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FIRE IN STEPPE VEGETATION OF THE NORTHERN INTERMOUNTAIN REGION

by
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Abstract

Managers often want to restore historical disturbance regimes. In the northern intermountain region, there is considerable interest in using fire as a management tool to accomplish a variety of objectives in steppe vegetation. Little information is available on the fire regimes of northern intermountain steppe vegetation before the arrival of Euroamericans. Similarly, we know little about how often Native Americans set fire to intermountain grasslands. Dry coniferous forests experienced frequent low-intensity fires, many of which resulted from human activities. It is likely that some of these natural and anthropogenic fires also burned steppe vegetation; however, the frequency and timing of those fires are not known. Soon after Euroamericans arrived in the region, fires may have become more frequent, but eventually fire suppression in uplands and the cessation of burning by Native Americans probably reduced the frequency of fire at moderate elevations. It is unlikely that fire suppression was effective in steep canyons.

Native perennial bunchgrasses are susceptible to damage by fire because their meristematic tissues are located near ground level, they grow by means of tillers rather than rhizomes, and they reproduce by seeds. In addition, species that form very compact tufts and are phenologically advanced are especially susceptible. Idaho fescue has all of these characteristics.

Native perennials are least vulnerable to fire when they are dormant, in summer. This is when most naturally started fires would have occurred in the past. Perennial forbs and shrubs that are able to regenerate from underground storage organs usually recover from burning.

There is evidence that seedling recruitment in the rare Spalding's catchfly increases when communities dominated by rough fescue are burned. This is thought to be due to the removal of litter by fire; however, it is less likely that litter limits recruitment in intermountain steppes, where less litter is produced.

Fire damages microbiotic crusts, and crust recovery after burning may take years or even centuries. Annuals increase after fires if enough seeds survive to repopulate a site or if they can colonize it. Before the arrival of Eurasian annuals with superior adaptations for colonizing disturbed sites, these postfire changes in community composition were transient, but this is no longer the case.

The fire ecology of intermountain steppe is influenced by its distinctive physiognomy and phenology. Although dry forests were negatively impacted by fire suppression, the evidence for a similar situation in steppe communities, which have much lower fuel loads, is less compelling. Furthermore, burned stands of native steppe vegetation are vulnerable to invasion by cheatgrass and other annual exotics, an event which can irreversibly alter community composition.

1. Introduction

In recent years, managers have come to appreciate the role of disturbances in shaping the structure and function of ecosystems. It has become clear that organisms are adapted to the disturbance regimes under which they evolved and that altering those disturbances regimes and reducing the natural variability in disturbance dynamics can have profound, and often unfortunate, consequences (Swanson et al. 1993; Morgan et al. 1994; Rogers 1996; Poff et al. 1997; Landres et al. 1999). For this reason, managers often seek to restore natural disturbance regimes.

In steppe vegetation of the Intermountain West, prescribed burning is often recommended as a means of accomplishing several objectives, including removing litter to enhance seedling recruitment; promoting plant vigor and site productivity; providing opportunities for species that require early seral stages; rejuvenating decadent stands containing large amounts of standing dead, leached vegetation; improving forage for wildlife and livestock; controlling exotic weeds; preventing shrub encroachment; enhancing structural diversity within habitats and landscape level diversity across habitats; decreasing the probability of severe fires in the future; and increasing ecosystem stability (McKell et al. 1962; Vogl 1974; Wright 1974; Peek et al. 1979; Antos et al. 1983; Adams 1989; Johnson 1989; Johnson et al. 1994; Fedrizzi 1998; Johnson 1998).

Fire management should maximize the beneficial effects of burning on native vegetation and minimize its negative effects. In order to do this, managers need to understand past disturbances and their consequences. This report reviews information about the nature, timing, and effects of fire on true steppe and meadow steppe communities of the northern intermountain region. This region, termed the northern section of the "*Agropyron spicatum*" Province by Daubenmire (1970), encompasses southeastern Washington, northern Idaho, northeastern Oregon, south-central British Columbia, and a disjunct area in northwestern Montana (Figure 1). Its climate is semiarid, with most precipitation falling in the cooler months (Figure 2), so that the region is characterized by summer drought (Weaver 1917; Daubenmire 1968*b*, 1972, 1978), although in some areas there is a secondary peak of precipitation in May and June (Tisdale 1986; Johnson and Simon 1987). Native steppe vegetation is dominated by perennial bunchgrasses accompanied by a microbiotic or cryptobiotic crust of mosses, lichens, algae, fungi, and cyanobacteria (Daubenmire 1942, 1970; Tisdale 1947, 1986; Cooke 1955; Poulton 1955; Mueggler and Stewart 1980; Johnson and Simon 1987; Mancuso and Moseley 1994; Lichthardt and Moseley 1997). The most common dominant grasses on zonal soils are bluebunch wheatgrass (*Pseudoroegneria spicata* ssp. *spicata*, formerly *Agropyron spicatum*) and Idaho fescue (*Festuca idahoensis*). In mesic environments, the perennial grasses and cryptogams are accompanied by a variety of forbs growing between the perennial grasses as well as low thickets of rose (*Rosa nutkana* and *R. woodsii*) and common snowberry (*Symphoricarpos albus*). This type of vegetation is termed meadow steppe. As the environment becomes even more mesic to the north and east, meadow steppe gives way to dry coniferous forests dominated by ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*) (Daubenmire 1970). To the west, the climate becomes more xeric, and shrub steppe (in which an overstory of big sagebrush, *Artemisia tridentata*, accompanies herbaceous steppe vegetation) is the predominant type of vegetation.

