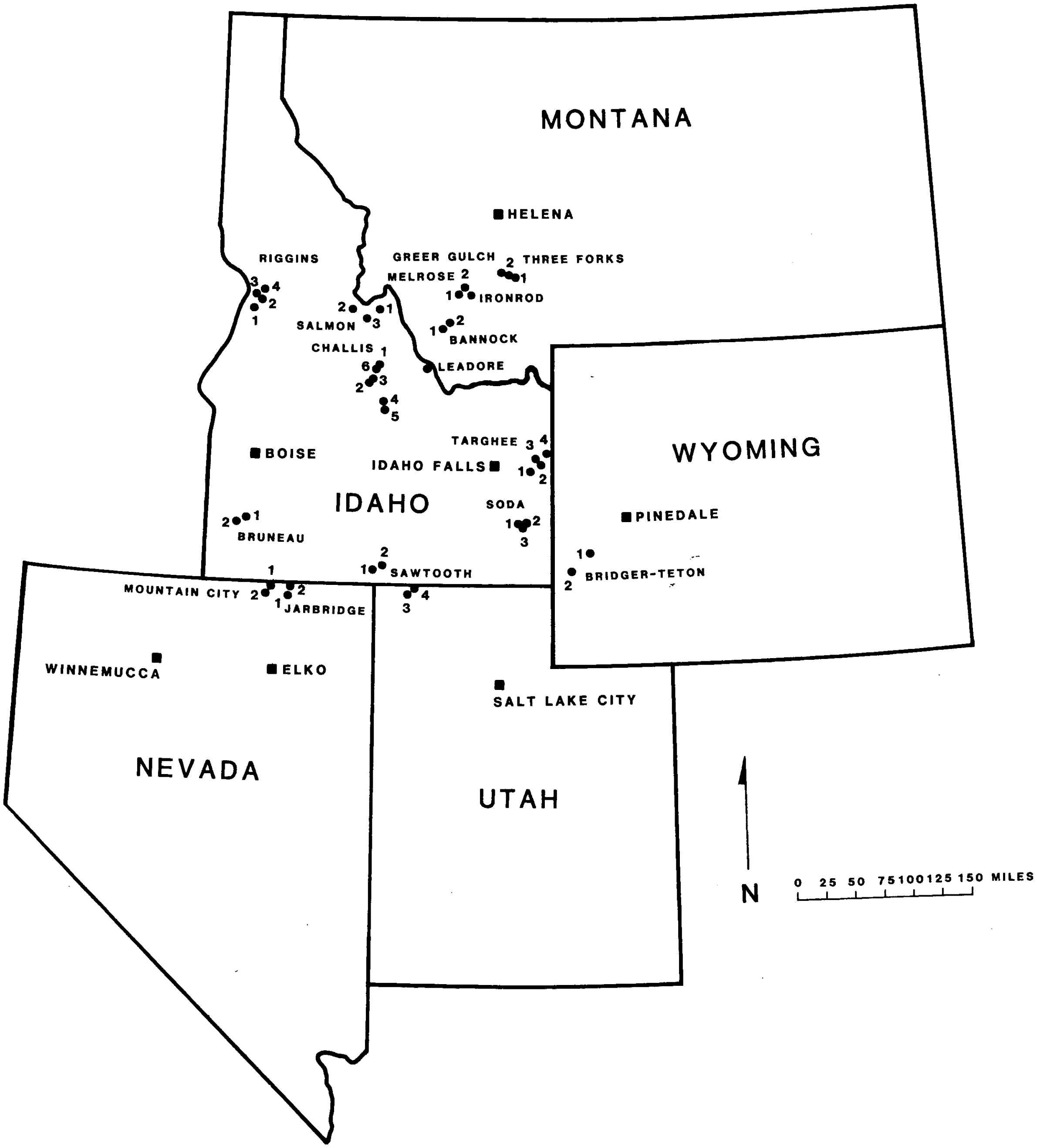

Figure 1.--Location of the 41 mahogany sampling sites. See table 1 for description of site characteristics.

and Nagy 1976; Claar 1973; Richens 1967). In southwestern Montana heavy utilization by ungulates was believed to have been responsible for a deterioration of mahogany stands (South 1957). In contrast, Claar (1973) concluded that decades of heavy browsing by big game in central Idaho had not caused mahogany to deteriorate. Plant losses were compensated by establishment of seedlings. Mackie (1973) concluded that high-level ungulate use over a 5- to 23-year period on two Montana winter ranges had not been responsible for decreased plant populations, browse production, or both.

Researchers working on the ecology of mahogany have postulated fire effects. Dealy (1975) in eastern Oregon and Scheldt (1969) in Idaho reported that the existence of mahogany was related to the fire protection afforded by rocky sites. They also concluded that most mahogany stands on deep soils were less than 100 years old and that tree age seemed to correlate closely to the advent of fire control and use of forage by livestock that otherwise would have fueled fires.

Montana studies that included age determination of mahogany implicitly showed the relationship of age to absence of fire. Duncan (1975) found an average age of 22 years (range 5 to 85 years) for 210 randomly chosen plants in 21 southwestern Montana stands. Lonner (1972) reports the average age of 62 mahogany plants collected on Montana big game winter ranges was 37 years (range 2 to 130 years).

The beneficial influence of fire has also been reported. Claar (1973) concluded that fire seemed to be essential to set succession back and maintain seral mahogany on drier sites associated with adjacent Douglas-fir/ninebark habitat types.

Mahogany, a weak sprouter (Wright and others 1979), is highly susceptible to fire, which results in heavy mortality. It sprouts from undamaged auxiliary buds on the stems or from adventitious buds beneath the bark. Unlike many shrubs, it has a thick bark that allows it to survive light fires when mature and does not sprout from a basal caudex or rhizomes. Sprouting may occur after light burning, but reproduction almost entirely depends on seedling establishment.

Mahogany has successfully regenerated from seed after stands were cut. Dealy (1975) reported that young stands in two Oregon localities developed following intensive cutting for firewood during the late 1800's and early 1900's. Experimental cutting and bulldozing of mahogany on the Targhee and Cache National Forests during the 1960's resulted in germination of many seedlings (Phillips 1970). Seedling germination was heavy on mineral soil that was bared of litter and plant competition. High seedling mortality may occur, however, apparently the result of summer drought.

Marked reductions in mahogany forage availability have led to attempts to increase productivity by top pruning (Austin and Urness 1980; Ormiston 1978; Phillips 1970; Thompson 1970). These experiments indicated that production can be temporarily increased in the browsing zone by pruning plants above a point where there are numerous live twigs. Where large treelike mahogany predominates, however, the scarcity of twigs within the browsing zone precludes pruning as a practical treatment measure. No sprouting from adventitious buds below the cut was reported. Attempts to improve forage availability by pushing over younger mahoganies with a bulldozer have succeeded (Phillips 1970); however, older mahogany usually die when pushed over (Dealy 1971).

HISTORICAL PERSPECTIVE

Examination of historical accounts showed that wildfire was a major perturbation in semiarid regions of the Interior West from at least 1776 to 1900 (Gruell in press). Many of these fires were set by Indians (Gruell in press). Some of these accounts described the beneficial effects of fire in stimulating grasses and suppressing woody plants.

Study of the scars on trees indicates that before Euroamerican settlement fire intervals averaged from 5 to 20 years in ponderosa pine/Douglas-fir (*Pinus ponderosa/Pseudotsuga menziesii*) forests in the Bitterroot Valley of western Montana (Arno and Peterson 1983). Scar data from higher and cooler Douglas-fir/sagebrush (*Artemisia tridentata* subsp. *vaseyana*) ecotones in Yellowstone Park and southwestern Montana indicated that fire intervals were 20 to 40 years (Houston 1973; Arno and Gruell 1983). Fire scar evidence in Ephraim Canyon, Utah, indicated an average fire interval of from 7 to 10 years in aspen (*Populus tremuloides*) during the period 1770 to 1875 (Baker 1925). Working in southwestern Idaho, Burkhardt and Tisdale (1976) reported that presettlement fire intervals were about 11 years in sagebrush-grass/western juniper (*Juniperus occidentalis*) ecotones.

An examination of early photographs provided insights about the historical appearance of mahogany stands (Gruell 1983). Figures 2 and 3 are some of the earliest scenes found within the study area. These 1868 and circa 1871 scenes show mahogany confined to protected rocky sites or thin soils where fire was infrequent. Recent field inspection revealed evidence of pre-1868 fire within the scene at figure 2. On other sites (fig. 3) some mahogany plants had apparently resisted light surface fires but were killed by a more severe fire before 1871. Figure 4 shows an example of mahogany regeneration following cutting.

METHODS

Mahogany density varied greatly among communities. To provide consistent sampling among study sites, stands had to meet the following criteria to be selected:

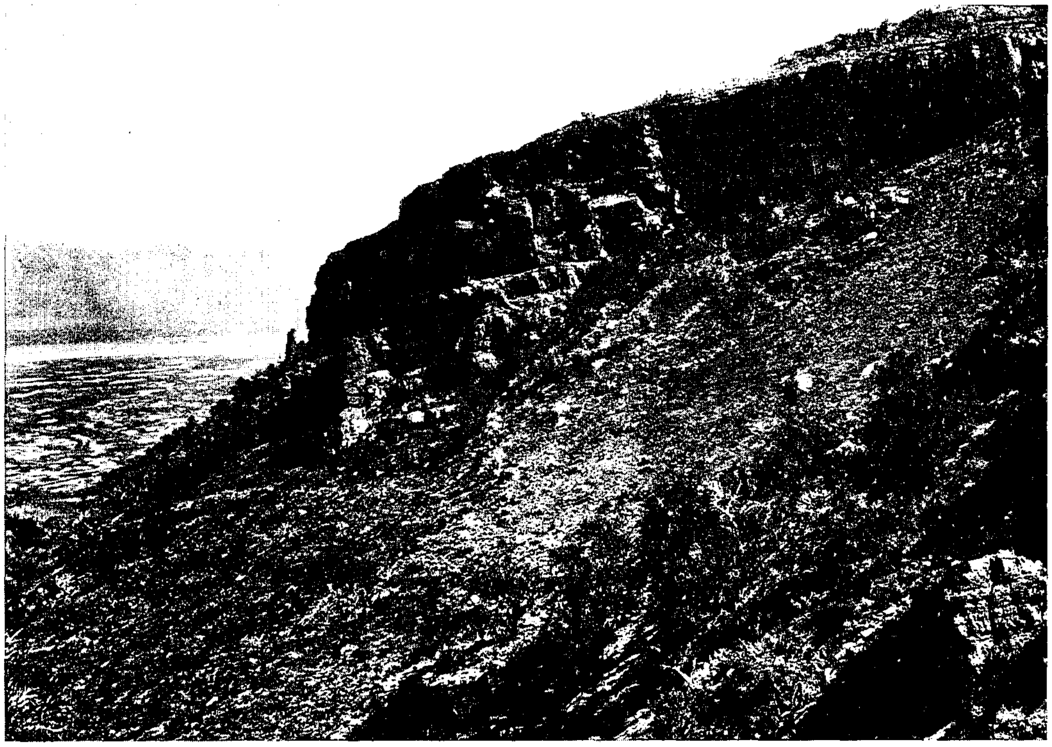

Figure 2a.--Looking east-southeast down canyon toward Ruby Marsh from a point about 1.5 miles above Flyn and Hager Spring (elevation 7,500 ft)(1868). Note the scattered distribution of living and dead fire-killed mountain-mahogany in lower left quarter of photo.

Photograph by Timothy O'Sullivan. Courtesy of U.S. Geological Survey, Denver, Colo.

Figure 2b.--Photo taken July 31, 1982. The absence of fire since the 1840's or earlier has allowed mountain-mahogany and other woody vegetation to increase. Charred material in mahoganies verified loss of mahogany to fire before 1868.

Photograph by G. E. Gruell.

Figure 3a.--Looking north from a point adjacent to county road in southeast quarter of City of Rocks, Idaho (elevation 6,400 ft). Woody plants include singleleaf pinyon pine (*Pinus monophylla*), Utah juniper (*Juniperus osteosperma*), and mountain-mahogany. Note the dead branches in foreground and absence of large woody plants in the smaller openings between rocks.

Photograph by Timothy O'Sullivan. Courtesy of U.S. Geological Survey, Denver, Colo.

Figure 3b.--Photo taken August 20, 1983. Absence of fire over 100 years has allowed woody plants to proliferate. Sagebrush has increased in opening at left and on flats at right. Mountain-mahogany mixed with pinyon pine and juniper have invaded the deeper soils in openings. Sometime after 1872, a fire swept the upper slopes on distant mountain on right.

Photograph by G. E. Gruell.

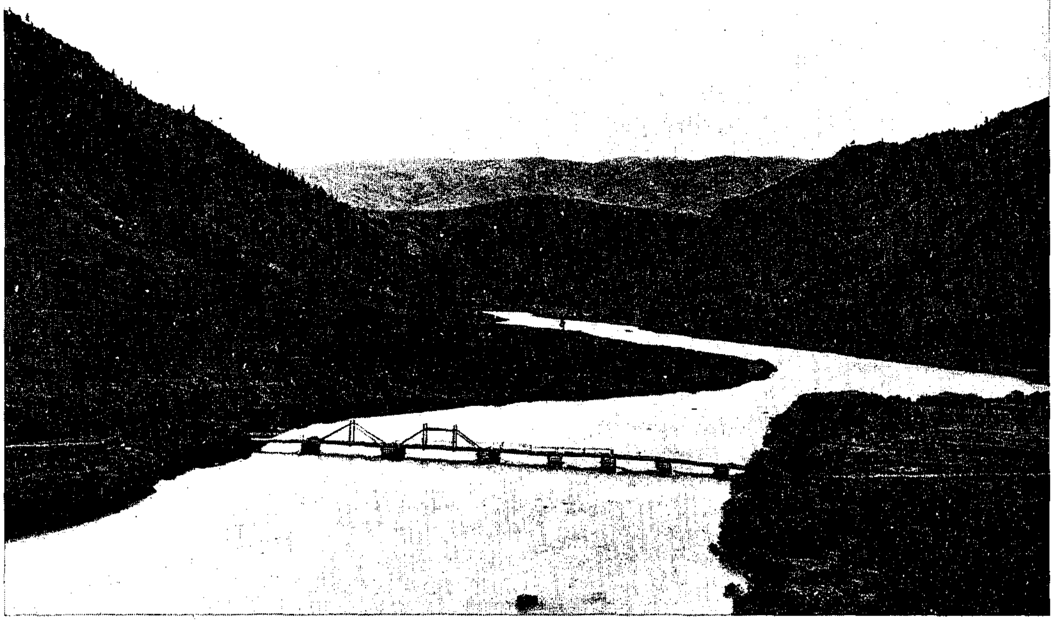

Figure 4a.--Photo taken in 1871. Camera faces south-southeast from position on west bank of Madison River near present day Highway 84 crossing at Beartrap Recreation area (elevation 8,500 ft). Distant slopes support Douglas-fir (*Pseudotsuga menziesii*), limber pine (*Pinus flexilis*), Rocky Mountain juniper (*Juniperus scopulorum*), and mountain-mahogany.

