
Distribution of a Restricted Locally Abundant Species: Effects of Competition and Nutrients on *Coreopsis lanceolata*

Author(s): Laurie A. Folgate and Samuel M. Scheiner

Source: *The American Midland Naturalist*, Oct., 1992, Vol. 128, No. 2 (Oct., 1992), pp. 254-269

Published by: The University of Notre Dame

Stable URL: <https://www.jstor.org/stable/2426459>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <https://about.jstor.org/terms>



is collaborating with JSTOR to digitize, preserve and extend access to *The American Midland Naturalist*

JSTOR

Distribution of a Restricted Locally Abundant Species: Effects of Competition and Nutrients on *Coreopsis lanceolata*

LAURIE A. FOLGATE AND SAMUEL M. SCHEINER¹

Department of Biological Sciences, Northern Illinois University, DeKalb 60115

ABSTRACT.—To determine if there is a trade-off between competitive ability and growth in unproductive conditions in *Coreopsis lanceolata* L. (Asteraceae), two studies were carried out. In one, a survey of natural populations quantified environmental parameters and plant traits. The results indicated that these habitats are characterized by low soil moisture and low nutrient availability; densities of *C. lanceolata* were negatively correlated with densities of other species. The second study was a transplant garden experiment in which three levels of nutrients and two levels of competition were manipulated. One garden was adjacent to a natural population and the second was in a more productive area where *C. lanceolata* did not occur. Plants grew, survived and reproduced better in the area where *C. lanceolata* did not occur if competitors were removed. Nutrient effects were transient and only affected growth soon after application. The trade-off between competitive ability and growth in unproductive habitats may be responsible for the distribution of *C. lanceolata* and other restricted locally abundant species which often are habitat specialists.

INTRODUCTION

A basic question in ecology is: what are the factors that limit the local distribution and abundance of species (Krebs, 1972)? The distribution of a species can be characterized by three traits: its geographic range (wide or narrow), its habitat specificity (broad or restricted), and its local population size (somewhere large or everywhere small) (Rabinowitz and Rapp, 1981). Local limits of plant species distributions can often be explained by dispersal ability, competitive ability, resource availability, disturbance rates, preferential herbivory and physiological tolerances over environmental gradients. Numerous studies have been made of the effects on the distribution and abundance of plant populations of competition (Goldberg and Werner, 1983; Rabinowitz *et al.*, 1984; Gurevitch, 1986; Wilson and Keddy, 1986a, b; McGraw and Chapin, 1989; Reader and Best, 1989), nutrient availability (Reader and Watt, 1981; Tilman, 1982; Goldberg and Miller, 1990), and the combination of competition with drought stress (Bauder, 1989) and with nutrients (Reader, 1990). Often the control of abundance cannot be attributed to a single process but to a combination of processes (Crawley, 1986).

The present study focuses on the herbaceous perennial *Coreopsis lanceolata* L. (Asteraceae), a species with a broad geographic range, restricted to specific habitats, and locally abundant. We will refer to this particular distribution as restricted locally abundant. This form of rarity is the most frequent for plants which are habitat specialists, *e.g.*, sand dune, marsh, bog and fen species (Rabinowitz *et al.*, 1986). Because these habitats are all resource-limited or characterized by extreme conditions (*e.g.*, pH in bogs), this category seems to represent species that specialize on stressful habitats and suggests the hypothesis that a trade-off exists between tolerance to extreme abiotic conditions and competitive ability (Grime, 1977; Goldberg and Miller, 1990).

Based on this hypothesized trade-off between competitive ability and stress tolerance, Grime (1977) proposed that superior competitors will be found in the most productive,

¹ Addressee for all correspondence

undisturbed environments and stress tolerators will be found in unproductive environments. A stress is any extreme environmental factor capable of inducing a potential injury in living organisms (Levitt, 1980). Grime (1979) reasoned that the outcome of intense competition largely determines plant density where relatively high soil fertility favors large, fast growing species; but on infertile soils, the limited nutrient supply restricts plant growth and stature, thus reducing the chance of interaction occurring between neighbors. A refinement of Grime's hypothesis is a prediction of the light-mortality hypothesis (Goldberg and Miller, 1990) that the species that are competitively displaced at high fertility levels are those that are slower growing, smaller, have leaves close to the ground or are physiologically shade-intolerant. An additional prediction of stress tolerance is that on very infertile soils, successful plants will be those exhibiting relatively slow and phenotypically unresponsive patterns of root development; survival and fitness are expected to be correlated with relatively low rates of nutrient uptake and with the tendency to accumulate stores of mineral nutrients within the plants (Sibly and Grime, 1986). Tilman (1982) has disputed the claim that competition is reduced in unproductive areas. The differences between Grime and Tilman are due mostly to discrepancies in their definitions of tolerance and competitive ability, although the two authors do have genuine differences in their views on the evolutionary trade-offs associated with productivity gradients (Grace, 1990). Therefore, we take as a reasonable working hypothesis the existence of the trade-off proposed by Grime.

We tested for the existence of a trade-off between tolerance for growth in unproductive conditions and competitive ability in the herbaceous perennial *Coreopsis lanceolata*. *Coreopsis lanceolata* is a rosette plant with prostrate, oblong, leathery leaves; it may have one to a few flowerstalks each possessing a few upper leaves and bearing 1–3 inflorescences (heads). *Coreopsis lanceolata* is found throughout most of the central and southern United States in a narrow range of habitats, usually in sandy, nutrient-poor soils in sand dune or oak savanna habitat types where it is locally abundant (Gleason and Cronquist, 1963; Swink and Wilhelm, 1979). Many habitats exist that are apparently similar but contain no individuals of *C. lanceolata*; where it is found, however, it is abundant (pers. observ.). This habitat specificity of natural populations leads us to ask what factors limit the local distribution and abundance of *C. lanceolata* populations.

We propose the following hypotheses. First, we predict that *Coreopsis lanceolata* possesses physiological tolerances which permit growth in soils with low nutrient and soil moisture levels. If so, we expect it to be able to grow and reproduce in poor environments. Second, we predict the restriction of habitat range is at least partially a result of competitive exclusion. If so, we expect (1) in natural populations a negative correlation between the density of *C. lanceolata* and other species and (2) under experimental conditions negative effects of competition on morphological traits and life history traits of growth rate, survivorship and reproduction.

