

APPENDIX D PNW Causal Paper Ungulates

The Influence of Ungulates on Non-native Plant Invasions in Forests and Rangelands: A Review

Catherine G. Parks, Michael J. Wisdom, and John G. Kie

U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station,
La Grande, OR.

Abstract

Herbivory by wild and domestic ungulates can strongly influence vegetation composition and productivity in forest and range ecosystems. However, the role of ungulates as contributors to the establishment and spread of non-native invasive plants is not well known. Ungulates spread seeds through endozoochory (passing through an animal's digestive tract) or epizoochory (attached to an animal's body); hence, animal-mediated spread of invasive plants is a common phenomenon. Manipulative experiments of ungulate grazing effects on non-native plant introduction, establishment, and spread are limited. Herbivory can alter successional patterns and rates when selective foraging favors survival, growth, and reproduction of plants with low palatability, although the impact can differ greatly among ecosystems. Descriptive studies in various habitats have shown that non-native species invade sites with or without livestock grazing, and other studies have tested the utility of prescribed grazing to reduce biomass and occurrence of invasive plants. Understanding the cause-effect relations between ungulates and invasive plant dynamics is a critical management need that deserves high priority for research. We summarize existing knowledge and identify gaps and research needs.

Additional Keywords.

Exotic plants, invasive plants, cattle grazing, herbivory.

The Influence of Ungulates on Non-native Plant Invasions in Forests and Rangelands: A Review

Introduction

Herbivory by wild and domestic ungulates has profound effects on vegetation development and productivity in forest and range ecosystems (Hobbs 1996). Livestock grazing has long been recognized as an agent of change affecting the composition, structure, and development of rangeland plant communities (Fleischner 1994, Milchunas et al. 1998). More recently, herbivory by wild ungulates also has been recognized as an ecological force in forest ecosystems (Augustine and McNaughton 1998, Riggs et al. 2000, Kie and Lehmkühl 2001). Substantial populations of domestic and wild ungulates, particularly cattle, elk (*Cervus elaphus*), and mule deer (*Odocoileus hemionus*), are present throughout expansive areas of western North America. An estimated population of 200,000 cattle and 430,000 mule deer and elk graze public lands in Oregon for at least part of each year (fig. 1). For example, ungulate densities on the Wallowa-Whitman National Forest in northeast Oregon typify the densities present on public lands in much of the intermountain West. Total ungulate numbers on the Wallowa-Whitman exceed 80,000 animals. Densities of elk and mule deer on winter range average 3 elk per square kilometer and 5 deer per square kilometer. In addition, cattle density averages about 3 cattle per square kilometer (table 1.)

Empirical studies have provided evidence that ungulate herbivory contributes to long-term changes in ecosystems by changing nutrient turnover; rates, patterns, and perhaps trajectories of succession; and competition among plant species (Molvar et al. 1993, Pastor et al. 1993, Hobbs 1996, Pastor and Cohen 1997, Augustine and McNaughton 1998). Ungulate grazing and browsing can function as a chronic disturbance, exerting a continuous influence over long periods, as opposed to episodic disturbances such as fire, epidemic insect defoliation, and timber harvest that change forest structure and composition dramatically at a given point in time (Klein 1968, Kie et al. 2003).

One aspect of ungulate herbivory is its potential as a contributor to the establishment, spread, and persistence of non-native invasive plant species. The establishment and spread of these plants is an increasingly important issue for land managers in western North America, who

are faced with expansive invasions of non-native plants that are displacing native plant communities at an alarming rate. Non-native plants are spreading and invading approximately 700,000 hectares of U.S. wildlife habitat per year (Babbitt 1998, Pimental et al. 2000). At least 17 million acres of western federal lands were reportedly infested in 1996, more than quadrupling the range affected between 1985 and 1995 (Westbrooks 1998). Invasive plants are having profound ecological impacts on Western landscapes, where they can form new metastable states that deflect or halt the natural dynamics of native ecosystems (Hobbs and Mooney 1993).

It has been asserted that livestock grazing is a major cause of non-native plant invasions (Belsky and Gelbard 2000). However, no manipulative studies, with appropriate treatments and controls, have rigorously tested this hypothesis. Likewise, to our knowledge, manipulative experiments of grazing effects of wild ungulates on non-native plant species dynamics have yet to be conducted. Although scientific support is growing for the hypothesis that large herbivores facilitate the invasion and establishment of non-native plants, substantial controversy exists about the specific processes in time and space and the associated predictions of effects. We summarize the current scientific understanding of the role of ungulates in the introduction, establishment, and spread of non-native plants in forest and rangeland ecosystems, and discuss associated knowledge gaps and research needs. We focus our summary on forest and rangeland ecosystems in western North America, where herbivory by a variety of wild and domestic ungulates is common, and where non-native plant species are supplanting native plant species at rapid rates.

Definitions

Invasive species are plants with the ability to spread into native ecosystems, expand over large areas, and often are considered “undesirable” by society owing to their ecologic or economic impacts. The majority of invasive species that are considered most deleterious to Western forests and rangelands were introduced to North America during the last century from other continents. For consistency, we use the term “invasive” to define a non-native plant species whose introduction does, or is likely to, cause economic loss or detrimental impact to native plant communities and ecological processes. Non-native means, with respect to a particular ecosystem, any species that is not indigenous to that ecosystem.

