

Competition at the population level along a standing crop gradient: a field experiment in successional grassland

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Abstract

I measured competitive responses of experimentally-established populations of the perennial grass, *Andropogon gerardi*, across a complex gradient of standing crop and species composition in the successional grasslands of southwest Michigan. The goal was to assess whether long-term (three year) population-level responses of *Andropogon* to competition matched the inferences made from a previous phytometer study that examined transplant responses to competition across this same gradient over a single growing season.

Replicate experimental populations of *Andropogon* were established at seven grassland sites by sowing seed into 0.5×0.5 m plots that had been denuded of all vegetation. During the first year of the study, all *Andropogon* populations were maintained as monocultures by hand weeding. At the end of the first growing season, half of the monocultures were selected for continued weeding and half were left open to invasion by competitors for three years. Invasion of the unweeded populations by neighboring plants varied strongly among sites and was positively correlated with standing crop. Increased susceptibility to invasion and competition resulted in the extinction of the unweeded *Andropogon* populations at the two most productive sites, supporting the hypothesis that *Andropogon* is restricted by competition to low productivity sites in these grasslands. The finding that the intensity of competition was positively correlated with standing crop is consistent with the previous transplant study, suggesting that short-term experimental assays of competition on the growth of individual transplants may have predictive value for longer-term outcomes of competition at the population level.

Introduction

Variation in the intensity of competition is thought to be an important factor producing variation in plant species composition within communities and along environmental gradients (Grubb 1977; Grime 1979; Huston 1979; Southwood 1988; Tilman 1988; Keddy 1989; Gurevitch et al. 1992). Over the past two decades, several plant neighbor removal experiments in the field have measured variation in plant competition, most often to test the hypothesis, originally offered by Grime (1973, 1979), that competitive intensity increases along gradients of plant productivity, soil fertility, or standing crop (Wilson & Keddy 1986; Wilson & Tilman 1991, 1993; Bonsor & Reader 1995; Kadmon 1995; Twolan-Strutt & Keddy 1996; Foster

& Gross 1997). The majority of these experiments examined the performance of target transplants over a single growing season, in the presence and absence of neighbors, at sites differing in standing crop. For understanding the role of competition in controlling the distributions of species across environmental gradients or in determining the composition and diversity of communities, these experiments have two potentially important limitations. First, the focus on individual target plants is problematic because it is uncertain how the effects of neighbors on the growth rates of individuals will translate into outcomes at the population-level (Grace 1990; Goldberg & Barton 1992). Second, because these experiments are short-term, they may merely capture transient dynamics, potentially yielding misleading inferences about

the long-term role of competition along environmental gradients. For example if the intensity of competition measured with phytometers over a single growing season is found to be the lowest in infertile or unproductive habitats, as has been found in several studies (Wilson & Keddy 1986; Shipley et al. 1991; Kadmon 1995; Bonser & Reader 1995; Foster 1999), does this mean that competition is less important in regulating species abundances in unproductive habitats over the long term compared to productive habitats? If the primary impact of productivity or fertility is on the rate of competitive exclusion (Huston 1979), then low intensities of competitive suppression in unproductive habitats measured over a single growing season may simply reflect slower transient dynamics relative to productive sites caused by slower rates of growth. Slower dynamics may or may not have any bearing on the ultimate outcome of competition at the population-level (Huston 1979; Goldberg & Barton 1992).

In this study I measured population-level responses of a native grass to competitors after three growing seasons across seven Michigan old-fields that span a complex gradient in soil fertility, standing crop, and plant species composition. In a previous single-season phytometer experiment in these same fields, Foster (1999) found that the relative intensity of competition experienced by transplants of the native grass, *Andropogon gerardi* Vitman (big bluestem) was positively correlated and increased logarithmically with standing crop (Figure 1). Because plant production integrates abiotic and biotic characteristics of a habitat, above-ground standing crop is used as a predictor of target plant performance and of the magnitude of competition occurring along this complex gradient. The main inference from the previous short term study was that intense competition experienced by *Andropogon gerardi* in the most productive habitats is responsible for restricting this species to unproductive habitats within the current landscape.