Our first study quantified the environmental, morphological and reproductive parameters of the natural populations to determine the environmental conditions of the habitats including the density of cooccurring species. Our second study was a transplant garden experiment in which competition, nutrients and site conditions were manipulated to determine if a trade-off between tolerance of unproductive conditions and competitive ability is partially responsible for the restricted locally abundant distribution.

SURVEY OF NATURAL POPULATIONS

We studied three natural populations of *Coreopsis lanceolata* in a range of environments to quantify habitat characteristics. The first two populations were located in Allegan State Game Area, Allegan Co., Michigan (Population A in the SW corner of T2N R14W Sect5

and Population B in the NW corner of T3N R15W Sect 35). The original vegetation of both areas was oak-pine forest (Kenoyer, 1934). Both populations were located in fire-maintained oak savannas dominated by *Carex pensylvanica*, *Hieracium pratense*, *Rumex acetosella*, *Lupinus perennis* and *Lithospermum croceum* (see Folgate, 1991, for further description of species composition). The areas had a high percentage of exposed ground. Population B is part of a controlled burning program by the Michigan Department of Natural Resources and was burned in April 1978 and April 1989. A noticeable feature of both populations was a well-defined boundary. Areas surrounding the populations were dominated by either graminoids or woody plants.

The third population, I, was located at Indiana Dunes National Lakeshore, Porter Co., Indiana (T36N R7 Sect35). This population occupied a late successional forest located on the W side of an inland backdune with large openings in the forest on S-facing slopes. This area was dominated by *Quercus alba*, *Rumex acetosella*, *Achillea millefolium*, *Solidago nemoralis* and *Artemisia caudata* (Folgate, 1991). Population I occurred in both shaded and open areas. All three sites had the same soil type, Oakville fine sand (Knapp, 1987; Furr, 1981).

MATERIALS AND METHODS

The habitat of *Coreopsis lanceolata* was quantified with regard to light, soil moisture, soil nutrients and vegetation during the summer of 1989. Solar irradiance was measured directly above the plants (approximately 10 cm above ground level) and recorded as percentage of full sunlight using a LI-Cor LI-185B quantum flux meter. Measurements were made on clear days and recorded at population I on 28 June 1990 at 11:15 A.M. and 3:30 P.M. and at populations A and B on 6 July 1990 at 11:15 A.M. and 3:00 P.M. and at 11:30 A.M. and 3:15 P.M., respectively. Soil moisture was measured using a Bouyoucos moisture meter. Bouyoucos gypsum blocks were buried at root level, 5 cm depth, 15 blocks per population, and measurements were recorded weekly from 6 June to 28 July 1989 as percent available soil moisture. Soil composition was analyzed at the Soil Testing Laboratory at Michigan State University, East Lansing. In June 1990, soil samples were taken from each population. Five samples each were removed from populations B and I; in population A five samples were taken from within the population and five from outside the population boundaries. Each soil sample consisted of four cores, 10 cm depth and 2 cm diam, and was analyzed for NO_3^- , NH_4^+ , P^{4-} , K^+ , Ca^{+2} , Mg^{+2} , and pH.

To quantify the apparent vegetational gradient, we established six transects, four in population A and two in population B. Each transect was 50 m long, beginning 25 m within the population's boundaries and extending 25 m outside the boundary, and consisted of a 0.5 m² quadrat placed every 5 m. We measured percentage vegetation cover, mean vegetation height, aboveground biomass (dry weights), species composition and solar irradiance. Aboveground dry biomass was determined in July after clipping all vegetation within each quadrat and drying at 60 C.

To compare variation in morphological traits among the natural populations and the experimental gardens (see below), 250 randomly chosen plants in each population were measured for traits involving size, biomass and reproductive effort. We counted the number of shoots and measured the lengths and widths of the three longest leaves per plant. Leaf shape was calculated as the ratio of leaf length to leaf width. Specific leaf weight was determined by weighing 3 dried leaf disks of a fixed area per plant. Flower measurements included: number of flowering stalks, flowerstalk length, number of heads, head diam, ray length, number of seeds per head and seed weight. All statistical analyses were performed using the SYSTAT statistical package (Wilkinson, 1987).

TABLE 1.—Environmental parameters (means ± SE) measured in the three natural populations; soil moisture (n = 300), irradiance levels (n = 102), soil nutrients (ppm) and pH (n= 15). Means having different superscripts are different based on a Tukey HSD Multiple Comparison Test (P < 0.05). F-values are from ANOVA

	Population			
	A	B	I	F
% soil Moisture	46.9 ^B ± 3.9	46.0 ^B ± 4.0	91.2 ^A ± 2.0	50.4****
% full Sunlight	85.1 ^A ± 2.7	85.3 ^A ± 3.8	60.2 ^B ± 3.7	17.5****
pH	5.70 ^A ± 0.09	5.32 ^B ± 0.06	5.42 ^B ± 0.07	6.93**
NO ₃ ⁻	0.330 ^A ± 0.101	0.000 ^B ± 0.000	0.000 ^B ± 0.000	10.729**
NH ₄ ⁺	1.910 ^A ± 0.242	1.530 ^A ± 0.290	1.510 ^A ± 0.228	0.785
P ⁻⁴	89.2 ^A ± 19.6	52.6 ^B ± 8.1	24.7 ^C ± 2.8	27.5****
K ⁺	10.8 ^B ± 2.2	20.4 ^A ± 2.0	19.5 ^A ± 3.4	16.8****
Ca ⁺²	216.0 ^{AB} ± 69.7	120.0 ^B ± 56.6	232.0 ^A ± 16.0	5.9*
Mg	11.5 ^B ± 0.0	11.5 ^B ± 0.0	17.0 ^A ± 0.0	U ⁺

* P < 0.05; ** P < 0.01; *** P < 0.001; **** P < 0.0001

+ The F-value is undefined because there was no variance

RESULTS

Environmental parameters.—The sites differed in soil moisture levels, light levels and soil composition (Table 1). Population I had significantly higher mean soil moisture levels than the others. Both A and B had similar irradiance levels that were significantly higher than Population I. Population A had significantly higher levels of NO₃⁻, pH and P⁻⁴ (Table 1). Population I had the highest concentration of Mg⁺². Populations B and I did not differ in concentrations of K⁺ but both were significantly higher than population A. All three populations had similar amounts of NH₄⁺.

