Livestock Grazing and Weed Invasions in the Arid West

by

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and
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Executive Summary

Nonindigenous plants (also referred to as alien, exotic, or introduced weeds) are invading arid and semi-arid grasslands, shrublands, and woodlands of the American West at an exponential rate. Management efforts intended to control their spread have been largely ineffective. This may be due to a lack of attention to domestic livestock grazing, the dominant land use of the region.

The contribution of livestock grazing to weed invasions has generally been downplayed while the effects of drought, historic overgrazing, fire, and seed introductions associated with outdoor recreation, roads, and wildlife have been emphasized. In this paper, we review the scientific literature relating livestock grazing to the invasion of nonindigenous plant species in the arid and semiarid lands west of the Rocky Mountains.

At the landscape and regional scales, livestock grazing is one of several factors causing and enhancing the invasion of alien weeds into grassland, shrubland, and woodland communities; but at the community scale, livestock may be the major factor causing these invasions. Most studies find that plant communities grazed by domestic livestock contain a greater density, frequency, or cover of nonindigenous plants than ungrazed communities. A few studies document positive, but only temporary, reductions of weed numbers by sheep and goats, but most weedy species are avoided by cattle.

Livestock contribute to alien weed invasions by:

(1) transporting weed seeds into uninfested sites on their coats and feet and in their guts,

(2) preferentially grazing native plant species over weed species,

(3) creating patches of bare, disturbed soils that act as weed seedbeds,

(4) destroying microbiotic crusts that stabilize soils and inhibit weed seed germination,

(5) creating patches of nitrogen-rich soils, which favor nitrogen-loving weed species,

(6) reducing concentrations of soil mycorrhizae required by most western native species, and

(7) accelerating soil erosion that buries weed seeds and facilitates their germination.

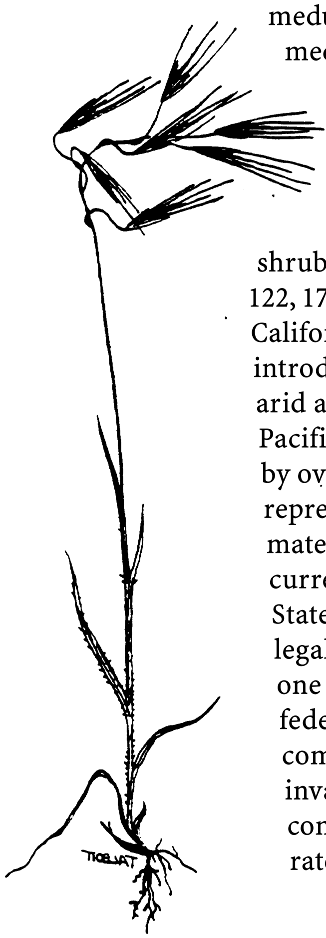
This review suggests that nonindigenous weeds will continue to spread through arid and semi-arid grasslands, shrublands, and woodlands in the western United States unless selective grazing, nutrient redistribution, and soil disturbances by livestock are greatly reduced or eliminated.

At the community scale, livestock may be the major factor causing weed invasions.

Introduction

Invasive, nonindigenous plants, also referred to as alien, exotic, or introduced weeds (i.e. species that have been moved beyond their natural range by humans (178)), are spreading through public and private grasslands, shrublands, and woodlands of the arid and semi-arid West at a rapid, and in some areas exponential, rate (65, 155). As a result, the region's native plant communities are being severely degraded.

Alien annual grasses such as cheatgrass (Bromus tectorum) and medusahead (Taeniatherum caput-medusae) and forbs such as the starthistles and knapweeds (Centaurea spp.) and leafy spurge (Euphorbia esula) have invaded over 40 million ha of western grasslands, shrublands, and woodlands (30, 104, 122, 173). Large, low-elevation areas of California are currently dominated by introduced annual grasses (14), and arid and semi-arid portions of the Pacific Northwest have been invaded by over 860 exotic plant species (65), representing over 20% of the estimated 3,700 alien plant species currently recorded in the United States (178). Of these, 115 have been legally declared "noxious weeds" by one or more states (65). In spite of federal, state, and local activities to combat spread of these weeds, weed invasions into western plant communities continue at epidemic rates (155).



Cheatgrass
(Bromus tectorum)

These findings are of serious concern because nonindigenous species are suspected of being the second main cause, following loss of habitat, for the listing of all threatened and endangered species in the United States (57, 177). According to a recent survey by Wilcove et al. (177), alien species have contributed to the endangerment or extinction of 33% of at-risk plant species. Additionally, invasions that alter the biological landscape constitute a significant component of global environmental change (168). Introduced weeds alter western ecosystems by increasing fire frequency (30, 36, 173), reducing biodiversity (126, 137, 178), reducing wildlife habitat (18, 90), disrupting nutrient cycling and hydrology (167), increasing topsoil loss (94), and altering soil microclimate (53). Long-term monitoring suggests that some weed-altered arid and semi-arid communities may never recover, even with the cessation of all anthropogenic disturbance (30, 31, 180).

Nonindigenous species are suspected of being the main cause following loss of habitat for the listing of all threatened and endangered species in the United States.

The rapid spread of nonindigenous plants in the West, estimated at 2,200 ha (5000 ac) per day on western federal lands (155) or 14% annually (158), indicates that weed management strategies currently used by federal land-management agencies have been largely ineffective (65, 155).

While most weed scientists and federal agencies conclude that the most effective and least expensive way of managing introduced plant species is to prevent new infestations (e.g. 79a, 140, 155, 163, 178), recent weed management plans and agency publications (e.g., 12, 65, 154, 155, 156, 157, 158, 162, 163, see also 141) have given little attention to prevention. Instead, these publications emphasize weed control and eradication using herbicides, biological control, mechanical weed removal, fire prevention, and plowing. Prevention is often limited to exhorting hikers to clean their boots, asking drivers to wash off their vehicle undercarriages, and recommending that owners of pack animals use weed-free feed (e.g., 141, 154, 155, 156, 163).

The Missing Component

Missing from these federal management plans is a thorough analysis of the relationship between livestock grazing and weed invasions. Not only has grazing long been the dominant land use of most western grasslands and shrublands (58), but livestock grazing has also been a major use of western woodlands (23) and low- and mid-elevation forests (24). The 100->200-year history of livestock grazing in the American West is known to have degraded stream and riparian ecosystems, stripped uplands of native grasses, severely depleted herbaceous plants in all plant communities, increased erosion, and endangered native species (8, 9, 25, 58, 116, 121, 183). Evans and Young (53) noted that significant portions of the sagebrush-grasslands in the Great Basin have been degraded to the point that they produce less than 50% of their biological potential.

Numerous scientific papers have listed the influence of past and current livestock grazing on the spread and ever-increasing dominance of introduced weeds (e.g., 14, 18, 38, 45, 78, 91, 113, 183, 185, among others). In Washington State, for example, 84% of yellow starthistle (Centaurea solstitialis) and 80% of diffuse knapweed (Centaurea diffusa) populations are found on lands predominantly used for livestock grazing (135). However, these conclusions about the causal relationship between livestock and weed invasions have not been translated into effective weed control policies, nor even discussed in most agency educational materials.