> *Managers often want to restore historical disturbance regimes. In the northern intermountain region, there is considerable interest in using fire as a management tool to accomplish a variety of objectives in steppe vegetation, but there is a need for information about the historical role of steppe fires.*

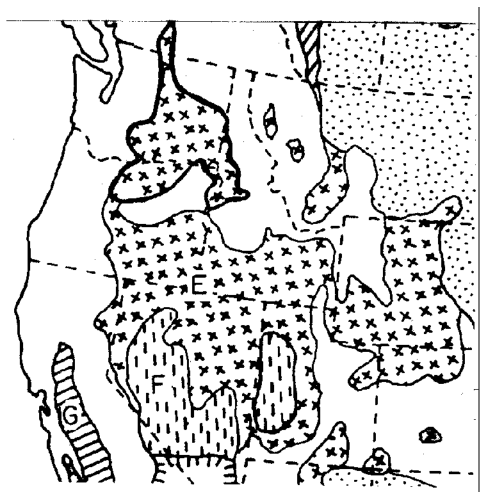

Figure 1. The northern section of the "*Agropyron spicatum*" Province (heavy black line). (After Daubenmire 1978).

2. Past fire regimes in northern intermountain steppe

2.1. Fire regimes prior to the arrival of Euroamericans

2.1.1. Naturally started fires

Information on past fires can be obtained from natural records, such as fire scars in tree trunks and charcoal deposits in sediment cores, as well as from historical records, such as journals, notes, sketches, and photographs. Because of the scarcity of woody material in steppe environments, historical records figure prominently in attempts to reconstruct their fire history. These materials provide a considerable amount of material pertaining to fire history, but they have some limitations (Nelson and England 1971; Gruell 1985; Swetnam et al. 1999). First, the events of some times and places are recorded in more detail than others. Whether or not an event was recorded depends upon chance (was an observer present in the right place at the right time?), interest (did the observer consider the event worth recording?), and opportunity (did the observer have the time and the equipment to record the event?). Cultural attitudes influence what an observer considers worth recording. Settlers may have been disinclined to record steppe fires because they were considered less economically and ecologically important than forest fires (Daubenmire 1968*a*; Gruell 1985). Second, it is often difficult to determine the extent of the geographic area that is covered by an account. Third, documents can be hard to interpret because they are unclear or because the document has deteriorated. Finally, the reliability of the documentary record depends upon the skill and honesty of the people who recorded past events and the technical capabilities of the cameras or other equipment used.

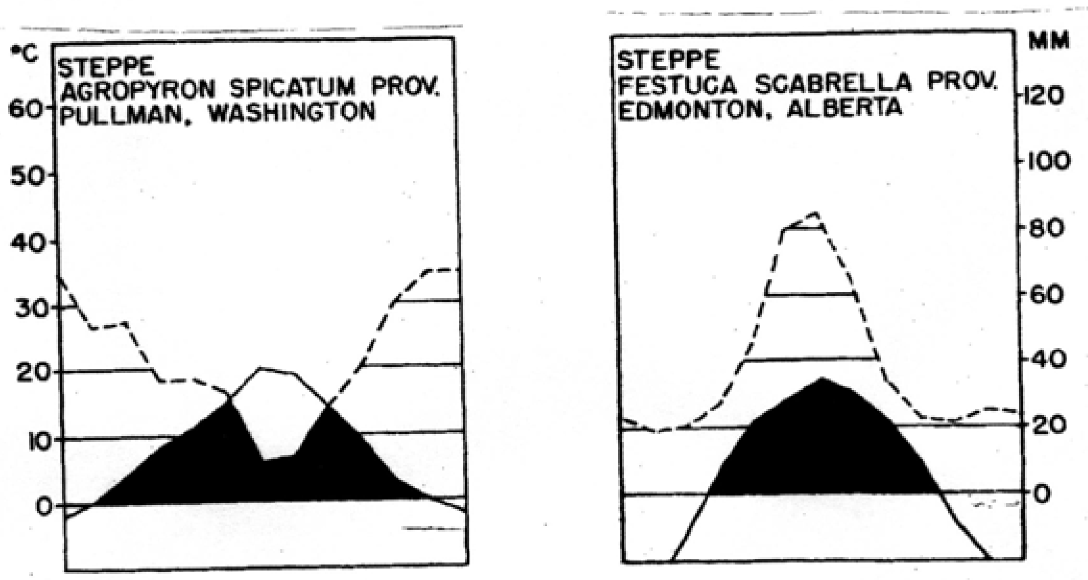

Fig ur e 2. Seasonal distribution of mean monthly temperature and precipitation in the "*Agropyron spicatum*" Province. Solid line = temperature; dashed line = precipitation. Note that in the "A*gropyron spicatum*" Province precipitation is at a minimum in summer, whereas in the "*Festuca scabrella*" Province precipitation peaks in summer. (After Daubenmire 1978.)

When white settlers arrived in the intermountain region, naturally started surface fires were frequent in dry, low-elevation forests and forest-steppe ecotones (Arno 1976, 1980; Hall 1980; Arno and Gruell 1983; Gruell 1983; Agee 1993; Kinateder 1998). There is also evidence that fires were common in the steppes of the northern Great Plains (Nelson and England 1971), and fire may have been an important influence on the composition of shrub steppe vegetation (Burkhardt and Tisdale 1976), although vegetation was less likely to burn where fine fuels were in short supply (Peters and Bunting 1994). Little is known about the frequency of fires in the intermountain steppes, however.