Vegetational gradient.—A vegetational gradient extended from within to outside both population A and B. Along the gradient, percent cover of *Coreopsis lanceolata* decreased from 12.5 ± 3.4% to 0 ± 0.0% (values are means ± SE over the six transects). Percent total dicot cover, including *C. lanceolata*, decreased from 16.5 ± 3.1% to 9.3 ± 1.9%. Percent vegetation cover increased (37.5 ± 6.2% to 65.8 ± 10.5%) with distance from the center of the population. Increases occurred in percent monocot cover (20.2 ± 4.6% to 52.5 ± 10.2%) (primarily *Carex pensylvanica*), percent litter cover (6.7 ± 5.0% to 36.8 ± 8.4%), and average canopy height (22.7 ± 1.8 cm to 35.9 ± 4.0 cm). Average biomass of quadrats within the population was 12.1 ± 3.1 g compared to an average of 18.9 ± 2.6 g in quadrats outside the population. Irradiance, at ground level, decreased along the gradient, from 78.7 ± 5.9% to 52.3 ± 10.3% of full sunlight. Percent *C. lanceolata* cover was negatively correlated with % vegetation cover (r = -0.32, df = 58, P < 0.02) and canopy height (r = -0.26, df = 58, P < 0.05); it was positively correlated with light levels (r = 0.32, df = 58, P < 0.02).

Morphological traits.—Populations A, B and I differed significantly in number of shoots/plant; population B had the greatest number of shoots (Table 2). For leaf length and leaf width, populations A and B were similar and both differed significantly from I. Leaf shape differed significantly among all three populations. Plants in population I had the longest and most narrow leaves compared to the shorter, wider leaves of plants in both Allegan populations.

Flowering traits.—The percentage of genets flowering in A, B and I was 40%, 58% and 42%, respectively, and differed significantly (G = 19.59, df = 2, P < 0.0001). The three populations were not significantly different for head diameter and ray length (Table 2).

TABLE 2.—Means (\pm SE) of traits measured in the natural populations. Means having different superscripts are different based on a Tukey HSD Multiple Comparison test ($P < 0.05$). F-values are from ANOVA

Trait	Population				F
	A	B	I		
Number of shoots	2.7 ^C \pm 0.1	8.1 ^A \pm 0.4	3.7 ^B \pm 0.2		98.6****
Leaf length (cm)	6.51 ^B \pm 0.11	6.37 ^B \pm 0.12	12.34 ^A \pm 0.17		618.16****
Leaf width (cm)	0.68 ^B \pm 0.01	0.71 ^B \pm 0.01	0.82 ^A \pm 0.01		38.88****
Leaf shape	9.93 ^B \pm 0.15	9.16 ^C \pm 0.15	15.96 ^A \pm 0.25		387.84****
Number of flowerstalks	1.6 ^C \pm 0.1	3.5 ^A \pm 0.3	2.5 ^B \pm 0.2		15.3****
Flowerstalk length (cm)	29.23 ^B \pm 1.3	28.14 ^B \pm 0.54	43.38 ^A \pm 0.88		128.54****
Disc diameter (cm)	1.00 ^A \pm 0.06	0.92 ^B \pm 0.02	0.92 ^{AB} \pm 0.03		1.33
Ray length (cm)	1.83 ^A \pm 0.10	1.93 ^A \pm 0.05	1.86 ^A \pm 0.05		0.61
Number of seeds per head	80.7 ^A \pm 9.6	96.0 ^A \pm 2.9	74.4 ^A \pm 3.0		13.2****
Seed weight (mg)	0.603 ^B \pm 0.100	0.775 ^{AB} \pm 0.030	0.863 ^A \pm 0.040		4.961**

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$
Sample sizes: number of shoots, leaf length, leaf width, and leaf shape ($n = 750$); number of flowerstalks ($n = 359$); flowerstalk length ($n = 239$); disc diameter and ray length ($n = 134$); number of seeds per head and seed weight ($n = 198$)

Population B had a significantly greater mean number of flowerstalks/plant while population I had the longest mean flowerstalk length (cm). There were significant site effects for mean number of seeds per head and seed weight. Overall, population B plants had the greatest number of flowerstalks and number of seeds per head.

TRANSPLANT GARDEN EXPERIMENT
MATERIALS AND METHODS

To test the hypotheses that competition or nutrient availability were limiting the local distribution and abundance of *Coreopsis lanceolata* populations, two transplant gardens were established. The first garden, Allegan Garden (AG), was located 20 m from the center of population A near the edge of the woods. The area was dominated by monocots, mainly *Carex pensylvanica*, *Panicum depauperatum*, *P. commonsianum* and *Agropyron repens* and no *Coreopsis lanceolata* naturally occurred there. The second garden, Loudon Garden (LG), was located in Loudon Field (T1S R9W Sect5), an old field last cultivated in 1951 (W.K. Kellogg Biological Station, Hickory Corners, Michigan, Stergios, 1970). This field was chosen because *C. lanceolata* had existed here during the early years of abandonment but was now absent (Steve Tonsor and Kay Gross, pers. comm.). Loudon field sloped from a xeric sandy area down to a more mesic area. The garden was located in the xeric area dominated by *Andropogon scoparius*, *Hieracium pratense*, *Rumex acetosella*, *Antennaria neglecta* and *Solidago nemoralis*.

