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MULTIPLE INDIRECT EFFECTS OF PLANT LITTER AFFECT THE ESTABLISHMENT OF WOODY SEEDLINGS IN OLD FIELDS[1]

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Abstract. I studied the effects of oak leaf litter, herb competition, and insect herbivory on the establishment of seedlings of *Ailanthus altissima* in New Jersey, USA. I performed two experiments in an early-successional site in two consecutive years. In the first experiment I tested the effects of litter and competition, and their interaction, on establishment and growth of tree seedlings. In the second experiment I studied the effect of insecticide application in combination with litter and herb competition on seedling establishment and growth, and on arthropod abundance. In the absence of competition, litter had no significant effect on the biomass of woody seedlings, though it delayed seedling emergence. Herb competition reduced the growth of the woody seedlings, but the addition of leaf litter reduced the density and biomass of the herbs, indirectly improving the growth of the woody seedlings. Litter increased both invertebrate damage to seedling cotyledons and seedling mortality. The application of insecticide increased seedling emergence and reduced seedling mortality, and more so in the presence of litter. The total number of arthropods and the number of plant-chewing arthropods were increased by the addition of litter and reduced by application of insecticide. Thus, litter had, simultaneously, a positive indirect effect on individual biomass through reduced competition, and a negative indirect effect on the number of individuals through increased seed and/or seedling predation, and a negative direct effect on seedling mortality.

Key words: Ailanthus altissima; *arthropods; Eastern deciduous forests; effects of plant litter; herb competition; herbivores; indirect effects; insects; invasive species; old fields; succession; tree establishment.*

INTRODUCTION

In the past few decades community ecologists have argued about whether competition or predation is the main interaction shaping community structure (see, e.g., Hairston et al. 1960, Connell 1983, Schoener 1983, Hairston 1989). This discussion not only disregards other interactions such as parasitism, symbiosis, etc., but is also biased by the assumption of the prevalence of one single interaction acting independently from other interactions. Herbivory, for example, may alter the outcome of competition (Bentley and Whittaker 1979, Lubchenco 1986, Louda et al. 1990), and competition may affect the susceptibility to herbivore attack (Dirzo 1986). To understand the role of biotic interactions in shaping communities it is necessary to include both direct and indirect effects integrated in an interaction web. Interaction webs differ from food webs in that the former also include the non-trophic relationships within and between trophic levels. Several studies have established the importance of indirect effects in the organization of various animal communities (e.g., Wilbur 1972, Morin 1981, Roughgarden and Diamond 1986). Far fewer studies focus on the importance of indirect effects in plant–plant or plant–herbivore systems (but see Bergelson 1990*a*). It is possible that indirect effects have been frequently confounded with direct effects in poorly designed experiments (e.g., apparent competition, Connell 1990).

The importance of both competition and herbivory in old-field communities is well established. Several experiments have documented strong effects of competition in herb-dominated old fields (see Hairston [1989] for a review). Herbivores in seral communities are usually reported to consume only a small proportion of the productivity (e.g., Odum 1960). However, exclusion of herbivores in old-field communities produces important changes in community structure and population dynamics (e.g., Brown 1985, Brown et al. 1987).

Recent research has pointed out the importance of direct and indirect effects of plant litter on the dynamics of plant communities (Grime 1979, Bergelson 1990*a*, *b*, Carson and Peterson 1990, Facelli and Pickett 1991*a*; see Facelli and Pickett [1991*b*] for a review). Direct

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and indirect effects produced by litter are conceptually interesting because the effect is produced by the activity of another population separated by time (Bergelson 1990*a*, *b*, Facelli and Pickett 1991*c*, Facelli and Facelli 1993) and, frequently, by space (Facelli and Carson 1991, Facelli and Pickett 1991*b*). C. R. Cid (*unpublished manuscript*) found that the competitive outcome between annual and perennial forest herbs was controlled by the presence of tree leaf litter. Grime (1979) suggested that tree leaf litter that accumulated close to old-field–forest borders could improve woody seedling establishment because litter could reduce the competitive effect of the herbs. Facelli and Pickett (1991*c*) found that the presence of oak leaf litter reduced the competitive effect of herbs on seedlings of *Ailanthus altissima* in a greenhouse experiment.

I report here the results of two field experiments performed in consecutive years to study how oak leaf litter, competing herbs, and invertebrate herbivores, acting alone and in combination, affect the establishment of tree seedlings in a 1st-yr old field. The first experiment was designed specifically to test in the field the prediction that the presence of litter should have an indirect positive effect on woody seedlings' growth (Grime 1979, Facelli and Pickett 1991*c*). The second experiment, based on observations and results from the previous one, was mainly designed to study the effect of litter on arthropod activity and the effect of herbivore arthropods on seedling establishment. The factorial designs employed allowed me to assess the importance of direct (main effects in the ANOVA) and indirect (interaction term) effects of the factors under study.

MATERIALS AND METHODS

Experimental system

The study was conducted at William L. Hutcheson Memorial Forest Center (HMF), East Millstone, New Jersey, USA (40°30′ N, 74°34′ W). The climate of the region is subcontinental, with a mean annual precipitation of 1120 mm evenly distributed throughout the year. Mean monthly temperatures range from 0.0°C in January to 24°C in July (United States Weather Bureau 1959); the growing season extends from 20 March to 20 November (Robichaud and Buell 1973). The soils are well-drained silty loam, derived from the Triassic red shales of the Brunswick Formation, included in the Penn B Silt Loam Series (USDA 1976).