It is often assumed that prior to the arrival of Euroamericans, fires were frequent in northern intermountain steppe vegetation. Fedrizzi based recommendations for fire management of steppe vegetation at Craig Mountain on the assumption that the natural fire regime was "nonlethal very frequent," "stand replacing frequent," or "mixed frequent" for bunchgrass and bunchgrass-shrub community types (Fedrizzi 1998:44-49). Johnson (1998) suggests that 80% of the canyon lands of northeastern Oregon experienced low-severity fires in the past, 6% experienced medium-severity burns, and 14% experienced high-severity burns. According to the Forest Service, fires of stand replacement severity occurred with a frequency of 0 to 35 years throughout the steppes and shrub steppes of the West and Midwest (http://www.fs.fed.us/fire/fuelman/firereg.htm, historical natural fire regimes, Version 3.0, November 3, 1999).

This author found little specific data bearing on the fire history of northern intermountain bunchgrass vegetation, however. The conclusion that bunchgrass vegetation burned often is based upon analogy with midwestern steppes or extrapolations from its nearest neighbors, shrub steppe and dry coniferous forest. Gruell (1985) collected 145 accounts of fires in Montana, Wyoming, Idaho, Utah, Nevada, and eastern Oregon, but none of these events occurred in the steppes of the northern intermountain region. It is not clear if this paucity of accounts in steppe reflects infrequent fires or a bias in the historical record. Unfamiliarity with bunchgrasses also led to some errors in interpretation, even among trained observers. The botanist Charles Geyer believed that the caespitose physiognomy was caused by annual frosts and summer fires acting to fragment the grasses, "separating one tuft into several" (Geyer 1846: 288, footnote).

A long-term fire history of Craig Mountain, which rises steeply from the Snake River approximately 30 km southeast of Lewiston, ID, has been reconstructed from charcoal-rich beds and microscopic charcoal in a sediment core taken from Blue Lake (Smith 1983). This site is located at the eastern edge of the intermountain region, at an elevation of 1,035 m, which puts it near the transition between canyon grasslands that rise steeply from the Snake River and forest vegetation at higher elevations. The frequency of macroscopic charcoal in the sediment cores suggests that from 4,300 to 700 years ago, fires severe enough to cause slope erosion burned the open Douglas-fir forests above Blue Lake once every 100 to 350 years.

Although the Blue Lake sediments provide information on the frequency of forest fires at the eastern boundary of the intermountain region, they do not resolve the question of the historical fire frequency of the adjacent steppe vegetation. We do not know if the slopes below Craig Mountain's forests burned as often as the forests. There are reasons to think that they did not. First, since fires move upslope more rapidly than downslope (Daubenmire 1968*a*), it is not warranted to assume that every fire that burned in the forests above Blue Lake also burned the steppe vegetation at lower elevations. Second, where bunchgrasses are widely spaced, as on rocky slopes, fuel continuity may be insufficient to carry fire (Steve Bunting, personal communication, January 29, 2001). Third, aerial photographs of canyon fires taken in the summer of 2000 show that often vegetation dominated by native bunchgrasses did not ignite, even when large fires burned at higher elevations (Dick Walker, personal communication, January 31, 2001.) Thus, although some of the fires that burned trees near Blue Lake undoubtedly also affected steppe vegetation downslope, the relationship between the frequency of fire in forests and in steppe at this site is not known.

2.1.2. Anthropogenic fires

If the frequency of past fires in the northern intermountain steppe region is difficult to determine, the question of how often those fires were started by Native Americans is equally troublesome. Most examples of anthropogenic burning in the northern intermountain region involve forests or shrub steppe, rather than true steppe vegetation. For example, Lewis and Clark (Thwaites 1959) and the botanist John Leiberg (1900) gave accounts of Nez Perce Indians setting fire to forests, and Shinn (1980) summarized historical accounts of broadcast burning by native people in shrub steppe vegetation in east-central Oregon.

Although there is not a large body of evidence pertaining specifically to the anthropogenic burning of intermountain steppe vegetation, there is ample speculation. Because Indian burning was important in many parts of North America, some authors have assumed it was uniformly important everywhere. Pyne (1982) argued that Native burning was ubiquitous throughout the New World. Following this line of reasoning, Robbins (1999:222), contended that "Indian incendiarism was a significant factor in the burning of grassland and forest alike" throughout the Inland Northwest. This conclusion was based on evidence for anthropogenic fires in California; the Willamette and Puget lowlands; central Oregon; the Blue Mountains; and the valleys of the Walla Walla, Powder, Grande Ronde, and Umatilla rivers. The physical, biotic, and cultural environments of the Northwest were not homogeneous, however, and therefore it is prudent to assume that the importance of human-caused fires varied "from place to place and culture to culture" (Agee 1993:55).

