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JOINT EFFECTS OF COMPETITORS AND HERBIVORES ON GROWTH AND REPRODUCTION IN *ARISTOLOCHIA RETICULATA*[1]

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Abstract. The separate and joint effects of herbivory and interspecific competition on an herbaceous plant were measured to determine to what extent, if any, herbivory and competition interact in their effects, and to test models of their joint effects. Plants of Texas Dutchman's pipevine, *Aristolochia reticulata,* were grown in a greenhouse, alone and in competition with either or both little bluestem grass, *Schizachyrium scoparium,* and southern dewberry, *Rubus trivialis.* Herbivory on *A. reticulata* by the pipevine swallowtail butterfly, *Battus philenor,* and on *S. scoparium* by cattle was simulated by clipping. Competition and clipping individually had the expected negative effects on *A. reticulata* growth and reproduction. The joint effect of competition and clipping on *A. reticulata* was best described as additive. The joint effect of the two competing species on *A. reticulata* in three-species mixtures was well predicted by a simple, but nonlinear, model that assumed that all three species competed for the same limiting resource. The results of this study suggest that the structure and dynamics of this community, and by extension those of other communities, can be understood by examining subsets of the community separately.

Key words: Aristolochia; Battus; *community structure; competition; herbivory; interspecific interactions;* Rubus; Schizachyrium.

INTRODUCTION

Ecologists have long sought to understand and predict the structure and dynamics of natural communities. They have generally examined only subsets of the species that make up communities, however, assuming, or hoping, that the dynamics and structure of whole communities can be understood from the behavior of their many component subsets. In its simplest form, this approach requires one to assume that the outcome of the interactions among three or more species is predictable from a knowledge of the interactions between pairs of species. If the effect of one species on a second depends on the presence or absence of a third species (e.g., Wilbur 1972, Neill 1974, Bentley and Whittaker 1979, Lee and Bazzaz 1980, Fowler 1981, Colton 1983), the prediction of multispecies interactions may be difficult. In such cases, simple additive models of the effects of two or more species on a third are inappropriate, and more complex, nonlinear models are required. The best form of these models, however, has not yet been determined, nor is it known how frequently interactions among species are nonadditive.

The study described here represents an initial attempt to address these issues by examining the interactions among three plant species and a specialist herbivore that commonly co-occur in the open pine uplands of east Texas. We examined the joint effects on the herbaceous plant *Aristolochia reticulata* of herbivory by the butterfly *Battus philenor,* simulated by clipping, and of interspecific competition from *Schizachyrium scoparium* and *Rubus trivialis.* We did not attempt to distinguish between the effects of exploitative and interference competition (e.g., allelopathy), and will refer to them collectively as competition. Our specific goals were to answer the following questions:

1) Do herbivory (simulated by clipping) and competition separately affect the growth and reproduction of *A. reticulata* adversely?

2) Are the effects on *A. reticulata* growth and reproduction of (a) competition and herbivory, and (b) competition from two different plant species, additive on either an arithmetic or a logarithmic scale? In other words, is the impact of one stress independent of the level of the other?

3) If these effects are not additive, can a biologically realistic model be developed that predicts the simultaneous effects on *A. reticulata* of the different stresses from the separate effect of each stress?

METHODS

Species

Texas Dutchman's pipevine, *Aristolochia reticulata* Nutt. (Aristolochiaceae), is a small perennial herb of the open longleaf pine uplands (the pine-bluestem savanna of Vogl 1972 and Streng and Harcombe 1982) of southeast Texas. It is winter deciduous and leafs out in mid-March. Caterpillars of the pipevine swallowtail

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butterfly, *Battus philenor,* feed on *A. reticulata* from early April to mid or late June. In a typical year, larvae consume 40–45% of the annual leaf crop of *A. reticulata* and can defoliate an individual plant several times (Rausher and Feeny 1980). Feeding by larvae decreases plant growth by ≈50% and increases the mortality rate of small plants significantly. For further description of the interaction between *B. philenor* and *A. reticulata,* see Rausher (1978, 1980, 1981, 1983) and Rausher and Feeny (1980).

