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Thomas E. Miller

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DIRECT AND INDIRECT SPECIES INTERACTIONS IN AN EARLY OLD-FIELD PLANT COMMUNITY

THOMAS E. MILLER*

Department of Biological Science, Florida State University, Tallahassee, Florida 32306-2043

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Abstract.—The success of species in a community is determined not only by the direct interactions between species but also by indirect interactions. Indirect effects will occur if an associate species changes the abundance of intermediate species in a chain of interactions that ultimately affect the growth of some focal species. A model of species interactions in a community is presented here and used to quantify direct and indirect effects in a five-species weedy plant community. This method quantifies indirect effects by measuring changes in the abundance of the intermediate species and then estimating how such changes will affect the focal species. The experiments demonstrated that the direct effects in this community were generally negative (competitive) and could be quite large. Indirect effects were positive (facilitative) and negatively correlated with the direct effects, which thus acted to mitigate the usually larger competitive effects. The magnitudes of most species interactions in this community were primarily determined by large direct effects of *Ambrosia artemisiifolia* and, to a lesser extent, *Agropyron repens*. The species that exhibited the least competitive release following the removal of a competitor were those that were the most suppressed, because of the nonlinear nature of their response to increasing abundance of competitors.

Each species in a community is affected by interactions with many other species. Understanding this complex set of interactions involves determining a combined effect of the many often simultaneous species interactions in which any single species is participating. This understanding has proven elusive, and several authors have even suggested that it may, at present, be beyond our grasp (Brown 1981; Simberloff 1982).

Much of the difficulty appears to stem from indirect effects through the linkages or loops (Levins 1975) of interactions connecting different species. I define an indirect effect of an "associate" species on a "focal" species as that produced when the associate species changes the direct effect of one or more other associate species on the focal species. This definition encompasses what other authors have termed *indirect effects* (see, e.g., Levine 1976; Schmitt et al. 1983; Abrams 1984, 1987), *higher-order interactions* (Vandermeer 1969; Wilbur 1972; Abrams 1983; Morin et al. 1988), and *apparent competition* (Holt 1977; Schmitt 1987). For example, a predator that changes the abundance or behavior of a prey species, and thus alters the effect of that species on its own prey, has an indirect effect across a trophic level on the resource species of its prey. Indirect effects

* E-mail: miller@bio.fsu.edu.

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can occur both between and within trophic levels and either in the absence of or simultaneously with direct interactions between two species. The net effect of any one species on another in a community is the sum of the effects produced through all direct and indirect pathways of interaction. The complex webs of direct and indirect pathways determine not only the abundance of individual species but also community characteristics such as diversity and stability.

The general mechanisms of plant-plant interactions create operational and semantic difficulties for understanding indirect effects in plant communities. Even direct interactions among plants are usually "indirect" in the sense that the interactions occur through shared resources such as light, water, and nitrogen. However, most published definitions of indirect effect specifically require an intermediate living individual or population (see, e.g., Miller and Kerfoot 1987; Stone and Roberts 1991; Wootton 1993). Thus, for the purposes of this article, *direct effect* will refer to the effect of one species on another through the consumption of shared, presumably abiotic limiting resources. *Indirect effect* will refer to the effect of one species on another through direct effects on the resource consumption of one or more intermediate species.

Many experimental studies have shown that indirect effects can qualitatively affect species abundances and have documented some of the different types of pathways that can be involved. For example, a predator can reduce the density of a prey species, which thus reduces the effect of the prey species on competitors (keystone predation; see, e.g., Paine 1966; Lubchenco 1978). However, early efforts to quantify indirect effects (Vandermeer 1969; Wilbur 1972; Neill 1974; Case and Bender 1981) have been subject to much later reanalysis and criticism (Brenchley 1979, 1981; Pomerantz 1981; Thomas and Pomerantz 1981; Vandermeer 1981; see discussion in Roughgarden and Diamond 1986). Indirect effects between two species are experimentally confounded with simultaneously occurring direct effects and by nonlinear interactions. Other methods proposed for quantifying indirect effects are quite restricted in their application, requiring stable communities (at or near equilibrium) and linear, Lotka-Volterra dynamics (Lawlor 1979; Davidson 1980; Bender et al. 1984). Thus, virtually all the evidence of indirect effects comes from situations in which either no direct effects are likely (e.g., across three distinct trophic levels; Werner et al. 1983) or the indirect effect is larger than and in the opposite direction from the direct effect (Silander and Antonovics 1982; however, see Dungan 1986). In these situations, the presence of indirect effects can be demonstrated by removing an associate species and measuring changes in the focal species ("press experiments," sensu Bender et al. 1984).

Although experimental quantification of indirect effects in the presence of simultaneous direct effects may be very difficult, there is certainly no reason to expect that such indirect effects are not important. In particular, although most studies of indirect effects have considered interactions between trophic levels, indirect effects among competitors may also be very important (see, e.g., Vandermeer 1969; Neill 1974; Silander and Antonovics 1982). Because direct effects between competitors are by definition negative, the simplest indirect effects (those involving only one intermediate competitor) must be positive. Also, al-

though only a single negative direct effect occurs between any pair of competitors, many indirect linkages are possible through intermediate competitors. Theoretical investigations have also suggested that indirect effects among competitors play a substantial role in structuring communities (see, e.g., Lawlor 1979; Schaffer 1981; Yodzis 1988; Stone and Roberts 1991).

