

Herbivore Influences on Plant Performance and Competitive Interactions

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I. Introduction

Both competition and herbivory can affect plant abundance and distribution (e.g., Harper, 1977; Whittaker, 1979; Crawley, 1983; Sih *et al.*, 1985; Fowler, 1986). However, it is still not clear when, how, or how often these two processes interact to determine plant community structure or dynamics. Theory predicts that consumers, including herbivores, will have major effects on their resource populations; the character of these effects depends on many factors, including feeding preferences, refuges, differential growth rates, differential recruitment rates, and competition among co-occurring plants (e.g., Crawley, 1983; Jeffries and Lawton, 1985; Holt, 1985; Maschinski and Whitham, 1989).

Leaf, root, and seed damage by herbivores is common and well documented (e.g., Harper, 1977; Edwards and Wratten, 1980; Hodgkinson and Hughes, 1982; Crawley, 1983, 1988a; Hendrix, 1988), as is selective consumption among co-occurring plants (e.g., Janzen, 1971; Morrow, 1977; Coley, 1983; Denno and McClure, 1983; Dirzo, 1985; Brown, 1985; Louda *et al.*, 1987a; Joern, 1989). But the significance of these observations remain controversial (e.g., Belsky, 1986; McNaughton, 1986). Fox and Morrow (1986), however, effectively argue that the effect of herbivory should be related to its differential impact on competing species and may be independent of the absolute amount of damage inflicted.

In this chapter, we consider three questions: (1) To what extent does herbivory affect plant growth and resource acquisition? (2) Will herbivory modify the intensity or alter the outcome of resource-mediated competitive interactions? and (3) When will such effects be most marked? By herbivory we mean consumption of living plant tissues, including grazing, browsing, defoliation, seed predation, parasitism, and disease. Our examples are generally drawn, however, from the interactions with which we are most familiar: insects feeding on foliage and seeds.

Herbivory can decrease growth and fecundity, stimulate compensatory regrowth, or cause mortality (Harper, 1977; Crawley, 1983). So, herbivory might influence competitive interactions: (1) by changing a plant's relative ability to acquire limited resources, or (2) by eliminating the plant as a competitor. We develop theory and review evidence bearing on both effects. Crawley (1983, p. 8) has suggested, "The principal effect of herbivores on plant species richness acts not through the animals eating plants to extinction (although this can happen), but through their feeding modifying the competitive abilities of *one* plant species with another." We suggest that the impact of herbivory on competitive interactions among plants is and should be greatest in general when environ-

mental constraints limit plant response and compensatory regrowth after selective consumption on one competitor. However, the available data are as yet insufficient for a definitive evaluation of this hypothesis. We conclude by suggesting methods for such studies.

II. Herbivory in Models of Competition

"Competition" generally means reciprocal negative interactions among individuals or populations. In ecological discussions, the term competition usually refers to negative interactions that arise from direct interference or, more indirectly, from the preemptive exploitation of limiting resources (Fig. 1). In multispecies communities, however, alternative indirect pathways leading to reciprocal negative interactions are possible, including shared natural enemies (Holt, 1977, 1984) and mixed mutual-

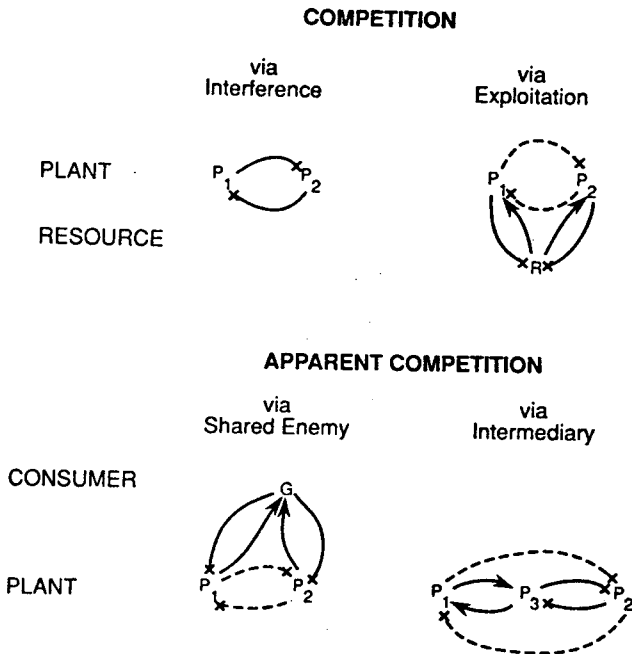


Figure 1 The conceptual model of competitive interactions and apparent competition. Adapted from Holt (1977, 1984) and Connell (this volume). The \times indicates negative effect, whereas the arrow indicates the direction of a positive effect. Solid lines represent *direct effects*, and dashed lines represent *indirect effects*. Two directly competing plant species, P_1 and P_2 are represented. P_3 is added to represent a plant for which facilitation occurs, such as by a mutualistic association. R represents a limiting resource, and G represents a generalist herbivore that is a shared natural enemy of P_1 and P_2 .

ism-competition systems (Connell, this volume); these alternatives are called "apparent competition" (Fig. 1).

In this chapter we schematically depict how herbivory can be included in the conceptual models corresponding to the disparate varieties of competition (Fig. 2). Furthermore, we examine how the impact of selective herbivory might influence competitive interactions. Specifically, we use a graphical model to examine two factors that will govern the impact of asymmetrical, selective herbivory on competing plants. The first factor is the benefit gained by the nonconsumed species. This benefit will vary inversely with the capacity of the consumed species to compensate for its losses. The second factor is the relationship of herbivore dynamics to plant dynamics; the effect on coexistence will reflect whether the selective herbivore acts as a density-independent *limiting* agent, with herbivore numbers set by mechanisms other than food availability or, instead, as a density-dependent *regulatory* agent.

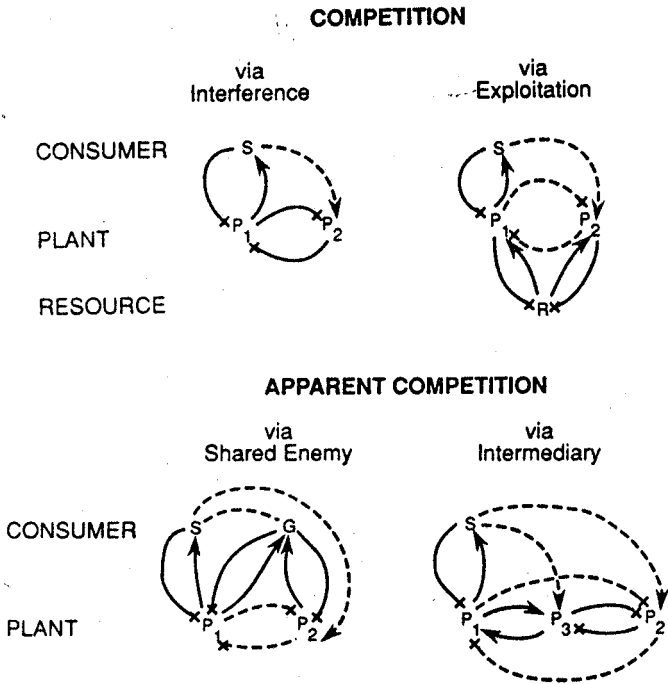


Figure 2 Incorporation of selective, differential herbivory into the conceptual model in Fig. 1. We divide the consumer trophic level into generalized, shared herbivores (G) and selective, more specialized herbivores (S). Other symbols follow Fig. 1. Selective consumers (S) feeding on competitor P_1 should indirectly benefit competitor P_2 , independent of whether the competitive mechanism involves interference, exploitation, or apparent competition.