Ungulates as Contributors to Plant Invasions

Both theoretical and empirical evidence suggest that domestic and wild ungulates may contribute to plant invasions by (1) selective foraging on and resultant reduction or elimination of native plant species, thus favoring an increase in invasive plants; (2) transport of invasive plant seeds into uninfested sites through endozoochory, which occurs when animals consume seeds in one area and later regurgitate or defecate them in another area; (3) epizoochory, which is the transport of seeds attached to animal skin, fur, or hooves, into another location where the seeds detach; and (4) disturbance or alteration of soils or trampling of vegetation, any of which confers advantage to invasive plant seeds that often are adapted for establishment in subsequent openings and bared soil.

Selective Foraging

Few studies have examined the effects of ungulate herbivory on ecosystem processes, but many have examined ungulate effects on the species composition of plant communities (Hobbs 1996, Augustine and McNaughton 1998, Vesk and Westoby 2001). Herbivores influence recruitment, growth, and mortality rates of plants, which are correlated with community traits and with interspecific competition (Huntly 1991). Herbivory is highly variable in space and time, and the spatial and temporal patterns of herbivory can modify the composition, structure, and dynamics of plant communities. Herbivory alters the profile of a plant community through differential use of palatable versus unpalatable plants, and thus can alter successional trajectories when selective foraging favors survival and reproduction of plants with low palatability. Palatable, native perennial plant species may produce fewer seeds and seedlings in heavily grazed or browsed situations (Crawley 1983, Parks et al. 1998) and thereby place unpalatable invasive species at a competitive advantage.

Secondary compounds (e.g., phenolics and tannins) and structural compounds (e.g., lignins and cellulose) in plants reduce their palatability to ungulates, thus conferring defense against herbivory and an advantage to plants that contain these compounds (Augustine and McNaughton 1998). Many invasive plants have such defenses, and thus are unpalatable to herbivores, or only palatable during short phenologic periods (Kelsy and Locken 1987, Sheley and Petroff 1999). As a consequence, less intensive grazing of the invasive plant provides

competitive advantage to these species over more palatable native plants, allowing the former to effectively invade, establish, and spread.

Despite the competitive advantages that ungulate herbivory may confer to invasive plants, the impact of grazing animals can differ greatly among ecosystems. Specific effects may depend largely on the response variables chosen to evaluate herbivory (Milchunas and Lauenroth 1993). For example, Stohlgren et al. (1999) evaluated 20 long-term livestock grazing exclosures in Colorado, Wyoming, Montana, and South Dakota, and concluded there was little evidence to suggest that grazing has an effect on native species richness or on the accelerated spread of most invasive plant species at landscape scales. This study, as with most other grazing studies, did not exclude native ungulates from ungrazed treatments. Other studies in various habitats have shown that non-native species can invade sites with or without livestock grazing (Lacey et al. 1990, Frank et al. 1995, Rambo and Faeth 1999). Moreover, Milchunas et al. (1998) concluded that the shortgrass steppe of North America is insensitive to cattle grazing because plants have evolved and adapted to long evolutionary history of grazing by native bison (*Bison bison*). Moreover, Milchunas et al. (1998) found ungrazed shortgrass steppe to be more susceptible to invasion by “weed” species than were heavily grazed communities. Mack and Thompson (1982) also found this true of steppe communities east of the Rocky Mountains. By contrast, however, Mack and Thompson (1982) argued that steppe communities west of the Rocky Mountains historically had few large herbivorous mammals and therefore lack herbivore-adapted traits and resiliency in response to current anthropogenic increases of both domestic and wild herbivores.

Despite research that questions the role of grazing as a major contributor to plant invasions, findings from many observational studies (as summarized by Belksy and Gelbard 2000) support this premise. Conducting research in a spotted knapweed (*Centaurea maculosa* Lam.) infested area that had been repeatedly grazed, Olson and Wallander (1997) found root and shoot biomass of Idaho fescue (*Festuca idahoensis* Elmer.) was significantly reduced from ungrazed controls, whereas the spotted knapweed biomass was unchanged with grazing. These results suggest that repeated grazing may reduce the ability of Idaho fescue to compete with spotted knapweed. Moreover, Sheley et al. (1997) found that clipping to simulate intensive livestock grazing enhanced the establishment of diffuse knapweed (*Centaurea*

diffusa Lam), but moderate defoliation had no effect. Such variability in results reflect the need for manipulative studies where confounding and extraneous factors are properly controlled or accounted for, and where effects of specific treatments of interest are evaluated in an experimental manner.

Numerous studies have tested the utility of “prescribed livestock grazing,” particularly with sheep and goats, to reduce biomass and composition of invasive plants. Olson et al. (1997) grazed sheep intermittently for 3 consecutive years on range infested by spotted knapweed; they found that knapweed density and seed viability were lower on grazed treatments versus ungrazed treatments. Grazing treatments also produced more Kentucky bluegrass (*Poa pratensis* L., a non- native grass) cover and increased bare soil. Other studies report some level of invasive plant reduction with controlled levels of grazing, selective timing of grazing, or multiple species of herbivores (Lacey and Sheley 1996, Sheley and Petroff 1999). Cattle appear to be less effective at reducing invasive plants than sheep or goats (Vallentine and Stevens 1994, Lawrence et al. 1995), or alternatively, can increase the cover of invasive plants in grazed treatments (Maxwell et al. 1992).

