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INTERACTIONS AMONG COLONIZING ANNUALS: IS THERE AN EFFECT OF GAP SIZE?'

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Abstract. Small-scale gaps are often colonized by more than one plant, yet few studies to date have directly investigated the interactions among co-invading individuals. We examined interactions among co-invading plants within small gaps in an old-field community as a function of the size of the gap being invaded. Several colonizing annual species were grown, as single individuals or in conspecific or heterospecific pairs, in artificially created gaps of 10, 20, and 40 cm diameter in a *Poa pratensis* L. background in two successive years.

The identity of the neighbor influenced plant survivorship for one of the two years studied, but had no effect on the probability of becoming reproductively mature, or on levels of seed production. In contrast, vegetative growth was influenced by neighbor identity in both years. Both positive and negative plant–plant interactions were found; the presence of a neighbor did not always result in competitive reduction in the target individual. Conspecific neighbors were found to reduce vegetative biomass to a greater extent than heterospecific neighbors for one of the two years studied, primarily due to the sensitivity of one species, *Setaria faberii*, to conspecific neighbors. We found no evidence of a consistent competitive hierarchy present in this system. Finally, although increasing gap size had significant, positive effects on survivorship, growth, and reproduction, the size of the gap being colonized had no effect on plant–plant interactions between co-invading individuals.

In this system the number and identity of invading individuals, as well as the characteristics of the gap itself, interact to dictate the composition of the invading community and the relative performance of each individual colonist. This complexity may contribute to increased diversity in plant communities in which small-scale disturbances provide opportunities for earlier successional species to persist in localized patches within later successional vegetation.

Key words: annual; beneficence; colonizing; competition; competitive hierarchy; conspecific; disturbance; gap size; heterospecific; neighbor; old field; plant-plant interactions.

INTRODUCTION

Small-scale disturbances generated by animal activities are known to influence plant community structure and dynamics in herbaceous systems, and often allow less competitive species to persist locally (e.g., Platt 1975, King 1977, Rabinowitz 1978, Hobbs and Mooney 1985). Community properties such as diversity, invasability, and the identities and characteristics of component species may be influenced by the frequency. distribution, and characteristics of such disturbances (see Bazzaz 1983, 1986, Tilman 1983, Pickett and White 1985, Inouye et al. 1987). Attention has been increasingly focused on the life-history and physiological attributes of colonizing species, and on characteristics of the gaps themselves (e.g., size, time of formation, resource levels) that might influence the response of the invading plant populations to these gaps (e.g., Davis and Cantlon 1969, Platt 1975, King 1977, Gross and Werner 1982, Goldberg and Werner 1983a, Hobbs and Mooney 1985, Rapp and Rabinowitz 1985, Goldberg 1987*a*, Koide et al. 1987, McConnaughay and Bazzaz 1987). However, the effects of small-scale gaps on community structure and dynamics depend not only upon species' responses to gap characteristics but also upon the interactions that occur among individuals colonizing a gap.

Small-scale gaps may be colonized by few (e.g., Platt and Weis 1985, this study) or many (e.g., Tilman 1983, Hobbs and Mooney 1985, Goldberg 1987a) individual plants, but few studies to date have directly investigated the interactions among co-invading individuals (Platt and Weis 1985, Rabinowitz and Rapp 1985). Consequently, little is known about how the number and identity of colonists will influence the survivorship, growth, and reproduction of individual plants within a gap. Co-invading plants must share gap resources, which may or may not be limiting, depending on gap characteristics and the number and resource requirements of the co-invaders. If complementarity in architectures, resource utilization, etc., among coinvading individuals reduces negative plant-plant interactions, heterospecific neighbors may reduce plant performance to a lesser extent than conspecific neighbors. Heterospecific interactions may be species-spe-

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cific (i.e., given neighbor species having different effects on each co-invading "target" species) or may be represented by a high degree of "competitive equivalency" (sensu Goldberg and Werner 1983b). They may or may not be characteristic of a competitive hierarchy. In some cases, interactions among co-invaders may be positive (Hunter and Aarssen 1988). For example, neighbors might serve as supports for climbing species, or ameliorate unfavorable environmental conditions, such as widely fluctuating temperatures, that are present in open habitats (Bazzaz 1979).