Photograph by W. H. Jackson. Courtesy of U.S. Geological Survey, Denver, Colo.

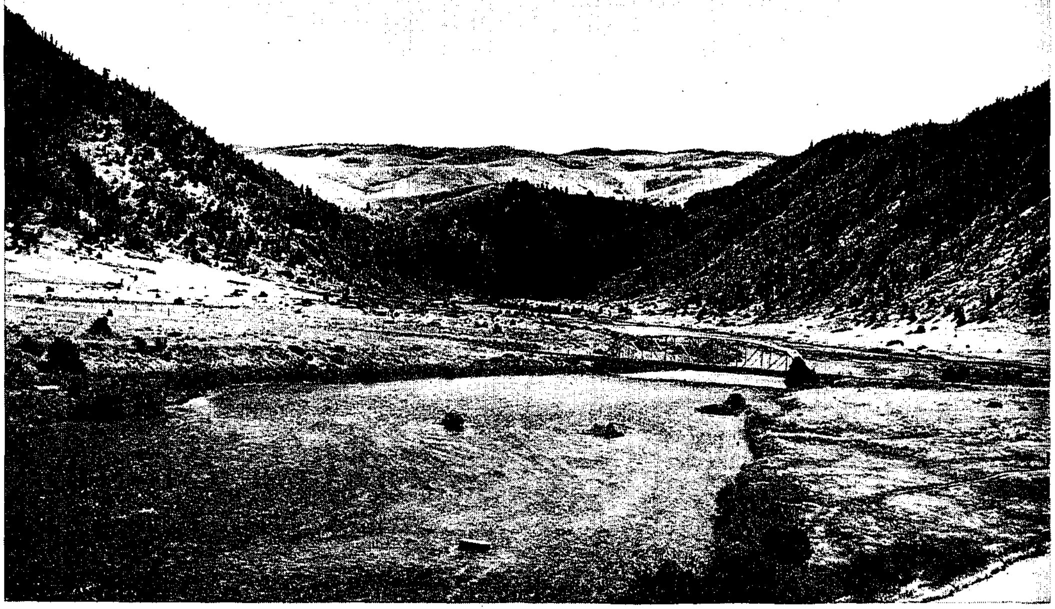

Figure 4b.--Photo taken August 31, 1982. Douglas-fir was cut after original photo was taken. Fire-scarred stumps indicate fires had occurred every few decades before settlement. Removal of conifers and absence of fire allowed great increase in mahogany. Note distant slopes above bridge.

Photograph by G. E. Gruell.

1. Minimum density of 10 mature mahogany per acre (25 per hectare) (in the case of recently burned stands the preburn density had to exceed 10 plants per acre).
2. A minimum stand diameter of 164 ft (50 m).
3. Reasonable accessibility.

Stands meeting these criteria were identified during a prestudy reconnaissance. A random sample of these stands was then selected using a random number table.

Fire-scarred cross sections were collected from all stands in which scarred mahogany occurred. These data aided in interpreting the role of fire in sampled communities. Stands burned on a known date or with a known history of other types of disturbance such as logging were chosen for sampling.

In each stand, the center points for four azimuths were randomly determined. Along each azimuth, a 13- by 66-ft (4- by 20-m) belt transect was used to measure the density of mahogany. The stem diameter near ground level was recorded. Where stands were dense, the belt transect was reduced to a width of 3.28 ft (1 m).

The age-diameter relationship for each stand was determined by randomly selecting 8 to 15 mahogany plants representing the size classes present. Height, maximum crown spread, and basal diameter of the plant were recorded, and a cross-section at the base was then collected. In the laboratory, cross-sections were sanded and annual growth rings counted with the use of a 10- to 50-power dissecting microscope. Ring counts were not considered precise because of the likelihood of false or missing rings. Data from 307 cross-sections were used in regression analysis to develop a model to estimate the age of mahogany.

Litter depth and seedling density were measured within a 3.28- by 66-ft (1- by 20-m) belt transect along each of the azimuths.

Cover of trees, mahogany, shrubs, perennial grasses, perennial forbs, annuals, and bare ground were estimated on circular plots with a radius of 3.28 ft (1 m). Five plots were located along each of the random azimuths at 16 ft (5 m) intervals. Mahogany canopy cover was also estimated by line intercept along the transect lines.

Additional site data collected on each stand included elevation, aspect, slope, vegetational competition, habitat type, surface soil texture, parent material, and time since last fire if known.

RESULTS

Age Determination

Results of the regression analysis indicated that basal diameter was the best single variable to estimate mahogany age. The regression equation is as follows:

$$Y = 11.66 + 5.90X$$

where:

Y = age (number of growth rings) of mahogany (years).

X = basal diameter (centimeters).

The coefficient of determination (r^2) for this equation was 0.75. Additional variables were included, and the sample was partitioned by such factors as habitat type and aspect in further regression analysis; however, the r^2 improved only slightly. Consequently, the simpler regression equation was used to predict age.

Stand Age And Structure

Forty-one mahogany stands in 13 habitat types were sampled (table 1). Stands were grouped into five categories by potential climax association and stand structure as follows:

Category 1. Mahogany is the potential climax. Stands are comprised of all age classes dating from pre-1830.

Category 2. Mahogany is the potential climax. Stands are almost entirely comprised of post-1900 age classes.

Category 3. Mahogany is seral. Conifers are present but scattered and not yet competitive.

Category 4. Mahogany is seral and is being replaced by conifers.

Category 5. Mahogany communities arising after post-1900 disturbances.

Analysis of stand age (categories 1 to 4) showed a great increase in mahogany density during the past 150 years (table 2). After 1940, the rate of increase accelerated (fig. 5). This rate is inflated because 11 of the 36 stands sampled were almost entirely comprised of young plants. The most noteworthy aspect of the data in figure 5 is that only 1 percent of the mahoganies in 1970 stands was present before 1830. We concluded that the 1980's sampling provided a reasonably accurate picture of the pre-1830 stand because there was little evidence of plant losses after 1830.

Separate analysis of the five categories revealed differences in stand development. Stand data were graphed to display changes in density over time.

Category 1 (All Aged Potential Climax Mahogany)

Historically, category 1 stands were protected from fire by rock outcrops or by discontinuous fuels. In 1855, some stands were lightly stocked (13 stems/acre; 31/ha), and a few stands were well stocked (203 to 329 stems/acre; 501 to 813/ha). Most stands regenerated after 1855. The rate of regeneration seems to have been strongly influenced by canopy coverage and competition from other plants. Closed canopy stands, such as Mountain City 2 (fig. 6), which

Table 1.--Characteristics of potential climax and seral mahogany stands in the five State study area

Stand	Habitat type	Parent material[1]	Aspect	Elevation	Slope	Average Cele cover	Evidence of past fires[2]
				---Feet---	-----Percent-----		
Category 1 (all aged potential climax mahogany)							
Riggins 1	Cele/Agsp	L	SSE	3,100	70	20	P
Riggins 2	Cele/Agsp	L	W	2,300	55	14	C
Riggins 4	Cele/Agsp	B	SW	2,200	32	31	C
Challis 3	Cele/Agsp	L	SSW	7,000	33	18	P
Bruneau 1	Artrva/Syor/Feid	B	SE	6,000	5	50	P
Bruneau 2	Artrva/Syor/Feid	B	N	6,100	8	15	P
Mountain City 2	Artva/Syor/Feid	B	WNW	6,500	7	49	N
Jarbridge 2[3]	Cele/Syor/Feid	R	W	7,600	46	69	P
Sawtooth 1	Artva/Syor/Feid	B	N	7,200	8	50	N
Bridger-Teton 1	Cele/Artva/Feid	S	W	7,800	35	29	P
Bridger-Teton 2	Cele/Artva/Feid	S	W	7,500	33	18	P
Ironrod 1	Cele/Agsp	G	W	6,200	26	38	N
Category 2 (young stands; mahogany potential climax)							
Riggins 3	Cele/Agsp	L	S	3,200	33	1	P
Challis 4	Artrva/Syor/Feid	L	ENE	7,500	47	55	P
Soda 2	Juos/Cele/Agsp	L	E	6,200	63	4	P
Bannock 1	Cele/Agsp	G	SW	6,200	47	23	N
Bannock 2	Pifl/Cele/Agsp	G	WSW	7,000	43	30	C
Melrose 1	Cele/Agsp	L	SW	6,300	32	11	N
Melrose 2	Cele/Agsp	L	WSW	6,300	18	16	N
Threeforks 1	Pifl/Cele/Agsp	L	NW	4,800	23	45	N
Threeforks 2	Pifl/Cele/Agsp	L	NW	4,800	25	25	N
Category 3 (seral mahogany with scattered conifers)							
Salmon 1	Pipo/Feid	G	SW	4,500	62	18	P
Salmon 3	Psme/Cele	G/L	S	4,600	62	21	P
Leadore	Pifl/Cele	L	W	7,500	42	24	P
Challis 5	Psme/Cele	L	NE	7,500	50	57	P
Jarbridge 1	Abla[5]	G	W	8,200	58	12	P
Sawtooth 2	Abla[5]	B	NW	7,100	14	59	N
Sawtooth 3	Pimo/Artrva/Agsp[5]	L	SE	8,000	26	31	N
Soda 1	Juos/Cele/Agsp[5]	L	S	6,200	39	40	N
Targhee 3	Psme/Syor	L	SW	6,300	51	19	P
Targhee 4	Pifl/Syor	L	SSE	7,200	52	57	P

See footnote at end of table.

continued

Table 1.--(continued)

Stand	Habitat type	Parent material[1]	Aspect	Elevation	Slope	Average Cele cover	Evidence of past fires[2]
				---Feet---	-----Percent-----		
Category 4 (seral mahogany with competitive conifers)							
Sawtooth 4	Pimo/Artrva/ Agsp[5]	L	S	7,500	35	8	N
Challis 1	Psme/Cele	L	N	8,000	5	34	N
Targhee 2	Psme/Syor	L	S	6,500	50	20	P
Greer Gulch	Psme/Cele	G	WSW	5,000	38	28	N
Category 5 (disturbed mahogany stands)							
Mtn. City 1	Artrva/ Syor/Feid	B	SW	6,500	20	6	Burned October 1975
Targhee 1	Psme/Syor	L	W	6,300	64	1	Burned 1966. Seeded to grass after fire
Challis 2	Cele/Agsp	L	SSW	7,000	35	1	Burned 1934. Very slow regeneration.
Salmon 2	Psme/Cele	G	W	4,800	64	37	Last burned in 1919.
Challis 6	Psme/Cele	L	NE	8,000	5	2	Timber harvested. Slash was piled and burned.
Soda 3[4]	Juos/Cele/ Agsp[5]	L	SE	6,200	46	20	Juniper had been cut for posts.

[1] B = basaltic; G = granitic; L = limestone; R = ryolite; S = sandstone.

[2] P = fire evidence present; C = circumstantial evidence present; N = no evidence of past fires.

[3] Sapling sized Abla establishing in former Cele stand.

[4] Post-cutting estimated to have occurred 30 to 50 years ago.

[5] This vegetation has not been adequately habitat typed in this region, consequently this designation has been tentatively applied by the authors.

Table 2.--Summary of number mahogany stems per acre (stand density) by period of establishment for all stands except disturbance stands in category 5

	Period of establishment							
	Before 1830	1831-1855	1856-1900	1901-1920	1901-1940	1921-1950	1941-1960	1961 1970
Statistic[1]								
Median	0	26	26	51	76	51	51	51
High	89	253	177	405	759	2277	3138	4200
Low	0	0	0	0	0	0	0	0

[1] Median data were used in place of mean because extraordinary high values reflective of young stands in category 2 tended to skew the mean unreastically high as an (average).

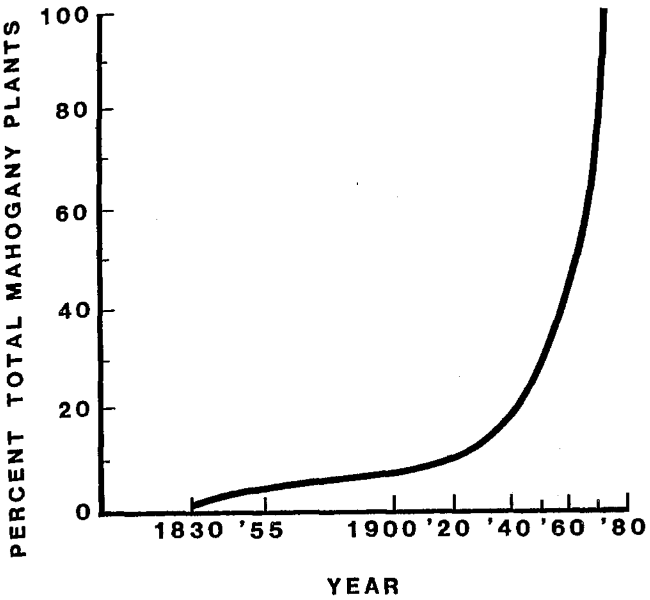

Figure 5.--Mountain mahogany densities in category 1-4 stands from 1830 to 1970. Percentage values for dates of record were calculated by dividing the number of stems per record date by the total number of stems in 1970. After 1830 percentage values are accumulative.

regenerated mostly after 1900, show a significant decline in regeneration since 1940. Shading, litter accumulation, and lack of bare soil apparently reduced the opportunity for seedling establishment. Foraging on seedlings by domestic livestock, deer, rabbits, and rodents may also be inhibiting regeneration. Stands with more open canopies and exposed bare soil such as Bruneau 2 have been regenerating at a sustained rate (fig. 6). Less open stands (B-T-1) continued to regenerate but at a slower rate; whereas others (Challis 3) have had a substantial increase in regeneration during the past 30 years (fig. 7). Accelerated rates of regeneration in recent decades seem to be strongly influenced by stands reaching a critical reproductive age. When this point is reached, seed is dropped and regeneration establishment takes place on suitable microsites.

Category 2 (Young Stands; Mahogany Potential Climax)

These stands occur typically on deep soils that historically have had grass cover. Except for Bannock 2 (table 1), past fires were not evident. We believe that surface fires were once frequent and completely consumed the light fuels, thus preventing the establishment of mahogany.

Some stands became established between 1900 and 1920, and regeneration accelerated after 1940 (fig. 8). Since about 1960, however, the rate of regeneration has sharply declined. Other stands, such as Threeforks 1 (fig. 9), did not become established until about 1940. This stand has been regenerating rapidly in recent decades.