Transport of Invasive Plant Seeds by Endozoochory and Epizoochory

Several intentional and unintentional introductions of invasive plants have been associated with livestock management, and some introductions have resulted in widespread invasions (Baker 1978, Mack 1991, Sheley and Petroff 1999). Landscape-scale spread of invasive plants can occur when seeds are moved along transportation corridors from infested sites or from infested ungulate forage, attached to or held within infested animals, or attached to vehicles used to transport infested forage or animals. Domestic and wild ungulates spread seeds through endozoochory or epizoochory (Janzen 1984). Animal-mediated spread of invasive plants is a common, world-wide phenomenon (Schiffman 1997). Although invasive plant foliage and other structures generally harbor unpalatable plant compounds and often are avoided, they can be consumed by large herbivores, even when not intentionally selected or preferred. Fruits and seeds are readily eaten by large herbivores intentionally or inadvertently in the course of general grazing, and may form a substantial part of their diet (Gill and Beardall 2001). By moving seeds away from parent plants, which are usually competitively superior, animal dispersers are likely to increase the probability of seedling survivorship

(Howe and Smallwood 1982, Herrera 1995). Because wild ungulates and livestock have predictable patterns of habitat selection (Johnson et al. 2000, Coe et al. 2001), animal-dispersed seeds are likely to be spread among environmentally similar sites. Consequently, invasive plants are often deposited in conditions similar to sites where such plants have already become established (Howe and Smallwood 1982). This role of ungulates to deposit seeds in environments where establishment can be successful can be particularly important for colonization of invasive plants in fragmented landscapes (Schiffman 1997).

Invasive species with thick seed coats dispersed by endozoochory, in addition to benefiting from transport, may have enhanced germination owing to gut scarification (Schiffman 1997). Invasive plant seeds have been recovered from feces and found viable in numerous studies. Seeds of leafy spurge (*Euphorbia esula* L.) are viable for 4 days following sheep ingestion (Olson and Wallander 2002). Thill et al. (1986) fed achenes of common crupina (*Crupina vulgaris* Cass.) to several large herbivores and found none in sheep feces; but horses, mule deer, and cows excreted 5, 3, and 25% respectively. The percentage of achenes consumed and excreted that are viable ranged from 29% in cows to 81% in deer. Seeds of spotted knapweed fed to mule deer and sheep were collectable and viable for more than 2 days (Wallander et al. 1995).

It is not certain how important endozoochory is in initiating or increasing infestations in natural systems (Gill and Beardall 2001). Malo et al. (2000), however, quantified seeds in dung deposited by domestic and wild herbivores in Mediterranean plant communities; they found that cows dispersed the most seeds (68%), followed by red deer (*Cervus elaphus*) (20%), rabbits (7%), and fallow deer (*Dama dama*) (5%). Malo et al. (2000) concluded that the effect of seed input to the seed bank from ungulate transport may be low at large and medium-sized spatial scales, but very important at small scales and for colonization processes.

Epizotic transport may also be an important mode of introduction and spread of invasive plants at several landscape scales. De Clerck-Floate (1997) suggests that cattle are effective dispersers of hound's-tongue (*Cynoglossum officinale* L.) on rangelands of British Columbia. Likewise, sheep are known to spread leafy spurge seeds (Olson et al. 1997). The fleece of a

single sheep grazing on calcareous grasslands of Germany was found to carry as many as 8,500 seeds of 85 vascular plant species (Fischer et al. 1996).

Effects of Site Disturbance or Alteration

Direct physical or chemical effects such as plant trampling, disturbance of soil crusts, creation of bare soil, and inputs of nitrogen to the soil through dung and urine, can influence the success of native species (Augustine and McNaughton 1998) and thereby the “invasibility” of a plant community by non-native species (Lonsdale 1999).

By consuming aboveground biomass of plants, domestic ungulates also reduce the amount of biomass available for conversion to litter. Substantial litter reduction can cause a subsequent increase in bare ground (Schulz and Leininger 1990), erosion, and soil compaction, all of which favor germination and establishment of invasive plants (Sheley and Petroff 1999). Many studies have shown that increased nitrogen availability (e.g. through animal dung and urine deposition) encourages community dominance by invasive plant species (Harris 1967, Hobbs 1989). A recent greenhouse study, however, evaluated five levels of nitrogen availability on the comparative growth of native and invasive plant species and found the invasive plants did not display a more positive response (Lowe et al. 2002).

Direct trampling by ungulates can alter the important symbiotic relations of microbiotic crusts and mycorrhizae with native plants, thus indirectly increasing the invasibility of the community by non-native plants that are enhanced by disturbed site conditions (Eckert et al. 1986, Rosentreter 1994). Microbiotic crusts are living mats of lichens, mosses, algae, and cyanobacteria that cover rangelands world-wide. Microbiotic crusts play a key role in nutrient cycling, increase soil stability and soil moisture, interact with vascular plants, and perform other important functions (Eldridge and Green 1994). The need for scientific understanding regarding the ecological role of these crusts is growing (Quigley and Arbelbide 1997), along with growing concern about management practices that adversely impact the crust layer. In general, trampling and grazing are deleterious to survival of microbiotic crusts (Brotherson et al. 1983, Johansen 1986, Jeffries and Klopatec 1987, Beymer and Klopatek 1992).

