

## EMPIRICAL APPROACHES TO QUANTIFYING INTERACTION INTENSITY: COMPETITION AND FACILITATION ALONG PRODUCTIVITY GRADIENTS

DEBORAH E. GOLDBERG,<sup>1,4</sup> TARA RAJANIEMI,<sup>1</sup> JESSICA GUREVITCH,<sup>2</sup> AND ALLAN STEWART-OATEN<sup>3</sup>

<sup>1</sup> Department of Biology, University of Michigan, Ann Arbor, Michigan 48109-1048 USA

<sup>2</sup> Department of Ecology and Evolution, State University of New York, Stony Brook, New York 11794-5245 USA

<sup>3</sup> Department of Ecology, Evolution, and Marine Biology, University of California,  
Santa Barbara, California 93106 USA

**Abstract.** Quantitative synthesis across studies requires consistent measures of effect size among studies. In community ecology, these measures of effect size will often be some measure of the strength of interactions between taxa. However, indices of interaction strength vary greatly among both theoretical and empirical studies, and the connection between hypotheses about interaction strength and the metrics that are used to test these hypotheses are often not explicit. We describe criteria for choosing appropriate metrics and methods for comparing them among studies at three stages of designing a meta-analysis to test hypotheses about variation in interaction intensity: (1) the choice of response variable; (2) how effect size is calculated using the response in two treatments; and (3) whether there is a consistent quantitative effect across all taxa and systems studied or only qualitatively similar effects within each taxon–system combination. The consequences of different choices at each of these stages are illustrated with a meta-analysis to examine the relationship between competition/facilitation intensity and productivity in plants. The analysis used a database of 296 cases in 14 studies.

The results were unexpected and largely inconsistent with existing theory: competition intensity often significantly declined (rather than increased) with productivity, and facilitation was sometimes restricted to more productive (rather than less productive) sites. However, there was considerable variation in the pattern among response variables and measures of effect size. For example, on average, competitive effects on final biomass and survival decreased with standing crop, but competitive effects on growth rate did not. On the other hand, facilitative interactions were more common at low standing crop for final biomass and growth rate, but more common at high standing crop for survival. Results were more likely to be significant using the log response ratio ( $\ln[\text{removal}/\text{control}]$ ) as the effect size than using the relative competition intensity ( $[\text{removal} - \text{control}]/\text{removal}$ ), although the trends for these conceptually similar indices did not differ. When all studies were grouped in a single meta-regression of interaction intensity on standing crop to test quantitative similarity among studies, survival showed the clearest negative relationship. However, when the same regressions were done for each unique combination of taxon and site within each study to test for qualitative similarity among studies, the slopes averaged over studies tended to be negative for biomass and growth rate, but not different from zero for survival. These results are subject to a number of caveats because of the limitations of the available data—most notably, the extension of effects of interactions on individual growth or survival to effects on population distribution and abundance or community structure is highly problematic. Nevertheless, the fact that none of the meta-analyses demonstrated a significant positive relationship between competition and standing crop but that we frequently found negative relationships is an important pattern that has not been apparent from qualitative surveys of individual studies, and it demonstrates the potential power of meta-analysis in ecology. We conclude with recommendations to overcome some of the limitations of the currently available data and meta-analytical procedures.

**Key words:** competition intensity; community ecology; effect size; facilitation; interaction intensity; meta-analysis; metrics, choice of; productivity gradients.

### INTRODUCTION

Testing hypotheses in community ecology often requires quantification of the magnitude of interactions

Manuscript received 9 January 1998; revised 22 July 1998; accepted 15 August 1998; final version received 15 September 1998. For reprints of this Special Feature, see footnote 1, p. 1103.

<sup>4</sup> E-mail: degold@umich.edu

between species so that these magnitudes can be compared among groups of taxa or of environments. For example, a number of models predict how the magnitude of competition varies along gradients of environmental favorability (e.g., Miller 1967, Grime 1973, Newman 1973, Connell 1975, Rosenzweig and Abramsky 1986, Menge and Sutherland 1987, Tilman 1988) or among taxa (e.g., Grime 1977, Tilman 1988). While many of these models have been tested empirically in

individual studies, examining their generality requires synthesis of results across many studies. To date, such synthesis has largely been based on narrative reviews or counts of significant/nonsignificant effects (e.g., Connell 1983, Schoener 1983, Sih et al. 1985, Goldberg and Barton 1992, but see Gurevitch et al. 1992). Instead of these qualitative summaries, quantitative synthesis that compares actual measures of the intensity of interactions across studies using meta-analytic procedures may provide a more powerful approach to test these models and evaluate their applicability. However, quantitative synthesis requires consistent indices of interaction intensity among studies.