Two other common plant species that grow in the sandy soils of these pine savannas are little bluestem grass, *Schizachyrium scoparium* (Michx.) Nash var. *virile* (Shinners) Gould (Gramineae), also referred to as *Andropogon scoparius* Michx., and southern dewberry, *Rubus trivialis* Michx. (Rosaceae). (Nomenclature follows Correll and Johnston 1970.) These two species, which are the first and third most abundant herbaceous species in the vegetation within 13 cm of *A. reticulata* plants (M. D. Rausher, *personal observation*), were used in different combinations to form the competitive regimes in which *A. reticulata* was grown in this experiment. The second most common species in the habitat, *Rhus radicans,* was not used for obvious reasons.

Experimental design

Plants of each of these three species were collected 29–31 May 1980 from the John Henry Kirby State Forest in Tyler County, Texas. The plants were taken in coolers to Austin, Texas and transplanted into a greenhouse there on 4–5 June 1980. Before transplanting, each *Aristolochia reticulata* plant was clipped to remove all aboveground material. The roots were then washed, blotted dry, and weighed. These root masses were the "initial masses" referred to below. Each *A. reticulata* plant was then planted in a separate standard 15-cm (6-inch) plastic pot in a mixture of sand and peat moss. Each pot also had transplanted into it either: (a) three small clumps of *Schizachyrium scoparium*; (b) one shoot of *Rubus trivialis*; (c) both of these; or (d) no other plants. In half of the pots containing *S. scoparium,* this species was clipped to 3 cm on 28 April, 22 June, and 1 Sept 1981 to simulate grazing by cattle, a common use of the pine savannas. There were therefore a total of six competitive regimes experienced by *A. reticulata*: (a) no competition; competition (b) with *Rubus* alone; (c) with unclipped grass; (d) with clipped grass; (e) with *Rubus* and unclipped grass; and (f) with *Rubus* and clipped grass. These six treatments constituted a 3 × 2 full-factorial design, with three levels of grass treatment (absent, present, or present but clipped) and two levels of *Rubus* treatment (absent or present).

To simulate herbivory by *Battus philenor, A. reticulata* plants were clipped to ground level so that only a small portion of the main stem remained. Three levels of clipping were imposed: (a) no clipping; (b) clipping once, on 28 April 1981; and (c) clipping twice, on 28 April 1981 and again 22 June 1981. These intensities of clipping correspond to degrees of defoliation of individual plants that are commonly observed in nature (M. D. Rausher 1981 and *personal observation*).

These clipping and competitive treatments were designed to simulate, as far as possible, stresses confronting *Aristolochia reticulata* in nature. Since transplants of all species were taken from the same site, the genotypes used in this experiment were appropriate ones. Total densities in the pots were high, but within the range of natural variation. Probably the greatest departure from natural conditions was the restricted depth of the available rooting zone in pots. Clipping may, in some instances, not fully duplicate natural herbivory (Dyer and Bokhari 1976, Crawley 1983, but see Detling et al. 1980). However, clipping is probably a good simulation of the feeding damage caused by *B. philenor.* In the field, large, wandering larvae commonly consume the entire aboveground shoot in a short period (1–2 h), leaving only a small piece of the main stem projecting above ground. The appearance of a defoliated and a clipped plant were therefore similar. The timing of the clipping treatments corresponded to the time of defoliation in nature (Rausher and Feeny 1980, Rausher 1981).

The greenhouse was divided into five blocks, with each block containing three replicates of each of the 18 possible combinations of clipping and competitive regimes. Pots were arranged randomly within each block.

All plants were harvested 22–25 October 1981, and the roots of each species separated from the soil and washed. After the *Aristolochia reticulata* plants were frozen and freeze-dried, masses were determined separately for three different parts of each plant: roots, reproductive parts (inflorescences and capsules), and shoots (stems and leaves). In addition, the root/shoot ratio was calculated for each plant as the ratio of root mass to shoot mass.

Analysis

The data were subjected to a series of analyses of covariance (ANCOVA) in which the root mass, shoot mass, reproductive mass, and root/shoot ratio of *Aristolochia reticulata* were the dependent variables and the initial mass of *A. reticulata* was the covariate. All analyses were performed both with untransformed variables and with all variables log-transformed before analysis. The analyses on untransformed data correspond to what we will term the "additive model." The logarithmic transformation of the data has the effect of making the linear statistical model of the ANCOVA into a "multiplicative model," since it is equivalent to assuming that final mass equals initial mass × competition effect × herbivory effect × competition-herbivory interaction effect, etc. The logarithmic transformation improved the fit of the residuals to the normality assumption of ANCOVA, and hence the significance tests associated with the multiplicative model are perhaps more reliable. However, because the departures from normality of the residuals of the additive model were not large (their distributions were unimodal with some skewing and kurtosis), significance tests using this model should be valid (Sokal and Rohlf 1981).