A number of other authors have speculated specifically about the role of Indian fires in intermountain steppes. On the basis of archaeological evidence, Johnston concluded that the Nez Perce deliberately set fire to steppe vegetation to improve the production of food resources and to provide grazing for their horses. Nez Perces reached relatively high population densities in the valley of the Clearwater River; this circumstance led Johnston to speculate that the region's resources could not have supported such high densities without resource management in the form of deliberate burning (Johnston 2000). Daubenmire (1970:7), on the other hand, reached the opposite conclusion. He suggested that since there were no large herds of game animals that could be concentrated by fires and "fire is of little use in warfare when villages are along rivers, the aborigines had little incentive to burn steppe." Similarly, Tisdale (1986:35) suggested that the scarcity of game and lack of shrub encroachment in canyon grasslands of Idaho "may have largely removed motivation for such action." Kaiser also thought that the Indians of eastern Washington rarely burned upland vegetation. His reasoning was based on the large amounts of organic matter in the deep, fertile Palouse soils, which he believed could not have accumulated if aboveground vegetation had been removed by frequent fires (Kaiser 1961). However, many intermountain steppe plants have extensive, deep root systems (Weaver 1917), which contribute large amounts of organic matter to the soil when they decay (Figure 3). Most of this underground biomass is not affected by burning, so the presence of soils high in organic matter tells us little about past fire regimes.

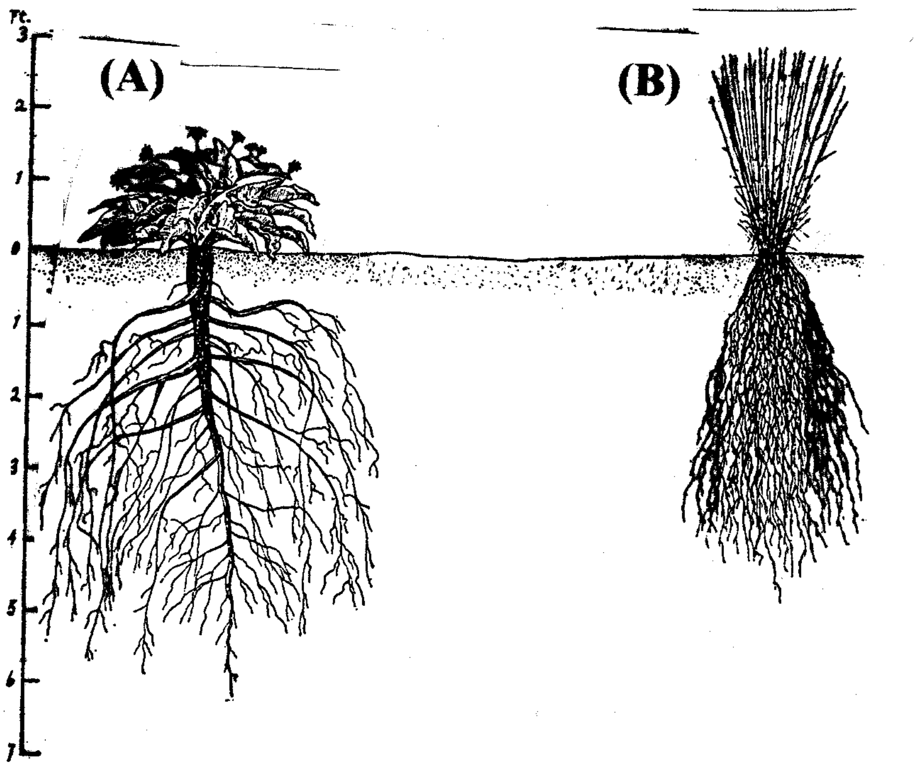

Figure 3. Roots of arrow-leaf balsamroot (A) and bluebunch wheatgrass (B). (After Weaver 1917.) Vertical scale is in feet.

In addition to this speculation, there is some specific data on the question of anthropogenic fires in northern intermountain steppes. During his ethnographic studies, Marshall was told by informants that the Nez Perce periodically set fire to grasslands for a variety of purposes, including enhancing the quantity and quality of food plants, improving winter habitat for elk, and concentrating game (Marshall 1977, 1999 and personal communications, May 8 and January 30, 2001). This is consistent with data from microscopic charcoal in the Blue Lake sediments, which indicate that light surface fires became more prevalent in the vicinity of Craig Mountain about 700 years ago when Nez Perce activity in the area intensified (Smith 1983).

Thus, data from anthropological studies and sediment cores suggest that Native Americans in the northern intermountain region did set fire to steppe environments. The frequency and intensity of these fires are not known, however.

2.2. Fire regimes after the arrival of Euroamericans

The arrival of Euroamericans in the Intermountain West brought far-reaching changes in land use and disturbance regimes. Agricultural burning, sparks from trains, and carelessness may have initially increased the frequency of fires. On the other hand, livestock grazing decreased the amount and continuity of fine fuel and therefore tended to decrease fire frequency. The drastic reduction in the area influenced by traditional Native American lifestyles probably also contributed to a reduction in fire frequency. Finally, the suppression of fires in accessible habitats also decreased fire frequency (Gruell 1983). It is doubtful that fire suppression would have been effective in the steeper canyons, however.

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3. Effects of burning on northern intermountain steppe

3.1. Effects of burning on vascular plants

3.1.1. Perennials

The responses of plants to fire depend upon species, weather, and fuel accumulations, as well as timing, intensity, and frequency of burning. The large number of relevant variables is one reason for apparent inconsistencies in the scientific literature on the effects of fire. To complicate matters, the parameters that are measured do not necessarily reflect the conditions experienced by burned plants. For instance, because the soil surface is typically darker and warmer on burned sites than on unburned sites, the former are generally phenologically advanced in comparison to unburned sites. Yet this is rarely taken into consideration when burned and unburned "controls" are compared (Daubenmire 1968*a*). Similarly, studies of the effects of fire intensity often report ambient temperature, but it is the temperatures of burning plant tissue that are ecologically important (Wright and Bailey 1982).