In this study I established replicate experimental populations of *Andropogon* at seven of the nine grassland sites used in the previous study. This was done to better evaluate the long-term consequences of competition for the distribution of *Andropogon* across complex grassland gradients in this region. In addition, I sowed seeds of *Andropogon* into undisturbed vegetation at each of the seven sites to examine the capacity of this species to colonize intact communities by seed at various positions along the gradient. The specific questions addressed by this study are as follows:

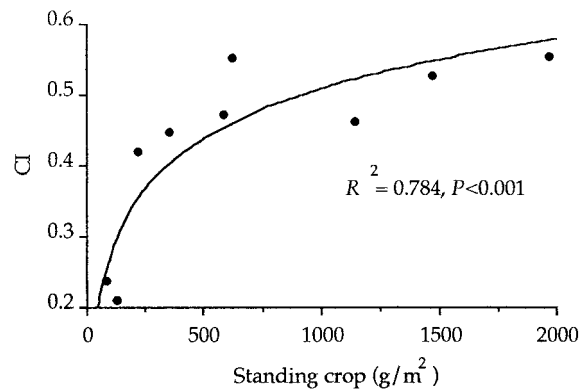


Figure 1. Relationship between relative competition intensity (CI) for *Andropogon gerardi* and standing crop from a previous study (Foster 1999) carried out across nine Michigan old-fields ($CI = -94 + 0.235 (\log \text{ standing crop})$). CI was measured for *Andropogon* using data from the relative growth rates of transplants grown in field plots in the presence and absence of plant neighbors. $CI = (RGR_{NR} - RGR_{NI}) / RGR_{NR}$, where RGR_{NR} is the relative growth rate of transplants in plots where neighboring plants had been removed and RGR_{NI} is the relative growth rate of transplants in plots where neighbors were left intact.

(1) Does the capacity of the experimental *Andropogon* populations to resist invasion by competitors, and to persist in the habitat, vary predictably with standing crop as suggested by the previous short-term phytometer study?

(2) Does the potential of *Andropogon* to invade intact grassland by seed vary with standing crop?

Methods

Study sites

The study was conducted from 1994 to 1997 in seven successional grassland sites at the W. K. Kellogg Biological Station (KBS) of Michigan State University in southwest Michigan (Kalamazoo County; 42°24' N, 85°24' W). Sites were selected for an earlier competition study (Foster 1999) to include a range of habitats that spanned a complex gradient of standing crop and species composition (Table 1). Each field site had been abandoned from row-crop agriculture (primarily corn production; Burbank et al. 1992) for at least 20 years prior to the start of the study. Soils at all sites are classified as Kalamazoo sandy loam, but differ in the degree of agriculturally-related soil erosion and thus the degree of exposure of the nutrient-poor, subsurface sand (Burbank et al. 1992). Site numbers (1–7) were assigned based on a ranking of standing crop

biomass measured at the sites in the previous study (Foster 1999; 1 = lowest and 7 = highest mean standing crop; Table 1). As is the case with virtually all grassland gradients in this landscape, the sites in this study with highly-eroded top-soils and relatively low standing crop (sites 1–3) are primarily dominated by native species, while the sites with relatively high standing crop (sites 4–7) are dominated by introduced C_3 grasses. Previous work has shown that soil nitrogen availability is positively correlated and light availability is negatively correlated with standing crop in these grasslands (Foster & Gross 1997).

Target species

Andropogon gerardi is a C_4 perennial grass that typically dominates native tall-grass prairies (Bazzaz & Parrish 1982), and which was widely distributed in southwest Michigan prior to settlement (Gotshall 1972). In the current successional landscape of southwest Michigan, this species is restricted to small isolated populations on unproductive soils and is largely absent from highly productive grassland habitats that are typically dominated by introduced C_3 grasses such as *Elytrigia repens* (quackgrass) and *Bromus inermis* (smooth brome). In this study, *Andropogon* was present at very low density prior to the start of the experiment within sites 1, 3 and 5.

