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A Review of Field Experiments with Plants**

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PATTERNS AND CONSEQUENCES OF INTERSPECIFIC COMPETITION
IN NATURAL COMMUNITIES: A REVIEW OF FIELD EXPERIMENTS
WITH PLANTS

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Abstract.—We present a quantitative literature review to assess the extent to which field experiments with plants have addressed questions about patterns of competition over time and space, consequences of competition for community structure, and comparisons of competitive ability among species. We outline the necessary treatment comparisons and statistical analyses to answer each question and then describe the number of experiments that meet these criteria and their results. Although we found a total of 101 experiments in 89 studies, 63% of these experiments only addressed whether competition significantly affected some component of individual fitness of a single species at a single time and site. Despite the limited data base to address more complex questions about competitive interactions, we did find consistent results for a few of the questions we reviewed. Where tested, competition always had significant effects on distribution patterns (five experiments), on relative abundances (two experiments), and on diversity (four experiments), consistent with the notion that competition has strong effects on community structure. On the other hand, intraspecific competition was not usually stronger than interspecific competition for either competitive effect (four experiments) or response (three experiments), which suggests that resource partitioning may not be an important mechanism of coexistence in plants.

Ecologists have long been interested in competitive interactions because of their great potential for shaping patterns of distribution and abundance and the traits of competing species (Darwin 1859; Tansley 1917; Clements 1929; Gause 1934). This interest has led to a large body of theory that addresses how competition influences community structure and the evolution of competitive ability (Roughgarden 1979). It has also led to an increasing number of experiments on competition in natural communities (reviews in Connell 1983; Schoener 1983; Fowler 1986a; Aarssen and Epp 1990). However, it remains unclear to what extent these theoretical and empirical literatures are connected, because the primary emphasis in recent reviews of field experiments on competition has been on whether or not competition occurs rather than on whether this competition does indeed have major ecological and evolutionary consequences in nature (Connell 1983; Schoener 1983).

In this article, we present a quantitative literature review of field competition experiments in plants to meet two primary goals: how specific questions about competitive interactions in nature other than whether it occurs or not should be investigated with field experiments, and to what extent experiments have been

TABLE 1

TREATMENTS NEEDED TO ADDRESS SEVERAL QUESTIONS ABOUT COMPETITIVE INTERACTIONS IN NATURAL COMMUNITIES AND THE NUMBER OF EXPERIMENTS THAT ADDRESS THESE QUESTIONS

QUESTION	NECESSARY TREATMENTS	INDIVIDUAL		POPULATION	
		Potential	Actual	Potential	Actual
1. Occurrence	Treatments differ in absolute abundance of neighbors (removal and phytometer experiments only)	75 (57)	71 (53)	21	18
Patterns of occurrence:					
2. Temporal heterogeneity	As in (1) repeated at >1 time	2 (1)	0	2	1
3. Spatial heterogeneity	As in (1) repeated at >1 site	19 (16)	7 (6)	8	0
4. Productivity gradients	As in (1) crossed with productivity treatment	4 (3)	2 (1)	2	1
	As in (3) with sites differing in productivity	5 (5)	3 (3)	1	0
5. Herbivory interactions	As in (1) crossed with herbivore density treatments	6 (3)	2 (1)	2	1
	As in (3) with sites differing in herbivore density	0	0	1	0
Community consequences:					
6. Distribution and abundance	As in (3) with sites differing in occurrence or abundance of the target species	14 (13)	4 (4)	6	0
7. Relative abundance	As in (1) and abundance of all species in the community monitored	7	2
	As in (7)	8	4
8. Diversity					
Competitive ability:					
9. Between species or groups:					
a) Effect	>1 neighbor species or group in separate treatments	21 (16)	15 (11)	5	0
b) Response	>1 target species or group	42 (29)	13 (8)	13	1
10. Intra- vs. interspecific:					
a) Effect	>1 neighbor species, with one neighbor being conspecifics of the target species	13 (9)	11 (9)	0	0
b) Response	>1 target species, with one target being conspecifics of the neighbor species	9 (6)	3 (2)	1	0

NOTE.—For each question, the "potential" column indicates the total number of experiments out of a total of 101 (in 89 studies) that included the necessary treatments. The "actual" column indicates the number of experiments that also included the appropriate statistical analysis to address each question (see text). "Individual" indicates that target species' responses were measured at the individual level (e.g., growth, survival), and "population" indicates that population size of the target species (e.g., density, cover) was measured. Because two studies included both individual- and population-level measurements, the total number of experiments noted for a question in the text does not always equal the sum of the individual and population columns in the table. Values in parentheses are the number of removal experiments only; because population-level measures cannot be obtained for phytometer experiments, values in the population column are already for removals only.

done that meet these criteria. We limit our review to plants because more field competition experiments seem to be available for plants than for other groups of organisms (Jackson 1981; Connell 1983; Schoener 1983), probably because of the relative ease of manipulating sessile organisms in the field.

We develop a series of questions about the phenomenon of competition and its consequences (summarized in table 1). These are all phrased in deliberately general terms, but in all cases there is at least some theory (formal mathematical or verbal) that makes specific predictions about the answers. They are also all questions that we felt are best answered by field experiments. Because of the diversity of questions we discuss, we do not attempt a general review of the competing hypotheses for any one question, but we do give some examples demonstrating the importance of each question for resolving current controversies in ecology or for assessing the validity of assumptions of current theories on competition. After describing the questions, we describe the scope of our review and our criteria for inclusion of experiments. For each question, we then outline the necessary experimental treatments and statistical comparisons that we argue are required to answer the question, tally how many studies meet these requirements, and summarize their results.

QUESTIONS

Occurrence of Competition

The most obvious question we can ask about competition is simply whether or not it occurs (question 1 in table 1). By itself, the answer to this question is not very informative, although it is by far the question most commonly addressed by field experiments on competition (see below).

Patterns of Occurrence of Competition

Broadening the question to ask whether the magnitude of competition varies over time (question 2; Schoener 1983; Fowler 1986a) or space (question 3) is important for assessing the generality of results for simple occurrence or any of the other questions below. Variation in magnitude of competition or relative competitive abilities over space and/or time is also an essential assumption of several models of the role of competition in community structure (Hutchinson 1961; Grubb 1977; Wiens 1977; Chesson and Warner 1981). Other theory makes more specific predictions about how the magnitude of competition should vary over particular types of environmental gradients. Productivity gradients, in particular, have interested plant ecologists because so many patterns in vegetation composition are associated with productivity (question 4). For example, a major debate among plant community ecologists is whether the magnitude of competition increases with increasing productivity (Grime 1973; Wilson and Keddy 1986) or stays similar along productivity gradients (Newman 1973; Tilman 1988). Similarly, Grime (1977, 1988) has argued that the traits that determine competitive ability are constant across productivity gradients, whereas Tilman (1982, 1988) has argued that trade-offs in competitive ability for different resources result

in changes in the traits that determine competitive success across productivity gradients. The abundance of predators, pathogens, or mutualists is another type of environmental gradient, and a number of researchers have hypothesized about how the magnitude of competition or relative competitive abilities depends on interactions with other trophic levels (question 5; Connell 1975; Menge and Sutherland 1976; Grime 1979; Oksanen et al. 1981; Coley et al. 1985; Louda et al. 1990).

Community Consequences of Competition

How does competition influence distributions across environments (question 6) and relative abundances (question 7) and diversity (question 8) within environments? These were central issues of the debate of the late 1970s and early 1980s on the "importance of competition" (Salt 1984; Strong et al. 1984; Diamond and Case 1986), and they still occupy much of the theoretical literature concerned with competitive interactions. Documenting that competition occurs does not necessarily imply that this competition has important consequences for ecological communities.