Old fields at HMF are small (>1–3 ha), with a relatively large proportion of their perimeter bordered by hedgerows or woodlots of various ages. When subject to disturbance in the spring, as was the site studied, *Setaria faberii* (nomenclature follows Gleason and Cronquist 1963) dominates the community, and *Solanum carolinense* and *Panicum dichotomiflorum* are subdominants (Facelli and Pickett 1991*a*). Litter distribution is heterogeneous in those old fields because of heterogeneous litter production and patchy deposition of tree leaf litter blown by wind from nearby woodlots (Facelli and Carson 1991).

The experimental site was located in an old field that was cultivated until 1985, when it was left fallow. The experiments reported here were performed in two adjacent portions of the same old field that had been previously used to study the effect of different types of litter on herb communities (Facelli and Pickett 1991*a*).

The target species in both experiments was *Ailanthus altissima* (henceforth mentioned only by its genus name). *Ailanthus* (Simaroubaceae) is an exotic, fast-growing, early woody colonist. It is found widely in forests and old fields throughout most of North America. In many areas *Ailanthus* is very abundant and can be considered naturalized. I selected it as the target species mainly because it is one of the first trees to successfully colonize old fields in the area (Facelli and Pickett 1991*c*; J. M. Facelli, *personal observation*).

Experiment 1989: effects of litter and competition

The experiment began on 4 June 1989, 5 d after the experimental area was tilled. This factorial experiment had two levels of herb competition (naturally growing herbs left intact or removed by hand) and two of litter (litter absent or oak leaf litter added at 150 g/m^2). The experimental addition of oak leaf litter simulated the patches formed by litter deposited in old fields by bordering woodlots (Facelli and Carson 1991). Each of the four possible factor combinations was replicated 10 times in a random 8 × 5 plot grid. Each plot was 1 m × 60 cm, and vegetation was cleared from the 1-m buffer strips between plots. In each of the plots I added 10 seeds of *Ailanthus*, to secure a reasonable number of seedlings emerging. A few naturally dispersed seeds were probably also present (see Facelli and Pickett 1991*c*). The seeds were locally collected during the previous fall and stored in a cold room at 4°C during the winter and early spring. Germination in the laboratory was 87 ± 6.78% (mean ± 1 SE). I used leaf litter of *Quercus alba*, collected from local woodlots at the beginning of the growing season. The material was air-dried, cleaned of extraneous material and partially decomposed leaves, and weighed into the amounts to be applied to each plot. All plots were covered with chicken wire (5 cm diameter openings) to prevent wind from removing the oak leaves. The chicken wire formed a cage, 5 cm high, that did not compress the litter. In the plots without competition all the herbs emerging were clipped at surface level, taking special care to minimize any physical disturbance. I began to remove the herbs on 12 June, and continued to do so roughly every week throughout the season. I also severed horizontal root connections from outside the plots by driving a spade 30 cm into the ground around the perimeter of each plot.

I counted the seedlings of *Ailanthus* approximately every 6 d from 18 June to 22 July, and on 22 August and 15 September. On each date I marked all newly emerged seedlings with color-coded toothpicks and recorded the number of dead (missing) seedlings. To reduce possible biases due to the different visibility of seedlings in the plots with and without litter, I considered a seedling "emerged" when its cotyledons were fully expanded. This is the stage when seedlings start to depend mostly on acquired resources rather than on seed reserves. On 30 June 1989, because I had observed that damage produced by herbivores on the cotyledons of the *Ailanthus* seedlings seemed to be increased by the presence of oak leaf litter, I estimated the percentage of the cotyledons (using 5% intervals) missing in each seedling.

On 15 September 1989 I harvested all the plots. I first clipped all aerial biomass of herbs, and then collected the seedlings of *Ailanthus* by gently removing the soil and pulling them by the base of the stem, thus retrieving as much root as possible. The herbs were sorted into grasses and dicots, and the woody seedlings were sorted into leaves, stem, and roots. All material was oven-dried for 48 h at 84°C, and weighed.

Experiment 1990: effect of litter on competition and herbivory

In the second experiment I manipulated three factors: herb competition (as in 1989), presence of oak leaf litter (as in 1989), and activity of invertebrates (present at natural densities, or reduced by application of insecticide). Each of the eight treatment combinations was replicated once in each of four blocks. Each plot was 1 m × 80 cm, separated by 1-m buffer strips cleared of vegetation. Twenty seeds of *Ailanthus* per plot were added.

I started the experiment on 30 May 1990, 3 d after having tilled the soil. I placed 20 seeds of *Ailanthus* in a square (side = 50 cm) at the center of each plot. The insecticide treatment consisted of the application of Carbaril dust 5%, which was selected because of its high persistence and wide-action spectrum. In all the plots that received insecticide, the soil was dusted with 5 g of active principle per square metre after the soil was tilled. This is the application recommended by the manufacturer for generalist herbivores. Plots were covered with chicken wire mesh as described for the 1989 experiment. Prior to manipulating the experimental factors I placed two pitfall traps in each plot, each 10 cm away from the 50-cm central square, in the direction of the longest axis of the plot. Pitfall traps mostly sample activity of large invertebrates living at the soil surface and in the litter mat (Southwood 1979) and are likely to efficiently trap seed and seedling predators. Each pitfall trap consisted of a plastic cup (8.5 cm in diameter, 12 cm in depth) buried into the ground to its rim, with a plastic funnel attached on the top to prevent insects from escaping from the traps. The traps were covered with a plastic lid at the beginning of the experiment and continued so until 14 August. On that date I removed the lids and placed into each trap a plastic container filled with soapy water to retain the invertebrates falling into the trap. The traps remained open for 24 h. The catches of the two traps in each plot were pooled together and preserved in ethyl acetate until identification. I only counted invertebrates >2 mm in length. The most frequent species (those found in at least 50% of the plots) were identified, at least to family. The rest were identified to higher taxa: order for insects, and class for other invertebrates. I also computed the total number of plant-chewing invertebrates, because they were the most likely to inflict the damage and mortality I observed in the *Ailanthus* seedlings (see *Results*).

