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PLANT COMPETITION AND HERBIVORY IN RELATION TO VEGETATION BIOMASS[1]

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Abstract. We tested whether effects of competition and herbivory on plant growth depend on the aboveground biomass of vegetation. Our objective was to test theoretical predictions about the site-dependence of biotic mechanisms of plant population regulation. Biomass ranged from a mean of 64 to 776 g/m^2 at the eight study sites, which included six old fields and two herbaceous plant communities near water. To measure effects of competition, 4–5 wk old plants of a perennial grass (*Poa compressa*) were transplanted into plots where neighboring plants were either left intact or removed and after 4 mo the shoot mass of transplants was compared in the two treatments. Transplants were caged in both treatments to exclude herbivores. Removing neighbors increased transplant shoot mass significantly at all sites, indicating that transplants experienced less competition for resources when their neighbors were removed. Regression analysis indicated that the increase in shoot mass due to neighbor removal was significantly greater at sites with higher biomass. This result supports theories that predict competition should increase with increasing biomass. To measure effects of herbivory, the growth of caged and uncaged plants was compared. Caging transplants did not increase their shoot mass significantly at the two sites with the lowest biomass. However, shoot mass was significantly greater for caged transplants than for uncaged transplants at all other sites. Caged transplants lost less tissue to herbivores such as small mammals and molluscs. Regression analysis indicated that the increase in shoot mass due to caging was significantly greater at sites with higher biomass. The combined effect of herbivory and competition was measured by comparing transplant growth in plots where transplants were caged and neighbors were removed with the growth of transplants in plots where transplants were not caged and neighbors were left intact. Transplant shoot mass was significantly greater where herbivores were excluded and neighbors were removed, especially at sites with high biomass. Our results indicate that competition and herbivory each have a greater effect on plant growth at sites with higher biomass and that herbivory has less effect than competition on plant growth at sites with relatively low biomass.

Key words: aboveground biomass; competition; herbivory; old field; Ontario, Canada; plant growth; Poa; *population regulation.*

INTRODUCTION

One goal of plant ecologists is to develop a model of population density regulation that can accurately predict population dynamics at any site. Achieving this goal will be especially difficult if mechanisms of population regulation are site dependent. It is not yet clear whether all regulatory mechanisms are site dependent, so we tested whether effects of two mechanisms (competition and herbivory) depended on the amount of aboveground plant biomass present at a site (henceforth called biomass). We chose competition and herbivory because each can be an important determinant of plant population dynamics (Harper 1977). We decided to examine these mechanisms (competition and herbivory) along a biomass gradient to test predictions of some current theories and to help explain inconsistent results of past experimental studies.

Current theories of plant community organization make different predictions about the relationship between competition and biomass. Some theories (e.g., Grime 1979, Keddy 1990) predict that competition should increase with an increase in biomass. The basis of this prediction is that plants are more likely to interact and to compete for resources at sites with higher biomass. In contrast, other theories (e.g., Taylor et al. 1990, Tilman 1988) predict that competition should not increase with an increase in biomass. Taylor et al. (1990) argue that competition reflects the ratio of resource demand to supply and that this ratio could be equally high at sites with low or high biomass. Tilman (1988) and others (e.g., Newman 1973, Grubb 1985) feel that competition for light may be greater where biomass is high but that competition for soil resources may be greater where biomass is low; consequently total competition could be about equal at sites with low vs. high biomass. Empirical tests are required to de-

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termine which of these theories best applies to natural communities.

The relationship between herbivory and biomass has received less attention from theorists. However, predictions made for a related variable, plant productivity, suggest that several relationships are possible. Oksanen et al. (1981) predicted that herbivory should increase with an increase in plant productivity from $\approx$30 $g \cdot m^{-2} \cdot yr^{-1}$ to 700 $g \cdot m^{-2} \cdot yr^{-1}$ because more herbivores could be supported at a site with higher productivity. With a further increase in productivity, herbivory should decrease because more carnivores would be present. These predictions assume that herbivores and carnivores do not move between sites differing in productivity. If animals move freely among sites, there could be less difference in herbivory among sites (Oksanen 1990, Oksanen et al. 1992).