Management plans for federal lands lack thorough analysis of the relationship between livestock grazing and weed invasions.

Livestock are not the only factors contributing to weed invasions in the West. Anthropogenic causes of soil disturbance such as outdoor recreationalists, off-road vehicles (ORVs), trucks, road construction, and logging; and natural causes such as wildfire, burrowing animals, wind, floods, and natural erosion enhance the vulnerability of communities to invasion. Resource availability (60, 77, 80, 146), distance to seed source (60, 146), drought (113, 148), and above-normal precipitation (50, 155) contribute to invasions at multiple spatial scales, while wildlife (48, 188), fire (173,187), soil chemistry, texture, and depth (80, 134, 182), and surface microclimate and microtopography (53) contribute to invasions at local scales. Rising levels of carbon dioxide in the atmosphere may also increase the growth rates of weedy annuals (44, 125).

The admitted lack of effectiveness of current federal weed prevention programs (65) can be traced to several causes. First, limited funds have been concentrated on weed control rather than on prevention (79a, 98). Second, unorthodox definitions of weed prevention, such as "early detection", "education, training, and inventory" (11) and "spot control" (162) have often been applied to weed management programs, rather than the more usual definitions of reducing the influx of weed seeds or reducing community vulnerability to invasion. Third, efforts have concentrated more on preventing the introduction and spread of weed seeds along roads and trails than on preventing activities that disturb soil surfaces and open plant communities to invasion. This is not to say that preventing invasions along roadsides is unimportant, since roads act as corridors for the movement of weeds into new regions and support high densities of nonindigenous plants. However, roadside disturbances are only part of the problem.

Recent BLM and US Forest Service plans to combat introduced weeds recommended neither significant changes in livestock management nor reductions in livestock numbers.

Finally, the ineffectiveness of current weed prevention programs in the arid and semi-arid West may result from insufficient attention being given to the multiple impacts of livestock grazing. Recent BLM and US Forest Service reports and management plans to combat introduced weeds (e.g., 157, 158, 162, 163) recommended neither significant changes in livestock management nor reductions in livestock numbers. In some cases, they even consider increasing livestock grazing in weed-dominated areas (157, 158, 163). Where changes in livestock management are considered, emphasis is on altering season of use by livestock or changing the grazing system, but little evidence is provided showing that these changes are effective. Surprisingly, some of the recommended grazing systems such as rest-rotation and time-controlled grazing have been found to favor weed growth (117, 183). In addition, changes in livestock management are usually recommended only after weed eradication programs are implemented, not before weeds have entered the community (e.g., 141, 163).

In this paper, we review the multiple influences of livestock grazing on invasions of nonindigenous plants in grasslands, shrublands, and woodlands of the American West. We include arid and semi-arid lands west of the Rocky Mountains, including California, but exclude the Sonoran, Mojave, and Chihuahuan Deserts of the American Southwest. Most of the studies discussed in this paper are from the described region, but papers from other regions are included if they describe general ecological factors not likely to differ among regions.

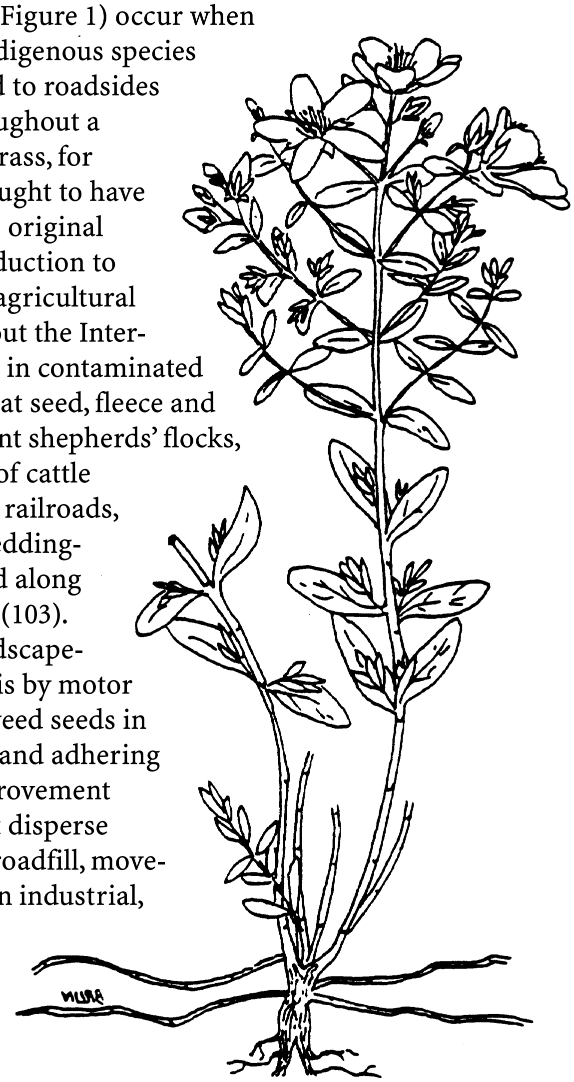
Weed Introductions at Different Ecological Scales

Inattention to the impacts of livestock grazing may be due, in part, to a confounding of ecological scale (7) by land managers. In this report, ecological scale refers to different levels of biological organization ranging from large, i.e. the continental or regional scale, to small, i.e. the local or community scale. Most federal land management plans concentrate on roadside invasions, thereby looking primarily at the landscape scale, not the full range of scales.

The invasion process begins with a regional-scale introduction of weed seeds and plant parts from overseas or distant geographic areas (Figure 1). Ships, trains, and trucks carry agricultural seed and animal feed contaminated with weed seeds over long distances, and weed seeds hitchhike in ship ballast, packing materials, and mud adhering to vehicles. Escape of introduced ornamental plants such as leafy spurge, Dalmation toadflax (Linaria dalmatica), and St. Johnswort (Hypericum perforatum) from gardens and parks and intentional introductions of alien species such as Johnsongrass (Sorghum halepense) have also led to widespread introductions (15, 105, 143, 175, 178). The introduction of cheatgrass into the western U.S. from southwestern Asia occurred both accidentally (in contaminated wheat seed) and deliberately (following a study to identify new grass species to reseed overgrazed rangelands in eastern Washington) (103).