Competitive Ability

Finally, several related questions require comparisons of competitive ability among species: To what extent do species differ in competitive ability, what traits determine relative competitive ability, and how do these traits change among environments (question 9)? Again, theoretical formulations suggest hypotheses about the answers to these questions for plants, including *r*- and *K*-selection theory (MacArthur and Wilson 1967; Pianka 1970), strategy theory (Grime 1973, 1977, 1979, 1988), and mechanistic models of competition (Tilman 1982, 1988; Smith and Huston 1989; Goldberg 1990). Question 10 concerns the relative intensity of intraspecific to interspecific competition in coexisting species. Until recently, most of the theory on coexistence within communities predicted that intraspecific competition should be consistently greater than interspecific competition for stable coexistence (Roughgarden 1979; Tilman 1982), although several alternative theories for trophically equivalent species now exist, for example, coexistence by equivalence of competitive abilities (Aarssen 1983; Hubbell and Foster 1986) and spatial and/or temporal variation in environment (Chesson and Warner 1981; Shmida and Ellner 1984).

Limitations of Review

Several caveats should be kept in mind while evaluating our results about the extent to which field experiments have addressed each of these questions. First, field experiments are not the only possible and useful way to address most of these questions, and abundant data to evaluate the answers may be available from sources outside the scope of our review. For example, numerous researchers have compared competitive ability among species in greenhouse and common-garden experiments (see Harper 1977; Keddy 1989). Second, we included two distinct steps in evaluating whether or not a given experiment addressed a particular question: whether or not the appropriate experimental treat-

ments were included in the design, and then whether or not the appropriate statistical analysis of those treatments was made. In many cases, experiments we included as meeting the first set of criteria may not have met the second because the authors were addressing very different questions and simply happened also to include the appropriate treatments for our question. Our goal here was simply to assess whether the questions we review are being addressed in the literature and not to indict particular studies for not addressing them (if it were the latter, the senior author would have to spend too much time saying "mea culpa"). Third, because our focus was on appropriate types of comparisons needed to answer particular questions about competition, we were liberal in our criteria for rigor in other aspects of experimental design and statistical analysis. Hurlbert (1984) and Underwood (1986) provide excellent reviews of these aspects of field experiments in ecology. Fourth, for clarity we use the term *competition* in the usual textbook definition of negative interactions (see Abrams 1987). However, in most cases these interactions could have arisen through several mechanisms, including those not traditionally thought of as competition such as those mediated by a herbivore (e.g., apparent competition; Holt 1977; Connell 1990). Similarly, for clarity we also often refer to experimental treatments that differ in abundance of potentially interacting plants as "competition experiments," although this basic experimental design could (and often does; see below) also detect positive interactions.

METHODS

General Criteria for Inclusion

We surveyed the 10-yr period 1979–1988 in seven journals (*Ecology*, *Ecological Monographs*, *Journal of Ecology*, *Oecologia* (Berlin), *American Journal of Botany*, *American Midland Naturalist*, and *American Naturalist*). By conducting an exhaustive search of a restricted set of journals and years, we gain the advantage of an unbiased data base. However, this procedure has the disadvantage that some excellent studies that meet all the criteria for addressing a particular question are excluded because they are outside the scope of the quantitative survey. Despite this limitation, it is unlikely that a broader survey would change the basic conclusions of the study.

All articles that contained experiments on interspecific plant-plant interactions in natural communities were included in the survey. We defined these as studies that included experimental manipulation of abundance (e.g., density, biomass, cover) of one or more plant species or group of species in a natural community and that recorded some aspect of performance of individual plants (e.g., survival, growth, physiological status), plant populations (e.g., density, biomass, cover), or plant communities (e.g., relative biomass, species diversity) as a dependent variable. We did not include experiments where only intraspecific interactions were examined, although we did include measurements of intraspecific interactions if interspecific interactions were also quantified. We included all studies on vascular plants, and we also arbitrarily decided to include studies of some nonvascular plants such as kelps with growth forms that generate a layered vege-

tation. We did not include studies on planktonic algae or sessile algae with strictly crustose growth forms.

Types of Manipulations Included

To describe the types of experimental manipulations we included, we distinguish between neighbor species and target species in an experiment. A neighbor species is the species or group (e.g., growth form) whose abundance differs between treatments (an independent variable). A target species is the species or group whose response to differences in neighbor abundance is being monitored (a dependent variable). We included experiments in which only the neighbor species, only the target species, or both targets and neighbors were manipulated. In "removal" experiments, neighbor abundance was experimentally reduced relative to controls, whether or not targets were also experimentally manipulated. Although neighbor abundance could also be experimentally increased, we did not find any such studies. In "phytometer" experiments, only target abundance was experimentally manipulated, and neighbor abundance varied because of natural causes (e.g., targets transplanted into tree-fall gaps vs. undisturbed forest or under individual plant canopies vs. between canopies). Because natural variation in neighbor abundance could arise from a number of (often unknown) factors that could also directly affect the target plants, we present data both on the total number of experiments we found that address a given question and the number excluding phytometer experiments.

Both removal and phytometer experiments allow assessment of the absolute magnitude of competition because treatments differ in the absolute abundance of at least one group of neighbors. We also included two other types of experiments in which treatments differ in neighbor identity but not absolute neighbor abundance. These allow comparison of the relative but not the absolute magnitude of the effects of different neighbors. In "comparison-phytometer" experiments, targets are planted in sites that differ naturally in identity of neighbor species or groups, but those neighbors do not necessarily (or at least are not reported to) differ in absolute abundance (e.g., seedlings planted under individual canopies of different shrub species; Fuentes et al. 1984). In "substitutive" experiments, only two species are present, total density is constant, but frequency of the two species is varied among treatments.

The "natural community" part of our definition of field experiments excludes common-garden experiments, where all vegetation was removed, typically the ground was prepared in some way, and all individuals of the experimental species were sown or transplanted back in at controlled densities (Grace and Wetzel 1981; Mitchley and Grubb 1986). We did, however, include experiments where target plants in pots were placed in environments that differed in absolute abundance of potential competitors (e.g., in closed canopy vs. tree-fall gaps; Chazdon 1986) or where both targets and neighbors were planted in pots but were placed back in the natural field situation (McCreary et al. 1983). There were only seven of these "field pot" experiments (one removal, five phytometer, and one substitutive experiment). Excluding these experiments does not change any of the basic patterns reported below.

Information Recorded from Experiments

For each distinct experiment (some articles contained more than one experiment), we recorded the type of manipulation, the level of response measured (individual or population; see below for explanation), the duration of the experiment, the number of sites and years in which the experiment was repeated, the number of different target and neighbor species or groups, the type of any additional treatments that were performed (e.g., herbivore protection, resource additions), and the types and outcomes of statistical comparisons of treatments (see Apps. A and B).

Throughout the presentation of the results, we separate experiments that measure response to competition at the individual and population levels because, as Abrams (1987) has emphasized, the magnitudes and even signs of interactions may change between individual and population levels and much of competition theory focuses only on the population-level consequences of competition for communities. Similarly, predictions about the traits that determine competitive ability may differ between individuals and populations (Goldberg 1990; Grace 1990). Individual-level responses include demographic parameters (e.g., probability of emergence, survival or reproduction, growth rate or size, reproductive output) and physiological and morphological measurements. Population-level measures include indices of total population size (density, biomass, or cover). Measures of abundance of only a part of the target population (e.g., number of new recruits) were included with the individual-level responses because it is not known whether changes in other components of the population could compensate for the changes in the measured component. Because phytometer experiments, by definition, incorporate experimental manipulation of the targets, population-level response cannot be measured in these experiments.

RESULTS AND DISCUSSION

We found a total of 89 articles containing 101 distinct experiments in our survey (see App. B for details for each experiment). These included 76 removal experiments, 18 phytometer experiments, 4 comparison-phytometer experiments, and 3 substitutive experiments. Most experiments (82) measured responses of individual plants, but we found 21 experiments with population-level responses. (Two experiments provided both individual- and population-level data, so the numbers in the individual and population columns in table 1 do not always add up to the total number of experiments reported in the text.) Similar to the findings of Schoener (1983), the majority of experiments (62%) lasted 1 yr or less, with a maximum duration of 7 yr (fig. 1). Thus, all the conclusions drawn below have the caveat that they only apply to short-term responses to competition.