The experiment was initially analyzed as a four-way full factorial design using both multiplicative and additive models, the four factors being the intensity of grass competition, the intensity of *Rubus* competition, the *A. reticulata* clipping regime, and block. Since block and the interaction terms containing block were found to explain little of the variance among plants and to have for the most part no statistical significance, the analyses presented here do not include any of the terms containing block effects. Instead, the data were reanalyzed as a three-way full factorial design without blocking. All statistical analyses were carried out using the Statistical Analysis System (Helwig and Council 1979). Because the designs were slightly unbalanced due to mortality (1%), absence of aboveground growth in survivors (10%), and failure to reproduce (51% of survivors), all tests of significance were based on Type IV sums of squares, which use estimable functions in which the coefficients of any effect are distributed equitably across higher level effects containing that effect, and hence are appropriate for unbalanced designs.

RESULTS

Main effects

The presence of the grass *Schizachyrium scoparium* or of *Rubus trivialis* in a pot had highly significant effects on all four measured *Aristolochia reticulata* characters, regardless of whether we analyzed the data using a multiplicative model or an additive model (Table 1). As expected, the presence of these competing species decreased root mass, shoot mass, and reproductive mass, and increased the root/shoot ratio (Table 2). The effect of clipping the grass (simulating cattle grazing) was also expected: the effect of the grass on *A. reticulata* was not as large if the grass was clipped than if it was not clipped.

Clipping of *A. reticulata,* simulating herbivory by *Battus philenor,* had the expected effect of reducing root mass and shoot mass (Table 2). These reductions and an increase in root/shoot ratio were all highly significant regardless of whether a multiplicative or additive statistical model was used (Table 1). Clipping had no significant effect upon reproductive mass in either analysis. Finally, the covariate, initial root mass, explained a significant fraction of the variation in all characters except reproductive mass in the multiplicative model.

The interaction of clipping and competition

Despite the presence of large main effects, none of the interaction terms involving the clipping and competitive regimes were significant in either the multiplicative or the additive model (Table 1). The results of these analyses therefore do not allow the rejection of the null hypothesis that clipping and competition affect *Aristolochia reticulata* independently. Instead, the results suggest that the effect of herbivory on *A. reticulata* does not depend on the competitive regime that the plant experiences. Further examination of the results of each set of analyses suggests that the additive model is the better predictor of the joint effects of herbivory and competition, since, of the 12 interaction terms involving clipping (4 variables × 3 terms per analysis), none have associated probabilities of <0.20 in the additive model, whereas 6 of these 12 terms have associated probabilities of <0.20 in the multiplicative model. Clipping and interspecific competition thus seem to be best modelled as additive.

The interaction of the effects of the two competitor species

The interaction of the effects of the presence or absence of the grass *Schizachyrium scoparium* and of *Rubus trivialis* had a highly significant effect on the magnitude of all four of the measured *Aristolochia reticulata* characters in both the additive and multiplicative analyses (Tables 1 and 2). Root mass, shoot mass, and reproductive mass were on average greater, and root/shoot ratio lower, than either model predicts in treatments with both competitor species present. In other words, the competition experienced by *A. reticulata* from these two species simultaneously was less than that predicted by the sum or product of their separate effects on *A. reticulata.*

The existence of such an interaction is not surprising if we consider the nature of the biological relationships that would lead to each model. Assume that a single resource limited the growth of *A. reticulata* in the experimental pots, and that the competing species reduced the growth of the *A. reticulata* by using portions of that resource and thus reducing the amount available for *A. reticulata.* The models differ in the way in which the competitors make the resource unavailable. The logarithmic transformation of all measurements converts the linear model of analysis of covariance into a multiplicative model. If its interaction terms are all zero, this model says that final root mass = initial mass × grass effect × *Rubus* effect × clipping effect, substituting, in turn, shoot mass, reproductive mass, and root/shoot ratio for root mass. Each "effect" is a treatment-specific constant. This model (henceforth Model I) is therefore equivalent to supposing that *S. scoparium* took some fixed proportion of available resources from *A. reticulata,* and that *R. trivialis* took a fixed proportion of whatever resources were left. This scenario does not seem to be very probable for these species. However, other plant species often differ in the timing of their major demands on resources. Plants whose peak demands occur later in the growing season