Experimental design and methods

Beginning in spring 1994, three experimental treatments were established at each of the seven study sites. The treatments included: (1) the introduction of experimental *Andropogon* populations to plots protected from invasion by weeding (weeded populations); (2) the introduction of experimental *Andropogon* populations to plots left open to invasion by neighboring species (unweeded populations); and (3) the addition of *Andropogon* seeds to intact neighbor vegetation (seed addition treatment). To establish these treatments, five experimental blocks were marked at each site in May 1994. Within each block, three 0.5×0.5 m plots were established such that each was separated by a 0.5 m buffer. At each site, the experimental blocks were separated from the next by a distance of 3–5 m. Within each block, two plots were randomly selected for the establishment of the experimental *Andropogon* populations, while the third plot was left unmanipulated until 1995 when *Andropogon* seeds were added to the intact vegetation (seed addition treatment; see below).

To establish the experimental *Andropogon* populations, Glyphosate herbicide (Roundup[®], Monsanto Inc.) was applied to the appropriate plots in early May 1994. One week after the application of herbicide, the dead plant material was removed and then locally collected seeds of *Andropogon* were hand sown at a rate of 3000 seeds m^{-2} across the plots. To assure adequate contact with the soil and to improve germination, the seeds were pressed into the bare soil by hand. During the 1994 growing season, all of the plots containing the *Andropogon* populations were hand-weeded to maintain them as monocultures. By the peak of the first growing season (September 1994), *Andropogon* had become well established, covering greater than 90% of the ground surface in all of the monoculture plots at all sites (data not reported).

At the end of the 1994 growing season (October 1994), one *Andropogon* monoculture was randomly selected from each block for continued weeding (weeded populations). The weeded populations underwent regular weeding throughout the remaining three years of the experiment while the other *Andropogon* plots were left open to invasion by the competitor species present in the neighboring vegetation (unweeded populations). To reduce root competition from outside of the weeded population plots, the perimeters of all weeded plots were trenched with a flat-blade shovel to a depth of 20 cm in early June and early August 1995–1997.

In early May 1995, seeds of *Andropogon* were sown at a rate of 3000 seeds m^{-2} into the intact vegetation of the seed addition treatment plots. The seed added to these plots came from the same lot of seed used to establish the *Andropogon* monocultures in the previous year. Seeds were added to these plots at the beginning of the 1995 growing season, rather than in 1994, to synchronize the start of the invasion of *Andropogon* by seed into the intact vegetation (seed addition treatment) with the start of the invasion of competitors into the unweeded *Andropogon* populations. This allowed a direct comparison of the capacity of *Andropogon* to invade intact vegetation with the capacity of this species to resist invasion by competitors over the same time interval.

The three experimental treatments (weeded populations, unweeded populations, and the seed addition treatment) were maintained until early September 1997 when above-ground standing crop in the plots was clipped at ground level and collected. In addition to within the three original treatments, standing crop was also clipped from a 0.50×0.50 m plot

Table 1. Species composition and standing crop at each of the seven study sites. Data are from Foster (1999). Nomenclature follows Gleason & Cronquist (1991).