Furthermore, characteristics of the gaps themselves may influence patterns of plant-plant interactions. Previous work in herbaceous communities found differences among species in response to gap size that could result in differing competitive outcomes in gaps of different sizes (McConnaughay and Bazzaz 1987). Gap size influences the amounts and patterns of distribution of resources (e.g., light, moisture, and nutrients), temperature and humidity profiles, and herbivore and pathogen pressure in complex ways in forest systems (see reviews by Bazzaz 1983, Collins et al. 1985, Runkle 1985, Canham 1988). Less is known about how resources might change as a function of gap size in herbaceous systems, and the few available data sets are inconsistent. Few differences were found in resources as a function of gap size in Michigan old fields (Goldberg and Werner 1983a, Bradshaw and Goldberg 1989). However, larger gaps in an Illinois old-field community had higher light intensities at canopy level and at the soil surface, and lower levels of soil nutrients (measured as total N, available P, K, Ca, Mg, and Na) and soil water (K. D. M. McConnaughay and F. A. Bazzaz, personal observation). Colonizing annuals exhibit increased growth and reproduction in larger gaps in this system (McConnaughay and Bazzaz 1987).

The present study examines the interactions among plants colonizing gaps of various sizes and addresses the following questions: (1) Can the performance (i.e., survivorship, growth, reproductive output) of an individual plant colonizing a gap be affected by the presence or the identity of a co-invading plant? (2) Is the effect of a given neighbor species similar for all target species, or are interactions species-specific? (3) Is there a consistent competitive hierarchy among these species? (4) Do the consequences of conspecific and heterospecific interactions differ? (5) Can the characteristics of the gap itself, specifically the size of the gap being invaded and consequent resource levels within the gap, influence plant–plant interactions among co-invading individuals?

MATERIALS AND METHODS

Experimental design

The research was conducted in 1984 and 1985 on a 10-yr-old field located in the University of Illinois Biological Research Area, located 6 km east of Urbana, Illinois. The soil was a nutrient-rich prairie soil (mollisol). Poa pratensis L. dominated the site, while Solidago altissima L., Erigeron species, and woody species, such as Rubus and Gleditsia, were present in lesser numbers. Natural levels of seedling establishment in artificial gaps in which the seed bank was left relatively intact were monitored in 1985 (Table 1). Levels of seedling establishment in 1984 were similar to those reported in Table 1. Based on the levels of natural seedling establishment in small gaps in this field, we chose to limit the number of potential colonists to two plants per gap.

Circular gaps of 10 cm, 20 cm, and 40 cm diameter were established at 1-m intervals in Poa neighborhoods by removing all above- and below-ground material to a depth of 15 cm and replacing the soil with unsterilized prairie soil of the same type from a nearby field. The species used, Abutilon theophrasti Medic., Setaria faberii Herm., Chenopodium album L., and Ipomoea hederacea Jacq., are natural colonizers of disturbed areas for this region. Chosen from a larger group of species used in a previous study that examined the response of individuals to a range of gap sizes (Mc-Connaughay and Bazzaz 1987), these species represent a diversity of growth form: Abutilon forms sturdy, upright seedlings with broad, long-petioled leaves; Setaria is an erect grass; Chenopodium forms tiny seedlings with many small leaves and has delayed maturation; and Ipomoea is a climbing plant derived from very large seeds and seedlings. Seedlings of similar age and size were chosen from populations of seeds collected from the same field and germinated in the greenhouse.

Pairs of seedlings were transplanted into the gaps on 7 June 1984. Each species was grown with every other species as well as with itself, and each of these "target × neighbor" treatments was replicated 10 times in each of the three gap sizes studied. The two individuals were planted 1–3 cm apart in the center of the gap, and this planting distance was maintained in each of the gap sizes. Each pair of seedlings was then enclosed by a wire mesh cylinder for protection against herbivory by rodents, which can be significant in this field (Kirk-patrick and Bazzaz 1979). Immediately following transplanting and for a few days afterward, the seedlings were watered to reduce mortality due to transplant shock.