I counted and marked the *Ailanthus* seedlings on 10 June, 20 June, 2 July, 15 July, 31 July, 30 August, 11 September, and 17 September. On the last date I harvested the plots to assess biomass of herbs and woody seedlings. Because I had observed some apparent toxic effects of the insecticide on the woody seedlings early in the experiment, I only harvested the plots that did not receive insecticide. The harvest procedures were identical to those detailed for the 1989 experiment.

Statistical analyses

I tested the effects of all the factors and their interactions on cumulative seedling emergence, and number of seedlings surviving at the end of the experiment by analysis of variance (SAS Institute 1985). The counts of seedlings per plot were transformed to $(\text{count} + 0.5)^{-1/2}$. Mean days to emergence was also analyzed by ANOVA after arcsine transformation. The effect of the treatments on cotyledon damage in the first experiment was tested by a two-way ANOVA on the arcsine-transformed data. To assess the effects of the treatments on woody seedling mortality, I used G tests of goodness of fit on the percentage of accumulated dead seedlings, and G tests of independence to assess the existence of interactions among the effects of the factors studied. For the 1990 experiment, and based on the visual observation of data, I assumed that no three-way interaction existed, and tested only for two-way interactions.

I analyzed the treatment effects on individual biomass of the woody seedlings by ANOVA. I used as an independent variable the average biomass of all *Ailanthus* seedlings in each plot. This procedure avoids inflated degrees of freedom for the experimental error (Hairston 1989). Log transformation of the biomass values increased normality and achieved variance homogeneity. Though litter significantly delayed the emergence of woody seedlings, the inclusion in the model of the age of the seedling as a covariate was not appropriate due to the different responses of seedling biomass to age observed in the different treatments. I used ANOVAs to assess how the presence of litter affected the performance of the competing herbs. I an-

TABLE 1. ANOVA for arcsine-transformed values of cumulative number of emerged seedlings of *Ailanthus* in the 1989 and 1990 experiments (10 and 4 replications per treatment combination respectively). L = litter present, C = competition from herbs, I = insecticide used.

Source of variation	df	F	P
	1989 experiment		
L	1	7.71	0.009**
C	1	0.01	$0.925^{\rm NS}$
L × C	1	3.53	$0.686^{\rm NS}$
	1990 experiment		
Block	3	1.25	$0.289^{\rm NS}$
L	1	8.43	0.007**
C	1	0.14	$0.713^{\rm NS}$
I	1	7.76	0.010*
L × C	1	0.16	$0.691^{\rm NS}$
L × I	1	0.02	$0.894^{\rm NS}$
I × C	1	0.01	$0.917^{\rm NS}$
L × C × I	1	0.19	$0.699^{\rm NS}$

* $P < 0.05$, ** $P < 0.01$, NS = nonsignificant.

alyzed herb density (as $[\text{count} + 0.5]^{-1/2}$) of grasses (mostly *Setaria faberii*) and herbaceous dicots, and total aerial biomass (after log transformation) in the competition treatments (the only treatments containing any herbs).

I analyzed the effects of litter, competition, insecticide, and their interactions on the total number of arthropods and on the abundance of plant-chewing arthropods, applying ANOVAs to the number of individuals per plot transformed as $(\text{count} + 0.5)^{-1/2}$. I also analyzed the treatment effects on those taxa that were found in at least half the plots: crickets (*Grillus pennsylvanicus*), adult ground beetles (*Calosoma* sp., Carabidae), larvae of ground beetles (probably also *Calosoma* spp.), ants (Formicidae), spiders, millipedes, and Orthoptera other than crickets. Because of the lack of normality in the data, I used Kruskal-Wallis tests, using each factor combination as a treatment. I calculated an approximate F using an ANOVA on the ranks obtained by the RANK procedure (SAS Institute 1985). This approximation is more reliable than the chi square approximation obtained by alternative procedures (SAS Institute 1985). Because of the non-independence of the tests, I corrected the estimated alphas by Bonferroni's correction for $n = 7$ comparisons.

RESULTS

Seedling emergence and survivorship

In both years litter significantly reduced the cumulative number of emerged seedlings (Table 1, Fig. 1) and delayed their emergence (from 18.2 to 35.7 d to mean emergence day in 1989, and from 12.5 to 24.3 d in 1990; ANOVAs, $P < 0.01$). The number of seedlings of *Ailanthus* per plot at the end of the experiments was lower in the treatments with litter (ANOVA, $P < 0.01$), partially because of higher mortality in those plots (Fig. 1, G test of homogeneity, df = 3, $P < 0.01$). The effect of litter on mortality was independent of the presence of herbs (G test of independence, df = 1, $P > 0.05$ in both years). In 1989 the presence of litter increased the percentage of cotyledon consumed at 30 June ($P < 0.01$), but the damage was reduced by the presence of herbs (Fig. 1). In 1990 the insecticide applications significantly increased the total number of emerged seedlings (Table 1, Fig. 1). The application of insecticide also reduced seedling mortality (G tests of homogeneity, df = 1, $P < 0.01$), and the effects of litter and insecticide were not independent (G test of independence, df = 1, $P < 0.01$). Neither competition nor any of the interactions had any significant effect ($P > 0.01$) on seedling mortality. At the end of the experiment the treatments with litter had the lowest seedling densities, and those with insecticide the highest (Fig. 1, ANOVA, $P < 0.01$).