Site	Five most abundant species	Species relative biomass (%)	Aboveground standing crop g m^{-2}
1	<i>Andropogon virginicus</i>	50.0	68.8 ± 15.2
	<i>Rubus alleghaniensis</i>	13.9	
	<i>Danthonia spicata</i>	9.9	
	<i>Solidago nemoralis</i>	5.7	
	<i>Hieraceum aurantiacum</i>	4.6	
2	<i>Rubus alleghaniensis</i>	27.8	109.6 ± 43.7
	<i>Danthonia spicata</i>	17.2	
	<i>Centaurea maculosa</i>	14.7	
	<i>Andropogon virginicus</i>	11.0	
	<i>Hieraceum aurantiacum</i>	7.8	
3	<i>Andropogon virginicus</i>	49.8	182.3 ± 15.1
	<i>Danthonia spicata</i>	9.8	
	<i>Rubus alleghaniensis</i>	6.0	
	<i>Desmodium rotundifolium</i>	4.8	
	<i>Centaurea maculosa</i>	4.3	
4	<i>Elytrigia repens</i>	85.2	259.6 ± 27.5
	<i>Achillea millefolium</i>	7.3	
	<i>Bromus inermis</i>	6.4	
	<i>Melilotus alba</i>	0.1	
	<i>Oxalis stricta</i>	0.1	
5	<i>Bromus inermis</i>	58.1	348.1 ± 17.9
	<i>Poa pratensis</i>	10.3	
	<i>Achillea millefolium</i>	10.1	
	<i>Elytrigia repens</i>	5.1	
	<i>Hypericum perforatum</i>	2.4	
6	<i>Bromus inermis</i>	78.0	398.8 ± 56.2
	<i>Elytrigia repens</i>	10.3	
	<i>Poa pratensis</i>	3.8	
	<i>Daucus carota</i>	3.2	
	<i>Dactylis glomerata</i>	1.7	
7	<i>Elytrigia repens</i>	71.0	745.2 ± 105.3
	<i>Arrhenatherum elatius</i>	28.3	
	<i>Silene alba</i>	0.1	
	<i>Polygonum scandens</i>	0.1	
	<i>Poa pratensis</i>	0.1	

placed at the end of each experimental block (0.5–2 m away from the nearest plot in each block). These new plots are subsequently referred to as unmanipulated vegetation plots and represent a fourth experimental treatment applied to each block ($n = 5$ at each site). Standing crop from the unmanipulated vegetation plots was used as an index of plant productivity for each experimental block. This treatment was also used as a control to compare to the unweeded populations and the seed addition treatment.

For the unweeded *Andropogon* populations, standing crop biomass was sorted to species. For the seed addition plots, standing crop was sorted into one of two categories: (1) *Andropogon* biomass; and (2) composite biomass of all other species (competitor species). Standing crop harvested from the unmanipulated vegetation was not separated to species. All plant material was oven-dried at 60°C to constant mass and then weighed.

Statistical analysis

All analyses were conducted on biomass data collected at the end of the 1997 growing season. To examine variation in aboveground standing crop among sites and among the four experimental treatments, a mixed-model within-subjects ANOVA (Zar 1996) was used. This ANOVA model accounted for one among-subjects grouping factor (site). The experimental blocks were treated as subjects of the analysis with each of the four treatments applied once to each block. Variation in standing crop among blocks within sites was considered a random effect, while site and treatment effects were treated as fixed effects. Error terms to test the significance of main effects and interactions all contain the random component of variance due to blocks within sites. The same ANOVA model was used to examine site and treatment effects on the biomass of *Andropogon* and on the composite biomass of competitor species (species other than *Andropogon*). The ANOVA for *Andropogon* biomass excluded the unmanipulated vegetation treatment because *Andropogon* was not present in this treatment. The ANOVA for competitor species biomass excluded the weeded population plots because competitors were intentionally weeded from these plots. In cases where there were significant interactions, Tukey's Honestly Significant Difference method was used to compare the appropriate treatment means (Zar 1996). Heteroscedasticity, evident in the raw biomass data, was improved through the use of log-transformations such

that the assumptions of ANOVA were met. All biomass data are presented in the figures untransformed.

To examine how the intensity of competition experienced by *Andropogon* in the unweeded populations varied as a function of standing crop, a relative competition intensity index (CI) was calculated for each site using site means of *Andropogon* biomass in the weeded and unweeded population plots:

$$CI = (B_{\text{weeded}} - B_{\text{unweeded}}) / P_{\text{weeded}},$$

where B_{weeded} = biomass of *Andropogon* in the weeded plots, and B_{unweeded} = biomass of *Andropogon* in the unweeded plots. Linear regression analysis was used to test for the dependence of CI on mean site standing crop harvested from the unmanipulated vegetation plots. Because CI showed evidence of non-linear saturating dependence on standing crop, standing crop was log-transformed prior to the formal analysis. These data are shown in a figure un-transformed with a logarithmic curve presented to illustrate non-linearity. SYSTAT statistical software (version 5.2.1; Wilkinson 1992) was used for all analyses. Nomenclature follows Gleason & Cronquist 1991.