An additional caveat applies to interpreting results for population-level responses. Because these experiments tended to be even shorter than the entire set of experiments (maximum duration of 3 yr; fig. 1), many of the measures of change in population size probably do not represent cross-generational responses. Instead, they may reflect mortality of already existing individuals or, for biomass

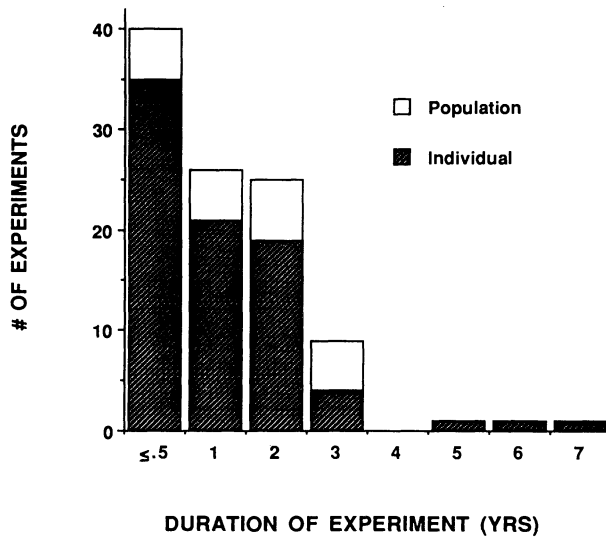


FIG. 1.—Frequency distribution of the number of experiments ($n = 101$) with different durations. Individual and population indicate the level at which responses of target species in an experiment were measured (see text for definitions).

or cover data, changes in growth rate of already existing individuals (i.e., results similar to that represented by individual-level data).

Occurrence of Competition

1. *Does competition occur?*—Operationally, this question can be translated to, Do components of fitness of individuals or total population size differ between treatments that differ in absolute abundance of neighbors? Therefore, all of the removal and phytometer experiments potentially could test for the occurrence of competition at either the individual (74% of all experiments) or population level (21% of all experiments; table 1). Of these, four experiments at the individual level and three at the population level did not statistically compare target response in low versus high neighbor abundance. Of the remaining 71 experiments at the individual level, 83% showed at least some significant negative effects, and 10% showed at least some significant positive effects of high relative to low neighbor abundance (App. B). Of the 18 remaining experiments at the population level, 61% had some significant negative effects, and 33% had some significant positive effects. The values for negative interactions, especially at the population level, are somewhat lower than the 92% of studies with at least some significant negative effects found by Schoener (1983) for terrestrial plants. Nevertheless, the results do agree with those of both Schoener (1983) and Connell (1983) on the relatively high frequency of occurrence of competition in natural communities. They also suggest that facilitation is common enough to deserve more investigation than it has received (Boucher 1985; Hunter and Aarssen 1988).

Patterns in the Occurrence of Competition

2. *Does the magnitude of competition vary over time?*—To answer this question, one must repeat experiments with treatments that differ in absolute neighbor abundance (competition treatments) at different times, and the time \times neighbor abundance treatment interaction must be tested. We use these fairly strict design and analysis criteria for two reasons. First, we required that the neighbor abundance treatments be reinitiated rather than maintained over time because in many cases variation in competition over time within the same experiment could reflect factors other than competition per se, such as life-history stage. For example, an experiment started with seedlings may show competition in year 1 but not in year 2 if seedlings are more vulnerable to competition than older plants. Thus, unlike Schoener (1983), we do not include studies with measurements in the same experiment over time as testing for variation in competition over time. Second, we required an explicit statistical test for variation in magnitude of competition over time (the neighbor abundance \times time interaction) rather than qualitative comparison of statistical analyses of competitive effects among times. The latter would be adequate to show variation over time if competitive effects were present at one time and nonsignificant at another but could not test for more subtle effects where the magnitude of significant competition differed over time.

We found only four experiments that reinitiated the same neighbor abundance treatments at different times and so potentially could test for variation in magnitude of competition over time (table 1). However, three of these analyzed competition effects independently for each season (Turner 1985) or year (Parker and Muller 1982; Miller and Werner 1987); these all found at least some significant effects of competition at all times. Only one study explicitly tested for variation in magnitude of competition over time, and in that case the time \times competition interaction was significant (Sousa et al. 1981), which indicates that the magnitude of competition differed among seasons.

3. *Does the magnitude of competition change over space?* 4. *Does the magnitude of competition change along productivity gradients?*—Both of these questions require that treatments differing in absolute abundance of neighbors (competition treatments) be repeated in different sites and that site \times competition interactions be tested. That is, the effect of neighbors must differ between sites to answer these questions in the affirmative. For question 3, the sites could differ in any environmental characteristic or even be chosen as replicates. For question 4, the sites must differ in productivity. These requirements also hold for question 6, where sites must differ in abundance of the target species (see Community Consequences of Competition).

Nearly 75% of the experiments were conducted in only a single site (fig. 2), and a further two experiments compared treatments differing only in neighbor identity but not in neighbor abundance. Of the remaining 25 experiments with the potential to examine how the magnitude of competition changes over space, only seven tested the site \times competition interaction at the individual level, while none did so at the population level; the remainder analyzed competition effects

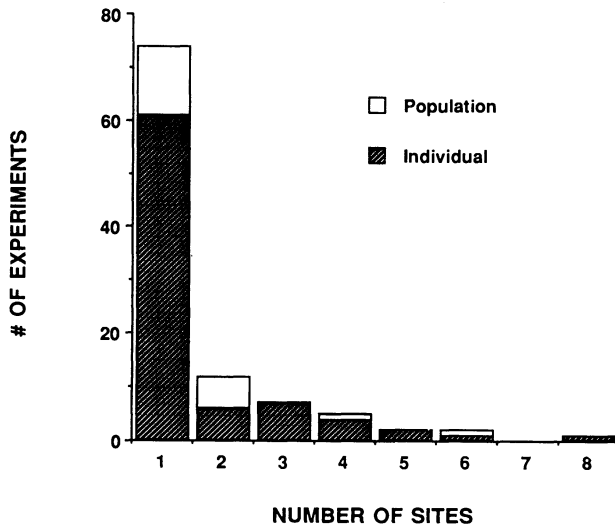


FIG. 2.—Frequency distribution of the number of experiments ($n = 101$) that were repeated in a given number of sites. Individual and population indicate the level at which responses of target species in an experiment were measured (see text for definitions).

independently at each site (table 1). All but two of the experiments that tested whether the magnitude of competition varied among sites addressed either productivity gradients or target species distributions; these are discussed below. Both of the “replicate” site experiments showed nonsignificant site \times competition interactions (Titus and Stephens 1983; Sork 1987), which indicates that the magnitude of competition did not depend on site, although both sites and competition were significant as main effects in at least some tests.

For question 4, five experiments were repeated on sites that differed explicitly in productivity (these were also all “distribution sites” for question 6; table 1). In three of these, site \times competition interactions were tested (table 1). All were significant, and all showed larger differences in target performance between low and high neighbor abundance (i.e., greater magnitude of competition) in sites with higher productivity (Gurevitch 1986; Reader and Buck 1986; Wilson and Keddy 1986).

An alternative approach to asking whether productivity influences the magnitude of competition is to create productivity gradients experimentally by resource additions. We found seven experiments that included factorial designs of neighbor abundance crossed with resource addition (all fertilization) treatments, of which only three tested for interactions between the two types of treatments. Of these, Reichman (1988) found no significant interactions, and Goldberg (1985) and Gibson (1988) both found 25% or fewer of interactions tested were significant. In all three cases, the main effect of resource addition was significantly positive, which indicates that a limiting resource was added.

Thus, the few available data from natural and experimental productivity gradients are conflicting. The natural gradient data are consistent with Grime's (1973)

hypothesis that competition is more intense on more productive sites and therefore might have larger effects on community structure. However, the data from experimental productivity gradients are consistent with the opposing hypothesis that competition does not change in intensity along productivity gradients (Newman 1973; Tilman 1988). Two more recently published studies not included in our survey are also consistent with this dichotomy of results. Using a natural gradient, Reader and Best (1989) found competition intensity was higher in more productive sites, and Wilson and Tilman (1991) found no change in intensity along an experimental nitrogen addition gradient.