The ramets for this experiment came from 180 genets randomly sampled from population A. The genets were washed, separated into two ramets, and weighed. Each ramet consisted of one shoot and a small amount of rhizome and root material. On 25–26 May 1989, 90 ramet pairs were transplanted into each of the two gardens. Each garden consisted of 30 1 m \times 1 m blocks arranged in three 1 m \times 10 m rows, and separated by 1 m wide walkways. Each block consisted of six treatments, two levels of competition (competition and no competition) and three levels of nutrients (ambient, medium and high) in a factorial com-

bination. Competition treatments were accomplished by randomly dividing each block into two 0.5 m × 1 m halves, one half left "as is" and the other half clipped to ground level of all standing vegetation. Competition plots were continuously clipped throughout the study whenever any regrowth appeared. The nutrient treatments were ambient, medium (95.5 g/m² Osmocote® 14-14-14 NPK), and high (382 g/m² Osmocote®) (based on levels in Goldberg and Miller, 1990); locations of nutrient treatments were randomized within half-blocks. For each nutrient treatment, a 10-cm diam ring was centered at 20 cm, 50 cm or 80 cm from the top of a block and the fertilizer spread evenly throughout the area of the ring. Genets were paired across competition treatments. Genets were randomized with respect to nutrient treatments because small plant size made it impossible to obtain six ramets from a genet. These nutrient treatments were reapplied to all living plants in June 1990. There were 30 ramets/treatment/garden for a total of 360 ramets.

In order to determine vegetation composition of the gardens, the vegetation clipped from each no-competition block was separated into monocots and dicots, bagged, dried at 65 C for 48 h, and weighed. Solar irradiance soil moisture and soil nutrients were measured in the gardens. Light measurements were recorded at plant level of *Coreopsis lanceolata* in both competition and no-competition blocks and at Allegan on 7 June 1990 at 10:30 A.M. and 1:15 P.M. and at Loudon on 8 June 1990 at 11:30 A.M. and 2:15 P.M. using the methods described above. Soil moisture was measured in each garden by placing six pairs of Bouyoucos blocks at root depth, half in competition blocks and half in no-competition blocks, with two pairs in each row and measurements were made weekly. Soil composition was determined as before from samples taken from each garden on 9 June 1990. In each garden, soil cores were removed from four blocks in which all plants had died, six samples per block, one from each treatment. These blocks were chosen because we did not want to disturb any living plants and interfere with the treatments. All soil samples were analyzed as above.

To quantify treatment effects, we measured survivorship, growth rate, morphology and reproductive success during the summers of 1989 and 1990. Survivorship was determined August 1989, June 1990 and August 1990. Growth rate was measured by counting the number of leaves for each ramet weekly for 8 wk beginning 8 June 1989; number of leaves was highly correlated with total plant biomass ($r = 0.90$, $df = 105$, $P < 0.0001$). At the end of 8 wk we measured length and width of the three longest leaves and specific leaf weight. As plants flowered we measured number of flowerstalks, flowerstalk length, number of heads, head diameter and ray length. Heads were bagged, seeds collected and number of seeds per head and seed weight were determined. On ramets surviving to 1990, we measured number of shoots and leaves and length and width of the three longest leaves. In late August 1990, we recorded the final number of leaves and shoots. All living ramets were removed from the gardens with rhizomes and most roots intact. Each ramet was divided into shoots and roots, dried at 60 C, and weighed.

Statistical analyses were carried out using the SAS (SAS Institute Inc., 1985) and SYSTAT (Wilkinson, 1987) statistics packages. SAS procedure GLM was used for 3-way ANOVAS using type III sums of squares and for repeated-measures MANOVAS. A repeated-measures MANOVA was used to analyze the growth data for plants that were measured more than once (Potvin and Lechowicz, 1990). The multivariate test was used to test if the growth curves have the same shape, because these growth curves violated the assumption of sphericity (homogeneity of the variance/covariance matrix) which must be met to use the univariate test. The MANOVA consisted of a factorial model with site, competition and nutrients all treated as fixed effects and initial ramet weight as a covariate. SYSTAT was used for basic statistics, G-tests, 3-way ANOVAS, and multiple comparison tests. In order to meet statistical assumptions, number of shoots (1990) was square-root

TABLE 3.—Environmental parameters (means ± SE) measured in the experimental gardens; soil moisture (n = 167), solar irradiance (n = 24), pH and soil nutrients (ppm) (n = 48), and vegetational composition (n = 60). F-values are from ANOVA

Trait	Site		F
	Louden garden	Allegan garden	
% soil moisture	84.4 ± 2.1	80.4 ± 2.3	1.67
% full sunlight with competition	51.7 ± 5.0	39.8 ± 8.6	†
% full sunlight with no-competition	93.0 ± 2.5	65.3 ± 12.1	†
pH	5.17 ± 0.02	5.28 ± 0.04	6.90**
NO ₃ ⁻	0.046 ± 0.014	0.158 ± 0.053	4.13*
NH ₄ ⁺	3.581 ± 0.298	3.360 ± 1.269	0.29
P ⁻⁴	7.2 ± 1.5	69.7 ± 11.3	120.7****
K ⁺	62.3 ± 7.1	19.0 ± 2.5	133.6****
Ca ⁺²	315.8 ± 27.9	144.5 ± 19.4	101.8****
Mg ⁺²	41.4 ± 5.4	11.5 ± 0.0	124.6****
Monocots (g)	30.70 ± 3.17	21.90 ± 0.95	7.18**
Dicots (g)	32.30 ± 3.90	8.00 ± 0.97	36.61****

* P < 0.05; ** P < 0.01; *** P < 0.001; **** P < 0.0001

† See text

transformed; number of leaves (1990), number of flowerstalks (1990), shoot dry weights, root dry weights and total dry weight were log₁₀ transformed.

RESULTS

Environmental parameters.—The environments of the gardens differed. For light levels, there were significant site differences (ANOVA F = 6.27, df = 1,44, P < 0.016) and highly significant competition effects (ANOVA F = 17.81, df = 1,44, P < 0.0001) but there was no significant interaction (ANOVA F = 0.996, df = 1,44, P < 0.324); LG had higher light levels (Table 3). Light levels in AG in the no-competition and competition treatments were 23% and 53%, respectively, lower than those in the Allegan natural populations (Tables 1 and 3). Soil moisture was similar between the gardens and was approximately double that of the Allegan natural populations (Tables 1 and 3). There were significant site differences in soil nutrient composition (Table 3). LG had higher levels of K⁺, Ca⁺², and Mg⁺², while AG had a higher pH and P⁻⁴ concentrations. There was no significant difference in the nutrient composition of the soil inside population A, the no-competition-ambient treatment in the Allegan garden, and an area immediately outside of population A. With regard to vegetation, LG had a significantly greater mean and range of biomasses of both monocots and dicots (monocots—Louden 5.4–77.4 g; Allegan 12.6–33.4 g; dicots—Louden 6.7–107.8 g; Allegan 1.2–21.2 g).