Results

Total above-ground standing crop varied significantly among sites, but did not differ among the four treatments at any site (Table 2). Standing crop ranged from a mean of 81 (± 14.8) g m⁻² at site 1 to 659 (± 96.3) g m⁻² at site 7.

By the end of the experiment, *Andropogon* had been completely displaced from the unweeded population plots and the seed addition plots at sites 6 and 7, the two most productive sites (Figure 2). As a result, data from sites 6 and 7 were excluded from the ANOVA. For sites 1–5, *Andropogon* biomass varied significantly among sites, among treatments (weeded populations, unweeded populations, and the seed addition treatment), and with the interaction between treatments and sites (Table 2, Figure 2). At the two least productive site (sites 1 and 2), *Andropogon* biomass did not differ among treatments. At sites 3–5, *Andropogon* biomass was significantly greater in the weeded populations than in the unweeded populations and the seed addition treatment. Across all sites, mean site biomass of *Andropogon* in the weeded population plots increased significantly with mean site standing crop (simple linear regression; $r^2 = 0.97$, $P <$

Table 2. ANOVA results summarizing the experimental treatment effects on (A) standing crop, (B) *Andropogon* biomass, and (C) competitor biomass. For standing crop, the treatments being compared include the unmanipulated vegetation, the unweeded populations, the weeded populations, and the seed addition treatment. For *Andropogon* biomass, the treatments being compared include the unweeded populations, the weeded populations, and the seed addition treatment. For competitor species biomass, the treatments being compared include unmanipulated vegetation, the unweeded populations, and the seed addition treatment.

Dependent Variable	Source of variation	MS	df	F	P
Standing crop	Between Blocks				
	Site	8.848	6	25.800	<0.001
	Block	0.173	4	0.258	0.902
	Error	0.548	24		
	Within blocks				
	Treatment	0.003	3	0.102	0.959
	Treatment \times site	0.097	18	0.704	0.796
	Treatment \times block	0.100	12	0.569	0.860
	Error	0.169	72		
<i>Andropogon</i> biomass	Between Blocks				
	Site	2.644	4	6.509	0.003
	Block	0.403	4	0.992	0.440
	Error	0.406	16		
	Within Blocks				
	Treatment	13.125	2	23.153	<0.001
	Treatment \times site	3.039	8	5.362	<0.001
	Treatment \times block	0.212	8	0.374	0.926
	Error	0.567	32		
Competitor biomass	Between Blocks				
	Site	16.657	6	16.210	<0.001
	Block	0.543	4	0.528	0.716
	Error	1.028	22		
	Within Blocks				
	Treatment	3.664	2	18.148	<0.001
	Treatment \times site	0.674	12	3.341	0.002
	Treatment \times block	0.208	8	1.031	0.428
	Error	0.202	44		

0.0001). In contrast, *Andropogon* biomass declined significantly with standing crop in the unweeded population plots and the seed addition plots (unweeded: $r^2 = 0.71$, $P < 0.05$; seed addition: $r^2 = 0.63$, $P < 0.05$). Competition intensity (CI), measured by comparing *Andropogon* biomass in the weeded and unweeded populations, increased logarithmically with standing crop (Figure 3).

The composited biomass of competitor species (all species other than *Andropogon*) also varied significantly among sites, among treatments (unmanipulated vegetation, unweeded populations, and the seed ad-

dition treatment), and with the interaction between treatments and sites (Table 2, Figure 4). At sites 1–3, competitor biomass was significantly lower in the unweeded population plots and the seed addition plots compared to the unmanipulated vegetation. At site 4, the only significant difference in competitor biomass was between the unweeded population plots and the unmanipulated vegetation. At the three most productive sites (5–7) there were no differences in competitor biomass among treatments.

