Competition vs. Facilitation of Tree Seedling Growth and Survival in Early Successional Communities

Alan R. Berkowitz; Charles D. Canham; Victoria R. Kelly

COMPETITION VS. FACILITATION OF TREE SEEDLING GROWTH AND SURVIVAL IN EARLY SUCCESSIONAL COMMUNITIES[1]

ALAN R. BERKOWITZ, CHARLES D. CANHAM, AND VICTORIA R. KELLY
Institute of Ecosystem Studies, Box AB, Millbrook, New York 12545 USA

Abstract. Competition has been widely assumed to be one of the principal mechanisms underlying the resistance of shrub and herbaceous communities to invasion by trees. However, there are potential mechanisms by which low-growing species, particularly in physically stressful sites, could enhance growth or survival of tree seedlings (facilitation). The balance of inhibition and facilitation will determine the net effects of a community on tree seedling growth and survival. We conducted a large-scale field experiment to quantify the net effects of four major physiognomic types (shrub thickets, shrubby grass meadows, grass meadows, and herbaceous meadows) commonly found both in old fields and along utility rights-of-way on the growth and survival of three common tree species: sugar maple (*Acer saccharum*), red maple (*Acer rubrum*), and gray birch (*Betula populifolia*). The eight community types were distributed in 23 sites representative of the range of upland environments present in the Hudson Valley of New York. Growth of planted seedlings of all three tree species was uniformly slow in all of the community types and environments. In all cases, the net effect of intact vegetation was to inhibit the growth of the tree seedlings. The intensity of competition varied substantially among the 23 sites but was not consistently related either to community type or to the biomass of the intact community. Instead, variation in the intensity of competition was related to the underlying favorability of the site for the growth of a particular target tree species. On physically unfavorable sites, tree seedlings grew slowly because of physical stress rather than competition with the intact vegetation. As site quality increased, the intensity of competition increased. Thus, competition and physical stress traded off along a site–quality gradient, with the result that tree seedling growth was uniformly slow. In contrast to the results for growth, there were cases in which the survival of these young tree seedlings was enhanced (facilitated) by the presence of intact vegetation. In particular, survival of the highly shade tolerant but drought intolerant sugar maple seedlings was facilitated by intact vegetation at many sites, especially for the 1988 cohort, which experienced a drought during its first growing season. Since we detected no consistent differences among communities in the *intensity* of competitive effects on seedling growth, the apparent differences among early successional communities in resistance to tree seedling establishment may be caused by variation in the *duration* of competition resulting from differences in height and canopy structure of the low-growing communities.

Key words: Acer rubrum; Acer saccharum; Betula populifolia; facilitation; neighbor analysis; plant competition; plant succession; productivity gradient; tree seedlings.

INTRODUCTION

For the past 20 yr, one of the most active debates among plant ecologists has been how the intensity of competition varies along environmental gradients and associated gradients in community productivity. Grime (1973, 1979) and others (e.g., Huston 1979, Keddy 1989) have proposed that the intensity of competition increases with increasing site quality, while Tilman (1988) and others (e.g., Newman 1973, Grubb 1985) have proposed that competition is intense even in harsh environments. Much of the literature on plant competition consists of case studies, frequently involving only a single site. As a result, there have been few

empirical data from which to develop generalizations about how the intensity of competition varies among different communities and environments. The empirical studies needed to resolve this debate have only recently begun to appear (e.g., Wilson and Tilman 1991).

While most studies of plant–plant interactions focus on the negative effects of competition, it is clear that there are processes by which intact communities can have positive effects on the performance of individual plants ("facilitation"). For example, desert shrubs often provide favorable sites for establishment of other species (Muller 1953, Muller and Muller 1956, Everett et al. 1986). While facilitation is widely assumed to be an important component of primary succession following colonization of a new substrate (Connell and Slatyer 1977), there is still debate over whether or not

facilitation is common during the secondary succession that occurs, for example, following the abandonment of land from agriculture (Pickett et al. 1987).

The resolution of this debate is likely to lie in determining the relative importance and underlying causes of both facilitation and inhibition. Its significance goes beyond our understanding of the natural dynamics of plant communities and applies to our ability to manage vegetation for desired goals. For example, competition between tree seedlings and low-growing plant communities has been widely assumed to be the principal mechanism in resistance by right-of-way vegetation to invasion by trees (e.g., Niering and Goodwin 1974, Bramble and Byrnes 1976). However, knowing under what circumstances facilitation, rather than inhibition, might occur will be essential in devising comprehensive management plans. Likewise, an understanding of the underlying mechanisms should help to identify specific management practices that might be used to maximize competition and minimize facilitation of seedling growth.

The effects of intact vegetation on tree seedling performance can be expected to vary significantly among tree species due to differences in the physiological and morphological traits that determine their responses to environmental conditions. As a result, an evaluation of the resistance of a shrub or herbaceous community to invasion by trees must take into account the characteristics of not only the low-growing community and its environment, but also the traits of the tree species dispersing into the community.

In this paper, we present the results of a large-scale field experiment designed to assess the net effects of a wide range of early successional communities, dominated by shrubs and herbaceous species, on the growth and survival of planted tree seedlings. We have deliberately avoided using the term competition at this point, because the research is designed to quantify the net balance of any positive effects of intact communities on seedling performance (facilitation) and the more traditionally recognized, negative, competitive effects (inhibition). This study addresses the following four basic issues:

1) What are the net effects of intact vegetation, compared to clipped sites, on the growth and survival of tree seedlings?

2) Are the net effects of intact vegetation related either to the average biomass of the community or to the biomass of vegetation in the immediate neighborhood of a tree seedling?

3) How do these effects vary among different community types and environments?

4) How do these effects vary among different species of trees?

Our approach was to select study sites that are representative of the major early successional community types common to abandoned agricultural land and rights-of-way in the mid-Hudson Valley of New York

(Canham and Kays 1993). For each community type, we selected sites across a broad range of environments. At each site, we transplanted newly germinated seedlings of three representative tree species into quadrats containing intact, undisturbed vegetation, and into adjacent quadrats from which the low-growing vegetation had been experimentally removed. The net effects of the low-growing vegetation were then assessed by comparing the growth and survival of the tree seedlings in clearings vs. those beneath intact vegetation.

METHODS

Study sites and species

The shrub and herbaceous vegetation of rights-of-way in the Hudson Valley of New York has been classified into 12 distinct community types (Canham and Kays 1993). These communities are quite similar to more traditionally defined old-field communities in terms of species composition and structure. In fact, many shrub and herbaceous communities along rights-of-way are true old fields, abandoned from agriculture either prior to or after construction of the right-of-way. We selected the eight most distinct community types for study, two in each of four major physiognomic types: shrub thickets, shrubby grass meadows, grass meadows, and herbaceous meadows (Table 1). There were six sites for each of the two most common communities: little bluestem (*Schizachyrium scoparium* (Michx.) Nash-Gould) grass meadows and gray dogwood (*Cornus racemosa* Lam.) shrub thickets, and two sites for each of the other six communities. One site for one of the perennial herb communities, purple loosestrife (*Lythrum salicaria* L.) wet meadows, had to be abandoned because it was flooded for too much of the growing season. The sites were chosen to span the full range of upland environmental conditions described in previous studies of these communities in the mid-Hudson Valley of New York. Ten of the 23 sites were located along rights-of-way in Dutchess and Ulster Counties of New York (41°45' to 42°00' N, 73°35' to 74°26' W) and 13 of the sites were located on ≈50-yr-old abandoned fields located within the Mary Flagler Cary Arboretum in Dutchess County (41°50' N, 73°45' W).