In this article, I present a model that quantifies direct and indirect species interactions among competitors. Parameters for this model were obtained from a five-species community of weedy plants. The specific problems addressed are assessing the relative strengths of the direct and indirect interactions between each pair of species and determining the ways in which various direct and indirect effects combine to account for the abundance of each species in the community.

A MODEL OF PLANT INTERFERENCE

I have constructed a model of plant interference to estimate the direct and indirect effects occurring between all possible pairs of species in a community. The model is based on the mean response of individuals of a focal species to the abundances of different associate species. In an n-species system, the growth response or biomass of the focal species is represented as a surface in $(n + 1)$-dimensional space. Each independent axis represents the abundance (biomass/area or yield) of a different associate species, and the dependent axis denotes the mean size of individuals of the focal species. A point on the response surface represents the growth of an individual of the focal species at a particular combination of the abundances of the different associate species. Indirect effects occur if one associate species changes the abundance of a second associate species, which thus changes the position of the focal species on the response surface (linkage indirect effect; Miller and Kerfoot 1987), or if one associate species interacts with another, which changes the per-unit effects of the second associate species and results in a change in the shape of the response surface (behavioral indirect effect; Miller and Kerfoot 1987; what some authors have termed *higher-order interaction;* see, e.g., Vandermeer 1969; Neill 1974).

Two assumptions permit simplification of this n-dimensional representation. First, two-species competition experiments (Peart and Foin 1985; Goldberg 1987; Miller and Werner 1987) have suggested that, in general, a focal species responds similarly to a given yield of any associate species, regardless of the identity of the associate species (competitor equivalence; see Goldberg and Werner 1983). Therefore, in the multidimensional representation, the individual curves representing the effects of the yields of different associate species on the focal species are identical.

Second, I assume that, if the effects of different associate species are equivalent on a per-gram basis, the yields of different associate species can be added for purposes of determining their net effect. This additivity suggests that no behavioral indirect effects (Miller and Kerfoot 1987) are occurring: the presence of a second associate species may change the yield of another associate species (its position on the response curve) but not the per-gram effect of that species on the focal species (the shape of the response curve).

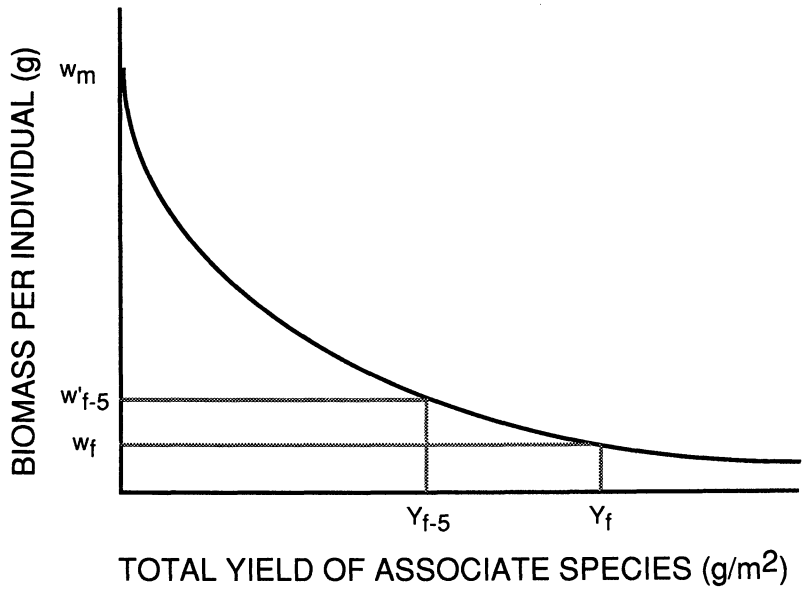

FIG. 1.—The expected relationship between the mean growth of individuals of the focal species and the total yield of the associate species (g/m^2). Values are defined in the text.

On the assumption that associate species effects are equivalent and additive, the independent axes in the n-dimensional space can be collapsed into a single axis. Figure 1 illustrates such a generalized response curve in which the total combined yield of all the associate species in the full community (Y_f) determines the mean biomass per individual of the focal species (w_f). The value w_m is the mean biomass of individuals of the focal species when no associate species are present.

The following section demonstrates how generalized response curves such as figure 1 can be used to quantify direct and linkage indirect effects in a multispecies plant community. In this method, the effect of a single associate species on the summed yield of all other associate species is separated into two components: the direct contribution of its own biomass and the indirect contribution it makes by changing the yields of other associate species. The response curve of the focal species is then used to convert these direct and indirect contributions of a single associate species to the summed yield of other associate species into direct and indirect effects on the focal species.

QUANTIFYING SPECIES INTERACTIONS

Consider a five-species community in which the focal species is species 1 and the associate species whose direct and indirect effects are to be quantified is species 5, which has a yield of Y_5. The total effect of associate species 5 on the focal species can be experimentally quantified as the response of the focal species

to the removal of species 5—that is, the difference in the mean biomass of the focal species with (w_f) and without (w_{f-5}) associate species 5 present, standardized by the maximum potential biomass of that focal species (w_m):

$$\text{total effect of associate 5 on } w = (w_f - w_{f-5})/w_m. \quad (1)$$

A negative term would indicate some antagonistic relationship between species; a positive term would indicate a facilitative relationship. This measure of species interactions is similar to that used by Silander and Antonovics (1982) to quantify species interactions in dune plant communities. The difficulty is that this total effect is some unknown combination of direct and indirect effects. I have estimated the direct and indirect components by noting that, when no indirect effects occur, the direct effect equals the total effect and so can be measured with equation (1). Experimentally, one could create such a situation by holding the abundance of the intermediate species constant while removing the associate species of interest (see Werner et al. 1983). However, this is not possible with plants: I cannot remove one species and then hold the growth of some group of the remaining species constant.

