

## UNGULATE EFFECTS ON THE FUNCTIONAL SPECIES COMPOSITION OF PLANT COMMUNITIES: HERBIVORE SELECTIVITY AND PLANT TOLERANCE

DAVID J. AUGUSTINE,<sup>1</sup> Biological Research Laboratories, Syracuse University, Syracuse, NY 13244, USA  
SAMUEL J. McNAUGHTON, Biological Research Laboratories, Syracuse University, Syracuse, NY 13244, USA

**Abstract:** Large mammalian herbivores not only depend on plant communities for their existence but cause major changes in plant community composition and structure. These changes have direct consequences for ecosystem processes, but recent studies of ungulate–ecosystem relations show widely divergent ungulate effects in different ecosystems. We reviewed studies of ungulate effects on plant community composition to gain insight into potential mechanisms of ungulate-induced changes in both community composition and ecosystem processes. Our analysis of these studies is based on the premise that the effect ungulates exert on plant communities depends on the balance between (1) feeding selectivity of herbivores (i.e., degree to which different plant species or ecotypes experience different levels of tissue loss), and (2) differences among plant species in their ability to recover from tissue loss. A large number of studies clearly show that selective ungulate herbivory leads to the dominance of unpalatable, chemically defended plant species in communities. However, many studies have also demonstrated that intensive long-term herbivory does not lead to the invasion of unpalatable species into the community, and can even increase the dominance of highly palatable species. Our review indicates that high levels of nutrient inputs or recycling and an intermittent temporal pattern of herbivory (often due to migration) are key factors increasing the regrowth capacity of palatable species and hence maintaining their dominance in plant communities supporting abundant herbivores. Key factors limiting ungulate foraging selectivity, again limiting herbivore-induced dominance of slow-growing, unpalatable species, include herding behavior, early growing season and postfire herbivory, asynchronous phenology of palatable versus unpalatable species, and low relative abundance of unpalatable species. Our review indicates differences among ecosystems in the role played by ungulate herbivory result from the relative strength of these factors enhancing plant tolerance to herbivory and limiting foraging selectivity. Anthropogenic changes in these factors (e.g., alteration of migration patterns) therefore have the potential to significantly alter the effects of ungulates on plant communities and ecosystem processes.

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Since the inception of wildlife management as a discipline in North America, researchers have recognized that large mammalian herbivores not only depend on plant communities but also generate strong direct and indirect feedbacks on plant community composition and structure. Today, native ungulate populations in all “natural” ecosystems have been affected by direct management through harvest, or by indirect human effects such as predator extirpation, introduced and controlled parasites, alterations in landscape structure, and food supplementation by agricultural practices. Managing ecosystems for objectives ranging from in-

creased yield of game species to the conservation of nongame species and fundamental ecosystem processes will therefore require a thorough understanding of how changes in ungulate populations and patterns of herbivory interact with and regulate plant communities and ecosystems.

Hobbs (1996) recently outlined how ungulates can influence such ecosystem processes as nutrient cycling, pathways of energy flow, and disturbance regimes. Plant–herbivore relations can play a central role in energy and nutrient cycling because the palatability, growth rate, and decomposition rate of plant species are often linked. When palatability is defined based on the degree to which a species is consumed

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<sup>1</sup> E-mail: djaugust@syr.edu

relative to its abundance, recent studies have documented a clear, positive correlation between palatability and both plant growth rate (Bryant et al. 1989) and decomposition rate (Grime et al. 1996). Many studies of the basis for herbivore selectivity have shown that structural compounds (e.g., lignin) and secondary compounds (e.g., phenolics) reduce plant palatability (Bryant and Kuropat 1980, Schwartz et al. 1980, Cooper and Owen-Smith 1985, Palo 1985, Bryant et al. 1991b, Palo and Robbins 1991, Bryant et al. 1992). These same compounds also reduce litter decomposition rates (Melillo et al. 1982, Flanagan and Van Cleve 1983, McClaugherty et al. 1985, Wedin and Pastor 1993) and plant growth rates (Coley et al. 1985, Herms and Mattson 1992), suggesting that these correlations are widely applicable to plant communities (Bryant et al. 1991b, Pastor and Cohen 1997).

Despite the predictable linkages among plant properties, results from recent ecosystem-level studies show that abundant native ungulate populations can have nearly opposite effects on primary productivity and nutrient flow in different ecosystems (Hobbs et al. 1991, Pastor et al. 1993, Frank and Evans 1997, McNaughton et al. 1997a, Ritchie et al. 1998). Ungulates can alter the flow of energy and nutrients by (1) changing plant species composition of the community, and hence litter inputs from uneaten plants; (2) altering the chemical composition of plant tissues during digestion; (3) altering inputs from eaten plants to the soil due to changes in the root system or leaf-litter quality; and (4) altering plant and soil microenvironments. The latter 3 factors act to increase the rate of nitrogen cycling and energy flow by returning nitrogen to the soil in forms that are readily mineralized (Floate 1981, Ruess and McNaughton 1984, McNaughton et al. 1997b), increasing root turnover and labile carbon inputs to the soil (Merrill et al. 1994, Kielland et al. 1997, Frank and Groffman 1998), reducing nitrogen immobilization by microbes (Holland et al. 1992), and increasing solar radiation reaching the soil surface. The overall effect of herbivores therefore depends on whether changes in species composition of the plant community act to offset these latter 3 factors by increasing the abundance of unpalatable, slow-growing, and slowly decomposing species, or amplifying the effects of these latter 3 factors by increasing the abundance of palatable, fast-growing, rapidly

decomposing species. In forests, changes in canopy species composition will be the primary determinant of how ungulates affect ecosystem dynamics because only juvenile stages of the dominant plants are consumed, and nearly all soil inputs are from tree litter and roots. In grasslands and shrublands, the effect of changes in species composition will also depend on the proportion of primary production consumed, plant physiological changes, and alterations of the soil microenvironment.

While few studies have explicitly examined the effects of ungulate herbivory on ecosystem processes, many have examined ungulate effects on the species composition of plant communities in systems ranging from tundra to temperate and tropical grasslands to temperate and boreal forests. Ungulate-caused changes in the functional properties of dominant plant species such as growth rate, nutrient uptake rate, and litter quality will clearly have subsequent effects on ecosystem processes and other trophic levels (Bryant et al. 1991b, Pastor and Cohen 1997). In addition, feedbacks from the plant community will affect long-term ungulate population growth (Pastor et al. 1993, McNaughton et al. 1997a). Thus, understanding how ungulate herbivory modifies plant community composition can, in turn, highlight the mechanisms and constraints that allow ungulates to have potentially opposite effects on processes in different ecosystems.