We selected three tree species for study: sugar maple (*Acer saccharum* Marsh.), red maple (*Acer rubrum* L.), and gray birch (*Betula populifolia* Marsh.). Red maple is the most common species of tree seedling found in utility rights-of-way in the region (Hill et al. 1994). The other two species have more restricted distributions, gray birch occurring primarily on dry, rocky sites and sugar maple on more mesic sites. The three species span a wide range of shade and drought tolerance. Seeds from regional populations of the three species were purchased each year from a local supplier (Sheffield Seed Co., Locke, New York), stratified, and germinated on sand or wet paper towels under mist. Newly

TABLE 1. The eight old-field community types studied in this experiment in the Hudson Valley, New York, and their four-letter codes. The communities are grouped into the four major physiognomic types they represent. The dominant species for each community are given (from Canham and Kays 1993), along with the range of biomasses of the surrounding vegetation measured at one to six sites studied for each community type. Biomass was not measured at the KAVA sites.

Community type	Code	Physiognomic type	Dominant species	No. sites	Community biomass (g/m²)
Gray dogwood thickets	CORA	Shrub Thicket	*Cornus racemosa, Bromus inermis, Agrostis* sp., *Solidago rugosa, Rubus flagellaris*	6	1455–13 483
Mountain laurel/blueberry thickets	KAVA	Shrub Thicket	*Kalmia latifolia, Myrica asplenifolia, Dennstaedtia punctiloba, Vaccinium angustifolium,* moss	2	. . .
Gray dogwood/grass meadows	GRCO	Shrubby Grass Meadow	*Cornus racemosa, Bromus inermis, Agrostis* sp., *Solidago rugosa,* moss, *Anthoxanthum odoratum*	2	448–487
Rubus/little bluestem meadows	RUSC	Shrubby Grass Meadow	*Rubus flagellaris, Schizachyrium scoparium, Solidago* spp., misc. grass spp., moss	2	181–406
Little bluestem meadows	SCSC	Grass Meadow	*Schizachyrium scoparium,* moss, *Rubus flagellaris*	6	177–494
Little bluestem mossy meadows	SCMO	Grass Meadow	*Schizachyrium scoparium,* moss	2	171–331
Rocky hayscented fern meadows	DEPU	Herbaceous Meadow	*Dennstaedtia punctiloba, Myrica asplenifolia,* rock, moss, *Vaccinium angustifolium*	2	255–361
Loosestrife wet meadows	LYSA	Herbaceous Meadow	*Lythrum salicaria,* moss, *Solidago rugosa, S. graminifolia*	1	630

germinated seedlings were transferred to seedling flats filled with sterilized commercial potting soil (including peat moss for maples). The volume of soil used was kept as small as possible to minimize carryover effects of the growth medium after the seedlings were planted in the field. Seedlings were raised in these flats for 7–9 wk after germination. At the time of planting, seedling height was ≈1 mm for gray birch and ≈4–5 cm for the maples. Two separate cohorts of newly germinated seedlings were planted, one in July 1988 and a second in June 1989. While the date seedlings were transplanted into the field was considerably later than when they germinated, transplant seedling sizes were similar to those of naturally occurring seedlings (Hill et al. 1994).

Plot layout

At each site, four 1.8 × 2.1 m quadrats were located within the intended community type to minimize variation within and between quadrats and to assure ample area with similar vegetation around each quadrat to minimize edge effects. Since quadrats were not randomly placed, they cannot be interpreted as sampling the full range of vegetation at a site; rather, they are representative of the particular community type sampled. To eliminate herbivory by small and large mammals, a large area around the quadrats was fenced to a height of 1.5 m, with a 50 cm wide strip of fine-mesh hardware cloth buried to a depth of 15 cm (where possible). In some sites, all four quadrats were within a

single enclosure; at others, two enclosures were required. The very low rate of seedling herbivory observed suggests that the fences were effective at excluding herbivores.

Two of the quadrats at each site were left undisturbed (INTACT treatment) and two were cleared and kept free of all aboveground vegetation (CLEAR treatment). CLEAR quadrats were hand-clipped to ground level and then raked in the spring of 1988. Glyphosate herbicide (Roundup) was sprayed on resprouting vegetation 2 wk after clipping, followed by spot applications once or twice more as needed. Black plastic was placed over the clipped vegetation in the LYSA (*Lythrum salicaria*) site to suppress regrowth, and seedlings were planted into holes made in the plastic. The perimeter of each CLEAR quadrat was trenched by driving a spade into the ground to a depth of 12–15 cm at the time of seedling planting, and additional regrowth was eliminated by hand removal. CLEAR quadrats were hand-cleared and trenched again at the beginning of the 1989 growing season.

For each cohort, 8–10 seedlings of each species were planted in each quadrat at randomized locations in a grid with ≥15 cm spacing between adjacent seedlings. The location of each seedling was marked with a plastic pot marker to ensure accurate identification of all seedlings, including dead ones.

Data collection

Seedlings.—Growth and survival of each seedling were determined each spring and fall, and seedling

shoot height and biomass were measured at the end of the second growing season for each cohort. At that time, seedlings were cut at ground level and leaves and stems were separated and dried at 60°C for ≥5 d. Shoot dry mass (in milligrams) was determined once drying was complete. The net effect of the intact vegetation on survival was assessed by calculating the difference between the survival of seedlings in CLEAR vs. IN-TACT quadrats. Positive values indicate competition and negative values indicate facilitation of survival. For seedling shoot mass, the difference between seedling sizes in CLEAR vs. INTACT plots was relativized by the shoot mass in the CLEAR treatment (i.e., [CLEAR − INTACT]/CLEAR) as per the measure of diffuse competition described by Wilson and Keddy (1986). This measure of competitive intensity (C.I.) is +1.0 if competitive inhibition is complete, approaches zero if effects are neutral, and is negative if facilitation occurs.

Neighboring vegetation.—In order to assess the effects of the biomass of neighboring low-growing species on seedling performance, we harvested 16 samples (15 × 15 cm) from INTACT quadrats at each site in the fall of 1990. These samples were centered on the location of red maple transplant seedlings from the 1989 cohort. Samples were dried at 60°C for ≥5 d and weighed. For the six gray dogwood (CORA) sites, only herbaceous plants were weighed directly. For the shrub itself, basal diameter of each stem was measured within a 30 × 30 cm square. Data were converted to biomass estimates using regressions developed from subsamples taken at each site (R^2 values of 80–95%). No biomass estimates were done for the mountain laurel (*Kalmia latifolia* L.) thickets (KAVA) because of the difficulty of accurate measurement in that community.

Data analysis

Growth and survival (arcsine square-root transformed proportion surviving) were assessed with ANOVA. Relationships between these parameters and various measures of site quality (community biomass or species-specific site quality) were examined with simple correlation or regression analyses. Species-specific site quality was calculated for each species × cohort combination at each site as the mean seedling shoot mass at that site in the CLEAR treatment, divided by the greatest average seedling shoot mass achieved in the CLEAR treatment in any site for that species × cohort combination. Thus, the site-quality indices provided unique rankings for each species × cohort combination, with site quality ranging from zero (if no seedlings survived) to one in the site where seedlings had the greatest average shoot mass in CLEAR quadrats.

RESULTS

Net vegetation effects on growth

Overall effects.—To isolate the effects of the communities on growth (vs. effects on survival), we ana-

TABLE 2. Shoot height, shoot biomass and etiolation (shoot height per shoot mass) of tree seedling transplants at the end of two growing seasons in the cleared and intact treatments, averaged across all community types (n = 23) in our Hudson Valley study sites.