The influence of grazing on mycorrhizae also is a concern because mycorrhizal fungi form symbiotic relations with the roots of most vascular plants native to North America (Molina et al. 1992). Allen et al. (1989), however, reported no detectible changes in vesicular-arbuscular mycorrhizal fungi in two species of semiarid tussock grasses after clipping. Conversely, Bethlenfalvai and Dakessian (1984) found that colonization of forage grasses by vesicular-arbuscular mycorrhizal fungi was significantly reduced by sheep grazing, but found no differences in colonization of grazed and ungrazed broadleaf plants. These authors documented that grazing causes a shift in the composition of the native vegetation and accompanying mycoflora.

Interactions Between Grazing and Other Disturbances

Most invasive species are extremely efficient at exploiting the initial decreases in native plant competition that can follow a disturbance. If native plant species vigor, abundance, or diversity are reduced following disturbance, invaders may establish vigorous populations that ultimately exclude the recovery of native species (Pimm 1984, Drake 1990). The interaction of multiple disturbances such as fire, logging, grazing, and road building have been noted to allow non-native species to invade or colonize native ecosystems (Vitousek et al. 1996). Predicting specific responses, however, is exceedingly complex. Grazing by ungulates reduces the standing biomass of plants available for burning, hence grazing can influence the frequency, extent, and intensity of wild and prescribed fires (Belsky and Blumenthal 1997). Fire, directly or indirectly, can influence the establishment and spread of many invasive plant species (D'Antonio and Vitousek 1992, Milberg and Lamont 1995, D'Antonio 2000, Goodwin and Sheley 2001, Harrod and Reichard 2001). Once established, the invasive plants themselves may modify fire frequency and intensity, as is the case with cheat grass (*Bromus tectorum* L.) which in some environments is a persistent species because of its synergistic relationship with fire (Mack and D'Antonio 1998).

Effects of Disturbance-Mediated Ungulate Distribution

Many factors beyond food availability regulate the distribution of ungulates (Coughenour 1991, Reimoser and Gossow 1996). Interference factors, such as postfire rehabilitation, logging, fuels reduction practices, and increased road traffic, can redistribute ungulates across landscapes (Wisdom 1998, Weisberg et al. 2002). As a result of such interference, herbivores

may concentrate their use, and hence their impacts, in a smaller portion of their habitats. Overall, grazing by livestock tends to be more intense and potentially deleterious to native plant communities than grazing by wild ungulates simply because livestock densities can be higher and spatially constant, owing to fencing, water improvements, mineral supplementation, and other management (Hobbs 1996). However, migratory wild ungulates and their effects are also highly influenced by management inputs. Setting ungulate density through hunting seasons is a traditional tool of wildlife managers, but managing game animal numbers alone may not alter the relative grazing pressure on plant communities. Historical patterns of wild ungulate grazing were based on migration that tracked the young, rapidly growing stage of development in plant communities along phenological gradients covering entire landscapes. Anthropogenic habitat fragmentation and the elimination of migration corridors, however, may have led to a homogenization of grazing intensities because these landscapes no longer receive the variable grazing pressure of nomadic ungulates (Knopf 1996). Extended or continual grazing may have major indirect effects on the functional composition of isolated reserves (Augustine and McNaughton 1998), and thereby could increase their risk of non-native plant invasion.

Knowledge Gaps and Research Needs

Current knowledge of ungulate herbivory as a contributor to the invasion, establishment, and spread of non-native plants is severely limited by a lack of manipulative experiments. Most studies to date have been observational, unreplicated, and lacking the experimental controls needed to eliminate or account for confounding sources of variation. For example, most studies have examined ungulate effects on composition or succession of plant communities by comparing only extant herbivory with total ungulate exclusion or evaluate the effects of only one ungulate species even though two or more species were typically present in the areas under study. Only a few studies evaluate multiple densities of ungulates. Inferring cause-effect relations from such studies is questionable. Importantly, we are unaware of any herbivory studies that were designed to make inferences to large landscapes typically of interest to resource managers.

Given the rapid rate of establishment and spread of invasive plants in Western landscapes, we feel that new research on the influence of ungulates should consider the following points in study design:

- (1) The influence of all ungulate species present in the system under study, including both wild and domestic species.
- (2) The effects of multiple densities of each ungulate species, including the evaluation of potential thresholds, below which the densities of ungulates may or may not contribute to spread and establishment of non- native plants.
- (3) The interactions of ungulate herbivory with episodic disturbances as potential joint contributors to non-native plant spread and establishment;
- (4) The specific mechanisms by which each species of invasive plant may be influenced by ungulate herbivory, such as through trampling of vegetation, soil disturbance, endozoochory or epizoochory, or interspecific competition.
- (5) Manipulative studies, with particular emphasis on experiments designed to evaluate specific effects of ungulates under appropriate treatments and controls needed to understand cause-effect relations and mechanisms.
- (6) Research that allows inferences to be made at large landscape scales of interest to managers such as watersheds that are typically managed for a variety of resources in an integrated manner (Hann et al. 1997).
- (7) Interdisciplinary research in various vegetation types to establish a multiple-scale framework for restoration of native communities on invasive-species-infested areas that have been historically overgrazed by domestic ungulates.