TABLE 1. Sums of squares and significance levels of *F* ratios from analyses of covariance of the effects of three levels of grass treatment (present, absent, or present but clipped) and two levels of *Rubus* (present or absent) upon four characters of *Aristolochia reticulata.*

Source of variation	df	Measured character: Root mass	Shoot mass	Reproductive mass	Root/shoot mass ratio
		A. Multiplicative model.			
Initial mass†	1	33.16***	9.65***	1.67	4.78***
Grass (G)‡	2	20.09***	47.85***	45.10***	11.41***
Rubus trivialis (R)	1	17.48***	66.70***	32.87***	23.82***
Clipping regime (C)	2	9.86***	22.91***	0.63	4.44***
G × R	2	3.94***	31.91***	12.53**	11.08***
G × C	4	1.55	4.46	4.20	2.36
R × C	2	0.06	0.36	0.01	0.31
G × R × C	4	2.09	3.71	1.16	2.00
Error 249/223/112/223§		57.59	129.98	98.22	69.56
		B. Additive model.			
Initial mass†	1	48.66***	4.49***	0.80**	293.60***
Grass (G)‡	2	42.13***	42.33***	1.02**	56.33
Rubus trivialis (R)	1	33.08***	35.46***	0.66*	309.90***
Clipping regime (C)	2	15.85***	5.92***	0.01	178.54*
G × R	2	17.13***	33.44***	1.19**	179.39*
G × C	4	1.78	0.79	0.71	111.37
R × C	2	0.23	1.03	0.21	48.24
G × R × C	4	2.03	0.79	0.05	42.55
Error 249/223/112/223§		105.71	77.20	11.99	4738.32

* $P < .05$; ** $P < .01$; *** $P < .001$.

† Covariate.

‡ *Schizachyrium scoparium.*

§ For the four characters, respectively.

may have available only those nutrients that have not been used by earlier growing species, which could meet the assumptions of this model.

The existence of highly significant interaction effects in the results of the analyses using the multiplicative model allow us to reject Model I. We calculated the masses predicted by Model I by assuming that the ratio of mean *A. reticulata* mass when grown with one competitor to its mass when grown alone is a measure of the resource remaining to *A. reticulata* after that competitor has removed its portion of the resource. The predicted mass of *A. reticulata* in three-species pots is therefore equal to its mass when grown alone multiplied by these two ratios (one for each competitor). A total of six predicted values (three clipping regimes × two grass treatments) were calculated for each of the dependent variables except root/shoot ratio. The actual values of *A. reticulata* in three-species pots show very poor agreement with the predicted values (Table 3). In all cases the observed values are much larger than the predicted values (mean percent deviation from expected values = 56.7%).

The additive model with no interactions (Model II) can be derived from a different set of biological assumptions. If *S. scoparium* and *A. reticulata* competed for a different part of the limiting resource than did *R. trivialis* and *A. reticulata* (e.g., for nutrients in different rooting zones), the effects of the two competitor species together on *A. reticulata* would have been additive. The difference between mean *A. reticulata* mass when

TABLE 2. Mean values of *Aristolochia reticulata* plants grown under different clipping* and competition treatments. Note that, while simple arithmetic means are given in this table, all statistical analyses were performed upon data adjusted for initial *Aristolochia* root mass.