Most of the large body of theory on the potential role of herbivory on plant species coexistence (see Abrams, 1977; Holt, 1985) relies on the following structure for plant dynamics:

$$dN_i/dt = N_i[f_i(N_1, N_2, \dots, N_j) - m_i(H, N_1, N_2, \dots, N_j)] \quad (1)$$

where H is herbivore density, and N_i is a measure of population size, such as density or biomass, for plant species i . The function f_i implicitly encapsulates both intra- and interspecific interactions among plants and, in particular, the negative density dependence inherent in competitive interactions (i.e., $\partial f_i/\partial N_j < 0$). The function m_i describes how herbivores depress the growth rate of population i , by increasing mortality or decreasing individual growth or reproduction. We use this basic theory and we assume both that the underlying competitive interaction between plants matches one of the models of Fig. 1, and that one competitor dominates the other, i.e., there are no priority effects.

In Fig. 3, we plot several possible density-dependent growth functions for the competitive dominant, species 1. The strength of density dependence is given by the slope of the per capita growth function, evaluated at density N_1 . In fact, the absolute value of the slope is the marginal effect of a small change in density on per capita growth rate. With logistic population growth (Fig. 3A) the strength of density dependence is independent of population density. Alternatively, with nonlogistic growth (e.g., Fig. 3B), the strength of density dependence may diminish (curve a) or intensify (curve b) with increasing density. Herbivory may thus reduce plant population size or growth rate in either a density-independent (Fig. 3A,B) or density-dependent manner (Fig. 3C). The plant population will be in balance when its per capita growth just matches the reduction in size or growth rate caused by herbivory.

This graphical model illustrates several important potential effects of selective herbivory. First, increasing the level of selective herbivory on a dominant plant will clearly lower its equilibrium population size (Fig. 3A-C), altering interactions with subdominant competing plants.

Second, however, the magnitude of the herbivore-caused reduction will depend on several factors. For density-independent herbivory on a plant population with logistic growth, lowering r will increase the impact of a given level of herbivory (e.g., from $N_1 = 1$ to $N_1 = 2$: Fig. 3A). With nonlogistic growth and weak density dependence near K (Fig. 3B: curve a), even low levels of herbivory can severely depress host plant abundance. In contrast, however, with strong density dependence near K (Fig. 3B, curve b), the plant population can compensate and is not as severely depressed, for even quite high levels of herbivory.

Third, density-independent herbivory can also reduce a population's rate of increase at low plant densities (Fig. 3A,B). High levels of her-

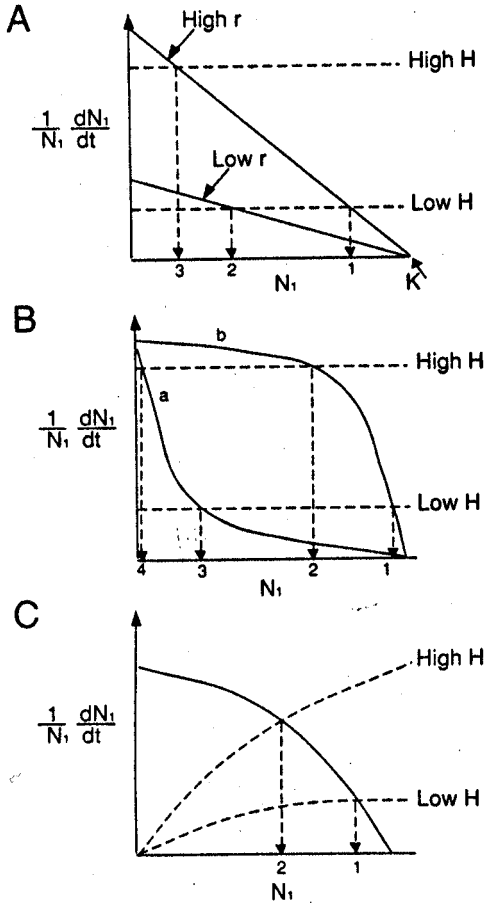


Figure 3 Effects of intraspecific density dependence and alternate population growth responses to herbivory. The solid lines in each part depict per capita growth rate as a function of density for the dominant competitor (N_1); the density dependence may include both direct interference and the effects of exploitative competition for a limiting resource, but it does not reflect effects of herbivores. In adding either density-independent (A, B) or density-dependent (C) herbivory, we assume for now that the impact of herbivores on plant populations is additive, decreasing population growth rate without modifying the underlying dynamics of intraspecific and interspecific competition. The difference between a given solid curve and the dashed line measures the realized intrinsic growth rate for the plant. Equilibrium density is determined by the density at which a solid curve and dashed line intersect. In A, the plant grows logistically and herbivory is density independent, as would be the case when herbivore dynamics are limited by factors other than plant density. With a low level of herbivory, a plant species with high r is depressed in abundance from K to the density denoted by 1, and a species with low r is depressed to the lower density denoted by 2. With a high level of herbivory, the high- r species is depressed to level 3, whereas the low- r species is completely eliminated. In B, the plant population grows nonlogistically, and herbivory remains density independent. Since the slope of the growth curve represents the

bivory may eliminate the plant from the local community (Fig. 3A), or reduce the relative growth rate of the competitive dominant significantly (Fig. 3B), potentially allowing it to be excluded competitively by the nonconsumed, subdominant plant species. Thus, density-independent herbivory is as likely to preclude coexistence as to allow it.

In contrast, if herbivory is strongly density dependent (Fig. 3C), it will only have a small effect on the capacity of the consumed species to increase when that species is rare. In this case, species with a density-dependent herbivore can be pushed to a lower density by consumption, permitting the coexistence of a competing species, but it should not itself tend to be excluded from the community by the herbivore.

In summary, this model suggests that selective herbivory on the competitive dominant will have its strongest effect when the plant has either a low r or weak density dependence near K , i.e., when the species has constraints on its capacity to compensate for reductions in abundance below its environmental carrying capacity. In these cases, the competitive dominant will be greatly reduced in density by herbivory, and its impact on competing, subordinate plant species will be correspondingly less. Conversely, a high level of compensatory recruitment by the consumed plant population should reduce the influence of selective herbivory on competitive interactions among co-occurring plants. Finally, the overall effect of selective herbivory on species coexistence will be sensitive to whether herbivory is density dependent or not.