I can, however, simulate this situation with a knowledge of the biomass of the other associate species from the five-species mixture and the relationship between associate species yield and focal species biomass (fig. 1). If no indirect effects occur, then the biomass of the intermediate three species, Y_{f-5}, would not differ with the presence or absence of species 5. I therefore use Y_{f-5} from the five-species community and the relationship between associate species yield and focal species biomass (e.g., fig. 1) to determine the expected response of a focal species to the removal of associate species 5 (w'_{f-5}). As in equation (1), w'_{f-5} can then be used to calculate the direct effect of an associate species on the focal species:

$$\text{direct effect of associate species 5 on } w = (w_f - w'_{f-5})/w_m. \quad (2)$$

The indirect effect is produced when species 5 changes the abundance of intermediate species, which thus changes the effect of these intermediate species on the focal species; it is represented by the difference between w'_{f-5} and w_{f-5}:

$$\text{indirect effect of associate species 5 on } w = (w'_{f-5} - w_{f-5})/w_m. \quad (3)$$

The total, direct, and indirect effects all represent the reduction in growth of individuals of the focal species from that in monoculture. Note that, because of the per-gram equivalence of competitive effects, the direct and linkage indirect effects are assumed by the method to sum to the total effect:

$$\text{direct effect} + \text{indirect effect} = \text{total effect}. \quad (4)$$

A strength of this approach is the straightforward meaning of the values obtained. In each case, the result represents an effect of an associate species on a focal species expressed in terms of the maximum possible growth of the focal species (i.e., growth in a monoculture in this environment). For example, a total effect of -0.30 indicates that the presence of the associate species suppresses the focal species by 30% of its maximum potential size in monoculture. Or, put

TABLE 1

MEAN DRY BIOMASS, YIELD, AND DENSITY OF EACH SPECIES FOR YEARS 1 AND 2

	YEAR 1			YEAR 2		
	Mean g	g/m^2	No./m^2	Mean g	g/m^2	No./m^2
Ambrosia artemisiifolia L.	1.53	137.17	89.8	1.60	140.55	88.0
Agropyron repens (L.) Beauvois	...	36.85	...	...	50.10	...
Plantago lanceolata L.	.87	32.07	36.9	.45	11.79	26.0
Chenopodium album L.	.06	2.56	45.3	.07	8.80	126.0
Lepidium campestre (L.) R. Brown	.05	1.96	40.4	...	...	...
Trifolium repens L.	...	...	...	.06	2.36	38.0

NOTE.—Values were determined in late September to early October of each year. Only yield was determined for *Agropyron repens* (see text).

another way, removal of the associate species caused an increase in biomass of the focal species amounting to 30% of its maximum potential size.

EXPERIMENTS IN A FIVE-SPECIES PLANT COMMUNITY

This method was used to quantify the direct and indirect effects among species in each of 2 yr in a first-year weedy community. The community studied was in an annually plowed area of Bailey Front Yard at the W. K. Kellogg Biological Station in southwestern Michigan. Plant growth is quite substantial in this community; seedling densities reach 300 individuals/m^2, and canopy height exceeds 1.5 m by late August. Resource addition experiments performed in this community suggest that light, water, and nitrogen may each limit plant growth at a different time of the season (Goldberg and Miller 1990).

The five most abundant species were used in each year of the experiments; individuals of all other species were removed from the experimental plots. The five species used in any given year made up over 95% of the biomass of the naturally occurring plant community. Three of the species were consistently codominants (by biomass) in Bailey Front Yard (*Ambrosia artemisiifolia,* common ragweed; *Agropyron repens,* quack grass; and *Plantago lanceolata,* narrow-leaf plantain), whereas a fourth species (*Chenopodium album,* lamb's-quarter) had one of the highest densities in both years (table 1). The fifth most abundant species was different in the 2 yr of the study (year 1, *Lepidium campestre,* field cress; year 2, *Trifolium repens,* red clover), and neither of the two contributed more than 1% to the total yield of the community (table 1). The six species have different life histories and growth forms, but all have very similar phenologies in this field (Miller 1987).

In both years, the field had been plowed the previous November to a depth of 20 cm. Square quadrats were marked out in April, prior to seedling emergence. The desired species mixtures were obtained by hand removal of unwanted seedlings immediately after emergence in late April and early May. This method prevented regrowth and did not significantly disturb the soil. The rhizomatous grasses (e.g., *A. repens, Bromus inermis*) could not be removed in this way

without disturbing the soil. These species were removed in year 1 by continuously clipping at the soil surface and in year 2 by applying a weak solution (3%) of the contact herbicide Round-Up.

The 2 yr of the study differed in the number of replicates and the types of treatments. In year 1 (1982), 63 2 × 2-m quadrats were used, and treatments were randomly assigned to each quadrat. The treatments consisted of all possible one-, two-, or four-species mixtures and the five-species full community; each treatment was replicated in three quadrats. In year 2 (1983), 230 1.3 × 1.3-m quadrats were marked out in a randomized block design, with five blocks. Again, all one-, two-, four-, and five-species mixtures were used; however, the monoculture treatments included both low (half of ambient) densities and ambient densities, whereas two-species mixtures were maintained at half:ambient, ambient:half, and ambient:ambient density combinations of the two species. In plots assigned low densities, randomly chosen plants were removed to obtain the desired densities.