Species	Treatment	1988 cohort		1989 cohort	
		Mean	CV	Mean	CV
		SEEDLING HEIGHT (cm)			
Gray birch	CLEAR	66.9	46.7	90.4	22.7
	INTACT	4.2	43.0	8.9	85.7
Red maple	CLEAR	23.4	48.6	25.6	45.3
	INTACT	8.5	30.5	8.5	30.3
Sugar maple	CLEAR	6.2	42.4	8.6	28.3
	INTACT	6.8	24.9	8.4	13.7
		SEEDLING SHOOT MASS (g)			
Gray birch	CLEAR	33.47	81.3	38.82	46.2
	INTACT	0.03	90.4	0.12	192.1
Red maple	CLEAR	4.59	120.7	4.95	104.2
	INTACT	0.09	41.5	0.10	83.3
Sugar maple	CLEAR	0.57	83.2	0.79	60.1
	INTACT	0.14	45.0	0.22	37.7
		SEEDLING ETIOLATION (cm/g)			
Gray birch	CLEAR	7.7	126.6	4.1	69.0
	INTACT	384.7	64.0	275.8	49.8
Red maple	CLEAR	14.5	92.7	14.1	83.4
	INTACT	128.1	21.6	135.3	48.8
Sugar maple	CLEAR	19.5	44.4	15.6	43.3
	INTACT	63.9	35.1	51.7	34.8

lyzed growth patterns only in those seedlings that survived for two full growing seasons. The net effects of intact vegetation on seedling height and shoot mass were quite negative and highly significant (Tables 2 and 3, ANOVA of TRT effect significant at P = 0.0001), and differed for the three tree species (Table 3, ANOVA of SPP × TRT effect significant at P = 0.0001 for both height and shoot mass). Expressed as a percentage of aboveground growth in the CLEAR treatment, shoot mass in the INTACT treatment was 0.09–0.3% for gray birch, 1.9–2.0% for red maple, and 25–28% for sugar maple. These differences are consistent with differences among the species in shade tolerance. While shoot mass did not differ significantly between the two cohorts, there were significant differences between cohorts in height growth (Table 3, ANOVA of COHORT main effects P = 0.0003 and CO-HORT × SPP × TRT interaction effects P = 0.0497). Sugar maple seedlings in the 1989 cohort were taller than the 1988 cohort in both treatments, while gray birch seedlings showed greater growth in the INTACT treatment in 1989 vs. 1988 but not in the CLEAR quadrats.

Seedling shoot mass was affected much more negatively by the intact vegetation than was height growth (Table 2). The relatively smaller differences in seedling height between CLEAR and INTACT quadrats reflect etiolation of the seedlings beneath intact vegetation (Table 3, ANOVA of all effects significant at P < 0.05 or higher). The degree of etiolation accorded with the

TABLE 3. Results of ANOVA for the overall model and species, treatment, cohort, and interaction effects for transplant seedling height, shoot mass and etiolation.

		Height		Shoot mass		Etiolation	
Source	df	F	P	F	P	F	P
Overall model	11	105.8	0.0001	41.8	0.0001	50.3	0.0001
Effects (Type III)							
Species (SPP)	2	164.0	0.0001	69.2	0.0001	76.6	0.0001
Treatment (TRT)	1	344.8	0.0001	116.6	0.0001	360.8	0.0001
SPP × TRT	2	177.0	0.0001	69.8	0.0001	90.9	0.0001
Cohort (COH)	1	13.2	0.0003	0.8	0.3592	5.8	0.0172
SPP × COH	2	6.5	0.0018	0.6	0.5731	4.2	0.0157
TRT × COH	1	5.3	0.0218	0.8	0.3838	4.4	0.0378
SPP × TRT × COH	2	3.0	0.0497	0.5	0.5843	3.9	0.0213
Error df		240		235		235	
Error mean square		151.5		97.3		4190.9	

species' relative shade tolerance, gray birch being the most plastic (INTACT etiolation 50–67 fold greater than in the CLEAR plots), followed by red maple (9–10 fold increase) and sugar maple (threefold increase).

Effects of local neighborhood biomass.—Local neighborhoods around individual red maple seedlings differed in biomass by over three orders of magnitude when including both shrub and herb communities, or over two orders of magnitude among herbaceous communities only (Fig. 1). This variation combined patchiness of the intact vegetation within sites and a regional productivity gradient across sites. Despite this enormous range, there was no significant correlation ($P > 0.05$) between red maple shoot mass or height and local neighbor biomass (combining all data from all sites). When analyzed within community type, there were still no significant correlations ($P > 0.05$ in all seven cases with sufficient data, Table 4A). Only among seedlings in the shrubby grass meadows (GRCO) was there even weak evidence of the expected negative relationship between neighborhood biomass and aboveground seedling growth (Table 4A). There were sufficient data from 16 of the 23 sites to determine the correlation between

local neighbor and red maple shoot biomass at the site level. Of the three significant results, one (RUSC) was a *positive* correlation, one (CORA) was based on only three live seedlings, and one (GRCO) was negative (Table 4B). These results, taken as a whole, provide very little evidence that natural variation in the local biomass of low-growing species translates into variation in net effects on seedling shoot growth.

Site and community effects.—We used the average biomass of the intact vegetation as one indicator of site "quality." Sites varied nearly fourfold in average standing vegetation biomass among the herbaceous communities, and by nearly two orders of magnitude when the dogwood (CORA) communities were included. However, the intensity of competitive effects on seedling growth across this wide range of site productivity did not vary in any consistent pattern (Fig. 2). There were no significant regressions of competitive intensity vs. community biomass (log(10)transformed) for any of the species × cohort combinations (R^2 values ranged from 0.1% to only 11.4%). The only notable trend was a positive relationship in the 1988 cohort for the two maple species in the dogwood (CORA) sites;

FIG. 1. Aboveground biomass (g) of individual red maple seedlings (1989 cohort) at the end of the 1990 growing season plotted against the biomass (kg/m²) of the surrounding vegetation in 15 × 15 cm quadrats around each seedling. Note log scales on both axes. Abbreviations for the different community types are defined in Table 1.

1989 COHORT RED MAPLE

COMMUNITY TYPES

grass: ■ SCSC, □ SCMO
shrub: ● CORA
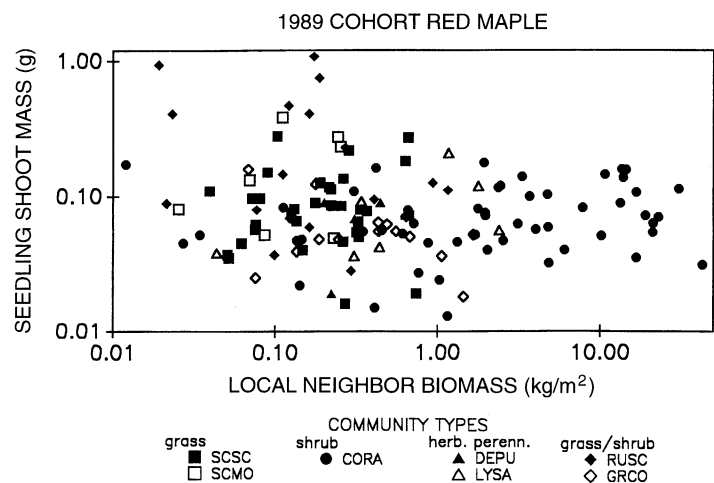herb. perenn.: ▲ DEPU, △ LYSA
grass/shrub: ◆ RUSC, ◇ GRCO

TABLE 4. Correlations (*r*) between aboveground biomass of transplanted red maple seedlings and local neighbor biomass. Analyses were done for all seedlings in each community type across sites (A), and for all seedlings at each site for the 1989 cohort (B). *n*, number of live seedlings in analysis; *P*, probability of correlation coefficient (NS = *P* > 0.10). Data for sites with insufficient surviving seedlings omitted. No community biomass was collected in the KAVA shrub sites.