We examined studies of ungulate effects on plant community composition and structure within the context of a central premise: ungulates directly affect vegetation through (1) feeding selectivity of herbivores, and (2) recovery capacity of plants fed upon. Too often, conceptual views of plant-herbivore interactions are predicated on the following sort of reasoning: (1) herbivores feed preferentially on plant species palatable to them; (2) this consumption reduces the fitness of palatable plants relative to neighbors of lower palatability; so (3) unpalatable plants replace palatable ones under herbivore pressure, acting to diminish habitat carrying capacity. This thinking focuses on chemical and physical properties of the plant and behavior of the animal; it commonly encompasses an estimate of herbivore intake, but such thinking does not consider the extent to which a plant is damaged by herbivore feeding or regrowth capacity of plants fed upon. Our literature synthesis reveals that palatable plants can

persist in ecosystems, even attain dominance, provided they are less severely damaged by herbivory, and therefore retain a greater growth potential than less palatable species.

Changes in the relative abundance of species in a plant community due to herbivory depend on the relative degree and temporal pattern of tissue loss experienced by each species (herbivore foraging behavior interacting with plant morphology) and how each species responds to tissue loss. Plant responses are of 2 major types: regrowth from, or death of, residual tissue, and morphological modification. The way in which regrowth capacity and morphological modifications determine a plant species' reproductive rate, survivorship, and competitive abilities within the community are the elements of plant tolerance. This includes tolerance to such non-feeding damage as trampling, crushing, and dung coverage. Management of both domestic and wild ungulate densities is well known to have a strong feedback on habitat quality through selective foraging behavior that can suppress palatable species in the community (Bryant et al. 1991b). Many ecophysiological studies of rangeland plants have addressed the role of plant tolerance in determining herbivore effects on plant communities (Caldwell et al. 1981, Brown and Stuth 1993, Anderson and Briske 1995, and others), but tolerance has received much less consideration in evaluating the role of native ungulates in plant community dynamics than the mere contrast of palatable and unpalatable food species.

We examined studies from a wide range of ecosystems concerning the effects of ungulate herbivores on plant community composition specifically to (1) evaluate the relative role of herbivore selectivity versus differential plant tolerance to tissue loss in determining plant community changes, and (2) identify characteristics of ecosystems which influence the relative effects of herbivore selectivity and plant tolerance on the functional composition of plant communities. We suggest that the relative importance of foraging selectivity and plant tolerance is the basic mechanism by which ungulate herbivory changes plant species composition and determines whether herbivory promotes or inhibits ecosystem nutrient cycling and energy flow. Thus, an understanding of the constraints that operate on foraging selectivity and plant tolerance will enable predictions of the effects of ungulates on any given ecosystem.

## EFFECTS OF HERBIVORE FORAGING SELECTIVITY

An individual ungulate may take up to  $10^7$  bites of vegetation in a year (Chacon et al. 1976) while moving through an extremely heterogeneous food environment. As a result, "generalist" ungulate herbivores forage selectively to increase their fitness. From the level of bites on a temporal scale of seconds, selectivity is expressed at scales up to the annual range movements of migratory herbivores (Senft et al. 1987, McNaughton 1989).

In forest ecosystems, studies of herbivore food preferences combined with long-term enclosure experiments show that foraging selectivity often drives changes in the abundance of palatable plant species (i.e., species consumed to a greater degree than expected based on their abundance). At Isle Royale National Park, moose (*Alces alces*) prefer deciduous leaves and twigs, eat large quantities of balsam fir (*Abies balsamea*) in winter when deciduous twigs cannot meet food demands, and do not eat spruce (*Picea* spp.) twigs (Peterson 1955, Miquelle and Jordan 1979, Risenhoover 1987). Intensive browsing therefore reduces the regeneration of palatable deciduous trees such as aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*), mountain ash (*Sorbus decorana*), and mountain maple (*Acer spicatum*; Risenhoover and Maass 1987, McInnes et al. 1992). Browsing suppresses balsam fir where fir is not extremely abundant (Brandner et al. 1990), while growth of uneaten spruce appears unaffected (McInnes et al. 1992). These changes have occurred in spite of the ability of some deciduous tree seedlings to increase shoot elongation in response to winter browsing (Bergstrom and Danell 1987, Edenius et al. 1993, Danell et al. 1994), perhaps due to the combined effects of summer browsing (Danell et al. 1994) and intensive winter browsing during periods of high moose density.

In northern hardwood forests, selective browsing by white-tailed deer (*Odocoileus virginianus*) can suppress regeneration of palatable sugar maple (*Acer saccharum*) and pin cherry (*Prunus pensylvanica*) in forest clearings, while less palatable American beech (*Fagus grandifolia*), birch, and striped maple (*A. pensylvanicum*) increase in relative abundance and eventually dominate the canopy (Tierson et al. 1966, Marquis 1981). Selective browsing on oak

(*Quercus* spp.) seedlings may also impede regeneration of this genus relative to other deciduous trees (Strole and Anderson 1992, Healy 1997). However, deer browsing also has the potential to eliminate all tree regeneration, contingent on factors such as deer density, overall tree seedling abundance (J. S. Jordan 1967, Marquis 1974), and tree seedling growth conditions (Tilghman 1989, Healy 1997). In New Zealand forests, browsing by introduced cervids favors regeneration of unpalatable tree species (e.g., *Pseudowinter colorata* attained a density of 1,780 stems/ha in the subcanopy layer of browsed stands and seedlings disappeared from 12–17-year-old ungulate exclosures), while highly palatable, fast-growing species dominate regeneration inside exclosures (e.g., *Geniostoma ligustrifolium* attained a density of 1,330 stems/ha in the subcanopy inside exclosures, but no stems reached this size class in browsed plots; Allen et al. 1984). In all of these systems, selective browsing of tree seedlings acts as a filter that determines eventual canopy composition and, potentially, many forest characteristics.

In African savannas, herbivores have pronounced effects on vegetation composition, ranging from determination of both the species composition (McNaughton 1983a) and the prevalent plant growth form (McNaughton 1984) of grasslands to regulation of the balance between arborescent and herbaceous layers (Laws 1970, McNaughton and Sabuni 1988). Ungulate effects on the composition of savanna communities depend on the relative abundance of browsers and grazers as well as the selectivity of foraging by any given herbivore. The relative influence of grazers and browsers also interacts with rainfall and fire to lead to the open, "typical" savanna of Africa (Vesey-Fitzgerald 1972, Norton-Griffiths 1979, Dublin et al. 1990, McNaughton 1992, Dublin 1995, Sinclair 1995).

