

Plant-animal interactions affecting plant establishment and persistence on revegetated rangeland

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Abstract

The role of ungulate grazing in shaping rangeland ecosystems is well known relative to other important plant-animal interactions such as pollination, seed dispersal, granivory, and belowground herbivory. Successful rangeland revegetation may be enhanced by strategies that favor certain groups of animals and discourage others. Many perennial forbs and shrubs require animals for successful pollination, reproduction, and subsequent maintenance of species on a site; however, pollination biology of many rangeland plants and pollinator abundances at potential revegetation sites are largely unknown. Granivory may be significant in some locations and planning and design of revegetation areas may be improved by implementing principles of seed escape mechanisms, such as predator satiation, seed escape in space (low perimeter-to-area ratio for revegetation site), and seed escape in time (synchronous or staggered timing for nearby revegetation sites). Seedling establishment may be associated with invertebrate population levels which need to be considered in future revegetation projects. Timing and site preparation are important in limiting belowground herbivory. Animals can serve as dispersal agents of seeds. Livestock dosed with desirable seeds can disperse them in their dung across the landscape, thereby creating patches of desirable plants. If revegetation sites will be grazed by livestock, then managers should choose plant species that tolerate rather than avoid grazing and should apply adequate management to establish and maintain plant populations. Seeds inoculated with mutualistic species such as mycorrhizae, nitrogen-fixing bacteria, or actinomycetes may enhance establishment, productivity, and nutrient quality of rangeland species while increasing rates of succession.

Key Words: defoliation, granivory, grazing, pollination, revegetation, seed dispersal, seed predation

An awareness of the dynamic interactions between plants and the heterotrophs which use them (e.g., microbes, granivores, frugivores, folivores, etc.) is central to understanding processes that regulate ecosystem structure, population dynamics, the flow of energy and the cycling of nutrients through time (see Crawley 1983). The role of herbivores in shaping ecosystem characteristics via grazing activities has been well-studied relative to other important plant-animal interactions such as microbial associations, pollination, seed predation, and seed dispersal. In our tendency to focus on how grazers modify plant species composition and productivity, we often overlook the reverse consideration that the mixture of plant species or of growth forms may dictate the kind and abundance of animals utilizing a site.

The success of restoration and reclamation efforts may be enhanced by formulating strategies which may favor certain

groups of animals and discourage others. For example, seed predation might be reduced by encouraging animals that prey upon granivores. Providing perching structures for birds of prey might also encourage frugivorous passerines to rest and defecate seeds on reclaimed sites, thereby enhancing plant immigration and species diversity (McDonnell and Stiles 1983, Vander Wall and MacMahon 1984). Strategies to encourage the dissemination of desirable or to discourage the dissemination of undesirable seeds by livestock may also warrant consideration. In a companion paper (Pyke and Archer 1991), we discussed interactions among autotrophic organisms in relation to plant establishment on revegetated rangeland. In this paper, we will address animal impacts on seedling establishment, where the term animal will take a broad definition including heterotrophic microbes such as fungi and bacteria.

Plant-Microbe Associations

The importance of plant-microbe relationships in ecosystem structure and function is widely recognized. In disturbed ecosystems, reductions in plant biomass reduce energy for soil organisms. Microbes associated with plants (rhizosphere organisms), do not, in general, appear to successfully switch from living plant substrates to detritus (Corman et al. 1987, Janos 1988, Perry et al. 1987). As a result, their abundance is linked directly to plant abundance and physiological activity. Reductions in activity of mutualistic or free-living rhizosphere microbes can subsequently influence soil fertility (e.g., by influencing nitrogen fixation) and structure (e.g., aggregate stability [Lynch and Bragg 1985]) and thus, the capacity of soils to store and deliver resources. The absence of microbes (e.g., mycorrhizae) can severely limit seedling establishment, plant growth, and plant survival. As a result, the success of revegetation efforts may be significantly influenced by the extent to which microbial activity in soils has been affected and by the extent to which linkages between plants and soil organisms are subsequently restored (Perry et al. 1989).