Activity of herbivores

In the 1990 experiment the total number of arthropods per plot and the abundance of plant-chewing arthropods were increased by the presence of litter and reduced by the application of insecticide (Table 2). There was also a significant litter × insecticide interaction (Table 2) because litter only increased the abundance of arthropods in the absence of insecticide. The treatments with litter but without insecticide had the highest abundance of crickets, ants, and millipedes, and the treatments with insecticide had the lower abundances (Kruskal-Wallis test, $P < 0.01$; Table 3).

Seedling biomass: effects of litter and competition

The herb community in all the plots was very simple, and similar to that documented in previous studies (Facelli and Pickett 1991*a*, *c*). *Setaria faberii* was the dominant species, and only a few individuals of *S. viridis*, *Panicum dichotomiflorum*, and of various forbs were observed. Litter reduced total herb biomass (Fig. 2, $P < 0.01$) and density of grasses ($P < 0.01$), but not that of the dicots ($P > 0.01$). The effect of litter on the density and biomass of the herbs was similar to that observed in previous field and greenhouse experiments (Facelli and Pickett 1991*a*, *c*).

Competition had a strong, negative effect on woody seedling biomass (Table 4, Fig. 2), and accounted for most of the variation. Litter had no significant effect on individual biomass (Table 4). The litter × competition interaction was highly significant (Table 4) because the presence of litter in the competition treatments increased the biomass of the seedlings compared to competition without litter (Fig. 2).

The aerial biomass of all herbs was lower in 1990 than in 1989, and the relative effect of litter on the herb biomass was seemingly stronger (from a reduction of 30 ± 8% in 1989 to a reduction of 44 ± 12% in

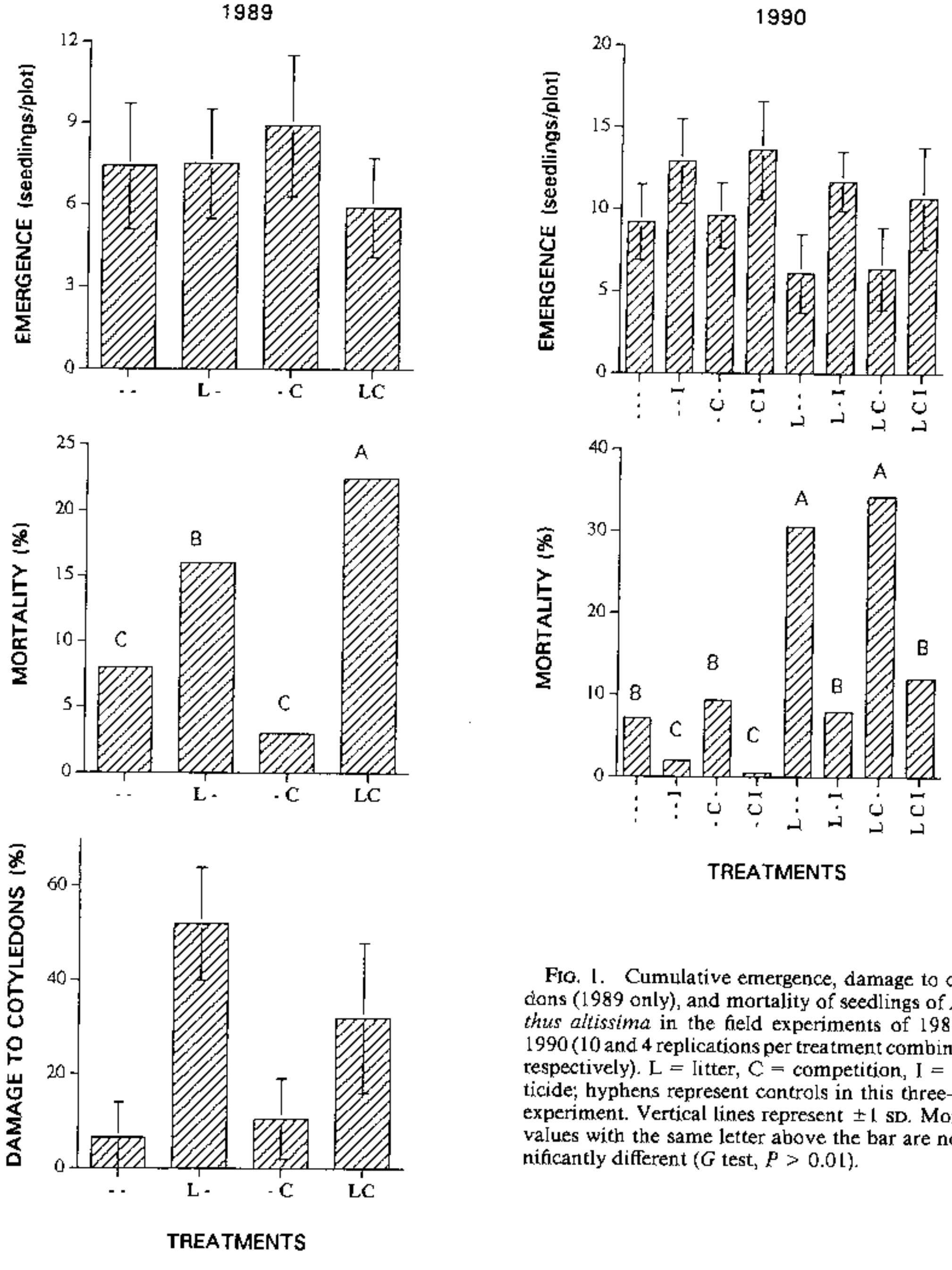

Fig. 1. Cumulative emergence, damage to cotyledons (1989 only), and mortality of seedlings of *Ailanthus altissima* in the field experiments of 1989 and 1990 (10 and 4 replications per treatment combination, respectively). L = litter, C = competition, I = insecticide; hyphens represent controls in this three-factor experiment. Vertical lines represent ±1 SD. Mortality values with the same letter above the bar are not significantly different (*G* test, $P > 0.01$).