The field evidence surveyed in our review (below) leads to similar predictions and, thus, appears consistent with these models. However, there are, as yet, few field experiments which simultaneously analyze herbivory and competition. Moreover, empirical studies of herbivore effects show that herbivores often modify individual plant traits in ways not yet incorporated into theoretical models (Louda and Keeler, 1989).

III. Herbivore Impact on Individual Plants

In many cases, chronic herbivory modifies the growth rate, the form, or the developmental timing of plants, and so changes plant traits that

degree of density dependence at any particular plant density, line **a** represents the case of weak density dependence at high N ; in this case, low levels of herbivory will severely depress abundance for a plant population (3) and high levels of herbivory will cause near extinction (4). Line **b** illustrates the case of strong intraspecific density dependence at high N ; in this case, high levels of herbivory are required to depress equilibrium abundance at all. In **C**, plant growth and herbivory are both density dependent. Here, if herbivory increases with population size, it may greatly depress the size of a plant population without affecting the rate at which the plant population can increase when its density is low.

appear critical to the acquisition of resources. In fact, the characteristics that determine competitive ability, either to deplete resources or to tolerate low resource levels (see Goldberg, this volume), are the traits most often modified by herbivores (Louda and Keeler, 1989). These observations lead to the hypothesis that herbivory can change the ability of a plant to acquire limited resources by altering key morphological traits.

Herbivores often slow growth, reduce biomass, or decrease plant stature (e.g., Gradwell, 1974; Morrow and LaMarche, 1979; Louda, 1984; Crawley, 1988a). Foliage consumption frequently modifies leaf traits, such as density, age structure, metabolism, and canopy shape (e.g., Mattson, 1977; Coley, 1983; Louda, 1984; Clark and Clark, 1985; Whitham and Mopper, 1985). Herbivory may also change (1) internal allocation of resources (e.g., Detling *et al.*, 1979; Chapin, 1980; Caldwell *et al.*, 1981; Mooney and Gulmon, 1982; Bazzaz *et al.*, 1987), (2) root:shoot ratios (e.g., Richards, 1984), (3) nutrient turnover rates (Mattson and Addy, 1975), and (4) litter accumulation rates (Belsky, 1986). All of these herbivore-induced modifications will influence plant performance, and thus potential competitive interactions among plants.

Plants with higher nutrient requirements (Berendse, 1985) or growth rates (Taylor and Bardner, 1968) were vulnerable to foliage losses. The quantitative impact of herbivory was then related to factors that determined the individual plant's ability to compensate for herbivore-caused foliage losses, such as its nutritional status (e.g., Karban and Courtney, 1987; Polley and Detling, 1989) or the specific growing conditions (e.g., Louda, 1982b, 1983; Maschinski and Whitham, 1989). Thus, generally, for plants with high resource requirements, herbivory should be expected to influence resource-mediated interactions when the limiting resource is scarce.

Factorial experiments designed to evaluate the effects of the impact of chronic herbivory on competitive interactions support the hypothesis that herbivores often modify individual plant growth and, in doing so, influence plant position in competitive hierarchies. Included in laboratory studies that are relevant here, is a 1964 study by Sibma *et al.*, summarized by Harper (1977). In this study, oats contributed disproportionately more to seed yield than did barley in a replacement series experiment in the greenhouse. However, the introduction of a root-feeding nematode (*Heterodera avenae*) depressed the competitive advantage of oats over barley and reversed the outcome of the interaction. Windle and Franz (1979) found similar results testing the effect of greenbugs on barley in a growth chamber experiment. Also, defoliation of *Holcus lanatus* had different effects on yield, depending on whether it was growing with versus without its competitor, *Lolium perenne* (Watt and Hagger, 1980). And, using clipping to simulate herbivory on competitive

mixes of plants in greenhouse pots, Fowler and Rausher (1985) observed that defoliation modified the competitive outcome for *Aristolochia reticulata* and a dominant grass.

Field experiments that we have found in the literature include a recent evaluation of herbivore impact on competitive interactions of *Rumex*. A specialized leaf beetle, *Gastrophysa viridula* (Chrysomelidae), changed the relative growth and success of *Rumex obtusifolius* and *Rumex crispus*: alone, with each other, and with co-occurring grasses (Bentley and Whittaker, 1979; Bentley *et al.*, 1980; Cottam *et al.*, 1986). Cottam *et al.* (1986) concluded that (1) herbivory made the critical difference in the outcome of competition between *Rumex* species and grasses, and (2) the magnitude of the effect of herbivores depended on "other factors which impinge on the growth of the plant." Similarly, another experiment demonstrated that the suppression of *Dactylis glomerata* (Poaceae) by larger-statured *Trifolium* species (Fabaceae) was reversed by preferential grazing of slugs on *T. repens* (Cottam, 1986). Insects or slugs are also known to influence the growth or relative competitive performance of pasture species (Dirzo and Harper, 1980, 1982), a prairie forb (Louda *et al.*, 1989), forest sedges (Handel, 1976), and a desert shrub (Parker and Salzman, 1985).

In summary, preferential consumption by herbivores among co-occurring plants is common and it can affect individual plant characteristics (see Louda and Keeler, 1989). As predicted theoretically, such modifications can lead to differential performance among co-occurring competitors, especially when the environment or resource constraints prevent full regrowth and complete compensation for losses. However, most of the extensive evidence supporting this prediction is observational. More studies that directly measure the influence of herbivory and its interaction with individual competitive performance are needed, especially for native plants under field conditions.

IV. Herbivore Alteration of Population Dynamics and Resource Demand

Clearly, herbivory that kills plants decreases plant density, affecting density-dependent interspecific interactions. Thus, when herbivory changes the density or distribution of a host population, it should also alter the competitive pressure exerted by that population on its competitors. Mortality caused by selective herbivory contributes to local spatial variation in density. Such variation reflects both central place foraging by herbivores (Reichman, 1979; Huntly, 1987) and changes in herbivore pressure correlated with environmental heterogeneity (e.g., Burdon and Chilvers,

1974; Halligan, 1974; Rausher and Feeny, 1980; Parker and Root, 1981; Louda, 1982b, 1983).

Herbivory can also have a differential effect on reproduction among co-occurring plants (see Janzen, 1971; Crawley, 1983, 1989a; Hendrix, 1988; Louda, 1989). Although compensatory flowering occurs (e.g., Hendrix, 1979; Paige and Whitham, 1987), flower and seed consumption generally decreases seed numbers or quality and lowers the potential recruitment component of fitness (Janzen, 1971; Louda, 1982b, 1983, 1989; Hendrix, 1988; Louda *et al.*, 1989; Maschinski and Whitham, 1989).

The evidence that herbivory reduces density or recruitment, leaving space unoccupied and resources unsequestered, comes from several bodies of literature, as discussed in the rest of this section.