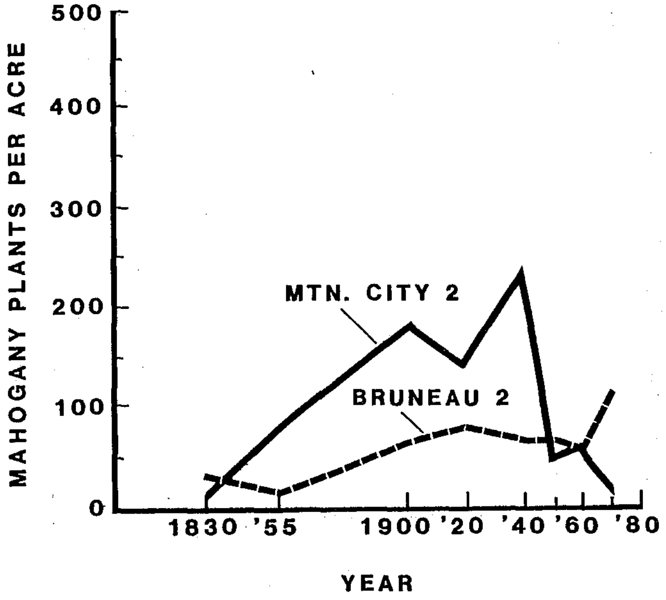

Figure 6.--Potential climax stands showing contrasts in reproduction. Mountain City 2 regenerated at an accelerated rate through about 1940 and then declined sharply. Bruneau 2 shows a lower rate of regeneration with an upturn since 1960.

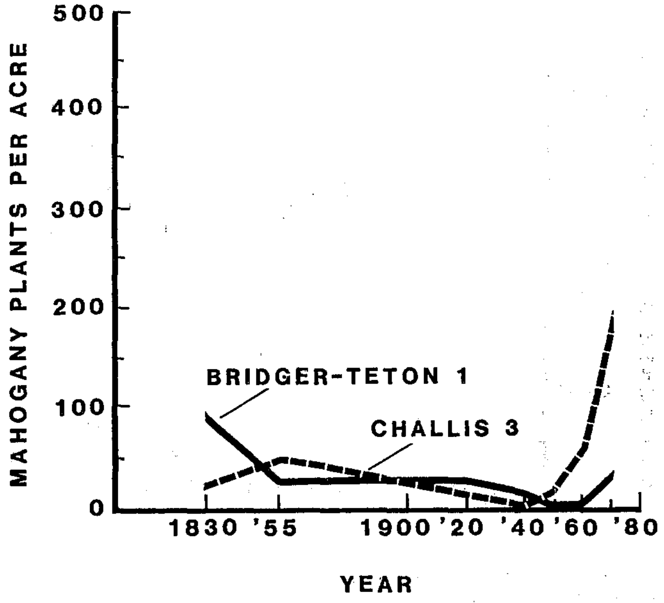

Figure 7.--Examples of potential climax stands that show differences in rates of regneration. Bridger-Teton 1 is an old stand that continues to regenerate at a low level. In contrast, Challis 3 shows accelerated regeneration during the past 30 years.

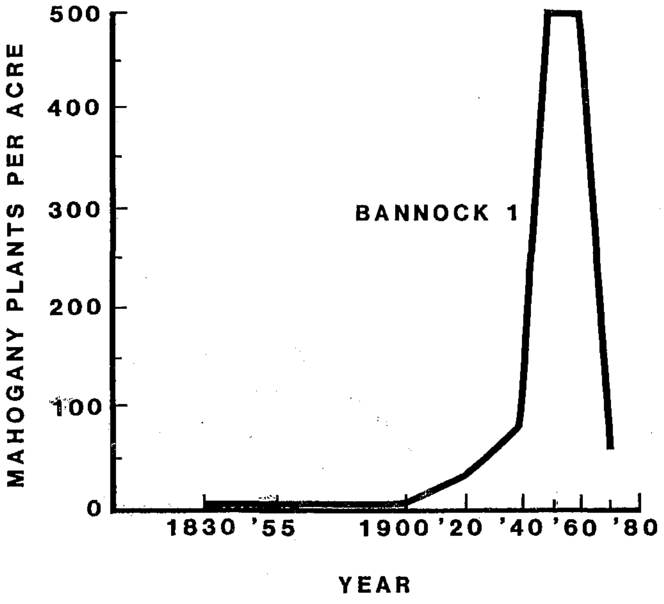

Figure 8.--Example of a potential climax stand in category 2 that regenerated on a site that was not occupied by mahogany prior to about 1920. Sharp decline in regeneration seems to be result of the site becoming fully stocked.

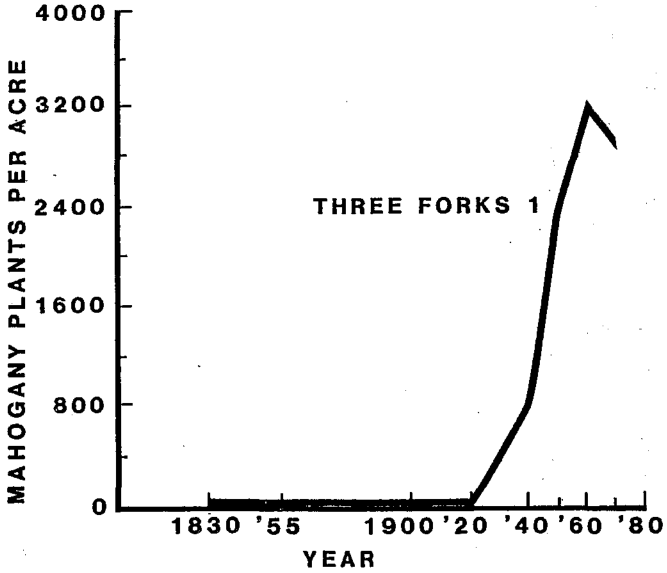

Figure 9.--Example of a potential climax stand that did not become established until about 1940.

Category 3 (Seral Mahogany With Scattered Conifers)

These stands are structurally similar to category 1 except that mahogany is seral. In regions of short fire intervals (mean intervals less than 30 years), fire suppressed conifers and kept the mahogany confined to rock outcrops or sites where sparse fuels did not allow fire to carry. Visual evidence suggests that when woody fuels had accumulated and burning conditions were extreme, fires killed portions of mahogany stands (fig. 2). In more moist communities, such as the Targhee 3 and 4 stands (table 1), infrequent severe fires killed conifers and mahogany over large areas.

Sawtooth 2 (fig. 10) is indicative of many stands having had a sustained increase in regeneration over the past 150 years. Most of the regeneration occurred after 1940. In contrast, other stands have had a marked reduction in regeneration. Regeneration on Targhee 3 (fig. 10) has declined markedly since 1920. Failure of some stands to regenerate seems to be influenced by closure of mahogany canopies and a marked reduction in conditions favorable for seedling establishment.

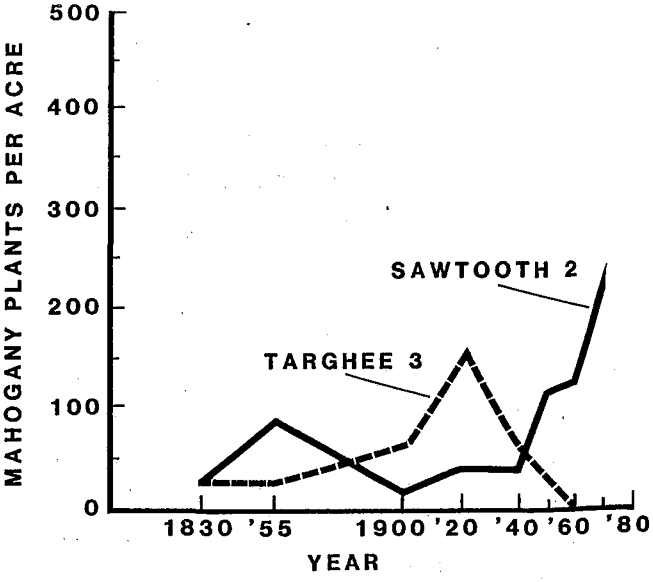

Figure 10.--Examples of seral mahogany stands in category 3 where conifers are not competitive. Sawtooth 2 shows accelerated regeneration after 1940, while regeneration on Targhee 3 has been on the decline or absent since 1920.

The trend in these stands has been a long-term increase in numbers of plants. During the past several decades, some stands have had increased regeneration; in others regeneration has subsided. Stands that contain old plants will become increasingly susceptible to fatal attacks by insects such as those described by Furniss and Barr (1975). Losses to insects and closure of conifer canopies will conceivably result in large-scale loss of mahogany.

Category 4 (Seral Mahogany With Competitive Conifers)

Many mahogany stands fall in this category; however, few met our criteria because the density of mahogany was too low to be included in the sampling. These stands vary most in age and stand structure. They frequently exhibit wide differences in the success of regeneration. For example, Targhee 2 had not regenerated successfully (except the 1970 age group) since about 1900 (fig. 11). In contrast, Greer Gulch (fig. 11) is almost entirely comprised of plants that regenerated post-1900. This stand is comparable to category 2 stands except for the presence of many conifers.

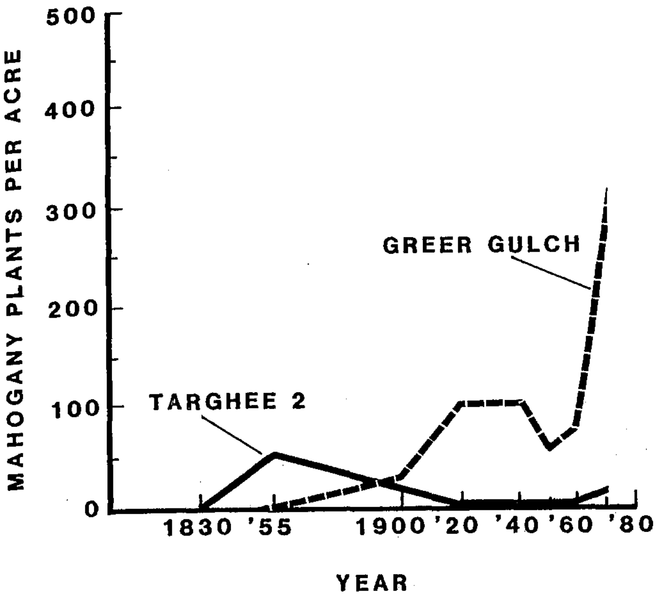

Figure 11.--Examples of differences in regeneration in mahogany stands in category 4 where conifers are competitive. Targhee 2 shows virtually no regeneration in an established stand of conifers since about 1900. In contrast, the Greer Gulch stand essentially regenerated since 1900 and at a much higher level in a developing conifer stand.

Mahogany in category 4 stands is being displaced by conifers. The level of competition varies from scattered conifers, beneath which are mahoganies in low vigor, to closure of conifer crowns and whole-scale loss of mahogany. Without disturbance, the long-term prognosis for category 4 stands is replacement of mahogany by conifers.

Category 5 (Disturbed Mahogany Stands)

Stands in this category were selected to determine the success of mahogany regeneration after disturbance. The time required for seedling establishment varied considerably. The Mountain City 1 stand (table 1) regenerated from seed following an October 21, 1975, fire that completely destroyed the parent stand. Over 4,000 seedlings per acre older than 3 years were tallied in 1982. Initial germination was from seeds of the 1975 crop that apparently had fallen to the ground or from seed banks stored in the litter. The likelihood of this quantity of seed having been transported from off-site sources is remote. Immediate seedling establishment following fire was also measured at the Targhee 2 site (table 1). Other examples of successful seedling establishment following fire were noted. Only 2 percent of the Mountain City 1 and 4 percent of the Targhee 1 stands regenerated from sprouting, which was confined to plants between 20 and 30 years old.

Measurement of the Challis 2 site revealed delayed regeneration within the 1934 Pats Creek burn. The preburn stand was of low density, and the stand did not regenerate until about 30 years after the fire. All parent trees except those on outlying ridges and in rock outcrops were killed by a severe summer wildfire that apparently destroyed the on-site seed source. Subsequent failure of seedling establishment may have resulted from limited seed dispersal and the warm south-southwest aspect, where temperatures were excessively hot for seedling survival. Shading from sagebrush and other ground cover in later years may have provided suitable microsites for seedling germination. Initially, seed dispersal from off-site locations was apparently inadequate; however, scattered mahogany seedlings eventually established themselves. As on-site mahogany regeneration reached seed-bearing age, the rate of regeneration increased dramatically.

Immediate establishment of mahogany following cutting was recorded on two sites. A selection cut in dense Douglas-fir (Salmon 2, table 1) that contained scattered old-growth mahogany resulted in establishment of many mahogany seedlings. Vigorous seedlings were observed growing where the slash had been piled and burned. Before the timber harvest, mahogany had not regenerated successfully since 1900. Sampling at the Soda 3 site (table 1) also documented accelerated mahogany regeneration following the cutting of juniper for posts and poles.

Sampling in disturbed stands that were logged or burned indicated that a reduction in competition and an increase in exposed mineral soil enhanced successful seedling establishment. Observations of other logged and burned mahogany stands that were not sampled suggested comparable relationships. Quantitative data from this study showed that successful seedling establishment was closely linked to condition of the soil surface. Most seedlings were found on exposed mineral soil. No seedlings over 2 years old were found where litter exceeded 0.25 inches (6 mm) in depth.

Regeneration following disturbance can vary greatly depending on intensity of treatment and availability of seed crop. Fires in very small stands kill most mahogany, thus removing the seed source. In large stands, however, many plants survive because of discontinuous fuels. This "fire mosaic" treatment allows seeds to disperse from surviving plants into openings, thus increasing the probability of successful seedling regeneration.

MANAGEMENT IMPLICATIONS

Our data and observations show the desirability of excluding fire from many communities, especially sites where mahogany is the potential climax and where stands are 50 years of age or less. Burning would cause marked retrogression in these communities. There are, however, many low-vigor mahogany communities that would respond positively to fire.

Following are some considerations that may prove helpful in determining where it would be desirable to exclude fire and where there is a solid ecological rationale for using prescribed fire.

Potential Climax Mahogany Stands.--Vigorous stands are not candidates for prescribed fire. Many of these stands are young, having regenerated since 1920. Prescribed fire is also not recommended in stands with woody fuels such as sagebrush where mahogany is scattered or in stands of 0.5 acre (0.20 ha) or less.

Prescribed fire can benefit old mahogany stands that support sufficient fuels to carry fire. The best opportunities include localities where rocky outcrops and sparse fuels allow mahogany to survive as scattered individuals and in clumps. The chances of mahogany surviving and serving as cover and a seed source for immediate mahogany regeneration are enhanced as the burn becomes larger. A fall prescription including several thousand acres of burned and unburned areas would be ideal, especially where mahogany is associated with woody, crown-sprouting shrubs and trees.

Seral Mahogany Stands.--Prescribed fire is most likely to improve mahogany productivity in seral mahogany stands. The higher priorities are in category 4 stands, where conifers are competitive and mahoganies have not been reproducing for many decades. The objective of burning would be to kill competing conifers, remove other plant competition, and promote conditions conducive to seedling establishment.