Several experimental studies have examined the relationship between herbivory (or competition) and biomass but they give inconsistent results. Some studies (e.g., Rice 1987, Boyd 1988, Reader 1992) indicate that herbivory increases with increasing biomass, while others (e.g., McAuliffe 1986, Ellison 1987) report that herbivory decreases with increasing biomass. For competition, some studies (e.g., del Moral 1983, Gurevitch 1986, Wilson and Keddy 1986, Reader and Best 1989, Campbell and Grime 1992) indicate that it increases with increasing biomass, while other studies (e.g., Fowler 1990, Wilson and Tilman 1991, 1993, Turkington et al. 1993, Reader et al. 1994) indicate that competition may not increase with an increase in biomass. It is difficult to generalize about the site dependence of competition or herbivory from these inconsistent results, especially since each study considered a relatively small range of biomass, and, further, these ranges frequently did not overlap (cf. Goldberg and Barton 1992, Gurevitch et al. 1992, Grace 1993).

In this study we used the entire range of biomass exhibited by herbaceous plant communities at a particular geographic location to examine the relationship between biomass and competition (or herbivory). We focused on plant communities with the same type of vegetation (i.e., herbaceous) at one geographic location to minimize potentially confounding effects of differences in plant type (e.g., herbaceous vs. woody) and differences in macroclimatic conditions. To ensure that any difference in competition (or herbivory) among sites was not confounded by differences among plants, we used transplants of the same species, size, and age at all sites. The effects of competition (or herbivory) on transplant growth were measured by removing neighbors (or excluding potential herbivores) of some transplants and comparing their growth with that of untreated transplants.

METHODS

Study site biomass and species composition

Eight sites were chosen for the study within a 10-km^2 area near Guelph, Ontario, Canada (43° 33′ N, 80° 15′ W). Six of the eight sites were old fields (Table 1). One of the remaining two sites was located alongside a stream and the other was next to a river. No site had been disturbed by human activity for at least 15 yr (R. Reader, *personal observation*).

Only herbaceous plants were present at each site and most shoots die during winter. Therefore, aboveground plant biomass ranges from near zero at the start of the growing season to some maximum value near the end of the growing season. To estimate the maximum aboveground biomass of vegetation at each site, aboveground plant material was collected from five randomly selected 1-m^2 areas per site in late September. This material was then dried (80°C) and weighed. Mean biomass was calculated for each site and the statistical significance of differences among means was determined using analysis of variance (ANOVA) followed by Tukey's honestly significant difference (HSD) test (Zar 1984).

The species composition of vascular plants was determined at each site using five randomly positioned 1-m^2 quadrats per site. Each quadrat was subdivided into twenty-five 20 × 20 cm units and species rooted in each unit were noted. The percentage of 125 units occupied (i.e., 25 units per quadrat × 5 quadrats) was calculated for each species to quantify its frequency at a site.

Experimental design

A randomized-block experiment with the following six treatments was set up at each site to measure effects of competition and herbivory on the growth of target plants:

1) Neighbors of the target plant left intact and the target plant placed in a full cage;

2) Neighbors removed and the target plant placed in a full cage;

3) Neighbors removed and the target plant not placed in a cage;

4) Neighbors left intact and the target plant not placed in a cage;

5) Neighbors removed and the target plant placed in a half cage; and

6) Neighbors left intact and the target plant placed in a half cage.

With this experimental design, competition could be measured by comparing the growth of target plants in treatments 1 and 2 (i.e., neighbors left intact vs. neighbors removed, with herbivores excluded by a full cage).

Herbivory could be measured by comparing target plant growth in treatments 2 and 3 (i.e., herbivores excluded by the full cage vs. herbivores not excluded by a cage, without any neighbors present). Since neighbor removal could affect herbivory (e.g., by making the target plant more apparent), herbivory was also assessed by comparing target plant growth in treatments 1 and 4 (i.e., with neighbors left intact).