Community type	Code	*r*	*n*	*P*
A) By community				
Gray dogwood thickets	CORA	+.07	55	NS
Gray dogwood/grass meadows	GRCO	−.42	17	0.0968
Rubus/little bluestem meadows	RUSC	−.26	17	NS
Little bluestem meadows	SCSC	+.17	34	NS
Mossy bluestem meadows	SCMO	+.28	7	NS
Rocky hayscented fern meadows	DEPU	+.46	5	NS
Loosestrife wet meadows	LYSA	+.32	8	NS
B) By site				
Gray dogwood thickets	CORA	−.07	12	NS
		+.35	8	NS
		−.99*	3	0.0881
		+.01	12	NS
		−.27	14	NS
		−.21	6	NS
Gray dogwood/grass meadows	GRCO	−.81†	9	0.0096
		−.06	8	NS
Rubus/little bluestem meadows	RUSC	+.86‡	6	0.0289
		−.29	11	NS
Little bluestem meadows	SCSC	+.36	10	NS
		−.24	15	NS
		+.46	5	NS
Mossy bluestem meadows	SCMO	+.28	7	NS
Rocky hayscented fern meadows	DEPU	+.05	4	NS
Loosestrife wet meadows	LYSA	+.32	8	NS

* Analysis of log(10) seedling shoot mass vs. log(10) neighbor biomass.
† Analysis of log(10) seedling shoot mass vs. neighbor biomass.
‡ Analysis of seedling shoot mass vs. neighbor biomass.

in these cases, the intensity of competition *increased* with community biomass (Fig. 2).

While there was considerable variation in the intensity of competition among the 23 sites, there were no consistent differences among the eight community types. In the ANOVA for seedling shoot mass, neither the main effect of community type nor the interactions between community type and species or treatment effects were significant (*P* values > 0.05). Inspection of the results in Fig. 2 reveals only a few trends. Negative effects on gray birch were virtually complete (i.e., competitive intensity (C.I.) = 1) in the shrub communities and several of the herbaceous communities. Only in some of the more open little bluestem (SCSC) communities was there a slight departure from this pattern (Fig. 2). There was greater variation among the sites in the intensity of competitive effects on red maple (C.I. ranged from 0.84 to 1); C.I. in a given site varied between the two cohorts (Fig. 2). Net intensity of competition varied most for sugar maple seedlings, with nearly complete suppression of growth in the high productivity gray dogwood thickets (CORA) and several of the drier herbaceous communities (DEPU). Net competitive effects were neutral or even positive (facilitation) in one dogwood (CORA) and one shrubby grass meadow (*Rubus*/bluestem, RUSC) site for seedlings from the 1988 cohort (planted during an unusual early-season drought in 1988), but the pattern changed con-

siderably for the 1989 cohort. More impressive than any of these patterns, however, is the overall *lack* of pattern, caused by the wide range of competitive intensities observed among the different sites representing each community type.

The lack of pattern in the above analyses is underscored by the absence of consistent and strong correlations between seedling shoot mass in the CLEAR treatments and community biomass at each site, especially across species and cohorts (Table 5). Thus, the productivity of the low-growing species at a site is not generally a good indicator of the site's favorability for the growth of any single tree species. In effect, each tree species responded individualistically to the environmental gradient each year (compare the sorting of sites along the site-quality axes in Fig. 3 for the different species × cohort combinations). This suggested to us that the best predictor of site "quality" would be the performance of each cohort of each species in the CLEAR treatment. Competitive intensity is clearly related to this species-specific site quality index for both of the maple species (Fig. 3). Competition is most intense on the most favorable sites and is reduced on poor sites.

In order to better evaluate this pattern, we compared the results to the curves shown in Fig. 3 for the maples. The curves show a particular null model: how apparent competitive intensity (C.I.) would change with site
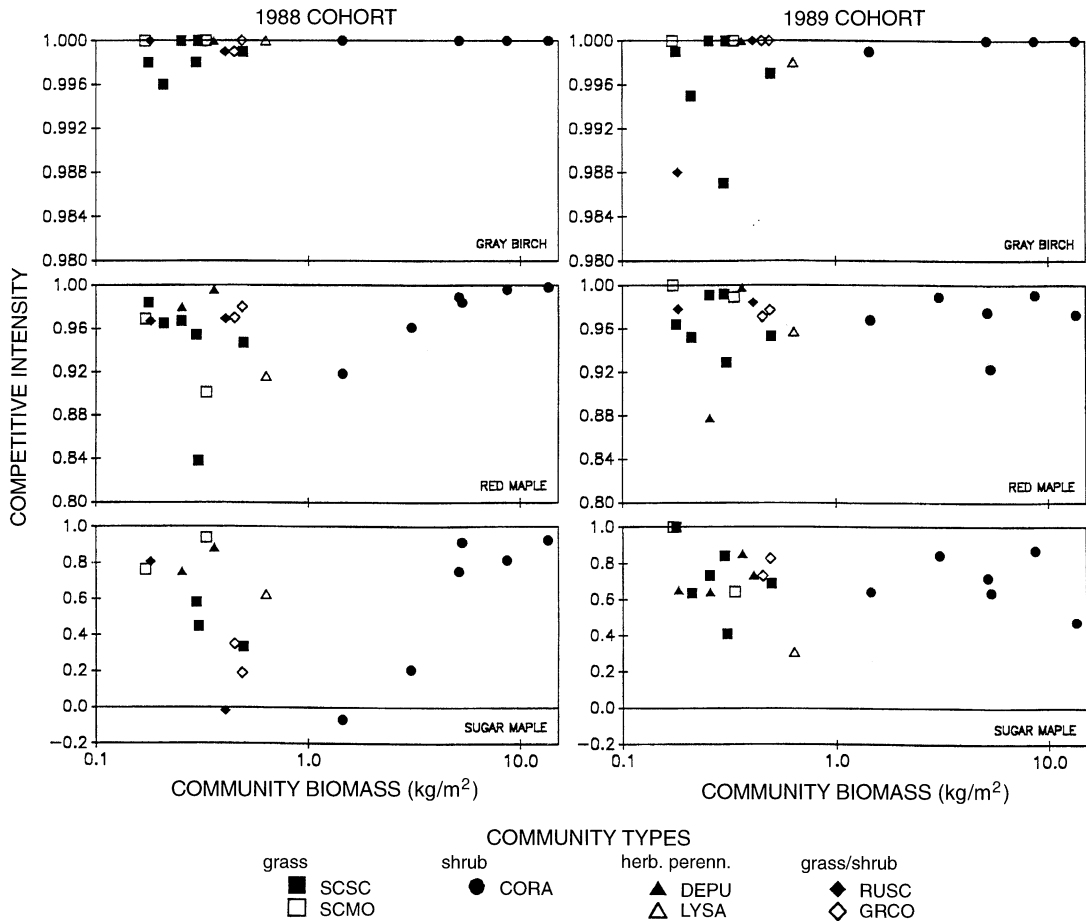
FIG. 2. Intensity of competitive effects (C.I.) on seedling aboveground growth (shoot biomass) as a function of average community biomass for 21 sites for which community biomass was measured. C.I. = [($\bar{X}$ CLEAR shoot mass) − ($\bar{X}$ INTACT shoot mass)] ÷ ($\bar{X}$ CLEAR shoot mass), where $\bar{X}$ is the mean of all surviving seedlings at each site. Negative C.I. (in two sites in the 1988 sugar maple cohort) indicates facilitation. Different symbols indicate different community types.

quality if seedling sizes were identical in all INTACT plots. They were calculated by substituting the overall mean of seedling shoot mass in all INTACT plots (from Table 2) in the computation of C.I. for individual sites. The actual C.I. data for red maple are not distinguishable from this calculated curve, suggesting that competition increased directly with site quality in both cohorts of this species. There is considerable departure from this curve for the sugar maple seedlings. The effects of competition on sugar maple were more severe

than would be predicted in certain grass (SCSC) and herbaceous meadow (DEPU) sites, as well as in the mountain laurel/blueberry thickets (KAVA). Competition was less severe in the grassy *Rubus* sites (RUSC) and other SCSC sites. We found no evidence that the intensity of competition lessened in sites that were most favorable for seedling growth in the absence of vegetation (Fig. 3).