A very clearly documented chain of cause-and-effect exists between the abundance of different herbivore species, the levels of herbivory they exert on different plant species, plant growth and survival, and the openness of savanna woodlands. Browsers feed preferentially on woody plants, grazers feed preferentially on herbaceous plants, and the uneaten herbaceous layer is consumed by fire, which, if intense, can be transmitted to the woody layer. If rainfall is high, a high fuel load in the herbaceous layer will be generated during the wet season, leading to the seemingly anomalous result of higher fire

frequency in wetter years (Norton-Griffiths 1979). When elephants (*Loxodonta africana*) are present, they destroy adult trees by bark-stripping and pushing them over during the dry season (Laws 1970) and prevent woodland reestablishment after fire (Dublin et al. 1990). Browsers, such as giraffe (*Giraffa camelopardalis*), also prevent vertical growth of tree saplings and shrubs, keeping them within fire-susceptible size classes (Pellew 1983a). Mixed-feeders, like impala (*Aepyceros melampus*), largely graze during the wet season but browse heavily in the dry season on small, accessible woody plants, which can prevent woodland establishment (Prins and Van der Jeugd 1993). Dry season fire burns seedlings and saplings back to ground level, preventing recruitment into the canopy class. Low densities of grazers, or years of particularly high rainfall, produce high fuel loads that can be sufficient to burn crowns of adult trees and hinder growth, sometimes to the extent of causing mortality.

Within the context of these factors regulating the balance of woody and herbaceous plant species, selective foraging by dominant browsers has the potential to drive changes in the woody plant community. In nutrient-poor broadleaf savannas, impala and kudu (*Tragelaphus strepsiceros*) show highly selective foraging that can be attributed to differences among species in the level of defensive chemical compounds (Cooper and Owen-Smith 1985, Owen-Smith and Cooper 1987). Such selectivity is likely the primary factor maintaining dominance of slow-growing woody species with high levels of condensed tannins and lignin in the infertile savanna (Owen-Smith and Cooper 1987, Scholes and Walker 1993). Similarly, foraging by elephants in a West African savanna severely suppressed common, palatable shrub species, while highly unpalatable species increased in relative abundance (Jachmann and Croes 1991). This type of direct, selective-foraging effect may be limited to particular savanna conditions, however, and may depend on edaphic factors that limit regrowth responses of damaged trees. For example, in a *Brachystegia* woodland of East Africa, intensive browsing by elephants damaged both palatable and unpalatable tree species, leading to an overall increase in the coppice regrowth of palatable species tolerant of high levels of elephant damage (Jachmann and Bell 1985).

Foraging selectivity can also determine species changes within herbaceous communities.

In both post-oak (*Q. stellata*) savanna and true prairie, Brown and Stuth (1993) and Anderson and Briske (1995) have clearly shown that although palatable grasses can regrow faster than unpalatable grasses following herbivory, strong selectivity by cattle overrides this differential tolerance and increases the abundance of less-palatable grasses. Many studies also have demonstrated that selective herbivory by livestock on palatable grasses allows forbs to invade or increase in the community (e.g., Jones 1933, Sala et al. 1986, Facelli 1988). Similarly, grazing by bison (*Bison bison*) alone and by black-tailed prairie dogs (*Cynomys ludovicianus*) and bison together causes declines in palatable graminoids and increases the abundance of uneaten or unpalatable forbs in tallgrass prairie (Fahnestock and Knapp 1994, Hartnett et al. 1996) and mixed-grass prairie (Coppock et al. 1983, Archer et al. 1987, Cid et al. 1991). Fahnestock and Knapp (1994) further demonstrated that enhanced water and light availability in patches where bison selectively removed graminoids contributed to the 39% increase in total biomass of the uneaten forb *Ambrosia psilostachya* and the 45% increase in reproductive biomass of *Veronia baldwinii* relative to ungrazed prairie. In forb communities of deciduous forests, selective grazing by white-tailed deer can even drive highly palatable species toward local extirpation, while less palatable species remain abundant in the understory (Anderson 1994, Balgooyen and Waller 1995, Rooney 1997, Augustine and Frelich 1998). In a nitrogen-poor savanna, selective grazing by deer also limited the abundance of fast-growing species of  $N_2$ -fixing legumes; after a period of 12 years, cover of *Lathyrus venosus* was more than 6 times greater in fenced compared to unfenced plots (Ritchie and Tilman 1995). Clearly, altered species composition due to selective foraging is a general feature of plant-ungulate interactions that extends across biomes.

## EFFECTS OF PLANT TOLERANCE

Because individual plants are not completely consumed by a herbivore, differences among plant species in their response to herbivory in terms of survivorship, growth, reproduction, and competitive ability can also be a critical determinant of community changes (McNaughton 1983b). While tolerance is conferred by physiological and morphological traits of plant species (McNaughton 1979a, Briske 1991), the ex-

pression of such traits is also affected by characteristics of a given ecosystem such as environmental conditions during periods of regrowth, and the intensity and frequency of tissue removal. By altering the competitive relationships among plant species, differential tolerance of co-occurring plant species appears to be an important determinant of the responses of both woody and herbaceous plant communities to herbivory by native ungulates.

In temperate forests, a large body of research has documented the severe detrimental effect that high densities of cervids can have on regeneration of conifer species such as hemlock (*Tsuga canadensis*; Anderson and Loucks 1979, Frelich and Lorimer 1985, Anderson and Katz 1993, Peterson and Pickett 1995, Alverson and Waller 1997), northern white-cedar (*Thuja occidentalis*; Beals et al. 1960; Verme and Johnston 1986), white pine (*Pinus strobus*; Ross et al. 1970), Canadian yew (*Taxus canadensis*; Beals et al. 1960; Allison 1990a,b), and silver fir (*Abies alba*; Motta 1996). This effect has been predicted to convert stands to a canopy dominated by deciduous species such as sugar maple (Frelich and Lorimer 1985, Alverson and Waller 1997, Tester et al. 1997), American beech (Peterson and Pickett 1995), or paper birch (Ross et al. 1970). Such conversion from conifer to deciduous species dominance appears to be due mainly to the inability of slow-growing conifers to tolerate tissue loss rather than to foraging selectivity. Although hemlock, yew, and cedar are often considered "highly preferred" winter forage (Dahlberg and Guettinger 1956, Beals et al. 1960), many of the previously cited studies document conifer regeneration failure in stands where deciduous seedlings are also intensively browsed. In addition, during the growing season, cervids such as white-tailed deer and moose consume deciduous leaves but not conifer needles, such that on a yearly basis, deciduous species may experience higher levels of tissue loss than co-occurring conifers. In northwestern European forests, effects of browsing by roe deer (*Capreolus capreolus*) and red deer (*Cervus elaphus*) on forest species composition are also due to the lesser ability of pedunculate oak (*Q. robur*) and silver birch (*B. pendula*) to tolerate intensive browsing as compared to beech (*F. sylvatica*; Van Hees et al. 1996). Similarly, changes in tundra species composition due to intensive summer herbivory by caribou (*Rangifer tarandus*) appear to be the result of