The combined effects of competition and herbivory

TABLE 1. Biomass and frequency of the most common species at the eight study sites near Guelph, Ontario, Canada (means ± 1 SD). Biomass values with the same superscript capital letter do not differ significantly ($P \geq 0.05$). Nomenclature follows Gleason and Cronquist (1963). Frequency values for all other species found at the eight sites are given by Bonser (1994).

Study site	Habitat type	Biomass (g/m^2)	Species	Frequency (%)
1	Old field	64 ± 26^{A}	*Poa compressa**	95 ± 11
			Lotus corniculatus	78 ± 30
			Daucus carota	46 ± 31
			*Panicum capillare**	42 ± 35
2	Old field	129 ± 28^{A}	*Poa compressa**	99 ± 2
			Echium vulgare	54 ± 24
			Medicago lupulina	44 ± 31
			Potentialla recta	34 ± 35
3	Old field	233 ± 42^{B}	*Hieracium floribundum*	100 ± 0
			*Poa compressa**	76 ± 10
			Medicago lupulina	55 ± 11
			*Poa pratensis**	30 ± 7
4	Old field	326 ± 64^{B}	*Poa pratensis**	100 ± 0
			Hieracium pratense	88 ± 6
			Satureja vulgaris	45 ± 13
			Solidago canadensis	33 ± 11
5	Old field	558 ± 80^{C}	*Bromus inermis**	100 ± 0
			*Poa pratensis**	100 ± 0
6	Streamside	579 ± 52^{C}	*Phalaris arundinacea**	100 ± 0
			Equisetum arvense	10 ± 17
			Cirsium arvense	6 ± 6
			Solanum dulcamara	2 ± 4
7	Old field	651 ± 162^{C}	*Solidago canadensis*	100 ± 0
			*Poa pratensis**	100 ± 0
			Aster novae-angliae	13 ± 8
			Linaria vulgaris	1 ± 1
8	Riverside	776 ± 184^{C}	*Aster puniceus*	52 ± 46
			*Glyceria striata**	45 ± 39
			Eupatorium maculatum	28 ± 40
			Clematis virginiana	12 ± 25

* = graminoid; other species are forbs.

could be measured by comparing the growth of target plants in treatments 2 and 4 (i.e., neighbors removed plus herbivores excluded by a full cage vs. neighbors left intact and herbivores not excluded by a cage).

The two half cage (HC) treatments (5 and 6) were included in the experimental design to be able to test for a potentially confounding effect of shading by the full cage. The half cage also shaded the target plant but it did not exclude herbivores, as described in more detail below. To assess the effect of shading, we compared target plant growth in treatments 3 and 5 (i.e., no cage vs. half cage, with neighbors removed) and in treatments 4 and 6 (i.e., no cage vs. half cage, with neighbors left intact). In each case, we found that target plant growth did not differ significantly between half cage and no cage treatments (Bonser 1994). This result confirmed that shading was not a confounding factor. Therefore, it was appropriate to assess herbivory by comparing target plant growth in full cage and no cage treatments. Results for the half cage treatments 5 and 6 are not presented here since they were not used to calculate effects of competition or herbivory.

Each of the six treatments was assigned randomly to one of six 1-m^2 plots in a block. Within a block, plots were set up about 1 m apart. Six blocks were set up at each site. Blocks were at least 2 m apart.

Experimental treatments were applied to transplants of a perennial grass, *Poa compressa* L., at all sites. This particular species (henceforth called *Poa*) was chosen because both factors of interest here (i.e., competition and herbivory) had affected its growth in a previous study (Reader and Bonser 1993) and abiotic conditions had less effect on its growth.

Experimental procedure

The experiment was conducted at sites with a medium amount of biomass (i.e., sites 3 and 4) in 1992 (but not in 1993) and extended to sites with lower biomass (i.e., sites 1 and 2) plus sites with higher biomass (i.e., sites 5 through 8) in 1993. Procedures used in the 2 yr were very similar but not identical, as explained below.

For the neighbor removal treatment, all aboveground vegetation and litter were removed after shoots were either clipped by hand (1992) or herbicide was applied (1993). It was impractical to clip shoots at all six sites in 1993 so herbicide (i.e., a 1% solution of glyphosate [N-phosphenomethylglycine], trade name Roundup) was applied instead. The herbicide was contained during application by enclosing the treated plot in a plastic container (1 × 1 m × 0.5 m tall) that had no top or bottom. In both years any regrowth in treated plots was removed by hand throughout the experiment.