Vesicular-arbuscular (VA) mycorrhizae and symbiotic nitrogen-fixing bacteria (*Rhizobium* spp.) or actinomycetes (e.g., *Frankia* spp.) may enhance host and nonhost plant establishment, increase productivity, enhance exploitation of soils for water and nutrients, increase nutrient quality of foliage, and increase rates of succession on reseeded sites (Parker and Chatel 1982, Miller 1987, Allen 1988). These root symbionts may be particularly important to seedlings, which have less storage tissue and smaller root systems than adult plants (St. John and Coleman 1983). Most inferences regarding the importance of root symbionts to nutrient uptake and plant production are based on examinations of surficial roots or on estimations of symbiont abundance in surficial soils. Rhizobial populations are often small or nondetectable under these circumstances; however, inferences based on these criteria may underestimate the importance of microbe-root associations. Large rhizobial populations and viable root nodules may occur deeper in the soil profile (e.g., 2 to 10 m for honey mesquite [*Prosopis glandulosa* Torr.]) where moisture conditions are more favorable and nutrient concentrations rarely reach inhibitory levels (Virginia et al. 1986, Jenkens et al. 1988, Johnson and Mayeux 1990).

Mycorrhizae, rhizobium, and actinomycetes are facultative symbionts that may or may not be present in rangeland soils in

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adequate numbers and of the appropriate species before reseeding. Levels of mycorrhizal infection can vary significantly between soils (Frankland and Harrison 1985). Erosion and soil disturbances can reduce the inoculation by VA mycorrhizae (Moorman and Reeves 1979, Powell 1980, Allen 1988), and *Rhizobium* (Trinick 1982, Lowther et al. 1987a,b) when native populations of these microbes do exist. Where microbial populations have been substantially reduced by severe disturbance, the probability and rate of spore dispersal into a site will depend on the geographic scale of the disturbance and on the proximity to less disturbed areas which serve as sources of spores (E. Allen 1989). Poor legume establishment on freshly plowed land in western Australia was attributed to soil fungi that produced antibiotics which inhibited *Rhizobium* growth (Holland 1966, Holland and Parker 1966). Plant establishment was enhanced by applying a fungicide or by allowing the field to remain fallow until the fungi became less prevalent.

Site conditions may dictate levels of infection, reproduction, and nutrient acquisition by these microbes. Soil pH influences the success of infection of several species of VA mycorrhizal fungi and *Rhizobium* and influences their saprophytic growth with host plants (Porter et al. 1987a,b, Rice et al. 1977). Post-establishment persistence and spread of alfalfa (*Medicago sativa* L. and *M. falcata* L.) inoculated with *Rhizobium* may depend on seedlings emerging within interplant zones and becoming infected with effective *Rhizobium*. *Rhizobium* density may decrease with increasing distance from inoculated plants, such that soil samples 50 to 100 cm from inoculated plants contain no *Rhizobium* (Lowther et al. 1987b). While seeds inoculated with VA mycorrhizae or with nitrogen-fixing bacteria before dissemination can facilitate plant-microbe symbiosis (Alexander 1977), this technology is available for only a few species (M. Allen 1989).

Establishment and persistence of vascular plants in restoration projects might be facilitated if concentrated efforts were made to introduce free-living nitrogen-fixing bacteria, lichens, or blue-green algae. Cryptogamic crusts may offer particular potential since they enhance surface soil stability, improve water infiltration, and provide pulsed inputs of plant-available nitrogen (Loope and Gifford 1972, Rychert and Skujins 1974, Kleiner and Harper 1977). Establishment of cryptogamic crusts in early stages of restoration may enhance chances for successful seedling establishment and for subsequent plant growth and reproduction (St. Clair et al. 1984).

Pollination

Persistence of a species on a site depends on vegetative regeneration, on the production of new offspring from seed, or on both. Long-lived perennials in arid and semiarid systems may endure adverse conditions and persist by vegetative propagation until the occurrence of a rare window of opportunity for seedling establishment. Allocation of resources to annual flower and seed production may be rather high since the appearance of such windows is unpredictable. Although the resource status of a plant strongly influences its seed output (Stephenson 1981), pollinator service and flower:pollinator ratios may also be important determinants of levels of seed production (Simpson et al. 1977, Silander and Primack 1978, Zimmerman 1980). In some cases, plants may compete for pollinators as well as for light or soil resources (Waser 1978).