Addressing these needs as part of future research on ungulate herbivory is critical to the design of effective management strategies to mitigate the continued spread and establishment of invasive plants, and to determine the best practices to reestablish native communities. Understanding the cause-effect relations between ungulates and native and invasive plant dynamics is a critical management need that deserves high priority for research.

Literature Cited

Allen, M.F., J.H. Richards, and C.A. Busso. 1989. Influence of clipping and soil water status on vesicular-arbuscular mycorrhizae of two semiarid tussock grasses. *Biology and Fertility of Soils* 8:285-289.

Augustine, D.J., and S.J. McNaughton. 1998. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. *Journal of Wildlife Management* 62:1165-1183

Babbitt B. 1998. Statement by Secretary of the Interior on invasive alien species. "Science in wildland weed management." Symposium, April 8-10, 1998. Denver, CO. US Department of the Interior.

Baker, J.G. 1978. Patterns of plant invasions in North America. Pages 44-57 in H.A. Mooney and J.A. Drake, eds. *Ecology of biological invasions of North America and Hawaii*. Springer Verlag, New York.

Belsky, A.J., and D.M. Blumenthal. 1997. Effects of livestock grazing on stand dynamics and soils in upland forests of the interior West. *Conservation Biology* 11:315-327.

Belsky, A.J., and J.L. Gelbard. 2000. livestock grazing and weed invasions in the arid West. Oregon Natural Desert Association, Bend, OR.

Bethlenfalvay, G.J., and S. Dakessian. 1984. Grazing effects on mycorrhizal colonization and floristic composition of the vegetation on a semiarid range in northern Nevada. *Journal of Range Management* 37:312-316.

Beymer, R.J., and J.M. Klopatek. 1992. Effects of grazing on cryptogamic crusts in pinyon-juniper woodlands in Grand Canyon National Parks. *American Midland Naturalist* 127:139-148.

Brotherson, J.D., S.R. Rushforth, and J.R. Johansen. 1983. Effects of long-term grazing on cryptogamic crust cover in Navajo National Monument, Arizona. *Journal of Range Management* 36:579-581.

Coe, P.K., B.K. Johnson, J.W. Kern, S.L. Findholt, J.G. Kie, and M.J. Wisdom. 2001. Responses of elk and mule deer to cattle in summer. *Journal of Range Management* 54: A51-A76. Available at <http://uvalde.tamu.edu/jrm/remote/auesursf.htm>.

Coughenour, M.B. 1991. Biomass and nitrogen responses to grazing of upland steppe on Yellowstone's northern winter range. *Journal of Applied Ecology* 28:71-82.

Crawley, M.J. 1983. *Herbivory: the dynamics of animal-plant interactions*. University of California Press, Berkeley.

- D'Antonio, C.M. 2000. Fire, plant invasions, and global changes. Pages 65-93 in H.A. Mooney and R.T. Hobbs, eds. *Invasive species in a changing world*. Island Press, Washington, D.C.
- D'Antonio, C.M., and P.M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics* 23:63-87.
- De Clerck-Floate, R. 1997. Cattle as dispersers of hound's-tongue on rangeland in southeastern British Columbia. *Journal of Range Management* 50:239-243.
- Drake, J.A. 1990. The mechanics of community assembly and succession. *Journal of Theoretical Biology* 147: 213-233.
- Eckert, R.F., Jr., F.F. Peterson, M.S. Meurise, and J.L. Stevens. 1986. Effects of soil-surface morphology on emergence and survival of seedlings in big sagebrush communities. *Journal of Range Management* 39:414-420.
- Eldridge, D.J., and R.S.B. Green. 1994. Microbiotic soil crusts: a review of their roles in soil and ecological processes in the rangelands of Australia. *Australian Journal of Soil Research* 32:389-415.
- Fischer, S.F., P. Poschlod, and B. Beinlich. 1996. Experimental studies on the dispersal of plants and animals on sheep in calcareous grasslands. *Journal of Applied Ecology* 33: 1206-1222.
- Fleischner, T.L. 1994. Ecological costs of livestock grazing in Western North America. *Conservation Biology* 8:629-644.
- Frank, A.B., D.L. Tanaka, L. Hofmann, and R.R. Follett. 1995. Soil carbon and nitrogen of northern Great Plains grasslands as influenced by long-term grazing. *Journal of Range Management* 48: 470-474.
- Gill, R.M.A., and V. Beardall. 2001. The impact of deer on woodlands: the effects of browsing and seed dispersal on vegetation structure and composition. *Forestry* 74:210-218.
- Goodwin, K.M., and R.L. Sheley. 2001. What to do when fires fuel weeds. *Rangelands* 23:15-21.
- Hann, W.J., J.L. Jones, M.G. Karl [et al.]. 1997. Landscape dynamics of the Basin. Pages 337-1,055 in T.M. Quigley and S.J. Arbelbide, eds. *An assessment of ecosystem components in the Interior Columbia basin and portions of the Klamath and Great Basins: Volume II*. Gen. Tech. Rep. PNW-GTR-405. USDA Forest Service Pacific Northwest Research Station. Portland, OR.
- Harris, G.A. 1967. Some competitive relationships between *Agropyron spicatum* and *Bromus tectorum*. *Ecological Monographs* 37:90-111.