At site 1, the major competitor species in the unweeded populations plots (Figure 5) were *Andropogon*

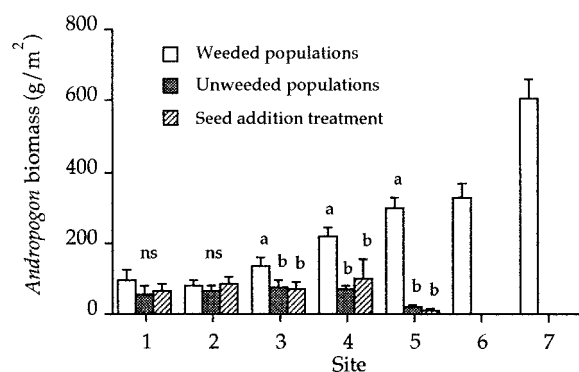


Figure 2. Aboveground biomass of *Andropogon* (mean \pm SE) in the weeded and unweeded *Andropogon* population plots, and in the seed addition treatment plots. For each site separately, treatment means with different lowercase letters are significantly different from each other ($P < 0.05$; Tukey's Honestly Significant Difference Method).

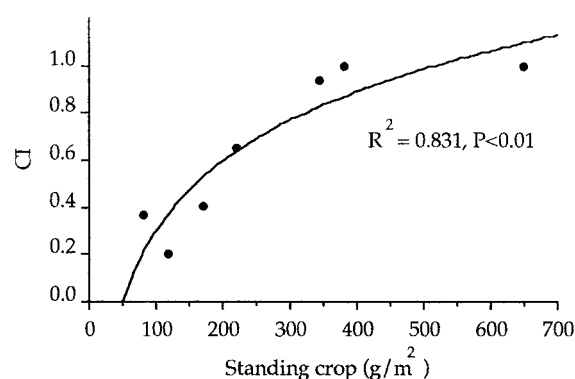


Figure 3. Relationship between relative competition intensity for *Andropogon* and standing crop in the current study. (CI = $-0.166 + 0.980 (\log \text{ standing crop})$).

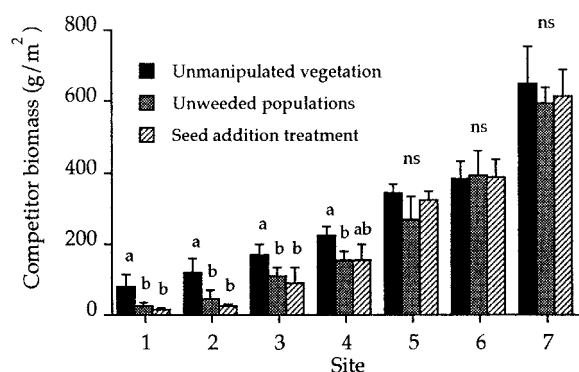


Figure 4. Aboveground biomass (mean \pm SE) of competitor species in the unmanipulated vegetation, in the unweeded population plots, and in the seed addition treatment. For each site separately, treatment means with different lowercase letters are significantly different from each other ($P < 0.05$; Tukey's Honestly Significant Difference Method).

virginicus (perennial grass), which was the dominant species in the neighboring vegetation, and *Hieraceum aurantiacum*, a perennial forb that was also present in the neighboring vegetation (Table 1). At site 2, the dominant competitors in the unweeded population plots were *Rubus* species (primarily *Rubus alleghaniensis*, a perennial woody vine) and *Centaurea maculosa* (perennial forb), which were both abundant in the neighboring vegetation. At site 3, the dominant competitor in the unweeded plots was *Centaurea maculosa*, which was present at relatively low abundance in the neighboring vegetation. *Andropogon virginicus* and *Rubus* species, which were present in the neighboring vegetation, were also abundant competitors in the unweeded population plots of site 3. At sites 4–7, the major competitor species in the unweeded population plots were primarily the introduced perennial grasses, *Elytrigia repens* and or *Bromis inermis*, which were the dominant species in the neighboring vegetation.