1990 [mean ± 1 SD]). The individual biomass of the seedlings in 1990 was lower than those of 1989 (Fig. 2).

Discussion

Effects of litter, competition, and herbivory

Competition by herbs, presence of litter, and seedling predation strongly influenced the establishment of *Ailanthus* seedlings. Litter had no significant direct effect on seedling biomass (although consistently tending to reduce it, see Fig. 2), but its presence controlled the effect of both competition and seedling predation. The results demonstrate that the indirect effects of litter on woody seedling biomass suggested by a previous greenhouse study (Facelli and Pickett 1991*c*) are also detectable under field conditions. This field study also unravelled the importance of the negative indirect effect of litter on the establishment of individual seedlings, through an increase in the activity of herbivorous arthropods.

TABLE 2. ANOVA on total number of arthropods and total number of plant-chewing insects per plot in the 1990 experiment (four replications per treatment combination). Data were transformed for the analyses to $(\text{count} + 0.5)^{-½}$. L = litter present, C = competition from herbs, I = insecticide used.

Source of variation	df	*F*	*P*
	Total number of arthropods		
L	1	15.85	<0.001***
C	1	0.03	0.859^{NS}
L × C	1	2.33	0.140^{NS}
I	1	32.65	<0.001***
L × I	1	5.61	0.010**
C × I	1	0.07	0.925^{NS}
L × C × I	1	0.06	0.815^{NS}
	Total number of plant-chewing insects		
L	1	26.43	<0.001***
C	1	2.18	0.152^{NS}
L × C	1	1.18	0.287^{NS}
I	1	56.43	<0.001***
L × I	1	25.70	<0.001***
C × I	1	2.35	0.140^{NS}
L × C × I	1	1.20	0.282^{NS}

** $P < 0.01$, *** $P < 0.001$, NS = nonsignificant.

Competition was the most important factor regulating the individual biomass of the *Ailanthus* seedlings. Litter indirectly reduced the strength of competition by reducing both the density and the biomass of the dominant herb, *Setaria faberii* (see also Facelli and Pickett 1991*a*). The main direct effect of litter on the woody seedlings was seemingly the delay of their emergence (which could account for the marginal negative effect of litter on seedling biomass). The observed reduction in establishment and increased mortality can be attributed to indirect effects, through increased activity of herbivores. In the presence of competitors the marginal negative effect of litter was overridden by its positive indirect effect through reduced competition. The relative importance of the positive indirect effect of litter on seedling biomass was far smaller than the direct competitive effect of herbs. However, the presence of litter in plots with competition increased seedling biomass by a factor of almost 2 and 3 in 1989 and 1990, respectively.

The reduced mortality and the increased emergence in the plots with insecticide strongly support the contention that the reduced establishment produced by litter was due, at least partially, to increased seed and/or pre-emergence seedling predation by invertebrates. Thus, litter indirectly controls the predation rate on the *Ailanthus* seedlings. Litter may prevent seedling emergence by mechanical impediment (Grime 1979, Bergelson 1990*a*, *b*). Longer confinement under dense litter mats may render the more tender tissues of the etiolated seedling more prone to pathogen attack and herbivore damage (Facelli and Pickett 1991*b*). Even though reduced emergence was also observed in greenhouse experiments (Werner 1975, Hamrick and Lee 1987) where herbivory is unlikely to occur, my results warn against automatically attributing reduced emergence in field experiments solely to the direct effects of litter (e.g., Werner 1975, Carson and Peterson 1990, Facelli and Pickett 1991*a*). In the parallel greenhouse experiment (Facelli and Pickett 1991*c*) I did not find any negative effect of litter on the emergence of seedlings of *Ailanthus*. The negative direct effect of litter is likely to be more important in small-seeded species (Peterson and Facelli 1992).

The increased activity of arthropods in the plots with litter may be explained because litter provided an environment with improved temperature and humidity (see review in Facelli and Pickett [1991*b*]). It is also possible that some arthropods may find refugia in the litter, while predators (carabids, spiders) may find higher prey abundance there. I did not find any significant effect of the presence of herbs on the abundance of

TABLE 3. Numbers of several taxa of arthropods, total number, and number of plant-chewing ("Chewers") arthropods per plot in the 1990 experiment. The contents of two pitfall traps per plot were pooled together.*