A. Rangeland Management

Enclosures of grazers, both native and domesticated, usually lead to shifts in species composition (see Scott *et al.*, 1979; Dyer *et al.*, 1982; Crawley, 1983, 1989a; Huntly and Inouye, 1988; Naiman, 1988; Naiman *et al.*, 1988). Selective use of plants by vertebrates provides a mechanism for such shifts (Harper, 1977), either by causing differential mortality or by changing competitive ability of the preferred plant. The plants that decrease under moderate grazing tend to be (1) relatively short-lived, often colonizing, perennials; (2) relatively palatable and nutritious to the large grazers; and (3) intermediate in growth rate and other life history traits between weedy annuals (ruderals) and long-lived, competitively dominant perennials. Interestingly, dominant grasses tend to respond positively to moderate-to-light grazing or clipping, *if* sufficient resources are available (e.g., Jameson, 1963; Norton-Griffiths, 1979; McNaughton, 1985; Painter and Detling, 1981; Archer and Detling, 1984; Seastedt, 1985). However, these responses also depend on the timing and severity of losses and the availability of resources for regrowth (Lee and Bazzaz, 1980; Wallace *et al.*, 1984; Coughenour *et al.*, 1985; Polley and Detling, 1989). Alternatively, nondominant grasses and forbs usually respond negatively to removal of leaf area (e.g., Bell, 1970; Crawley, 1983; Coughenour *et al.*, 1985).

Insect and nematode feeding is also selective, and its effects on plant morphology, growth, and reproduction could influence competitive interactions in rangelands. Examples of invertebrates using and differentially affecting grassland plants include foliage-feeding grasshoppers (e.g., Chandra and Williams, 1983; Landa and Rabinowitz, 1983; Joern, 1989), flower- and seed-feeding insects (e.g., Henderson and Clements, 1979; Kinsman and Platt, 1984; Louda *et al.*, 1987b), and root-feeding invertebrates (Ueckert, 1979; Ingham and Detling, 1986; Seastedt *et al.*, 1987). Exclusions of insects, such as fruitfly (*Oscinella* sp.), have led to

changes in plant species composition, with decreases in the weedier species in British grasslands (Clements and Henderson, 1979). Consumers and plant competition also interact to determine the recruitment of a native, monocarpic thistle (*Cirsium canescens*) in Sandhills Prairie (Louda *et al.*, 1989). In this case, predispersal seed predation by insects restricted both the number of viable seeds and the number of seedlings established (Table 1). Additionally, seedling recruitment was 16 times higher in the open than in grass (8 versus 0.5%). Seedling survivorship was reduced in proximity to switchgrass (*Panicum virgatum*; Table 2). In this case, insect seed destruction and subsequent interaction of thistle seedlings with established grasses should jointly determine population density and growth rate (Louda and Potvin, in preparation). Many other studies also suggest that both herbivory and competition may be important to population dynamics (see Janzen, 1971; Hendrix, 1988; Louda, 1989).

Table 1 Effects of Flower and Seed Herbivory on Seed Production, Average Seedling Establishment, and Subsequent Survival of Platte Thistle (*Cirsium canescens*) in Disturbed Blowouts at Arapaho Prairie, in the Sandhills Prairie Ecosystem of Arthur County, Nebraska^{a,b}

| | Control, Water Only | | Insecticide in Water | |
|---|------------------------|------|-------------------------|------|
| | \bar{X} | SE | \bar{X} | SE |
| 1984 Exclusion Experiment ($N = 6,5$) | | | | |
| Total seeds | 487 | 89 | 651 | 101 |
| Viable seeds | 27 | 6.3 | 105 | 20.1 |
| 1985 seedlings | 0.6 | 0.37 | 3.3 | 0.71 |
| 1988 adults | 0.05 | 0.03 | 0.33 | 0.16 |
| 1985 Exclusion Experiment ($N = 6,6$) | | | | |
| Total seeds | 652 | 76 | 783 | 121 |
| Viable seeds | 53 | 5.6 | 105 | 12.3 |
| 1986 seedlings | 0.35 | 0.20 | 2.7 | 0.69 |
| 1988 adults | 0.07 | 0.05 | 0.41 | 0.16 |

^a The data given here were taken from Louda and Potvin (in prep.) and were calculated per plant by blowout for each treatment, N being the number of blowouts per treatment; establishment and survival were recorded in the third week of May (1985–1988); the same blowouts were used in 1985, with treatments reversed. By May 1988, we had accounted for the fate of 96.4 and 78.0% of all seedlings established in the 1984 and 1985 experiments, respectively.

^b Two-way ANOVA model explained a significant portion of the variance ($p < 0.01$); there was a significant treatment effect for all stages (all $p < 0.03$) subsequent to the initial one (total seeds); years were not significantly different.

Table 2 Survival of Thistle (*Cirsium canescens*) Seedlings Transplanted Into Open Areas of a Grass (*Panicum virgatum*) Clone and into the Open Area Adjacent to the Clone^a

| | Number Surviving ^b | | Percent Surviving |
|---------------|-------------------------------|------|-------------------|
| | \bar{X} | SE | |
| After 9 weeks | | | |
| In grass | 0.14 | 0.14 | 4.8 |
| In open | 1.29 | 0.36 | 42.9 |
| After 2 years | | | |
| In grass | 0.00 | — | 0.0 |
| In open | 0.29 | 0.18 | 9.5 |

^a From Louda et al. (1989).

^b \bar{X} , Average for the 7 replicates of 3 seedlings per treatment replicate, with two treatments: (a) in open areas within a clone of grass (*Panicum virgatum*), and (b) in open areas adjacent to the clone; univariate ANOVA on arcsine-transformed proportions, $p < 0.02$ after 9 weeks. The study was carried out from May 22, 1986 to May 20, 1988 at Arapaho Prairie, Arthur County, Nebraska.

Vertebrate and invertebrate herbivores may have different, and at times conflicting, effects on plant dynamics and thus on the competitive interactions among plants (e.g., Inouye et al., 1980; Davidson et al., 1985; Gibson et al., 1987; Crawley, 1989b). However, the actual role of chronic, differential insect herbivory, as well as its interactions with vertebrate herbivory in plant competitive interactions, remains to be assessed directly under field conditions for the majority of plants in most natural communities.

B. Outbreaks

Significant temporal and spatial patterns of damage and influence are correlated with eruptions of herbivores. Outbreaks usually reduce the growth and resource acquisition of dominant plants (see Mattson, 1977; Barbosa and Schultz, 1987; Mattson and Haack, 1987; Joern, 1989), as well as accelerate nutrient turnover and regeneration in the community (e.g., Mattson and Addy, 1975).