The following year, we reduced the test species to *Abutilon, Chenopodium*, and *Ipomoea.* The experimental design was identical to that used in 1984, except that each species was also grown as individuals in the absence of any neighbor at all. Seedlings were transplanted into the gaps on 4 June 1985. The plants were handled in the same fashion in both years.

At the end of each growing season (mid-October), the above-ground parts of the surviving plants were measured for height, harvested, and separated into seeds, flowers, fruits, and vegetative parts. All samples were ovendried to a constant mass and subsequently weighed.

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TABLE 1. Mean numbers of naturally recruited seedlings and/ or shoots per gap (n = 10). Data were taken on 4 June 1985 and represent peak populations.

	Gap diameter (cm)				
Species	10	20	40		
Daucus carota	0.0	0.5	0.2		
Trifolium sp.	0.0	0.1	0.1		
Polvgonum pensvlvanicum	0.0	0.0	0.2		
Chenopodium album	0.0	0.4	0.0		
Abutilon theophrasti	0.0	0.2	0.0		
Grasses	0.0	0.3	1.8		
Unknown	0.0	0.0	0.6		
Total	0.0	1.5	2.9		
Range	0–0	0-3	0-12		

Statistical analyses

The proportions of plants that survived, flowered, and set seed were compared across neighbor treatments and gap sizes for each target species in each year using log-likelihood calculations (the 1984 BMDP Statistical Software Package BMDP4F, Dixon 1985). Log-linear models (described in Bishop et al. [1975], and Sokal and Rohlf [1981]) are additive, which is particularly useful for experimental designs in which the number of cells in each combination of treatments is preassigned, as was true for the present study. Accordingly, all of the models we examined included fixed interaction terms that could not be directly estimated (see Brown [1985] and Sokal and Rohlf [1981] for discussion). Thus, in order to determine the effect of gap size and neighbor treatment on survivorship for a given target species, our preliminary models necessarily included the gap size \times neighbor treatment interaction term. We then fit models that included the terms of interest (i.e., gap size and neighbor species) and obtained log-likelihood ratio (G^2) values through subtraction. All hypotheses tested were assumed to be twotailed.

Analysis of variance tests were performed for each year on log-transformed values of plant height, number of seeds produced, and vegetative biomass using the General Linear Modelling procedure (GLM) in the Statistical Analysis System (Joyner 1985). The transformed parameters and the residuals obtained via our models were all judged to be normally distributed. F_{max} tests (Sokal and Rohlf 1981) indicated that the variances were not significantly different. The models examined were full factorial models using target species, neighbor treatment, and gap size as fixed main effects. All main effects and interactions were tested using the residual (error) variance. To further elucidate the effect of neighbor treatment on plant performance, contrasts were specified to test for differences between conspecific and heterospecific interactions (1984 and 1985 data) and between the presence or absence of a neighbor (1985 data). F tests were constructed for these comparisons by calculating the mean square (variance) associated with the effect in question and dividing by the residual (error) variance. In all cases Type III sums of squares were employed. In cases where there was a significant neighbor treatment or neighbor treatment interaction term, least-square means were computed, and *t* tests with associated Bonferroni probabilities (adjusted for multiple comparisons) were computed to assess differences between treatments.

RESULTS

Including year as a random effect in our models showed significant main effects of year and many significant interactions between year and one or more of the other effects (target species, gap size, and neighbor treatment) included in the models. Thus, for statistical reasons as well as for simplicity in interpretation, data were analyzed separately for each year.

Survivorship, flowering, and seed set

Survivorship was generally high (91% for all target species and treatments combined) in 1984 (Fig. 1A). While there were no significant effects of neighbor species on the probability of survivorship or reproduction for any of the target species, there were some effects of gap size (Table 2). Chenopodium and, marginally, Ipomoea had greater survivorship in larger gaps (Fig. 1A). Furthermore, the proportions of plants that flowered and set seed increased with gap size for both Chenopodium and Ipomoea. When the proportions of plants that flowered or that set seed were analyzed using only those plants that had survived or that had flowered, the effects of gap size disappeared for Chenopodium (Table 2). Thus, although the probabilities of surviving, flowering, and setting seed were all greater in larger gaps for Chenopodium, the probability of surviving plants becoming reproductive was unaffected by the size of the gap. In contrast, Ipomoea had a higher probability of developing mature fruits (given that flowers were present) as the size of the gap was increased, and had marginally higher probabilities of flower initiation and survivorship as well.