Net vegetation effects on survival

Overall effects.—While the net effects of old-field vegetation on seedling growth were predominantly negative (inhibition), seedling survival was facilitated by the presence of intact vegetation in many cases (ANOVA of TRT effect significant at $P = 0.0008$, Tables 6 and 7). As was the case for growth, the net effect of intact vegetation on seedling survival was strongly dependent on the shade tolerance of the target tree species (ANOVA SPP × TRT interaction significant at $P = 0.0001$). The species ranked as before, with survival in the INTACT treatment (expressed as a percentage

TABLE 5. Correlations (r) between transplant seedling performance (shoot mass) in the CLEAR treatments and total aboveground community biomass at each site. P, significance value.

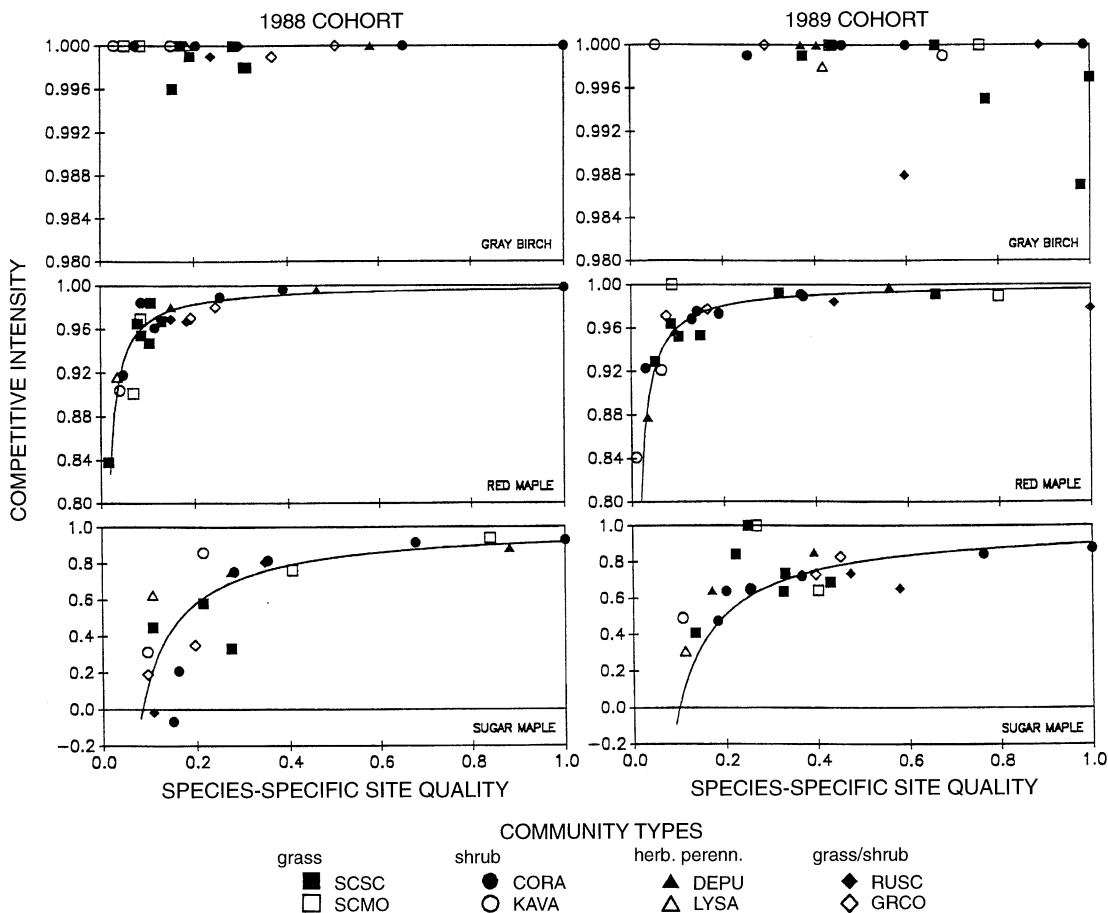| Species	1988 cohort		1989 cohort	
	r	P	r	P
Gray birch	+.272	0.23	−.003	0.99
Red maple	+.782	0.001	−.125	0.59
Sugar maple	+.515	0.017	+.201	0.38

FIG. 3. Intensity of competitive effects (C.I. defined as in Fig. 2) on seedling aboveground growth (shoot biomass) as a function of species-specific site quality indices for the eight community types. Negative C.I. (in two sites in the 1988 sugar maple cohort) indicates facilitation. Different symbols indicate different community types. Curves for the two maple species are not fitted regression lines, but rather illustrate how C.I. would vary under the following null hypothesis: competitive intensity varies directly with site quality such that seedling size in the intact plots is constant across the entire gradient. It is calculated using the overall mean seedling biomass for that species × cohort in intact vegetation (averaged over all 23 sites).

of that in the CLEAR plots) ranging from 18 to 21% for gray birch, 73 to 133% for red maple and 95 to 246% for sugar maple (Table 6). However, unlike the results for growth, the differences among species and between treatments also varied significantly among co-

TABLE 6. Fraction of transplanted tree seedlings surviving to the end of the second growing season in each treatment for each cohort, averaged across all 23 sites.

Species	Treatment	1988 cohort Mean	1988 cohort CV	1989 cohort Mean	1989 cohort CV
Gray birch	CLEAR	.479	60.8	.477	49.5
	INTACT	.088	129.7	.101	93.0
Red maple	CLEAR	.481	44.6	.644	39.6
	INTACT	.642	32.5	.470	54.6
Sugar maple	CLEAR	.233	74.0	.514	47.5
	INTACT	.573	49.2	.487	51.6

horts (Table 7, ANOVA of interaction terms significant: COHORT × TRT $P = 0.0002$ and COHORT × TRT × SPP $P = 0.0023$). While gray birch survival was consistently low under competition, survival of the maples was facilitated in the 1988 but not in the 1989 cohort. The 1988 growing season was characterized by an unusual drought early in the growing season (Canham and Kelly 1993). Our results suggest that intact vegetation may have buffered the seedlings from effects of the drought, though much of the actual seedling mortality occurred over winter. As a result, divergence in survivorship curves between INTACT and CLEAR treatments was most pronounced during the dormant season between the fall and spring censuses (Fig. 4).

Local neighbor effects.—We used logistic regression (SAS Institute 1987) to test for effects of local neighborhood biomass on survival of red maple seedlings from the 1989 cohort. When all sites were combined,

TABLE 7. Results of ANOVA for tree seedling survival (after angular transformation) in cleared vs. intact sites.

Source	df	F	P
Overall model	11	17.52	0.0001
Effects (Type III)			
Species (SPP)	2	38.14	0.0001
Treatment (TRT)	1	11.45	0.0008
SPP × TRT	2	37.31	0.0001
Cohort (COH)	1	1.39	0.2398
SPP × COH	2	1.14	0.3215
TRT × COH	1	14.23	0.0002
SPP × TRT × COH	2	6.21	0.0023
Error df			264
Error mean square			0.079

there was no significant relationship between neighbor biomass and seedling survival. This result is strongly influenced by the relatively high survival of red maple seedlings in gray dogwood thickets with very high biomass. Analysis within individual community types indicated a significant relationship between neighborhood biomass and red maple seedling survival only for the little bluestem-dominated communities ($\chi^2 = 5.50$, df = 1, $P = 0.019$ for SCSC, SCMO, and RUSC sites combined; $n = 145$ seedlings). However, the relationship was *positive*: red maple seedling survival was slightly higher in neighborhoods with higher biomass of surrounding low-growing species (primarily little bluestem grass).