The interpretation of this contrast due to methodology is obscure, especially because there have been no direct comparisons of natural and experimental productivity gradients in the same system. However, it does suggest that the two approaches may not be comparable, although it is difficult at this point to suggest which approach is more appropriate because both have potentially important artifacts. For example, natural gradients may typically be confounded by some other factor that covaries with productivity such as herbivory (Oksanen et al. 1981; Louda et al. 1990; Oksanen 1990), physical disturbance (Wilson and Keddy 1986), or fire (Barton 1991). On the other hand, experimental productivity gradients produced by nutrient addition may not adequately mimic the temporal patterns of supply of nutrients in natural systems, which could have strong effects on the apparent magnitude of competition (see Goldberg and Miller 1990).

In addition, none of the experimental or natural gradient studies have presented the data relative to maximum potential performance in each site in the absence of competition. Comparing absolute differences in performance of target plants with and without neighbors would tend to bias results in favor of increasing competition with increasing productivity, although this bias should apply equally to both experimental and natural gradients and so does not help explain the dichotomy of results we found. All the results also compare total effects of all vegetation present among sites rather than adjust for differences in standing crop or productivity of neighbors between sites so that per-gram competitive effects could be compared. Because natural productivity gradients have presumably developed over long periods of time, differences in initial biomass of neighbors between low and high productivity should be much greater along natural gradients. This would tend to bias toward finding larger effects of removing neighbors and hence greater competition intensity at high productivity in natural gradients, consistent with our results. Finally, none of the experiments that address competition along productivity gradients have been carried out for more than 3 yr (App. B). If the major effect of productivity is on the rate of competitive displacement (Huston 1979), smaller magnitudes of competition measured over a short time period are expected in less productive sites, with lower individual growth rates, again consistent with our results. Although this would have no effect on the equilibrium outcome of competition, Huston (1979) has argued that the interaction of disturbance and rate of competitive exclusion would produce much stronger effects of competition on high productivity sites.

5. *Does the magnitude of competition depend on herbivory?*—To answer this question, both neighbor abundance and herbivore abundance must be manipu-

lated and the competition \times herbivore interaction tested. We found eight experiments where presence-absence of herbivores was fully crossed with presence-absence of neighbors in a factorial design, but only three of these tested for significant interactions (table 1). Although the main effects of both herbivory and neighbors were usually significant, the results for interactions were variable among the few studies with tests: Parker and Salzman (1985) found that the magnitude of competition did not depend on herbivory, Sousa et al. (1981) found strong dependence, and Sork (1987) found rare dependence (one out of six possible tests). As with productivity-competition interactions, an alternative approach is to repeat competition experiments on sites that differ naturally in herbivore density. We found only one study like this, which did not include statistical comparisons between sites (Lubchenco 1980). We also found no studies that examined how the interaction of herbivory and competition changed along productivity gradients to test the ideas of Oksanen et al. (1981) and Louda et al. (1990).

Community Consequences of Competition

6. *Does competition influence the distribution and absolute abundance of species among environments?*—Whether competition influences species' distributions was potentially investigated by 19 experiments that repeated neighbor abundance (competition) treatments in sites that differed in abundance of the target species (table 1). In most cases, the choice of sites was made explicit by the authors, but in a few cases we inferred a choice based on target distribution from vegetation descriptions of each site. Only four of these tested for competition \times site interactions; most of the remaining experiments with suitable data did separate analyses of competition effects at each site (table 1). All of those tested showed significant interactions, and all showed greater negative effects of neighbors in sites where the target species was absent or at low abundance than where it was present or at higher abundance (van der Meijden and van der Waals-Kooi 1979; Gurevitch 1986; Reader and Buck 1986; Cid-Benevento 1987).

These consistent results suggest that competition from neighbors does often influence distribution and abundance patterns, especially when contrasted with the two nonsignificant interactions from experiments that use "replicate" sites (see question 3). However, such results may not always be sufficient. If identical results were found for a second target species that does occur in all sites, this would suggest that competition alone could not be responsible for the distribution of the first species. Therefore, a completely satisfactory affirmative answer to question 6 would include significant site \times target species \times competition interactions, with the target species showing greater negative effects of high neighbor abundance where it does not occur than where it does occur *and* greater effects where it does not occur than for a species that does occur there. We found two studies that included this additional level of comparison (see McGraw and Chapin 1989 for an excellent study meeting this criterion, but outside the scope of our quantitative review). Gurevitch (1986) found that *Stipa neomexicana*, a C₃ grass restricted to drier tops of ridges, was less affected by competition in these sites than in wetter sites where it did not naturally occur. However, the same pattern

was found for seedlings of a group of C_4 species that do occur in the wetter sites (i.e., nonsignificant target species \times neighbor abundance \times site interaction). This analysis by itself suggests that differences in competitive ability between the two groups are not responsible for their different distributions, although other data reported in the same article do suggest (but do not test explicitly) that the C_3 species is a poorer competitor in wetter sites. Cid-Benevento (1987) analyzed response to neighbors of an old-field and a woodland annual in both habitats. Although the full analysis was not reported (each species was analyzed separately), the old-field annual was significantly less affected by competition in the old field than the woods, whereas the reverse was true for the woodland annual (both significant site \times neighbor abundance interactions).

7, 8. *Do plant-plant interactions influence relative abundances (7) or species diversity (8) within environments?*—To answer both of these questions, one must consider the necessary conditions, again, of competition treatments that differ in absolute abundance of neighbors and measurement of response of the (initially similar) entire community to these treatments. This requirement eliminates both phytometer and comparison-phytometer experiments because the neighbor treatments in these designs are sites chosen because of natural differences in neighbor abundance or identity and therefore are possibly different in community composition as well. Substitutive experiments are also eliminated because in all examples we found the original community comprised more than the two species used in the experiment. Finally, the question can only be asked at the population level, which eliminates all experiments with only individual-level responses.

These restrictions left only nine experiments. Of these, only two were tested for response of the entire community; both found significant effects of experimental manipulation of neighbor abundance on composition of the rest of the community using multivariate analyses (Gibson 1988; Johnson and Mann 1988). In most of the remaining studies, changes in absolute abundance of each species were analyzed independently. Thus, parallel responses of all species in the community to competition treatments (i.e., no change in relative abundances) cannot be distinguished from change in relative abundances. Four of the nine studies also presented data on species diversity; these all involved removal of one or a few dominant species from the community. In all four studies, diversity was significantly higher in removal treatments than in controls in all or most tests (Armesto and Pickett 1985; Duggins and Dethier 1985; Turner 1985; Gibson 1988), which suggests that numerical (or biomass) dominants do often exclude other species from a community.

Competitive Ability

9. *To what extent do species differ in competitive ability, what traits determine competitive ability, and how do these traits change among environments?*—To answer all parts of this question, one must compare competitive ability among species. The definition of competitive ability is a hotly debated topic (Thompson 1987; Tilman 1987), but for our purposes we define it in two distinct ways: competitive effect or ability to suppress other plants and competitive response or ability to avoid or tolerate suppression. This definition corresponds to comparison

of effect of different neighbor species (or groups of species such as growth forms) on a single target species or group and comparison of response of different target species to a single neighbor species or group (Goldberg and Werner 1983a). Distinguishing between these is important because different traits may be related to rankings of competitive effect and of competitive response (Goldberg 1990; Goldberg and Landa, in press). Comparisons of competitive effect and competitive response also require different statistical analyses. Significant differences in competitive effect are detected by significant main effects of neighbor treatment, where the treatments differ in identity of the neighbor species or group. However, significant differences in response to competition are detected by significant interactions between target species and neighbor abundance treatment (i.e., all target species should be considered in the same analysis). Significant target main effects, but not target \times treatment interactions, indicate that the target species differ overall in the trait measured but not that they differ in their response to competition.