	Treatments†							
Taxa	---	--I	-C-	-CI	L--	L-I	LC-	LCI
Carabidae								
Adults	0.75^{B}	0.00^{B}	0.75^{B}	0.50^{B}	1.50^{B}	1.00^{B}	3.25^{A}	1.00^{B}
Larvae	2.00^{B}	0.50^{B}	2.75^{B}	1.50^{B}	4.50^{AB}	3.75^{AB}	7.50^{A}	2.50^{B}
Crickets	1.00^{B}	0.75^{B}	0.75^{B}	0.25^{B}	3.50^{A}	1.00^{B}	3.75^{A}	1.50^{B}
Millipedes	1.00^{B}	1.25^{B}	2.75^{AB}	0.50^{B}	4.75^{A}	2.00^{B}	3.25^{A}	1.00^{B}
Spiders	2.00^{A}	1.00^{A}	2.25^{A}	2.75^{A}	2.25^{A}	1.75^{A}	1.00^{A}	0.25^{A}
Ants	1.25^{B}	0.25^{B}	2.00^{B}	1.00^{B}	17.50^{A}	3.25^{B}	12.00^{B}	2.50^{B}
Other	6.25^{A}	5.50^{A}	8.00^{A}	5.00^{A}	7.00^{A}	1.75^{A}	6.75^{A}	2.50^{A}
Total	14.25^{B}	8.78^{C}	19.25^{B}	11.50^{BC}	41.00^{A}	14.50^{B}	37.50^{B}	11.25^{BC}
Chewers	3.25^{B}	4.25^{B}	5.25^{B}	2.25^{B}	11.25^{A}	3.75^{B}	8.50^{A}	2.75^{B}

* See Table 2 for statistical analyses of total number, and of number of plant-chewing arthropods. The other classes were analyzed by Kruskal-Wallis test; same superscript letters within a column means that differences were not significant (LSD on ranks, $P < 0.01$).

† Hyphens in the treatment codes indicate controls in the three-factor design. L = litter presence, C = competition from herbs, I = insecticide used.

arthropods, although presence of herbs reduced damage to cotyledons in 1989. The structural complexity of the plant community strongly affected the arthropod community in other studies (e.g., Riechert and Bishop 1990, see review in Lawton [1983]). The presence of alternative food items could reduce herbivore pressure (Fenner 1987), but the sensitivity of seedlings to herbivory may be increased by competition (Dirzo 1986). These two effects may have compensated each other in my experiment. I did not observe any evidence of damage by mammals, which contrasts with results from another study performed in the same field using seedlings of *Carya* sp. (Myster and McCarthy 1989). This may be due to differences in the species and age of the seedlings used in the experiments, or to seasonal differences in herbivore activity.

Unfortunately, the inability to get an accurate measurement of biomass in the treatments with insecticide prevented the assessment of possible direct and indirect effects of insects on herbs and woody seedling biomass. Riechert and Bishop (1990) found that mulching (i.e., litter addition) increased predation by spiders, which resulted in reduced damage to plants by insect herbivores. Detailed studies of the effects of litter on the arthropod community could reveal further indirect effects.

The long interval between some of the samplings may have resulted in the underestimation of mortality in the 1990 experiment, but that would only make the results more conservative. Though I observed possible signs of insecticide toxicity in the *Ailanthus* seedlings in the insecticide plots, I could not find any evidence of negative effect on emergence and survivorship. That effect would have partially masked the protection against arthropods, making my conclusions even more conservative.

Though the amount of biomass consumed is small, the reduction in the density of woody seedlings may have important effects on the community structure later in the successional process. The effect of herbivory on plant populations may be disproportionate to the amount of biomass removed, especially if biomass is removed during sensitive parts of the life cycle, or if meristems are damaged (Crawley 1983, Dirzo 1986, Edwards and Gillman 1987, Verkaar 1987, Louda et al. 1990).

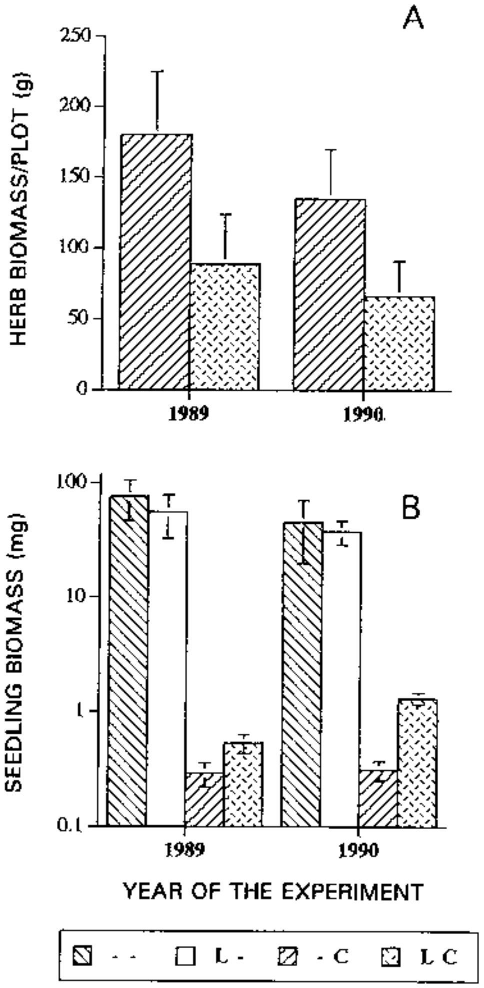

FIG. 2. (A) Aerial biomass of herbs (mostly the grass *Setaria faberii*) in the plots with competition in the 1989 and 1990 experiments. The narrow bars represent 1 SD for total herb biomass. (B) Total mean individual biomass of seedlings of *Ailanthus altissima* in the 1989 and 1990 experiments. The narrow bars represent ± 1 SD. Notice the logarithmic scale. L = litter, C = competition; hyphens indicate control treatments.

TABLE 4. ANOVAs for log-transformed values of mean biomass of seedlings of *Ailanthus* in the 1989 and 1990 experiments (10 and 4 replications per treatment combination, respectively). In 1990 only the treatments that had not received insecticide were harvested. L = litter, C = competition.