Site and community effects.—We assessed the net effect of vegetation on seedling survival by computing the difference in survival between CLEAR and INTACT treatments. Gray birch seedling survival was inhibited by intact vegetation in virtually all of the sites, regardless of community type or biomass of the surrounding community (Fig. 5). In contrast, there were clear cases of facilitation of seedling survival for both cohorts of both maple species (Fig. 5). For the 1988 cohorts of both red maple and sugar maple, facilitation of survival was relatively uniform, regardless of community biomass. The 1989 cohort of maples fared less well in the herbaceous communities than did their 1988 counterparts (separate ANOVA of community type × cohort effects on the difference in survival was significant for red maple, $P = 0.0016$, but not for sugar maple). This resulted in a generally negative relationship between seedling survival and community biomass for maples in the 1989 cohort (regression analysis: red maple, $R^2 = 35.5\%$, $P < 0.01$; sugar maple, $R^2 = 18.3\%$, $P < 0.10$). These are the only instances in which we obtained results consistent with the hypothesis that competition is less intense at the most favorable end of a resource gradient.

In contrast to the patterns of seedling growth, net effects of old-field vegetation on seedling survival generally were not related to the species-specific indices of site quality (Fig. 6). The clear exception was the 1988 cohort of gray birch, where the intensity of com-

petition increased directly with site quality (regression analysis: $R^2 = 72.1\%$, $P < 0.001$). Otherwise, the intensity of competitive effects on seedling survival was unrelated to site quality.

DISCUSSION

One of the most striking results of this experiment was the relatively minor variation in growth of tree seedlings beneath a wide range of intact communities. While growth of seedlings of all three tree species was uniformly poor across the entire range of communities and environments, the role of competition in this pattern varied with site quality (Fig. 3). On sites that were potentially favorable for a species (as measured by growth of that species in cleared quadrats), intact vegetation strongly inhibited tree seedling growth. However, in sites that were physically unfavorable (i.e., stressful even in cleared quadrats), the presence of intact vegetation had little negative effect on seedling growth. In two extreme cases, intact vegetation on particularly stressful sites actually facilitated growth of sugar maple seedlings (Fig. 3). Although the communities differed significantly in amount of shade cast by
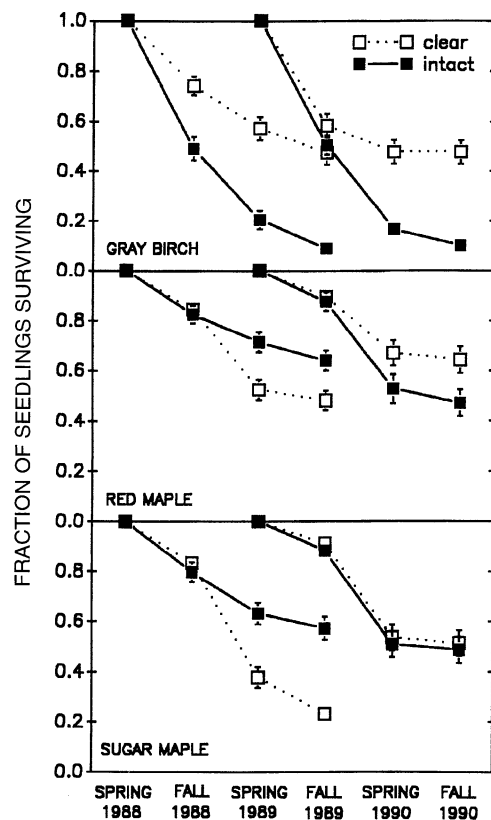

FIG. 4. Fraction of transplanted seedlings surviving over time for each cohort of each of the three tree species. 1988 cohort survival is calculated from spring 1988 to fall 1989 and 1989 cohort survival from spring 1989 to fall 1990. Data are averaged over all 23 sites by treatment. ■, INTACT treatment; □, CLEAR treatment. Error bars show ±1 SE.
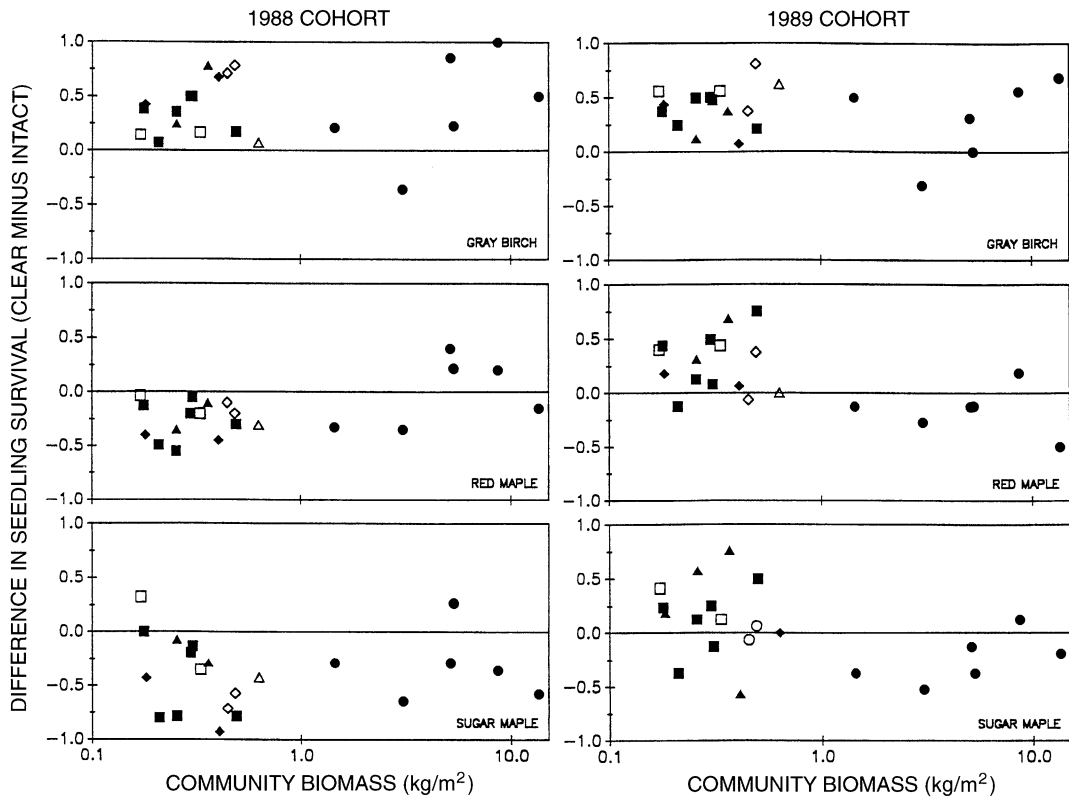
FIG. 5. Differences in the fraction of seedlings of each cohort surviving to the end of the second growing season in CLEAR vs. INTACT treatments, as a function of average community biomass in a site. The two KAVA sites are excluded because no community biomass estimates were made there. Different symbols represent different community types (see Fig. 3). A positive value indicates inhibition of seedling survival; a negative value indicates facilitation.

the intact canopy (Canham and Kelly 1993), they did not differ consistently in either absolute magnitude of seedling growth (beneath intact canopies) or intensity of competitive inhibition of young tree seedlings.