For the full-cage and half-cage treatments a target plant was either fully enclosed or half enclosed, respectively. A full cage consisted of a wire mesh (6 mm) cylinder (10 cm diameter × up to 50 cm tall) that was supported by a short plastic tube (8 cm tall × 10 cm diameter). The cylinder was closed at the top but open at the bottom. The open end of the cylinder fit snugly around the top of the plastic tube. The plastic tube was hammered 4 cm into the ground to exclude crawling herbivores such as slugs. The plastic tube did not shade the transplant but it may have restricted lateral movement of roots within the top 4 cm of the soil. However, any such restriction did not have a significant effect on plant growth in a previous experiment (Reader 1992). At three sites (2, 3, and 4) it was also necessary to place a wire fence (60 cm tall, 2.5-cm mesh) around plots assigned to the full-cage treatment to prevent mammals (e.g., rabbits) from pushing over the cages. A half cage consisted of the same 6-mm wire mesh but it was placed only on the south side of a target plant to give the same amount of shading experienced by a plant in a full cage. The half cage was not intended to exclude herbivores so plastic tubes were not used in this treatment because they could have excluded crawling herbivores.

To assess effects of experimental treatments on plant growth, young plants (4–5 wk old) of the target species were transplanted into experimental plots after the last spring frost (i.e., late May–early June). Transplants were used so that plant size and age could be standardized among treatments. The initial height of transplants differed by < 1 cm. Young plants were used to ensure that early growth stages, which may be especially susceptible to effects of competition (Goldberg 1990) and herbivory (Reader 1992), were included. Either three transplants (in 1992) or four transplants (in 1993) were spaced uniformly within a plot. A plastic marker was placed next to each transplant to distinguish it from naturally occurring plants.

Transplants were grown from *Poa* seeds collected at site 3. Seeds were germinated in Petri dishes and seedlings were transferred to small pots (3 × 4 cm × 5 cm deep) that contained a commercially prepared potting medium (Promix, Les tourbieres premier, Canada). Seedlings spent 4–5 wk in the greenhouse to become established, then they were transplanted into field plots. A total of ≈0.2 L of tap water was applied per transplant during their 1st wk in the field to minimize transplant shock.

After 4 mo, shoots of transplants were harvested, dried at 80°C, and weighed. Mean values of shoot mass were calculated and the statistical significance of differences in mean shoot mass among treatments was tested using a two-way ANOVA (i.e., neighbor removal and caging), followed by Tukey's HSD test, for each study site. Data were $\log_e$-transformed to meet assumptions of ANOVA.

Competition and herbivory in relation to biomass

To compare effects of competition (CI), herbivory (HI) and competition plus herbivory (CHI) at different sites, values of the following indices were calculated for each site, based on recommendations of Grace (1995):

$$CI = (NR - NI)/NR, \quad (1)$$

where NR and NI are the mean shoot masses of transplants in treatments with neighbors removed and left intact, respectively, in fully caged plots (i.e., effects of herbivory excluded);

$$HI = (FC - NC)/FC, \quad (2)$$

where FC and NC are the mean shoot masses of transplants within a full cage or with no cage, respectively, in plots where neighbors were removed (i.e., effects of competition excluded). HI was also calculated for plots where neighbors were left intact since neighbor removal could have affected herbivory, as explained above. Student's t test was used to test for a significant ($P < 0.05$) difference between values of HI with neighbors left intact vs. neighbors removed.

$$CHI = (FCNR - NCNI)/FCNR, \quad (3)$$

where FCNR is the mean shoot mass of transplants within a full cage and with neighbors removed and NCNI is the mean shoot mass of transplants not in cages and with neighbors left intact.