Recently, attention has been drawn to the importance of deriving measures of interaction intensity from particular ecological models (Laska and Wootton 1998, Osenberg et al. 1999). This approach requires an explicit, appropriate model, as well as assumptions about factors such as equilibrium status of a population or the time scale of interactions (Laska and Wootton 1998). However, in many cases, this will not be possible and, therefore, it will be necessary to use more empirical considerations to choose appropriate indices of interaction intensity. Such empirically derived indices of interaction intensity are not suitable for parameterizing models or for testing quantitative predictions (Osenberg et al. 1999) but yield valuable information on patterns in the consequences of interactions to test qualitative predictions and generate new hypotheses.

In this paper, we provide guidance both on choosing appropriate indices and on using these indices in meta-analyses to test hypotheses about variation in the consequences of interactions, especially competition and facilitation (see Navarrete and Menge [1996], Osenberg et al. [1997], and Wootton [1997] for recent discussions of predator-prey interaction strength). We then illustrate these issues using data on competition and facilitation along productivity gradients for plants. Whether competition is more important at high productivity (Grime 1973, 1977) or similarly important regardless of productivity (Newman 1973, Tilman 1988) has been a very controversial area in plant ecology. While numerous relevant experiments have been performed (e.g., Wilson and Tilman 1991, 1995, Reader et al. 1994, Twolan-Strutt and Keddy 1996), there has not yet been a quantitative synthesis.

#### AN EMPIRICAL APPROACH TO CHOOSING METRICS OF INTERACTION INTENSITY

Testing hypotheses about variation in interaction intensity involves choices at three stages of quantification: (1) the response variable that is actually measured on the targets in each treatment, (2) how the change in the response variable between treatments is quantified (e.g., using absolute or relative differences), and (3) how this effect size is compared among taxa or environments. In this section, we describe general criteria for choices at each stage. Most previous discus-

sions of interaction intensity have focused on the second of these stages; as we illustrate in the following section, results of synthesizing interaction intensity can also depend on the choices at the first and third stages.

We first define some terminology to facilitate clear definitions of different kinds of metrics of interaction intensity. The individual or taxon whose response is being measured is referred to as the "target" and the organisms causing any suppressive or facilitative effect as the "associates" (cf. Goldberg and Scheiner 1993). For most organisms, the most common type of field experiment on interactions includes only two treatments that differ in abundance of the associates: presence of the associate at its natural abundance (control treatment) vs. its complete absence (removal treatment). In plants (and sessile animals), where the limiting resources tend to be similar among taxa within a community, the associate is most commonly all vegetation other than the target (Goldberg and Barton 1992). The descriptions of indices below assume this kind of experiment, although they can easily be used for other types of data.

#### *Response variable*

The response variable is what is actually measured or estimated about the targets in each abundance treatment. For each taxon of targets, this could be an individual-level measure (e.g., a behavioral descriptor or a component of individual fitness such as growth rate, survival, reproduction) or a population-level measure (e.g., population size or growth rate, relative abundance). For parameterizing population-dynamic models or testing hypotheses about the effect of competition on distribution and abundances, population-level responses should be measured (e.g., Paine 1992). However, data on population abundances and, especially, population dynamics in response to competition are relatively rare for large or long-lived organisms (Sih et al. 1985, Goldberg and Barton 1992). Instead, various logistical constraints dictate that most experiments on the consequences of competition quantify effects on components of individual fitness. Therefore the challenge is to use individual-level data to infer something about populations. One approach is to integrate effects of interactions throughout the life history by parameterizing a demographically based model of population growth (Gurevitch 1986, McPeck and Peckarsky 1998). When the entire life cycle cannot be followed, inferences from individuals to populations can still be made if the chosen individual-level response variable strongly influences population dynamics. This has usually been implicitly assumed rather than explicitly justified in experimental studies, but it may be possible to make non-arbitrary choices of individual response variables based on attempts to categorize organisms by the life-cycle stages most important for population growth (e.g., for plants: Silvertown et al. 1993, Franco and Silvertown 1996). The choice of response variable is

not trivial—a number of studies have quantified interactions for different demographic parameters or at different life-history stages and found that both the overall magnitude of interactions (and even their sign) and the relative competitive abilities of different taxa depend on the response variable (e.g., DeSteven 1991a, b, Howard 1998, and see *Example: . . .*, below). McPeck and Peckarsky (1998) showed that even strong effects on several components of individual fitness could translate into minimal effects on population growth rate.