Discussion

In this study, the susceptibility of the experimental *Andropogon* populations to invasion by the competing species varied strongly among sites and increased with standing crop. This increased susceptibility to invasion led to a decline in the biomass of *Andropogon* in the unweeded plots and thus increasing competition intensity along this complex grassland gradient. Intense competition resulted in the extinction of *Andropogon* populations at the two most productive sites, supporting the hypothesis that *Andropogon* is restricted by competition to low productivity sites in these old-fields. These results are consistent with the previous study (Foster 1999), suggesting that short-term phytometer experiments may in some cases have predictive value for long-term competitive outcomes at the population level. The results from the present study not only confirm a positive relationship between competition intensity and standing crop, but also confirms that this relationship is non-linear. In both experiments competition intensity tended to increase rapidly across a narrow range of low standing crop and then saturate between approximately 250 and 300 g m⁻² (Figures 1 and 3).

Although data are lacking on the specific mode of invasion by competitors into the unweeded *Andropogon* populations, field observations suggested that clonal expansion from plot edges represented the

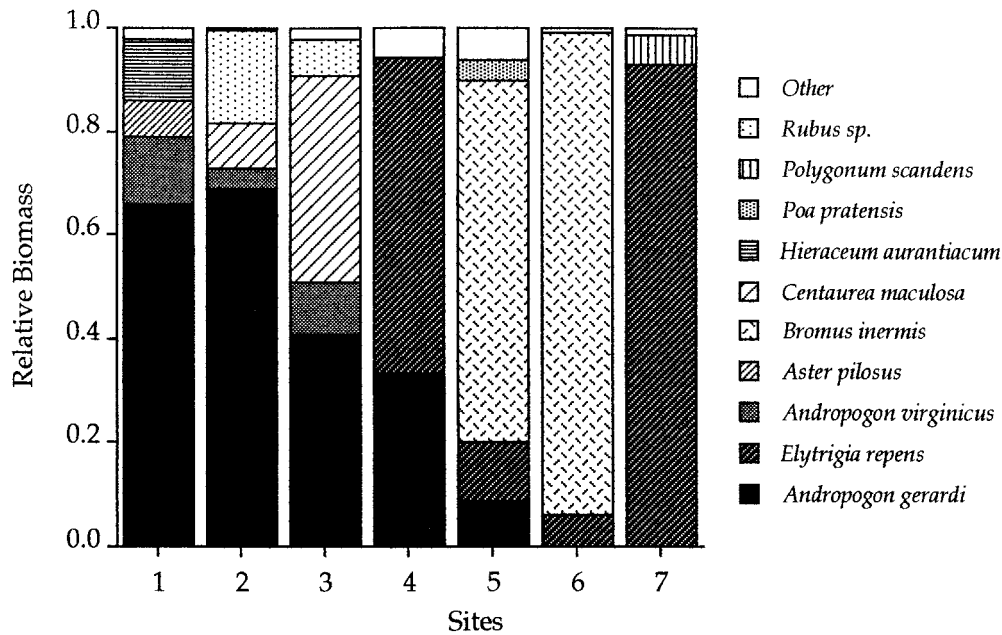


Figure 5. Relative biomass of abundant species in the unweeded population plots.

most common avenue of invasion. This is particularly likely in the case of sites 4–7 which had communities dominated by fast-growing clonal and carpet forming grasses. At site 1, *Hieraceum aurantiacum* invaded primarily via stolons that grew from rosettes present at the perimeter of the unweeded plots, while *Andropogon virginicus* appeared to have invaded primarily from seed. At site 2, *Rubus* species invaded via resprouting rhizomes and invading runners from the plot edges. At site 3, *Centaurea maculosa*, a prolific seed producer appeared to invade entirely through the establishment of new seedlings.

It can be argued that three years is still not long enough to judge long-term population consequences of neighborhood competition for the target species in these sites. However, there are two reasons to believe that this time period was adequate for this purpose. First, the unweeded populations of *Andropogon* declined to extinction in the two most productive sites within three years, thus capturing the ultimate consequence of competition for this species at these sites. Second, *Andropogon* had become a dominant species in the unweeded plots at the three least productive sites, where many individuals flowered and produced seeds, a strong indication that *Andropogon* will persist in these sites for some time.