In contrast to 1984, survivorship was quite low in 1985 (<50% for all species combined, Fig. 1B). We observed a great deal of physical damage both within gaps and in the surrounding vegetation in our experimental area, possibly due to the activities of dogs, deer, or other mammals. Partially as a consequence of this damage, survivorship was particularly low in the 40cm gaps, making comparisons within this gap size difficult. Ipomoea was the only target species for which there was a significant effect of gap size on survivorship in the second year (Table 2), and this effect may have been partially due to the reduction in survival in the 40-cm gaps (Fig. 1B). Ipomoea also had higher probabilities of flowering and seed-set in larger gaps, and higher probability of developing mature fruits from flowers (Table 2). As in 1984, the probability of flowering and setting seed in *Chenopodium* was directly related to survivorship: virtually all surviving individ-



FIG. 1. Percentage of individuals surviving, flowering, and setting seed, over an 18-wk period, in relation to (A) gap size in 1984, (B) gap size in 1985, and (C) neighbor treatment in 1985.

uals went on to produce mature seed. No reproductive *Abutilon* individuals were present in the 1985 cohort.

In 1985 there were significant effects of neighbor treatment (including no-neighbor treatment) on survivorship for both *Abutilon* and *Chenopodium* (Table 2, Fig. 1C). *Chenopodium* survivorship was lower when grown with *Ipomoea*, regardless of gap size, whereas survivorship for *Abutilon* was apparently lower for individuals grown with either *Ipomoea* or *Chenopodium* (except in the 40-cm gaps, for which the data are least complete due to the aforementioned damage). *Ipomoea* was not affected by neighbor treatment.

Growth and fecundity

Plant height, vegetative biomass, and reproductive output were all significantly affected by gap size in both years (Table 3). All target species and target species \times gap size interaction terms were also significant (marginally significant for height in 1985), except that for number of seeds produced in 1985. Although all target species studied produced more biomass in larger gaps (Fig. 2), the significant interaction indicates that the target species differed in their sensitivity to variation in gap size. For example, in 1984, *Setaria* was quite responsive to differences in gap size, while *Abutilon* and particularly *Ipomoea* were less affected (Fig. 2). Furthermore, some target species apparently differed in sensitivity to gap size from one year to the next (cf. *Ipomoea* in 1984 vs. 1985). Height growth patterns in relation to gap size (data not shown) resemble those for vegetative biomass presented in Fig. 2. *Chenopodium*, and to a lesser extent *Ipomoea*, produced greater numbers of seeds in larger gaps, and seed production for *Chenopodium* in 1984 was particularly sensitive to differences in gap size (Fig. 2).

The height of a target plant was also responsive to the neighbor treatment, although levels of significance were marginal in both years (Table 3). However, we found no evidence of a simple trend in presence vs. absence of neighbor or in conspecific vs. heterospecific TABLE 2. Results of log-likelihood tests of association of gap size and neighbor treatment on the proportions of individuals surviving, flowering, and setting seed, by the end of the growing season, for each target species.

Proportion of individuals	Abutilon		Chenopodium		Ipomoea		Setaria	
at end of season	Gap size	Neighbor	Gap size	Neighbor	Gap size	Neighbor	Gap size	Neighbor
			A) 1984	1				
Surviving	NS	NS	**	NS	(*)	NS	NS	NS
Flowering a) all individuals b) surviving individuals	NS NS	NS NS	*** NS	NS NS	** (*)	NS NS	NS NS	NS NS
Setting seed					()			
a) all individuals b) flowering individuals	NS NS	NS NS	*** NS B) 1085	NS NS	*** *	NS NS	NS NS	NS NS
Surviving	NS	*	NS	**	*	NS		
Flowering								
a) all individuals b) surviving individuals	† †	† †	NS NS	** NS	* NS	NS NS		
Setting seed								
a) all individuals b) flowering individuals	† †	† †	NS NS	** NS	**	NS NS		