#### *Comparison of two treatments*

Once a response variable is chosen, the next stage involves deciding on the functional form used to measure the change in the response variable between abundance treatments, i.e., the effect size as defined by meta-analysts (Gurevitch and Hedges, 1993, 1999) and interaction strength as defined by ecologists (Laska and Wootton 1998, Paine 1992). Metrics of interaction intensity as quantified empirically differ primarily in the kinds of standardizations applied to a raw difference between response in control and removal treatments. At least three kinds of standardizations are relevant:

1. *Absolute vs. relative differences.*—The difference between control and removal responses can be expressed as an absolute value or a relative value standardized to some other value, most often the response in the absence of interactions (Goldberg and Scheiner 1993). If the goal of the meta-analysis is to parameterize models of species interactions, absolute values are appropriate. However, if the goal is to quantify the observed consequences of interactions, without assuming any underlying mechanisms, relative values are more appropriate because they eliminate confounding due to any direct effects of the environment on the response variable (Grace 1995, and see Miller [1996] for some cautions); the effect is relative to the target's intrinsic capacity in that particular environment. Most field experimental work in plant ecology has used a relative metric, specifically, relative competition intensity (RCI):

$$RCI = (X_{\text{removal}} - X_{\text{control}})/X_{\text{removal}}$$

where  $X$  is some measure of individual performance such as growth or survival (e.g., Wilson and Keddy 1986: Fig. 1 legend). Less commonly, RCI has also been used for population-level data (e.g., Campbell and Grime 1992). This metric has a simple intuitive interpretation; proportional reduction in some response due to the presence of associates (for modifications when facilitative effects are common, see Markham and Chanway [1996], Suding and Goldberg [1999]). However, although the statistical properties of RCI for use in meta-analysis have not been investigated in detail, its properties are likely to be problematic (e.g., because it is a simple ratio, Hedges et al. 1999). As result, Hedges et al. (1999) advocate using the log response ratio:

$$\ln RR = \ln(X_{\text{removal}}/X_{\text{control}})$$

which is mathematically related to RCI ( $\ln RR = -\ln(RCI - 1)$ ). Further, Hedges et al. (1999) have thoroughly examined the statistical properties of the log response ratio in the context of meta-analysis. The log response ratio may thus provide a more suitable measure of relative response than RCI, although Osenberg et al. (1999) discuss some possible theoretical limitations associated with the general applicability of both.

2. *Total or per unit effects.*—The difference between the response variable in control and removal treatments can be expressed as the total effect of associates at their natural abundance in the control plots or as a per-unit effect (e.g., effect per unit biomass of associate). Most population and community-dynamic models use a per capita effect (e.g., the alpha of Lotka-Volterra models) and therefore associate-standardized effects are necessary if the goal is to parameterize models. However, most available data from field experiments only quantify total effects at natural abundance (equivalent to species impacts defined by Wootton [1997] or population interaction strengths defined by Navarette and Menge [1996]). While it is possible to estimate per unit effects by dividing total effects by natural abundance (e.g., Paine 1992, Navarette and Menge 1996, Laska and Wootton 1998), this can only be extrapolated to other densities if interactions are linear with the density of the associates. Linearity of per capita competitive effects is rarely tested in the field but is probably uncommon (e.g., Schoener 1986, Goldberg 1987, Miller and Werner 1987). On the other hand, for testing hypotheses about the consequences of interactions in the field, total effects of associates at their natural abundance will often be more relevant, and so unstandardized measures can be used.

3. *Rates and time scales.*—The response of the control and removal treatments can be expressed as rates (e.g., change in biomass per unit time) or as a state variable (e.g., final biomass) (see Billick and Case 1994, Osenberg et al. 1997). Given that most ecological experiments are short in duration (and thus are still undergoing dynamic change and have not re-equilibrated), rates may often be the focus of a quantitative synthesis (e.g., Osenberg et al. 1997, 1999). However, ecological processes are not linear over all time periods, so extrapolating to interaction intensity per unit time may not be possible with data from only a single time. Thus, experiments that differ in duration present a severe problem to any data synthesis, including meta-analysis (Osenberg et al. 1997, 1999, Downing et al. 1999). In many plant systems, however, field experiments are carried out over time periods with a relatively consistent biological context, e.g., for one growing season, regardless of the duration of the growing season. For interpretations of consequences of interactions in the field, standardizing to such time intervals (or re-

stricting meta-analyses to results for a state variable after a particular number of seasons) could be more relevant for comparison than standardizing to an absolute time scale.