About 25% of all experiments used more than one neighbor species or group (fig. 3, top) so that competitive effects potentially could be compared, but 36% of these did not contain any statistical comparisons of the effects of different neighbor groups (table 1). The remaining 16 experiments can be broken down according to the way comparisons were made among neighbors (some experiments had more than one type of comparison, so the numbers add up to greater than 16). Most commonly, researchers compared species or groups of species such as growth forms at their natural abundances by removing all individuals of one species or group at a time. Thus, comparisons of competitive effect from this kind of analysis are potentially confounded by differences in abundances among species, and it is impossible to relate traits of individuals to their competitive effect. Removal experiments where only one species or group is removed at a time also measure the total of direct and indirect effects of the removed species, so that comparisons among species or groups cannot be extrapolated to other communities where the potential complex of indirect effects may be different. Only six experiments compared species on a per-plant basis (Berendse 1983; McCreary et al. 1983; Fuentes et al. 1986; Schoen et al. 1986; Goldberg 1987; Zammit and Westoby 1988). All these measured only direct effects because only one neighbor species or group was present in each treatment. The only one of these that did not show at least some significant differences among neighbor species in competitive effect was a comparison of two species of *Impatiens* that used a substitutive design replicated in two sites (Schoen et al. 1986).

Because individual plants within a species can vary so enormously in size, even comparisons of competitive effect on a per-individual basis may be difficult to interpret in terms of the physiological or morphological basis of competitive ability. For addressing mechanisms of competition, comparisons among species on a per-unit size basis may be more informative. Only two experiments compared neighbor species or groups on a per-unit biomass basis; in both cases, neighbor effects were generally not significantly different on a per-gram basis (Goldberg 1987; Miller and Werner 1987). This contrasts with comparisons of per-gram competitive effect among neighbor species in more controlled greenhouse or

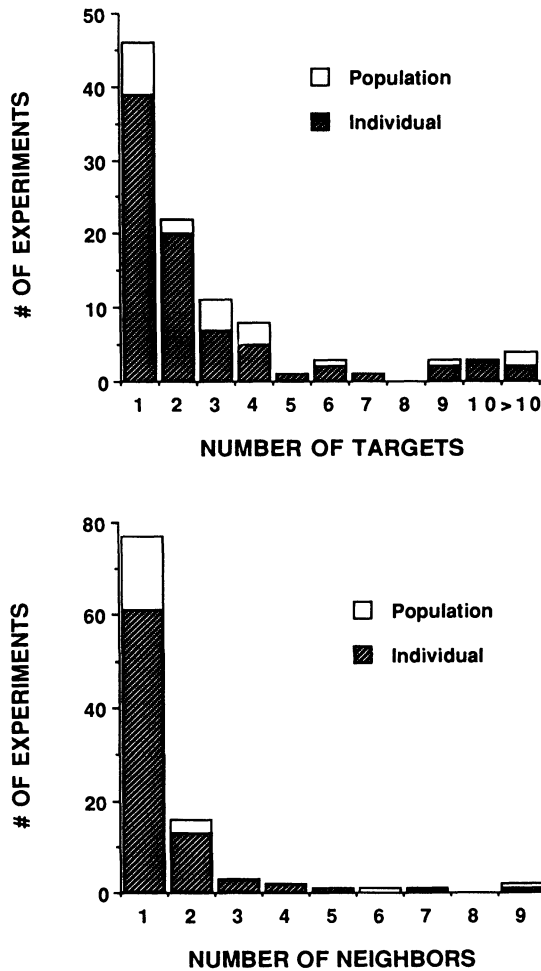


FIG. 3.—Frequency distribution of the number of experiments ($n = 101$) with different numbers of target species (*top*) and neighbor species (*bottom*). Individual and population indicate the level at which responses of target species in an experiment were measured (see text for definitions).

common-garden experiments, where species usually do differ significantly (see, e.g., Goldberg and Fleetwood 1987; Gordon et al. 1989; Goldberg and Landa, in press).

Many more studies had the potential to compare competitive responses than competitive effect, but many fewer actually did so. Over half of all the studies used more than one target species or group and so potentially could have compared competitive responses, but only 25% of these (14 experiments) actually did the appropriate statistical test (table 1). In contrast, only 25% of all experiments used more than one neighbor species and so could have compared competitive effects, but 64% of these did the appropriate statistical test. One likely cause of

this discrepancy is the greater complexity of the statistical analyses to compare responses than effects. Although differences in competitive responses are detected by the target species \times competition treatment interaction, the common approach when more than one target species is used is to treat each species as a separate dependent variable and analyze the effects of competition on each species independently (Goldberg 1985).

A second possible reason for the rarer occurrence of statistical comparisons of competitive response among target species derives from the way classical competition theory is formulated. The outcome of competition in models based on the Lotka-Volterra competition equations depends on the relative carrying capacities and the relative competition coefficients, which are defined as comparisons of competitive effects between hetero- and conspecifics. Competitive response is implicitly incorporated because the equilibrium outcome of competition depends on the values of all the reciprocal comparisons of intra- or interspecific effect. Nevertheless, the definition of the competition coefficients suggests that the essential comparisons of competitive ability are of competitive effects on a single target species at a time. Our results suggest that this is indeed the typical comparison made. Similarly, the standard analysis of substitutive experiments provides for an explicit test only of the relative intensity of inter- and intraspecific competitive effect.

There are actually even fewer response comparisons among species than suggested in table 1 because four of the 14 comparisons were among groups within a single species. These were included in the survey because all the target groups were responding to heterospecific neighbors in all four cases. Excluding these intraspecific comparisons, half of the response comparisons showed no significant differences among target species (McCreary et al. 1983; Fuentes et al. 1984 [2 experiments]; Schoen et al. 1986; Zammit and Westoby 1988), and half showed at least some significant differences in response (Gurevitch 1986; Collins and Pickett 1988a [population level]; Pons and van der Toorn 1988; Popma and Bongers 1988; van der Toorn and Pons 1988). The intraspecific comparisons showed a similar variable pattern. Crawley and Nachapong (1985; seed size), Winn (1985; seed size), and Turkington and Harper (1979; clones originally growing with different neighbor species) all found some differences in competitive response among target groups, but Goldberg (1988; clones) found no differences.

Whether differences in competitive ability among species are greater for effect or for response has an important bearing on the design of experiments to analyze the influence of competition on communities. For example, Goldberg and Werner (1983a) suggested that effect on a per-unit size basis might be more similar among species than is response. If correct, this could greatly simplify analysis of competitive relationships within a community because we then only need to measure response of individual species to the entire community of neighbors. The only studies to include both effect and response comparisons in the same experiment were all comparisons of intra- and interspecific competition; these are discussed below (question 10). Across studies, whether co-occurring species differ more in effect or response seems to depend on the type of comparison of effect of neighbors. Across studies, species differed in response in about half the comparisons.

Per-individual effects of neighbors were almost always different among neighbor species, and so effects seem to differ more than response. However, consistent with Goldberg and Werner (1983a), the two sets of comparisons of per-gram effects found very few differences among neighbors and so effects seem to differ less than response.

To assess what traits influence competitive ability, one must compare in either effect or response species that differ in some specified trait, with several species at each level of the trait (e.g., evergreen vs. deciduous species, small vs. large seeded species) or sufficient species for a valid regression on a continuously varying trait (e.g., seed size or root allocation). We checked all studies with four or more neighbor or target groups and found that these conditions were met in only two experiments. For effect, Goldberg (1987) compared competitive effect among three growth forms (2–3 species each) and among all seven species as a function of aboveground size of an average neighbor plant and found that growth form and species differences in per-individual effect could be largely accounted for by differences in biomass. Winn (1985) compared competitive response among six seed size classes within a species in each of two sites and found individuals from larger seeds were generally better response competitors (i.e., they showed less of a negative response to high neighbor abundance treatments).

The final part of question 9 is whether relative competitive ability or the traits determining competitive ability change between environments. Treatments comparing neighbors or targets repeated in more than one site are required to address this point. Of the experiments listed in table 1 for competitive abilities, five of the potential effect comparisons and 17 of the potential response comparisons were repeated in more than one site (App. B). Of these, only two experiments assessed whether relative competitive abilities changed between sites, and both did so at the individual level. Schoen et al. (1986) compared both effect and response in two sites and found relative effects of two *Impatiens* species changed between sites but relative responses did not. As already discussed under question 6 on distribution patterns, Gurevitch (1986) compared relative growth responses of a C₃ grass and a group of C₄ grasses to competition among three sites and found no significant change in relative response among sites.