For example, the interaction of heather, heather beetles, and grasses provides a case where experimental data suggest a coupling between cycles of insect abundance and of vegetation change (see Berdowski and Zeilinga, 1983, 1987; Heil and Diemont, 1983). In the heathlands of The Netherlands declines in abundance of the dominant heather (*Calluna*

vulgaris, Ericaceae) and simultaneous expansions of subdominant grasses are correlated with the opening of the canopy by outbreaks of the monophagous heather beetle. Field experiments showed that (1) removal of heather led to increased grass cover, (2) increases were greatest in heather removal plots that were fertilized, and (3) feeding and growth of heather beetles increased most on fertilized plants (Brunsting and Heil, 1985). Such experimental data are especially intriguing since in England cycles in abundance and dominance of heather have been explained as cycles of plant senescence (e.g., Watt, 1985).

Similarly, outbreaks of beetles (*Trirhabda*) on goldenrods (*Solidago*) are often observed in prairie grasslands. McBrien *et al.* (1983) found that, after an outbreak of beetles, grasses invaded large areas previously monopolized by goldenrods. Medium intensity, early defoliation retarded clonal development and reduced flowering, and heavy defoliation caused clonal mortality. Beetle herbivory also eliminated goldenrod transplants in the drier portion of a soil moisture gradient in prairie (Werner, 1989). Such observations suggest that periodic episodes of intense herbivory interact with high levels of competition for soil resources in the prairie in the determination of goldenrod establishment and persistence. However, a direct test of this hypothesis for the interaction of herbivory with competition in relation to changing environmental conditions is still needed for goldenrod dynamics.

C. Biological Control of Weeds

Successful biological control projects show that specialized insect herbivores can lead to dramatic reductions in host plant densities, and they also suggest properties that may promote strong herbivore effect (Goeden, 1978; Julien, 1984). Less successful projects can provide insight into those factors that limit herbivore impact (Goeden and Louda, 1976; Murdoch *et al.*, 1984). We summarize two cases to make these points clear.

In the first case, the degree of control of *Hypericum perforatum* (Saint-John's-wort, Clusiaceae) by the introduced insects varied geographically. In northern California, an area with dry summers, the introduction of a specialized leaf beetle led to drastically reduced total plant density and to a severe compression of its realized distribution (Huffaker and Kennett, 1959; Harper, 1969). The exact mechanism may be more complicated than originally thought. Damage by herbivores appears to have interacted with soil moisture deficits in determining this result. Growth was reduced and plants eliminated only in the open sun and not in the shade (Huffaker, 1951; Harris, 1980). Also, in areas where control was incomplete, such as British Columbia (Goeden, 1978) and New Zealand (Cameron, 1935), soil moisture remained high throughout the growing sea-

son, allowing compensatory regrowth and maintenance of competitive position even after beetle herbivory (Cameron, 1935; Clark, 1953; Williams, 1985). Such results provide indirect evidence for the simultaneous interaction of competition and herbivory in the net outcome.

In the second case, the degree of control of tansy ragwort (*Senecio jacobaea*, Asteraceae) by a moth (*Tyria jacobaeae*, Arctiidae) also varied geographically and it was also correlated with growing conditions. Defoliation usually does not kill individuals, but it does reduce plant growth and size. These losses to herbivores limited tansy ragwort populations, but only where the physical conditions, particularly dry soils, prevented sufficient compensatory regrowth (van der Meijden, 1979; Myers, 1980; Dempster and Pollard, 1981; Cox and McEvoy, 1983; Islam and Crawley, 1983). Thus, the persistence of tansy ragwort, relative to its potential competitors, was inversely correlated with the environment and the plant's regrowth capacity after herbivory.

D. Experimental Studies

Most tests of herbivory on native plants have evaluated the direct effects of consumption on plant growth or fitness. These studies show, in general, that consumption (1) is variable in both space and time and selective among species (see Crawley, 1983, 1989a,b; Hendrix, 1988; Louda, 1989), (2) often alters plant growth and reproduction (Waloff and Richards, 1977; Louda, 1984; Marquis, 1984; Parker, 1985; Paige and Whitham, 1987), (3) can change abundance (e.g., Cantlon, 1969; Rausher and Feeny, 1980; Kinsman and Platt, 1984; Stamp, 1984; Parker, 1985), or (4) modify distribution (Parker and Root, 1981; Louda, 1982a,b, 1983). However, very few studies (see below) explicitly evaluate the joint effects of herbivore consumption and plant competitive interactions over a relevant spectrum of field conditions.

V. Spatial Variation in Herbivore Effect

If herbivore impact has a spatial dimension, then the influence of herbivory on plant competition should also vary in space. Our model for selective herbivory (Fig. 3) predicts that the impact of loss will depend inversely on the plant population's capacity to compensate for losses. Clearly, if the ability to compensate for consumption is related to environmental conditions, then variation in impact along environmental gradients is to be expected. Interactions for which data exist from several locations support the suggestion that the contribution of herbivory to plant dynamics and potential interactions shifts as growing conditions shift.

A. Herbivore Impact along Environmental Gradients

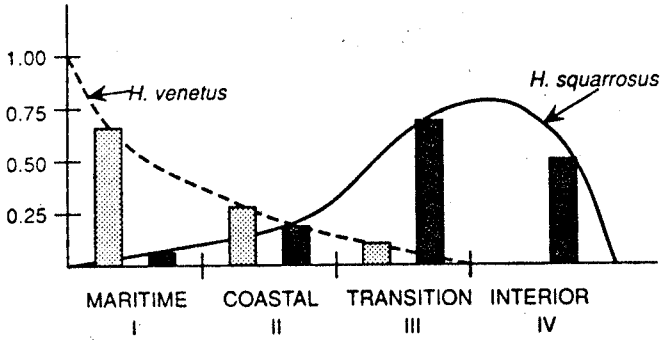
Consumer effects can, in fact, often be ordered along gradients: geographic gradients (Levin, 1976), productivity gradients (Fretwell, 1977; Oksanen *et al.*, 1981), elevational gradients (Louda, 1982a, 1983), disturbance gradients (Huntly, 1987; Coley, 1987), and local gradients (Handel, 1976; Louda *et al.*, 1987a-c; Louda, 1988).

On the geographic scale, several examples demonstrate spatial variation in herbivore influence. The effectiveness of control of Saint-John's-wort increased along a wet-to-dry regional gradient in the Pacific northwest (e.g., Harris, 1980). Herbivore pressure on native ginger (*Asarum caudatum*, Aristolochaceae) changed along the Pacific Coast: plants from moist northern areas with high exposure to slugs had slower growth, higher investment in defense, and lower seed output than plants in drier southern areas with less herbivore pressure (Cates, 1975). Frequency of cyanogenic morphs of *Lotus corniculatus* (Fabaceae) in Europe was directly correlated with herbivore pressure and inversely correlated with time available for regrowth (Jones, 1973). Such observations suggest that herbivory could be a major pressure affecting relative growth and resource exploitation, and thus the balance between competition and predation effects, along geographic gradients (Menge and Sutherland, 1976).