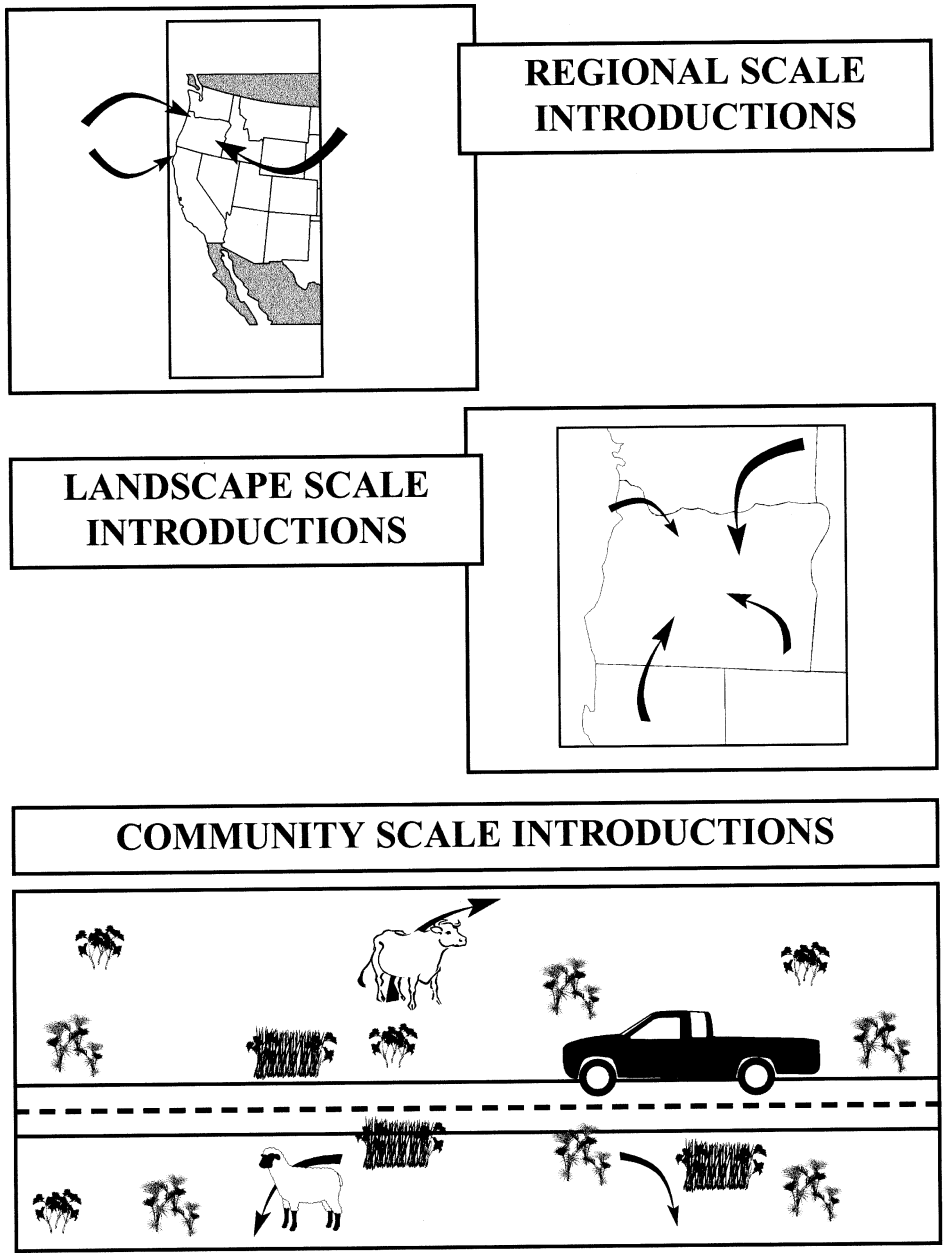
Introductions of alien species at the regional scale create localized points of infestation, usually around sea ports, train stations, and industrial sites frequented by commercial trucks, as well as in and surrounding agricultural fields and along major highways.

The second or landscape-scale introductions (Figure 1) occur when seeds of nonindigenous species are transported to roadsides and fields throughout a region. Cheatgrass, for example, is thought to have spread from its original points of introduction to roadsides and agricultural lands throughout the Intermountain West in contaminated alfalfa and wheat seed, fleece and dung of itinerant shepherds' flocks, dung and hair of cattle transported on railroads, and in cattle bedding-straw discarded along railroad tracks (103). Additional landscape-level dispersal is by motor vehicles with weed seeds in their radiators and adhering mud, road improvement operations that disperse contaminated roadfill, movement of unclean industrial, logging, and agricultural equipment (155), and



St. John's Wort (*Hypericum perforatum*)

FIGURE 1:
WEED INTRODUCTIONS AT DIFFERENT ECOLOGICAL SCALES



Introductions of nonindigenous plants at different geographic scales into arid and semi-arid shrublands, grasslands, and woodlands of the American West.

livestock trucks transporting animals from infested into uninfested areas (135). Flowing water, wind, and far-ranging birds also transport weed seeds throughout regions (133, 135). Landscape-level introductions typically result in infestations along secondary roads, throughout agricultural lands, and along the banks of streams and irrigation ditches (135).

At the third and smallest level, local- or community-scale introductions (Figure 1) occur where weed seeds are transported from travel corridors, agricultural areas, and stream banks onto adjacent plant communities. Natural vectors such as wind, flowing water, and native wildlife, and anthropogenic vectors such as livestock, hikers, ORVs , and agricultural equipment move seeds into and throughout native communities (133, 135, 138).

Livestock as Vectors of Nonindigenous Plants

Although weed seeds may be introduced into communities by natural vectors or recreationalists (133), the more than 20 million cattle and sheep grazing western grasslands, shrublands, and woodlands of the American West (160) may be the most pervasive factor moving seeds into and throughout plant communities. Unlike large wildlife species, which are sparse in the arid West (106), and outdoor recreationalists, who for the most part are restricted to trails, roads, and campgrounds, cattle and sheep are far-ranging; they reach all but the steepest slopes and areas farthest from water (38). While in some areas, Off Road Vehicles, mountain bikes, or hikers may be the dominant source of weed introductions, livestock are more likely the cause of weed introductions into non-recreational or remote areas away from roads or trails.

The effectiveness of livestock as weed seed vectors is illustrated by their ability to transport viable seeds in their hair and digestive tracks, and in mud on their feet (91, Table 1). One study found that in one grazing season, a single cow in a pasture in Alberta, Canada, redistributed over 900,000 viable seeds (42). Dore and Raymond (42) also reported that a single cow deposited an average of 37,000 viable seeds of late-season annuals in dung per day in the fall. The authors concluded that cattle were the most important dispersers of seeds of pasture species. In other studies, individual sheep were found to transport up to 17 viable leafy spurge seeds per day in their dung (119) and 14 viable halogeton (Halogeton glomeratus) seeds per 500

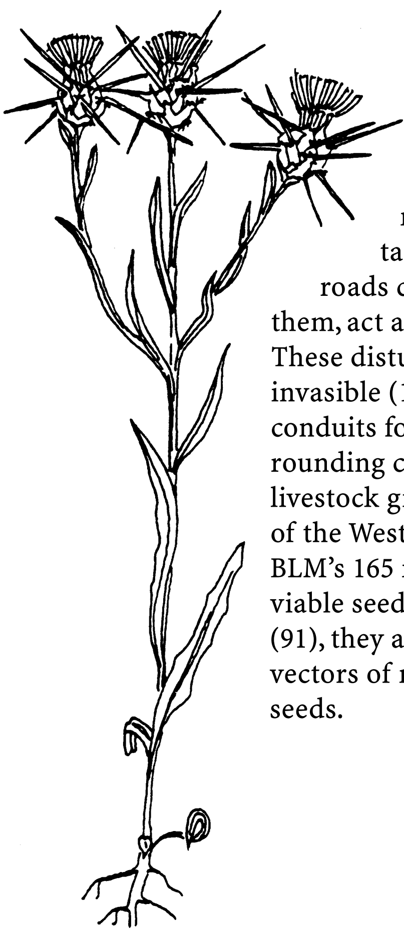
TABLE 1. Livestock as Vectors of Seeds of Nonindigenous Plant Species.