An alternative approach to testing whether relative competitive abilities change with environmental conditions is to combine manipulation of neighbor or target identity with experimental manipulations of the environment. When we included presence-absence of herbivores as an environmental condition, we found five experiments that potentially could have compared competitive effects across environments, of which two explicitly tested such comparisons. Parker and Salzman (1985) tested the response of shrub seedlings to removal of conspecific adults versus removal of all grasses with and without removal of a grasshopper herbivore of the shrub. Although both neighbor abundance and grasshoppers significantly influenced target growth, the relative effects of the two groups did not change depending on herbivore protection treatment. In contrast, McCreary et al. (1983) did find significant changes in relative effects depending on a variety of environmental treatments in a field pot experiment with two species of aquatic macrophytes, although the two species did not differ significantly in their effects

averaged over all environmental treatments. McCreary et al.'s (1983) experiment was also the only study to test explicitly whether relative competitive responses of target species change over environments, although a total of 10 experiments potentially could have done so. In this case, the species did not differ in relative responses averaged over all experimental environments, and the relative responses did not change among environments.

10. *Is intraspecific competition consistently stronger than interspecific competition?*—The requirements to address this question are the same as for comparisons of effect or response among any group of species with the additional stipulation that at least one of the target-neighbor combinations must be intraspecific. For effect, we found 13 experiments with the potential to compare the direct effects of intraspecific competition versus interspecific competition, all at the individual level (table 1). In most of these (85%), competitive effects were statistically compared, but, as with the more general comparisons of competitive effects, most of the comparisons confound the effect of total abundance of a species with its per capita or per-unit biomass effect. Only one of the four per-individual comparisons (all substitutive or comparison phytometer experiments) found that intraspecific competition was consistently greater than interspecific competition. In this case, two grassland species appeared to partition soil resources through different rooting depths (Berendse 1983). The remaining three experiments found no consistent pattern of intraspecific relative to interspecific effect (McCreary et al. 1983; Schoen et al. 1986; Zammit and Westoby 1988).

For response, we found 10 experiments with more than one target species and where the neighbors included conspecifics of at least one of the targets; all but one of these measured individual-level responses. Only three of these tested for differences in response (all also compared effect; see above), and all found no consistent pattern of intraspecific response being greater than interspecific effect (McCreary et al. 1983; Schoen et al. 1986; Zammit and Westoby 1988). Unfortunately, no statistical comparison of competitive responses was made in the one study that found intraspecific greater than interspecific effects (Berendse 1983).

The very limited field evidence available for coexisting species thus suggests that conspecifics do not usually compete more strongly than heterospecifics. There are, of course, many reasons why these data are inadequate to test the classical prediction that stable coexistence requires intraspecific competition to be greater than interspecific competition, through the mechanism of greater similarity in resource use. Most important, all of the comparisons are for only one of several possible life-history combinations, and all are for responses of individuals rather than populations, whereas the theory that generates the prediction was developed at the population level. Nevertheless, the results are consistent with the idea that resource partitioning is not an important mechanism of coexistence in plants, as a number of plant ecologists have argued in recent years (Werner 1979; Aarssen 1983; Goldberg and Werner 1983a; Hubbell and Foster 1986; Shmida and Ellner 1986; Mahdi et al. 1989). Instead, mechanisms of coexistence involving spatial or temporal variation in competition (see questions 2 and 3; Chesson and Warner 1983; Shmida and Ellner 1986) or equivalence of competitive ability (see question 9; Aarssen 1983; Shmida and Ellner 1985; Hubbell and Foster

1986) may be more important. However, rarely have both resource partitioning and alternative modes of coexistence been tested directly in a single system.

CONCLUSIONS

Although like other recent reviewers (Jackson 1981; Connell 1983; Schoener 1983; Aarssen and Epp 1990) we found a large number of studies containing field competition experiments, fewer than half of these (37/89 studies, 38/101 experiments) contain experiments that explicitly address questions about inter-specific competition in natural communities other than simply whether or not it affects components of individual fitness for a single species at a single site and time. In many cases, the lack of information to address any of the more complicated questions in table 1 is a function of lack of appropriate experimental treatments (24/89 studies, 26/101 experiments). This is hardly surprising. Given the time and expense involved in even a simple field competition experiment, it is a daunting prospect to repeat experiments at several times or sites, with many target or neighbor species, or combined with other experimental treatments to address more complicated questions about species interactions.

The more surprising result of the survey is that an equally important cause of lack of information to address most of the questions in table 1 is lack of appropriate statistical analyses of appropriately designed experiments (28/89 studies, 37/101 experiments). This is particularly striking in the case of competitive response. Over half of all the experiments we found used two or more target species and thus could have compared response competitive ability among species, but only 14 of these 55 experiments actually did the appropriate analysis of testing target species \times competition treatment interactions.

Some of this underutilization of available data is undoubtedly because the authors of the study never intended their experiment to address a given question, although the data turn out to be available. However, in many cases it *was* the authors' stated intention to address the question we pose. In these cases, a likely explanation is that many of the comparisons we argue are critical to addressing these questions concern interaction terms rather than main effects in an analysis. Questions 2–6, and 9*b*, and 10*b* all require tests of the interaction between competition treatments and either site or time (2–6) or target species (9*b*, 10*b*). In complex, multifactor experimental designs, interaction terms are often viewed as complications in an analysis, and the instinct seems to be to conduct a larger number of simpler analyses. However, for many of the important theoretical issues concerning species interactions, statistical interaction terms are clearly the point of biological interest.

Our results suggest three general recommendations for future field experiments on species interactions. First, we need larger and more complicated experiments if we are truly concerned with asking questions about the consequences of competition for community structure and how competition shapes species traits. Second is the less obvious but equally important recommendation that appropriate statistical comparisons be made to test specific hypotheses, such as the use of interaction terms to test changes in magnitude of competition over time or across sites.

This is quite apart from the important need for greater rigor in designing and analyzing experiments emphasized by Underwood (1986) and Hurlbert (1984), such as better-designed controls and real replication rather than pseudoreplication. Third, we need to incorporate measures of population-level response to competition and other treatments and to measure these responses for longer periods of time. It may be that the short-term individual-level responses that are more commonly measured always translate into short- and long-term population-level responses, but this is currently only an assumption with very little empirical basis.

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APPENDIX A

TABLE A1

DEFINITIONS OF VARIABLES FOR DESCRIPTION OF EXPERIMENTS IN APPENDIX B

Parameter	States
Level	IND = response of target individuals measured (e.g., survival or growth) POP = response of target population measured (e.g., density or cover) BOTH = individual and population target responses measured
Duration	No. of years experiment monitored .5 = one growing season .1 = only emergence measured
Experiment type	REMO = removal, neighbor abundance experimentally manipulated PHYT = phytometer, neighbor abundance differs naturally, targets experimentally planted CPHY = comparison phytometer, neighbor identity differs naturally, targets experimentally planted SUBS = substitutive, total density constant, species proportions varied experimentally -P = targets or targets and neighbors grown in pots placed in original field site
Other	Treatments fully crossed with neighbor abundance treatments: NO = none F = fertilizer additions H = herbivore density treatments SO = different soil types (not clearly differing in potential productivity) MY = mycorrhizal abundance Outcome of tests of other treatment \times competition interaction: NT = not tested † = tested and not significant * = tested and significant (pattern of results in text)

TABLE A1 (Continued)

Parameter	States
Years	No. of years or seasons experiment reinitiated Outcome of test of year \times competition interaction (codes as for Other)
Sites	No. of sites in which experiment repeated Type of variation among sites: D = target species differ in abundance among sites DP = sites differ in target species abundance and total productivity R = other
Relative abundance	Outcome of test of site \times competition interaction (codes as for Other) Measurement of response of all species or groups in a community to competition treatments (No/Yes)
Diversity	Outcome of test of changes in relative abundances (codes as for Other) Measures of no. of species in all competition treatments (No/Yes)
Effect	Outcome of tests of changes in diversity (codes as for Other) No. of neighbor species or groups manipulated in distinct treatments Type of comparison among neighbors: A = effects of neighbors at their natural abundances compared I = per-individual effects compared
Response	Outcome of tests of comparisons of neighbor species or groups: NT = not tested † = neighbors not significantly different in competitive effect * = at least some neighbor pairs significantly different
Intraspecific effect	No. of target species or groups monitored in experiments (C = all targets were conspecifics but of different genotypes or phenotypes) Outcome of tests of comparisons among target species or groups (i.e., target \times neighbor abundance interactions): NT = not tested † = targets not significantly different in response to competition * = at least some target pairs significantly different
Intraspecific response	Potential for comparison of intra- vs. interspecific effect (No/Yes) Type of comparison among neighbors (codes as for Effect) Outcome of comparison between intra- and interspecific effect: NT = not tested † = intraspecific effect not consistently stronger than interspecific effect * = intraspecific effect consistently stronger than interspecific effect
% Negative	Potential for comparison of intra- vs. interspecific response (No/Yes) Outcome of comparison between intra- and interspecific response (i.e., target \times neighbor identity interactions): NT = not tested † = intraspecific response not consistently stronger than interspecific response * = interspecific response consistently stronger than interspecific reasons
% Positive	Percentage of all possible comparisons within an experiment that were significantly negative (competition)
	Percentage of all possible comparisons within an experiment that were significantly positive (facilitation)

NOTE.—More details about appropriate treatment comparisons and statistical analyses to address specific questions about competition are given in the text, as are patterns for significant tests.