Plants were visually monitored throughout the season for herbivore or pathogen damage. No significant insect or pathogen damage was noted, but three plots in year 1 and two plots in year 2 were removed from the analyses because of damage caused by deer grazing.

Annual species (and larger perennial individuals) in this community begin to set seed in early October. At this time, individual plant biomass is highly correlated with seed set (Miller 1987). In both years, plants in all quadrats were harvested in late September and early October. Only the center of each plot (1 m × 1 m in year 1, 0.6 m × 0.6 m in year 2) was harvested because of possible edge effects. Each individual plant was clipped at ground level, pressed, dried for 72 h at 65°C, and weighed to yield aboveground dry mass.

A critical requirement for the analysis is that the mean biomass of the focal species be a function of the total yield of all the associate species. The relationship between mean dry mass of each species and total associate species yield was determined for the quadrats containing the focal species at ambient density and any mixture of associate species, and the relationships were analyzed by linear regression. The data were transformed as noted when the transformation led to a more normal and homoscedastic distribution of residuals. The values of w_m, the mean dry mass of the focal species in the absence of associate species, were measured directly from monocultures of each species maintained at ambient densities.

Total effects (eq. [1]) were calculated from the plant biomass from monocultures (for w_m), the full five-species community (w_f), and the four-species communities (w_{f-5}). Because the analyses are based on means from plots, I have assumed that the data are normally distributed on the basis of the central limit theorem. Tukey's honestly significant difference (HSD) tests (Sokal and Rohlf 1981) were then used to test the significance of total effects by comparison of the mean biomasses of the focal species with and without the presence of each associate species. Analyses using nonparametric Mann-Whitney U-tests yielded very similar results. The yield of the other species in the community, Y_{f-5}, was determined from each of the replicate plots containing the five-species mixture. Each

Y_{f-5} was then used to determine a w'_{f-5}, by means of the focal biomass versus total yield regressions. The measures of direct and indirect effects were tested for significance by determining whether w_f and w_{f-5}, respectively, were significantly different from w'_{f-5} for each focal-associate pair, again by Tukey's HSD. The tests of significance of direct and indirect effects should be evaluated with some caution, as they are based on estimated values from regression; they are included to provide comparison with the measures of total effects.

Note that, with this experimental design, the model of plant interference does not quantify intraspecific effects: Y_5 includes the yield of all associate species but not the yield of the focal species itself, and w_m represents the mean growth of the focal species in monoculture, not of an isolated individual. While theoretically it is possible to quantify intraspecific effects, such an approach was not taken in this experiment for two reasons. First, mean mass as the dependent variable would not be statistically independent of the combined yield of all species (intra- and interspecific). This problem could be overcome using a target-neighbor design (see, e.g., Goldberg and Werner 1983), but this was not possible in the experiments presented here because of the vast increase in the number of plots required. Second, intraspecific effects were generally thought to be small for all species but *Ambrosia*. The mean plant mass and yields of *Plantago, Chenopodium, Lepidium,* and *Trifolium* in the full community were quite low (table 1), with conspecific individuals seldom in physical proximity to one another.

RESULTS

Each species varied greatly in biomass, both in the absence of associate species (w_m) and when grown with competitors (figs. 2, 3). The biomasses of *Plantago, Chenopodium* in both years, *Lepidium* in year 1, and *Trifolium* in year 2 were functions of the total yield of associate species; in each case, the response curve appears to be strongly nonlinear (figs. 2, 3). The yield of *Agropyron* was a linear function of total associate species yield in both years of the study. For *Ambrosia,* no significant effect of associate species was apparent in year 1, and only a very weak relationship appeared in year 2 ($r^2 = 0.16$). This result may be caused, in part, by the consistently low yield of other species when grown in the presence of *Ambrosia*.

The equations describing the relationship between focal species success and total yield (given in figs. 2 and 3) were used to determine w'_{f-5}, the expected mean biomass of the focal species if only direct effects occur. Because no consistent relationship was found between associate species yield and mean biomass of *Ambrosia,* it was not possible to determine w'_{f-5} and, thus, the direct and indirect effects of other associate species on *Ambrosia*. The direct and indirect effects for all associate-focal species pairs (except those with *Ambrosia* as focal species) were then determined from equations (2) and (3).

Most of the total effects, as measured by the response of focal species to the removal of single associates (eq. [1]), were less than zero, which indicates net competitive interactions (table 2). The main factor that determined the magnitude of each effect was the identity of the associate species involved. *Ambrosia* ap-