Survivorship.—Survivorship over the 2 yr was affected by site and competition (Table 4). Independent of treatments, plants in LG had a greater overall survivorship to the end of the experiment than those in AG (43% vs. 20%, respectively) (G = 49.1, df = 10, P < 0.0001). Plants in the no-competition treatment had more than twice the survivorship of plants in the competition treatment (45% vs. 17%, respectively) (G = 26.8, df = 10, P < 0.005). The greatest mortality occurred over the winter (54.5%). Size affected survivorship; plants surviving the winter had more leaves in August 1989 (7.8 ± 0.3) than those that died (4.8 ± 0.2) (F = 23.5, df = 1,207, P < 0.0001).

Growth rate.—There were significant differences between treatments in both the means

TABLE 4.—Percentage survivorship with respect to site, competition and nutrient effects in the two transplant gardens. The values given for June 1989 are the initial number surviving transplantation; values thereafter are percentage survivorship to that time period. *See* text for significance tests

Site	Treatment		June 1989	August 1989	June 1990	August 1990
	Competition	Nutrient				
Louden garden	Comp.	Ambient	28	68	36	32
	Comp.	Medium	28	82	29	18
	Comp.	High	29	66	28	28
	No Comp.	Ambient	29	79	66	66
	No Comp.	Medium	30	80	53	53
	No Comp.	High	29	97	69	59
Allegan garden	Comp.	Ambient	27	44	4	4
	Comp.	Medium	27	48	4	4
	Comp.	High	28	61	21	18
	No Comp.	Ambient	26	73	12	15
	No Comp.	Medium	28	82	32	39
	No Comp.	High	30	87	37	37

and the shapes of the growth curves (Table 5). Tests for differences in treatment means averaged over the entire 8-wk period are shown as between-subject effects. Significant differences in grand means were found for the effects of site, competition, site-competition and nutrients. Ramets in the LG no-competition treatments had the most leaves (Fig. 1a) and increased nutrient additions corresponded with increased number of leaves (Fig. 1b). Tests for time*treatment effects determined if the curves have the same shape and are shown as within-subject effects. Significant differences in growth curves were found for the effects of site, competition, and nutrients. LG no-competition plants had the greatest growth as did those plants with the high nutrient treatments. LG no-competition plants showed increased growth over the entire 8 wk compared to periods of decreased growth in the other three treatments (Fig. 1a). High nutrient treatments had the greatest initial effect on growth, seen during the 1st 3 wk (Fig. 1b), whereas ambient and medium nutrient treatments both resulted in decreased growth between weeks 2 and 3. Over the 8-wk period, plants in ambient nutrient treatments showed little growth (Fig. 1b).

Growth patterns.—Patterns of growth differed over the 2 growing seasons in both leaf and shoot production. At the end of the summer 1989, the number of leaves per plant in both gardens ranged from 2–20 in LG and from 1–13 in AG and the majority of plants had only one shoot. Plants which survived the winter had increased leaf and shoot production the next summer (Table 8).

Morphological traits.—The treatments affected the majority of morphological traits (Tables 6, 7 and 8). In 1989, LG no-competition treatment plants had the greatest number of leaves, widest leaves and greatest specific leaf weight (Tables 6 and 8). Competition effects were apparent in LG; means differed significantly between competition treatments (Table 8). In 1990, LG no-competition plants had the greatest leaves, shoots, leaf width and total biomass (Table 8). The gardens differed in number of leaves, leaf length and leaf width in 1989 (Table 6) and in 1990 (Table 7). Competition had significant effects on number of leaves and leaf shape in 1989 and 1990 (Tables 6 and 7), with larger plants in the no-competition treatment. Significant nutrient effects existed for number of leaves, leaf length and leaf width in the 1st year only (Table 6). There were significant garden effects on aboveground biomass and competition and garden-competition interaction effects on above- and below-

TABLE 5.—Repeated-measures MANOVA of 1989 growth measured as number of leaves. The effects are computed as either (A) between subjects or (B) within subjects

A) Between subjects (Comparison of grand means)				
Sources	MS	F	df	P
Initial weight	468.1	21.1	1	0.0001
Site	842.8	37.9	1	0.0001
Competition	411.5	18.5	1	0.0001
Site•Comp.	272.4	12.3	1	0.0006
Nutrients	359.5	16.2	2	0.0001
Site•Nut.	42.1	1.9	2	0.1533
Comp•Nut.	6.3	0.3	2	0.7537
Site•Comp•Nut.	3.5	0.2	2	0.8537
B) Within subjects (Comparison of shapes of growth curves)				
Sources	Pillai's trace	F	df	P
Time	0.159	5.6	7	0.0001
Time•Weight	0.132	4.5	7	0.0001
Time•Site	0.152	5.3	7	0.0001
Time•Comp.	0.091	3.0	7	0.0055
Time•Site•Comp.	0.042	1.3	7	0.2582
Time•Nut.	0.144	2.3	14	0.0047
Time•Site•Nut.	0.074	1.1	14	0.3217
Time•Comp.•Nut.	0.046	0.7	14	0.7705
Time•Site•Comp.•Nut.	0.029	0.4	14	0.9628

ground biomasses (Table 7); ramets in LG no-competition treatments had the greatest biomasses (Table 8). The two traits showing no significant effects were leaf width in 1990 and shoot:root ratio. At the end of both years, the plants with the greatest biomass were those in the LG no-competition treatments; the number of both leaves and shoots was approximately three times that of the other treatments.

