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Intraspecific Competition in Chenopodium album Varies with Resource Availability

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ABSTRACT.—The intensity of intraspecific competition under different levels of light and nitrogen supply was assessed for the temperate zone herb, Chenopodium album. Plants were grown at two densities (one or six plants/pot) in a modified factorial design with three levels each of light and nitrogen availability. This yielded five light/nitrogen treatments which comprised two gradients, one extending from low light and nitrogen to conditions of high light and nitrogen, the other from conditions of low light/high nitrogen to conditions of low nitrogen/high light. Competition among plants grown six per pot significantly affected growth in all treatments and was most intense where resource supply was greatest. When one or both resources were limiting, competition was less intense. This pattern held whether assessed for total biomass, aboveground biomass, or belowground biomass only. Thus, it seems that the relative amount of resource limitation, not the source (light or nitrogen limitation), determined the intensity of intraspecific competition for this species. Those resource conditions most conducive to intense competition were also the most conducive to high productivity (dry biomass of plants grown alone). The pattern of competitive intensity observed in Chenopodium album suggests that the intensity of intraspecific competition is greatest under optimal resource conditions. We suggest that patterns of intraspecific competition may be important in community dynamics, and that the interpretation of future interspecific competition studies would be more complete if intraspecific competition were also considered.

INTRODUCTION

The importance of intraspecific competition to the ecology and evolution of species is widely recognized. However, most investigations of intraspecific plant competition have focused on tests of the −3/2 thinning rule (e.g., Kikuzawa, 1988; Firbank and Watkinson, 1990), on the development of size hierarchies (e.g., Weiner, 1985; Weiner and Thomas, 1986; Jurik, 1991), on the characteristics of neighborhood competitive interactions (e.g., Pacala and Silander, 1985; Silander and Pacala, 1985), or on variation in competitive ability among ecotypes under different environmental conditions (e.g., Clay and Levin, 1986; Linnhart, 1988). Mechanistic studies of the effect of resource availability on the intensity or importance of intraspecific plant competition in nonagricultural species are particularly few (Clay and Levin, 1986). For many species, especially those that establish dense, primarily monospecific stands, intraspecific competition can be critical to the growth, survival and reproductive success of individuals (e.g., McAuliffe and Janzen, 1986; Ungar, 1992; Aguilera and Lauenroth, 1993).

In contrast to intraspecific competition, the importance and intensity of interspecific plant competition under different resource availability regimes, and the effects of interspecific plant competition on community structure, have been investigated by numerous researchers. Some of these studies show that at low resource levels interspecific competition between individuals is less intense (Grime, 1979, 1987; Wilson and Keddy, 1986; Wilson,

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1988; Reader and Best, 1989; Goldberg, 1990; Aerts et al., 1991; Campbell et al., 1991), perhaps because under such conditions individuals are too sparse or slow-growing to affect neighbors strongly. Other studies (Tilman, 1988; Tilman and Cowan, 1989; Wilson and Tilman, 1991; Reader et al., 1994) show that interspecific competition is equally intense along a gradient of increasing plant productivity (defined as standing biomass). The latter studies suggest that resource limitation typically shifts from belowground to aboveground as light limitation increases and nitrogen limitation decreases.

Studies of interspecific plant competition often either do not consider the importance of intraspecific competition (e.g., Reader et al., 1994), or use plants grown in monoculture as control treatments (e.g., Tilman and Cowan, 1989; Aerts et al., 1991; Campbell et al., 1991; Wilson and Tilman, 1991; Wilson and Tilman, 1993). In these studies, different interspecific competition mixtures are compared to the intraspecific competition control. However, changes in the dynamics of intraspecific competition along density or resource supply gradients are rarely explicitly examined within the monoculture control groups. The intensity of intraspecific competition probably varies across density or resource supply gradients, and such changes might influence interpretation of interspecific interactions.