*** P < .001, ** .01 > P > .001, * .05 > P > .01, (*) .10 > P > .05, NS P > .10. † Insufficient data to perform analyses.

neighbors. Furthermore, there was no significant neighbor treatment \times target species interaction in either year. Pairwise multiple comparisons yielded few significant differences at either the .05 or the .10 level; a

notable exception was that in 1985 *Ipomoea* plants grown with *Abutilon* neighbors were significantly taller when compared to all other neighbors or no neighbor (Fig. 3). Thus, for both years, the height of the target

TABLE 3. Analysis of variance of plant height, vegetative biomass, and numbers of seeds produced. The model tested is a full-factorial, fixed-effects model. Refer to *Materials and methods: Statistical analyses* for a discussion of the additional contrasts.

	Height			Vegetative biomass			Number of seeds produced		
Source of variation	MS	df	P	MS	df	P	MS	df	Р
		A) 198	4						
Gap size	11.5327	2	.0001	0.0570	2	.0001	4.0047	2	.0014
Target species	11.2634	3	.0001	0.0210	3	.0001	42.4278	3	.0001
Neighbor treatment	0.4381	3	.0529	0.0029	3	.1612	0.1024	3	.9141
Gap size \times target species	0.5423	6	.0044	0.0066	6	.0008	2.0102	5	.0058
Gap size \times neighbor treatment	0.2627	6	.1608	0.0011	6	.6880	0.2490	6	.8636
Target species \times neighbor treatment	0.1780	9	.3995	0.0042	9	.0096	0.2203	9	.9466
Gap size \times target species \times neighbor									
treatment	0.1805	18	.3866	0.0017	18	.4655	0.6494	12	.3622
Residual (error)	0.1697	445		0.0017	445		0.5899	174	
Total		492			492			214	
Conspecific vs. heterospecific neighbors	0.0017	1	.9204	0.0178	1	.0013	0.0546	1	.7620
		B) 198	5						
Gap size	3.9590	2	.0001	0.0216	2	.0001	2.8552	2	.0017
Target species	9.9571	2	.0001	0.0233	2	.0001	30.3724	1	.0001
Neighbor treatment	0.4629	3	.0840	0.0090	3	.0019	0.3215	3	.5197
Gap size \times target species	0.4694	4	.0622	0.0049	4	.0264	0.0638	2	.8604
Gap size \times neighbor treatment	0.1003	6	.8171	0.0029	6	.1284	0.1704	6	.8765
Target species \times neighbor treatment	0.2693	6	.2550	0.0046	6	.0168	0.0210	3	.9853
Gap size \times target species \times neighbor									
treatment	0.1803	11	.5644	0.0025	11	.1557	0.1783	6	.8639
Residual (error)	0.2057	182		0.0017	182		0.4239	117	
Total		216			216			140	
Conspecific vs. heterospecific neighbors	0.2600	1	.2606	0.0037	1	.1504	+		
Presence vs. absence of neighbor	0.0429	1	.6470	0.0001	1	.8469	0.4521	1	.2968

† Insufficient data to perform contrast.



FIG. 2. Vegetative dry biomass and numbers of seeds produced over an 18-wk period, in relation to gap size, for two successive years (means \pm sE). Means have been adjusted for main effects of neighbor treatment.

individual was only moderately influenced by the identity of its neighbor, with no significant difference in the way each target species responded to the neighbor treatments.

Vegetative biomass was significantly affected by neighbor treatment in 1985 and by neighbor treatment \times target species in both years. The accumulation of dry mass of the target individual was influenced by the neighbor treatment, but the nature of that relationship differed among the target species examined. Examination of the additional contrasts shows that in 1984 there was a highly significant effect of conspecific vs. heterospecific target-neighbor pairs. Individuals grown in conspecific pairs had on average less vegetative biomass at the end of the season than did individuals grown in heterospecific pairs. This was obvious only in the case of Setaria, however (Fig. 3). Contrasts of conspecific vs. heterospecific neighbors and the presence vs. absence of neighbors were not significant in 1985. Consistent with the height response, there were few significant pairwise contrasts between neighbor treatments. Ipomoea plants grown with Abutilon neighbors in 1985 were significantly heavier when compared to all other neighbors or no neighbor, also consistent with the height response (Fig. 3).