Source of variation	df	F	P
	1989 experiment		
L	1	3.35	0.086^{NS}
C	1	549.73	<0.001**
L × C	1	18.84	<0.001**
	1990 experiment		
Block	3	1.10	0.399^{NS}
L	1	3.89	0.081^{NS}
C	1	166.63	<0.001**
L × C	1	15.36	0.003**

** $P < 0.01$, NS = nonsignificant.

Conceptual implications

While interest in indirect effects is relatively recent, several experimental studies have shown their presence in animal communities (Wilbur 1972, Morin 1981, Davidson et al. 1984, Martin et al. 1989). In contrast, and despite theoretical formulations (Vandermeer et al. 1985), examples of indirect effects in plant communities are scant (Hunter and Aarsen 1988), and in most cases the effects are mediated by herbivores (Harper 1969, Bentley and Whittaker 1979, Lubchenco 1986). Cases of one plant favoring another plant by suppressing a third, competing plant are scarce and inconclusive (see review in Hunter and Aarsen [1988]). Indirect effects among competing plants may be unimportant if plant competitors within a given size range are essentially equivalent, as proposed by Goldberg and Werner (1983). Indirect effects among three competing populations could result from asymmetric and intransitive relationships among competing species. Experimental studies (Gaudet and Keddy 1988, Keddy 1989) show that interspecific plant competition is almost always asymmetric and transitive.

Important indirect effects among plants may be mediated by environmental changes produced by living or dead plants, which alter the outcome of the interactions between other plant populations (Bergelson 1990*b*, Facelli and Pickett 1991*b*, *c*) and between plants and herbivores (Facelli and Pickett 1991*b*). The indirect effect of oak leaf litter reported here and in Facelli and Pickett (1991*c*) seems to be a novel one. The influence of the plants that produce the litter can be remote in space when litter is deposited away from the plant (Shure and Phillips 1987, Facelli and Carson 1991). This effect can also have a historical component, since the amount of litter accumulated depends on past events controlling production and destruction of biomass in the system (Bergelson 1990*a*, *b*, Facelli and Pickett 1991*b*).

In this study I documented that even in a simple, early successional community the web of interactions can be of considerable complexity. In addition to the expected direct effects (i.e., competition, herbivory, litter interference), I detected two indirect effects, one positive and one negative, each acting on different aspects of the plant population dynamics (i.e., on individual biomass and on seedling mortality, respectively). These indirect effects produced a twofold (or larger) increase in biomass and mortality over the "natural" condition (competition treatments). It has been argued that the strength of the indirect effects may be relatively small in comparison to that of the direct effects (Vandermeer 1981). However, as pointed out by Morin et al. (1988), they are large enough to be detected over the fairly large "background noise" that characterizes ecological systems. While there is little evidence to support Patten's (1991) claim that indirect effects may dominate ecological systems, it is probably safe to assume that understanding them will increase the predictive and explanatory power of community ecology. The theoretical and experimental investigation of entire, albeit necessarily simple, interaction webs will further our understanding of the structure of ecological communities better than the evaluation of the relative importance of different, isolated interactions.

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LITERATURE CITED

Bentley, S., and J. B. Whittaker. 1979. Effects of grazing by a Chrysomelid beetle, *Gastrophysa viridula*, on competition between *Rumex obtusifolia* and *Rumex crispus*. Journal of Ecology **67**:79–90.

Bergelson, J. 1990*a*. Spatial patterning in plants: opposing effects of herbivory and competition. Journal of Ecology **78**:937–948.

———. 1990*b*. Life after death: site pre-emption by the remains of *Poa annua*. Ecology **71**:2157–2165.

Brown, V. K. 1985. Insect herbivory and plant succession. Oikos **44**:17–22.

Brown, V. K., A. C. Gange, I. M. Evans, and L. Storr. 1987. The effect of insect herbivory on the growth and reproduction of two annual *Vicia* species at different stages in plant succession. Journal of Ecology **75**:1173–1189.

Carson, W. P., and C. J. Peterson. 1990. The role of litter in an old-field community: impact of litter quantity in different seasons on plant species richness and abundance. Oecologia **85**:8–13.

Connell, J. H. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. American Naturalist **122**:661–696.

———. 1990. Apparent versus "real" competition in plants. Pages 9–26 *in* J. B. Grace and D. Tilman, editors. Perspectives in plant competition. Academic Press, New York, New York, USA.

Crawley, M. J. 1983. Herbivory. The dynamics of plant–animal interactions. Blackwell Scientific, Oxford, England.

Davidson, D. W., R. S. Inouye, and J. H. Brown. 1984. Granivory in a desert ecosystem: experimental evidence for indirect facilitation of ants by rodents. Ecology **65**:1780–1786.

Dirzo, R. 1986. The role of the grazing animal. Pages 343–355 *in* J. White, editor. Studies in plant demography. Academic Press, London, England.

Edwards, P. J., and M. P. Gillman. 1987. Herbivores and plant succession. Pages 295–314 *in* A. J. Gray, M. J. Crawley, and P. J. Edwards, editors. Colonization, succession, and stability. Blacwell, Oxford, England.

Facelli, J. M., and W. P. Carson. 1991. Heterogeneity of plant litter accumulation in seral communities. Bulletin of the Torrey Botanical Club **118**:62–66.

Facelli, J. M., and E. Facelli. 1993. Interactions after death: plant litter controls priority effects in a successional plant community. Oecologia **95**:277–282.

Facelli, J. M., and S. T. A. Pickett. 1991*a*. Plant litter: light interception and effects on an old-field plant community. Ecology **72**:1024–1031.