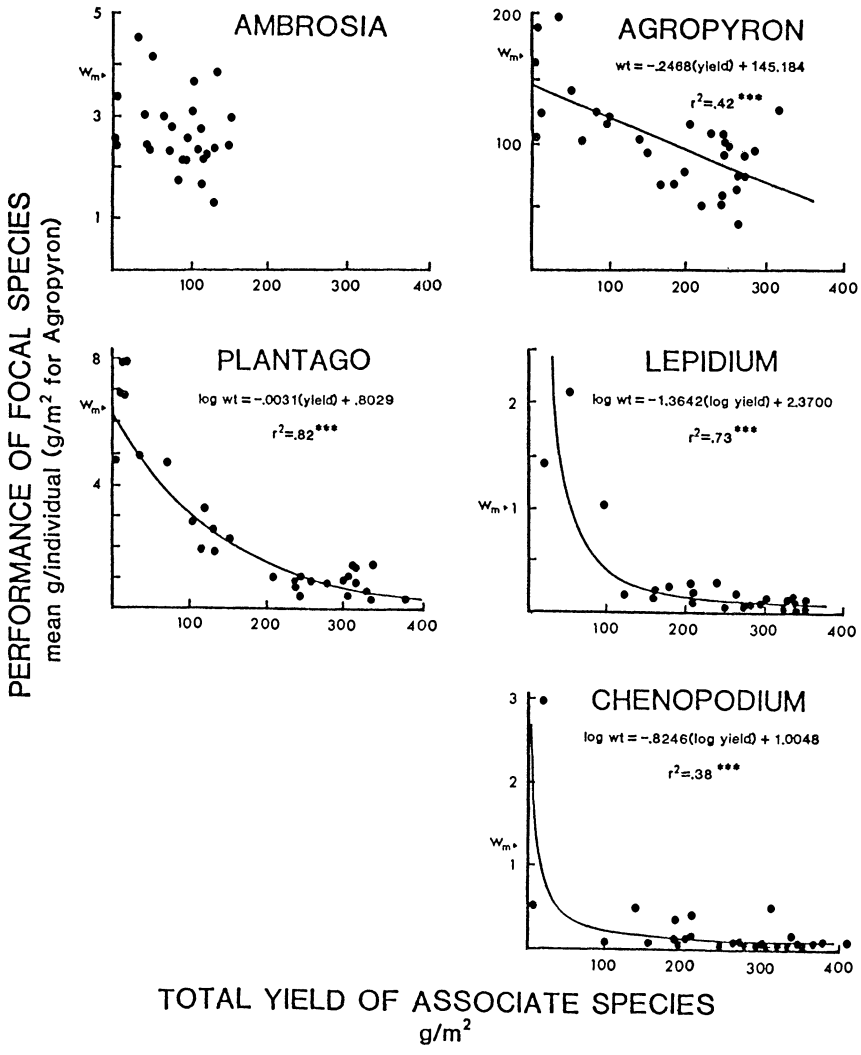

FIG. 2.—The effects of the total yield of associate species on the growth of each of the five species as focal species in year 1. Each *point* represents the mean dry mass/individual of the focal species when it was grown in a single plot with either one, three, or all four of the associate species. The value w_m is the yield of each species in monoculture (with no associate species present). *Three asterisks* denote $P < .001$.

peared to have the greatest competitive effects on other species; other species showed an average 15% increase in growth following the removal of *Ambrosia* in year 1 and a 24% increase in growth in year 2. *Agropyron* had the second largest effect (year 1 and year 2 = 9%), followed by *Plantago,* which had only very small effects on the other species. *Chenopodium, Lepidium,* and *Trifolium* as associates had no significant total effects on other species.

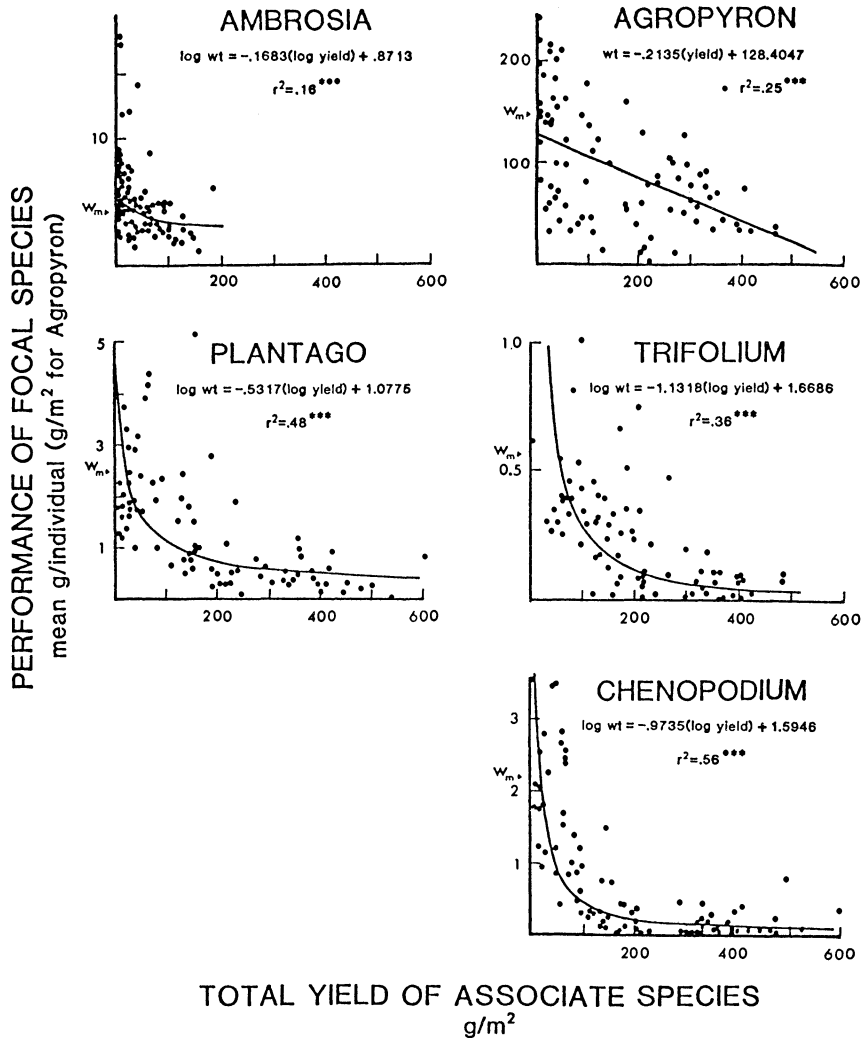

FIG. 3.—The effects of the total yield of associate species on the growth of each of the five species as focal species in year 2. Each *point* represents the mean dry mass/individual of the focal species when it was grown in a single plot with either one, three, or all four of the associate species. The value w_m is the yield of each species in monoculture (with no associate species present). *Three asterisks* denote $P < .001$.