In steppe associations, Idaho fescue and needle-and-thread (*Hesperostipa comata*, formerly *Stipa comata*) tend to be damaged by fire and to recover relatively slowly, whereas damage to bluebunch wheatgrass, Sandberg bluegrass (*Poa secunda*), and prairie junegrass (*Koeleria macrantha*, formerly *Koeleria cristata*) is often relatively slight, and these species may be stimulated after burning (Daubenmire 1975; Tisdale 1986; Johnson and Simon 1987; Johnson 1998). Similar differences in susceptibility have been observed in shrub steppe vegetation (Blaisdell 1953; Pechanec et al. 1954; Moomaw 1956; Mueggler and Blaisdell 1958; Wright and Klemmedson 1965; Conrad and Poulton 1966; Harniss and Murray 1973; Uresk et al. 1976, 1980; Nimir and Payne 1978; Clifton 1981; Kuntz 1982). (See Wright et al., 1979 and http://www.fs.fed.us/database/feis/plants/graminoid/ for reviews.)

Bunchgrasses grow in compact tufts of densely clustered culms. Their meristematic tissue is in the form of buds located near the soil surface, and new growth is produced by the formation of new lateral shoots, or tillers, rather than by rhizomes. Since they lack rhizomes, caespitose grasses reproduce from seeds. These traits make them particularly vulnerable to damage from fire. Their densely clustered culms and leaves create compact bundles of fuel that may smolder for hours, and the resulting prolonged exposure to heat can damage plant tissue (Conrad and Poulton 1966).

Steppe vegetation generally burns at lower temperatures than vegetation dominated by shrubs or trees (Bailey and Anderson 1980). Bunchgrasses that have spreading leaves are less likely to be damaged by fire than species that form compact clumps. Because open clumps burn quickly, little heat is transferred to the soil surface, and the basal meristems of species with loose clumps are likely to survive. Bluebunch wheatgrass, which has an open growth form, is less likely to be harmed by fire than Idaho fescue, which has compact tufts that are severely damaged by burning (Conrad and Poulton 1966). In experiments in which Idaho fescue and bluebunch wheatgrass plants were burned at controlled temperatures, Idaho fescue plants subsequently developed damaged leaves, presumably because of destruction of meristematic tissue, but bluebunch wheatgrass did not (Defossé and Robberecht 1996). In addition, bluebunch wheatgrass buds are located slightly below ground level, which gives them some protection from fire (Antos et al. 1983).

Similarly, bottlebrush squirreltail (*Elymus elymoides,* formerly *Sitanion hystrix*) has features that make it resistant to fire, whereas the characteristics of needle-and-thread make it vulnerable to fire. Squirreltail tussocks have low density and burn quickly. Needle-and-thread forms denser bunches, which burn at higher temperatures and continue to burn long after a passing fire ignites the outer leaves. As a result, needle-and-thread plants are likely to be killed by fire, but meristematic crown tissue of burned squirreltail plants generally survives (Wright 1971; Young and Miller 1985).

It has also been suggested that grass clumps which have become elevated or “pedestaled,” either because of overgrazing or age, are particularly vulnerable to fire because their roots are exposed. This phenomenon has been reported in Sandberg bluegrass (Young 1943; Wright and Klemmedson 1965; Clifton 1981).

The position of seeds and buds and the amount of moisture they contain likewise influence susceptibility to fire. In general, the higher these organs are, the more likely they are to be damaged. Plants that burn before seeds have been shed suffer more damage than plants that have dropped their seeds, because seeds that are held aloft are exposed to more intense heat.

Seeds that are beneath a layer of litter are less likely to be damaged than seeds exposed on bare ground, and seeds lying on the soil surface are more vulnerable than seeds that are partially buried (Daubenmire 1968*a*). Managers can take advantage of this fact to burn exotic species when their seeds will be most vulnerable. For instance, burning medusahead (*Taeniatherum caput-medusae*) while seeds are still in the head is more effective than burning plants that have dropped their seeds (McKell et al. 1962).

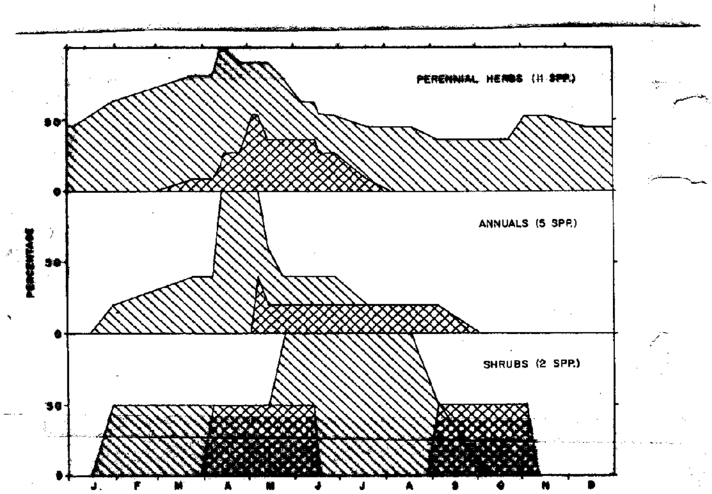
Like perennial bunchgrasses, the forbs and dwarf shrubs of steppe and meadow steppe respond to fire in various ways depending on their growth form and phenology. Forbs that are able to regenerate from underground organs are usually not harmed by fire. Those with buds or rhizomes below the mineral soil surface or with taproots that can regenerate from below their crowns are most resistant to fire, especially if it occurs during the summer drought (McLean 1969; Antos et al. 1983). For example, arrowleaf balsamroot (*Balsamorhiza sagittata*) has a deep taproot (Figure 3) and often increases after burning, although repeated fires can cause severe crown injury that nevertheless prevents regeneration (Young 1943; Johnson 1998). Rhizomatous forbs generally increase after burning, whereas woody-based (suffrutescent) forbs are slow to recover (Blaisdell 1953). Daubenmire noted an instance in which prairie star (*Lithophragma*) increased after a fire swept through a bluebunch wheatgrass–Idaho fescue stand the preceding fall, and attributed this to dormant bulbils or seeds in the soil "that are far more abundant in virgin grassland than would appear from the normal populations" (Daubenmire, unpublished notes for steppe stand no. 41, Gooseneck Ridge, available at Washington State University Library, Manuscript, Archives, and Special Collections).