differential tolerances to tissue loss among species because slow-growing lichens have declined dramatically, but palatable shrubs and graminoids have remained constant or increased slightly (Manseau et al. 1996).

Ungulates can also cause palatable but highly tolerant plant species to increase relative to intolerant but less-palatable species. Tilghman (1989:529) found that white-tailed deer densities above 15 deer/km<sup>2</sup> in Allegheny hardwood forests resulted in the development of monocultures of black cherry (*P. serotina*), a species of moderate preference to deer, "because black cherry grows rapidly in full sunlight, [and] many of the seedlings were able to survive under intense browsing pressure." We previously noted similar effects of intensive elephant browsing on the woody species of an East African *Brachystegia* savanna (Jachmann and Bell 1985).

Species composition of the open grasslands of the Serengeti Plains is influenced by the balance between plant palatability and susceptibility to damage by herbivores. Low-palatability grasses and forbs do not increase to the exclusion of the dominant palatable species, because the former are very prone to many types of damage by herbivores. Many unpalatable invaders invest considerable resources in stem production and are subject to breakage due to trampling by large mammals. Although less palatable species come to dominate exclosures (McNaughton 1983a), such species survive poorly in unfenced grasslands. In spite of an increase in the abundance of wildebeest (*Connochaetes taurinus*) in the Serengeti ecosystem during the 1960s and 1970s from 250,000 to approximately 1.3 million, the abundance of unpalatable dicots such as *Solanum incanum* has not changed on the southeastern plains over the past 20 years, while percent cover of the highly palatable sedge *Kyllinga nervosa* has increased from 6.5 to 18% (Sinclair 1995).

The plant species that dominate unfenced grasslands occur as different growth forms inside and outside exclosures. Within 10–12 years of protection from grazing, those species that remain inside exclosures are ecotypes much more erect in stature than the plants of the same species outside fences (McNaughton 1979b, Detling et al. 1986). Similarly, species that occur across sites widely varying in the grazing intensity they experience have differentiated genetically into a series of ecotypes with progressively more prostrate genotypes pre-

vailing as grazing intensity increases (McNaughton 1984). Grazed Serengeti grasslands are a mixture of predominately prostrate, rapidly growing genotypes and rare erect, slower growing forms; across genotypes, relative growth rate is a negative function of height growth potential (Hartvigsen and McNaughton 1995). Fencing, therefore, tips the balance between the 2 types, favoring the more erect genotypes in the closed-canopy environment.

As in the Serengeti grasslands, herbaceous communities in some North American ecosystems have exhibited a high degree of stability in response to intensive grazing by elk (*Cervus elaphus*). In Yellowstone National Park, while elk populations increased nearly 6-fold between 1968 and 1988 in response to the cessation of culling by park managers, the species composition of grasslands inside 30-year exclosures remained nearly identical to the grazed communities, with no evidence of invasions by unpalatable species (Houston 1982, Coughenour 1991, Singer 1995). In the understory of old-growth spruce–hemlock forests, elk herbivory maintains patches of palatable graminoids and hence increases the quantity and quality of elk forage, while such communities are replaced by a mixture of mosses, ferns, and shrubs following elk exclusion (Schreiner et al. 1996). Less palatable species are more subject to reduced growth resulting from the cumulative activities of the herbivores than species that come to dominate in the presence of elk. At the same time, palatable species that cannot tolerate intensive herbivory due to poor growing conditions can remain severely suppressed by elk, as observed for willows (*Salix* spp.) on Yellowstone's northern winter range throughout this century (Houston 1982, Singer et al. 1994).

These North American and African examples of plant community stability in spite of dramatic increases in ungulate populations during the past half century underscore the importance of different plant species' abilities to tolerate the cumulative effects of large-mammal activities. Studies we outlined also show that foraging selectivity and differential plant tolerance can both be important determinants of community change in systems ranging from xeric grasslands to mesic forests. Given the direct links between plant community change and overall ecosystem processes, these studies suggest that ungulates can promote or inhibit rates of energy flow and nutrient cycling in any biome, depending on the

balance between foraging selectivity and plant tolerance patterns. Building upon the studies outlined in the previous 2 sections, we examine ecosystem characteristics that may operate on both foraging selectivity and the tolerance capacity of plant species to determine ungulate effects on plant communities and ecosystems.

## UNDERLYING INFLUENCES ON FORAGING SELECTIVITY AND PLANT TOLERANCE

### Effects of Herbivore Density

Understanding the effect of ungulate density on plant communities is critical from a management perspective because setting animal density is 1 of the main tools wildlife managers can use to manipulate ecosystems. Changes in ungulate numbers alone cannot alter the relative abundance of a plant species if foraging selectivity and plant tolerance remain constant. In such a situation, herbivores will continue to have the same relative effect on the competitive abilities of different species at all levels of herbivore abundance. The only exception is when a particular species is never eaten by ungulates (e.g., spruce in boreal forests), in which case increasing herbivore density will increasingly favor the uneaten species.

However, changes in herbivore density are expected to affect both foraging selectivity (due to changes in absolute forage abundance) and plant tolerance (due to changes in the frequency and amount of tissue loss). As herbivore density increases, selectivity is expected to decline because of reduced availability of preferred forage per animal. Where herbivores are maintained at low densities, the most preferred species may therefore experience the highest level of tissue loss per plant, but the low absolute number of herbivores may result in no significant effect on any species. At moderate densities, the degree of discrimination among plant species may be slightly reduced, but increasing total amounts of tissue removal per plant are still likely to result in significant effects on species composition due to selective foraging (Marquis 1981, Tilghman 1989, Brown and Stuth 1993). At high ungulate densities, if heavily defended species are present that still experience relatively low herbivory levels, major selectivity effects can be observed, as with the development of spruce savannas at Isle Royale (McInnes et al. 1992). However, high-density un-

gulate populations have the potential to cause a complete switch in community type if all species in a given community are edible, as in the conversion of forests to grassland by white-tailed deer (Marquis 1974, Healy 1997).