Most grasses used in revegetation of rangelands are wind pollinated and are not dependent on animals. In contrast, many perennial forbs and shrubs are insect pollinated and are facultative or obligate outcrossing plants. Cross-pollination is desirable, since the offspring of self-pollinated plants may suffer inbreeding depression. The availability of pollinators for many plants may not be a problem (Bierzychudek 1981, 1982). Pollination success in other cases may largely depend on the presence of a certain insect

species (Augspurger 1980, 1981). The pollination biology of many rangeland plants is largely unknown. In addition, the functional abundance of pollinators on sites slated for restoration may be difficult to determine. In the absence of such information, inferences may be drawn from small-plot experiments where resource limitations to seed production are overcome. If seed production among plants on such plots remains low, the possibility of inadequate pollination should be considered.

Seed Predation

Seeds are subject to predation before, during, and after dispersal (Janzen 1971). The primary granivores of arid and semiarid regions of North America are rodents, whereas in South America, Australia, and Africa ants may be the primary seed predators (Mares and Rosenzweig 1978, Buckley 1982). Levels of seed predation by rodents may be particularly high in disturbed habitats, which may serve as dispersal sinks (Martell 1983). Where granivores are abundant, the composition and spatial pattern of vegetation may reflect seed consumption and the differential distribution of seed predators as well as edaphic variation and interspecific competition (e.g., Bartholomew 1970, Louda 1982, Smith et al. 1989). Rodents and ants have been shown to decrease seed reserves in annual grasslands and desert annual communities by 30 to 80% (Batzli and Pitelka 1970, Nelson and Chew 1977, Borchert and Jain 1978, Reichman 1979, Abramsky 1983). In old-field communities, forb seeds were removed at rates of 3 to 45% per day (Mittlebach and Gross 1984). Seed predation is potentially a major factor contributing to the failure of vegetation establishment when seed is broadcast (Nelson et al. 1970), but drilling of seeds may not insure their escape from predators. Excavation of buried seeds, especially large seeds like vetch (*Vicia* spp.), is known to occur (Reynolds 1950, 1958). Applications of rodenticides and colored dyes have been suggested to reduce seed losses due to rodents and birds during revegetation (Valentine 1989), but these may not be economically feasible.

There are several evolutionary mechanisms which enable seeds to persist in the face of predation. Janzen (1970) has proposed 2 escape mechanisms: escape in space and in time. Escape from predators in space can occur when seeds are dispersed away from parent plants or from cover which may harbor predators (Wilson and Janzen 1972, Webb and Wilson 1985). In planning revegetation areas, a site with a low perimeter-to-area ratio (e.g., large, circular area) will provide escape in space for the majority of seeds by providing a smaller edge from which predators may penetrate the revegetation area. Escape from predators in time can result when seeds are dispersed at unpredictable times or at times when predators are not abundant. Escape can also occur when plants produce more seeds than predators can consume. Known as predator satiation, this phenomenon is exemplified by mast seeding in trees, which appears to correspond to random fluctuations in weather (Silvertown 1980). Predators surviving lean periods between crops will be swamped by food in mast years.

Application of these concepts to revegetation would involve documenting seasonal population dynamics of seed predators to assure that sowing and germination of seeds would occur during periods of low predator abundance. Where adjacent sites are slated for revegetation, seed should be sown in all sites in the same year. This synchronous approach to revegetation will minimize the likelihood that seed predator populations will increase or be maintained over a series of years as might be the case where the same (or a greater) number of seeds are sown in different locations over a series of years. A synchronous approach is similar to the evolved mechanism of synchronous seed production found in bamboo (Janzen 1976). An alternative method of revegetating adjacent sites would be to stagger revegetation so that granivore populations on the treated site return to pre-reseeding levels before nearby sites are

seeded. Providing perching or nesting structures (natural or artificial) for raptors (MacMahon 1987) or approach cover for fox, coyote, bobcat, etc., may help increase predation on granivorous rodents and mitigate their impact. Providing alternative, preferred foods for granivores can reduce the seed consumption of desirable species in the short term, therefore allowing desirable seeds to germinate before predator populations increase. For example, survival of Douglas fir seed was improved from 5 to 50% by providing sunflower seeds in clear-cut areas of forest (Sullivan 1979). Allowances for seed predation should be taken into account when estimating seeding rates that may be required to achieve desired plant densities.