Animal Vector	Weed Species	Viable Seeds Transported	Citation Reference #
Cattle	Many	A maximum of 37,000 viable seeds/cow/day in dung	42
Cattle	Houndstongue	65% of burrs per stalk attach to cattle	40
Sheep	Halogeton	14 seeds/500g dung	91
Sheep	Knapweed species	Up to 17 seeds/sheep/day in dung; up to 39 seeds in fleece	119
Sheep	Squarrose knapweed	4.5 achenes per 10 grams wool from head	136
Sheep	13 non-indigenous species	In dung	74

Non-native weeds are most likely to invade sites that experience disturbances that differ in type or frequency from their natural disturbance regimes.

grams of dung (91). Sheep also carried an average of 39 leafy spurge seeds in their fleece (119). Cattle dispersed seeds of houndstongue (Cynoglossum officinale) on their heads, chests, and undersides, brushing them off on shrubs, poles and other animals (40).

By dispersing seeds into and throughout communities, livestock facilitate invasion of entire landscapes. In Australia, Brown and Carter (33) found the invasion of an alien shrub into a grassland to have been caused by a shift to cattle as the dominant livestock species. In addition, range developments such as water tanks and ponds, and the roads constructed to access them, act as loci for weed spread. These disturbed sites are highly invasible (129, 149) and act as conduits for invasion into surrounding communities. Given that livestock graze 70% of the land area of the West (164), including 94% of BLM's 165 million acres, and carry viable seeds for as long as ten days (91), they are undoubtedly major vectors of nonindigenous plant seeds.



Yellow starthistle (*Centaurea solstitialis*)

Livestock Grazing and the Invasibility of Arid and Semi-Arid Communities

For nonindigenous species to become important constituents of plant communities, not only must their seeds enter the communities, but the communities must be open to invasion. In other words, the communities must be invasible (127). The primary determinants of plant community invasibility are the number of safe sites for seed germination in the community (53, 68), the amount of plant cover or biomass (127), and perhaps resource availability (146). Community invasibility is enhanced by increases in soil disturbance (178), which aids seed establishment by creating safe sites for seeds and temporarily increasing soil nitrogen. Invasibility is also enhanced by reductions in plant cover, which reduce competition for limited resources (77, 78, 127). Crawley (34) and Rejmanek (127) found that the most invasible communities were those with low average levels of plant cover and frequent disturbance (see 17 for additional examples). Schiffman (139) concluded that nonindigenous plant species are most likely to invade sites that experience disturbances that differ in type or frequency from their natural disturbance regimes.

The rapid invasion of nonindigenous plants recorded throughout the West suggests not only that weed seeds are being transported into native grasslands, shrublands, and woodlands at high rates, but that these communities are highly invasible (30, 104, 106, 184). This invasibility can best be explained by low plant cover, which is common in arid and semi-arid regions; an absence of co-evolved predators, competitors, and parasites in the new environments; climates similar to those in the invasive species's area of origin; and exotic forms of disturbance.

Evolutionary Vulnerability

Grasslands, shrublands, and woodlands west of the Rocky Mountains may be more vulnerable to disturbances by domestic livestock and to weed invasions than other regions. For thousands of years prior to the arrival of livestock, large grazers were sparse in the Intermountain West and California (14, 79b, 106, 109, 112, 121, 169). Native herbivores such as deer, elk, and pronghorn are not thought to have been abundant enough to have exerted strong selective pressures on native grasses and broadleaved herbaceous species (38, 104, 113). Thus, the introduction of domestic livestock in the 1800s added a new type of perturbation to western ecosystems, e.g. heavy grazing and trampling (79b, 106, 139). In the classic discussion of this topic, Mack and Thompson (106) concluded that unlike grasses of the Great Plains, which evolved under thousands of years of intense grazing by American bison, bunchgrasses west of the Rocky Mountains were only lightly grazed. Consequently, these species evolved little tolerance of intense grazing and trampling, causing them to be highly sensitive to the actions of introduced cattle and sheep. As a result, within 20-40 years of the beginning of livestock production west of the Rockies, many western grasslands and shrublands were reported to be severely damaged (73, 103,189).

Unlike grasses of the Great Plains, bunchgrasses west of the Rocky Mountains evolved with little tolerance for intense grazing and trampling, causing them to be highly sensitive to introduced cattle and sheep.

Livestock Disturbances

Livestock increase the invasibility of plant communities by disturbing vegetation and soils (138) and by altering ecosystem processes such as fire frequency and nutrient cycling (10, 79a). These impacts act together to increase community invasibility.

1) Selective Grazing

A major cause of increased community invasibility is selective grazing by livestock (14, 45, 91, 117b, 183). Livestock, especially cattle, preferentially graze native plant species while avoiding most weeds, which are poor forage and have low palatability due to toxins, spines, and distasteful compounds (17, 34, 91, 117, 166, 181). As a result, the size, density, and competitive vigor of native plants are reduced while weedy species are released from competition (18, 91, 101, 117, 142). With continued livestock grazing, native species decline in density and cover, leaving bare patches that are readily colonized by weedy annuals (48, 72, 129).

Most studies suggest that livestock grazing leads to reductions of native species while pastures become increasingly dominated by alien species.

Examples of declines in vigor by native species and increases in density of nonindigenous species are numerous (Table 2). In Utah, individual plants of cheatgrass, halogeton, and Russian thistle (Salsola pestifer) were larger, sometimes by an order of magnitude, in heavily grazed communities than in ungrazed communities (71); and three years of repeated sheep grazing in Montana significantly reduced shoot and root biomass of the native bunchgrass, Idaho fescue (Festuca idahoensis), but had no effect on spotted knapweed (Centaurea maculosa) (118). Clipping studies (which duplicate grazing studies but without the trampling) of two bunchgrasses and two sod-forming grasses in eastern Washington resulted in significantly higher numbers of yellow starthistle in clipped than unclipped plots (134); while a single clipping of Idaho fescue (30% or 90% of shoot removed) increased spotted knapweed biomass and numbers (81). In a follow-up study, Jacobs and Sheley (82) found that clipping bunchgrasses more than once on a grass-dominated site reduced cover and density of the grasses but increased the cover of knapweed. Although not all species and habitats have been rigorously tested, most grazing and clipping studies (Table 2) suggest that livestock grazing leads to reductions of native species while pastures become increasingly dominated by alien species.

2) Trampling

Trampling also increases plant community invasibility (78, 104, 129). Through hoof action, livestock damage biological soil crusts, create safe sites for weed seeds, increase soil nitrogen levels, and create competition-free patches of bare ground that are open to invasion (48, 77, 78, 129, 137, 138). Trampling can also injure the shoots of native plants (171), reducing their competitive and reproductive capacities. The most severe effect of trampling may be compaction of soils, which damages plant roots (171) and causes roots to

TABLE 2. IMPACTS OF LIVESTOCK GRAZING ON INVASIVE, NONINDIGENOUS PLANT SPECIES.