In neither year was number of seeds produced affected by the neighbor treatment, nor were there any significant interactions between neighbor treatment and target species. Finally, none of the traits showed any evidence for either a neighbor treatment \times gap size or a neighbor treatment \times target species \times gap size interaction in either year.

Environmental heterogeneity

Environmental variation within seasons may affect plant performance and competitive relationships (Fowler 1982). As noted, the study site is a relatively recently abandoned agricultural field. It overlies a single soil type and exhibits little variation in topography. Furthermore, the gaps were located in a single background vegetative matrix and were created within weeks of each other. We therefore expected that environmental heterogeneity would be quite low. Nevertheless, we performed a posteriori tests to assess the effects of any potential microenvironmental heterogeneity on the results of the model presented. Including within-field location in our model did not improve normality of the data or of residuals, nor did this allow us to explain more of the variation. The inclusion of this factor did not change the relationships examined more than would be expected by chance alone.

A further test of the importance of small-scale environmental heterogeneity was performed by careful examination of the residuals obtained via our original model using both plant height and vegetative biomass produced as independent variables. Due to the low number of reproductive individuals, pairs in which both plants produced seed were too scarce to permit



FIG. 3. Height and vegetative dry biomass produced by the end of an 18-wk period, in relation to neighbor treatment, for two successive years (means \pm sE). Means have been adjusted for main effects of gap size. Neighbor treatments different at Bonferroni-adjusted P = .05, based on pairwise t tests, are marked by different lowercase letters.

this analysis using numbers of seeds produced. Residuals from pairs of plants (corresponding to the pairs present in each individual gap) were correlated to assess any possible interdependence. Positive correlations indicate that both members of a pair deviated from our model in similar fashion; i.e., either both plants were larger or both were smaller than would be predicted by our model. This would be indirect evidence that microenvironmental heterogeneity was an important force in this study (cf. Mitchell-Olds 1987). We did this for each gap size and for each target \times neighbor species pair and found significant positive correlations only in the 10-cm gaps. Furthermore, while none of the correlations for heterospecific pairs were significant (min. P = .276), correlations for all conspecific pairs, with the exception of *Ipomoea* pairs, were significantly positive (max. P = .011). Thus, while there may have been some effect of heterogeneity in this field, it seems that only conspecific pairs in the smallest gaps exhibited a measurable response to it.

DISCUSSION

Plant performance and year-to-year variation

Although results from the two years agreed well on a coarse level (e.g., greater performance in larger gaps, plant-plant interactions independent of gap size), a number of subtle differences between the years emerged. Overall survivorship (Abutilon, Fig. 1), vegetative growth in relation to gap size (Abutilon and Ipomoea, Fig. 2) and to neighbor treatment (Ipomoea, Fig. 3), and seed production in response to gap size (Chenopodium, Fig. 2) differed between the two years studied. This year-to-year variation in species' responses suggests that relative species' abundances will fluctuate in this community. Consequently, the persistence of any one species is more probable over time. Temporal heterogeneity in species' response is also evident when comparing results from the present study to those obtained in previous work that examined the response of single individuals to these same gap sizes in 1982 (McConnaughay and Bazzaz 1987). Most strikingly, overall levels of survivorship (1985), growth, and reproduction were considerably reduced in the present study relative to values obtained in 1982, as was the rate of above-ground gap closure (K. D. M. Mc-Connaughay, personal observation). The fact that we were unable to detect any differences, in any trait measured, between plants with and without neighbors in 1985 suggests that competitive reduction cannot explain the reduced performance observed in the present study.