Changes in herbivore density also affect the ability of plants to tolerate herbivory by determining the intensity and frequency of plant tissue removal. After a foraging event, the plant can respond in 3 ways: (1) relative growth rate (RGR) can be inhibited, including to the point of death of remaining tissue, even the entire plant; (2) RGR can remain the same as before herbivory; or (3) RGR can increase after herbivory. Which response predominates will depend on the intensity and timing of herbivory, as well as on plant genotypic properties and plant environment (McNaughton 1979a,b; Maschinski and Whitham 1989). For plants to recoup lost tissue, RGR must increase (Hilbert et al. 1981; Oesterheld and McNaughton 1988, 1991). If RGR remains the same or declines, biomass accumulation will be reduced compared to ungrazed plants. Although the prediction from these facts, the herbivore optimization curve (Dyer 1975, McNaughton 1979a), has been heatedly disputed (Belsky 1986), studies testing the herbivore optimization curve for grasses have been reviewed in detail by Hobbs (1996; and see Wegener and Odasz 1997, Hamilton et al. 1998) and provide strong support for the predicted increase in plant productivity at moderate levels of defoliation for grazing-adapted species. Compensatory growth following herbivory has also been documented in woody species from a wide range of ecosystems (Aldous 1952, Pellew 1983b, du Toit et al. 1990, Hjalten et al. 1993, Danell et al. 1994, Escos et al. 1996, Alados et al. 1997, Escos et al. 1997, Keya 1997). We reemphasize that given the appropriate environmental conditions and sufficient time between herbivory events, plants with a greater ability to compensate for tissue loss from herbivory will be able to better tolerate herbivory than neighbors and, therefore, to persist or even dominate in a plant community (Fig. 1, solid-line trajectory). In the absence of appropriate growth conditions or when tolerant plants are absent from a community, increasing levels of herbivory will simply shift competitive relationships among species to permit the invasion and dominance of unpalatable species (Fig. 1, dashed-line trajectory); plants damaged by herbivory will be eliminated. As a



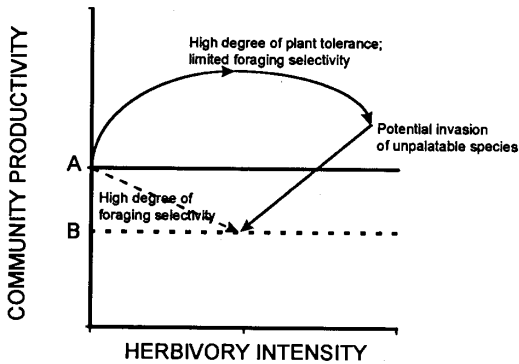


Fig. 1. Predicted relations between aboveground plant productivity and herbivory intensity under conditions favoring plant tolerance conditions (solid line) and conditions where foraging selectivity drives changes in species composition with increasing herbivory (dashed line). In the absence of herbivory, a community including palatable, herbivory-tolerant species has a control productivity level represented by the heavy solid line (A), while a community consisting of only unpalatable species is expected to have a lower productivity level represented by the heavy dashed line (B). Even in a community with herbivory-tolerant species, invasions of defended, unpalatable species or soil degradation with consequent declines in overall primary productivity may be expected under extremely intensive herbivory levels.

result, plant tolerance likely will be an important component of ungulate effects on plant communities at moderate ungulate densities (based on the herbivore optimization curve, Fig. 1).

These patterns suggest that while ungulate density will affect both foraging selectivity and plant tolerance, changes in animal density will not be the sole determinant of changes in community composition. Selectivity and tolerance can both increase in importance at low to moderate ungulate densities, while the role of selectivity and tolerance at high ungulate densities will depend on a range of additional ecosystem characteristics influencing plant growth, plant chemical defense, and herbivore foraging behavior.

### Factors Enhancing Plant Tolerance

**Constraints on Plant Chemical Defense.**—Chemicals synthesized by plants that deter herbivores incur a metabolic cost (Hermes and Mattson 1992), and plants that forgo these costs can use rapid regrowth as an alternative to defense (McNaughton 1983a, van der Meijden et al. 1988). Increasing nutrient stress appears to favor investment in chemical defenses (Bryant and Kuropat 1980, Bryant et al. 1983, Coley et al. 1985, Bryant 1987, Bryant et al. 1989, Mih-

aliak and Lincoln 1989, Bryant et al. 1991a), while above a critical level of nutrient availability, undefended plants experiencing high herbivory levels can compensate for lost tissue through rapid regrowth (McNaughton et al. 1983, Chapin and McNaughton 1989, Georgiadis et al. 1989, Wegerner and Odasz 1997, Hamilton et al. 1998). Thus, a tight coupling between tissue consumption and nutrient supply back to the soil by herbivores (Ruess and McNaughton 1984, 1987; Jeffries et al. 1994, Hamilton et al. 1998), as well as high rates of abiotic nutrient inputs to the ecosystem (Coley et al. 1985, Bryant et al. 1991a), can limit the competitive advantages of chemical defense. This limitation in turn increases the importance of plant regrowth in determining plant community changes due to herbivory. Further empirical analyses of the magnitude of the costs of chemical defense in terms of growth and reproduction in ecosystems with varying levels of soil nutrient availability are clearly needed.

Investment in chemical defense can also be constrained by disturbances that remove aboveground tissue nonselectively or that disproportionately affect chemically defended plants. For example, systems with greater fire frequencies are expected to impose greater costs on slow-growing species as the aboveground biomass is removed (Norton-Griffiths 1979, Briggs and Gibson 1992, Pastor and Cohen 1997). While reduced soil nitrogen availability at high fire frequency (Risser and Parton 1982, Ojima et al. 1994, Turner et al. 1997) may increase the advantages of chemical defense against herbivory, the direct effect of fire will be to favor species which can regrow rapidly. The use of silica by grasses to deter herbivores (McNaughton et al. 1985) may in part reflect this tradeoff. Although most defensive chemicals are volatilized following fire, silica is returned to the soil where it can be reused as plants recover from fire. Overall, short fire return intervals can exert a strong limitation on chemical defense against herbivores simply due to the constant loss of aboveground plant investments. In ecosystems where fire or other canopy disturbances occur at longer intervals, disturbance is an important force "resetting" the system for herbivores by releasing nutrients from slow-growing, defended species (Jeffries et al. 1994). Other disturbances such as trampling (Sun and Liddle 1993a,b) and outbreaks of specialist insects on unpalatable plants (Mattson et al. 1991, Hadley and Veblen



1993, Scholes and Walker 1993) can also act to limit the benefits to plants of investing energy and nutrients in defenses that deter herbivores.