APPENDIX B

TABLE B1

EXPERIMENTAL DESIGN AND OUTCOME OF TREATMENT COMPARISONS FOR 101 EXPERIMENTS IN 89 STUDIES

Study	Level	Dur.	Expt. Type	Other	Years	Sites	Relat. Abun.	Diver.	Effect	Resp.	Intra. Effect	Intra. Resp.	% Neg.	% Pos.
1	POP	3.0	REMO	MY	1	1	No	No	1	1	No	No	0	75
2	POP	.5	REMO	NO	1	2/D/NT	Yes/NT	Yes*	1	15/NT	No	No	35	12
3	IND	1.0	PHYT	NO	1	1	No	No	1	9/NT	No	No	100	0
4	IND	.1	PHYT	NO	1	1	No	No	1	1	No	No	0	100
5	IND	2.0	SUBS	F/NT	1	1	No	No	2/I*	2/NT	Yes/I*	Yes/NT	ND	ND
6	IND	7.0	REMO	NO	1	1	No	No	1	1	No	No	100	0
7	IND	2.0	REMO	NO	1	1	No	No	1	1	No	No	33	33
8	IND	2.0	PHYT-P	NO	1	1	No	No	1	3/NT	No	No	100	0
9	IND	.5	REMO	NO	1	3/D*	No	No	1	2/NT	No	No	17	4
10	POP	3.0	REMO	NO	1	1	No	No	1	4*	No	No	0	0
11	POP	3.0	REMO	NO	1	1	No	No	1	3/NT	No	No	ND	ND
12	IND	2.0	CPHY	NO	1	1	No	No	2/A*	1	No	No	ND	ND
13	IND	.5	REMO	NO	1	1	No	No	1	2C*	No	No	100	0
14	IND	2.0	REMO	NO	1	3/D/NT	No	No	7/A/NT	6/NT	No	No	93	0
15	IND	2.0	REMO	NO	1	4/DP/NT	No	No	1	10/NT	No	No	ND	ND
15	IND	1.0	REMO	NO	1	6/DP/NT	No	No	1	14/NT	No	No	ND	ND
15	POP	2.0	REMO	F/NT	1	6/DP/NT	No	No	2/A/NT	ND	No	No	ND	ND
16	POP	2.0	REMO	NO	1	1	No	No	1	1	No	No	50	0
17	POP	1.0	REMO	H/NT	1	2/R/NT	Yes/NT	Yes*	1	3/NT	No	No	83	0
18	IND	2.0	REMO	NO	1	1	No	No	2/A*	1	No	No	75	0
19	IND	.5	REMO	NO	1	5/D/NT	No	No	1	1	No	No	67	0
20	IND	2.0	REMO	NO	1	1	No	No	2/A†	2/NT	Yes/A†	Yes/NT	67	0
21	POP	2.0	REMO	NO	1	1	Yes/NT	Yes/NT	9/A/NT	16/NT	No	No	16	5
22	POP	2.0	REMO	NO	1	1	No	No	1	4/NT	No	No	0	0
23	IND	.5	PHYT-P	NO	1	1	No	No	2/I/NT	2†	Yes/I/NT	Yes/NT	100	0
23	IND	.5	PHYT	H/NT	1	1	No	No	1	3†	No	No	0	100
24	IND	1.0	REMO	H/NT	1	1	No	No	1	2/NT	No	No	0	100
24	IND	1.0	PHYT	H/NT	1	1	No	No	1	2/NT	No	No	0	75
24	IND	1.0	CPHY	H/NT	1	1	No	No	2/I*	2/NT	Yes/I/NT	Yes/NT	ND	ND
25	IND	6.0	REMO	F/NT	1	1	No	No	1	1	No	No	63	0
26	POP	.5	REMO	F*‡	1	1	Yes*	Yes*	1	4/NT	No	No	50	0

27	IND	3.0	PHYT	F*‡	1	1	No	No	1	2/NT	No	No	0	50
27	IND	1.0	REMO	NO	1	1	No	No	3/A/NT	1	No	No	50	0
28	IND	.5	REMO	NO	1	1	No	No	9/A*§	1	Yes/A†	No	33	0
29	IND	.5	REMO	NO	1	1	No	No	1	10C†	No	No	100	0
30	IND	1.0	REMO	NO	1	1	No	No	1	2/NT	No	No	63	12
31	IND	1.0	REMO	NO	1	1	No	No	3/A/NT	1	No	No	23	0
32	IND	2.0	PHYT	NO	1	3/D/NT	No	No	1	4/NT	No	No	52	0
32	IND	.5	REMO	NO	1	1	No	No	1	2/NT	No	No	75	0
33	IND	3.0	REMO	NO	1	3/DP*	No	No	1	2*	No	No	88	0
34	IND	2.0	PHYT	NO	1	1	No	No	1	1	No	No	50	0
35	IND	.5	CPHY	NO	1	1	No	No	3/A*	1	Yes/A†	No	ND	ND
36	IND	5.0	REMO	NO	1	1	No	No	1	1	No	No	100	0
37	POP	.5	REMO	NO	1	1	Yes/NT	Yes/NT	6/A/NT	3/NT	No	No	0	0
38	IND	.5	REMO	NO	1	1	No	No	1	3/NT	No	No	60	0
38	IND	.5	PHYT	NO	1	1	No	No	1	3/NT	No	No	60	0
39	POP	3.0	REMO	NO	1	1	No	No	1	1	No	No	100	0
40	IND	.1	REMO	NO	1	1	No	No	1	1	No	No	100	0
41	IND	.5	REMO	NO	1	1	No	No	1	1	No	No	75	0
42	BOTH	1.0	REMO	NO	1	2/D/NT	Yes*	Yes/NT	2/A/NT	9/NT	No	No	16	2
43	IND	.5	REMO	NO	1	1	No	No	1	4/NT	No	No	25	0
44	IND	1.0	REMO	NO	1	1	No	No	1	2	No	No	50	0
45	IND	2.0	REMO	NO	1	2/R/NT	No	No	1	4/NT	No	No	25	0
46	IND	3.0	PHYT	NO	1	1	No	No	1	1	No	No	100	0
46	IND	3.0	PHYT	NO	1	1	No	No	1	1	No	No	100	0
47	IND	.5	REMO	NO	1	1	No	No	1	1	No	No	33	33
48	POP	3.0	REMO	NO	1	2/D/NT	No	No	1	2/NT	No	No	50	0
49	IND	1.0	REMO	NO	1	1	No	No	2/A†	2/NT	Yes/A†	Yes/NT	50	0
50	BOTH	1.0	REMO	NO	1	4/R/NT	No	No	1	1	No	No	0	0
51	IND	.5	REMO-P	NO	1	1	No	No	1	7/NT	No	No	71	0
52	IND	.5	SUBS-P	SO	1	1	No	No	2/I*	2†	Yes/I†	Yes†	ND	ND
53	IND	.5	REMO	NO	2/NT	1	No	No	5/A*§	5/NT	Yes/A†	Yes/NT	27	0
54	IND	2.0	REMO	H/NT	1	1	No	No	1	1	No	No	100	0
55	IND	1.0	REMO	NO	1	1	No	No	2/A*	1	Yes/A†	No	33	0
56	IND	.5	PHYT	SO	2/NT	1	No	No	1	3/NT	No	No	90	0
57	IND	1.0	REMO	H†	1	1	No	No	2/A/NT	1	Yes/A†	No	50	0
58	IND	.1	REMO	NO	1	1	No	No	1	3/NT	No	No	33	67
59	IND	.1	REMO	NO	1	1	No	No	1	1	No	No	ND	ND