Seed Dispersal

Dispersal of plant propagules (see review by van der Pijl 1972 and Willson et al. 1990) is of central importance in succession and restoration. This is especially true when dealing with large areas where it is not economically feasible to conduct extensive reseeding or when the probability of achieving successful establishment in any given year is low. In such cases, one strategy might be to concentrate resources such that plant establishment is facilitated on smaller patches arranged in a pattern across the landscape. These intensively managed patches could then serve as nuclei of seed production and as future sources of propagules for the surrounding area. Such patches might be initiated from seed or via transplantation of entire plants, plugs, or sods using specialized equipment (DePuit 1988). Groups of tree and shrub species and their associated soils have been transplanted on mined lands using tree spades and front-end loaders (McGinnies and Wilson 1982). Although labor intensive and costly, transplant approaches may ensure ecotypic adaptation, introduction of soil microorganisms, introduction of species that are incapable of rapid establishment from seed, and ensure the establishment of larger plants that are more capable of coping with competition and herbivory.

Moody and Mack (1988) analyzed factors that contribute to the spread of invading plants by simulating various regimes of repeated control. Control regimes included reducing the area of the main stand or destroying some proportion of the smaller satellite stands. Results indicated that spread of species was primarily regulated by the dynamics of satellite stands rather than expansion of the initially large stand. Their simulations suggest that the rate of spread of desirable species might be enhanced by concentrating resources (e.g., seed, fertilizer, and water) to facilitate the development of satellite stands that could subsequently produce seed for natural dispersal rather than spreading those same resources uniformly across an area. Determining the size and arrangement of satellite patches on the landscape falls under the purview of landscape ecology (Neveh and Lieberman 1984, Forman and Godran 1986, Urban et al. 1987) and will not be explored in this paper. A knowledge of seed dispersal patterns and processes would be useful when planning and designing the placement of patches or satellite stands on the landscape. Wind and water are important vectors of seed dispersal for many species. In this paper, we will focus on animals as dispersal agents. Although opportunities exist to utilize wild and domestic animals as agents of seed dispersal to enhance restoration efforts, these must be weighed against negative aspects that may jeopardize the success of the restoration effort (e.g., granivory, dispersal of undesirable species, and excessive herbivory on desirable species).

The relative effectiveness of various agents of seed dispersal are difficult to evaluate, since there is no necessary correlation between numbers of seeds distributed by a particular agent and the value of that form of dispersal (Davidson and Morton 1984). The most effective agent of seed dissemination would transport large numbers of seeds and would deposit them in a germinable form in a microenvironment suitable for establishment. Thus, an animal

that simply transports large numbers of seeds is not necessarily an effective agent of dispersal. Conversely, animals that transport relatively fewer seeds are not necessarily poor vectors.

There is a fine line separating seed predation from seed dispersal in many instances. Seeds dispersed by some animals may escape predation by others. Seeds that escape mastication after ingestion by animals may be regurgitated or survive passage through the digestive tract and be deposited with feces. Ants in some cases (myremecochory), discard seeds after nutrients have been extracted from external structures (elaiosomes). Granivorous rodents may place seeds in caches where seeds may remain unutilized. Recruitment could be enhanced in each of these cases if probabilities of seed germination and seedling establishment were increased relative to those of undispersed seed.