For each index, the reduction in potential transplant mass due to competition and/or herbivory (i.e., the numerator) was expressed as a fraction of the potential transplant mass at that site (i.e., denominator). This accounted for variation in potential transplant mass among sites and years (i.e., 1992 vs. 1993) due to differences in abiotic conditions or transplant density. An index value of 0 would indicate that competition (or herbivory) did not reduce a transplant's mass from its potential value at a site. An index value of 1 would indicate that competition (or herbivory) reduced a transplant's potential mass to 0.

Index values calculated for the eight sites were plotted against mean values of biomass to examine the relationship between competition and/or herbivory and biomass. The statistical significance of these relationships was determined using nonlinear regression analysis (SAS Institute 1988) to estimate the slope of a relationship and to test whether the slope differed significantly from 0. The model $Y = a(1 - e^{-bX})$ was used in the analysis because it accounted for more of the

TABLE 2. Comparison of the mean* shoot mass (in grams) of target *Poa* plants in pairs of experimental treatments (NI = neighbors left intact, NR = neighbors removed, FC = full cage, NC = no cage) used to assess the effects of competition and/or herbivory at each of the eight study sites.

		Competition without herbivory			Herbivory: Without neighbors			Herbivory: With neighbors			Competition plus herbivory		
Site		NI FC		NR FC	NR NC		NR FC	NI NC		NI FC	NI NC		NR FC
1	$\bar{X}$	0.54	<	1.21	2.41	>	1.21	0.50	=	0.54	0.50	<	1.21
	1 SD	± 0.21		± 0.63	± 1.60		± 0.63	± 0.12		± 0.21	± 0.12		± 0.63
2	$\bar{X}$	1.09	<	4.58	4.32	=	4.58	0.80	=	1.09	0.80	<	4.58
	1 SD	± 0.53		± 2.66	± 3.47		± 2.66	± 0.52		± 0.53	± 0.52		± 2.66
3	$\bar{X}$	0.29	<	2.26	0.12	<	2.26	0.15	<	0.29	0.15	<	2.26
	1 SD	± 0.17		± 1.48	± 0.14		± 1.48	± 0.12		± 0.17	± 0.12		± 1.48
4	$\bar{X}$	0.28	<	3.22	0.13	<	3.22	0.15	<	0.28	0.15	<	3.22
	1 SD	± 0.16		± 2.82	± 0.24		± 2.82	± 0.12		± 0.16	± 0.12		± 2.82
5	$\bar{X}$	0.73	<	25.45	16.72	<	25.45	0.02	<	0.73	0.02	<	25.45
	1 SD	± 0.29		± 15.14	± 16.01		± 15.14	± 0.06		± 0.29	± 0.06		± 15.14
6	$\bar{X}$	0.44	<	10.90	1.88	<	10.90	0.02	<	0.44	0.22	<	10.90
	1 SD	± 0.22		± 4.66	± 1.40		± 4.66	± 0.06		± 0.22	± 0.06		± 4.66
7	$\bar{X}$	0.30	<	1.27	0.22	<	1.27	0.00	<	0.30	0.00	<	1.27
	1 SD	± 0.19		± 0.51	± 0.23		± 0.51	± 0.00		± 0.19	± 0.00		± 0.51
8	$\bar{X}$	0.24	<	4.15	0.26	<	4.15	0.01	<	0.24	0.01	<	4.15
	1 SD	± 0.15		± 1.54	± 0.18		± 1.54	± 0.04		± 0.15	± 0.04		± 1.54

* < or > indicates $P < 0.05$; = indicates $P \geq 0.05$.

variation in the data than did a linear model (i.e., $Y = a + bX$). The independent variable (X) was mean biomass and the dependent variable (Y) was either CI, HI, or CHI. Similar results were obtained using data collected in 1993 (i.e., at sites 1, 2, 5, 6, 7, and 8) vs. data collected in 1993 plus 1992 (i.e., at all eight sites). Therefore, only results for all eight sites are presented here.

RESULTS

Biomass and species composition

Biomass differed significantly among the eight sites, ranging from a mean of 64 g/m² to 776 g/m² (Table 1). Biomass was lowest (i.e., 64–129 g/m²) at sites 1 and 2, medium (i.e., 233–326 g/m²) at sites 3 and 4, and highest (i.e., 558–776 g/m²) at sites 5 through 8.