The size of the burn would depend upon type of terrain, fuels, and the abundance of mahogany. In most instances a burn of several hundred acres would be advisable to avoid excessive browsing of seedlings by wild ungulates and livestock. In remote regions where wildlife values and livestock grazing are primary considerations, there are opportunities to use fall burning prescriptions and natural features of the terrain to execute prescribed burns of several thousand acres. These burns would result in differential burning by removing groups of mahogany where woody fuels were plentiful and leaving mahogany unharmed where woody fuels were sparse. Our observations suggest that mahogany stands will not carry fire unless there are sufficient surface fuels. Large treelike stands supporting grassy fuels and minimal litter usually survive the fire.

In some areas, old-growth mahogany is associated with patches of commercial-sized saw timber. In this circumstance, there is an opportunity to encourage new mahogany plants by making small block cuts of 0.50 to 2 acres (1.23 to 1.94 ha). Opening of the conifer canopy, mechanical disturbance, and prescribed fire used in slash cleanup can provide conditions that permit seeds to disseminate on exposed mineral soil and thus establish seedlings. Leaving several seed-producing mahoganies in openings increases the probability of successful regeneration provided grazing impacts are not excessive.

Fire management plans that include unscheduled (lightning or human) ignitions can be a useful tool in future management of mahogany. It is particularly apparent that there is little or no rationale for suppressing wildfires in localities where mahogany is being outcompeted by conifers. Prolonged fire suppression will continue to reduce the numbers of seed- producing plants and thus will markedly reduce recovery potential following a hot wildfire.

Prescribed fire to enhance the condition of mahogany should be considered on a case-by-case basis. Applying prescribed fire through planned or unscheduled ignitions has a place in mahogany management. We suggest that managers responsible for ecosystems that include mahogany strongly consider the consequences of continually protecting declining stands. The future viability of this important plant will depend on whether we take the short-term approach of protection or the long-term view that recognizes disturbance as essential in promoting productive mahogany stands.

SUMMARY AND CONCLUSIONS

The combined quantitative and historical evidence strongly suggests that before European settlement fire significantly influenced mahogany in the Northern Rockies by restricting stand development. A reduction of fire periodicity and size following Euroamerican settlement apparently allowed mahogany seedlings to regenerate far in excess of former levels. The absence of fire for long periods has resulted in great variation in structure of mahogany stands. Many stands are declining because of losses to insects and conifer competition. In other areas, vigorous young mahogany predominate. These wide differences in stand conditions suggest different management strategies are needed at the local level. Fire management strategies may be used to manage mahogany stands.

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MANAGING WILDLIFE HABITAT WITH FIRE IN THE ASPEN ECOSYSTEM

Norbert V. DeByle

ABSTRACT: Much of the nearly 7 million acres (2.86 million ha) of aspen in the western United States is seral to conifers. Also, most aspen stands are old, in excess of 60 years. Proper treatment of these aspen forests will retain the aspen and can produce optimum wildlife habitat. Optimally, all age and size classes of aspen should be present on the landscape. Fire is often the most economical and, ecologically, the most natural treatment applicable in the many acres of unmerchantable but burnable aspen community types in the West. Fire of sufficient severity will kill the old stand, cause profuse aspen root suckering, and increase forage production. Currently, baseline data are being gathered for developing fire prescriptions and describing the fuels in Wyoming and Idaho aspen types. The effects of fire on the aspen plant community, especially on its value as wildlife habitat, is also being assessed.

INTRODUCTION

In the interior western United States there are 7,067,200 acres (2 859 944 ha) of aspen (*Populus tremuloides*). Of this, some 2,664,200 acres (1 078 163 ha) are noncommercial (Green and Van Hooser 1983). In addition, many millions of acres of aspen occur in the western provinces of Canada and Alaska.

Wildlife managers generally agree that the aspen forest type is especially valuable habitat for a variety of upland species of birds and mammals, both game and nongame (Gullion 1977b). In the interior West, aspen takes on a particularly important role for wildlife, because it is the only upland hardwood tree species and it frequently is found in groves in the coniferous forests or as isolated stands in mountain grasslands and shrublands. In the conifers, the aspen groves may be the only source of abundant forage; in the grasslands they may be the sole source of cover.

I recently reviewed the literature and contacted several sources to compile a listing of birds and mammals that occupy the aspen type in the West (DeByle in press). Some 134 species of birds and 55 species of wild mammals were included. Among the game birds, there are six species of ducks, two forest grouse (blue and ruffed), two pigeons (band-tailed and mourning dove), the sharp-tailed grouse, and the wild turkey (*Meleagris gallopavo*). Among the larger mammals, there are moose, elk, white-tailed deer, mule deer, snowshoe hare, cottontail rabbit (*Sylvilagus nuttallii*), bison (*Bison bison*), raccoon (*Procyon lotor*), mountain sheep (*Ovis canadensis*), mountain lion (*Felis concolor*), black and grizzly bears (*Ursus americanus and U. arctos*), and several furbearers.

Aspen is a seral forest type on the majority of sites. It is a relatively short-lived tree (about 100 to 125 years in the West) that readily gives way to longer lived and more shade-tolerant conifers. If a conifer seed source is present, the typical aspen stand responds approximately as shown in the model developed by Bartos and others (1983). Herb biomass peaks first, then shrubs (fig. 1). As long as aspen dominates, there is a large herbaceous or shrub biomass in the understory, but as conifers take over, this source of forage and low cover largely is lost.

Most of our western aspen stands have reached maturity because they have been protected from wildfire and have not been marketable for most of this century. In a Colorado survey, Shepperd (1981) measured an average age of 80 years, with stands younger than 50 years difficult to find. Single-aged stands predominated, but two-aged and all-aged stands were frequently found.

Treatments are needed to retain aspen on sites where it is seral. And, whether seral or not, treatments are needed if we wish to have a variety of aspen age and size classes represented on the landscape. In the natural setting, wildfire probably was the most common cause of widespread even-aged regeneration, although insect and disease outbreaks may have played a role, too. In the managed forest, clearcutting, herbicides, or prescribed fire may be used to effectively treat aspen stands by killing the overstory and triggering abundant aspen regeneration.

Aspen regenerates by producing root suckers in large numbers after the parent tree is top-killed. Such vegetative reproduction over several generations has produced a mosaic of aspen clones (groups of genetically identical stems) on the landscape (Barnes 1966). In the West, regeneration by seed is rare because a continuously moist, mineral soil seedbed is required throughout the first growing season (McDonough 1979).

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Norbert V. DeByle is Principal Plant Ecologist, Intermountain Research Station, Forest Service, U.S. Department of Agriculture. He is stationed at the Forestry Sciences Laboratory, Logan, Utah.

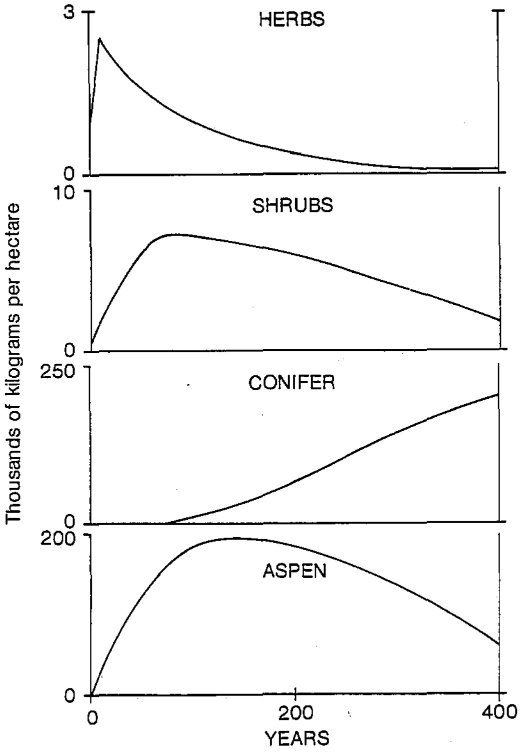

Figure 1.--Expected biomass of four vegetation components through time after a severe fire in aspen on a typical mesic site in the West. A conifer seed source is assumed. (From Bartos and others 1983, fig. 29a, p. 27.)

Sudden top-killing of an aspen stand upsets the hormone balance in the roots. Auxins, produced in tree crowns, are no longer supplied, and cytokinens, produced in roots, are no longer moved into the crowns. The lack of auxins, an increase in cytokinens, and warmer soil temperatures help stimulate abundant sucker production from roots near the soil surface (Schier 1981a, 1981b). If, say, the parent stand consisted of 200 stems per acre (494/ha), by the end of the second growing season after fire or clearcutting, there often will be some 40,000 suckers per acre (98 842/ha). Suckering response varies widely, due to genetic and site factors as well as the density of aspen roots near the soil surface. A good rule of thumb is 10,000 suckers per acre (24 710/ha) will produce a satisfactory forest stand--if roundwood products are being grown on the site.

The concern that high densities of young aspen will produce a stagnated stand is not justified because aspen is self-thinning. Disease, insects, browsing animals, snow breakage, and shading of these intolerant aspen suckers all take their toll. By maturity, a stand of 200 stems per acre (494/ha) again might be expected. During the 70- to 100-year interim, from a dense stand of young suckers to a mature stand of aspen trees, a progression of habitats will have been made available for a variety of wildlife species.

CASE STUDIES

There are many references in the literature about the effects of fire, usually wildfire, on aspen regeneration. There are far fewer on the effects on wildlife populations, and many of these are somewhat speculative. Usually the effects on plant communities are measured and the effects on associated wildlife are inferred.

Scotter (1972) points out that fire is at least partly responsible for maintaining extensive stands of aspen and other seral species in the boreal forest region but that the influence of fire on the animals cannot be easily evaluated--some members are benefited while others are disadvantaged. For optimum elk or moose habitat, both Gruell and Loope (1974) and Spencer and Hakala (1964) describe the benefits of fire in the aspen type. In the North, both Lutz (1956) and Viereck (1973) feel that fire may be deleterious on caribou (*Rangifer tarandus*) winter range because fire destroys lichens; on the other hand, it benefits moose and snowshoe hares because they depend upon the successional plant communities, notably aspen, that are produced. Much further south, Patton and Avant (1970) found that fire is an effective tool for producing deer and elk browse in the mixed aspen-conifer forests of New Mexico.

Those animal species that depend upon the forage or cover produced in a young aspen community will benefit from fire. They include some of the more important (game) species of wildlife--moose, elk, deer, ruffed grouse, and snowshoe hare. Others may do well in old, sometimes derelict, aspen stands--cavity-nesting birds for example. For these, fire is not necessary for habitat management if the aspen on the site is stable or climax. Other species of wildlife, such as red-backed voles (*Clethrionomys gapperi*), red squirrels (*Tamiasciurus hudsonicus*), and pine martens (*Mustela americana*), do best in coniferous forests. Fire to set back succession and retain aspen will be deleterious for these species. If diversity of habitats and a diversity of wildlife species are wanted, fire can play an important role in maintaining the mosaic of plant communities and age-size classes within these communities on the overall landscape. If edge is wanted, fire again is a tool to provide maximum edge between the patches in this mosaic. Thus, we must be specific what we want before prescribing fire or any other treatment.

The Role of Fire in Habitat Management of a Few Key Species

Elk.--The wapiti, or elk (*Cervus elaphus*), are grazing animals that prefer grassland, shrubland, and recent burns over the mixed forest community (Rounds 1981). They choose aspen over coniferous communities in summer and winter (Ackerman and others 1983), although conifers may be used for hiding (security) and thermal cover during times of harassment or severe weather (Thomas 1979).

Elk prefer grasses, then forbs; as curing or loss of herbaceous material occurs, they use deciduous browse species first and coniferous browse last. Aspen is avidly sought from among the browse species (Kufeld 1973; Nelson and Leege 1982). The aspen suckers themselves, however, will extend their crowns above the reach of elk in 6 to 8 years if growing in the open and not browsed (Patton and Jones 1977). In summer, the combined values of good forage and cover in the aspen forest make it especially valuable to elk; at this time they may select aspen stands over adjacent clearcut areas that have even more palatable forage (Collins and Urness 1983).

To provide optimum habitat for elk, Thomas (1979) recommended that 60 percent of the land area be managed to provide forage. Good forage is provided by the herbaceous and shrubby understory in the aspen as well as by aspen suckers less than 6-1/2 ft (2 m) tall. Peak production of this component is reached within a few years after burning (Bartos and others 1983).

In the Jackson Hole area of western Wyoming a combination of factors is causing the demise of aspen on big game winter ranges. Fire protection has permitted large areas of aspen to reach maturity and to begin the successional process toward conifers (Gruell and Loope 1974; Gruell 1979), and concentrations of big game, especially elk near winter feedgrounds, in some instances are eating every sucker that arises (Beetle 1979; Weinstein 1979). If nothing is done, aspen over large areas will disappear within a century (Krebill 1972). If protection can be provided from browsing elk (DeByle 1979), then fire can be used to regenerate the declining aspen stands. Somewhat similar conditions occur in and near Rocky Mountain National Park in Colorado (Olmstead 1979).

In recent years fire has been used on an experimental basis in the Jackson Hole area (Bartos 1979; Bartos and Mueggler 1979, 1981). They found that understory production decreased in the first postburn year, then increased to well over that on the unburned sites in the second and third postburn growing seasons. On one site in the second year there were 3,211 lb/acre (3 600 kg/ha) produced, about double that found before burning. Most of this was fireweed (*Epilobium angustifolium*)--a species palatable to cattle and elk. Production of aspen suckers was greatly increased by burning, enough to replace the parent stand where browsing pressure is not too great. On the sites where elk browsing pressure was greatest, there were 5,665 to 8,094 suckers per acre (14 000 to 20 000/ha) present in the declining aspen stands before burning; this density nearly doubled in the second postburn year, but by the end of the third postburn year, sucker densities had returned to near preburn levels (Bartos and Mueggler 1979, 1981). Even though over 1,000 acres (405 ha) was burned, elk use of aspen was deterred only one winter. Elk browsing the third winter averaged 44 percent of current annual growth and eliminated the height growth from the previous summer (Basile 1979). Under current browsing pressures on heavily used areas, the small increase in sucker numbers after burning is not expected to regenerate these aspen stands.

Moose.--The largest member of the deer family, the moose (*Alces alces*), extensively uses the aspen ecosystem. They are primarily browsers, especially in winter (Peek 1974). Forbs are also extensively used when available in spring and summer. Usually moose first select willow (*Salix* spp.) and then aspen as browse. The typical understory forbs and shrubs in the aspen type as well as young aspen are favorite moose forage.

Moose can utilize larger saplings than can deer or elk. Their height of reach is 8 ft (2.4 m), and they will break down saplings up to 4 inches (10 cm) in diameter to reach higher browse (Telfer and Cairns 1978).