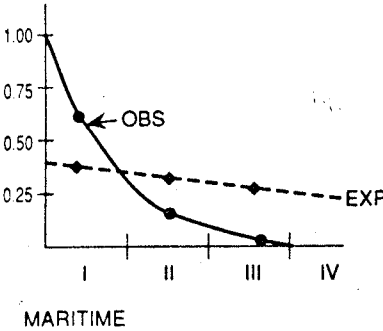
On the regional scale, plant species often replace each other along elevational gradients. One hypothesis for such replacement is that physiologically superior species competitively displace each other as the environment changes (Cody, 1978; Bunce *et al.*, 1979). However, herbivore abundances and damage also change along elevational gradients (Janzen and Schoener, 1967; Janzen *et al.*, 1976; Louda, 1982b, 1983; Randall, 1982), and thus the effect of herbivory also can change along the gradient. For example, control of gorse (*Ulex europaeus*, Fabaceae) by introduced seed predators shifted along an elevational gradient in Hawaii (Goeden, 1978). Thus, an alternative hypothesis is that differential consumption along such gradients may also lead to the observed replacement of plant species.

In a test of this hypothesis, Louda (1982a,b, 1983) excluded predispersal seed predators from two native goldenbushes (*Haplopappus squarrosus* and *Haplopappus venetus*, Asteraceae) at sites along an ocean-to-mountains gradient over which those species replace each other (Fig. 4A). Insect seed predation limited the production and the release of viable seed and, subsequently, the establishment of seedlings by both species (Louda, 1982a,b, 1983). The limitation was disproportionately strong near the coast for *H. squarrosus*, limiting its recruitment coastally and restricting it to the inland part of the gradient (Fig. 4C; Louda, 1982b). In addition, for the other, more coastal species (*H. venetus*), more intense

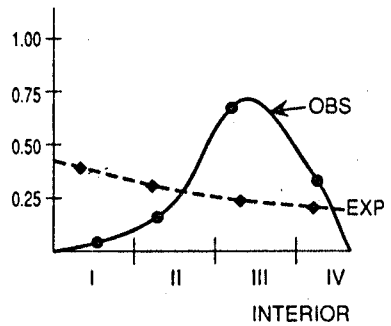
A



B *H. venetus*



C *H. squarrosus*



ZONES OF SAN DIEGO COUNTY

Figure 4 (A) Replacement of two goldenbushes, *Haplopappus venetus* by *Haplopappus squarrosus*, along the complex environmental gradient from maritime coast to interior mountains in San Diego County, California. Bars represent observed relative frequency of each species in a zone [stippled, *H. venetus*, adapted from Louda (1983); solid, *H. squarrosus*, adapted from Louda (1982b)], $N = 15,250$. (B, C) Comparison of observed frequency of each species after herbivory (solid line) against the potential distribution without herbivory (dashed line). The expected (= potential) distribution in the absence of consumption was projected on the basis of several measures of individual performance of control plants, especially flower and seed production, when insects were excluded (details in Louda, 1982b, 1983). These experiments demonstrated that consumption played a significant role in determining the coastal abundance of *H. venetus* and the more inland distribution of *H. squarrosus* along the gradient.

seedling consumption inland on the gradient followed the seed predation (Louda, 1983). The higher mortality inland compressed the realized adult distribution toward the coast (Fig. 4B). So, seed predation reduced density, and differential levels of total consumption by herbivores along

the gradient dramatically changed the subsequent spatial pattern of both species along the gradient. Using only the observational data (Fig. 4A), the replacement of these species along the gradient might have been interpreted as driven by competition. However, the experiments showed that the replacement was actually caused by herbivore consumption that caused disproportionate reductions in densities of *H. squarrosus* near the coast and of *H. venetus* inland. These decreases in density presumably released resources for other coastal scrub and chaparral plants in specific portions of the gradient, potentially affecting other, competitive-mediated interactions.

On the local scale, herbivory also varies along topographic gradients. Handel (1976) found that significant differential feeding by slugs on *Carex platyphylla* along a soil moisture gradient in northeastern deciduous forest altered *Carex* distribution. Insect consumption of *Cleome serrulata* (Capparidaceae), a fugitive annual of shortgrass prairie, shifted the population's mode for most successful seed set from the wet to the medium-wet portion of a 30-m soil moisture gradient (Louda *et al.*, 1987b; Fig. 5A). Plants grew larger and flowered more, but both foliage and seed losses to insects were much higher, in the wettest part of the gradient.

To summarize, such cases illustrate that herbivory can dramatically alter plant population dynamics along environmental gradients, thereby changing the intensity, character, and possibly outcome of competitive interactions among plants along these gradients. More studies are required to identify the characteristics, or groups, of species vulnerable or resistant to such herbivore interference in plant-plant interactions along various environmental gradients.

B. Herbivore Impact across Habitat Discontinuities

We predicted, and found, that the *net* impact of consumption generally changed in relation to conditions for regrowth. Growing conditions usually vary substantially between adjacent habitats. Herbivore pressure also often varies between adjacent habitats, including between sun versus shade sites (e.g., Huffaker and Kennett, 1959; Lincoln and Langenheim, 1979; Lincoln and Mooney, 1983; Louda and Rodman, 1983; Louda *et al.*, 1987a,c). Thus, consistently different levels of herbivory could determine comparative plant performance and relative competitive ability in adjacent habitats.

The best-known example of a case where herbivory appears to determine habitat-specific competitive ability is that of Saint-John's-wort (Clark, 1953). Insect herbivory was greater in the sun (Huffaker and Kennett, 1959). In addition, water deficits limited compensatory regrowth in the sun, presumably lowering the ability of attacked plants to compete with unconsumed neighbors (Clark, 1953; Williams, 1985).

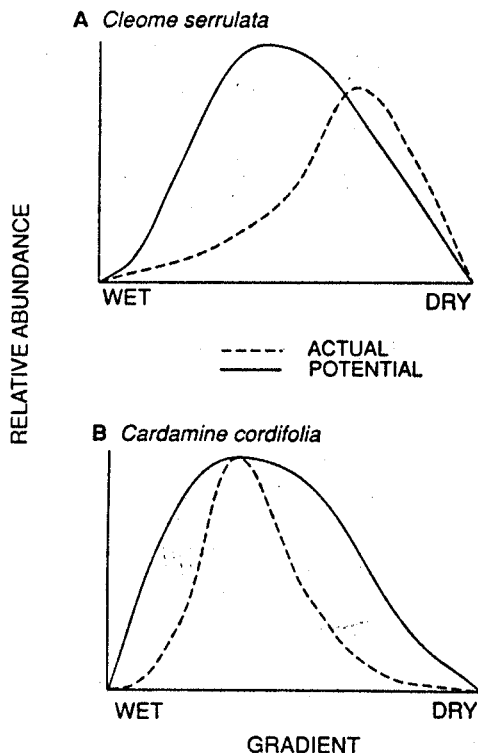


Figure 5 Schematic representation of herbivore-caused shifts in plant performance along small-scale topographic soil gradients: (A) Rocky Mountain bee plant, *Cleome serrulata*, in dry, shortgrass prairie of eastern Colorado (adapted from Louda et al., 1987b); and (B) bittercress, *Cardamine cordifolia*, within wet, willow-shaded habitats in a montane area of the Rocky Mountains, central Colorado (see Louda and Rodman, 1983; Louda, 1988).