**Convergent Selection Pressures.**—When plant traits that improve the ability of individuals to tolerate ungulate herbivory also adapt plants to other major biotic and abiotic constraints on growth and survival, strong selection for these traits may be expected. Regardless of their evolutionary origins, traits that enable plants to survive drought (i.e., basal meristems, small stature, high shoot density, belowground nutrient reserves, rapid transpiration) also enable plants to tolerate herbivory (Coughenour 1985). Given these dual trait functions, a large body of research concerning ungulate effects on grassland communities has identified limited rainfall as a major convergent selection pressure for plant tolerance of herbivory (Milchunas et al. 1988). A wide range of convergent selection pressures such as parasite resistance and pollinator attraction could potentially interact with secondary plant metabolites related to herbivory avoidance, but we are unaware of studies demonstrating multiple functions, including herbivory deterrence, of specific secondary metabolites in plants. To predict how an ecosystem will respond to changes in ungulate populations, it is important to recognize that any convergent selection pressures imposed by characteristics of that particular ecosystem will affect the relative costs and benefits of chemical defense versus plant tolerance strategies.

**Herbivore Return Intervals.**—The ability of plants to tolerate tissue loss depends on the timing of herbivory relative to the growing season and the length of regrowth periods between bouts of herbivory. These factors have long been known to dramatically affect pasture communities with managed livestock (Jones 1933; Milton 1940, 1947). In particular, Milton (1940, 1947) showed that short but intensive periods of sheep herbivory, which minimizes foraging selectivity, followed by a period of no grazing, can increase the relative abundance of palatable versus unpalatable species in fertilized pastures. Similar conditions clearly result from migratory behavior of ungulates because many of the communities used during the migratory cycle experience herbivory for only part of the growing season (Klein 1965, P. A. Jordan 1967, McNaughton 1985, Frank and McNaughton 1992). A critical determinant of compensatory growth is the length of time for regrowth in both grass-

es (Oosterheld and McNaughton 1988, 1991) and tree seedlings (Hjalten et al. 1993, Danell et al. 1994).

Periods of regrowth made possible by the migration patterns of dominant ungulates in grazing ecosystems such as the Serengeti and Yellowstone National Park (Frank et al. 1998) likely are a key, but not the only, factor allowing palatable species to maintain their competitive status within the community. In contrast, in systems such as the southern boreal forest at Isle Royale National Park, the year-round browsing pressure exerted by moose removes twigs during the winter and new leaves and shoot tips during the growing season. Such constant pressure results in much more severe effects on seedling growth and mortality than either summer or winter browsing alone (Danell et al. 1994). Migration may be most important in alleviating deleterious effects on palatable species on winter, dry season, and transitional ranges, since the animals are absent during most of the growing season. However, even in grazing ecosystems dominated by migratory ungulates such as the Serengeti and Yellowstone, summer and wet season ranges can experience herbivory throughout the period of plant growth (McNaughton 1985, Frank and McNaughton 1992). In these communities, factors other than the temporal pattern of herbivory must underlie lack of invasion by unpalatable species. While ungulate migration patterns may not be the sole determinant of community response to herbivory, reduced migratory behavior combined with increased ungulate densities can severely inhibit the regrowth capabilities of palatable species.

### Factors Limiting Herbivore Foraging Selectivity

**Herd Membership.**—Many ungulates move and forage in herds, and the close proximity of other animals may limit the opportunity for an individual to forage selectively among plant species. The benefits of herd membership to the individual in terms of improved forage quality and concentration per bite (McNaughton 1984) likely exceed the cost of occasionally consuming unpalatable species. This constraint on selectivity may be an important factor preventing unpalatable, chemically defended species from increasing in grazing lawns, but we are unaware of studies experimentally documenting the effect of ungulate social organization on forage selection. Other reasons for the formation of

dense ungulate aggregations, such as forage mineral content (McNaughton 1988, 1990) and the distribution of predator territories (Mech 1977), could also outweigh the cost to herbivores of reduced foraging selectivity and occasional consumption of chemically defended plants. Direct observations of an ungulate species that exhibits plasticity in social organization (for example, across habitat types or among locations differing in predation pressure) could provide insight to the degree to which herd membership influences plant selectivity at the scale of feeding stations (1–10 m<sup>2</sup>) and the selection of foraging patches within the landscape (10–1,000 m<sup>2</sup>).

*Foraging Selectivity in Relation to Plant Phenology.*—Variation in the chemical composition of co-occurring plant species over time (phenology) can interact with the temporal pattern of herbivory pressure to influence the degree to which herbivores discriminate among plant species. Migrations often track the young, rapidly growing stage of development in plant communities along phenological gradients covering entire landscapes (Klein 1965, P. A. Jordan 1967, McNaughton 1985, Frank and McNaughton 1992, Frank et al. 1998). As plants develop photosynthetic tissue early in the growing season, they are under extreme allocation constraints: early investment in chemical defense as opposed to photosynthetic enzymes represents the highest long-term cost in terms of growth during the growing season. In addition, young, actively growing tissues have minimal amounts of structural carbon such as lignin and cellulose. Thus, in ecosystems with abundant migratory ungulates, most herbivory occurs when differences among plant species in the level of secondary compounds, lignin, and cellulose are likely to be minimized, hence limiting foraging selectivity. When combined with the effect of migratory behavior on the length of plant regrowth periods between episodes of herbivory, this limitation on selectivity may enhance the dominance of palatable plant species. Reduced migratory behavior is a direct consequence of anthropogenic habitat fragmentation and the elimination of migration corridors; hence, such changes in landscape structure may be causing major indirect effects on the functional composition of plant communities in isolated parks and reserves.