In general, burning favors herbaceous vegetation at the expense of trees and shrubs (Vogl 1974), but there is little evidence that fire limits the distribution of shrub or trees in steppe and shrub steppe. This is not surprising since snowberry and other low shrubs of meadow steppe resprout readily from rhizomes and return to their prefire state within three years (Daubenmire 1970; Kinateder 1998), and limited soil moisture in summer prevents trees from becoming established in this zone even in the absence of fire (Daubenmire 1968*b*).

In shrub steppe associations, the major shrubs are killed by fire, and responses to fire are influenced by loss of the sagebrush overstory. The death of the overstory dominants releases resources for grasses and forbs on burned shrub steppe sites, whereas this is not the case in true steppe or meadow steppe. For this reason, the contrast between the prefire and postfire environments is far greater in shrub steppe than in steppe, and comparisons between responses to fire in these two types of vegetation should be made with care.

Phenology also affects vulnerability to fire. Seasonal activity patterns are especially important in the intermountain region, where moisture and temperature do not peak at the same time. Because moisture is available during the cooler months, many steppe plants are dormant in summer but photosynthetically active from autumn through spring (Daubenmire 1972). This was noticed by early botanists who visited the region. Geyer remarked that native grasses renewed their growth "about the middle of September, during a series of wet, foggy cloudy days," and even after the first frosts they continued to "grow a little" (Geyer 1846:287 footnote). Daubenmire estimated that about half the perennial herbaceous species in the bluebunch wheatgrass-Sandberg bluegrass association and one third of the species of perennial herbs in the Idaho fescue/common snowberry association produce new foliage at the beginning of the rainy season and remain photosynthetically active throughout the winter (Daubenmire 1970) (Figure 4).

(A)



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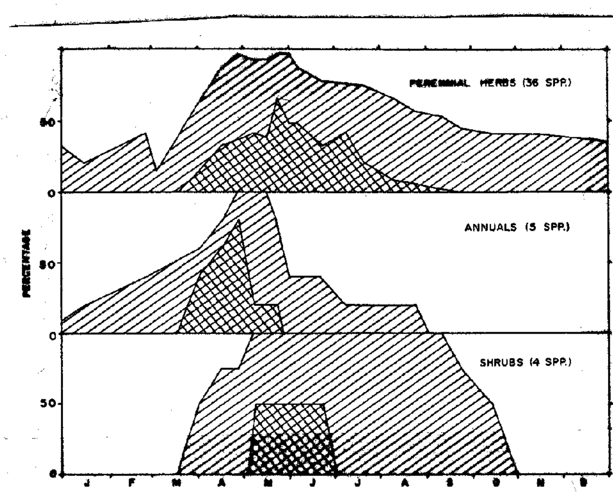

Figure 4. Phenology of native herbaceous species in an Idaho fescue/common snowberry association (A) and a bluebunch wheatgrass-Sandberg bluegrass association (B) in eastern Washington. Diagonal lines = actively growing; cross-hatching = pollinating. (After Daubenmire 1970.)

Burning is most damaging if it is conducted when plants are metabolically active. In regions with summer drought, this means that burning during the cool season entails a risk of damaging native perennials. Caespitose grasses typically produce tillers after the summer resting period. For example, bluebunch wheatgrass resumes growth slightly before rain moistens the soil of the root zone (Daubenmire 1972). Tillers become visible several weeks later and produce two or three fully expanded leaves by winter (Mueller and Richards 1986). These tissues are vulnerable to fires in autumn, winter, and spring, when they are photsynthetically active. The phenology of Idaho fescue is particularly advanced in comparison to other perennial grasses (Borman et al. 1990), which makes it especially vulnerable to early spring burning.

The annual cycles of a plant's energy reserves also affect its susceptibility to fire. It has been suggested that burning is especially detrimental if it occurs when carbohydrate reserves in underground storage organs have been depleted to produce foliage or fruits (Wright and Klemmedson 1965; Daubenmire 1968*a*; Beardall and Sylvester 1976).

Most natural burns of intermountain steppe vegetation would have occurred in mid or late summer, when the vegetation contained little moisture and lightning strikes were likely. We would expect native plants that evolved under this disturbance regime to have adaptations allowing them to survive late summer fires, and in fact they do. Most herbaceous plants are dormant at this time, so their aboveground tissues are not damaged by burning, and they regenerate readily from underground organs. For these reasons, late summer fires cause minimal damage to many native species (Daubenmire 1968*a*).