In contrast to the absence of community differences found in this study, long-term demographic studies of naturally occurring seedlings (Hill et al. 1994) found significant differences in overall resistance to invasion by trees. Such variation in resistance might be due to differences among communities in the *duration* of competition (i.e., the number of years until seedlings outgrow the competitive effects of the surrounding low-growing species) rather than to differences in the annual *intensity* of competition. The number of years required for a seedling to grow tall enough to escape the effects of shading or to establish a large enough root system to lessen the effects of belowground competition should vary with the structure of the low-growing community. In community types in which a seedling takes longer to escape the competitive effects of surrounding species, the cumulative risk of mortality will be higher because of the compounding of annual mortality rates (Hill et al. 1994).

Our results documenting strong competitive effects of old-field vegetation on the growth of transplanted

tree seedlings are consistent with similar studies in more fertile regions of New York (Gill and Marks 1991) and North Carolina (DeSteven 1991*b*). We found evidence that short-term survival of newly established transplants was in some cases facilitated by the presence of intact vegetation. DeSteven (1991*a*) also detected significant positive effects of intact vegetation on survival of pine and several large-seeded hardwoods, including red maple. The net effect of intact vegetation on seedling survival in our study clearly depended on the shade tolerance of the target tree species. Both cohorts of gray birch, a highly shade intolerant species, showed very low survivorship under intact vegetation. In contrast, survival of sugar maple, a highly shade tolerant species (Canham 1988), was either facilitated (1988 cohort) or unaffected (1989 cohort) by intact vegetation. This variation between years in the degree of facilitation suggests that net effects of intact communities on the survival of young tree seedlings cannot be reliably judged by one year's results. In the 1988 cohort, on average, intact vegetation facilitated the survival of newly-planted red maple seedlings. One year later, intact vegetation significantly reduced the survival of red maple seedlings (Fig. 4). Facilitation of survival of red and sugar maple seed-
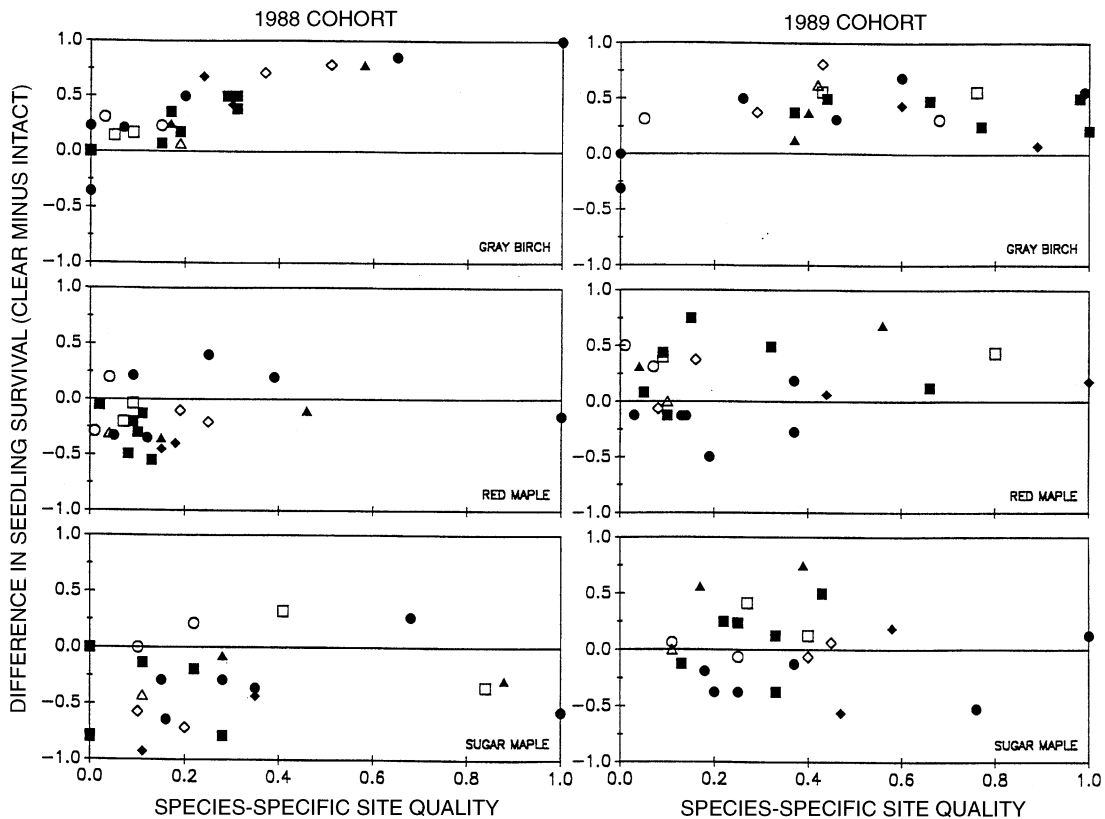
FIG. 6. Differences in the fraction of seedlings of each cohort surviving to the end of the second growing season in CLEAR vs. INTACT treatments, as a function of species-specific site quality (measured by seedling growth in the CLEAR treatments). Different symbols represent different community types (see Fig. 3). A positive value indicates inhibition of seedling survival; a negative value indicates facilitation.

lings planted in 1988 may be related to the extreme drought that year. We suspect that intact vegetation protected the young seedlings from drought and heat stress, while seedlings in cleared quadrats experienced high light levels and correspondingly high leaf temperatures. Both DeSteven (1991a) and Gill and Marks (1991) propose similar explanations for the facilitation of survival they observed.

It is important to emphasize that the patterns of seedling survival we described reflect direct effects of plant–plant interactions during only the first 2 yr of seedling invasion. The very low seedling growth rates observed in this field experiment and in our comparative study of tree invasion in a wide range of right-of-way communities (Hill et al. 1994) suggest that seedlings may require much longer periods of time (as many as 10–20 yr) to emerge above the canopy of the low-growing community. Although annual mortality rates generally decline after seedlings are 1-yr-old (Hill et al. 1994), in subsequent years, growth reduction caused by intact vegetation will increase cumulative seedling mortality because annual mortality rates are compounded over the longer period required for the seedling to emerge above the low-growing species.

Although we observed significant facilitation of seedling survival in some cases, it is important to note that the entire study was performed in the absence of herbivores. Experiments by Gill and Marks (1991) and Ostfeld and Canham (1993) demonstrate that intact vegetation can have a significant *indirect* negative effect on seedling survival by providing habitat for small mammal herbivores, such as meadow voles (*Microtus pennsylvanicus*), that are voracious consumers of newly emerged tree seedlings. Seedlings in areas cleared of vegetation apparently escape predation at least in part because herbivores are reluctant to venture into the clearings and expose themselves to the risk of predation (Gill and Marks 1991, Ostfeld and Canham 1993).

Our experiment was not designed specifically to test the effects of canopy disturbance on growth and survival of tree seedlings. However, the design does allow us to make limited inferences about the potential effects of plant canopy disturbance by natural processes or vegetation management. To the extent that seedling growth in the clearings in our study may indicate how seedlings would perform in natural or human-caused clearings, our results suggest that sites inherently favorable to the growth of a tree species should be sus-

ceptible to rapid seedling establishment and growth *of that species* if they are disturbed. On the other hand, disturbance should have less effect on invasion by a species in sites that are inherently less favorable for its growth. The critical proviso here is that the prediction is specific to individual tree species, not to overall invasion of the site by other tree species. Since the forests surrounding a right-of-way are expected to be dominated by species adapted to the local environment, the tree seeds arriving in the right-of-way are likely to be of species for which the site is relatively favorable (McDonnell and Koch 1993). This strongly suggests that disturbance to the canopy of low-growing species will reduce resistance to tree invasion in all but the extremely stressful environments.