Selection of recently burned, regrowing vegetation by many ungulate species (McNaughton

1985, Coppock and Detling 1986, Hobbs et al. 1991, Vinton et al. 1993, Wilsey 1996) may also result in grazing when differences among species are minimized in the level of chemical defense. Grasses that are unpalatable, such as members of the genus *Cymbopogon*, have that property because of the accumulation of secondary chemicals distasteful to grazers. Low herbivory on such unpalatable grasses leads to the accumulation of substantial fuel loads. In addition, the grasses can burn when green due to terpenoid contents, and fire is a common annual occurrence in *Cymbopogon* grasslands (McNaughton 1983b). Once regrowing, however, the grasses are highly palatable (Vesey-Fitzgerald 1972), which can result in very heavy grazing intensities as grazers concentrate on the postfire green flush (McNaughton 1985). These “unpalatable” grasses, in turn, are highly damaged by grazing when it occurs, so that a combination of fire followed by heavy grazing can eliminate them or severely restrict their abundance.

Finally, as discussed in our consideration of white-tailed deer effects on conifer species in much of eastern North America, seasonal asynchrony in growth patterns of palatable and unpalatable plants may limit differences among species in the amount of tissue loss experienced over an entire year. During summer, when all plant species are growing, white-tailed deer and moose consume only herbs and leaves of deciduous trees. During the winter, however, consumption shifts to include the needles of less palatable but green conifers (Peterson 1955, Dahlberg and Guettinger 1956). Similarly, in African savannas, leaves of mopane (*Colophospermum mopane*) trees and broadleaf evergreens that contain high levels of secondary compounds are generally considered of low palatability to ungulates, but these species experience intensive browsing pressure during the dry season when the leaves are actively growing and most other species have senesced (Owen-Smith and Cooper 1987, Cooper et al. 1988, Styles and Skinner 1997). Where traits of unpalatable, slow-growing species are linked to other ecological factors affecting their persistence in the community (i.e., increased leaf longevity permitting growth during a greater proportion of the year), discrimination among plant species by herbivores may be limited when considered over an entire yearly or wet–dry seasonal cycle.

*Effects of Plant Community Composition.*—

The relative and absolute abundance of plant species in a community are not only influenced by ungulate herbivory but may also have an important influence on foraging selectivity and the degree of tissue loss a given plant population experiences. The effect of community composition on foraging patterns can operate in addition to the effects of herbivore abundance and differences among plant species in leaf tissue chemistry. At the scale of an individual herbivore's home range, plant community composition affects foraging selectivity by setting the options available to the herbivore. These options include not only plant density and species composition in small-scale patches of vegetation (e.g., the relative abundance of deciduous and coniferous seedlings in a forest clearing; Heikkila and Harkonen 1996), but also the spatial distributions of discrete patches of different forage species (e.g., the presence of agricultural fields adjacent to a forest; Augustine and Jordan 1998).

Empirical evidence that plant species abundance influences ungulate effects on plant communities is limited but growing. Studies of elephants and trees in the Serengeti-Mara ecosystem (Dublin et al. 1990, Dublin 1995, Sinclair 1995) and white-tailed deer and understory forbs in fragmented deciduous forests (Augustine et al. 1998) show that herbivory can regulate populations of palatable plant species at low abundance where the species is rare, but herbivory does not cause the species to decline where populations are abundant. Similarly, whether browsing by white-tailed deer prevents tree regeneration in northern hardwood forests appears to depend on the density of tree seedlings in a stand at the time of canopy disturbance (J. S. Jordan 1967, Grisez and Peace 1973, Marquis 1974). However, community response to browsing is also related to tree growth conditions (e.g., under different canopy-thinning treatments; Tilghman 1989, Healy 1997) and the regrowth capacity of different tree species (Tilghman 1989). Abundance of a plant species influences herbivore effects because herbivore consumption becomes saturated where the plant species is extremely abundant (i.e., there is more than could possibly be consumed by herbivores), while in areas with low density of the plant species, the same number of herbivores are able to exert a high level of herbivory (Noy-Meir 1975, Schmitz and Sinclair 1997). Dynamics documented in empirical

studies appear possible because alternate sources of forage maintain the ungulate population when the palatable plant species or guild in question is rare: grass in the case of elephant-tree dynamics, agricultural crops in the case of deer-forest forb interactions, and herbaceous species in the case of white-tailed deer-tree regeneration relations.

Interactions between plant species abundance and ungulate herbivory pressure may also limit the ability of chemically defended, unpalatable species to avoid herbivory. A large body of research on domestic livestock has shown that forage with defensive compounds may only be avoided when high levels of the compound accumulate in the ungulate rumen and trigger aversive postingestive responses (Bryant et al. 1991b). As a result, chemically defended species may experience high levels of herbivory where they are not abundant enough to constitute a large proportion of the herbivore diet. In other words, chemical defenses may be ineffective where such species are rare (Bryant et al. 1991b).

This hypothesis is consistent with the observations that large generalist herbivores avoid patches of the landscape where unpalatable plants are abundant (McNaughton 1978), and that relatively unpalatable plants are suppressed by ungulate herbivores where they are rare in the overall plant community (Brandner et al. 1990, Heikkila and Harkonen 1996). In these latter 2 studies, the ability of moose to suppress regeneration of relatively unpalatable conifers where conifer seedlings occurred at low density may have depended on the availability of an alternative local forage source, deciduous tree seedlings, to maintain moose presence in the area. Furthermore, ungulate digestion can be enhanced by including a diversity of plant species in the diet, such that relatively unpalatable plants are still included in the diet but in small amounts. For example, in cafeteria trials, moose do not choose a monospecific diet of the most palatable browse species even when it is supplied in abundance in captivity and when it is abundantly available in natural mountain situations (Miquelle and Jordan 1979), and mountain hares (*Lepus timidus*) fed a pure diet of their most preferred plant species lose weight over time (Pehrson 1981). Thus, if chemically defended plants experience high levels of herbivory where they are rare because insufficient quantities are present to have toxic effects on ungulate diges-

tion, then we expect (1) invasions of chemically defended plants into communities will be prevented by their initial rarity, and (2) recovery of these species will be inhibited after any type of disturbance (e.g., fire) reduces their abundance.