#### *Among-study comparisons*

The third stage concerns the way in which effects are compared among taxa or environments or both. An important distinction here is whether the hypothesis being tested implies a consistent quantitative effect across all taxa and systems studied or only that qualitatively similar effects should be seen within each taxon–system combination. In the first case, the hypothesized pattern is that there is a single “true” effect, which may be a number or, more often, a function of known predictor variables. The effects observed in each study differ from the true effect only because of random variation. In this case, all effects from all studies should be put into the same meta-analysis, using standard meta-analytical techniques (Gurevitch and Hedges 1999). For example, to test the hypothesis that competition intensity increases at high productivity (Grime 1977), one could regress a metric of interaction intensity on productivity using appropriate data from all species in all studies in a single meta-analytical regression. Or, to test the hypothesis that higher potential growth rate is associated with greater ability to suppress other plants (Grime 1977), one could regress a metric of interaction intensity of different associate species on maximum potential growth rate of each associate, using data from all studies in a single regression.

This approach assumes that the dynamics of competitive interactions can be described by the same functional form and the same parameter values in all cases (Osenberg et al. 1999). Because this seems unlikely, an alternative approach is to calculate a pattern of effect sizes *within* each study (or part of a study) and to compare these patterns in meta-analyses across studies. For example, the above hypothesis about growth rate and competitive suppression implies “other things being equal”—e.g., similar targets or environmental conditions. To test this, a separate regression should be done of interaction intensity on growth rate for each study, using all the associate species tested within that study. The slopes of these regressions are then the appropriate effect pattern to be compared across studies in a meta-analysis. The prediction to be tested is not whether the regressions are the same—it could be whether the slopes are all the same (i.e., deviate from a “true” positive slope due only to within-study randomness), or whether the mean slope across studies is positive. Further analyses can then be done to examine the sources of variation in slope among studies—e.g., do the within-study slopes vary consistently among habitats? This approach assumes that similar qualitative relationships hold for different systems, but not that

either the functional form or parameter values are the same.

#### EXAMPLE: PLANT COMPETITION AND FACILITATION ALONG PRODUCTIVITY GRADIENTS

##### *The problem*

Patterns in the importance of competition and facilitation along productivity or favorability gradients has been a controversial issue in community ecology. Some models predict that competition is more important at the more favorable end of a gradient, while abiotic factors are more important at less favorable or “stressful” ends (Miller 1967, Kruckeberg 1969, Grime 1973, 1977, Rosenzweig and Abramsky 1986, Keddy 1990, and see Connell [1975] and Menge and Sutherland [1987] for variants also incorporating predation). In contrast, other models suggest that competition is important regardless of environmental favorability, although the limiting resource may well change among environments (MacArthur 1972, Newman 1973, Tilman 1988).

In plant ecology these two classes of models have given rise to the “Grime-Tilman” debate (Thompson 1987, Tilman 1987, Thompson and Grime 1988). Grime (1973) has argued that competition is more important at high productivity where plant biomass is greater and effects of abiotic conditions on survival are minimal. In contrast, Newman (1973) and Tilman (1988) have argued that productivity will determine the major limiting resource, from nutrients or water at low productivity to light at high productivity, but not whether or not plants compete for that limiting resource. More recently, Goldberg and Novoplansky (1997) predicted that which of these predictions holds depends on the response variable measured—competitive effects on survival are more likely to increase with productivity than competitive effects on growth. Effects on population dynamics would be determined by how survival and growth interact to determine population growth. Finally, Bertness and Callaway (1994) have added to this controversy about competition by predicting that facilitative interactions should be more common at low than high productivity. To test these ideas, numerous experiments have investigated whether the intensity of competitive/facilitative effects on some component of individual plant fitness changes consistently with productivity. Results as assessed by vote counting or narrative reviews are mixed, with some studies showing significant increases and some showing constancy of competition (reviews in Goldberg and Barton [1992], Kadmon [1995], Twolan-Strutt and Keddy [1996], Goldberg and Novoplansky [1997]). No studies to date have attempted a quantitative synthesis.