The identity of the focal species affected the magnitude of the total response: *Plantago* was the most sensitive associate species, increasing by some 9% in year 1 and 17% in year 2 following removal of associates. The rankings of effect, but not response, are similar to the ranking of competitive ability observed for these species in two-species mixtures (Miller and Werner 1987).

Virtually all of the direct effects in both years (table 3) were less than zero, so the direct effects of associate species on focal species were generally

TABLE 2

THE TOTAL EFFECTS BETWEEN SPECIES IN YEARS 1 AND 2

	ASSOCIATE SPECIES				
FOCAL SPECIES	*Ambrosia*	*Agropyron*	*Plantago*	*Lepidium*	*Chenopodium*
Year 1:					
Ambrosia	· · ·	−.08	−.04	−.02	−.03
Agropyron	−.30**	· · ·	.03	−.03	−.10
Plantago	−.24**	−.07	· · ·	−.03	−.03
Lepidium	−.08	−.03	−.07**	· · ·	.00
Chenopodium	−.07	−.16	−.02	−.05	· · ·
	ASSOCIATE SPECIES				
	Ambrosia	*Agropyron*	*Plantago*	*Trifolium*	*Chenopodium*
Year 2:					
Ambrosia	· · ·	−.11	.03	−.09	−.07
Agropyron	.02	· · ·	.07	−.02	.02
Plantago	−.47*	−.10	· · ·	−.03	−.07
Trifolium	−.33*	−.09*	−.03	· · ·	−.02
Chenopodium	−.17*	−.05	−.02	−.06	· · ·

NOTE.—Values represent the proportional effect on the maximum potential growth of individuals of the focal species. Negative values indicate a competitive effect, and positive values indicate a facilitative effect. Values followed by asterisks are significantly different from zero (Tukey's HSD).
* $P < .05$.
** $P < .01$.

competitive. Some of the direct effects were quite large; for example, the direct effect of *Ambrosia* in the five-species community reduced the biomass of *Plantago* by 53% in year 1 and *Trifolium* by 73% in year 2. In other cases, the direct effects were minor: *Lepidium, Trifolium,* and *Chenopodium* had relatively small direct effects on other species.

Of particular interest is that the indirect effects were generally greater than zero, which indicates facilitative effects (table 3). Facilitative indirect effects would be expected for first-order indirect effects among competitors (those involving a single intermediate species), whereas higher-order indirect effects alternate between positive and negative. This method quantifies the sum of all the possible indirect effects. The results indicate that the indirect effect of removal of an associate species is usually to increase the total yield of other associate species. Indirect effects ranged from 0.43 to −0.09. The magnitude of the indirect effect was related to the identity of the associate species: *Ambrosia* generally had quite large indirect effects on other species, and *Agropyron* and *Plantago* also had significant indirect effects in some cases.

Species that had large competitive direct effects generally had almost as large facilitative indirect effects, so that the two effects almost canceled each other out. In both years, the indirect effect was significantly correlated with the direct effect (year 1: $r = -0.83$, $P < .001$; year 2: $r = -0.73$, $P < .001$). Similarly, total effects were significantly correlated with direct effects in both years (year 1: $r = 0.76$, $P < .001$; year 2: $r = 0.63$, $P < .01$). However, total effects were

TABLE 3

THE ESTIMATED DIRECT (D) AND LINKAGE INDIRECT (I) EFFECTS BETWEEN SPECIES IN YEARS 1 AND 2

	Associate Species									
	AMBROSIA		*AGROPYRON*		*PLANTAGO*		*LEPIDIUM*		*CHENOPODIUM*	
Focal Species	D	I	D	I	D	I	D	I	D	I
Year 1:										
Agropyron	−.43**	.13	...	...	−.19	.22	−.02	.00	−.16	.06
Plantago	−.53**	.29**	−.17*	.10	...	...	−.06	.04	−.07	.04
Lepidium	−.35**	.28*	−.07*	.04	−.04*	−.03	...	...	−.04	.05
Chenopodium	−.22**	.15**	−.11	−.05	−.06	.04	−.06	.01	...	...
	Associate Species									
	AMBROSIA		*AGROPYRON*		*PLANTAGO*		*TRIFOLIUM*		*CHENOPODIUM*	
	D	I	D	I	D	I	D	I	D	I
Year 2:										
Agropyron	−.41**	.43**	...	...	−.09	.16	.06	−.08	−.03	.05
Plantago	−.38*	−.09	−.19**	.10	...	...	−.03	.00	−.10	.03
Trifolium	−.73**	.41*	−.38**	.29*	−.26**	.23**	...	...	−.10	.08
Chenopodium	−.30**	.13*	−.27**	.22**	−.15**	.13**	−.05	−.01	...	...

NOTE.—Values represent the proportional effect on the maximum potential growth of individuals of the focal species. Negative values indicate a competitive effect, and positive values indicate a facilitative effect. Values followed by asterisks are significantly different from zero (Tukey's HSD).