On the surface, the results of this study are consistent with the view of Grime (1973, 1979), that plant

competition intensity increases with increased productivity or standing crop, but is inconsistent with the view that competition intensity is constant along gradients in productivity (Newman 1973; Tilman 1988). In this study, *Andropogon* was able to successfully colonize the intact vegetation of the unproductive sites by seed (Figure 2), and eventually reduce the biomass of the competitor species (Figure 4). This result suggests that the relatively low intensity of competition experienced by the experimental *Andropogon* populations in the least productive sites may have occurred as a result of its own strong competitive effect on its competitors, which in turn may have reduced the capacity of competitors to significantly affect *Andropogon*. It appears then, that the ability of *Andropogon* to establish and persist in the unproductive sites is not merely the result of its capacity to tolerate stressful conditions, as might be assumed based purely on the relationship observed between competition intensity and standing crop, but also because of the capacity of *Andropogon* to compete for soil resources. It is likely that both a tolerance of low resource levels and a capacity to reduce resource supply to neighbors, contributed to the high competitive ability of *Andropogon* in these unproductive habitats (e.g., good response and effect competitor; Goldberg 1990).

That *Andropogon* exhibited tolerance of low resource levels is evident from the observation that this

species was able to successfully colonize the unproductive habitats from seed. The *Andropogon* seedlings that emerged from seed were initially able to establish and maintain positive growth at resource levels undoubtedly determined by the abiotic environment and by the uptake and non-uptake effects of the dominant resident species (Goldberg 1990). Being able to tolerate these low resource levels through the initial seedling establishment stages of the life history likely allowed *Andropogon* to grow and to attain the prominence necessary to eventually negatively impact the resource levels of its neighbors. This finding emphasizes the importance of understanding both the response and effect components of competition for a target species when testing for the general importance of competition in regulating species abundances and distribution.

The outcome of competition in this study appears to have been the same regardless of starting conditions as found for *Andropogon* by Wedin and Tilman (1993) in pair-wise competition experiments. In unproductive habitats, *Andropogon* showed the capacity to: (1) resist invasion by competitors and maintain dominance; and (2) invade intact vegetation from seed, increase in abundance, and then displace competitors. It is my interpretation that *Andropogon* is absent from high productivity habitats in this region because it is both a poor colonizer and a poor competitor there, and that it is present in low productivity habitats because it can colonize from seed and then compete effectively for soil resources in such areas. This finding runs counter to the argument that the competitive ability of individual species remain constant along productivity gradients (Grime 1973). However, this interpretation is consistent with the view of Tilman (1988) that shifts in overall competitive ability occur along such gradients because of trade-offs in competitive ability for above- and below-ground resources. So although competition intensity measured for this single species was lowest in the unproductive sites and increased with standing crop, this does not necessarily support the view that competition in general is less important in regulating species abundances, composition or diversity in unproductive habitats as proposed by Grime (1973, 1979). Results from this study make it clear that variation in competitive ability plays a major role in regulating the distribution of *Andropogon* in this landscape.

Although measures of competition in this study were correlated with standing crop, it is not known whether these correlations reflect the direct effects

of standing crop or productivity on competition or if they reflect the impact of some other factor that covaries with standing crop among the field sites such as species composition. Indeed, the strong competitive suppression of *Andropogon* observed in this study at the productive sites could be because these sites were dominated by introduced C₃ grasses. The C₃ grasses grow relatively fast and begin their growth earlier in the season than the native C₄ grasses, potentially pre-empting available resources before the native grasses can take advantage of them (Waller & Lewis 1979). Novel experimental approaches are needed to tease apart the relative importance of standing crop and species composition in determining the outcome of competition along productivity gradients (see Peltzer et al. 1998). Nevertheless, the results of this study indicate that standing crop can be a powerful integrative predictor of the long-term outcome of competition in these successional grassland communities.

In combination with earlier work (Foster 1999), the results of this study suggest that short-term removal experiments using target transplants can be utilized to better understand competition and its role in regulating long-term competitive outcomes at the population level and in affecting the distribution of species across environmental gradients. The results also suggest that to properly test general hypotheses about the importance of competition in regulating species distributions across environmental gradients it is important to address both the effect and response components of competition.

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