TABLE 6.—Results of ANOVAs for leaf traits measured in summer 1989. Values given are Mean Squares

Source of variation	df	No. of leaves	Leaf length	Leaf width	Leaf shape	Specific leaf weight
Initial weight	1	1.57	35.82*	0.11	41.82**	0.00
Site	1	302.01***	347.78***	4.31***	3.15	0.02
Competition	1	149.40***	11.90	0.64*	171.58***	1.97**
Site•Comp.	1	69.42***	4.30	0.26	50.39***	0.67*
Nutrients	2	57.54***	69.08***	0.89***	0.85	0.18
Site•Nut.	2	3.60	6.27	0.09	0.65	0.82
Comp.•Nut.	2	4.93	1.96	0.002	0.60	0.16
Site•Comp.•Nut.	2	0.92	5.48	0.01	1.38	0.21
Error		7.81	8.66	0.10	4.74	0.17
R ²		0.313	0.236	0.272	0.238	0.201

* P < 0.05; ** P < 0.01; *** P < 0.001

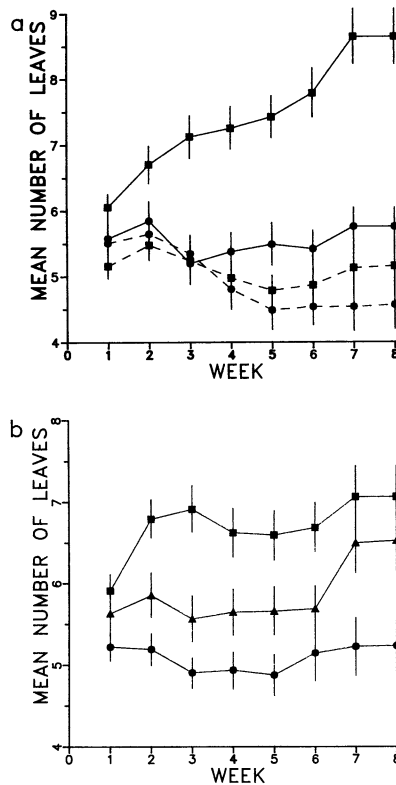


FIG. 1.—Growth curves of the weekly mean number of leaves of plants in the transplant gardens in the summer of 1989; bars indicate standard errors. a. The effects of site and competition: Allegan (dashed line), Loudon (solid line), No Comp. (square), and Comp. (circle). b. The effects of nutrients: ambient (circle), medium (triangle), and high (square). Flowering was occurring from weeks 2–6

Flowering traits.—More flowering occurred in LG both years. The percentage of individuals flowering for LG and AG was 24.4% and 5.6% in 1989 and 54.1% and 27.3% in 1990, respectively. There were significant site effects on percentage flowering both seasons at the end of 1989 ($G = 29.1$, $df = 10$, $P < 0.005$), in June 1990 ($G = 27.8$, $df = 15$, $P < 0.05$), and in August 1990 ($G = 43.8$, $df = 16$, $P < 0.001$). A significant competition effect on flowering was only apparent in August 1990 ($G = 44.3$, $df = 16$, $P < 0.001$). Only site differences were compared for flowering traits due to the small number of plants that flowered in the competition treatments. In 1989, plants in LG had the greater flowerstalk length, ray length, number of seeds/head, and seed weight (Table 9). In 1990, the greater percentage flowering in LG was evident by the greater number of flowerstalks/plant, seeds/head, and seed weight (Table 9). Overall, plants in the LG no-competition treatments were most successful; they had the greater survivorship, growth rate and percentage flowering.

DISCUSSION

Coreopsis lanceolata is found in habitats with low soil nutrients and soil moisture (Table 1). A trade-off between tolerance to unproductive conditions and competitive ability apparently is important in determining this distribution pattern. The ability of this species to

TABLE 7.—Results of ANOVAs for leaf traits and biomass measurements in summer 1990. Values given are Mean Squares

Source of variation	No. of leaves	No. of shoots	Leaf length	Leaf width	Leaf shape	Shoot dry wt.	Root dry wt.	Total dry wt.	Shoot : Root ratio
Initial weight	0.18	0.002	0.00	0.04	2.46	0.08	0.01	0.08	11.02
Site	4.60**	2.58*	45.47***	0.27*	7.39	7.59**	3.28	6.41**	11.09
Competition	7.11***	3.91**	6.98	0.09	61.78**	5.20*	5.14*	5.04*	0.11
Site•Comp.	3.63**	2.51*	7.03	0.00	12.70	9.53**	6.19**	7.18**	0.50
Nutrients	1.00	0.27	11.48	0.17	15.61	2.23	0.70	1.79	6.34
Site•Nut.	0.05	0.003	9.70	0.10	5.60	0.64	0.50	0.64	1.17
Comp.•Nut.	0.92	0.30	8.38	0.01	12.74	1.66	1.48	1.33	1.12
Site•Comp.•Nut.	0.41	0.09	7.84	0.04	7.50	0.89	0.66	0.93	1.87
Error	145.3	2.40	5.50	0.065	9.46	1.21	0.981	0.983	3.54
R ²	0.182	0.163	0.294	0.191	0.169	0.325	0.360	0.417	0.133

* P < 0.05; ** P < 0.01; *** P < 0.001

TABLE 8.—Means (\pm SE) for leaf traits measured in both 1989 and 1990. Means having different superscripts are different based on a Newman-Keuls Multiple Comparison test ($P < 0.05$)

Trait	Allegan Garden		Louden Garden	
	Comp.	No Comp.	Comp.	No Comp.
1989*				
No. leaves	4.6 ^A \pm 0.4	5.2 ^A \pm 0.4	5.8 ^B \pm 0.3	8.7 ^C \pm 0.4
Length (cm)	5.4 ^A \pm 0.34	5.2 ^A \pm 0.27	8.2 ^C \pm 0.49	7.4 ^B \pm 0.44
Width (cm)	0.6 ^A \pm 0.03	0.6 ^A \pm 0.03	0.8 ^B \pm 0.04	1.0 ^C \pm 0.06
Shape	9.1 ^C \pm 0.30	8.3 ^B \pm 0.26	10.3 ^D \pm 0.41	7.4 ^A \pm 0.20
Specific weight (mg)	1.8 ^A \pm 0.07	1.9 ^B \pm 0.04	1.7 ^C \pm 0.06	2.1 ^D \pm 0.06
1990**				
No. shoots	1.6 ^A \pm 0.30	2.2 ^A \pm 0.27	1.7 ^A \pm 0.28	6.2 ^B \pm 0.78
No. leaves	11.7 ^A \pm 2.56	19.4 ^B \pm 2.26	14.3 ^A \pm 2.33	62.8 ^C \pm 7.48
Length (cm)	7.4 ^A \pm 0.68	6.7 ^A \pm 0.41	8.9 ^C \pm 0.41	8.9 ^C \pm 0.40
Width (cm)	0.7 ^A \pm 0.07	0.8 ^B \pm 0.05	0.8 ^B \pm 0.05	0.9 ^C \pm 0.04
Shape	11.4 ^C \pm 1.17	8.4 ^A \pm 0.44	11.5 ^C \pm 0.71	10.2 ^B \pm 0.42
Dry wts. (g)				
Shoot	0.3 ^A \pm 0.06	0.5 ^A \pm 0.09	0.5 ^A \pm 0.10	2.1 ^B \pm 0.30
Root	0.1 ^A \pm 0.02	0.3 ^A \pm 0.04	0.2 ^A \pm 0.03	0.8 ^B \pm 0.11
Total	0.4 ^A \pm 0.08	0.7 ^A \pm 0.12	0.7 ^A \pm 0.13	2.9 ^B \pm 0.40
Shoot : Root	2.0 \pm 0.27	1.8 ^A \pm 0.19	2.9 \pm 0.79	2.5 \pm 0.15
* Sample sizes:	AG-Comp.	AG-No comp.	LG-Comp.	LG-No comp.
No. lvs. length, width, shape	37	62	53	72
Specific wt.	24	47	44	66
** Sample sizes:	AG-Comp.	AG-No comp.	LG-Comp.	LG-No comp.
Length, width, shape	7	23	26	53
All others	7	26	22	52