The objective of this study was to test whether the intensity of intraspecific plant competition varies under different conditions of resource supply. Because limiting resources such as light and soil nutrients often interact in their effects on plant traits (Peace and Grubb, 1981; Swank and Oechel, 1991), and because it has been proposed that competition for above- and belowground resources changes over resource supply gradients (Tilman, 1988; Wedin and Tilman, 1993), we considered the effects of both above- and belowground resource limitation on the intensity of intraspecific competition. Resource effects and the intensity of intraspecific competition were assessed by growing Chenopodium album alone and in competition with conspecific neighbors in a modified factorial design with three levels each of light and nitrogen availability.

METHODS

Study species.—The study species, Chenopodium album, is an annual herb that is widely distributed as a weed in the temperate zone. Chenopodium album has a rapid growth rate (Pearcy et al., 1981), very plastic growth form (Morgan and Smith, 1981), and occurs under a wide variety of environmental conditions (Holm et al., 1977), making it particularly well suited to a study of growth responses along resource availability gradients.

Experimental design.—Seedlings, 5–8 cm tall, were selected from a wild monospecific stand in Wellesley, Massachusetts, in June 1989. Seedlings were transplanted to 5 liter plastic pots and maintained in a greenhouse. Seedlings were planted at one plant or eight plants per pot; the latter were thinned to six plants per pot on the 15th day of the experiment. The potting medium consisted of two parts sand and one part perlite. These materials were chosen because they would not contribute to or accumulate nutrients added in solution.

Five days after planting, five replicate pots of each density were assigned to each of five nitrogen/light treatments (five treatments × two densities × five replicates = 50 pots). The five resource treatments can be seen as comprising two contrasting gradients. One gradient extends from conditions of low light and low nitrogen to conditions of high light and high nitrogen (treatments LL:LN, ML:MN, and HL:HN; herein called environmental gradient (1)); the other runs from conditions of low light and high nitrogen to conditions of low nitrogen and high light (LL:HN, ML:MN, HL:LN; herein called environmental gradient (2)).

Plants were watered with 200 ml of distilled water every other day. This volume was sufficient to saturate the soil without leaching nutrients from pots. To ensure that water
was not limiting, soil was kept damp to the touch. Soil and air temperatures were measured hourly for 3 days with a 21X Micrologger and model 107 temperature probes (Campbell Scientific Inc., Logan, Utah); neither differed significantly among treatments (Kruskal Wallis tests: soil temperature, n = 72, H = 1.8, df = 2, P > 0.25; air temperature, n = 76, H = 0.9, df = 2, P > 0.50). Pot locations within treatments were randomized every 5 days.

Light levels were reduced from ambient with opaque (black) fiberglass screen which covered low and medium light treatments. This type of screen was chosen in order to decrease light quantity without changing light quality. Mean (sd) photon flux densities (400-700 nm) were: 79 (65), 215 (199) and 530 (434) µmol m−2 sec−1 for the low, medium and high light levels, respectively. Light levels are the average of 3 sampling dates when measurements were taken at 10 randomly selected positions during a 5-min period within each light treatment (with a LI-190SA quantum sensor and Li-Cor LI-1000 datalogger; LiCor, Inc., Lincoln, Nebraska). In the high light treatment, light levels were consistently above the light saturation point of photosynthesis reported for Chenopodium album (Morgan and Smith, 1981). The low light level was above the instantaneous light compensation point for photosynthesis for most C₃ sun plants (Fitter and Hay, 1987).

Nutrient supply was maintained by weekly fertilization with a modified Hoagland’s solution that varied in nitrogen (nitrate) concentration but had ample amounts of all other nutrients. Nitrate concentrations of nutrient solutions were determined using the cadmium reduction method (Hach Chemical Company, 1980). Nitrogen supply levels were chosen to encompass the range used in similar studies (e.g., Tilman and Cowan, 1989); they were 5, 20 and 200 mg per weekly aliquot for the low, medium and high nitrogen treatments, respectively. Plants showed no signs of adverse effects of high nitrogen levels.