Vegetation at each site was dominated by graminoids and forbs (Table 1). The target species *Poa* occurred naturally at three sites (1, 2, and 3).

Competition and herbivory in relation to biomass

Competition with herbivores excluded.—Where herbivores were excluded by a full cage, the mean shoot mass of target plants was significantly greater with neighbors removed than with neighbors left intact, at all eight sites (Table 2). The increase in shoot mass due to neighbor removal ranged from 0.67 g at site 1 to 24.72 g at site 5.

Values of the competition index (CI) ranged from 0.56 at site 1 to 0.97 at site 5 (Fig. 1a). CI increased significantly (Table 3) from 0.56 at the site with the lowest biomass (site 1) to 0.94 at the site with the highest biomass (site 8). This increase in CI was greater between low and medium biomass (i.e., 64 to 326 g/m²) than between medium and high biomass (i.e., 326 to 776 g/m²).

Herbivory with neighboring plants removed.—Where neighbors were removed, the mean shoot mass of target plants was significantly greater for fully caged plants than for uncaged plants, at each of six sites (3–8; Table 2). At these sites the increase in shoot mass due to caging ranged from 1.05 g at site 7 to 9.02 g at site 6. At the other two sites, shoot mass either did not differ significantly between fully caged plants and uncaged plants (i.e., site 2) or was significantly greater for uncaged plants than for caged plants (i.e., site 1).

Values of the herbivory index (HI) ranged from −0.99 at site 1 to 0.96 at site 4 (Fig. 1b). HI increased significantly (Table 3) from −0.99 at the site with the lowest biomass (site 1) to 0.94 at the site with the highest biomass (site 8).

Herbivory with neighboring plants left intact.—Where neighbors were left intact, the mean shoot mass of target plants was significantly greater for fully caged plants than for uncaged plants, at each of six sites (3–8; Table 2). At these sites the increase in shoot mass due to caging ranged from 0.13 g at site 4 to 0.71 g at site 5. At the other two sites (1–2), shoot mass did not differ significantly between fully caged plants and uncaged plants.

Values of the herbivory index (HI) ranged from 0.07 at site 1 to 1.00 at site 7 (Fig. 1b). HI increased significantly (Table 3) from 0.07 at the site with the lowest

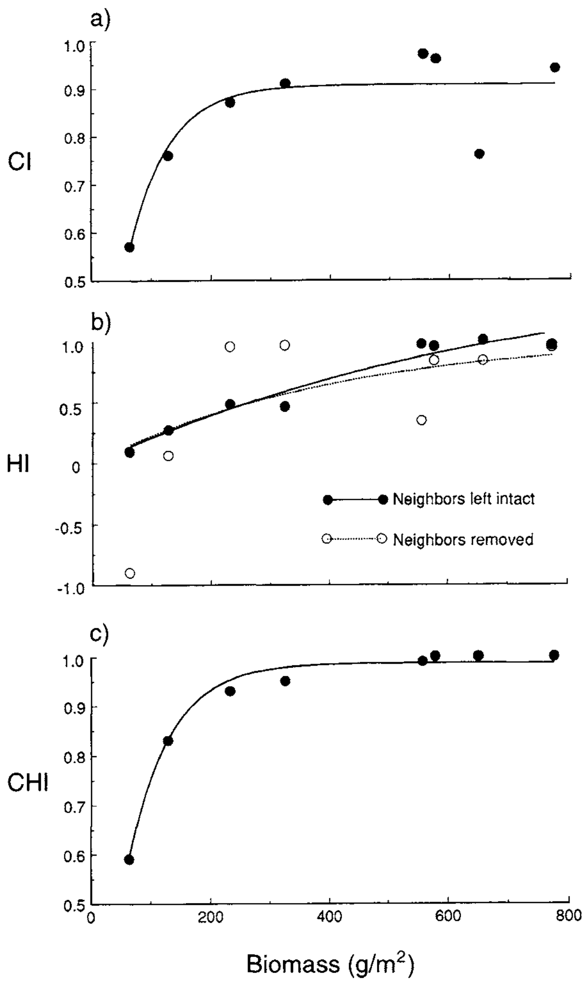

FIG. 1. Relationship between biomass and index values of (a) competition (CI; see Eq. 1), (b) herbivory (HI; see Eq. 2), and (c) competition plus herbivory (CHI; see Eq. 3). Lines were fitted by nonlinear regression (see Table 3).

biomass (site 1) to 0.95 at the site with the highest biomass (site 8).