* $P < .05$.

** $P < .01$.

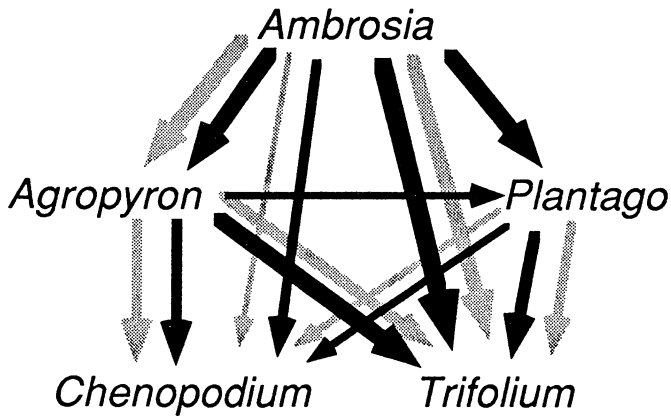

FIG. 4.—All significant direct and indirect interactions between species in Bailey Yard in 1983. Direct effects are shown with *solid arrows;* indirect effects are shown with *shaded arrows*. Arrow width is roughly proportional to the strength of the interaction.

not significantly correlated with indirect effects in either year (year 1: $r = -0.27$; year 2: $r = 0.07$).

The plant populations in Bailey Yard in the 2 yr did not differ greatly (table 1). Mean biomass of *Plantago* was twice as large in the first year, and *Chenopodium* density increased almost threefold in the second year. But, in general, mean plant size and density in the 2 yr were relatively similar. However, the relative importance of total, direct, and indirect interactions did differ somewhat between the 2 yr. For example, in year 1, the total effect of *Ambrosia* on *Agropyron* was large, primarily because of a large direct effect and a relatively small indirect effect (tables 2, 3). In year 2, the large direct effect is almost balanced by a large indirect effect, which results in a nonsignificant total effect. Overall, direct effects in the 2 yr were positively correlated ($r = 0.75$, $P < .05$). However, total and indirect effects in the 2 yr were not correlated ($r = 0.41$ and -0.28, respectively).

DISCUSSION

Species in this community can be put into three different groups on the basis of their interactions with other species. First, *Ambrosia,* the competitive dominant, had strong direct suppressive effects on all the other species (table 3; fig. 4). No evidence was found that the presence of any other species affected the biomass of *Ambrosia*. It is likely that *Ambrosia* individuals had a strong competitive effect on one another, but the method used in this study does not measure intraspecific competition. Monocultures established over a range of densities have shown that the naturally occurring intraspecific densities were high enough to suppress the biomass of individuals of *Ambrosia* (Miller and Werner 1987).

Second, *Agropyron* and *Plantago* had significant effects on species and yet were significantly suppressed themselves. *Ambrosia* exerted strong direct effects

on *Agropyron* and *Plantago*. These strong direct effects were generally countered by strong indirect effects: the strongest linkage indirect effect found in the community was the effect of *Ambrosia* on *Agropyron* in year 2 (table 3; fig. 4). Both *Agropyron* and *Plantago* had significant direct and indirect effects on subordinate species. Intraspecific effects were not determined, but it is possible that *Agropyron* was also limited to some degree by its own abundance (Miller and Werner 1987).

The majority of the species were in a third group at the far end of the competitive hierarchy. *Lepidium, Trifolium,* and *Chenopodium* were all significantly suppressed in the full community, primarily by the strong direct effects of *Ambrosia* and *Agropyron,* yet had no significant effects on any other species (table 2; fig. 4). It is likely that the growth of these species was not affected by intraspecific competition. Individuals were all small and rarely found in physical contact with other individuals of the same species.

Previous results from two-species mixtures (Miller and Werner 1987) led me to expect that many direct effects would be very large (especially those of *Ambrosia* and *Agropyron* on all other species). Further, I expected indirect effects to be generally positive and correlated with the strength of the direct effects. For example, it is known from two-species mixtures at ambient densities in Bailey Yard that *Ambrosia* has a strong competitive effect on *Agropyron* and that *Agropyron* has a strong competitive effect on *Trifolium* (Miller and Werner 1987). Therefore, I would predict that *Ambrosia* would have a strong positive or facilitative abundance indirect effect on *Trifolium* by suppressing the intermediate species, *Agropyron*.

These expectations were largely met by the results. Many total and direct effects were indeed quite large, and yet, because they act in opposite directions, the total effects were often quite small. For example, in two-species mixtures, *Ambrosia* reduced the biomass of *Chenopodium* by some 94%–98% of its maximum potential biomass (Miller and Werner 1987). Yet, the removal of *Ambrosia* from the full community had a relatively small total effect on *Chenopodium* (table 2), because strong negative direct effects were mediated by strong facilitative indirect effects (table 3).

In fact, what was surprising was the large magnitude of the indirect effects relative to direct effects. Indirect effects were generally facilitative: 14 of 16 indirect effects in year 1 and 13 of 16 indirect effects in year 2 were greater than zero. Indirect effects were generally one-half to two-thirds the magnitude of direct effects (table 3), so large direct effects were often matched by large indirect effects. In several cases, the magnitude of the indirect effect was actually larger than the direct effect, which resulted in a facilitative total effect (e.g., *Ambrosia* on *Agropyron* in year 2). This pattern could arise when the associate species suppresses other competitors of the focal species more than it suppresses the focal species itself: however, none of these facilitative effects was significant (table 2). There were notable exceptions to this pattern. In some interactions, the indirect effect was not facilitative but competitive (e.g., *Agropyron* on *Chenopodium* in year 1); however, none of these negative indirect effects was statisti-

cally significant. This pattern could occur when the presence of the associate species actually enhances the competitive effects of other associate species.