do well in unproductive conditions is demonstrated by a comparison among the three natural populations. The two Michigan populations had a low density of co-occurring species. The Indiana population differed in having a high density of other species, greater percent soil moisture and lower light levels. These factors suggest that Indiana is the most productive site of the three. Yet, plants in populations A and B had a greater percentage of flowering. Plants in population B had the greatest number of flowerstalks, seeds per head and seed weight (Table 2).

The transplant garden experiments showed that *Coreopsis lanceolata* does better in areas where it is not found naturally if competitors are removed (Table 8, Fig. 1a). Loudon Field was more productive and more heavily vegetated than the garden area in Allegan. When competitors were removed, plants were most successful in Loudon Garden. Growth rate and survivorship were greatly increased in the absence of competitors and with the addition of nutrients. Thus, this field is a more favorable site for *C. lanceolata* even though it does not now occur here. *Coreopsis lanceolata* is capable of growth in more fertile soils but cannot compete. Different treatment effects were important at different stages of the life cycle. Growth soon after transplanting was affected by nutrient additions and competition. Nutrient effects were transient, which may have resulted from the poor soil quality; plants may have

TABLE 9.—Means (\pm SE) for flowering traits in the gardens measured in both 1989 and 1990. F-values are from ANOVA

Traits	Gardens 1989				Gardens 1990			
	Allegan	n	Louden	F	Allegan	n	Louden	F
No. of flowerstalks	1.0 \pm 0.0	10	1.4 \pm 0.09	49	0.5 \pm 0.15	33	1.6 \pm 0.34	80
Flowerstalk length (cm)	19.5 \pm 1.7	10	26.9 \pm 0.76	49	36.4 \pm 3.4	10	35.7 \pm 1.1	50
Disc diameter (cm)	0.7 \pm 0.05	6	0.9 \pm 0.03	49	1.0 \pm 0.08	10	1.1 \pm 0.03	50
Ray length (cm)	0.9 \pm 0.06	6	1.5 \pm 0.05	49	1.7 \pm 0.08	10	1.9 \pm 0.05	50
No. seeds per head	20.6 \pm 5.3	5	46.1 \pm 4.0	45	38.9 \pm 5.5	13	87.8 \pm 6.3	40
Seed weight (mg)	0.2 \pm 0.04	5	0.8 \pm 0.05	43	1.0 \pm 0.16	13	1.5 \pm 0.09	40

* P < 0.05; ** P < 0.01; *** P < 0.0001

incorporated any fertilizer additions into their tissues soon after application. Survivorship, growth after plant establishment and reproduction were affected both years by site differences and competition. Plants in LG no-competition treatments had the greatest survivorship, were the largest, and had the greatest seed production and seed weight.

The habitat specificity of *Coreopsis lanceolata* appears to be related to its tolerance to low nutrient availability. Grime and Hunt (1975) showed a strong correlation between a slow growth rate and tolerance of mineral deficiencies. There is a tendency for plants found in low nutrient environments to possess characteristic features. The most conspicuous features include: small size, tendency to have small, leathery, long-lived leaves, and high root:shoot ratios. Because ramets have relatively small shoot systems, plant populations on nutrient-poor soils tend to be open, with bare gaps between plants. These morphological and habitat features are characteristic of *C. lanceolata*. Even stronger evidence that the distribution of *C. lanceolata* is based on a trade-off between tolerance and competitive ability would be a reciprocal transplant experiment of this species' competitors, especially *Carex pensylvanica*, into areas now dominated by *C. lanceolata*. We predict that the other species would grow poorly in those areas even in the absence of competition by *C. lanceolata*.

Several studies have found support for Grime's hypothesized trade-off between competitive ability and survival in stressful habitats (Willis, 1963; Reader and Watt, 1981; Rabinowitz *et al.*, 1984; Wilson and Keddy, 1986a; Bauder, 1989; McGraw and Chapin, 1989; Reader and Best, 1989; Reader, 1990), although only one study (Gurevitch, 1986) showed that the nonstress-tolerant competitors were truly limited by abiotic factors and not competition. Such a trade-off appears to be responsible for the restricted but locally abundant distribution of *Coreopsis lanceolata* and to be a general characteristic of stress-tolerant species. This trade-off can be seen in the fact that restricted locally abundant species often specialize on stressful habitats (Rabinowitz *et al.*, 1986). Stress tolerance allows for local abundance of populations and competition restricts the population to specific habitats. Not all species exhibiting this type of rarity are stress-tolerant; for example, weeds are also restricted locally abundant species. Weeds are classified as ruderal strategists according to Grime's C-S-R model (1977). The main difference between stress-tolerators and ruderals is the type of stress imposed, that is, unproductive habitats vs. disturbed habitats. However, in both cases the distribution and abundance appears to be determined by the trade-off between physiological tolerances and competitive abilities.