There are numerous examples demonstrating enhanced germination among seeds manipulated by animals relative to seeds not manipulated (Howe and Smallwood 1982). Enhanced establishment could also be achieved if dispersed seeds were consistently deposited in "safe sites" (Harper 1977). Safe sites for establishment may occur away from conspecific adults which harbor seed or seedling predators or may occur in selected habitats and microsites where resource availability is greater. For example, caching by rodents may result in seeds being buried at depths conducive to germination (Howe 1977), in the placement of seeds in microsites where seedling survival may be enhanced as a result of better light or soil properties, and in escape from seed and seedling predators associated with parent plants (Janzen 1970, Lignon 1978, Webb and Wilson 1985, Howe et al. 1985). Seed-caching or scatterhoarding by rodents has been implicated as important for indian ricegrass (*Oryzopsis hymenoides* (R. & S.) Ricker; McAdoo et al. 1983), bitterbrush (*Purshia tridentata* (Pursh) DC.; West 1968), creosotebush (*Larrea tridentata* (DC) Cov.; Chew and Chew 1970, Sheps 1973), *Opuntia* spp. and mesquite (*Prosopis juliflora* (Sw.) DC.) (Reynolds and Glendening 1949, Reynolds 1950), and oak (*Quercus* spp.) and beech (*Fagus* spp.) (Jensen 1985, Miyaki and Kikuzawa 1988). Smith and Reichman (1984) present an in-depth review of seed caching by birds and mammals.

Other factors held equal, recruitment on a site could be increased by increasing the immigration of seeds. This could be achieved in several ways. One approach would be to design the size, arrangement and density of seed-producing "islands" on a site so as to reduce distances seeds must travel. Where animals are important agents of dispersal, provisions for suitable cover and food should be made in reclamation plans. For example, the seed rain of bird-dispersed plants into abandoned fields was increased an order of magnitude when natural and artificial perching structures were provided (McDonnell and Stiles 1983).

Given the large numbers and high concentrations of livestock on many rangelands, their role in seed dispersal warrants specific consideration. Seed dispersal by adhesion (epizoochory) is an evolved adaptation of many low-statured plants of woodlands and disturbed areas (Sorenson 1986), and livestock have contributed to the introduction and spread of exotic weeds via this dispersal method (Benson and Walkington 1965, Mack 1981). Observations of large numbers of seedlings of *Prosopis* and *Acacia* spp. emerging from dung of ungulates have been made on 4 continents (Paulsen 1950, Lamprey et al. 1974, Gutierrez and Armesto 1981, Harvey 1981) and the rapid spread of these hard-seeded legumes is testimony to the effectiveness of livestock as dispersal agents (Brown and Archer 1987). Livestock grazing in autumn or winter breaks inflorescences of crested wheatgrass (*Agropyron desertorum* (Fisch. ex Link) Shultz.), thereby increasing the potential for germination of seeds retained on the spike by placing them in contact with soil (Pyke 1990). In this example, season of grazing is an important consideration.

Ungulates may also ingest and disperse seeds of a variety of herbaceous species while consuming foliage (Janzen 1984); however, there have been few attempts to use this knowledge of livestock as agents of seed dispersal to aid the establishment and spread of desirable species. Livestock could be strategically fed seeds of desirable species or allowed to graze in areas where the density of desirable, seed-producing plants is high. Once dosed, animals could be released to disseminate seeds into areas targeted for improvement.

This approach, if successful, could potentially offer several biological and economic advantages over conventional reseeding approaches. The most extensive and least expensive methods of seed application (e.g., broadcast seeding) typically meet with the lowest success. Practices ensuring good seed-soil contact are expensive and difficult to apply extensively, especially where brush, rocks, and rough topography predominate. In contrast, a potentially significant proportion of seeds ingested by cattle would be deposited in a moist, nutrient-rich medium that may facilitate germination and establishment. Depending on rate of seed passage and on patterns of animal movement, viable seeds could be distributed over large areas for several days after dosing. The cost of this approach would be relatively low. Emergence of seedlings in dung may occur over long periods, especially where hard-seeded species are involved. The result could be the development of a high density of patches of desirable species that could subsequently serve as local seed sources in the community. For this scheme to work, grazing management would have to be closely regulated, especially at the critical seedling establishment stage, so that livestock did not over-utilize and eliminate the very plants they were spreading.