Competitors		Root mass (g) No. times clipped			Reproductive mass (g) No. times clipped			Shoot mass (g) No. times clipped			Root/shoot mass ratio No. times clipped		
Rubus	*Schizachyrium*	0	1	2	0	1	2	0	1	2	0	1	2
Absent	absent	3.00	2.57	2.36	0.58	0.60	0.35	2.59	2.21	1.79	1.34	1.32	1.38
Absent	clipped	1.64	1.28	1.36	0.14	0.09	0.07	0.82	0.56	0.61	2.99	2.88	3.93
Absent	unclipped	1.73	1.05	0.71	0.08	0.03	0.04	0.81	0.32	0.19	2.33	6.15	5.50
Present	absent	1.48	1.27	0.91	0.06	0.05	0.08	0.48	0.39	0.27	5.04	4.84	7.78
Present	clipped	1.41	0.70	0.90	0.02	0.02	0.16	0.46	0.27	0.23	3.59	3.16	8.29
Present	unclipped	1.06	0.84	0.67	0.04	0.02	0.02	0.39	0.19	0.21	3.83	5.92	5.57

* *Aristolochia* plants were cut off at ground level.

TABLE 3. Comparison of predicted (P) and observed (O) values of three *A. reticulata* characters for plants in three-species pots using three different models (see Results: the Interaction of the Effects of the Two Competitor Species).

Number of *Aristolochia* clippings	Grass treatment	Root mass		Shoot mass		Reproductive mass	
		P	O	P	O	P	O
				A. Model I (multiplicative)			
0	Clipped	0.81	1.41	0.15	0.46	0.01	0.02
0	Unclipped	0.85	1.06	0.15	0.39	0.01	0.04
1	Clipped	0.63	0.70	0.10	0.27	0.01	0.02
1	Unclipped	0.52	0.84	0.06	0.19	0.00	0.02
2	Clipped	0.52	0.90	0.09	0.23	0.01	0.16
2	Unclipped	0.27	0.67	0.03	0.21	0.01	0.02
				B. Model II (additive)			
0	Clipped	0.12	1.41	−1.29	0.46	−0.38	0.02
0	Unclipped	0.21	1.06	−1.30	0.39	−0.44	0.04
1	Clipped	−0.02	0.70	−1.26	0.27	−0.56	0.02
1	Unclipped	−0.25	0.84	−1.50	0.19	−0.52	0.02
2	Clipped	−0.09	0.90	−0.91	0.23	−0.20	0.16
2	Unclipped	−0.73	0.67	−1.33	0.21	−0.23	0.02
				C. Model III			
0	Clipped	1.05	1.41	0.34	0.46	0.05	0.02
0	Unclipped	1.09	1.06	0.34	0.39	0.04	0.04
1	Clipped	0.84	0.70	0.26	0.27	0.03	0.02
1	Unclipped	0.74	0.84	0.19	0.19	0.02	0.02
2	Clipped	0.71	0.90	0.21	0.23	0.04	0.16
2	Unclipped	0.48	0.67	0.16	0.21	0.03	0.02

grown alone and when grown with one competitor would then be a measure of the resources taken from *A. reticulata* by this competitor, expressed as units of *A. reticulata* mass. Under this model the predicted mass of *A. reticulata* in competition with both species is equal to its mass when grown alone minus both of these differences. The existence of highly significant interaction effects in the additive statistical analysis (Table 1) indicates that Model II is a poor predictor of the effects of competition from two species simultaneously. Once again the predicted values are much smaller than the observed values, and are often negative. The mean percent deviation is even greater than that of Model I (98.4%; 0 was substituted for each negative value for this calculation).

The existence of statistical interaction effects in these analyses does not necessarily imply that the effects of competition on *A. reticulata* are complex, nor that they are unpredictable from the behavior of species in pairs. We now consider a third model (Model III), which is both simpler and, to us, more biologically plausible, than the two previous models. We assume that all three species compete for the same limiting resource. If they were also completely equal competitors, the presence of one competing species would reduce *A. reticulata* mean mass to one-half, and the presence of two competitors would reduce it to one-third, of its value when grown alone. Generalizing to the case of unequal competitors, *A. reticulata* grown with *S. scoparium* was reduced to $1/m$ of its mass when grown alone, implying that the resource was being used by the two species in the ratio $1/m$:$(1 - 1/m)$, or 1:$(m - 1)$. One grass plant (actually a unit of three clumps in this experiment; see Methods) was thus equivalent to $(m - 1)$ *A. reticulata* plants and preempted $(m - 1)$ times as many units of resource as the *A. reticulata* plant with which it competed. Analogously, when *A. reticulata* was grown with *R. trivialis,* its mass was reduced to $1/n$ of its mass when grown alone, and the resource was split by these two species in the ratio 1:$(n - 1)$. The simplest possible model is that these relationships were maintained in the three-species mixture such that the resource was used in the ratio 1:$(m - 1)$:$(n - 1)$. The *A. reticulata* individual therefore got a fraction $1/[1 + (m - 1) + (n - 1)]$ of the resource, and its mass in a three-species pot is thus predicted to be this fraction of its mass when grown alone.