Harrod R.J. and S. Reichard 2001. Fire and invasive species within the temperate and boreal coniferous forests of western North America. Pages 95-101. In K.E.M. Galley and T.P. Wilson, eds. Proceedings of the invasive species workshop: the role of fire in the control and spread of invasive species. Fire conference 2000: the first national congress on fire ecology, prevention, and management. Miscellaneous Publ. No. 11. Tall Timbers Research Station, Tallahassee, FL.

Herrera, C.M. 1995. Plant-Vertebrate seed dispersal systems in the Mediterranean: ecological, evolutionary, and historical determinants. *Annual Review of Ecology and Systematics* 26:705-727.

Hobbs, N.T. 1996. Modification of ecosystems by ungulates. *Journal of Wildlife Management* 60:695-713.

Hobbs, R.J. 1989. The nature and effects of disturbance relative to invasions. Pages 389-405 in J.A. Drake, H.A. Mooney, F. Di Castri [et al.], eds. *Biological invasions: a global perspective*. John Wiley and Sons, Chinchester, Great Britain.

Hobbs, R.J., and H.A. Mooney. 1993. Restoration ecology and invasions. Pages 127-133 in D.A Saunders, R.J. Hobbs, and P.R. Ehrlich, eds. *Nature Conservation 3: reconstruction of fragmented ecosystems*. Surrey Beatty and Sons, Chipping Norton, Great Britain.

Howe, H.F., and J. Smallwood. 1982. Ecology of seed dispersal. *Annual Review of Ecology and Systematics* 13:201-228.

Huntly, N. 1991. Herbivores and the dynamics of communities and ecosystems. *Annual Review of Ecology and Systematics* 22:477-503.

Janzen, D.H., 1984. Dispersal of small seeds by big herbivores: foliage is the fruit. *American Naturalist* 123:338-353.

Jeffries, D.L., and J.M. Klopatec. 1987. Effects of grazing in the vegetation of the blackbrush association. *Journal of Range Management* 40:390-392.

Johansen, J.R. 1986. Importance of cryptogamic soil crusts to arid rangelands: implications for short duration grazing. Pages 58-64 in Tiedeman, J. ed. *Short duration grazing*. Washington State University, Pullman, Wa.

Johnson, B.K., J.W. Kern, M.J. Wisdom, S.L. Findholt, and J.G. Kie. 2000. Resource selection of mule deer and elk during spring. *Journal of Wildlife Management* 64:685-697.

Kelsy, R.G., and L.J. Locken. 1987. Phytotoxic properties of cnicin, a sesquiterpene lactone from *Centaurea maculosa* (spotted knapweed). *Journal of Chemical Ecology* 13:19-33.

Kie, J.G., and J.F. Lehmkuhl. 2001. Herbivory by wild and domestic ungulates in the intermountain West. *Northwest Science* 75(Special issue): 55-61.

Kie, J.G., R.T. Bowyer, and K.M. Stewart. In Press. Ungulates in western forests: habitat requirements, population dynamics, and ecosystem processes. Pages 000-000 In C. J. Zabel and R.G. Anthony, editors. Mammal community dynamics in coniferous forests of western North America: management and conservation. Cambridge University Press, New York.

Klein, D.R. 1968. The introduction, increase, and crash of reindeer on St. Matthew Island. *Journal of Wildlife Management* 32:350-367.

Knopf, F.L. 1996. Prairie legacies--birds. Pages 135-148 in F. B. Samson and

F.L. Knopf, eds. *Prairie conservation: preserving North America's most endangered ecosystem*. Island Press, Covelo, Calif.

Lacey, J.R., P. Husby, and G. Handl. 1990. Observations on spotted and diffuse knapweed invasion into ungrazed bunchgrass communities in western Montana. *Rangelands* 12: 30-32.

Lacey, J.R., and R.L. Sheley. 1996. Leafy spurge and grass response to picloram and intensive grazing. *Journal of Range Management* 49:311-314.

Lawrence, B.K., S.S. Waller, L.E. Moser [et al.]. 1995. Weed suppression with grazing or atrazine during big bluestem establishment. *Journal of Range Management* 48:307-313.

Lonsdale M., 1999. Global patterns of plant invasions and the concept of invasibility. *Ecology* 80:1522–1536.

Lowe, P.N., W.K. Lauenroth, and I.C. Burke. 2002. Effects of nitrogen availability on the growth of native grasses and exotic weeds. *Journal of Range Management* 55:94-98.

Mack, M.C., and C.M. D'Antonio. 1998. Impacts of biological invasions on disturbance regimes. *Trends in Ecology and Evolution* 13:195-198.

Mack, R.N. 1991. The commercial seed trade: an early disperser of weeds in the United States. *Economic Botany* 45:257-273.

Mack, R.N., and J.N. Thompson. 1982. Evolution in steppe with few large, hooved mammals. *American Naturalist*. 119:757-773.

Malo, J.E., B. Jiménez, and F. Suárez. 2000. Herbivore dunging and endozoochorous seed deposition in a Mediterranean dehesa. *Journal of Range Management* 53:322-328.