Values of HI were significantly greater with neighbors left intact than with neighbors removed at sites 1 and 5 (64 and 558 g/m^2, respectively; Fig. 1). In contrast, HI was significantly lower with neighbors left intact than with neighbors removed at sites 3 and 4 (233 and 326 g/m^2, respectively; Fig. 1).

Combined effects of competition and herbivory.—The mean shoot mass of target plants was significantly greater with neighbors removed and plants fully caged than with neighbors left intact and plants not caged, at all sites (Table 2). The increase in shoot mass ranged from 0.61 g at site 1 to 25.43 g at site 5.

Values of the competition plus herbivory index (CHI) ranged from 0.59 at site 1 to 1.00 at site 7 (Fig. 1c). CHI increased significantly (Table 3) from 0.59 at the site with the lowest biomass (site 1) to 0.99 at the site with the highest biomass (site 8).

DISCUSSION

Competition and herbivory in relation to biomass

Our experimental results indicate that target plants competed for resources where their neighbors were left intact and that this competition increased as biomass increased. Values of the competition index (CI) increased more between low and medium biomass than between medium and high biomass. A similar nonlinear relationship between competition intensity and biomass has been described for some wetland plants by Shipley et al. (1991). These results imply that a study conducted from low to medium biomass is more likely to find a difference in competition intensity than a study conducted from medium to high biomass, especially if a narrow range of biomass is examined. This may help to explain the inconsistent results of past studies.

The relatively large increase in CI between low and medium biomass is consistent with biomass-dependent theories of plant community organization (e.g., Grime 1979, Keddy 1990), which predict that competition should increase with increasing site biomass. This result is not consistent with biomass-independent theories (e.g., Tilman 1988, Taylor et al. 1990), which predict that competition should not increase with increasing site biomass. However, it should be noted that the absence of a large increase in CI from medium to high biomass is more consistent with biomass-independent theories than with biomass-dependent theories. Of course, when the whole range of biomass (64–776 g/m^2) is considered, our results are only consistent with

TABLE 3. Results of regression analysis using the model $Y = a(1 - e^{-bX})$. The independent variable (X) is mean biomass and the dependent variable (Y) is either the intensity of competition (CI), or herbivory (HI), or competition plus herbivory (CHI). "a" and "b" are model coefficients to be estimated and e is the Napierian constant.

	a		*b*			
Y	$\bar{X}$	1 SD	$\bar{X}$	1 SD	*F*	*P*
CI	0.908	0.030	0.0152	0.0028	593.0	<0.0001
HI (neighbors removed)	1.029	1.111	0.0025	0.0054	5.7	<0.05
HI (neighbors left intact)	1.619	0.555	0.0014	0.0007	243.3	<0.0001
CHI	0.988	0.007	0.0144	0.0006	11 714.7	<0.0001

biomass-dependent theories. Our results indicate that biomass-independent theories may only be appropriate at sites with medium to high biomass.

We measured effects of competition on plant growth by comparing the shoot mass of transplants with neighbors removed vs. left intact. While neighbor removal is used commonly to measure competition (Aarssen and Epp 1990), Campbell et al. (1991) have questioned its use because dead roots of neighbors are usually not removed completely. As roots decompose in removal plots, nutrient supply may increase, especially at sites with low soil fertility and low biomass, where plants may store more nutrients in roots. Consequently, the increase in target plant growth due to neighbor removal may be greater at sites with low biomass than with high biomass due to differential nutrient release from decomposing roots. In this study, the increase in target plant growth due to neighbor removal was greater at sites with high biomass than low biomass, despite the fact that differential nutrient release among sites should favor target plants at sites with low biomass. Consequently, correcting for differential nutrient release among sites would only amplify the existing trend of a greater response to neighbour removal at sites with higher biomass.