This model predicts the mean values of root mass and shoot mass in three-species mixtures quite well; predictions for reproductive mass are not as good but are better than those of either Model I or Model II (Table 3, Fig. 1). The mean percent difference between predicted and observed values is 29.6%. Although the lack of independence among many of the predicted values precludes a formal statistical test of the goodness of fit of the predictions, it is clear that Model III provides a better prediction of the effect of three-species mixtures on *A. reticulata* than do Models I and II.

DISCUSSION

Effects of individual stresses

Each noncontrol *Aristolochia reticulata* plant in this experiment was confronted with some combination of three different stresses: clipping (simulating herbivory), competition from *Rubus trivialis,* and competition from the grass *Schizachyrium scoparium.* Acting singly, each of these stresses had the expected negative effect on *A. reticulata* growth and reproduction, with the exception that clipping did not significantly affect reproduction. Competition with *R. trivialis* and with *S. scoparium* produced approximately the same reduction in *A. reticulata* size (e.g., reductions of 51 and 42% in root mass, respectively). The similarity in effect of these two competitor species is probably in part a consequence of the approximately equal biomass of the initial transplants of these two species. Clipping of *A. reticulata* in the absence of competition was less detrimental than was competition, reducing root mass by only 14% (one clipping) or 21% (two clippings). Although the absence of an effect of clipping on reproduction is consistent with the results of field experiments that have examined the impact of natural populations of *Battus philenor* on *A. reticulata* (Rausher and Feeny 1980) the reason for the lack of such an effect is unclear. The level of reproduction may be determined by the amount of photosynthate stored during the previous year, or photosynthate that would normally be diverted to storage in roots may be used instead by defoliated plants to maintain normal levels of reproduction. Such compensation is a common response to herbivory (Crawley 1983).

Joint effects of herbivory and competition

Numerous experiments have shown that selective herbivory can affect the composition of plant communities. For example, the well-documented changes in vegetation that occur following the imposition or cessation of grazing are frequently considered to be partly the result of a shift in the balance of competition between less palatable and more palatable species, in addition to being the result of the direct effects of grazing (Harper 1977, Watkin and Clements 1978).

It is less clear whether variation in the competitive regime experienced by a plant commonly influences the impact of a given level of herbivory on that plant. Harper (1977) has discussed how such effects could arise. For example, under conditions in which light was limiting, two species might be equal competitors. Growing alone or under uncrowded conditions, individuals of each species might recover quickly from aboveground herbivory, but when growing together in dense mixtures, whichever species was subject to herbivory would lose its position in the height hierarchy and be quickly overtopped and shaded. Subsequent regrowth would then be slow. Experiments by Lee and Bazzaz (1980) demonstrate this phenomenon for plants grown in monocultures, but little evidence is available to indicate that it also occurs in mixtures of species.

By this argument, the effects of herbivory and competition should not be independent of each other, i.e., the effects of a given level of herbivory are expected to depend on the competitive environment of the plant experiencing the herbivory. Our results, however, indicate that this expectation is not always met. In our experiments, neither an additive nor a multiplicative model exhibited significant interaction terms. The additive model seems a more appropriate description of the data because the interaction terms in the multiplicative model approached statistical significance more closely. Under an additive model, the combined effects of competitive regime and clipping are simply the sum of the two separate effects. It thus appears that the impact of clipping on *A. reticulata* growth and reproduction does not depend on the competitive regime in which that plant grows. It is not clear to us why such independence should exist. Apparently the loss of position in the competitive hierarchy in response to herbivory does not occur as envisioned by Harper (1977).