Moose have a high tolerance for cold; they will occupy willow bottoms without much thermal cover early in winter. As winter progresses and snowpacks deepen, however, they move into densely forested uplands with less snow (Rolley and Keith 1980). Moose in Alberta selected aspen stands less than 33 ft (10 m) tall as preferred habitat (Rolley and Keith 1980). In Montana, Gordon (1976) described ideal upland moose habitat as having a good distribution of aspen and associated trees and shrubs in a mosaic of age classes. Conifer patches for hiding cover also are desirable, perhaps essential.

In Minnesota, Irwin (1975) found that moose selected deciduous forest stands, especially postburn communities that produce large amounts of preferred forage, during the summer-fall period. Willows and the sprouts of aspen, birch (*Betula* spp.), and maple (*Acer* spp.) were the most important browse species used.

Seral aspen being replaced by conifers in south-central Montana were burned to enhance winter moose habitat (Gordon 1976). Aspen suckers increased to 27,400 per acre (67 700/ha). After the second growing season they averaged 3 ft (91 cm) tall, and both they and willow sprouts could be utilized. Gordon found that the heaviest use of aspen and shrubs was adjacent to the unburned area, where cover was quite dense.

From work done in Alaska (LeResche and others 1974), Minnesota (Irwin 1975), Wyoming (Gruell 1980), and elsewhere (Gullion 1977b) it is evident that regeneration of young vigorous stands of aspen, willow, and associated shrubs, usually after fires, improves moose habitat and results in a moose population increase. After this browse grows out of reach, the moose population drops. LeResche and others (1974) noted that fire-induced seral communities in Alaska have the greatest moose densities.

Deer.--Mule and white-tailed deer (*Odocoileus hemionus and O. virginianus*, respectively) are common throughout the range of aspen in the West.

The mule deer predominates in the States with the most aspen. Deer herds in these States are migratory--they spend summers at high elevations within the aspen zone and winters on steppe and brushlands at lower elevations, usually below the aspen. Thus aspen is largely summer and fall range for deer in the West. During these seasons both thermal and hiding cover are abundant in the aspen type. Leckenby and others (1982) rated aspen communities on the shrub-steppe western range second only to riparian zones in value to mule deer. Deer prefer to feed in the aspen forest rather than in forage-rich clearcut openings, and they commonly bed down in the aspen forest as well (Collins and Urness 1983).

In spring and early summer deer prefer herbaceous forage, primarily forbs. As these cure, deer shift increasingly to browse; by winter their diets are three-fourths browse (Kufeld and others 1973). Aspen is among the top eight species of preferred browse for mule deer. Hungerford (1970) noted that aspen sprouts became a key food only after new growth matured, usually in July. Upon leaf fall in autumn, deer consume large quantities of aspen leaves (Julander 1952). In addition to the aspen itself, deer forage upon many of the common understory shrubs (snowberry, serviceberry, barberry, pachistima, chokecherry, rose, willow) and forbs (yarrow, aster, milkvetch, fleabane, geranium, peavine, lupine, knotweed, cinquefoil, dandelion, valerian, vetch) in the aspen forest type (Collins 1979; Kufeld and others 1973).

The impact of deer on aspen regeneration can be greatest in late summer and autumn. They will readily take young, succulent aspen sprouts on recent burns and clearcuts. They also browse on aspen up to a 5-ft (1.5-m) height, and therefore can have a significant impact on aspen suckers younger than 4 or 5 years or those suppressed by browsing to heights of less than 5 ft. Mueggler and Bartos (1977) noted that deer browsing prevented aspen regeneration in small clearcuts and in the uncut aspen forest, but nearby large burned areas regenerated successfully. They felt that burns or clearcuts less than about 5 acres (2 ha) would concentrate deer use and would be less likely to successfully regenerate than would larger areas.

Deer on their summer range will benefit from having plenty of aspen habitat available, especially if it contains an abundance of understory forbs and shrubs. Since both aspen suckers and the aspen understory are in greatest abundance within a few years after burning (Bartos and others 1983), it appears that management to provide an array of aspen age classes on the range would provide the best overall habitat. The burn units should be of adequate size, however, to prevent overbrowsing of the aspen regeneration. Perhaps 10- to 40-acre (4- to 16-ha) units burned or clearcut at intervals of 40 to 80 years would provide optimum deer habitat.

Snowshoe hares.--Snowshoe hares (*Lepus americanus*) are present throughout much of the aspen range in the West; however, they are more common in the associated coniferous forest types. In the Rocky Mountains, winter hare habitat is lacking in most pure aspen stands due to deep snowpacks. In northern Utah, Wolfe and others (1982) found 85 percent of winter use by hares was in vegetation types that had cover densities of at least 40 percent immediately above the snowpack. Sometimes aspen with a very dense understory of tall shrubs fits this criterion, but usually only conifers provide this much winter cover.

During the summer growing season, snowshoe hares disperse somewhat from coniferous winter cover (Wolff 1980). The aspen type then provides adequate cover and excellent forage. Aspen is nutritious and choice food for hares (Walski and Mautz 1977), although new suckers may not be as palatable as twigs on the mature growth because of their high terpene and resin contents (Bryant 1981). In Alberta, Pease and others (1979) found aspen to be among the six most common browse species. During summer the hares shift largely to a diet of succulent plant material (Wolff 1980). Since the aspen type has much more herbaceous and shrub cover than most coniferous types, in summer it probably is the more desirable habitat.

The aspen type, if well interspersed with dense conifer patches, provides adequate snowshoe hare habitat in the West. Marginal habitat is provided with aspen and a dense understory of tall shrubs if this understory is not covered with deep winter snowpacks. It is doubtful that even the peak density of aspen suckers and shrubs on most aspen burns or clearcuts in the West provides adequate snowshoe hare habitat in winter (Wolfe and others 1982). Perhaps the best recommendation for management is one developed in Michigan (Conroy and others 1979), where clearcuttings managed for hares were recommended as small and shaped so adequate canopy cover remained within 200 to 400 yards (about 200 to 400 m) of all parts of the opening. In the western United States and adjacent Canada, perhaps small irregularly shaped clearcuts or burns and encouragement of small but dense conifer patches throughout the aspen forest will provide maximum snowshoe hare habitat in the aspen type.

Ruffed grouse.--The ruffed grouse (*Bonasa umbellus*) has a wide range across North America (Aldrich 1963), is associated with hardwood and hardwood-conifer mixed forests, and is primarily a bird of the aspen and associated forest types. Gullion (1977a) opined that there is an obligatory relationship between ruffed grouse and the aspen type wherever snow covers the ground between November and April. Aspen is heavily used as food and as cover; it provides a highly nutritious food source (Gullion and Svoboda 1972), protection from the weather (Bump and others 1947), and escape from predation (Gullion and others 1962). Wherever aspen and grouse ranges overlap in the West, the grouse selects aspen habitat during part or all of the year, as shown by Phillips (1964, 1967) and Landry (1982) in Utah, Stauffer and Peterson (1982) in Idaho, and Rusch and Keith (1971) and Doerr and others (1974) in Alberta.

Management for optimum ruffed grouse habitat must center on the aspen ecosystem and nearby dense, brushy vegetation. For Idaho and Utah conditions, Stauffer and Peterson (1982) recommended a diversity of habitat structure within 40- to 50-acre (16- to 20-ha) units. Drumming (breeding) sites should have 200 to 450 trees per acre (about 450 to 1 100/ha) that provide 80 to 95 percent tree cover and at least 2,500 small stems (shrubs and aspen sprouts) per acre (about 6 000/ha). Hens with broods prefer 50 to 75 percent tree cover, about 600 to 2,800 small stems per acre (1 500 to 7 000/ha), and openings with abundant herbaceous cover more than 20 inches (about 50 cm) tall. Winter cover should have large mature aspen for food and perhaps some conifers for cover. For Minnesota conditions, Gullion (1977a) recommended practices that maintain heavily stocked, fast-growing aspen stands in a variety of age (size) classes within the daily range of grouse. The value of conifers was questioned because they harbor avian predators. Stauffer and Peterson (1982) and Landry (1982) both emphasized the importance of a dense shrub layer in aspen or mixed aspen stands for our western conditions.

Even-aged management of 10-acre (4-ha) units on rotations of about 60 years perhaps will produce the best ruffed grouse habitat in the montane West. One unit should be treated (burned or clearcut) every 15 years within each 40- to 50-acre block, thus producing the diversity of habitat needed within the range of individual grouse. Clearcutting units as small as 10 acres is the most feasible treatment; then burning within a year afterward may provide the best brood habitat (Sharp 1970). Larger areas that are being taken over by conifers may be burned to set back succession, then later put into the rotation system of small 10-acre units (Stauffer and Peterson 1982).

Sharp-tailed grouse.--The sharp-tailed grouse (*Tympanuchus phasianellus*) in the parklands aspen habitat will use aspen trees in the winter and spring, but they prefer and select grassland and grassland-low shrub cover throughout most of the year. During winter, small aspen and shrubs offer sharp-tailed grouse protective cover and food. The grouse feed on aspen buds in winter and spring (Hamerstrom 1963; Moyles 1981). Aspen is useful as small thickets of young growth (3 to 6 ft or 1 to 2 m tall) and as larger patches of taller trees for winter use (Evans 1968; Hamerstrom 1963). During much of the year, aspen, except as a shrub, seems to be of little or no importance and is perhaps even a detriment to the sharp-tailed grouse. The presence of aspen near breeding arenas discourages use by these grouse (Moyles 1981). Moyles cites evidence that invasion of grassland by aspen reduces sharp-tail habitat.

It appears that the sharp-tail is a bird characteristic of early successional stages in the aspen ecosystem. Sharp-tails use frequently burned areas in which aspen regeneration is mostly shrub-size except for some scattered stands of mature trees that have escaped the fires. As extensive stands of trees return to this setting, the sharp-tail gives way to the ruffed grouse. Fire in relatively short intervals, say 20 years, could be used for management of sharp-tail grouse habitat. Large units of several hundred acres could be burned if patches of large aspen trees were protected.

OUR CURRENT RESEARCH

In 1981 the Intermountain Forest and Range Experiment Station commenced a prescribed fire study in the aspen on the Bridger-Teton and Caribou National Forests in western Wyoming and southern Idaho, respectively. There are two primary objectives: (1) to develop prescriptions for the use of fire to regenerate aspen and (2) to determine postfire plant succession and production. The research focuses on aspen sites that are being invaded by conifers or are susceptible to such invasion. Facets of the study include:

1. Probabilities of achieving weather conditions meeting specific prescribed fire conditions.

2. A method for predicting water contents of live herbaceous fuels.

3. A classification within the aspen ecosystem of fuels and their flammability.

4. The relation of overstory tree mortality to fire severity as evidenced by visible bole damage and fuel consumption.

5. The relation of aspen sucker populations to overstory mortality.

6. Vegetation response to fire, both with and without postburn grazing.

Adjunct to this research are two cooperative studies being conducted by Utah State University and the Intermountain Station. In the first study, forage quality is being assessed for several plant species on burned and unburned aspen sites during the first and second years after prescribed fire. In the second study, tame elk are being used to determine habitat selection, foraging behavior, and dietary nutrition during the second and third postburn years on burned sites and in the surrounding habitat.

A progress report that covered all facets of the primary study was given at the end of the 1982 field season (Brown and DeByle 1982). Research continues; however, data gathering and analyses for predicting fire weather (facet 1), for estimating water contents of live fuels (facet 2), and for developing a fuel classification (facet 3) are essentially complete. The fuel classification scheme was outlined by Simmerman (1983) and will be expanded into a more definitive publication in the near future. The results from the cooperative studies, when combined with the results from facets 4 and 5, should be of considerable interest to managers of wild ungulate habitats.

On most of the mid- to high-elevation aspen range in the West, the deep snowpacks do not melt away until spring greenup. Spring burning is not possible under these conditions, hence, we concentrated on developing prescriptions for autumn burns. Summer generally is dry in northern Utah, southern Idaho, and Wyoming. Fuels cure through late summer and autumn. As autumn approaches, the probability of major precipitation from a frontal storm system increases. To predict the probabilities of such storm systems, we analyzed the long-term weather records for several stations. Two prediction lines are shown in figure 2. The solid line represents the accumulative frequency of a storm that temporarily prevents burning; subsequent drying, however, would return prescribed burning conditions that season. The dotted line essentially predicts the end of the burning season. For example: in half of the years a frontal storm that delays burning for several days can be expected by mid-September, and the burning season will end, probably with a snowstorm, by approximately October 25.

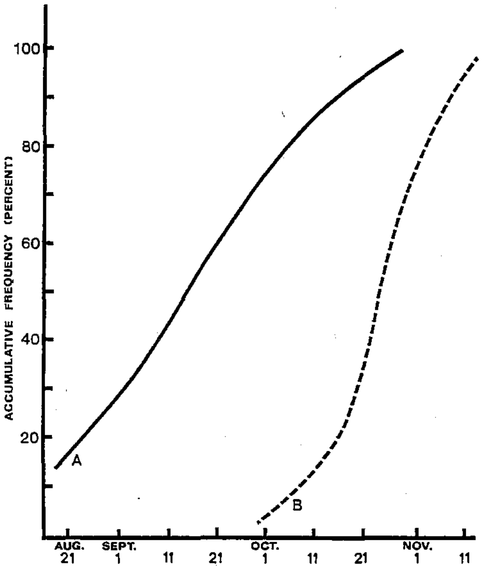

Figure 2.--Cumulative frequency curves of estimated dates before first major interruption of the prescribed burning season (curve A) and the last date of the prescribed burning season (curve B).

Fuel classification in the aspen ecosystem is based primarily upon understory characteristics (community types) and, to a lesser extent, upon successional status, amount of downed woody fuels, and grazing. Some of the major classes and their potential for prescribed burning are:

Overstory	Understory	Potential for prescribed fire
Aspen	Shrub	Good
Aspen/conifer mix	Shrub	Good
Aspen	Tall forb	Fair
Aspen	Shrub (grazed)	Fair
Aspen/conifer mix	Forb	Fair
Aspen	Low forb	Poor
Aspen	Tall forb (grazed)	Poor

NEEDS

It is generally accepted that managing western wildlands to provide an optimum amount of aspen on the landscape will benefit some key species of wildlife. It is generally accepted that managing this aspen to provide an array of age and size classes, perhaps in even-aged units of a few acres each will provide the best habitat for these key wildlife species. For most wildlife species, however, far too little is known about habitat needs to do a top-quality job of intensive aspen management to produce optimum habitat.

Several key wildlife species for which habitat management in the aspen type could be important have been used as examples in this paper. It is apparent that moose, elk, deer, snowshoe hare, and ruffed grouse will benefit by having an optimum amount of aspen in a variety of size classes on their range. Just how much is needed in relation to the mix and juxtaposition of other habitats is not known. For some species in some environments, aspen perhaps is all that is needed--an example is ruffed grouse in northern Minnesota (Gullion 1977a). For others, such as snowshoe hares in the montane West (Wolfe and others 1982), aspen alone will not provide satisfactory habitat. For still other species, aspen forest plus some other habitat variable is needed. Beavers (*Castor canadensis*), for example, use aspen (or willow) along streams and rivers. In addition, many species are migratory, such as most passerine birds, and use the aspen forest only during part of the year, but often during the all-important breeding season. These species are equally dependent upon habitats elsewhere for their year-round welfare. Manipulating the aspen type will not provide optimum habitat for this total mix of wildlife species.