Maxwell, J.F, R. Drinkwater, D. Clark, and J.W. Hall. 1992. Effect of grazing, spraying, and seeding on knapweed in British Columbia. *Journal of Range Management* 45:180-182.

Milberg, G.P., and B.B. Lamont. 1995. Fire enhances weed invasion of roadside vegetation in southwestern Australia. *Biological Conservation* 73:45-49.

Milchunas, D.G., and W.K. Lauenroth. 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecological Monographs* 63: 327-366.

Milchunas, D.G., W.K. Lauenroth, and I.C. Burke. 1998. Livestock grazing: animal and plant biodiversity of shortgrass steppe and the relationship to ecosystem function. *Oikos* 83:65-74.

Molina, R., H.B. Massicotte, and J.M. Trappe. 1992. Specificity phenomena in mycorrhizal symbiosis: Community-ecological consequences and practical implications. Pages 358-423 in E.M. Allen, ed. *Mycorrhizal functioning*. Chapman & Hall, New York.

Molvar, E.M, R.T. Bowyer, and V. Van Ballenberghe. 1993. Moose herbivory, browse quality, and nutrient cycling in an Alaskan treeline community. *Oecologia* 94:472-479.

Olson, B.E., and R.T. Wallander. 1997. Biomass and carbohydrates of spotted knapweed and Idaho fescue after repeated grazing. *Journal of Range Management* 50:409-412.

Olson, B.E., and R.T. Wallander. 2002. Does ruminal retention time affect leafy spurge seed of varying maturity? *Journal of Range Management* 55:65-69.

Olson, B.E., R.T. Wallander, and R.W. Kott. 1997. Recovery of leafy spurge seed from sheep. *Journal of Range Management* 50:10-15.

Parks, C.G., L. Bednar, and A.R. Tiedemann. 1998. Browsing ungulates—an important consideration in dieback and mortality of Pacific yew (*Taxus brevifolia*) in a northeastern Oregon stand. *Northwest Science* 72:190-197.

Pastor, J., and Y. Cohen. 1997. Herbivores, the functional diversity of plants species, and the cycling of nutrients in ecosystems. *Theoretical Population Biology* 51:1-15.

Pastor, J., R.J. Naiman, B. Dewey [et al.]. 1993. Moose browsing and soil fertility in the boreal forests of Isle Royale National Park. *Ecology* 74: 467-480.

Pimental, D., L. Lach, R. Zuniga, and D. Morrison. 2000. Environmental and economic costs of non-indigenous species in the United States. *BioScience* 50:53-65.

Pimm, S.L. 1984. The complexity and stability of ecosystems. *Nature* 307:321-326.

Quigley, T.M., and S.J. Arbelbide. 1997. An assessment of ecosystem components in the interior Columbia basin and portions of the Klamath and Great Basins. Gen. Tech. Rep. PNW-GTR-405. USDA Forest Service, Pacific Northwest Research Station, Portland, OR.

Rambo, J.L., and S.H. Faeth. 1999. The effect of vertebrate grazing on plant and insect community structure. *Conservation Biology* 13:1047-1054.

Reimoser, F. and H. Gossow. 1996. Impact of ungulates on forest vegetation and its dependence on the silvicultural system. *Forest Ecology and Management* 88:107-119.

Riggs, R.A., A.R. Tiedemann, J.G. Cook [et al. 2000]. Modification of mixed-conifer forests by ruminant herbivores in the Blue Mountains Ecological Province. Research Paper PNW-RP-527. USDA Forest Service, Pacific Northwest Research Station, Portland, OR.

Rosentreter, R. 1994. Displacement of rare plants by exotic grasses. Pages 170-175 in S.B. Monsen and S.G. Kitchen, eds. Proceedings--ecology and management of annual rangelands. General Technical Report INT-GTR-313. USDA Forest Service, Intermountain Research Station, Ogden, UT.

Schiffman, P.M. 1997. Animal-mediated dispersal and disturbance: driving forces behind alien plant naturalization. Pages 87-94 in J.O. Luken and J.W. Thieret, eds. Assessment and management of plant invasions. Springer-Verlag, New York.

Schulz, T.T., and W.C. Leininger. 1990. Differences in riparian vegetation structure between grazed areas and exclosures. *Journal of Range Management* 43(4):295-299.

Sheley, R.L., B.E. Olson, and L. Larson. 1997. Effect of weed seed rate and grass defoliation level on diffuse knapweed. *Journal of Range Management* 50: 39-43.

Sheley, R.L., and J.K. Petroff, eds. 1999. Biology and management of noxious rangeland weeds. Oregon State University Press, Corvallis, OR.

Stohlgren, T.J., L.D. Schell, and B.V. Heuvel. 1999. How grazing and soil quality affect native and exotic plant diversity in Rocky Mountain grasslands. *Ecological Applications* 9:45-64.

Thill, D.C., D.L. Zamora, and D.L. Kambitsch. 1986. The germination and viability of excreted common crupina (*Crupina vulgaris*) achenes. *Weed Science* 34:237-241.

Vallentine, J.F., and A.R. Stevens. 1994. Use of livestock to control cheatgrass--a review. Pages 202-206 in S.B. Monsen and S.G. Kitchen, editors. Proceedings--ecology and management of annual rangelands. General Technical Report INT-GTR-313. USDA Forest Service, Intermountain Research Station, Ogden, UT.