Another striking result of our experiment was the absence of any clear relationship between various measures of site quality or neighborhood biomass and net effects of old-field vegetation on seedling growth or survival. Many studies of plant competition have successfully predicted the intensity of competitive effects on growth of individual plants from the abundance or biomass of neighbors (e.g., Goldberg and Werner 1983, Goldberg 1987, Pacala and Silander 1987). However, we found no clear relationship between natural variation in neighborhood biomass of low-growing species and either the growth or survival of red maple seedlings. The distinction between our results and those of Goldberg and Werner (1983) may reflect different effects of "disturbed" vs. "undisturbed" variation in neighborhood biomass. Goldberg and Werner (1983) examined effects of variation in neighborhood biomass created by experimentally manipulating (removing or adding) biomass within a relatively uniform environment. The natural analogue to this would be variation in community biomass due to recent disturbances. Under those conditions, it is reasonable to expect that competition will be less intense in neighborhoods with lower biomass (Goldberg 1987). In effect, our CLEAR vs. INTACT quadrats represent the two extremes of a gradient in local neighbor biomass that could be created by either natural disturbance or experimental manipulation. Viewed in that light, our results clearly show an effect of local neighbor biomass on seedling growth, since seedlings of each species grew more, on average, in neighborhoods with zero biomass of low-growing species. However, our results suggest that it is not valid to generalize from the effects of transient variation in neighborhood biomass to naturally occurring ("undisturbed") variation in neighborhood biomass across a range of site conditions.

For the past 15 years, one of the most active debates in resource competition has been how intensity of competition varies along environmental gradients and associated gradients in community productivity. Grime (1973, 1979) and others (e.g., Huston 1979, Keddy 1989) have proposed that the intensity of competition increases with increasing site quality, while Tilman

(1988) and others (e.g., Newman 1973, Grubb 1985) have proposed that competition is intense even in harsh environments. Our experiment provides a direct test of these competing hypotheses and shows that the resolution of this debate lies in how site quality is defined. Tilman's view is supported if overall productivity of the site (average biomass of low-growing species) is used to define site quality (Fig. 2). While our sites varied considerably in competitive intensity, there was little relationship to community biomass; many sites with low community biomass had high-intensity competition. However, if site quality is defined by the performance of seedlings in the absence of intact vegetation (species-specific index of site quality), then our results (Fig. 3) clearly support Grime's contention. These two competing hypotheses are founded more on intuition than on any underlying mechanistic model of the relationships between environmental conditions, community productivity and the intensity of competition. Thus, it is not surprising that resolution of the debate may lie in the semantics of defining site quality and productivity (Thompson 1987, Tilman 1987*a, b*). We conclude (as have others; see Grace and Tilman 1990) that both hypotheses have merit when carefully applied.

Literature Cited

Bramble, W. C., and W. R. Byrnes. 1976. Development of a stable, low plant cover on a utility right-of-way. Pages 167–176 *in* R. Tilman, editor. Proceedings of the First National Symposium on Environmental Concerns in Rights-of-Way Management. Mississippi State University, State College, Mississippi, USA.

Canham, C. D. 1988. Growth and architecture of shade-tolerant trees: response to canopy gaps. Ecology **69**:786–795.

Canham, C. D., and J. S. Kays. 1993. Classification and gradient analysis of right-of-way vegetation in the mid-Hudson valley. Pages 7–30 *in* C. D. Canham, editor. Vegetation dynamics along utility rights-of-way: factors affecting the ability of shrub and herbaceous communities to resist invasion by trees. Final Technical Report to the Empire State Electric Energy Research Corporation.

Canham, C. D., and V. R. Kelly. 1993. The dynamics of resource supply and depletion in right-of-way vegetation. Pages 183–208 *in* C. D. Canham, editor. Vegetation dynamics along utility rights-of-way: factors affecting the ability of shrub and herbaceous communities to resist invasion by trees. Final Technical Report to the Empire State Electric Energy Research Corporation.

Connell, J. H., and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. American Naturalist **111**:1119–1144.

DeSteven, D. 1991a. Experiments on mechanisms of tree establishment in old-field succession: seedling emergence. Ecology 72:1066–1075.

———. 1991b. Experiments on mechanisms of tree establishment in old-field succession: seedling survival and growth. Ecology 72:1076–1088.

Everett, R. L., S. Koniak, and J. D. Budy. 1986. Pinyon seedling distribution among soil surface microsites. USDA Forest Service Research Paper INT-363 1986;1–4.

Gill, D. S., and P. L. Marks. 1991. Tree and shrub seedling colonization of old fields in central New York. Ecological Monographs 61:183–205.

Goldberg, D. E. 1987. Neighborhood competition in an old-field plant community. Ecology 68:1211–1223.

Goldberg, D. E., and P. A. Werner. 1983. Equivalence of competitors in plant communities, a null hypothesis and a field experimental approach. American Journal of Botany 70:1098–1104.

Grace, J., and D. Tilman, editors. 1990. Perspectives on plant competition. Academic, New York, New York, USA.

Grime, J. P. 1973. Competitive exclusion in herbaceous vegetation. Nature 242:344–347.

———. 1979. Plant strategies and vegetation processes. John Wiley and Sons, Chichester, England.

Grubb, P. J. 1985. Plant populations and vegetation in response to habitat disturbance and competition: problems of generalization. Pages 595–621 in J. White, editor. The population structure of vegetation. Dr. W. Junk, The Hague, The Netherlands.

Hill, J. D., C. D. Canham, and D. M. Wood. 1994. Patterns and causes of resistance to tree invasion in rights-of-way. Ecological Applications 5, in press.

Huston, M. A. 1979. A general hypothesis of species diversity. American Naturalist 113:81–101.

Keddy, P. A. 1989. Competition. Chapman and Hall, London.

McDonnell, M. J., and J. M. Koch. 1993. Woody plant seed dynamics in powerline corridors located in southern New York. Pages 87–128 in C. D. Canham, editor. Vegetation dynamics along utility rights-of-way: factors affecting the ability of shrub and herbaceous communities to resist invasion by trees. Final Technical Report to the Empire State Electric Energy Research Corporation.

Muller, C. H. 1953. The association of desert annuals with shrubs. American Journal of Botany 40:53–60.

Muller, W. H., and C. H. Muller. 1956. Association patterns involving desert plants that contain toxic products. American Journal of Botany 43:354–361.

Newman, E. I. 1973. Competition and diversity in herbaceous vegetation. Nature 244:310.

Niering, W. A., and R. H. Goodwin. 1974. Creation of relatively stable shrublands with herbicides: arresting "succession" on rights-of-way and pastureland. Ecology 55:784–795.

Ostfeld, R. S., and C. D. Canham. 1993. Effect of meadow vole population density on tree seedling survival in old-fields. Ecology 74:1792–1801.

Pacala, S. W., and J. A. Silander, Jr. 1987. Neighborhood interference among velvet leaf, Abutilon theophrasti, and pigweed, Amaranthus retroflexus. Oikos 48:217–224.

Pickett, S. T. A., S. L. Collins, and J. J. Armesto. 1987. Models, mechanisms and pathways of succession. Botanical Review 53:335–371.

SAS Institute. 1987. SAS/STAT guide for personal computers: Version 6 edition. SAS Institute, Cary, North Carolina, USA.

Thompson, K. 1987. The resource ratio hypothesis and the meaning of competition. Functional Ecology 1:297–303.

Tilman, D. 1987a. The importance of the mechanisms of interspecific competition. American Naturalist 129:769–774.

———. 1987b. Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. Ecological Monographs 57:189–214.

———. 1988. Plant strategies and the dynamics and structure of plant communities. Princeton University Press, Princeton, New Jersey, USA.

Wilson, S. D., and P. A. Keddy. 1986. Measuring diffuse competition along an environmental gradient: results from a shoreline plant community. American Naturalist 127:862–869.

Wilson, S. D., and D. Tilman. 1991. Components of plant competition along a productivity gradient. Ecology 72:1050–1065.