Soil nutrient levels were tested at the start and end of the experiment. A Spurway solution was used for nitrate extraction and nitrate concentration was determined with spectrophotometric analysis using chromotropic acid (West and Ramachandran, 1966). Soil analyses were carried out by the Cornell Nutrient Analysis Laboratories (Cornell University, Ithaca, New York). Soil nitrate concentration measured before and after the experiment never exceeded 6 ppm in any treatment, indicating that nitrogen did not accumulate in the soil. As leaching was minimized by watering only to the point of soil saturation, added nutrients were most likely assimilated by the plants.

Plant height was measured from soil surface to the tip of the apical meristem and total number of fully expanded leaves per plant was counted before harvest. Plants were harvested on the 40th day of the experiment and separated into leaves, stems and roots. Roots were washed in a solution of tetrasodium pyrophosphate (Na₄O,P₂, concentration: 270 g/100 liters), to facilitate removal of soil particles, and then rinsed in tap water to remove salts. Plant parts were dried for 48 h at 80 C. Dried samples were weighed to the nearest 0.001 g. Aboveground biomass was defined as the sum of the masses of stems and leaves; total biomass included roots and aboveground biomass.

Analyses.—Intensity of intraspecific competition was measured within each treatment as the proportional reduction in biomass per plant attributed to the presence of neighboring plants; i.e.:

\[
\frac{\text{dry biomass of plants grown singly} - \text{mean dry biomass of plants grown 6 per pot}}{\text{dry biomass of plants grown singly}}.
\]

For each treatment, replicates of plants grown singly were matched by random selection with a replicate of plants grown 6 per pot. The index of competitive intensity ranges from zero, for no effect, to one for complete competitive inhibition, and is a commonly used measure of competition (Aerts et al., 1991). Plant productivity of each treatment was de-
TABLE 1.—Comparison of growth characters (mean ± SD) of *Chenopodium album* grown under differing supplies of light and soil nitrogen: LL:LN is low light and low nitrogen; ML:MN is medium light and medium nitrogen; HL:HN is high light and high nitrogen; LL:HN is low light and high nitrogen; HL:LN is high light and low nitrogen. See text for treatment values of light and nitrogen.

<table>
<thead>
<tr>
<th>Character</th>
<th>Plant density</th>
<th>Resource supply treatments</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Height (mm)</td>
<td>1</td>
<td>158 ± 28b1</td>
<td>170 ± 30b</td>
<td>214 ± 61b</td>
<td>125 ± 53b</td>
<td>379 ± 65a</td>
<td></td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>105 ± 33c</td>
<td>155 ± 46b</td>
<td>113 ± 33c</td>
<td>93 ± 28c</td>
<td>272 ± 80a</td>
<td></td>
</tr>
<tr>
<td>P^2</td>
<td>&lt;0.01</td>
<td>0.41</td>
<td>&lt;0.01</td>
<td>0.22</td>
<td>0.01</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number of leaves</td>
<td>1</td>
<td>15.4 ± 2.1b</td>
<td>26.0 ± 6.0b</td>
<td>26.6 ± 6.5b</td>
<td>12.6 ± 5.0b</td>
<td>118.4 ± 13.9a</td>
<td></td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>11.5 ± 1.7c</td>
<td>20.7 ± 7.0b</td>
<td>11.9 ± 1.8c</td>
<td>9.8 ± 2.1c</td>
<td>41.1 ± 10.3a</td>
<td></td>
</tr>
<tr>
<td>P</td>
<td>&lt;0.01</td>
<td>0.14</td>
<td>&lt;0.01</td>
<td>0.26</td>
<td>&lt;0.01</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total dry biomass (g)</td>
<td>1</td>
<td>0.28 ± 0.11c</td>
<td>0.63 ± 0.14b</td>
<td>0.76 ± 0.15b</td>
<td>0.36 ± 0.05c</td>
<td>4.69 ± 0.5a</td>
<td></td>
</tr>
<tr>
<td></td>
<td>6^3</td>
<td>0.14 ± 0.04d</td>
<td>0.35 ± 0.06b</td>
<td>0.24 ± 0.07c</td>
<td>0.21 ± 0.05c</td>
<td>1.29 ± 0.2a</td>
<td></td>
</tr>
<tr>
<td>P</td>
<td>&lt;0.01</td>
<td>0.03</td>
<td>&lt;0.01</td>
<td>0.01</td>
<td>&lt;0.01</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