LOCATION	GRAZER	EFFECT OF GRAZING	REFERENCE #
California	Cattle	Medusahead was abundant on grazed but not ungrazed stands that were high in clay	147
Nevada	Cattle, sheep, horses	Cheatgrass, peppergrass, and halogeton increased "to an extreme degree" during 50 years of grazing	131
Oregon	Cattle, sheep	Cheatgrass cover and density were extremely low on a relict site but had up to 11% cover and 254 plants/m^2 on grazed sites	62
Washington	Cattle, sheep	In undisturbed vegetation, cheatgrass was sparse and the plants dwarfed	38
Washington	Cattle	After three years light grazing, cheatgrass and tumblemustard invaded areas where cattle congregated	129
Montana	Livestock	Ungrazed rough fescue and bluebunch wheatgrass communities were "fairly resistant" to invasion by diffuse knapweed	93
British Columbia	Cattle	Knapweed cover on a site sprayed with herbicide was higher in grazed than ungrazed plots	107

become more concentrated near the soil surface (43). These changes may prevent native plants from acquiring sufficient resources for vigorous growth

Soil compaction by large grazing mammals also locally reduces populations of soil decomposers and lowers soil hydrologic conductivity, aeration, and redox potential (20, 43, 174), changes that appear to favor weedy species over native bunchgrasses (41, 20). Rickard (129) recorded the effects of livestock trampling in Washington State, where he found that cheatgrass and tumble mustard (Sisymbrium altissimum) invaded a trampled grassland, but not nearby untrampled grasslands. In another study, the cover of introduced species in a site trampled by humans in Utah was significantly greater than in undisturbed sites (20).

Where livestock reduce vegetative cover and disturb soil surfaces, they also increase wind and water erosion (21, 43, 48, 102, 174). Soil movement resulting from erosion often buries weed seeds with loose soil particles, increasing the probability of their germination (51). Evans and Young (51) found that cheatgrass emergence was 30 times greater, tumblemustard emergence 20 times greater, and medusahead emergence eight times greater when their seeds were buried 1 cm deep than when their seeds were broadcast on a smooth soil surface. Fall grazing is especially conducive to cheatgrass invasion since livestock are more likely to bury cheatgrass seed in the soil profile when soil surfaces are dry (R. Rosentreter, pers. comm.). Thus, disturbances that loosen surface soils may increase nonindigenous plant invasions.

Native wildlife species such as gophers, ground squirrels, and deer also disturb soils and create bare patches. Although sometimes implicated in the spread of invasive species into intact communities (e.g. 153), native species do not appear to be major causes of community invasibility (139). Grasslands and shrublands that have long been protected from livestock disturbance, such as the US Department of Energy's Hanford Site in eastern Washington and a semi-isolated plateau known as The Island in central Oregon, still posses their native wildlife species but, except along roads, are relatively free of nonindigenous plant species (62, A.J. Belsky, personal observation). This difference between wildlife and livestock impacts may be, as Schiffman (139) discusses, due to native wildlife species creating disturbance types that are "evolutionarily and ecologically usual" while livestock create disturbances that differ in type, frequency, and intensity from the normal disturbance regimes. Holland and Keil (79b) and Archer and Smeins (10) similarly concluded that native herbivores such as elk, pronghorn antelope, and deer differ from livestock in their impacts on the vegetation by having different grazing patterns. They noted that native wildlife graze an area and then move on, allowing the vegetation to recover, while domestic livestock graze the same area repeatedly. In addition, livestock, but not native grazers, graze bunchgrasses down to their bases, damaging their growing buds.

Native wildlife create disturbance types that are "evolutionarily and ecologically usual" while livestock create disturbances that differ in type, frequency, and intensity from normal disturbance regimes.

3) Impacts on Soil Crusts

Microbiotic crusts (also referred to as biological, cryptobiotic, cryptogamic, or microphytic crusts) are living mats of lichens, mosses, algae, and cyanobacteria that blanket exposed soils in deserts, dry grasslands, and shrublands around the world. These crusts are important components of arid and semi-arid ecosystems in that they increase soil stability (21) and fix atmospheric nitrogen (N) (55). Cyanobacteria in these crusts may be the main source of N input into arid and semi-arid ecosystems (54, 55). In the western United States, microbiotic crusts have also been found to enhance soil fertility, increase elemental content of plant tissues, increase water infiltration and holding capacity, and contribute to mycorrhizal colonization (reviewed in 69, 70, 96).

By trampling these fragile crusts, livestock disturb, and in some cases completely destroy, this important component of arid ecosystems. Disturbance of these fragile crusts by cattle and sheep hooves (29, 83), which is widespread over the American West, most likely reduces the establishment and vigor of native plants (22,70), thus indirectly increasing community invasibility (20,46, 55, 137).

There is also evidence that intact microbiotic crusts reduce weed invasions directly by preventing the germination and establishment of annual weed seeds (46, 64a, 104, 137, 138), even when abundant seed sources are nearby. Crusts appear to have less effect on germination and establishment of native perennials (84). Two mechanisms have been proposed. The first is that crusts act as physical barriers to weed establishment by preventing seeds or their roots from contacting mineral soil (104). Some native species overcome this barrier by having special structures such as genticulate awns, which drill seeds through the crust into the soil (84).

A second mechanism is that crusts may prevent burial and germination of weed seeds by stabilizing soils (J. Belnap, personal communication). This idea is supported by Evans and Young (51), who found that emergence and growth of cheatgrass, medusahead, and tumble mustard were substantially enhanced by seed burial. Whatever the causal mechanism, sites with intact microbiotic crusts seem to be significantly more resistant to invasion than sites with disturbed crusts (84, 104). For example, Gelbard (unpublished data) found in a multivariate analysis of data from over 650 sites in southern Utah and eastern Nevada that in sites lacking microbiotic crusts, 20% of the plant species were aliens, while in sites with intact crusts, only 9% of species were aliens. In addition, Gelbard (1999) found that cheatgrass cover was four times higher on sites lacking microbiotic crusts than sites with crusts (16% vs. 4%). Approximately 64% of these sites had been disturbed by livestock, 25% by wildlife, 12% by outdoor recreationalists, and 2% by fire. Destruction of microbiotic crusts may therefore be one of the major ways that livestock predispose communities to weed invasions.

Livestock disturb and sometimes destroy microbiotic soil crusts, which reduce weed invasions directly by preventing the germination and establishment of annual weed seeds.

Nonindigenous plants are sometimes found in high numbers in areas with undisturbed microbiotic crusts, especially under conditions of high soil nitrogen or above-average rainfall. In a year of unusually frequent rainfall, for example, cheatgrass appeared at high density in an undisturbed community having well developed microbiotic crusts in Canyonlands National Park, Utah (49). Before this, the community had resisted cheatgrass invasion for 60 years, even though it was surrounded by communities with high cheatgrass densities (J. Belnap, personal communication). In another case, cheatgrass increased substantially after an unusually heavy spring rain in a kipuka, i.e., an island of soil and vegetation protected from grazing animals by old lava flows (87). However, a nearby kipuka supporting a similar shrub-steppe community was not invaded.