Major questions relative to actively utilizing livestock as agents of seed dispersal of desirable species pertain to seed survival, to the rate of passage through the digestive tract (a function of seed size, hardness and specific gravity, and of animal diet), to rates of germination in dung, and to subsequent seedling establishment (Fig. 1). Soft-seeded species may lose viability and germinability

1985, Simao Neto et al. 1987, Jones and Simao Neto 1987). Results to date suggest sufficient potential to warrant continued investigation.

Herbivory

Herbivory is the main plant-animal interaction which has been investigated in rangeland ecosystems. Activities of root-feeding nematodes, leaf-chewing grasshoppers, termites, herbivorous rodents, lagomorphs, and large mammals interact with livestock to affect rangeland vegetation. Seasonal and annual fluctuations in the abundance of arthropod and wildlife populations are difficult to obtain. As a result, estimates of numbers of these organisms and of their impact on plants relative to that of livestock is difficult to determine.

The debate over the effects of grazing (positive, neutral, negative) with regard to aboveground net primary production (Belsky 1986, 1987, McNaughton 1986) is often confounded by comparing across levels of organization (e.g., individual plants versus plant communities) and across gradients of resource availability. In addition, the debate may be largely academic for arid and semiarid regions where livestock grazing intensity is usually far in excess of that which might optimize aboveground net primary production (Piper and Heitschmidt 1988). Community-level response to grazing will vary, depending upon the evolutionary history of the species and the systems in which they occur (Milchunas et al. 1988). Plant response to herbivory will depend on an array of interacting factors including the frequency, magnitude, and season of tissue removal; the type of plant part(s) lost; levels of resource availability and competition; and stage of life cycle (Archer and Smeins 1991, Briske 1991). Species-rich plant communities are potentially more resilient than species-poor communities following grazing (Brown and Ewel 1988).

Most research has emphasized the effects of aboveground grazers on vegetation, but belowground herbivores may consume more plant material (Coleman et al. 1976, Stanton 1988). Nematodes, grass grubs (beetle larvae in Scarabacidae), and scarab larvae (*Phyllophaga crinita* (Burm.)) that consume roots cause significant plant mortality and reductions in shoot production (Ueckert 1979, Detling et al. 1980, Stanton et al. 1981). Estimates of decreased plant production resulting from nematode herbivory range from 6-13% in grassland ecosystems (Ingham and Detling 1984) to 1-10% in agricultural systems (Sohlenius et al. 1988). Aboveground grazing on grasses appears to increase their susceptibility to parasitic nematodes belowground (Stanton 1983, Ingham and Detling 1984). Methods for preparing a site for revegetation that kill the existing vegetation may reduce numbers of belowground herbivores by reducing their food supply. However, if seeds are sown and germinate before reductions in these invertebrate populations occur, or are sown into land with existing vegetation, then these unseen organisms could potentially limit the establishment of seedlings. This is an area of limited research and warrants further study.

Plant adaptations to herbivory fall into 2 major categories: grazing tolerance and grazing avoidance (Table 1). Grazing tolerant plants have characteristics that facilitate the reestablishment of foliage following grazing, whereas plants that avoid grazing have morphological or physiological characteristics (e.g., thorns, secondary chemical compounds) that minimize the probability of defoliation (Archer and Tieszen 1980, Mooney and Gulmon 1982, Briske 1986). Plants with traits conferring grazing avoidance are typically stress tolerators, whereas plants tolerant of defoliation often have characteristics of competitive plants (Pyke and Archer 1991). Trade-offs between competitive ability and tolerance to defoliation may also exist. Windle and Franz (1979) found that cultivars susceptible to insect attack were the superior competitors

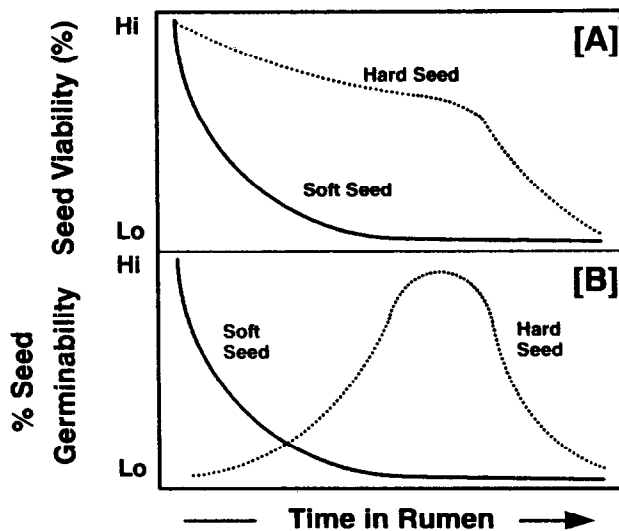


Fig. 1. Hypothetical functions for ingested seeds relating changes in seed viability and germinability to time in rumen.