Wildlife managers first must choose what key wildlife species are to be encouraged. Then they must determine what those species habitat needs are. Habitat needs must not be confused with preferences for some particular habitat components; instead, focus must be kept on what each species requires to maintain health, vigor, and an acceptable rate of reproduction (Peek and others 1982). The managers also must ascertain what the trade-offs are--what wildlife species are going to be placed in a disadvantageous position through some particular habitat management strategy. This is a difficult job, perhaps impossible with our present level of knowledge of habitat requirements for many species.

If the chosen key wildlife species are deer, elk, and moose (they usually are in the montane forested habitats of the West), perhaps enough is known about their preferences and some of their needs to make reasonable habitat management recommendations. Aspen clearly is preferred by these ungulates. On most of their ranges, aspen should be encouraged. A mix of habitats, consisting of mountain brush, meadows, conifers, and aspen may be best, but the proportions can only be speculated upon. Aspen on up to one-half of the range of these ungulates is perhaps most acceptable. Management of this aspen in even-aged units of 5 to 60 acres (2 to 24 ha) each on a rotation of 60 to 100 years will probably supply the greatest variety of habitats within the aspen type and will ensure a considerable amount of edge around these units. With this management strategy, fire becomes a feasible option for killing 60- to 100-year-old aspen stands, at least those with a shrubby understory, thereby triggering abundant even-aged aspen regeneration.

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MODELING SHRUB SUCCESSION FOLLOWING

CLEARCUTTING AND BROADCAST BURNING

Penelope Morgan and L. F. Neuenschwander

ABSTRACT: This conceptual model of early seral shrub succession following clearcutting and broadcast burning synthesizes ideas from previous research and modeling approaches into a simple diagrammatic model of the critical successional influences and processes. Illustrative examples are drawn from observations of successional development following high-and low-severity burns on the *Thuja plicata/Clintonia uniflora* habitat type in northern Idaho.

INTRODUCTION

The general trend in the study of succession following fire is from natural history descriptions to quantitative models that yield predictions of community development. The study of shrub succession in northern Idaho is a typical example.

Early seral shrub development following fire in the moist cedar-hemlock forests of northern Idaho was described by Leiberg (1900) and has since been studied in detail by Mueggler (1965), Lyon and Stickney (1976), and others. Shrubs rapidly invade burned areas and may dominate a site for many years (Mueggler 1965). Large-scale fires in the early 1900's created many shrubfields that provided abundant browse for big game. This prompted many studies, particularly of the shrub species important for big game forage. Early descriptions of succession following fire were general, seldom quantitative, often limited to one or two species, and usually poorly documented. Information useful in drawing a cohesive understanding of the factors affecting shrub succession is therefore often scattered, unpublished, incomplete, or otherwise unavailable.

Existing models that predict change in forest understory communities are often unsatisfactory to meet more than the specific needs for which they were developed. The goal of this report is to review some of these models and their limitations and to present a general conceptual model for early shrub succession.

Development of our model draws heavily on the previous work of Lyon and Stickney (1976), the existing literature, and our documentation of shrub succession following clearcutting and broadcast burning. We have been studying shrub succession following clearcutting and burning of dense coniferous forests on the *Thuja plicata/Clintonia uniflora* habitat type (Cooper and others 1983) in northern Idaho. Here, early seral communities are often dominated by shrubs that establish themselves immediately following fire. Native forbs and grasses do not have the potential to dominate the site and the forb/grass stage of succession is short lived. Forbs are common, and grasses are uncommon in this habitat type. More than 30 different shrub species grow on the habitat type, many of which are critical to timber and wildlife resource management.

We are building a simulation model based on the conceptual model presented here. The simulation model will predict regeneration, establishment, and subsequent changes in species composition in the early seral shrub communities that develop following high- and low-severity burns.

Ecological impact of fire on understory vegetation depends on burn severity. Severity is a function of the total fuel consumed by fire, a reflection of both total heat produced and duration of heating of the soil surface. We evaluated burn severity using visual criteria based on litter and duff consumption, evidence of mineral soil alteration due to heating, and size and depth of char on large woody fuels remaining after the burn. These criteria are similar to those developed for depth of char (Ryan and Noste, in press) and depth of burn (Rowe 1983). Burn severity may be unrelated to fire intensity. Fire intensity refers to maximum above-ground heat pulse and principally depends on consumption of fine fuels. In contrast, the degree of soil heating depends on consumption of duff and large woody fuels. Burn severity affects response of understory species and cambial damage to tree boles and roots more than fire intensity does.

PREVIOUS MODELS

Most existing forest successional models include only trees. If understory vegetation is considered, it is only by general growth form (Shugart and West 1980). The model of Bartos and other (1983) is a good example. Understory development affects aspen and conifer succession in

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Penelope Morgan is Doctoral Fellow and Leon F. Neuenschwander is Associate Professor, Department of Forest Resources, University of Idaho, Moscow.

this model; however, all understory species are grouped into shrub and herb components. More detailed descriptions of understory successional dynamics are needed in many disciplines. These descriptions should include changes in community structure, species composition, and growth rates of important understory species (Pfister 1982).

The stand prognosis model (Stage 1973; Wykoff and others 1982) predicts forest vegetation development following stand disturbance. It applies primarily to trees, but one can predict percent canopy cover, biomass, and height of some important understory shrub and grass species. The predictions are based on regression equations developed by Irwin and Peek (1979). Extensions to the model are being developed to predict total shrub cover, probability of establishment, percent canopy cover, and height of 42 shrub species (Laursen 1984). The regression equations were developed from empirical data collected in various forest habitat types and stand ages under different site conditions, tree stand densities, and types of disturbance (Stage 1973; Wykoff and others 1982). The regression approach is fairly easy to use as it does not require inclusion of mechanistic relationships, but it is data intensive. Predictions may have limited reliability for stand conditions, areas, or treatments other than those included in the original data base. The stand prognosis model does not consider the influences of severity of fire disturbance or existing understory vegetation on successional development.

The forest habitat type classification system provides a common means of stratifying the physical environment and is, therefore, a logical framework for studying secondary succession (Arno 1982). The secondary succession classification systems being developed by Arno and Simmerman (1982) and Steele (Steele and Geier-Hayes 1982) are diagrammatic models of tree and understory succession on selected habitat types in Montana and Idaho. Both approaches allow for different pathways of successional development depending on the nature of disturbance and initial stand conditions. However, neither is quantitative and neither identifies causal factors of observed successional patterns.

Recent descriptions of succession emphasize the influence of initial stand and site conditions, nature of disturbance, and life history characteristics of individual species as determinants of the multiple pathways of succession following disturbance. These include models based on the vital attribute concept of Noble and Slatyer (1980), and the JABOWA model (Botkin and others 1972) and its derivatives.

Vital attributes are those life history characteristics of a species that determine disturbance response. They include means of arrival and persistence, establishment, and timing of critical life stages (Noble and Slatyer 1980). The approach provides a conceptual framework for predicting response of individual species to disturbance based on general ecological and morphological characteristics. These characteristics are known for many understory species for which more detailed autecological data are unavailable. Local applications have been to trees only, including models of tree succession following fire in Glacier National Park (Cattelino and others 1979) and some forest communities in Montana (Kessell and Potter 1980). Multiple pathways of succession depend on vegetation existing before disturbance and the fire return interval. These and other vital attribute models (Noble and Slatyer 1980; Noble 1981) are diagrammatic, but the approach need not be limited to nonquantitative applications. Kessel and Potter (1980) provided general predictions of abundance for common understory species.

JABOWA and its derivatives are forest gap regeneration models (Shugart and West 1980). Predictions of regeneration, establishment and changing species composition of trees through time are stochastic. Life history characteristics of individual species determine successional development. Despite simplistic representations of growth and competition, the models have been successfully adapted to many forest ecosystems and a variety of disturbances (Shugart and others 1981). This illustrates the importance of recognizing the influence of disturbance, existing vegetation, and individual species characteristics on the major processes of regeneration and establishment. The models do not include understory species or effect of severity of disturbance.

The BRIND model (Shugart and Noble 1981) predicts successional dynamics following fire in Australian forests. It is derived from JABOWA but differs by including fire intensity effects on tree regeneration and mortality. Fire kills trees directly by scorching crowns or increasing susceptibility to other sources of tree mortality in the model. Germination of tree seeds is enhanced or stimulated by fire depending on fire intensity. This model thus recognizes that not all fires have the same ecological impact on ecosystems. Although fire intensity and severity both affect fire damage of trees, severity would be a better indicator of seed germination effects and some of the tree mortality factors. Species characteristics are important in the model, but the vital attribute approach is not specifically incorporated in the BRIND model.

Two particularly useful conceptual models applicable to shrub succession are those of MacMahon (1980, 1981), developed as a general model of succession, and Lyon and Stickney (1976), developed to describe succession following northern Rocky Mountain wildfires. Both emphasize the importance of on- and off-site propagule sources; the processes of survival, dissemination, and establishment; and the importance of individual species characteristics as determinants of the pattern of successional development.

The variety of modeling approaches reflects recognition of need for predictions of early succession following forest disturbance (Pfister 1982; Franklin 1982), yet few theories have been advanced to describe the causes of early successional patterns (Zamora 1982). Modeling of early succession in forests has been largely avoided due to its apparent complexity. Large numbers of species are involved, autecological data for even the most important species are often lacking, and species exhibit a wide array of life-cycle strategies (Zamora 1982). Few models of understory succession exist, as there is a belief that once communities reach the forest stage, the sequence of successional events becomes more predictable.

Early succession is neither too complex nor too variable to defy prediction. Previous research and modeling attempts have identified critical successional influences and useful approaches to handling them in a modeling context. Identifying critical life history characteristics of successional species (Gill 1977, 1981; Naveh 1975; Noble and Slatyer 1980; Rowe 1983); stratifying environments by habitat type (Arno 1982; Arno and Simmerman 1982; Stage 1973); and describing differential species response to burn severity (Rowe 1983) provide means to reduce variability and allow prediction. Availability of these ideas has greatly simplified our conceptual development to one of synthesis. We have combined the best characteristics of previous research and modeling approaches into a simple conceptual model of shrub succession following clearcutting and burning.

CONCEPTUAL MODEL

Our model of early succession (fig. 1) is briefly outlined in an overall description of the linkage of major successional processes and influences. More detailed treatment of successional processes included in the model follows in subsequent sections. A separate section is dedicated to the role of chance and our incorporation of stochastic and deterministic approaches into the conceptual model.

Those propagules (seeds, buds, rootstocks, and others) that survive disturbance on-site or are disseminated from off-site sources give rise to the initial flora. The initial flora includes those species available for colonizing the site following disturbance. The likelihood that the initial flora includes a particular species depends on environmental conditions (e), existing vegetation (v), and chance (c). Through the process of ecesis (Clements 1916), some of the initial flora establish and grow to form the vegetation in the first year after disturbance(s). Individuals may establish whenever suitable conditions for ecesis occur in the years following disturbance; however, establishment is limited to the first year following clearcutting and fall broadcast burning on the *Thuja plicata/Clintonia uniflora* habitat type. The process of ecesis is strongly influenced by burn severity (b), life history characteristics of individual species (l), and chance (c). Change in vegetation from the first year (S$_1$) to subsequent years (S$_N$) is the result of growth and the biotic interactions that affect growth. Growth and biotic interactions are affected by chance (c) and the life history characteristics of the successional species (l).

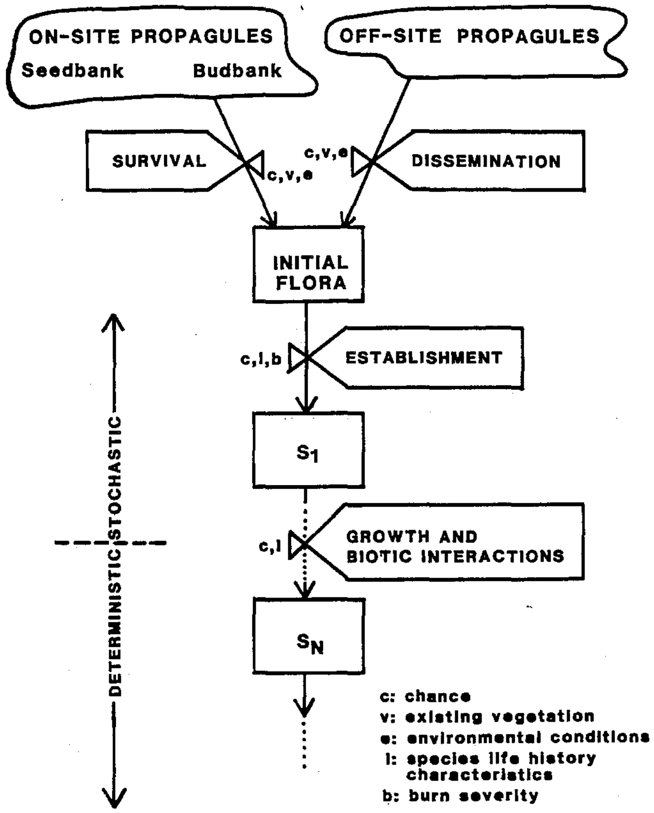

Figure 1.—Conceptual model of shrub succession following clearcutting and broadcast burning. The initial flora includes those species available for postburn colonization. It consists of those propagules surviving the burn on-site and those disseminated from nearby off-site areas. Species composition of the initial flora depends on chance (c), the vegetation existing before disturbance (v), and environmental conditions (e). Some of the initial flora establish to form the first year shrub community (S$_1$). The establishment process is affected by chance (c), life history characteristics of individual species (l), and burn severity (b). After establishment, changes in shrub communities to those of subsequent years S$_N$ are the result of growth and biotic interactions. These processes are strongly influenced by chance and the life history characteristics of individual species.

The major postburn successional influences identified in the conceptual model are environmental conditions (e), existing vegetation (v), burn severity (b), life history characteristics of species (l), and chance (c). Environmental effects include physical site conditions such as soil conditions, elevation, slope, aspect, and forest habitat type. Tree canopy closure and seed bank and live shrub species composition of the forest vegetation existing before clearcutting may strongly influence successional development. Life history characteristics of species that affect disturbance response include possible reproductive modes, intrinsic growth rates, longevity, and shade tolerance. Burn severity affects the potential contribution of various reproductive modes to postburn regeneration, establishment and growth of species. Chance plays an important role in all early successional processes.

We incorporate the effect of chance on succession through stochastic modeling in addition to deterministic approaches. Shrub community dynamics in the first few postburn years are modeled stochastically. These include the processes of determination of the initial flora, establishment, early growth, and biotic interactions. Subsequent changes in shrub communities are represented deterministically.