Examination of climatological data collated by the Urbana, Illinois weather station reveals that, overall,



FIG. 4. Mean daily temperature and total monthly precipitation, from June through October, collated from Illinois State Water Survey data, 1890–1985.

year-to-year variation in climate among the three years was modest, and that all three years fell within the range of climate observed in this area (Fig. 4). June 1984, however, did exhibit relatively high temperatures and low precipitation (Fig. 4), and this may have contributed to reduced performance relative to the previous study. While temperatures and precipitation levels during the growing season for 1985 were quite normal (Fig. 4), the relatively low number of clear days (39 vs. 65 in 1982), or climatological or biological variables not measured, may have been responsible for reduced survivorship and growth in this year.

Plant-plant interactions in relation to gap size

Surprisingly, there was no evidence that the nature of the relationship between individuals sharing a gap was influenced by the size of that gap. There were no significant interactions between neighbor treatment and gap size, or neighbor treatment, target species, and gap size, for any trait measured in either year. Thus it appears that resource levels within the gaps, which are a function of gap size, had no effect on interactions between co-invading plants. This could indicate that plant growth in these gaps was not resource limited (unlikely given the increased levels of growth seen in larger gaps), that interactions among co-invading plants are very weak or absent over the range of gap sizes examined (unlikely given the significant neighbor effects seen), or

that survivorship and growth of invading seedlings was primarily influenced by competition with the existing perennial matrix. Alternatively, because these species are characterized by a relatively high degree of niche overlap and competitive equivalency (Bazzaz 1987), the outcome of specific interactions may appear random. Fowler (1990) has interpreted such interactions as "disorderly", and lists a number of deterministic and stochastic factors that contribute to the "disorderliness" of plant-plant interactions, and thus the significance of chance events (e.g., time of germination, microsite effects), in predicting competitive outcome. Although studies have shown that plant-plant interactions can change as a function of resource levels under controlled greenhouse conditions (Pickett and Bazzaz 1976, 1978, Fowler 1982, Bazzaz and Garbutt 1988), the situation in the field is more complex (Berendse 1983, Fowler, in press, this study). We know of no data sets that clearly demonstrate changes in competitive relationships with varying levels of resources in the field.

Plant performance and gap size

In an earlier study conducted in the same field in 1982 (McConnaughay and Bazzaz 1987), individuals of both *Setaria* and *Chenopodium* displayed greater survivorship in larger gaps, and all species except *Ip*omoea had greater probabilities of reproducing in largOctober 1990

er gaps. In contrast, in this study *Ipomoea* was the only species for which gap size affected the ability to initiate or mature fruits and seeds. Survivorship in relation to gap size for these various species also differed from our previous findings: *Ipomoea* was responsive in both years, *Chenopodium* in 1984 only, and *Setaria* was not responsive to differences in gap size at all. Thus, in the earlier experiment *Ipomoea* was unique in its lack of response to gap size, whereas it was one of the most responsive species in the present study.

In both studies vegetative growth was greater in larger gaps (except for *Ipomoea* in 1982), although the degree of sensitivity to gap size differed among species and years. However, the increases in growth seen at the largest gap size in this study were not as dramatic as those found in the earlier study, nor was there any evidence of increased reproductive output in larger gaps, a result that was very striking in the previous study. As has been discussed in the previous section, however, year-to-year differences in gross climatological patterns may have contributed to differences in survivorship, growth, and reproduction.

Plant performance and the presence/identity of a neighbor

The presence of a neighbor did not result in a simple trend of reduced performance for target plants, in contrast with other recent field studies (Goldberg 1987*b*, Fowler, *in press*; see Connell [1983] and Schoener [1983] for earlier references). It was not the presence of a neighbor, but rather the identity of that neighbor, that was of critical importance in determining the response of the target individual in the present study. This suggests that some species pairs may have had good "ecological combining abilities" (sensu Aarssen 1983) and thus were not actually competing. Furthermore, some combinations resulted in positive interactions and can be described as "beneficent" (sensu Hunter and Aarssen 1988).

The greater performance of *Ipomoea* individuals growing with *Abutilon* in 1985 are suggestive of beneficent interactions (Fig. 3). *Ipomoea* is a climbing plant and might easily benefit from a neighbor's presence. *Setaria*, a grass, produces fairly erect, sharp-edged, silicon-laden blades, while *Chenopodium* has a delayed phenology, remaining quite small throughout most of the growing season. These traits might make these species less desirable than *Abutilon* as supports. It is unclear why the same increase in performance of *Ipomoea* targets grown with *Abutilon* neighbors was not seen in 1984, however.