quickly. Species with hard seed coats may lose viability more slowly. However, seeds passing through the rumen quickly may not be scarified and hence have low germinability. Once scarified in the rumen, additional time in the rumen may be detrimental to seed viability and germinability (Fig. 1). These issues have been addressed to varying degrees for some plant and livestock species (Burton and Andrews 1948, Yamada and Kawaguchi 1972, Welch

Table 1. Characteristics of plants that resist grazing either by tolerating or avoiding defoliation (adapted from Briske 1986).

Grazing tolerance	Grazing avoidance
	Morphological
High number of active meristems present after grazing.	Horizontal leaf and branch angles.
Axillary buds near soil surface or on less preferred branches.	High stem and sheath to leaf blade ratio.
	Prostrate growth form.
	Mechanical defenses — e.g., awns, pubescence, spines and thorns.
	Small foliage elements.
	Physiological
High relative growth rate.	High content of lignin, silica or epicuticular waxes.
High nutrient reserves.	
High carbohydrate reserves?	High levels of secondary compounds.

in the absence of insect pests; when insect interactions occurred, grazing-resistant cultivars replaced the more grazing-sensitive cultivars. The relative merits of adaptations conferring competitive ability versus tolerance to herbivory must therefore be considered in relation to the probability of the plant being defoliated at a given frequency and intensity.

The importance of carbohydrate reserves for regrowth in grazing tolerant plants has been a widely taught concept in range management (Stoddart et al. 1975, Holechek et al. 1989); however, experiments involving dark regrowth of plants and involving grafting indicate that the role of carbohydrate reserves may be less important than shoot characteristics that favor rapid regrowth following grazing (Richards and Caldwell 1985, Fankhauser and Volenec 1989). High frequency, high intensity defoliation of water sedge (*Carex aquatilis* Wahlenb.) tillers over 2 consecutive growing seasons reduced leaf production only on nonfertilized plots, suggesting that nutrients rather than declining plant carbohydrate reserve levels were limiting plant regrowth following defoliation (Archer and Tieszen 1986). Nutrient and moisture limitations to plant growth under field conditions are accentuated by reductions in root initiation, extension, and activity which accompany defoliation (Archer and Tieszen 1983, Richards 1984). Genotypes of perennial ryegrass (*Lolium perenne* L.) with high root to shoot ratios were found by Troughton (1973) to be least sensitive to defoliation, reflecting the importance of roots in plant recovery from grazing. Functional differences in the ability of species to maintain root activity and mass following grazing (Caldwell et al. 1987) are surely an important component of grazing tolerance, but are largely unknown.

Species whose adaptations to the prevailing climate and soils would make them the competitive dominants of the community under conditions of light grazing may assume subordinate roles or face local extinction as grazing intensity increases. Up to a point, grazing may substitute for death or reductions in growth and recruitment that might otherwise be produced by density alone. Grazing may adversely affect plant growth rates, viable seed production, seedling establishment, vegetative regeneration, and plant longevity or survival directly or indirectly (Crawley 1983, Archer and Tieszen 1986). Direct effects are those associated with alterations in plant physiology and morphology resulting from defoliation (Briske 1991). Alterations in microclimate, soil physicochemical properties and plant competitive interactions constitute indirect effects which influence plant response to leaf removal and seedling establishment (Archer and Smeins 1991).