## CONCLUSIONS

Our synthesis indicates that the relative importance of foraging selectivity versus plant tolerance in driving ungulate effects on plant communities will be the proximate determinants of ungulate effects on plant community composition and whether ungulates promote or inhibit rates of nutrient turnover and energy flow in ecosystems. These effects are not separate phenomena. Plant persistence, invasion, or disappearance will have consequences for nutrient cycling, energy flow, and other ecosystem processes (Bryant et al. 1991b, Hobbs 1996). Where selective foraging among chemically defended plant species predominates, long-term increases in the abundance of unpalatable species will reduce primary productivity, secondary productivity, and the return rate of nutrients to the soil (Pastor and Cohen 1997). Where plant tolerance of herbivory predominates, unpalatable species will not be able to dominate the community, and herbivores will increase primary productivity, secondary productivity, and nutrient turnover. The type of effect that is desirable from a management perspective will, of course, vary according to the objectives of that management, including factors such as sustainable yield, endemic and endangered species, and the conservation of ecosystem processes.

Analyses of the factors controlling selectivity and tolerance can assist managers in the development of predictions concerning the response of plant communities to both management directed at ungulate populations and other anthropogenic effects on the landscape and its components. Available empirical evidence emphasizes foraging in herds, seasonal asynchrony in growth among plant species, early growing-season and postfire herbivory, and low relative abundance of unpalatable species as potential constraints on selective foraging (Fig. 2). Pri-

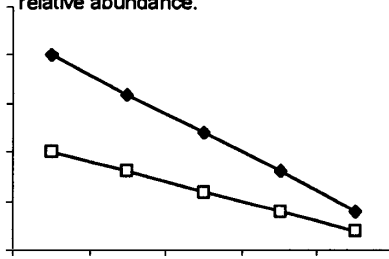
mary factors enhancing the ability of palatable species to tolerate herbivory include high rates of nutrient recycling or input and pulsed rather than continuous herbivory (Fig. 2). In arid grasslands, convergent selection for drought and herbivore tolerance will also restrict the invasion of unpalatable plant species (Milchunas et al. 1988). Influences of ungulate social organization and plant species rarity on forage consumption patterns in particular have received little empirical attention. Palatable, tolerant plant species will play a central role in long-term system dynamics by buffering ungulate populations against changes in the availability of less-tolerant forage species and inhibiting competitive abilities of less-palatable invaders. Identifying such species and understanding environmental variables regulating their growth can also assist in formulating habitat management plans and predicting how anthropogenic influences will affect the role of ungulate herbivory in an ecosystem.

A simple comparative analysis of ecosystems where ungulates have or have not enhanced the dominance of unpalatable species cannot disentangle the relative importance of various ecosystem characteristics directing the effects of ungulates. In systems such as the northern Yellowstone winter range and the Serengeti, the combination of seasonal migration, ungulates foraging in large, sometimes dense herds, high input rates of nitrogen to the soil system on growing-season ranges, and regular plant disturbance by trampling likely all play a role in limiting the abundance of unpalatable species. In contrast, examples where selective foraging has clearly driven community changes (e.g., moose in boreal forests, white-tailed deer in oak savannas, impala and kudu in *Brachystegia* woodlands) involve more sedentary ungulates which forage singly or in small groups and live in an environment with extremely low soil nutrient availability and higher rainfall. Most likely, a composite of the individual factors operates in different directions, and several examples of community response to ungulate herbivory in-

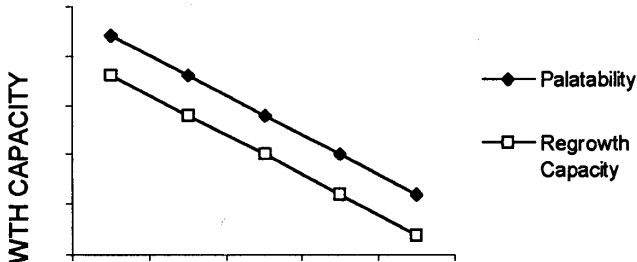
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Fig 2. Three potential distributions of species traits in a community when each species is plotted in terms of its palatability (% tissue loss relative to its abundance) versus its tolerance to tissue loss (relative ability to regrow after defoliation). Points represent individual species, while lines represent the community's distribution of species traits. Factors affecting the distribution of species traits in the community as depicted in (B) and (C) are predicted to increase the dominance of palatable species capable of rapid recovery from herbivory damage.

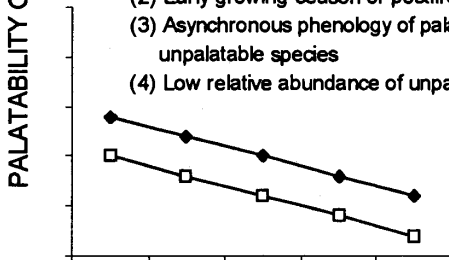
(A) Species with identical palatability:regrowth capacity ratios; no predicted herbivore-induced changes in relative abundance.



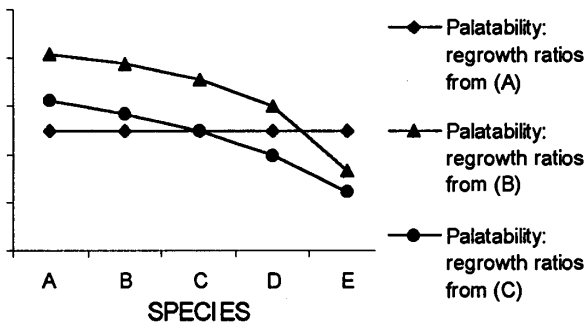
(B) Increased differential regrowth capacity of species due to  
 (1) High soil nutrient inputs or recycling  
 (2) Intermittent herbivory.



(C) Reduced differential palatability of species due to  
 (1) Herbivores in herds  
 (2) Early growing-season or postfire herbivory  
 (3) Asynchronous phenology of palatable versus unpalatable species  
 (4) Low relative abundance of unpalatable species.



(D) Palatability:regrowth capacity ratios based on species trait distributions in the 3 previous graphs. Factors listed in (B) and (C) lead to the highest ratio for the most palatable species in the community.



cluded both promotion and inhibition of different palatable plant species.

Consideration by wildlife managers of how each of these factors are operating in a particular system can clarify thinking about how ungulate population management, habitat restoration, and ongoing anthropogenic influences to the ecosystem will, in turn, affect the ecosystem-level role of ungulate herbivory. At the same time, adaptive research programs (Lancia et al. 1996) explicitly addressing the importance of specific controls on selectivity and tolerance in ecosystems are needed to test how ungulate populations can be manipulated to effect desired ecosystem-level changes. Further recognition of how changes in climate, nutrient inputs, and ecosystem boundaries affect the underlying mechanisms regulating ungulate effects on ecosystems will also be necessary to mitigate undesirable changes in ecosystem functioning and set ungulate population and habitat management into comprehensive ecosystem-based management plans.

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