The identity of a neighboring plant in the same gap had varied effects on the performance of an individual colonist. While survivorship was unaffected by neighbor treatment in 1984, it was significantly affected for two of three target species in 1985. In neither year was the likelihood of an individual plant flowering or setting seed affected by neighbor treatment. In contrast,

vegetative growth was influenced by neighbor treatment in both years. The two measures of growth, height and biomass, were affected in very different ways, however. Plant height was only marginally affected by the main effect of neighbor treatment, and there were no significant target species × neighbor treatment interactions. In contrast, there were significant target species × neighbor treatment interactions for vegetative biomass in both years. Thus, the accumulation of biomass was affected in a species-specific manner. Species-specific responses are less likely to result when access to the limiting resource(s) is ordered (i.e., asymmetrical), as has been found in respect to competition for light (Miller and Werner 1987). The fact that interactions were species-specific in the present study suggests that plant growth was limited primarily by soil resources or by a number of resources simultaneously. Therefore, in the present study biomass accumulation may be a more integrated estimate of overall plant performance than is plant height. These broad-scale conclusions aside, it is notable that relatively few of the pairwise comparisons of neighbor treatments were significant. Furthermore, the results of specific target \times neighbor species comparisons were not consistent among years (e.g., Ipomoea's response to Abutilon in 1984 vs. 1985). Thus no clear competitive hierarchy can be constructed from these data.

The present study did not detect any effect of neighbor treatment on either the probability of a target plant becoming reproductive or the number of seeds produced by that plant, both of which were lower than we expected based on our previous work with these species in this field. While it is possible that if the growing season had been more favorable for plant growth and reproduction in general (i.e., cooler, sunnier, wetter), plant–plant interactions might have had an effect on reproductive output, the two years of the current study are representative of the range of climatic variation seen in this area (Fig. 4).

Other studies have recently addressed plant-plant interactions in gaps in herbaceous systems. Rabinowitz and Rapp (1985), working in small (5.8 cm diameter) artificial gaps in Missouri tallgrass prairie, followed the fate of colonizing perennial seedlings and shoots for several years. They found little evidence of any densitydependent mortality in these populations, indicating that plant-plant interactions have little effect on the survivorship of individuals colonizing gaps, a result that is partially consistent with the findings of the present study.

Platt and Weis (1985) examined plant-plant interactions in large gaps (50–60 cm diameter) in tallgrass prairie in Iowa. Similar to the results obtained by Rabinowitz and Rapp (1985), they found little evidence that competitive neighborhood influenced the survivorship of the perennial plants colonizing the gaps. However, the presence of a co-invading plant consistently resulted in a reduction in vegetative growth and reproduction, in contrast with the findings of this study. In addition, they were able to demonstrate the existence of a clear competitive hierarchy. Conspecific interactions were shown to result in greater reductions in plant performance than heterospecific interactions, a result that is only partially consistent with our findings.

Conclusion

Our results indicate that the identity of a co-invading individual can have significant effects on the performance of annuals colonizing small-scale gaps in this herbaceous community. These effects were found primarily in differences in vegetative growth, although survivorship was influenced by neighbors in one of the two years studied. The presence of a neighbor did not, however, result in a simple competitive reduction in plant growth; both positive and negative plant-plant interactions were found. One species, Setaria faberii, had significantly reduced growth in the presence of conspecific neighbors relative to heterospecific neighbors. We did not find a consistent competitive hierarchy in the present study. Rather, competitive relationships appeared to be complex, and to differ between years. Finally, perhaps as a consequence of the complexity of interactions among co-invading plants, gap size did not affect plant-plant interactions among coinvading individuals, even though the size of the gap had many significant effects on the survivorship, growth, and reproduction of these species. Thus, in this system, the number and identity of invading individuals, as well as the characteristics of the gap itself, interact to dictate the composition of the invading community and the relative performance of each individual colonist. This complexity may contribute to increased diversity in plant communities in which small-scale disturbances provide opportunities for earlier successional species to persist in localized patches within later successional vegetation.

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