Other cases in which herbivory appears significant and varies in magnitude between adjacent habitats include *Lotus corniculatus* (Fabaceae) off versus on minetailings (Jones, 1966); *Machaeranthera canescens* (Asteraceae) in open versus in more closed vegetation in cool desert (Parker and Root, 1981); and *Cardamine cordifolia* (Brassicaceae) in dry, sunny habitats versus in adjacent moist, shaded habitats (Louda and Rodman, 1983; Collinge and Louda, 1988a,b).

For the latter species, field experiments have shown (1) consistently higher levels of herbivory in sun than in natural shade (Louda and Rodman, 1983; Collinge and Louda, 1988a,b); (2) increased vulnerability of shade plants to insects after removal of overhanging willow branches (Table 3); (3) growth and survival in the sun when insects were excluded (Table 3); and (4) decreased vertical growth, reduced leaf initi-

Table 3 Insect Herbivory and Bittercress (*Cardamine cordifolia*) Survival and Growth in a Transplant Experiment^{a,b,c}

| | Control (Water Only) | | No Insects (Insecticide in Water) | |
|---|----------------------------|------|---|------|
| | \bar{X} | SE | \bar{X} | SE |
| Increase in leaf area removed (mm ² /leaf) ^d | | | | |
| Sun | 68.2 | 1.93 | 5.3 | 1.94 |
| Shade | 9.5 | 0.5 | 3.2 | 0.55 |
| Ramet height (cm) | | | | |
| Sun | 13.1 | 1.7 | 18.5 | 1.9 |
| Shade | 20.6 | 3.6 | 24.2 | 2.6 |
| Number of fruits per plant | | | | |
| Sun | 0.2 | 0.1 | 0.6 | 0.2 |
| Shade | 0.8 | 0.2 | 0.7 | 0.2 |

^a From Louda (in review).

^b Half of the ramets were transplanted into the sun (one portion was used as controls, and the other portion was treated with pyrethrum to reduce foliage-feeding by insects) and half were transplanted back into the shade (one portion used as controls, the other treated with pyrethrum to reduce foliage-feeding by insects) at First Ford Meadow, Copper Creek, Gothic area, Gunnison County, Colorado (1980).

^c MANOVA, Wilks-Barr Trace, $p < 0.01$.

^d Damage evaluated using square-root transformed data.

ation, accelerated leaf senescence, lowered total leaf area, and reduced seed set caused by chronic insect herbivory (Louda, 1984). The more intense herbivory imposed on plants in the sun and in drier areas restricts the local population to moist and shaded areas (Fig. 5B) and thus releases resources for other, co-occurring plants in the adjacent sunny habitats.

Most work on herbivory has assessed the contribution of losses to the performance of established plants, i.e., their growth, survival, and seed production. However, in some cases herbivory on seedlings may be even more important in determining establishment, abundance, and subsequent competitive potential (e.g., Cantlon, 1969; Louda, 1983; Mills, 1983, 1984; Clark and Clark, 1985). Further direct tests of this hypothesis, especially along gradients, appear warranted.

Controlled field experiments that actually evaluate herbivory as a mechanism altering competitive ability and outcome are rare. However, the experimental studies that we did find do show that herbivory does

not have to cause mortality in order to affect relative competitive performance. Herbivore defoliation in these cases removed a demonstrated competitive advantage or changed the expected outcome of competition (Bentley and Whittaker, 1979; Windle and Franz, 1979; Bentley *et al.*, 1980; Watt and Hagger, 1980; McBrien *et al.*, 1983; Fowler and Rausher, 1985; Parker and Salzman, 1985; Cottam, 1986; Cottam *et al.*, 1986). However, such tests need to be extended to other species and to a range of environmental conditions.

Herbivory could also be an important aspect of temporal variation in plant interactions. Differential herbivory on plants occurring at each stage of succession could either augment or inhibit competitively driven changes in species composition (Ellison, 1960; Cates and Orians, 1975; Reader and Southwood, 1981; Brown, 1985; Mills, 1986). Foraging by vertebrate herbivores, including deer, elk, and rabbits, has been observed to cause changes in species composition (e.g., Leopold, 1956; Watt, 1957; Crawley, 1983). Also, the activities and feeding of fossorial herbivores disturb plants, influencing plant densities and interactions. These herbivores have an effect both by consumption and by indirect facilitation of soil turnover and nutrient cycling (e.g., Reichman and Smith, 1981; Tilman, 1983; Huntly, 1987; Inouye *et al.*, 1987). Such herbivory could be a particularly important modifier of competitive interactions during succession.

VI. Discussion

A. Predictions of the Effect of Selective Herbivory

Inclusion of selective herbivory into Holt's (1977, 1984) conceptual model (Fig. 1) suggests how herbivore consumption could be imposed and influence the various types of competitive interactions among plants (Fig. 2). The graphical analysis of selective herbivory on a competitive dominant (Fig. 3) shows that the net effect of selective herbivory should depend on (1) the plant's intrinsic rate of increase (Fig. 3A), a key aspect of compensatory ability; (2) the strength of the plant's density dependence near K (Fig. 3B); and (3) the degree of density dependence in the herbivory (Fig. 3C). The empirical evidence, especially the few experimental studies, broadly supports these expectations. The impact of selective herbivory varied in relation to (1) regrowth capability (a dimension of compensatory ability), and (2) competitive rank in the absence of herbivory. Our review also suggests that by inducing shifts in plant shape, phenology, resource allocation, recruitment patterns, etc., herbivores could frequently alter competitive interactions between plants in complex, nonadditive ways.

B. Environmental Context and Net Herbivore Effect

In most cases, the actual impact of herbivory was scaled by abiotic conditions. Losses had greater demographic and competitive repercussions under harsher physical conditions or under more limited resource conditions. Thus, herbivore-caused decreases in density or plant growth generally changed along environmental gradients, i.e., with elevation, habitat, gap occurrence, or soil moisture. Spatial variation in insect herbivory along gradients is correlated with differences in insect activity and abundance (Clark, 1953; Janzen and Schoener, 1967; Williams, 1985), or with plant physiological condition and foliage quality for insect feeding and growth (Lincoln and Langenheim, 1979; Lincoln and Mooney, 1983; Louda, 1986; Louda *et al.*, 1987b,c; Collinge and Louda, 1988a). However, this prediction and the relative importance of such mechanisms in creating spatial variation in herbivory, and thus in plant-plant interactions, along gradients still needs to be evaluated experimentally for a broader range of plant species and communities.