4) Impacts on Mycorrhizae

Besides damaging microbiotic crusts, grazing disturbances may enhance community invasibility by reducing colonization of grasses by vesicular-arbuscular mycorrhizae (VAM) (1, 27, 28, 176). VAM fungi form symbiotic relationships with plant roots, improving transport of essential nutrients and water from the soil into the roots of the colonized (mycorrhizal) plants (4). Allen et al. (5) suggested that VAM fungi reduce community invasibility by increasing native plant vigor. When VAM numbers are reduced due to disturbance or fire, plant species that require VAM fungi for vigorous growth, which include most native species in arid and semi-arid communities of the West (6, 176), are less vigorous and are put at a competitive disadvantage relative to weeds that do not require VAM fungi (5, 41, 61).

In a few cases, but not all (e.g., 6), livestock grazing has been found to reduce mycorrhizae numbers in the soil as well as to reduce their ability to form symbioses with host plants. Bethlenfalvay and Dakessian (27) explored the effects of livestock grazing on mycorrhizal colonization in a sagebrush (Artemesia tridentata) community and found VAM colonization of five native perennial grasses in a grazed community to be 28-60% lower than in an adjacent ungrazed community. Broadleaved plants were not affected. A follow-up study by Bethlenfalvay et al. (28) found that VAM colonization of Fairway crested wheatgrass (Agropyron desertorum), an introduced perennial forage grass, was 50% lower in a grazed than ungrazed sagebrush community. Similarly, Harper and Pendleton (70) found lower mycorrhizal infection in plants in uncrusted than crusted soils. In a study using mycorrhizal native grasses and mechanical disturbances of the soil, Doerr et al. (41) found that mycorrhizal infections declined with increasing soil disturbance. They concluded that the effects of mycorrhizae on plant community succession are so substantial that if perennial grasses are desired, then disturbances should be minimized.

Livestock grazing has been found to reduce mycorrhizae numbers in the soil as well as to reduce their ability to form symbioses with host plants.

While mycorrhizal species are benefited by VAM colonization, nonmycorrhizal weeds such as Russian thistle and halogeton may not be. VAM fungi can parasitically extract carbohydrates from nonmycorrhizal plants and kill their roots or root segments (2, 3, 5). Allen and Allen (3) found that in one site in Wyoming, inoculation of soils with mycorrhizal fungi reduced the cover and density of Russian thistle by 30% and 40%, respectively. Similarly, Allen et al. (5) found that the cover of early seral nonmycorrhizal species, including halogeton and black mustard (Brassica nigra), could be reduced by as much as 40% with the addition of mycorrhizal fungi. Thus, VAM inoculation of soil may be a tool to control some nonindigenous plant species.

5) Impacts on Soil Nitrogen

Livestock also increase the invasibility of grass-, shrub-, and woodland communities by redistributing soil nitrogen (N), creating locally enriched areas. High soil N content favors the establishment of weeds that prefer high N concentrations (55, 77). Such N "hot spots" occur in areas where animals deposit N in urine and dung or where disturbances increase N mineralization rates in the soil. Nitrogen hot spots are concentrated where livestock congregate near streams, fences, water tanks, and salt licks (10, 115, 149).

High soil N increases invasion by nitrophilous weeds such as cheatgrass and medusahead by stimulating germination of their seeds and enhancing their growth over that of native species (17, 52, 144, 150, 184). A study of competition between cheatgrass and the native perennial bluebunch wheatgrass (Pseudoregnaria spicata) found that application of nitrogen fertilizer quadrupled the number of cheatgrass plants but depressed wheatgrass yields by 50% (179). In a study examining the effects of both fertilization and grazing on competition between cheatgrass and intermediate wheatgrass (Elytrigia intermedia), Kay and Evans (85) found that applied nitrogen favored cheatgrass at the expense of the perennial grass. They also found that a combination of grazing and fertilization favored cheatgrass over wheatgrass more than fertilization alone. Hobbs and Atkins (76) working in Australia concluded that introduced annuals respond more favorably than native plants to a combination of soil disturbance and fertilization. Disturbance significantly increased the establishment of introduced annuals while fertilization significantly increased their biomass. Native annuals, however, showed little response to soil disturbance. Such combinations of disturbance and fertilization, in the form of trampling and dung, are common in grazed communities.

Application of nitrogen fertilizer quadrupled the number of cheatgrass plants but depressed native bluebunch wheatgrass yields by 50%.

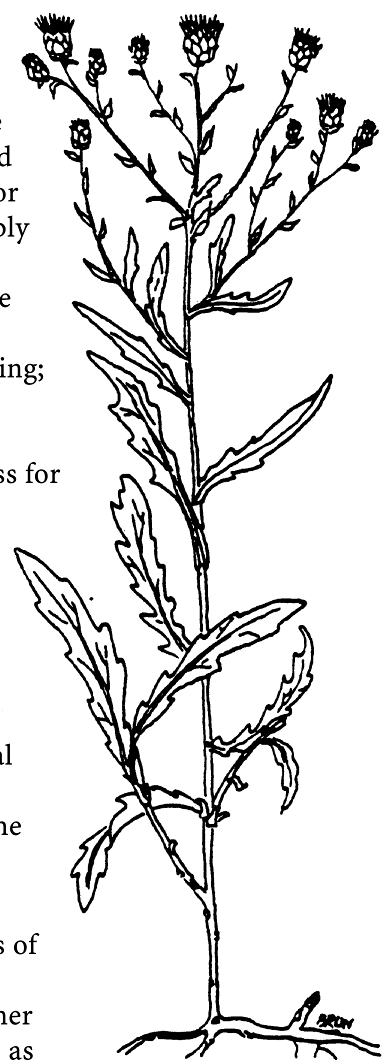
6) Impacts on Fire Regimes

Finally, dominance by alien species in arid and semi-arid communities is increased by the shorter fire-return intervals that often occur when annual weed cover is high. Once a grazed area is invaded by cheatgrass, which is denser than native bunchgrasses and dries out earlier in the growing season, fires become more frequent (30, 123, 173, 187). Frequent, early-season fire is lethal to many species of native bunchgrasses and shrubs, opening up communities to fire-tolerant alien species (30, 36, 187). One of the long-term consequences of nonindigenous plant invasions in the Intermountain West may be the absence of community recovery once flammable weeds have produced a permanently shortened fire-return cycle (30, 173, 187).

Can Ungrazed Communities Resist Invasions of Nonindigenous Species?

In most cases, established perennial grasses and healthy grasslands are able to retard, if not completely prevent, invasions by nonindigenous species (169, 184). Nonindigenous plants are generally absent or sparse in undisturbed grasslands and shrublands (39, 62, Tables 2), or their invasions are considerably slowed (93). Pickford (123) found that cheatgrass was rare (<1% cover) in communities protected from livestock grazing; and, as noted above, a site in Canyonlands National Park resisted invasion by cheatgrass for 60 years. Likewise, Daubenmire (38, 39), Goodwin et al. (62), and Belnap (20) observed few cheatgrass plants growing in undisturbed bunchgrass and blackbrush communities. Even where introduced annual species had established, their populations were small and the plants dwarfed (38).