Plants that decrease under grazing do so either because they are intolerant of defoliation or because they are highly preferred and are grazed more heavily than other plants. Inherent morphological

and physiological adaptations for tolerance to herbivory must therefore be evaluated in the context of relative grazing intensity among species in a stand. Plants which are highly tolerant of defoliation will be disadvantaged when competing with associated species which, although less tolerant of grazing, may be defoliated less frequently or intensely (Mueggler 1972, Archer and Detling 1984, Caldwell 1984). For this reason, species chosen for revegetation of rangelands that will be grazed should be dominated by plants with adaptations conferring grazing tolerance. Mixing grazing-tolerant and grazing-avoidance species will inevitably lead to dominance by species which avoid grazing.

Grazing during early stages of seedling establishment may be considered predation based on the strict definition by Thompson (1982) if it causes death of the plant. Seedlings are particularly sensitive to herbivory in that they have low levels of nutrient or energy reserves and shallow, low-density root systems relative to adult plants. Stage of root development is important for anchoring grazed plants. Meadow voles (*Microtus montanus* Peale) are capable of uprooting grass seedlings during the grazing process (Pyke 1987). Species differ in how soon after germination they can be grazed without being uprooted. The desire to have livestock graze plants as early as possible after revegetation has led to the development of grasses such as 'Hycrest' crested wheatgrass (*Agropyron cristatum* (L.) Gaertn. × *desertorum*). The lateral root production of 'Hycrest' is similar to that of cheatgrass (*Bromus tectorum* L.) (Aguirre and Johnson 1991) indicating that these species may be similar in their ability to resist uprooting while young.

Differences in seed size within and between species affects the rate and timing of germination and the subsequent growth rate and competitive ability of seedlings. There is generally a direct relationship between seed size and seedling performance (Harper 1977). As a result, use of large-seeded taxa with their greater seedling growth rates, may improve chances of establishment in the face of herbivory, competition, and various abiotic stresses. Defoliation can influence subsequent seedling recruitment and stand dynamics by reducing the number and size of seeds that plants produce (Crawley 1983, Jameson 1963, Maun and Cavers 1971a,b).

Because plants are relatively sensitive to defoliation early in their life cycle, deferment of grazing is often helpful, if not necessary, to ensure plant establishment. Deferment during early stages of restoration represents a "cost" in terms of missed opportunity (e.g., loss of revenue) and in terms of expenditures associated with supplementation or boarding of animals elsewhere. However, if grazing too soon after seeding significantly jeopardizes plant establishment, then the restoration effort is doomed to economic failure from the outset. Similarly, the long-term success of a restoration project will hinge on post-establishment grazing management. Plant recovery from grazing can be enhanced while persistence, productivity, and botanical composition can be sustained, but only if proper stocking rates are maintained. This requires matching grazing and rest intervals with the phenology and life history attributes of key plant species (Holechek 1983, Valentine 1989, Heitschmidt and Stuth 1991).

Conclusions

Land managers in the past selected species for revegetation by relying heavily on phytosociological correlations between late-successional species and their environment. Although phytosociology is important in species selection, the land manager of the future should be more like a repair person than a sociologist (Harper 1987). If a piece of equipment is broken, the repair person need not categorize or correlate the equipment (vegetation community) with the place it is used (environment) to fix it. They require a kit of appropriate tools and components and they require a knowledge of the mechanisms that interact in the equipment to

make it work. Land managers require certain tools and components (e.g., plant materials, nutrients, equipment) to use in conjunction with a knowledge of ecosystem processes for successful rangeland revegetation or restoration.

An understanding of plant autecology and plant-environment relationships is crucial to the success of restoration efforts. Biotic interactions, both plant-plant and plant-animal, will operate against a backdrop of edaphic and climatic constraints to further regulate and determine patterns of species distribution, abundance, and persistence over time. Much of our knowledge of the outcome of biotic interactions has come from and will continue to come from attempts to solve applied problems (Harper 1987, Slobodkin 1988) such as those associated with the reconstruction of vegetation communities on disturbed lands. In addition, revegetation and restoration projects offer unique opportunities to investigate species interactions at spatial and temporal scales not generally available in most research environments. Properly designed baseline studies aimed at ascertaining the mechanisms involved in biotic interactions would make a significant contribution to our working knowledge of ecological principles pertinent to rangeland revegetation and restoration.

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