C. Exploitation versus Compensation in Net Herbivore Effect

Logically and empirically it seems clear that the relationship between herbivory and ultimate plant performance is determined by the opportunity for compensatory responses at both individual and population levels (see above, and Maschinski and Whitham, 1989). In theory, factors that determine the opportunity and capacity for compensatory responses include (1) physical constraints on plant growth, (2) resource constraints on plant growth, (3) flexibility in internal resource allocation, and (4) type of intraspecific density dependence. Thus, prediction of plant responses to herbivory requires analysis of environmental controls on those responses, such as (a) resource distributions, (b) resource levels, (c) resource renewal rates, as well as (d) spatial and temporal variation in these variables. Both spatial and temporal variation in resources may limit plant capacity to make up for losses and, thus, influence net herbivore impact and plant-plant interactions. Relevant temporal variables include (i) length of growing period, (ii) fluctuations in resource regeneration rates, and (iii) frequency of external disturbance. Theory and observation suggest the importance of each of these constraints on regrowth, and thus on the ability of herbivores to influence relative competitive ability; however, all of these ideas require more experimental analysis under field conditions.

Plants with significant, selective insect herbivores did not grow as well, nor succeed in maintaining themselves as long, when *both* herbivory and potential resource limitation occurred. Given time and resources for regrowth, compensation for loss of leaf tissue or seeds often occurred. However, compensatory physiological responses and growth depend on

physical conditions and require resources (Belsky, 1986). When abiotic environmental conditions or time precluded full recovery, or when individual compensatory responses required diversion of limited resources and thus delayed relative growth and reproduction, damaged plants appeared to be at a significant competitive disadvantage. As a result, we expect compensatory responses to become more restricted as the species' distributional boundaries are approached, or as limiting resources become scarce. We predict that the importance of chronic herbivory, for the establishment of seedlings and for maintenance of relative competitive position of established plants, will increase *in general*: (1) as environmental conditions decrease plant capacity for compensatory regrowth, and (2) as herbivore pressure on competitors declines. When net losses (the excess of exploitative loss over compensatory regrowth) are differential among competitors, herbivory should make a substantial contribution to the character and outcome of interactions among competing plants.

A controversy exists over whether herbivory generally harms or benefits plants (e.g., Seastedt, 1985; Belsky, 1986; McNaughton, 1986; Paige and Whitham, 1987; Maschinski and Whitham, 1989). However, our arguments do not depend on whether herbivory, in isolation from its community context, is injurious or beneficial to the plant eaten. The evidence suggests that, if competition for limited resources exists and if levels of herbivory and plant compensatory responses vary in either direction among co-occurring plants, then herbivores could be critical in the determination of relative competitive ability. In such cases, herbivory leads to patterns in the plant community that would be unlikely in the absence of herbivory.

D. Detection of Interaction between Herbivory and Competition

The abundant evidence for the *potential* impact of herbivores suggests that relative resistance to herbivory is an important part of the suite of competition-mediating characteristics of plants. Few analyses have been done to assess this expectation. Herbivory needs to be assessed more routinely in studies of plant competition, and, vice versa, examination of the competitive milieu would benefit studies of herbivory. Such assessments could be made by first comparing spatial and temporal differences in plant traits, resource use, and herbivore damage (e.g., Tingey, 1986), and then by doing the appropriate factorial experiments in the field.

There are several ways to facilitate the detection and evaluation of herbivory in competition studies. Obviously, both herbivory and competition need to be examined. Competition needs to be quantified in the absence of natural enemies (e.g., in enclosures), and response to limiting resources needs to be identified. The effect of herbivory on competing

plants should be characterized experimentally if possible. Additionally, since physical conditions influence compensatory growth and thus actual herbivore impact, the experiments should evaluate competition and consumption over the range of abiotic conditions under which the plants occur. The models presented here suggest that intraspecific density dependence of the dominant species needs to be studied along with interspecific competition and herbivory.

Patterns in damage among competitors provide clues to potential effects, suggesting the relevant spatial or temporal dimensions. However, observed losses of leaf area or of seeds tend to underestimate actual herbivore impact (e.g., Coley, 1983; Louda, 1984; Fox and Morrow, 1986; Anderson, 1988). Consistent, differential patterns of herbivory can be important, often independent of the absolute amount of loss (Fox and Morrow, 1986). So, variation in herbivory among populations, sites, habitats, regions, and so forth, should be measured in relation to plant abundance, resource availability, and total plant biomass. An inverse relationship between damage and plant occurrence along a particular gradient, for example, suggests that differential herbivory cannot be ruled out as an explanation. In addition, we recommend simple exclusion tests and bioassays, done by placing vulnerable plants in different habitats. These allow spatial, temporal, and species-specific variation in damage to be categorized and quantified throughout the plant's range of habitats.

The obvious subsequent step is to evaluate the interaction of herbivory and resource competition experimentally in the field, modifying both herbivore load (Harper, 1969, 1977) and plant growing conditions (Ehlenberg, 1954). The basic experimental design should include decreases and enhancements of herbivory, resources, and competitors, singly and in combination. The specific system and particular subsidiary questions will determine the details of the design.

Given the evidence for variation along gradients in both plant abundance (Austin, this volume) and herbivory (above), the most important experiments will clearly be those that are done in more than one portion of a biologically interesting gradient and repeated along replicate gradients. We also need long-term, multiyear experiments. The contribution of herbivory to plant growth, density, or competitive ability may well shift with population age or size structure or with changes in the background vegetation.

In summary, herbivory can be a critical aspect in plant competitive interactions. We recommend an approach for the further analysis of this hypothesis that integrates both observational and experimental tests of theoretical and empirically based predictions for the role of both physical and biological variation in such interactions. We predict integrated stud-

ies of competition and predation in plant communities will yield a more robust, synthetic picture of the functioning of such assemblages.

VII. Summary

Herbivory can influence plant competitive interactions in two ways. First, herbivory often modifies plant growth or morphology, changing access to resources. Thus, when resources are limited, differential losses to herbivores could be critical, qualitatively altering the interaction among competing plants. Second, herbivory affects population distribution and abundance of some species, thereby changing resources for competitors. Generalist herbivores often modify total resource demand by plants. Selective herbivores in some cases shift relative competitive abilities. Either can cause predator-mediated patterns that mimic those generated by resource competition.

We incorporate selective herbivory into conceptual and graphical models of competition. The models suggest that the impact of selective herbivory on plant competition will reflect both the plant's compensatory responses to herbivory, including intraspecific density dependence, and the strength of density dependence of the herbivory. Our literature review leads to the same hypotheses. The net effect of herbivory generally depended on the balance between loss and compensatory regrowth. Also, the relative influence of herbivory on plant performance, and thus competitive potentials, often changed along environmental gradients. Herbivory was particularly important where constraints in resources, growing season, or growth strategies limited plant compensation for losses, and diminished the species's capacity to maintain itself against competitors.

We conclude that herbivory, by modifying individual traits and affecting population dynamics, represents a potentially significant dimension of competitive interactions among plants. However, few studies have as yet directly tested the interaction of herbivory and competition. So, we end by suggesting methods for doing so in future research.

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