On-site Propagule Sources

Understory vegetation is usually top killed by fire; therefore, most understory vegetation is adapted to regenerate after fire. Sources of regeneration are of two general types: on- and off-site (Lyon and Stickney 1976), which have also been called residuals and migrants (Clements 1916; MacMahon 1980, 1981). On-site sources may be dormant buds on surviving plants parts (the "bud bank") or dormant seeds stored on site in duff and surface soil (the "seed bank") (Roberts 1981).

The above ground parts of understory plants are usually partially or totally consumed and the cambial tissue killed or damaged by fire; however, the root system and subsurface plant parts may survive even intense fires. Understory vegetation commonly resprouts from previously dormant buds on rhizomes, root crowns, bulbs, corms, and other plant parts (Gill 1981; Heinselman 1981). Postburn sprouting is widespread in ecosystems worldwide (Keeley 1981). Postburn shrub growth from sprouts is often abundant and vigorous, particularly for low shrubs such as *Rosa, Symphoricarpos,* and *Spiraea* (Lyon and Stickney 1976). Root crown sprouting has been called the most important fire survival adaptation for northern Rocky Mountain shrub species (Lyon and Stickney 1976). It is particularly important for tall shrubs such as *Acer, Salix, Alnus,* and others (Lyon and Stickney 1976). Severe or deep burns, those that consume organic layers and heat the soil surface for some time, result in reduced sprouting response (Flinn and Wien 1977; Ohmann and Grigal 1979; Rowe 1983). This is likely due to direct lethal heating of the plant tissues but may also be due to changes in the postburn microenvironment such as soil water and temperature regimes or nutrient availability (Heinselman 1981). Generally, on-site seedling or sprout regeneration occurs even on severe burns (Heinselman 1981).

Seed banks may contribute significantly to postburn regeneration (Archibold 1979; Roberts 1981; and others). Seeds may lie dormant on site for many years, often through an entire successional cycle. For instance, many *Ceanothus* species apparently produce abundant seed beginning shortly after establishment. These accumulate in the soil until dormancy is broken, often by heat from fire (Gratkowski 1973). Postburn seedling regeneration from seed bank sources may be very abundant. We found that eight of 12 common and abundant shrub species on the *Thuja plicata/Clintonia uniflora* habitat type relied on seed banks for postburn regeneration (Morgan and Neuenschwander, in preparation). Live fruiting shrubs of these mostly shade-intolerant early successional species were not present in the undisturbed forests, nor is off-site dispersal likely (Morgan and Neuenschwander, in preparation). Thus, the majority of seeds in the duff and soil seed bank must have been produced on-site in a previous shrub stage.

Some seeds are specifically adapted to lie dormant until stimulated to germinate by heat from fire or the changed postfire environment. Germination of *Ceanothus* species is stimulated by heat scarification (Gratkowski 1973). *Ribes* (Quick 1956) and other species appear similar in their germination response to fire. Seeds of other species that lack specific adaptations for heat tolerance may survive fire by chance. The seedbed created by fire is seldom uniform. Even severe fires often leave small islands of unburned or only partially consumed duff. Seedling composition on such microsites is often different from that on more severely burned microsites. Regeneration from seed banks may be enhanced by moderately severe fires (Heinselman 1981).

The on- and off-site propagules sources that predominate on a given site affect successional dynamics. On-site sources are immediately available and postburn response may be rapid as is the case when sprouting is abundant and vigorous. Off-site sources may be but are most often not as quickly available and abundant postburn.

Off-site Propagule Sources

Propagules may be disseminated from areas adjacent to burns by wind, animal, bird, or water vectors. Usually the propagules are small airborne seeds or fruits (Lyon and Stickney 1976). The importance of off-site sources to a particular species varies with availability of suitable vectors and proximity of flowering source plants in unburned areas within or at the edge of burns. These factors are highly subject to topography and chance. Therefore, the postburn abundance of vegetation with off-site origins may be highly unpredictable (Lyon and Stickney 1976).

Species vary greatly in their adaptations to dispersal. Occasionally, off-site sources enable species to be very abundant postburn, as is often true with *Epilobium* species. Generally, however, off-site sources lead to infrequent and continuous establishment through time (Lyon and Stickney 1976). Shrubs that have seed adapted for wind dispersal (such as *Salix, Acer, Betula,* and *Alnus* species) also rely heavily on sprouting for postburn regeneration.

Initial Flora

The on- and off-site propagule sources determine the initial flora, those species available for postburn establishment (Lyon and Stickney 1976). The composition of the initial flora is strongly influenced by environment, existing vegetation, and chance. The environmental conditions of the site influence successional pathways (Zamora 1982) by limiting the species potentially present on-site and in adjacent areas that might provide off-site sources of propagules. On-site sources are particularly affected by the vegetation existing before disturbance. Sprouting potential is a function of age and vitality of shrubs (Naveh 1975; Gill 1981). Thus, post-burn sprouting depends on the presence of vigorous shrubs in the undisturbed understory. Many of the species important in early seral shrub communities are shade intolerant and unable to exist under the closed canopy of the undisturbed forest. Such species will sprout if they are present in the stand before disturbance, but many rely on dormant seed stored on-site in duff and soil seedbanks. Stand history may affect seedbank composition. On-site propagule sources will be nonexistent if the time since on-site seed production exceeds seed longevity.

Many shrub species regenerate from more than one propagule source on a given site. *Salix scouleriana* may establish post-burn from root crown sprouts or from wind-blown seed (Lyon and Stickney 1976). *Rubus parviflorus* may sprout from rhizomes and regenerate from seed stored on-site in the seedbank. Establishment probabilities and early growth rates of seedlings and sprouts of the same species often differ greatly, hence it is useful to treat the reproductive modes of the same species as separate entities in the model until they become difficult to differentiate in the field. Seedlings and sprouts of the same species are probably sufficiently similar to be treated as equivalents in the model after the first few post-burn growing seasons.

Establishment

The species present in the first post-burn growing season will depend on the initial flora, but not all initial flora will survive and regenerate after fire. It is unlikely that establishment success will be proportionate to the abundance of propagules in the initial flora.

Successful establishment depends on the kind and severity of disturbance, mode of reproduction, and other factors, including weather, microsite conditions, and herbivory. Burn severity affects the overall postburn abundance of shrub seedlings and sprouts. Both rhizomatous and root crown sprouts are more abundant on low-severity than on high-severity burns. Burn severity reflects the potential damage to seeds and plant organs in the duff and soil (Flinn and Wien 1977). It also strongly affects the postburn microenvironment. Thus, burn severity may strongly influence the likelihood of establishment from both seed and sprout propagules.

In the simplest case, establishment is limited to immediately following fire. Virtually all important early successional species establish in the first postburn year (Lyon and Stickney 1976; Gomez-Pompa and Vazquez-Yanes 1981; Zamora 1982). No significant additional establishment of either shrub seedlings or sprouts occurred after the first growing season on the fall broadcast burns we observed. Immediate establishment of shrubs is similarly probable for productive sites where establishment is primarily from on-site sources. Factors affecting regeneration are particularly important influences on successional pattern when establishment is immediate and characteristics of the species that do establish may strongly affect the pattern of successional development for many years. For instance, the apparent forb, shrub, and tree "stages" of succession are the result, not of successive establishment and replacement, but of differential growth rates of species that establish simultaneously (Lyon and Stickney 1976).

Growth and Biotic Interactions

Shrub community dynamics subsequent to establishment are the result of survival and differential growth of individuals (Lyon and Stickney 1976). It is useful to treat growth and establishment as separate processes even if they occur simultaneously, which accommodates the site poor for establishment but favorable to growth (Stage and Ferguson 1982).

In our conceptual model, growth is expressed as net growth, including mortality. Biotic interactions include competition, interference, and any other influences of one organism upon another that contribute to differential growth and size potential. Growth and biotic interactions encompass all processes, including the innate characteristics of individual shrub species, which determine apparent dominance over time (Lyon and Stickney 1976).

The mechanisms of growth and biotic interactions are difficult to quantify. Growth is a function of intrinsic growth rate, competition, mode of reproduction, physical site characteristics, weather, time, and other factors. Chance plays a major role, contributing to the spatial and temporal variability of these effects. Early growth is especially subject to a variety of factors. A few of these can be identified and quantified. Others may best be treated as chance influences. In a model, this is accomplished through use of stochastic functions. Growth and biotic interactions may be adequately represented by simple stochastic equations as in JABOWA (Botkin and others 1972) and the many models derived from it (Shugart and others 1981).

Role of Chance

Chance plays an important role in succession (Franklin 1982). It affects every successional process, whether that effect is identified and quantified in the model or not. The role of chance can be represented in simulation models by random and probabilistic components. Models that incorporate such effects are stochastic. Predictions of stochastic models are not single, absolute numbers; instead, they consist of a range of numbers with associated probabilities that express the likelihood that a particular outcome will occur. Inclusion of a separate stochastic element in a model stresses the important influence of chance on successional pattern (Franklin 1982). Models are simplifications. The effort to build an accurate model forces an elucidation of the most critical processes and controlling influences of succession. Many less important effects must be excluded. Stochastic elements may be used in simulation models to represent the influence of some of these excluded effects. Thus, stochastic functions may be used in simulation models to represent both natural variation due to chance and variability due to other influences on successional processes than those included in the model.

Deterministic models are usually simpler and less expensive to execute than stochastic models. Stochastic predictions more realistically represent natural variability in postburn succession.

We believe that a combination of stochastic and deterministic approaches provides flexibility and accuracy in a less expensive model. Stochastic functions can be used to represent processes that are strongly influenced by chance and by many factors that are difficult to identify and quantify, namely determination of initial flora, establishment, early growth, and biotic interactions. Shrub community dynamics following establishment and early growth are less subject to the vagaries of chance. A deterministic model may adequately represent successional development after the first few postburn years.

LIMITATIONS

The conceptual model presented here and the examples used to demonstrate it draw heavily on our experience with postburn shrub succession in northern Idaho. We hope that this model is generally applicable to postburn succession; however, differences in detail are likely. For instance, seed banks are probably not as significant as contributors to postburn regeneration of understory vegetation in some other habitat types. Johnson (1975) found evidence for lesser importance of seed banks in northern ecosystems. Relative contribution of on- and off-site sources may also be strongly influenced by fire regimes (Keeley 1981). Establishment may extend through many years elsewhere, especially if off-site sources predominate. This could strongly affect successional dynamics. In such situations, the relative importance of the successional processes and influences may differ from the one we described.

Much data may be required to obtain the knowledge of the on- and off-site propagule sources needed to apply this model. This is a serious limitation unless indicators of disturbance response can be easily identified. Seed morphology may be indicative of the likelihood of long-lived dormancy in seedbanks, the potential importance of seedbanks may be predictable by habitat type, and rooting habit may offer clues to sprouting potential. Ideally, adaptive characteristics of species could be simply identifed from such general morphological and ecological characteristics.

The conceptual approach is untested. Pilot simulation model development suggests that the modeling approach has promise. Once complete, the simulation model will be tested against field observations of shrub succession on the *Thuja plicata/Clintonia uniflora* habitat type. Results should reflect whether the conceptual approach is appropriate.

CONCLUSIONS

The complexity of early seral succession can be unraveled when casual factors are identified. We have outlined a conceptual model of shrub succession following clearcutting and broadcast burning. The model incorporates the critical influences and processes determining successional development. Environmental conditions, existing vegetation, life history characteristics of species available for colonization, kind and severity of disturbance, and chance are identified as important influences on successional patterns. The critical successional processes are determination of the initial flora, establishment, growth, and biotic interactions. Many of these influences and processes have been previously identified as important determinants of successional patterns. Here they are synthesized into a simple conceptual model of shrub succession following fire.

Development of our conceptual model draws heavily on the conceptual models presented by MacMahon (1980, 1981) and Lyon and Stickney (1976), existing literature, and previous successional modeling approaches. The best attributes of many separate approaches are combined in the conceptual model. The resulting integration differs substantially from any of the parts. We recognize the role of chance in successional development. Chance is most influential in the first few postburn years, and we represent early successional processes stochastically. Deterministic equations are adequate representations of community dynamics subsequent to establishment and early growth, when changes in the community are less subject to the vagaries of chance. This time-dependent linkage of stochastic and deterministic equations in a single successional model is unique. The conceptual model provides a valuable synthesis of ideas valuable in developing an understanding of the course of early seral shrub succession following clearcutting and burning.

Forest successional models have been used to integrate existing knowledge, explore theories, test specific hypotheses, and stimulate critical thinking about the causes and consequences of successional dynamics (Shugart and West 1980; Franklin 1982). We hope that the conceptual model presented here will stimulate similar critical thinking about succession of forest understory species.

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INFLUENCE OF FIRE SEVERITY ON RESPONSE OF EVERGREEN CEANOTHUS

Nonan V. Noste

ABSTRACT: Fire plays an important role in *Ceanothus velutinus* habitat. Its impact varies with season and severity of fire. Knowledge of the interaction between fire severity and evergreen ceanothus habitat can assist managers in estimating the effect of fire on evergreen ceanothus and in developing burning prescriptions.

INTRODUCTION

Ceanothus velutinus (Dougl.), evergreen or snowbrush ceanothus, is an important wildlife browse species that provides a critical winter food resource for deer and elk (Klebenow 1962; Martinka 1976). Evergreen ceanothus is a component of seral shrub fields, as well as of open xeric or developing early seral conifer stands. Evergreen ceanothus is also of special interest to managers because it fixes nitrogen (Zavitkovski and Newton 1968; Jurgensen and others 1979) and competes with tree seedlings (Gratkowski and Lauterback 1974). Fire plays a prominent, if not critical, role in establishing and maintaining these shrub fields and forest stands. Fire can be used in managing stands with a *Ceanothus* component (Hall 1977).

The following discussion of the response of evergreen ceanothus to fire emphasizes the effect of fire treatment severity. This paper summarizes information on the biology of evergreen ceanothus and emphasizes management strategies for using fire to encourage or discourage reproduction and growth.

SPECIES CHARACTERISTICS

Evergreen ceanothus commonly grows in dense clumps or patches but ranges from scattered individual plants to nearly complete site domination. There are two varieties of *Ceanothus velutinus*. *Ceanothus velutinus* var. *laevigatus* (Hook.) Torr. and Gray is distinguished by smooth (glabrous) leaves, at least on the veins on the underside of the leaves. Its range is the west Cascade Mountains from British Columbia to northern California. *Ceanothus velutinus* var. *velutinus* has pubescent leaves covered with short fine hairs. It is found east of the Cascade Mountains from British Columbia to California and Nevada and east to South Dakota and Colorado (Hitchcock and Cronquist 1961). Evergreen ceanothus is known under several aliases, including shinyleaf, varnish leaf, buckbrush, wild-lilac, stickylaurel, grease wood, and tobacco-brush. The seasonal growth patterns of evergreen ceanothus in the Rocky Mountains can be inferred from published phenological information (Schmidt and Lotan 1980; Schopmeyer 1974). The western variety (*laevigatus*) is sometimes treelike and reaches a maximum height of 20 ft (6 m) (Little 1979). The eastern variety (*velutinus*) is approximately 2 to 6 ft tall (0.5 to 2 m), occasionally up to 13 ft (4 m) Hitchcock and others 1961).