Vesk, P.A., and M. Westoby. 2001. Predicting plant species' responses to grazing. *J. of Applied Ecology* 38:897-909.

Vitousek, P.M., C.M. D'Antonio, L.L. Loope, and R. Westbrooks. 1996. Biological invasions as global environmental change. *American Scientist* 84:468-478.

Vitousek, P.M., and L.R. Walker. 1989. Biological invasion by *Myrica faya* in Hawai'i: Plant demography, nitrogen fixation, ecosystem effects. *Ecological Monographs* 59:247-265.

Wallander, R.T., B.E. Olson, and J.R. Lacey. 1995. Spotted knapweed seed viability after passing sheep and mule deer. *Journal of Range Management* 48:145-149.

Weisberg, P.J., N.T. Hobbs, J.E. Ellis, and M.B. Coughenour. 2002. An ecosystem approach to population management of ungulates. *Journal of Environmental Management* 65:181-197.

Westbrooks, R. 1998. Invasive plants, changing the landscape of America. Fact Book. Federal Interagency Committee for the Management of Noxious and Exotic Weeds (FICMNEW), Washington, DC. 109 pp.

Wisdom, M.J. 1998. Assessing life-stage importance and resource selection for conservation of selected vertebrates. Ph.D. dissertation, University of Idaho. Moscow, Idaho.

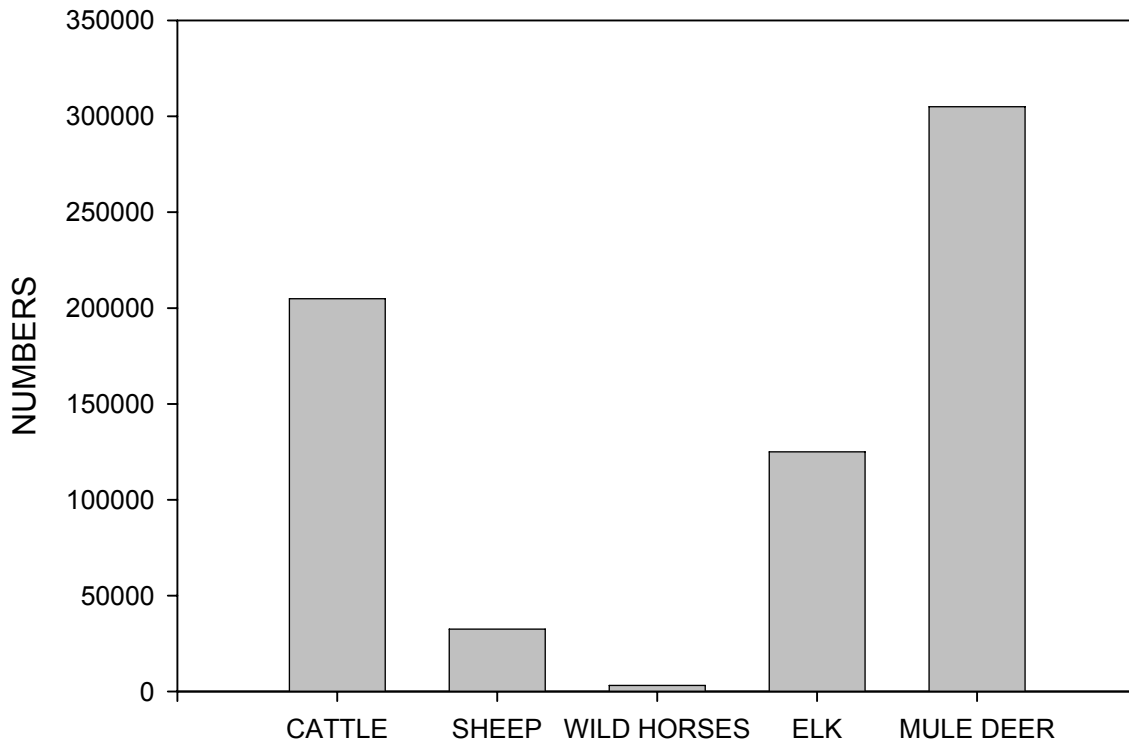


Figure 1. Numbers of ungulates that spend some time each year on public lands in Oregon. Based on 2001 data from Oregon Department of Fish and Wildlife reports and U.S. Forest Service national grazing statistics.

| Ungulate Type | Number of Animals | Area(km ²) | | Density | |
|------------------------------|----------------------|-------------------------|--------------|----------------------|----------------------|
| | | Total range | Winter range | Total range | Winter range |
| Mule Deer^a | 36,680 | 18,076 | 7,543 | 2.03/km ² | 4.86/km ² |
| Elk^b | 19,740 | 13,497 | 5,869 | 1.46/km ² | 3.36/km ² |
| Cattle^c | 24,150 | 7,725 | _____ | 3.13/km ² | _____ |
| Total | 80,570 | 39,298 | 13,412 | 6.63/km ² | 8.22/km ² |

Table 1. Density of grazing ungulates on the Wallowa Whitman National Forest in northeast Oregon

^a1998 population census (personal communication, Tim Schommer, Wallowa Whitman National Forest)

^b 2000 population census (personal communication, Tim Schommer, Wallowa Whitman National Forest)

^c2001 grazing statistics, Wallowa Whitman National Forest