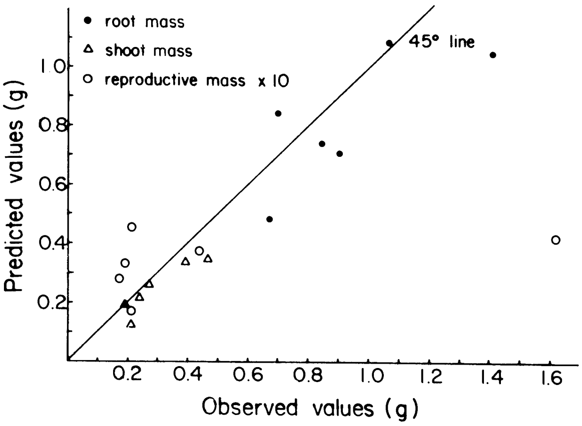

FIG. 1. Observed and predicted masses of *Aristolochia reticulata* when grown in three-species mixtures. Predictions were calculated from the mean masses of *A. reticulata* when grown alone and with one other species, and Model III (see Results: the Interaction of the Effects of the Two Competitor Species).

Our results are comparable with those of Bentley and Whittaker (1979), who examined the interaction between the effects of grazing and competitive regime on two species of *Rumex.* At low grazing intensities, these two effects were additive for both species. At high grazing intensities, they were additive for *R. obtusifolius.* For *R. crispus,* there were significant interactions between these two effects at high levels of grazing, but interpretation of these interactions is difficult because the experimental grazer, the beetle *Gastrophysa viridula,* had a marked preference for *R. obtusifolius.* Consequently, grazing on *R. crispus* when grown alone was likely to have been much heavier than grazing on that species when grown with *R. obtusifolius.* The significant interaction terms may thus reflect differences in the amount of actual feeding damage experienced by *R. crispus* plants in the two treatments rather than differences in the *effect* of a constant amount of feeding damage under different competitive regimes. Current evidence thus argues against the validity of the hypothesis that the impact of a given amount of grazing depends on what other species a plant is competing with.

Joint effects of competition among three species

In contrast with the effects of herbivory and competition, the joint effects of the two competitor species, *Schizachyrium scoparium* and *Rubus trivialis,* upon *Aristolochia reticulata* did not fit either a multiplicative model (Model I) or an additive one (Model II). However, the observed mean masses of *A. reticulata* in three-species mixtures were well predicted from its mean masses grown alone and in two-species mixtures, and a simple model that assumes that all three species compete for the same limiting resource (Model III, see Results). Model III is not a linear model, and therefore the interactions among these species are technically "nonlinear." However, the nonlinearity of this system is a consequence of its simplicity, not of its complexity.

Model III predicts greater masses of *A. reticulata* in three-species mixtures than do Models I and II. The most probable cause of these greater masses is that the other two species also competed with each other, reducing one or both species' biomass and thus reducing their impact on *A. reticulata.* However, other explanations of the fit of Model III are, of course, possible, as are a variety of other algebraic models.

The behavior of multispecies mixtures

Despite the attention that it has received, the question of to what extent the dynamics and structure of complex natural communities can be understood and predicted from the behavior of subsets of their species is still the subject of debate. The prediction of the behavior of three- and four-species mixtures from the behavior of pairs of species is a simple aspect of the general problem. Because attempts to make such predictions, usually for sets of competing species, have had variable success (e.g., Vandermeer 1969, Wilbur 1972, Neill 1974, Akre and Johnson 1979, Fowler 1981, 1982, Morin 1981, 1983, Colton 1983), some workers have concluded that assemblages of species have emergent properties ("higher order interactions") not predictable from the behavior of subsets of their species. However, in all studies, predictions concerning the behavior of multispecies mixtures from the behavior of pairs of species must be based on specific models. The failure to predict the behavior of the more complex system may indicate only that the model is inappropriate, not that the system really has emergent, nonpredictable properties.

Normally the models considered are standard additive or multiplicative statistical models. We found that these models were adequate for describing the joint effects of herbivory and competition, but inadequate for describing the joint effects of two competitor species, on *A. reticulata.* However, by considering a third simple and biologically realistic model, we were able to make accurate predictions about the behavior of a three-species mixture of competitors from measurements of growth and reproduction in pairwise mixtures. Our results thus suggest that the dynamics of complex communities can be studied profitably by examining the interactions between subsets of that community. They also indicate that in some cases the failure to predict the dynamics of multispecies communities from the dynamics of species pairs may be due simply to a lack of appropriate models. The development of such models is therefore of top priority.

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