Native Americans were more likely to set fires in spring and fall than in summer, however. It is not clear to what extent these intentional burns had selected for adaptations to spring and fall burning.

3.1.2. Annuals

Annual forbs and grasses increase following fire if sufficient seeds survive or if a source of seeds is nearby. A few of these increasers, such as tall annual willowweed (*Epilobium brachycarpum,* formerly *paniculatum*), are native, but most are not. When livestock grazing and agriculture increased the frequency and the size of disturbances in the intermountain region, these changes favored European annuals such as cheatgrass or downy brome (*Bromus tectorum*), which had evolved with agriculture and livestock grazing (Mack 1981, 1986, 1988). The native grasses, on the other hand, were not well adapted to the new disturbance regime because they had never evolved adaptations to large-scale grazing and trampling. Although some large ungulates are native to intermountain steppes, huge herds of massive grazing mammals never roamed the region, so the dominant grasses did not evolve under the kind of grazing pressure that guided the evolution of steppe grasses exposed to bison herds in the Great Plains. The exotic species that were accidentally or deliberately introduced from Eurasia, however, had evolved with frequent and widespread disturbances and were able to exploit the newly disturbed environments (Tisdale 1961, Daubenmire 1970, Mack and Thompson 1982, Mack 1986).

Initially, cheatgrass colonized only sites that had been disturbed by grazing, farming, fires, or other events that removed native vegetation, but eventually cheatgrass became so ubiquitous that it was even able to invade relatively pristine sites (Mack 1986; Brandt and Rickard 1994). Once established, cheatgrass affects native species unfavorably by successfully competing with them for moisture (Melgoza et al. 1990).

More recently, other alien annual grasses, such as medusahead (Torell et al. 1961), and forbs, such as yellow star-thistle (*Centaurea solstitialis*), have become serious problems (Kiemnec and McInnis 1994) in intermountain steppes. These exotics have the potential to increase flame lengths (Dick Walker, personal communications, January 26 and 31, 2001) and to alter fire frequency and intensity.

3.1.3. Rare plants

Over a dozen rare plant taxa, many of them endemics, occur in the northern intermountain steppes (Hill 1995*a*,*b*, 1996, Hill and Gray 1998*a*,*b*; Weddell and Lichthardt 1998). Like other plants of the region, these species evolved under the selective pressures exerted by the historical fire regime. The specific effects of fire on their demography are not well understood, however.

One species of particular concern is Spalding's catchfly, *Silene spaldingii*, a perennial forb that has been proposed for listing as federally threatened (Federal Register 64(232), December 3, 1999). In the Tobacco Plains of northwest Montana, at a site dominated by Idaho fescue and rough fescue (*Festuca altaica* ssp. *scabrella*, formerly *Festuca scabrella*), burning was followed by enhanced Spalding's catchfly recruitment (Lesica 1999). This effect was more pronounced with spring burning than with fall burning and was attributed to the removal of litter and creation of safe sites for germination. Fire might not have similar results in steppe habitats to the west of that study, however. The Tobacco Plains site is transitional between intermountain steppes and the steppes of the northern Great Plains, a region which is ecologically quite different from the intermountain region. Rough fescue is a coarse grass that produces "thick mats of persistent sheaths and culms bases" (Hitchcock et al. 1994:587), which create large amounts of litter that decomposes slowly. For these reasons, burning might have quite different effects on Spalding's catchfly populations east and west of the Rocky Mountains.

3.2. Effects of burning on microbiotic crusts

Many investigators have reported that in arid and semiarid environments burning decreases the biomass and cover of microbiotic crusts and alters their species composition (Countryman and Cornelius 1957; Antos et al. 1983; Schulten 1985; West and Hassan 1985; Johansen et al. 1984, 1993; Johansen and St. Clair 1986; Kaltenecker and Wicklow-Howard 1994; Johnson 1998; Youtie et al. 1999). (See Johansen and Rayburn 1989, West 1990, and St. Clair et al. 1993 for reviews.) On sites dominated by Idaho fescue, mosses and lichens located beneath bunchgrass tufts have especially high mortality (Johnson 1998), perhaps because of the high temperatures generated in the compact crown of this species. (See Section 3.1.1.) Soil algae typically recover after several years, but the recovery of mosses and lichens may take decades or centuries (Belnap 1993). Since the microbiotic crust affects soil texture and infiltration, nitrogen fixation, carbon cycling, plant nutrient status, and seedling establishment, its destruction has far-reaching consequences (Evans and Johansen 1999). Aggregations of dead crustal material persist initially, but eventually they disintegrate, exposing the soil surface to wind and water erosion and to weed invasion (Johansen and Rayburn 1989). In addition, nutrient and hydrological cycles are altered.

3.3. Effects of burning on plant community composition

In forested landscapes, where light is a limiting factor, fire sets back succession, creating openings that can be colonized by pioneer species of seral communities. There is little evidence for fire-maintained species or communities in intermountain steppes, however. Neither Daubenmire (1970) nor Tisdale (1986) felt that historic fires had been a major force determining the composition or distribution of steppe communities in eastern Washington and west-central Idaho. Burning certainly favors some species over others and creates openings that can be exploited by pioneer species, but before the arrival of exotic grasses and forbs from Eurasia, the increases in ruderal species that followed burning probably lasted only a few years.