^1 Treatment means with a different letter were significantly different at the P < 0.05 level according to Tukey's Studentized Range test (SAS Institute Inc., 1989)

^2 Comparisons between high and low plant densities

^3 High density plantings were compared by using nested ANOVA—plants were nested within pots; all dry biomass values were log_{10} transformed to meet the assumptions of ANOVA

Intraspecific competition occurred in every treatment and significantly affected plant growth (Table 1). For example, within the LL:LN, ML:MN and HL:HN treatments, plant height and number of leaves were significantly smaller at high density (*i.e.*, six per pot) than at low density (*i.e.*, grown alone). Resource supply treatments also affected plant growth: LL:LN plants grown alone were 58% shorter and had 87% fewer leaves than HL:HN plants grown alone. Total biomass was significantly altered by both light/nitrogen treatment and density in all treatments; HL:HN plants were significantly larger than those grown in other treatments at both densities (Table 1).

Reduced levels of either light or nitrogen significantly lowered the intensity of competition (Table 2). The significant interaction between light and nitrogen treatments indicated that the effect of either limiting factor on the intensity of competition was dependent upon the level of the other. Thus, along environmental gradient 2 (extending from low light and high nitrogen to high light and low nitrogen), competition was less intense when either light or nitrogen was in short supply (LL:HN or HL:LN) than when both light and nitrogen were available at intermediate levels (ML:MN, Table 3). Limitation by low soil nitrogen and limitation by low light resulted in statistically equivalent levels of intraspecific competitive
TABLE 2.—Results of a two-way ANOVA testing the effects of light, soil nitrogen and their interaction on the intensity of competition\(^1\) in *Chenopodium album*. Coefficient of determination (R\(^2\)) for the model was 0.78

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>Sum of squares(^2)</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Light</td>
<td>1</td>
<td>0.066</td>
<td>12.47</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Nitrogen</td>
<td>1</td>
<td>0.079</td>
<td>14.92</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Light*nitrogen</td>
<td>1</td>
<td>0.072</td>
<td>13.60</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Error</td>
<td>17</td>
<td>0.090</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

\(^1\) Intensity of competition was defined as the proportion (dry biomass of plants grown singly — dry biomass of plants grown 6 per pot)/(dry biomass of plants grown singly); a square transformation (\(Y' = Y^2\)) was performed because treatment variances were inversely proportional to their means

\(^2\) Type III sum of squares (SAS Institute Inc., 1989)

intensity for *Chenopodium album* (compare LL:HN to HL:LN on environmental gradient 2; Table 3). Considering environmental gradient 1 (extending from low light and nitrogen to high light and nitrogen), competition was greater when high levels of both resources were present (ML:MN and HL:HN) than when both light and nitrogen were limiting (LL:LN, Table 3).

We assessed the intensity of competition using total biomass, aboveground biomass only, or belowground biomass only, and found that the pattern was equivalent in each case (Table 3). There was no indication of effects of competition on allocation pattern, nor any indication of a switch from aboveground competition at limiting light levels to belowground competition at limiting nitrogen levels.

Productivity of the treatments, assessed as log total dry biomass of plants grown singly, was significantly correlated with intensity of competition (Spearman’s rank correlation, \(r = 0.77, \text{df} = 20, P < 0.01; \text{Fig. 1}\)). At HL:HN, where productivity was greatest, competition was most intense. Where one or both resources were strongly limiting, both productivity and intensity of intraspecific competition were less.