Acknowledgments.—We thank Steve Banovetz for extensive assistance with the field work and the staffs at Indiana Dunes National Lakeshore, Allegan State Game Area and Kellogg Biological Station for their assistance and cooperation. Kay Gross provided needed advice and counsel. The comments of Gabriel Holbrook, Carl von Ende and three anonymous reviewers greatly improved the manuscript. Partial funding was provided by the Graduate School of Northern Illinois University.

LITERATURE CITED

- BAUDER, E. T. 1989. Drought stress and competition effects on the local distribution of *Pogogyne abramsii*. *Ecology*, **70**:1083–1089.
- CRAWLEY, M. J. 1986. Life history and environment, p. 253–290. *In*: M. J. Crawley (ed.). *Plant ecology*. Blackwell Scientific Publications, Boston, Mass.
- FOLGATE, L. A. 1991. Competition and nutrient effects on the local distribution and abundance of *Coreopsis lanceolata*. Master's Thesis, Northern Illinois University, DeKalb. 69 p.
- FURR, G. F. 1981. Soil survey of Porter County, Indiana. U.S. Dep. Agric. and Soil Conserv. Serv. in coop. with Purdue University Agric. Exp. Sta., Indiana Department of Natural Resources, Soil and Water Conservation Committee. 172 p.
- GLEASON, H. A. AND A. CRONQUIST. 1963. *Manual of vascular plants of northeastern United States and adjacent Canada*. D. Van Nostrand Co., New York, N.Y. 810 p.

- GOLDBERG, D. E. AND T. E. MILLER. 1990. Effects of different resource additions in species diversity in an annual plant community. *Ecology*, **71**:213–225.
- AND P. A. WERNER. 1983. Equivalence of competitors in plant communities: a null hypothesis and a field experimental approach. *Am. J. Bot.*, **70**:1098–1104.
- GRACE, J. B. 1990. On the relationship between plant traits and competitive ability, p. 51–65. *In*: J. B. Grace and D. Tilman (eds.). *Perspectives on plant competition*. Academic Press, New York.
- GRIME, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Am. Nat.*, **111**:1169–1194.
- . 1979. *Plant strategies and vegetation processes*. John Wiley and Sons, New York, N.Y. 222 p.
- AND R. HUNT. 1975. Relative growth-rate: its range and adaptive significance in a local flora. *J. Ecol.*, **63**:393–422.
- GUREVITCH, J. 1986. Competition and the local distribution of the grass *Stipa neomexicana*. *Ecology*, **67**:46–57.
- KENOYER, L. A. 1934. Forest distribution in southwestern Michigan as interpreted from the original land survey (1826–32). *Pap. Mich. Acad. Sci. Arts Lett.*, **19**:107–111.
- KNAPP, B. D. 1987. Soil survey of Allegan County, Michigan. U.S. Dep. Agric. Soil Conserv. Serv. in coop. with Michigan Agric. Exp. Stn. 176 p.
- KREBS, C. J. 1972. *Ecology: the experimental analysis of distribution and abundance*. Harper & Row, Publishers, New York, N.Y. 800 p.
- LEVITT, J. 1980. Responses of plants to environmental stresses, Vol. II. Water, radiation, salt and other stresses. Academic Press, New York. 607 p.
- MCGRAW, J. B. AND F. S. CHAPIN. 1989. Competitive ability and adaptation to fertile and infertile soils in two *Eriophorum* species. *Ecology*, **70**:736–749.
- POTVIN, C. AND M. J. LECHOWICZ. 1990. The statistical analysis of ecophysiological response curves obtained from experiments involving repeated measures. *Ecology*, **71**:1389–1400.
- RABINOWITZ, D. AND J. K. RAPP. 1981. Dispersal abilities of seven sparse and common grasses from a Missouri prairie. *Am. J. Bot.*, **68**:616–624.
- , J. K. RAPP AND P. M. DIXON. 1984. Competitive abilities of sparse grass species: means of persistence or cause of abundance. *Ecology*, **65**:1144–1154.
- , S. CAIRNS AND T. DILLON. 1986. Seven forms of rarity and their frequency in the flora of the British Isles, p. 182–205. *In*: M. E. Soule' (ed.). *Conservation biology: the science of scarcity and diversity*. Sinauer, Sunderland, Mass.
- READER, R. J. 1990. Competition constrained by low nutrient supply: an example involving *Hieracium floribundum* Wimm & Grab. (Compositae). *Func. Ecol.*, **4**:537–577.
- AND B. J. BEST. 1989. Variation in competition along an environmental gradient: *Hieracium floribundum* in an abandoned pasture. *J. Ecol.*, **77**:673–684.
- AND W. H. WATT. 1981. Response of Hawkweed (*Hieracium floribundum*) patches to NPK fertilizer in an abandoned pasture. *Can. J. Bot.*, **59**:1944–1949.
- SAS INSTITUTE INC. 1985. SAS user's guide: statistics, version 5. SAS Institute, Inc., Cary, N.C. 956 p.
- SIBLY, R. M. AND J. P. GRIME. 1986. Strategies of resource capture by plants—evidence for adversity selection. *J. Theor. Biol.*, **118**:247–250.
- STERGIOS, B. G. 1970. Seed dispersal, seed germination and seedling establishment of *Hieracium aurantiacum* in an old-field community. Masters thesis, Michigan State University, East Lansing 79 p.
- SWINK, F. AND G. WILHELM. 1979. Plants of the Chicago region. The Morton Arboretum, Lisle, Ill. 922 p.
- TILMAN, D. 1982. *Resource competition and community structure*. Princeton University Press, Princeton, N.J. 296 p.
- WILKINSON, L. 1987. SYSTAT: the system for statistics. SYSTAT, Evanston, Ill. 822 p.
- WILLIS, A. J. 1963. Branton burrows: the effects on the vegetation of the addition of mineral nutrients to the dune soils. *J. Ecol.*, **51**:353–374.

- WILSON, S. D. AND P. A. KEDDY. 1986a. Species competitive ability and position along a natural stress/disturbance gradient. *Ecology*, **67**:1236–1242.
- AND ———. 1986b. Measuring diffuse competition along an environmental gradient: results of a shoreline plant community. *Am. Nat.*, **12**:862–869.

SUBMITTED 5 JUNE 1991

ACCEPTED 22 MAY 1992