Facelli, J. M., and S. T. A. Pickett. 1991*b*. Plant litter: dynamics and effects on plant community structure and dynamics. Botanical Review **57**:1–32.

Facelli, J. M., and S. T. A. Pickett. 1991*c*. Direct and indirect effects of plant litter on woody seedlings subject to competition. Oikos **62**:129–138.

Fenner, M. 1987. Seedlings. New Phytologist **106**:35–47.

Gaudet, C. L., and P. A. Keddy. 1988. A comparative approach to predicting competitive ability from plant traits. Nature **334**:242–243.

Gleasson, H. A., and A. Cronquist. 1963. Manual of vascular plants of Northeastern United States and adjacent Canada. Van Nostrand Reinhold, New York, New York, USA.

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

Grime, J. P. 1979. Plant strategies and vegetation processes. John Wiley & Sons, New York, New York, USA.

Hairston, N. G. 1989. Ecological experiments. Purpose, design, and execution. Cambridge University Press, Cambridge, England.

Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. American Naturalist **44**:421–425.

Hamrick, J. L., and J. M. Lee. 1987. Effects of soil surface topography and litter cover on germination, survival and growth of musk thistle. American Journal of Botany **74**: 451–457.

Harper, J. L. 1969. The role of predation in vegetational diversity. Brookhaven Symposia in Biology **22**:48–62.

Hunter, A. E., and L. W. Aarsen. 1988. Plants helping plants. BioScience **38**:34–40.

Keddy, P. A. 1989. Competitive hierarchies in herbaceous plant communities. Oikos **54**:234–241.

Lawton, J. H. 1983. Plant architecture and the diversity of phytophagous insects. Annual Review of Entomology **28**: 23–29.

Louda, S. M., K. H. Keeler, and R. H. Dolt. 1990. Herbivore performance and competitive interactions. Pages 413–444 *in* J. B. Grace and D. Tilman, editors. Perspectives in plant competition. Academic Press, New York, New York, USA.

Lubchenco, J. 1986. Relative importance of competition and predation: early colonization by seaweeds in New England. Pages 537–555 *in* J. Diamond and T. J. Case, editors. Community ecology. Harper & Row, New York, New York, USA.

Martin, T. H., R. A. Wright, and L. B. Crowder. 1989. Nonadditive impact of blue crabs and spot on their prey assemblages. Ecology **70**:1935–1942.

Morin, P. J. 1981. Predatory salamanders reverse the outcome of competition among three species of anuran tadpoles. Science **212**:1284–1286.

Morin, P. J., S. P. Lawler, and E. A. Johnson. 1988. Competition between aquatic insects and vertebrates: interaction strength and higher order interactions. Ecology **69**: 1401–1409.

Myster, R., and B. C. McCarthy. 1989. Competition vs. herbivory: survival of *Carya tomentosa* seedlings in a forest–field ecotone. Oikos **56**:145–148.

Odum, E. P. 1960. Organic production and turnover in old field succession. Ecology **41**:34–49.

Patten, B. C. 1991. Network ecology: indirect determination of the life–environment relationship in ecosystems. Pages 288–351 *in* M. Higashi and T. P. Burns, editors. Theoretical studies of ecosystems: the network perspective. Cambridge University Press, New York, New York, USA.

Peterson, C. J., and J. M. Facelli. 1992. Contrasting germination and seedling growth of *Betula alleghaniensis* and *Rhus typhina* subject to various amounts and types of plant litter. American Journal of Botany **79**:1209–1216.

Riechert, S. E., and L. Bishop. 1990. Prey control by an assemblage of generalist predators: spiders in garden test systems. Ecology **71**:1441–1450.

Robichaud, B., and M. F. Buell. 1973. Vegetation of New Jersey. Rutgers University Press, New Brunswick, New Jersey, USA.

Roughgarden, J., and J. Diamond. 1986. The role of species interactions in community ecology. Pages 333–343 *in* J. Diamond and T. D. Case, editors. Community ecology. Harper & Row, New York, New York, USA.

SAS Institute. 1985. SAS user's guide: statistics. Version 5 edition. SAS Institute, Cary, North Carolina, USA.

Schoener, T. W. 1983. Field experiments in interspecific competition. American Naturalist **122**:240–285.

Shure, D. J., and D. L. Phillips. 1987. Litterfall patterns within different sized disturbance patches in a Southern Appalachian Mountain forest. American Midland Naturalist **118**:348–357.

Southwood, T. R. E. 1979. Ecological methods. Chapman and Hall, London, England.

United States Weather Bureau [Department of Commerce]. 1959. Climate of the states—New Jersey. United States Government Printing Office, Washington, D.C., USA.

USDA [United States Department of Agriculture]. 1976. Soil survey of Somerset County, New Jersey. U.S. Department of Agriculture, Washington, D.C., USA.

Vandermeer, J. H. 1981. A further note on community models. American Naturalist **117**:379–380.

Vandermeer, J. H., B. Hazlett, and B. Rathcke. 1985. Indirect facilitation and mutualism. Pages 326–343 *in* D. H. Boucher, editor. The biology of mutualism, ecology and evolution. Croom Helm, London, England.

Verkaar, H. J. 1987. Population dynamics—the influence of herbivory. New Phytologist **106**:49–60.

Werner, P. A. 1975. The effect of plant litter on germination in teasel, *Dipsacus sylvestris* Huds. American Midland Naturalist **94**:470–476.

Wilbur, H. M. 1972. Competition, predation, and the structure of the *Ambystoma–Rana sylvatica* community. Ecology **53**:3–20.