Ungrazed and lightly grazed but still healthy stands of perennial grasses have been found to deter invasion by other nonindigenous weedy species as well. Yellow starthistle (134), medusahead (35, 181, 186), bull



Russian Knapweed (*Centaurea repens*)

thistle (59), diffuse knapweed (26), halogeton (32, 128), dyer's woad (Isatis tinctoria) (108); musk thistle (56), and Russian thistle, tumble mustard, alfalfa (Medicago sativa), sweetclover (Melilotus officianalis), horseweed (Conyza canadensis), and storksbill (Erodium cicutarium) (39) were all found to be less frequent in ungrazed or lightly grazed communities than in more disturbed ones. These reports provide strong evidence of the effectiveness of healthy native plant communities in deterring weed invasions.

Some weed species have been found to invade undisturbed grasslands and shrublands (e.g., 49, 73, 87, 89, 91, 93). Spotted knapweed, for example, invaded fescue (Festuca spp.) communities adjacent to roadsides in Glacier National Park (153), and leafy spurge invaded the remote Danaher Creek area of the Bob Marshall Wilderness (18). In spite of these and other reports, serious weed infestations in ungrazed, undisturbed grasslands and shrublands appear to be limited.

Can Range Communities Recover when Livestock are Removed?

The elimination of livestock grazing from grasslands and shrublands has often, but not always, been found to result in a reduction in weed numbers (Table 3). In eastern Oregon, the frequency of the alien grass Bromus hordeaceus declined in wet meadows that had been protected from grazing for 15 years, but increased 2-48% where grazing continued (63). In the same community the frequency of the introduced grass timothy (Phleum pratense) declined from 33% to 3% where protected and the frequency of tall buttercup (Ranunculus acris) declined from 55% to 12%. Similarly, after 20 to 40 years of protection from livestock grazing in British Columbia, cheatgrass cover was 1% (versus 3% on a grazed site), and its frequency was 4 % (versus 12% on a grazed site.) (111). In addition, seedlings of native perennial bluebunch wheatgrass were able to invade cheatgrass stands after ten years of protection in western Montana (72). Finally, Monsen (114) reported that protection from grazing for 58 years in southcentral Idaho allowed native species to increase in density and cover on north exposures, although not on south and west exposures.

Little research has focused on the environmental conditions necessary for weed-dominated arid and semi-arid communities to recover through natural successional pathways, or for native species to recolonize weed-dominated stands (114). Since several important weedy species, e.g., cheatgrass, medusahead, leafy spurge, and knapweeds, outcompete native species for water (72, 188), reestablishment of native perennials is most likely to result from the elimination of livestock in high rainfall areas (114) or in habitats characterized by high soil moisture availability (38). However, Monsen (114) also noted that during a recent drought, cheatgrass disappeared from extensive sagebrush communities in Nevada, Idaho, and Utah and was replaced in some areas by perennial bunchgrasses.

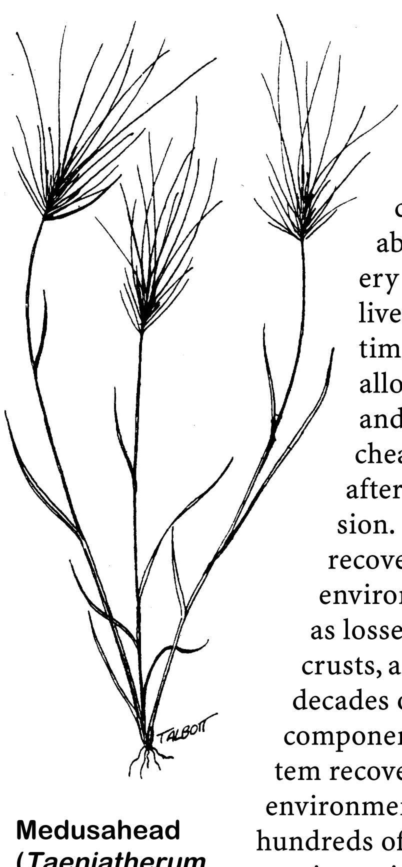
A number of studies have not found a decline of nonindigenous weeds when disturbances, including livestock grazing, were eliminated (e.g. 31, 39, 128, 130, 172). However, some of these results are not clear-cut. Robertson (130), for example, found that cheatgrass increased 38% during 30 years of protection from livestock grazing in a eroded

TABLE 3. Effects of Protecting Previously Grazed Communities from Livestock Grazing.

Location	Grazer	Years of protection	Effect on plant community	Citation Reference #
California	Cattle, sheep	4 years	Cheatgrass cover was three times higher in grazed vs. protected pastures	85
California	Cattle	6 years	Cover of native species was significantly higher and the cover of introduced species was significantly lower in protected than grazed coastal prairies	47
California	Cattle, sheep	10-15 years	Scattered plants and small stands of perennial grasses appeared in annual grassland	16
California, Channel Islands	Cattle, sheep	Variable	Native vegetation recovered while alien species declined in cover	64b
Colorado	Cattle, sheep	10 years	Cheatgrass, pepperweed, and other annual weeds were less frequent in protected than grazed plots	152
Utah	Cattle	5-40 year	Perennial grass cover averaged 23% and 10% on protected and grazed plots, respectively. Cheatgrass cover averaged 1.3% and 2.3% on protected and grazed plots, respectively	123
Utah	Cattle, sheep	6-15 years	Reduced occurrence of halogeton in exclosures	128
Oregon	Cattle	10 years	*Phleum pratens* frequency declined from 33% to 3% and tall buttercup frequency decreased from 55% to 12% in protected stands while remaining stable in grazed stands	63
Idaho	Cattle, sheep	16-23 years	No exotics recorded in ten community types	67
British Columbia	Cattle	30-40 years	Perennial grass cover was 3-10 times higher in protected pastures while cheatgrass cover was 3 times higher in grazed pastures	111

sagebrush-grass community in Nevada. However, the cover of native perennial grasses, forbs, and shrubs also increased during this period.

Studies of grassland restoration suggest that livestock grazing inhibits community recovery. Young and Evans (186), for example, found that application of the herbicide 2,4-D to remove low sagebrush in California resulted in an increase of native grasses in ungrazed plots, but to a severe invasion of medusahead on grazed plots. Another study suggested that weed-dominated communities in Idaho can be restored to communities more closely resembling native communities by reseeding with native or other perennial grasses in conjunction with removal of livestock (84).



Medusahead (*Taeniatherum caput-medusae*)

Although often attributed to weeds having established a new climax or steady state in western grassland and shrubland communities (100), the absence of community recovery following elimination of livestock grazing may sometimes be due to the short time allowed for recovery. McLean and Tisdale (111) found that cheatgrass began to decline only after 30 years of livestock exclusion. In other cases, lack of recovery may be due to severe environmental degradation, such as losses of topsoil, microbiotic crusts, and mycorrhizae, following decades of heavy grazing. These components are important for ecosystem recovery (e.g. 30, 41, 174). Such environmental damage may require hundreds of years before reversal (19) or require active restoration by land managers.