TABLE B1 (Continued)

Study	Level	Dur.	Expt. Type	Other	Years	Sites	Relat. Abun.	Diver.	Effect	Resp.	Intra. Effect	Intra. Resp.	% Neg.	% Pos.
60	IND	.5	PHYT-P	NO	1	1	No	No	1	1	No	No	100	0
61	IND	.1	REMO	NO	1	1	No	No	1	2*	No	No	0	0
62	IND	.5	PHYT-P	NO	1	1	No	No	1	10*	No	No	100	0
63	IND	2.0	REMO	NO	1	1	No	No	1	11/NT	No	No	67	17
64	IND	2.0	REMO	NO	1	1	No	No	1	2/NT	No	No	0	0
65	IND	1.0	REMO	NO	1	1	No	No	1	1	No	No	50	0
66	IND	.5	REMO	NO	1	2/DP*	No	No	1	1	No	No	0	0
67	POP	1.0	REMO	NO	1	2/D/NT	No	No	1	3/NT	No	Yes/NT	50	0
67	POP	.5	REMO	NO	1	1	Yes/NT	Yes/NT	1	6/NT	No	No	71	14
68	IND	.5	REMO	F†	1	1	No	No	1	1	No	No	67	0
68	IND	.5	PHYT	NO	1	1	No	No	1	1	No	No	17	17
69	POP	2.0	REMO	NO	1	1	No	No	2/A/NT	2/NT	No	No	0	0
70	IND	.5	SUBS	NO	1	2/R*	No	No	2/I†	2†	Yes/I†	Yes†	ND	ND
71	IND	1.0	REMO	NO	1	1	No	No	1	1	No	No	100	0
72	POP	1.0	REMO	NO	1	1	No	No	1	1	No	No	ND	ND
73	IND	2.0	PHYT	H*‡	1	3/R†	No	No	1	1	No	No	50	0
74	POP	.5	REMO	H*	2*	1	No	No	1	1	No	No	0	0
75	IND	2.0	REMO	NO	1	1	No	No	1	1	No	No	50	0
76	IND	.1	REMO	NO	1	1	No	No	1	1	No	No	0	100
77	IND	.5	REMO	NO	1	3/R†	No	No	1	1	No	No	0	0
78	IND	1.0	REMO	NO	1	1	No	No	4/A*	1	No	No	100	0
79	IND	1.0	REMO	NO	1	1	No	No	4/A*	4C*	No	No	100	0
80	IND	.1	REMO	NO	1	1	No	No	1	1	No	No	0	100
81	POP	2.0	REMO	NO	2/NT	2/D/NT	No	Yes*	1	1	No	No	100	0
82	IND	.5	REMO	NO	1	5/D/NT	No	No	1	1	No	No	80	0
83	IND	1.0	REMO	NO	1	3/D*	No	No	1	1	No	No	83	17
84	IND	2.0	REMO	NO	1	1	No	No	1	2*	No	No	100	0

85	IND	2.0	REMO	NO	1	2/D/NT	No	No	1	4/NT	No	No	71	0
85	IND	2.0	REMO	NO	1	2/D/NT	No	No	1	1	No	No	50	0
86	IND	.5	REMO	F/NT	1	1	No	No	1	1	No	No	100	0
87	IND	1.0	REMO-P	NO	1	8/DP*	No	No	1	3/NT	No	No	ND	ND
88	IND	.1	PHYT	NO	1	4/R/NT	No	No	1	4C*	No	No	100	0
89	IND	1.0	CPHY	NO	1	4/R/NT	No	No	2/I*	2†	Yes/I†	Yes†	ND	ND

NOTE.—Parameters and their possible states are defined in App. A. ND indicates no data; for % negative and % positive this usually means neither statistical comparisons of competition treatments nor confidence intervals were reported. Because it was sometimes necessary to make arbitrary decisions about what category we use for a particular experiment, there are undoubtedly errors in this table, and we welcome corrections by the authors of the studies listed. However, it is unlikely that changing the categories for these errors would have any impact on the main conclusions of this survey. Code numbers for articles: 1 = Allen and Allen 1988; 2 = Armesto and Pickett 1985; 3 = Augsberger 1984; 4 = Bell and Ungar 1981; 5 = Berendse 1983; 6 = Bridge et al. 1986; 7 = Burton and Mueller-Dombois 1984; 8 = Chazdon 1986; 9 = Cid-Benevento 1987; 10 = Collins and Pickett 1988a; 11 = Collins and Pickett 1988b; 12 = Collins and Quinn 1982; 13 = Crawley and Nachapong 1985; 14 = Dayton et al. 1984; 15 = del Moral 1983; 16 = Duggins 1980; 17 = Duggins and Dethier 1985; 18 = Eissenstat and Caldwell 1988; 19 = Ellison 1987; 20 = Fonteyn and Mahall 1981; 21 = Fowler 1981; 22 = Fowler 1986b; 23 = Fuentes et al. 1984; 24 = Fuentes et al. 1986; 25 = Gerrish et al. 1988; 26 = Gibson 1988; 27 = Goldberg 1985; 28 = Goldberg 1987; 29 = Goldberg 1988; 30 = Goldberg and Werner 1983b; 31 = Gross 1980; 32 = Gross and Werner 1982; 33 = Gurevitch 1986; 34 = Hanzawa 1988; 35 = Hartnett and Bazzaz 1985; 36 = Hibbs et al. 1980; 37 = Hils and Vankat 1982; 38 = Horn 1985; 39 = Hughes et al. 1988; 40 = Inouye 1980; 41 = Inouye et al. 1980; 42 = Johnson and Mann 1988; 43 = Keizer et al. 1985; 44 = Klinkhamer and de Jong 1988; 45 = Knoop and Walker 1985; 46 = Lebron 1979; 47 = Lee and Bazzaz 1982; 48 = Lubchenco 1980; 49 = Manning and Barbour 1988; 50 = Matlack 1987; 51 = McConnaughay and Bazzaz 1987; 52 = McCreary et al. 1983; 53 = Miller and Werner 1987; 54 = O'Dowd and Gill 1984; 55 = Parker 1982; 56 = Parker and Muller 1982; 57 = Parker and Salzman 1985; 58 = Pemadasa and Amarasinghe 1982; 59 = Petranka and McPherson 1979; 60 = Pitelka et al. 1985; 61 = Pons and van der Toorn 1988; 62 = Popma and Bongers 1988; 63 = Primack et al. 1985; 64 = Rabinowitz and Rapp 1985; 65 = Rapp and Rabinowitz 1985; 66 = Reader and Buck 1986; 67 = Reed and Foster 1984; 68 = Reichman 1988; 69 = Schmid 1985; 70 = Schoen et al. 1986; 71 = Smith 1980; 72 = Sobey and Kenworthy 1979; 73 = Sork 1987; 74 = Sousa et al. 1981; 75 = Stevens 1987; 76 = Taylor and Zisheng 1988; 77 = Titus and Stephens 1983; 78 = Turkington et al. 1979; 79 = Turkington and Harper 1979; 80 = Turner 1983; 81 = Turner 1985; 82 = Ungar et al. 1979; 83 = van der Meijden and van der Waals-Kooi 1979; 84 = van der Toorn and Pons 1988; 85 = Walker and Chapin 1986; 86 = Whigham 1984; 87 = Wilson and Keddy 1986; 88 = Winn 1985; 89 = Zammit and Westoby 1988.

* See App. A for definition.

† See App. A for definition.

‡ For these studies, $\leq 25\%$ of interactions tested were significant.

§ Both these studies also tested per-gram effects and found no significant differences among neighbor species. Study 28 also tested per-individual effects and did find significant differences.

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