The shape of the species response curves will have a large effect on the magnitude of total, direct, and indirect effects. Most of the response curves are strongly nonlinear. In these cases, the total biomass of associates growing in the full community (Y_f) is in the region of the response curve that is asymptotic to the X-axis (figs. 2, 3). In this region of the response curve, changes in the abundance of associate species, such as would be caused by most species removals, may not result in any significant effect on the focal species. Paradoxically, therefore, some of the most suppressed species (e.g., *Chenopodium, Lepidium*) will be the least responsive to the removal of an individual competitor species (table 2). On the other hand, species with less concave response curves (e.g., *Agropyron, Plantago*) will be relatively more sensitive to the removal of a competitor species. Note that this is exactly the opposite of what happens in two-species mixtures (Miller and Werner 1987), in which indirect effects do not act to ameliorate the competitive direct effects.

Will the basic patterns of direct and indirect effects found in this study extend to other competitive communities? In general, the large indirect effects found in this study qualitatively support theoretical expectations (Yodzis 1988; Stone and Roberts 1991); if anything, the indirect effects found in this study were larger in magnitude than suggested by theoretical studies. I would tentatively predict that the patterns of direct, indirect, and total effects found in this study will commonly be found in other plant communities. That is, the response of species to the removal of a competitive dominant will frequently be smaller than expected, because large direct effects are counteracted by large indirect effects. This prediction is based on the generality of concave species response curves in plants, which forms the basis for the well-established reciprocal yield law (Harper 1977). As found in this study, species that are somewhat less inhibited may show the greatest response to competitive release, whereas very suppressed species may show little response. For most species, however, the full shape of the response curve is not known (cf. Schoener 1983), and, for the highly nonlinear response curves, the magnitude of the response depends on both the initial position on the curve and the magnitude of the perturbation along the curve.

Assumptions of the Method

One of the obstacles to studying indirect effects has been that an associate species can simultaneously have both direct effects and various indirect effects on other species, and it can be very difficult to separate the two. The method used here in a herbaceous plant community quantifies direct and indirect effects by assuming that per-gram competitive effects of different associate species on the same focal species are equivalent, that the abundances of different associate species can be added to quantify a total effect of associate species, and that indirect effects are mediated only by species on the same trophic level (the effects of herbivores and pathogens were minimal in this community). The results need to be discussed in the context of these assumptions.

Two-species competition experiments support the existence of a general per-unit equivalence of competitive effects among these species (Miller and Werner 1987). These experiments compared the effects of different associate species on the same focal species, generally revealing no difference between the effects of associate species at the same yield. However, not all associate species could be compared, as it was difficult to obtain low yields of some associate species because of their large mean size and high yields of other associate species because of their small mean size.

A general per-gram equivalence of competitive effects has also been found by Peart and Foin (1985) in a grassland community and by Goldberg (1987) in a midsuccessional old-field community. Goldberg and Werner (1983) have argued that a per-gram equivalence of competitive effects would be expected among plant species with similar growth forms. They suggest that homogeneity of resource requirements, low encounter probabilities between individuals of any particular species pair (diffuse interactions), and strong size asymmetries between competing individuals will lead to a general equivalence of competitive effects. The weedy community in Bailey Yard has these characteristics: although all individuals begin as similar-sized seedlings, strong size asymmetries develop within 4–6 wk (T. E. Miller, unpublished data).

However, experiments done on plants grown in more controlled environments have revealed at least some differences in per-gram effects of different species (Goldberg and Fleetwood 1987; Gordon et al. 1989). Goldberg and Landa (1991) also found significant differences in per-gram effects among seven species in a greenhouse study. They suggest that the greater variation in growth seen in field experiments than in greenhouse experiments may mask real differences in per-gram competitive effects.

The assumption of equivalence is important in allowing the construction of a simple method for quantifying direct and indirect effects, but the assumption can be relaxed without changing the general conclusions. The method presented here could still be used if equivalence applied to transformed species abundances (e.g., if the yield of *Plantago* could be converted to a yield of *Ambrosia* having the same effect) and if these converted abundances were still additive. Nitrogen fixation and herbivory are two factors that might lead to nonequivalence.

The assumption of additivity is less well supported. In this study, nonadditivity would have resulted in a weak relationship between focal species success and total associate species yield (figs. 2 and 3), but additivity is difficult to test directly. When the yields of different associate species are similar, a method based on isobole properties can be applied (Berenbaum 1985). The isobole method cannot be used in this study, but it has been used to show that associate species yields are additive in three-species plant mixtures (T. E. Miller, unpublished manuscript). Future work will be needed to evaluate the additivity assumption.

The use of this model of plant multispecies interactions suggests that the importance of direct and indirect effects among competitors in this community depends on the interaction pathway and the species involved. Direct effects are all competitive and can be quite large. Linkage indirect effects between species are generally

facilitative and almost as large as direct effects. The overall pattern is of a community structured by large direct effects of *Ambrosia* and, to a lesser extent, *Agropyron*. Indirect effects tend to reduce the strength of direct, competitive effects, which could have important implications for the diversity and stability of plant communities.

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