Burning decreases litter, and this can increase opportunities for seedling establishment. (See Section 3.1.3.) This effect is short-lived where annuals invade burned sites, however. In northeastern Oregon, burning decreased litter initially, but within a few years litter exceeded preburn levels because of the additional biomass contributed by annuals (Johnson 1998).

Native perennial bunchgrasses are susceptible to damage by fire because their meristematic tissues are exposed near ground level, they grow by means of tillers rather than rhizomes, and they reproduce by seeds. In addition, species that form very compact tufts and are phenologically advanced are especially susceptible. Idaho fescue has all of these characteristics.

Perennial forbs and shrubs that are able to regenerate from underground storage organs usually recover from burning. Native perennials are least vulnerable to fire when they are dormant, in summer. This is when most naturally started fires would have occurred in the past.

There is evidence that seedling recruitment in the rare Spalding's catchfly increases when communities dominated by rough fescue are burned. This is thought to be due to the removal of litter by fire. In intermountain steppes, where less litter is produced, it is less likely that litter limits recruitment.

Fire damages microbiotic crusts, and the recovery of crusts after burning may take years or even centuries. Annuals increase after fires if enough seeds survive to repopulate a site or if they can colonize it. Before the arrival of Eurasian annuals with superior adaptations for colonizing disturbed sites, these postfire changes in community composition were transient, but this is no longer the case.

4. Exotic species and changing fire regimes

As early as 1932, Pickford noted a positive feedback between fire frequency and cheatgrass invasion: "On promiscuously burned areas which have long been protected from grazing . . . burning tends to deplete the stand of perennial grasses and to allow annual grasses, chiefly downy brome, to increase sharply in density" (Pickford 1932:171). In addition to displacing native species and causing a decline in forage quality, this shift in species composition has another serious consequence: cheatgrass increases the fire hazard because it provides large amounts of fine, highly flammable fuel. This in turn favors cheatgrass and other fire-adapted species (Peters and Bunting 1994). The destruction of the microbiotic crust by fire also favors disturbance-adapted species. In a cultivated field that was abandoned in 1920 and subsequently burned, cheatgrass became dominant by the second postfire season and remained so for at least 52 years (Daubenmire 1975).

The ubiquity of Eurasian annuals with superior ability to exploit disturbed areas has changed the consequences of fire in intermountain steppes. Cheatgrass and other alien annuals increase the supply of fine fuels, thereby increasing the likelihood of fires, a change which further favors annual exotics. Fire now "alters the biotic and abiotic factors enough that the plant community crosses a threshold from a perennial-dominated to an annual-dominated community" (Tausch et al. 1995:252).

After cheatgrass colonizes burned sites, it increases the supply of fine fuel, which promotes additional fires and leads to further increases in non-native species at the expense of natives.

5. Conclusions

Fire has effects at many levels of organization. After reviewing the effects of prescribed burning on an endangered forb of wetland prairies in the Willamette Valley, Pendergrass et al. (1999:1420) concluded that "the consequences of reintroducing burning must be considered at all ecosystem levels. A fire regime that is beneficial at one level of organization may be neutral or even detrimental at other scales, and managers need to be aware that potential benefits for one species or community may disadvantage others."

Although restoring natural disturbance regimes is generally considered desirable, exotic species complicate the picture. Because species vary in their responses to burning, fires favor some species over others. Where aggressive, disturbance-adapted exotic species are present, fire can promote their establishment (Christensen and Burrows 1986; Hobbs and Huenneke 1992), and once invading species become established they may alter many properties of ecosystems, including their disturbance regimes (Vitousek 1990; D'Antonio and Vitousek 1992). In some cases, changes in species composition following fire lead to irreversible changes that prevent a return to the predisturbance community. This scenario differs from conventional models of succession, in which fire sets back succession and is followed by a predictable sequence of stages culminating in the re-establishment of a climax community. Rather, the introduced species create a new stable state. This appears to be the case when cheatgrass comes to dominate intermountain steppes (Tausch et al. 1993, 1995).

These circumstances create a dilemma for managers of intermountain steppes. Attempts to restore a natural ecosystem process to the landscape through prescribed burning may have unintended consequences. Given the ubiquity of exotic annual forbs and grasses, fire is likely to favor the spread of non-native species at the expense of natives. This means that managers must decide which species they wish to manage for, and consider carefully the consequences of increasing the level of disturbance in an environment within which exotics are poised to take advantage of disturbance (Fox and Fox 1986), especially if populations of rare taxa could be harmed by the encroachment of annuals.

Efforts to restore fire to northern intermountain steppes should be evaluated carefully, for two reasons. First, it is not clear that the intermountain steppes have suffered dramatic negative consequences as a result of a change in fire frequency. While it seems likely that fires now occur less often than they did prior to the arrival of Euroamericans, we do not know the magnitude of that change in frequency or its consequences. Second, the benefits of burning are equivocal. There are some situations where the removal of accumulated litter may benefit native plants, but these benefits must be weighed against the risk that increases in exotic annuals will lead to irreversible losses of native vegetation.

The fire ecology of intermountain steppe is influenced by its distinctive physiognomy and phenology. Although dry forests were negatively impacted by fire suppression, the evidence for a similar situation in steppe communities, which have much lower fuel loads, is less compelling. Furthermore, burned stands of native steppe vegetation are vulnerable to invasion by cheatgrass and other annual exotics, an event which can irreversibly alter community composition.

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