Our experimental results indicate that herbivory had a significant effect on the growth of uncaged target plants, especially at sites with higher biomass. Cuts on the stems of uncaged plants showed that some had been grazed by rabbits and others by deer. Shoots of other uncaged plants were clipped off at ground level, suggesting that herbivores such as meadow voles (*Microtus* sp.), slugs, and snails were also involved. In contrast, fully caged plants showed little or no evidence of tissue loss to these herbivores. Less herbivory on fully caged plants probably accounts for their greater shoot mass at sites 3 through 8. A full cage did not exclude herbivorous insects < 6 mm wide, so caged and uncaged plants probably did not experience differential tissue loss to insects.

Values of the herbivory intensity index (HI) increased significantly with an increase in biomass from 64 to 776 g/m^2. Presumably, HI increased because sites with more biomass supported more herbivores, due to greater plant cover and food availability. Oksanen et al. (1981) predicted that herbivory should increase with an increase in plant productivity from 30 $g \cdot m^{-2} \cdot yr^{-1}$ to 700 $g \cdot m^{-2} \cdot yr^{-1}$. While productivity and biomass are not necessarily equivalent, the similarity of their prediction and our results for the range of biomass from 64 g/m^2 to 776 g/m^2 is worth noting.

Values of HI were also affected by within-site variation in biomass resulting from neighbor removal. Removing neighbors (i.e., biomass) from 1-m^2 plots reduced HI at site 5, probably because there was less incentive for herbivores to forage in plots with less cover and food. (The reduction in HI to a negative value at site 1 [Fig. 1b] is due to some other, unknown factor). In contrast, removing neighbors increased HI at sites 3 and 4, perhaps because target plants were now more visible to herbivores at these sites. It is not clear why HI increased in response to neighbor removal at some sites and HI decreased at other sites. This difference may reflect differences in the foraging behavior and/or types of herbivores present at these sites. Previous studies have also shown that HI may increase (e.g., Ellison 1987) or decrease (e.g., Rice 1987, Reader 1991) where vegetation has been removed by a localized disturbance.

Our results show that the relationship between HI and biomass depends on the range of biomass considered. For a relatively small range of biomass (e.g., within a site), HI either increased or decreased as biomass increased. Over a wider range of biomass (e.g., between sites), HI increased as biomass increased.

Plants may experience both herbivory and competition under natural conditions. Our results indicate that the total effect of competition and herbivory increased as biomass increased. Values of the competition plus herbivory index (CHI) increased significantly with an increase in biomass from 64 to 776 g/m^2. At the two sites (1 and 2) with the lowest biomass, herbivory probably contributed little to the total effect because target plant growth did not increase significantly in treatments where only herbivores were excluded. In contrast, only excluding herbivores had a significant effect on target plant growth at sites with higher biomass, so herbivory probably contributed more to the total effect at sites with high biomass than at sites with low biomass.

In summary, it appears that there was both a quantitative and qualitative change in the effects of competition and herbivory as biomass increased. Competition and herbivory each increased significantly as biomass increased (i.e., quantitative change). Herbivory had less effect than competition at sites with low biomass but not at sites with higher biomass (i.e., qualitative change).

Generality of the relationship between competition (or herbivory) and biomass

Our results indicate that competition and herbivory both increased with increasing biomass. To establish the generality of these relationships, additional studies are needed since our analysis involved only one species (i.e., *Poa*) and one measure of plant performance (i.e., shoot mass). Another study (Bonser 1994) used a subset of the eight study sites (i.e., sites 1, 2, 5, 6, 7, and 8) to compare effects of competition and herbivory on two species (i.e., *Poa* and another species chosen from species present at a particular site). The following six measures of plant performance were recorded at each site: shoot mass, root mass, total plant mass, mortality rate, seed production, and vegetative reproduction. Effects of competition (or herbivory) were highly correlated among the six measures of plant perfomance and also between the two species per site. These results indicate that the relationship between competition (or herbivory) and biomass reported here for *Poa* should be applicable to other species and measures of plant performance.

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