The loss of native seed sources following heavy livestock grazing also prevents recovery. For example, when livestock were removed from California grasslands that no longer contained native plant species, introduced species continued to dominate (16). However, in California's coastal prairies where native bunchgrasses still occurred, less than 10 years of protection from livestock grazing led to increases in native perennial grasses and reductions in introduced species (16).

Alien weeds may also maintain their dominance in western communities by having traits such as rapid growth rates, high seed production, and tolerance of grazing and fire (e.g. 30, 72, 130, 132). In addition, native species may be unable to recolonize weedy sites due to difficult-to-detect microsite changes, such as changes in microbial concentrations in the soil (e.g. 41, 71). Whatever the explanation, the failure of many communities to recover after disturbance is eliminated underscores the importance of preventing the disturbances and seed introductions that encourage weed invasions in the first place.

Can Livestock Be Used to Control Nonindigenous Plants?

Range scientists and land managers have suggested that livestock be used to control invasive plant species (e.g., 117, 163) since, theoretically, grazing would reduce the vigor, seed production, and seedbanks of palatable nonindigenous species and reduce the probability of destructive wildfires. Evidence to support the long-term effectiveness of this form of weed control is scant, although short-term reductions in weed cover are not uncommon (e.g. 97).

Goats and sheep are more successful at controlling alien weeds than cattle (reviewed in 117), although control by any of these species is seldom complete (92, 97, 117). Not only are many weedy species unpalatable even to goats and sheep (e.g. 108), but livestock commonly select native or introduced forage species over weeds. For example, in a feeding trial in Idaho, goats avoided the noxious weed leafy spurge when also offered the introduced perennial grass, crested wheatgrass (Agropyron cristatum), but preferred leafy spurge over the native forb arrowleaf balsamroot (Balsamorhiza sagittata) (170). In this same study, sheep avoided leafy spurge when paired with either balsamroot or crested wheatgrass. In another study, sheep reduced the density of spotted knapweed; but one year after grazing had ceased, grazed areas had twice as much knapweed as ungrazed areas (120). In this study sheep disturbances also increased the area of bare ground and the frequency of another introduced weed, Kentucky bluegrass (Poa pratensis). Finally, sheep in a mixed meadow of spotted knapweed and Idaho fescue reduced the root and shoot biomass of the fescue, but had no effect on the weed (118). The authors concluded that sheep grazing reduced the ability of the native bunchgrass to compete successfully with spotted knapweed.

Cattle have not been found to reduce leafy spurge, knapweed, or other broadlef species (88, 91, 95). They do, however, reduce the biomass of cheatgrass, which is palatable in the winter and spring. Such grazing is counterproductive since cattle grazing on grasslands in the spring also weakens native perennial grasses and disturbs wet soils (113, 184). These activities increase weed growth and enhance the probability of future invasions. Vallentine and Stevens (165) concluded that the use of cattle to reduce cheatgrass and enhance establishment and growth of perennial grasses would require a high degree of grazing control, which may be a major limitation under practical management situations. The absence of studies showing the long-term effectiveness of weed control by cattle supports their conclusion.

Other studies also confirm this conclusion. Cattle in a study in Nebraska selectively grazed some weed species, but not others (99). The cattle, therefore, did not provide effective weed control. Finally, in a clipping study of different combinations of spotted knapweed and bluebunch wheatgrass, the grass was found to be less tolerant of defoliation than the weed (86). These authors concluded that the feasibility of controlling knapweed with livestock was doubtful.

Many weedy species are unpalatable, even to goats and sheep, and livestock commonly select native or introduced forage species over weeds.

Other range scientists appear to agree. Not only did Young (183) report that tumblemustard and Russian thistle take over cheatgrass sites that have been heavily grazed by cattle, but both Lacey (91) and Tucker (151) concluded that the use of livestock to control range weeds was limited. Finally, Vallentine and Stevens (165) concluded that with a few possible exceptions, grazing is not an effective general tool for cheatgrass control. By disseminating weed seeds in dung and fur, disturbing soil surfaces, creating nutrient hot-spots, and grazing preferentially on native species, livestock are more likely to create and maintain weedy communities than to control them.

Conclusion

The spread of nonindigenous plants through grasslands, shrublands, and woodlands of the American West has been described as one of the greatest environmental threats facing native species and ecosystems of the region (30, 104, 177). Although invasion by nonindigenous species is usually ranked as a threat separate from livestock grazing (e.g., 57, 177), we suggest that in many areas of the West, current extensive invasions by nonindigenous plants should be classified as a subset of livestock grazing, not an independent threat. Without disturbance to native plants, microbiotic crusts, and soils resulting from livestock grazing and trampling, and corresponding increases in light, water, and nutrients for the remaining weeds, it is doubtful that alien plants would have spread so far or become so dense. At least they would not be invading as rapidly, and certainly not over the vast area of western grasslands, shrublands, and woodlands as they now are. Neither would these weeds achieve the same degree of community dominance.

The spread of exotic weeds throughout grasslands, shrublands, and woodlands in the West has been described as one of the greatest threats facing the region's native species and ecosystems.

Recent research showing that livestock significantly increase invasions by nonindigenous plants in the western U.S. is persuasive. Similar results were found in all western states and for nearly every introduced species that has been studied. Although many of these studies would have benefited from both better replication and more recent research techniques, the pattern of evidence is overwhelming.

By ignoring the relationship between livestock grazing and nonindigenous plant invasions, rangeland managers have been unsuccessful at stopping or even slowing these invasions. A new draft management plan for 73 million acres of public lands in the Columbia River Basin (163) and another for 6 million acres of BLM lands in southeastern Oregon (157) call for restoration of weed-dominated communities. However, they propose neither reducing livestock numbers nor significantly altering livestock management.

Recent research showing that livestock significantly increase invasions by nonindigenous plants in the western U.S. is persuasive.

Another proposal for restoring weed-dominated communities in the Great Basin (158) also avoids implicating livestock grazing more recent than the 1800s. All such plans are doomed to failure.

Most of the current recommendations in management plans for stopping nonindigenous plant invasions on public lands in the West focus on preventing landscape-level introductions of weed seeds by washing vehicles and using

Not until plant communities and soils are allowed to recover their natural defenses (such as healthy, deep-rooted native plants and intact microbiotic crusts) will the spread and dominance of exotic weeds in the American West be reduced or reversed.

weed-free livestock feed. Although useful, these strategies are similar to rearranging deck chairs on the Titanic. Similarly, recent calls to use livestock to control weed infestations appear unlikely to succeed. Preferential grazing of native plant species over non-indigenous species by livestock, combined with livestock's disturbances of soils, microbiotic crusts, mycorrhizae, nutrients, and fire cycles, will likely keep these communities open to invasion and prevent community recovery. Not until plant communities and soils are allowed to recover their natural defenses such as healthy, deep-rooted native plants and intact microbiotic crusts will the spread and dominance of nonindigenous weeds in the American West be reduced or reversed.

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