**DISCUSSION**

A strong and consistent effect of intraspecific competition on growth of *Chenopodium album* was demonstrated under experimental conditions chosen to represent a wide range of light and nitrate availabilities experienced by plants under natural field conditions. Intensity of intraspecific competition in *C. album* increased with increasing resource availability and with increasing plant productivity. Competition was most intense at high light and high nitrogen (HL:HN), and at intermediate availability of light and nitrogen (ML:MN). Where light or nitrogen was strongly limiting, the *response* (sensu Goldberg, 1990) of the plants to intraspecific competition was reduced. Thus, it seems that the amount of resource limitation, not the source (light or nitrogen limitation), determined the intensity of intraspecific competition for this species.

Our results are similar to those of interspecific competition studies that show that the intensity of competition significantly decreases with decreasing resource availability (*e.g.*, Reader and Best, 1989; Aerts *et al.*, 1991; Campbell *et al.*, 1991; Campbell and Grime, 1992). The results are qualitatively different, however, from interspecific studies showing that intensity of competition is constant across resource supply or productivity gradients (Tilman and Cowan, 1989; Tilman, 1990; Wilson and Tilman, 1991, 1993; Reader *et al.*, 1994), or most intense where supply of soil resources is lowest (Wilson, 1993). Furthermore, the
TABLE 3.—Intensity of competition1 (mean ± sd) among Chenopodium album as determined using total plant, aboveground, or belowground biomass. Plants were grown under different availabilities of light and soil nitrogen representing two environmental gradients (1) extending from low light and low nitrogen (LL:LN) to high light and high nitrogen (HL:HN), and (2) extending from low light and high nitrogen (LL:HN) to high light and low nitrogen (HL:LN).

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Environmental gradient 1</th>
<th>Environmental gradient 2</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Total biomass2</td>
<td>Aboveground biomass</td>
</tr>
<tr>
<td>LL:LN</td>
<td>0.44b ± 0.18</td>
<td>0.48b ± 0.19</td>
</tr>
<tr>
<td>ML:MN</td>
<td>0.69a ± 0.06</td>
<td>0.72a ± 0.05</td>
</tr>
<tr>
<td>HL:HN</td>
<td>0.70a ± 0.06</td>
<td>0.72a ± 0.07</td>
</tr>
</tbody>
</table>

1 Intensity of competition was defined as the proportion (dry biomass of plants grown singly – dry biomass of plants grown 6 per pot)/(dry biomass of plants grown singly); larger values indicate more intense competition.

2 Comparisons among treatments; means with a different letter were significantly different at the P < 0.05 level according to Tukey's Studentized Range Test (SAS Institute, Inc., 1989).
pattern of intensity of competition in the present study was identical, whether assessed by total, above- or belowground biomass; thus there was no indication of a switch from below to aboveground limitation with increasing productivity, as suggested for interspecific competition (Tilman, 1988; Wilson and Tilman, 1991).

Many competition studies focus primarily on issues of community structure, dominance and competitive exclusion. These studies generally do not discuss the importance of intraspecific competition processes; rather, these are subsumed into ‘competition’ as a general phenomenon. Studies of intraspecific competition, however, have shown that intraspecific competition can affect the growth, survival, and fecundity of individual plants (McAuliffe and Janzen, 1986; Ungar, 1992; Aguilera and Lauenroth, 1993). Intraspecific effects over environmental gradients can be complex, and may vary greatly with plant age or size or with population density (Firbank and Watkinson, 1990). Previous studies have shown that when conspecifics differ in size or age, the magnitude of intraspecific effects may actually be larger than interspecific effects (Parrish and Bazzaz, 1985; Connolly et al., 1990).

Intraspecific competition has obvious implications for the evolution of species and the fitness of individuals, and studies of intraspecific competition may reveal patterns of com-
petition intensity or mechanisms of competition that cannot be identified by studies of interspecific competition alone. The effects of intraspecific competition on the growth and fecundity of individuals may affect their interactions with neighbors of other species. Consequently, intraspecific competition may affect the ability of species to coexist, and may indirectly be important in determining community structure. Our results indicate that future studies that consider interspecific competition, especially those that use intraspecific competition as background or control, would be more complete if the complex and varying patterns of intraspecific competition across environmental gradients were also considered.

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LITERATURE CITED