In Montana, Morris and others (1962) associate evergreen ceanothus with Douglas-fir and spruce-fir zones. In north central Washington, evergreen ceanothus is responsible for much of the difference in shrub cover in the ponderosa pine and Douglas-fir forests (Tiedemann and Klock 1976). Average cover 4 years after burning was 12.7 percent on south slopes compared to 6 percent on the west aspects.

Explosive flammability in these stands is attributed to retention of dead leaves on sclerophyllous (thick hard leaves) understory vegetation such as evergreen ceanothus. Fuel from winter dieback of evergreen ceanothus could increase flammability. Stickney (1965) attributed dieback during the winter of 1962-63 in the Missoula, Mont., area to a severe drop in temperature followed by a mild period.

Some of the species that dominate early successional phases often have dormant, ground-stored, fire-activated seeds. This is true of evergreen ceanothus, whose seeds are characteristically small (61,400 to 152,000/lb) (Schopmeyer 1974), rounded to spherical, smooth texture, and without obvious means of dispersal much beyond the limits of the parent plant (Lyon and Stickney 1976). Evergreen ceanothus seeds are long-lived, viable on forest sites for 200 to 300 years (Gratkowski 1962), and require heat treatment to germinate (Dyrness 1973). Pressure of the two edges of the hilar fissure against each other is sufficient to prevent moisture penetration into the seed. Heat induces germination by opening the hilar fissure sufficiently to permit passage of water into the seed (Gratowski 1962). The species can resprout from the root crown after being burned and is intolerant to shade.

Lyon and Stickney's (1976) model for predicting a plant species' success links fire survival strategy to its abundance in early seral communities. Evergreen ceanothus fits two fire survival categories.

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Nonan V. Noste is Research Forester, Intermountain Research Station, Forest Service, U.S. Department of Agriculture, Missoula, Mont.

When the on-site survival mechanism (meristematic tissue) is sprouting from burned root crowns, their model predicts a minor decrease in response to severe wildfire. If the survival mechanism is long viability on-site seed, a large increase after these severe wildfires is expected.

FIRE SEVERITY

The concept of fire severity combines the effect of the heat pulse up to the above-ground vegetation and down into the soil (Ryan and Noste in press). The heat pulse down has been termed ground char and is evaluated by classifying postburn soil and fuel characteristics. When used in relation to *Ceanothus velutinus* reproduction and regeneration, the term "fire severity" inplies that the heat pulse is down to the soil. It is difficult to separate fire intensity and the upward heat pulse from ground char in evaluating measures to characterize fire in relation to fire effects. In the literature, ceanothus response has been related to several fire measures such as intensity and percent duff reduction. This information will be interpreted in accordance with the concept of fire severity.

Critical soil temperature inducing germination range from 113° to 149° F (45° to 65° C) (Gratowski 1962). A minimum 8-minute exposure to dry heat induces germination, with further exposure having no additional influence. Mortality increases heat treatment information on the western variety (*laevigatus)*, and it is commonly inferred that it also applies to the variety *velutinus*. Solar insolation on unburned sites apparently also is often sufficient to stimulate germination (Dyrness 1973). The general relationship of *Ceanothus velutinus* to fire severity is illustrated in table 1.

Table 1.--Response of *Ceanothus velutinus* (CEVE) to fire severity[1]

Preburn condition	Response				
Extant plants (CEVE shrubs present)	Aerial crown	Kill		Shrub	Mortality
	All shrubs resprout	Most shrubs resprout		Few shrubs killed	Many shrubs killed
Dormant, viable seed (CEVE seed present in forest floor or ground)	Untreated	Fire treated			
	(below critical temperature)	(above critical min. temp.)			
		Nonlethal range		Lethal range	
	Seeds remain dormant	Uppermost seeds activated	Most activated	Few seeds killed	Many seeds killed
No seeds or extant plants present (CEVE absent from site in all forms)		NO RESPONSE			
	No resprouts or seedling evident in postfire community				
	Low	FIRE SEVERITY GRADIENT			HIGH

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[1] Personal communication, Peter F. Stickney, Missoula, Mont.: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station, Forestry Sciences Laboratory, Feb. 1984.

FIRE SEVERITY RELATIONSHIP

Preliminary results of a study by Arno and Simmerman (1982) describe a relationship between fire severity and establishment of evergreen ceanothus. On the Douglas-fir/ninebark (*Pseudotsuga menziesii/Physocarpus malvaceus*) habitat type (Pfister and others 1977), a medium or hot wildfire or broadcast burn on a site with evergreen ceanothus seed in the soil produces an evergreen ceanothus community type. In Douglas-fir/blue huckleberry (*Pseudotsuga menziesii/vaccinium globulare*) types, a severe burn produces an evergreen ceanothus community type.

In a forest succession study, Stickney (1980) provides data on plant response in relation to fire severity for the larch/Douglas-fir forests of western Montana. There was no evergreen ceanothus on the plots before treatment. The subalpine fir/queencup beadlily (*Abies lasiocarpa/Clintonia uniflora*) habitat type was treated at the Miller Creek prescribed fire study area on the Flathead National Forest. Evergreen ceanothus became established at low levels (5 and 7 percent cover in 6 years) on two south exposure plots burned by wildfire (table 2). This wildfire could be judged severe based on Stickney's observation that no duff layer remained (DeByle 1981).

The western redcedar/queencup beadlily (*Thuja plicata/Clintonia uniflora*) grand fir/queencup beadlily (*Abies grandis/Clintonia uniflora*), and Douglas-fir/blue huckleberry habitat types were sampled at the Newman Ridge prescribed fire study area on the Lolo National Forest (Stickney 1980). The cold, north-slope western redcedar/queencup beadlily site had no ceanothus response (see unit N2 in table 2).

The four plots in the grand fir/queencup beadlily habitat type had varied response, with no evergreen ceanothus on a west exposure plot (W2) burned by a relatively severe fire. Lack of seed source may explain the absence.

A west slope site on Newman Ridge burned (W3) by a low-severity fire had a relatively high evergreen ceanothus cover (24 percent in 6 years). When treated with fires of similar severity, evergreen ceanothus cover was 22 percent after 6 years on a south slope (S2) compared to 11 percent on an east slope. A Douglas-fir/blue huckleberry plot on a south slope treated with a severe fire had 41 percent cover in 6 years, which must approach the maximum potential for evergreen ceanothus establishment and growth.

Table 2.--Fire effects on Miller Creek-Newman Ridge sites in western Montana (Stickney 1980)

Location, unit no.	Habitat[1] type	Fire intensity (water loss)	Postburn duff depth	Duff reduction	Evergreen ceanothus Preburn	Evergreen ceanothus 6-year postburn
		gm	cm	Percent	Percent	Percent
Miller Creek						
N6	Subalpine fir	303	7.0	14	0	0
N7	Subalpine fir	242	4.5	49	0	0
N8	Subalpine fir	266	6.0	6	0	0
E6	Subalpine fir	243	2.7	49	0	0
E8	Subalpine fir	881	6.6	31	0	0
E9	Subalpine fir	834	4.7	38	0	0
S1	Subalpine fir	286	4.3	16	0	0
S2	Subalpine fir	--	--	--	--	--
W3	Subalpine fir	423	4.5	11	0	0
W10	Subalpine fir	519	2.4	52	0	0
W15	Subalpine fir	228	6.4	11	0	0
Newman Ridge						
E3	Grand fir	820	2.0	35	0	11
N2	Western redcedar	1,297	2.7	51	0	0
S2	Grand fir	813	1.9	47	0	22
W2	Grand fir	1,253	2.2	59	0	0
W3	Grand fir	283	1.0	63	0	24
S3	Douglas-fir	1,976	.3	94	0	41
Wildfire in standing timber						
S12	Subalpine fir	--	--	--	--	7
S13	Subalpine fir	--	--	--	--	5
W6	Subalpine fir	--	--	--	--	0

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[1] All units were in the *Clintonia uniflora* phase of the habitat type except unit S3, which is in the *Vaccinium globulare* phase.

Percent duff reduction is an index of depth-of-char, so the concept of fire severity can be applied to the data in table 2. There is a direct trend between percent duff reduction and ceanothus cover. The wildfires and prescribed fires with ceanothus response were severe.

SPRING AND FALL BURNS

The effect of spring and fall prescribed burning is being studied on a seral shrub field in a Douglas-fir/ninebark (*Pseudotsuga menziesii/physocarpus malvaceous*) habitat on O'Keefe Creek near Missoula, Mont. The area is a critical big game winter range, and evergreen ceanothus is an important browse species on the site. The idea that more severe fall prescribed fires provide an alternative to traditional spring fires to rejuvenate seral shrub fields is being evaluated. Fall fires are generally more severe because the larger fuels are drier and soil moisture lower.

Plots of 50 and 125 acres (20 and 50 ha) were burned on October 3, 1979, and April 16, 1980, respectively. The fall of 1979 was dry, and the fire was intense considering the limited fuels on the site. Flame lengths on the fall fire averaged 9 ft (3 m) and contrasted to 3 ft (1 m) flame lengths on the spring burn. A detailed description of fuel loadings, fuel moisture, weather conditions, and fire behavior, which were needed to develop a burning prescription, has been published along with vegetation sampling methods (Noste 1982).

Twenty individual evergreen ceanothus plants were observed before the burns and 1 year after (1980). Twelve of 20 marked plants were killed on the more intense fall burn; there was no mortality on the spring burn. Thus, first growing season survival rates of mature plants were 40 percent on the fall burn and 100 percent on the spring burn.

Evergreen ceanothus seedlings were not counted the first growing season after the fall burn (1980), but many were present. Wildlife grazing during the relatively open (free from snow) 1980-81 winter severely reduced the number of ceanothus seedlings. In 1981, evergreen ceanothus seedlings occurred on 38 percent of the plots (0.5 by 0.5 m) on the fall burn, and the seedlings count indicated a density of 18,000 seedlings per acre (45,000/ha). Seedlings have not been seen on the spring burn. A sample of 50 plots (0.5 by 0.5 m) in both the spring and fall burn during the fourth growing season (1983) indicates 6,500 seedlings per acre (16,000/ha) surviving on the fall burn and none on the spring burn.

The differential response of evergreen ceanothus to fall and spring burning is shown in measurements of percent cover in the following tabulation:

Treatment year	Percent cover
Spring	
preburn	11.5
1980	12.7
1981	19.6
1982	21.5
Fall	
preburn	18.5
1980	0.2
1981	6.7
1982	10.4

During the first growing season following the spring burn, treatment cover (12.7 percent) exceeded the preburn value (11.5 percent). Cover has nearly doubled (21.5 percent) during the third growing season. All of these plants resprouted from root stocks. The fall burn set evergreen ceanothus cover back to 0.2 percent the first year and in the third growing season had expanded to about half of preburn coverage (18.5 and 10.4 percent). This cover nearly all originated from plants that resprouted; small seedlings accounted for very little.

DISCUSSION

Knowledge of the relationship between fire severity and evergreen ceanothus can facilitate development of burning prescriptions. Severe fires are generally needed to establish evergreen ceanothus seedlings. Some interactions between fire severity, aspect, and habitat type are also significant. More severe fires are needed in cool moist habitat types than in warm habitat types. The greatest potential for establishing evergreen ceanothus is on south slopes, followed in order by west and east slopes. The Douglas-fir habitat types have more potential for ceanothus than grand fir habitat types. Subalpine fir habitat types have more potential for evergreen ceanothus than western redcedar habitat types on north slopes or northeast slopes.

Success in regeneration and rejuvenation of evergreen ceanothus following burning is extremely variable, presumably due to variation in duff moisture and fire severity (Wright and others 1979). Late summer or fall burns, however, do increase the number of seedlings and resprouts (Wright and others 1979). The O'Keefe Creek results support this claim. The more intense fall fire produced seedlings at O'Keefe Creek, whereas the spring fire increased evergreen ceanothus cover in the short run.

Martin (1982) has described an effort to reduce evergreen ceanothus in central Oregon ponderosa pine (*Pinus ponderosa*). A burning treatment is designed to exploit stress on the plant and increase the probability of mortality. The treatment combines a preharvest underburn to weaken mature plants and germinate some seed, with a subsequent postharvest burn. This concept of frequent, less intense fires is being evaluated. Successive fires at relatively short intervals have been shown to retard shrub growth (Isaac 1940; Gratowski 1962).

The information presented here, although not in the form of a predictive model, can be used as a guide for estimating the effect of fire on evergreen ceanothus. The manager wanting to increase or decrease the evergreen ceanothus component of a seral shrub field or a forest stand can be more specific in setting objectives and evaluating results and through this process can learn to manipulate this species through the use of fire. Weather conditions and fuel availability may limit attaining the severity of treatment required to accomplish burning objectives.

Low-severity spring burns can increase ceanothus cover immediately and relatively inexpensively through regrowth from root crowns. Severe summer and fall burns stimulate germination of ground-stored seed to produce young plants, thus providing a long-term increase. Multiple low-severity fires provide an approach for reducing the ceanothus component. Objectives should reflect realistic attainable increases in cover or number of seedlings and should only reduce ceanothus cover enough to allow tree seedlings to compete.

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A compilation of 11 papers in which authorities discuss the impacts of fire on wildlife habitat and wildlife populations. Presentations cover bobwhite quail, nongame birds, white-tailed deer, bighorn and Stone's sheep; and the response to burning of curlleaf cercocarpus, aspen, evergreen ceanothus, and antelope bitterbrush.

KEYWORDS: wildland fire, fire management, wildlife habitat, prescribed burning, wildlife management, fire ecology, postfire succession, wildland management, fire effects

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The Intermountain Research Station, headquartered in Ogden, Utah, is one of eight Forest Service Research stations charged with providing scientific knowledge to help resource managers meet human needs and protect forest and range ecosystems.

The Intermountain Station's primary area includes Montana, Idaho, Utah, Nevada, and western Wyoming. About 231 million acres, or 85 percent, of the land area in the Station territory are classified as forest and rangeland. These lands include grasslands, deserts, shrublands, alpine areas, and well-stocked forests. They supply fiber for forest industries; minerals for energy and industrial development; and water for domestic and industrial consumption. They also provide recreation opportunities for millions of visitors each year.

Several Station research units work in additional western States, or have missions that are national in scope.

Field programs and research work units of the Station are maintained in:

Boise, Idaho

Bozeman, Montana (in cooperation with Montana State University)

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Missoula, Montana (in cooperation with the University of Montana)

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Ogden, Utah

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