##### *Designing a meta-analysis*

A quantitative synthesis of data requires consistency across studies in the response variable and the measure

of effect size for that response variable. The appropriate kind of response variable to test the relationship between the importance of competition/facilitation and productivity depends on exactly what is meant by “importance.” Experimentally this has most often been taken implicitly to mean the magnitude of effects on a component of individual fitness (Goldberg and Barton 1992), but a close reading of the conceptual papers cited above suggests that population-level (or even community-level, see *Future developments*, below) responses are often the implicit response variable. That is, competition is “important” for a taxon when the presence of interspecific competitors decreases the population size or growth rate of that taxon and therefore limits its distribution and abundance. Unfortunately, population-level responses are rarely available to address this question directly. More typically, plant size, individual growth rate, or survival are measured. Thus, we focus our meta-analysis on these response variables, with the caveat that extensions to population consequences of interactions are unknown.

If, as argued above, the effect of competition on distribution and abundance is of primary interest in testing current hypotheses, the measure of effect size should

1) standardize the difference in the response variable between removals and controls for target performance in the absence of interactions to eliminate confounding due to direct effects of the environment on the response variable,

2) not standardize for abundance of associates to reflect the actual magnitude of interactions experienced by the targets. Variation in the abundance of associates among environments, with constant per unit associate effects, could well be part of the explanation of variation in target abundance (Grime 1977), and

3) be expressed as a change in equilibrium response rather than as a rate to better reflect effects on population persistence. The first two of these points are straightforward and generally easy to accomplish with available data—either RCI (relative competition intensity) or  $\ln RR$  (log response ratio) as described above (see *An empirical approach: . . . Comparison of two treatments*) would be suitable indices. However, in practical terms, the third point on time standardization is probably moot—most experiments do not last long enough for re-equilibration to occur and therefore only rate data (for individual-level responses) are available.

Finally, qualitative similarity across systems in the relationship between interaction intensity and productivity is the more appropriate hypothesis to test than quantitative similarity because it is unlikely that growth of individuals or population dynamics will be controlled by the same model (including parameter values) for all the different taxa and habitats included in a meta-analysis. Nevertheless, we included both types of analyses to determine if they give substantially different answers.

### Database

We used four earlier reviews of experiments on competition in plants (Goldberg and Barton 1992, Gurevitch et al. 1992, Goldberg 1996, Goldberg and Novoplansky 1997) as the main source of references for the meta-analysis data base. From this database we selected all field experimental studies of competition in terrestrial plants that (1) included data on standing crop as a surrogate for productivity and (2) provided a measure of RCI or  $\ln RR$  or sufficient data to calculate them. For the analysis in this paper, we further restricted the final database to studies that removed above- and belowground material of all naturally occurring neighbors around individual target plants (either transplanted or naturally occurring), or that assumed belowground biomass was dead. This type of experiment measures the net effect of all potential competitors on a component of individual fitness, and represents the great majority of field competition experiments in plants (Goldberg and Barton 1992). We also restricted the analysis to studies with herbaceous plants as both targets and neighbors (eliminating only one study) because the great difference in potential size and growth rate between herbs and trees makes it more likely that their competitive dynamics are functionally distinct, making it inappropriate to lump them in a single analysis. In addition, most relevant experiments use standing crop as a surrogate for annual productivity; while this may be reasonable for those herbaceous communities that regrow aboveground biomass annually, it is definitely not reasonable for woody communities that accumulate aboveground biomass over years. Finally, because only one study in the database (Gurevitch 1986) had data on the same target plants for more than one year, we restricted the analysis to results after a single growing season—the actual duration of the experiments ranged from 60 to 150 d. Thus, the effect sizes reported below have implicit time units of “per growing season” and apply only to initial effects of manipulation of associate abundances.

The database contained 15 suitable studies with a total of 321 cases. This is a relatively small subset of potentially relevant experiments; probably the single most common reason for exclusion was lack of data on standing crop. Within this data set, we restricted our analyses to the 14 studies reporting one or more of three response variables: biomass accumulation at the end of a study (86 cases in 7 studies), exponential growth rate based on biomass (182 cases in 4 studies), and probability of survival (28 cases in 6 studies) (see legend to Fig. 1 for references; data in Appendix). To compare these response variables between control and removal treatments, most of the studies reported RCI, although Hedges et al. (1999) recommend using  $\ln RR$  in meta-analyses because of its statistical properties. In this data set we could not take advantage of these improved statistical properties for two reasons. First,

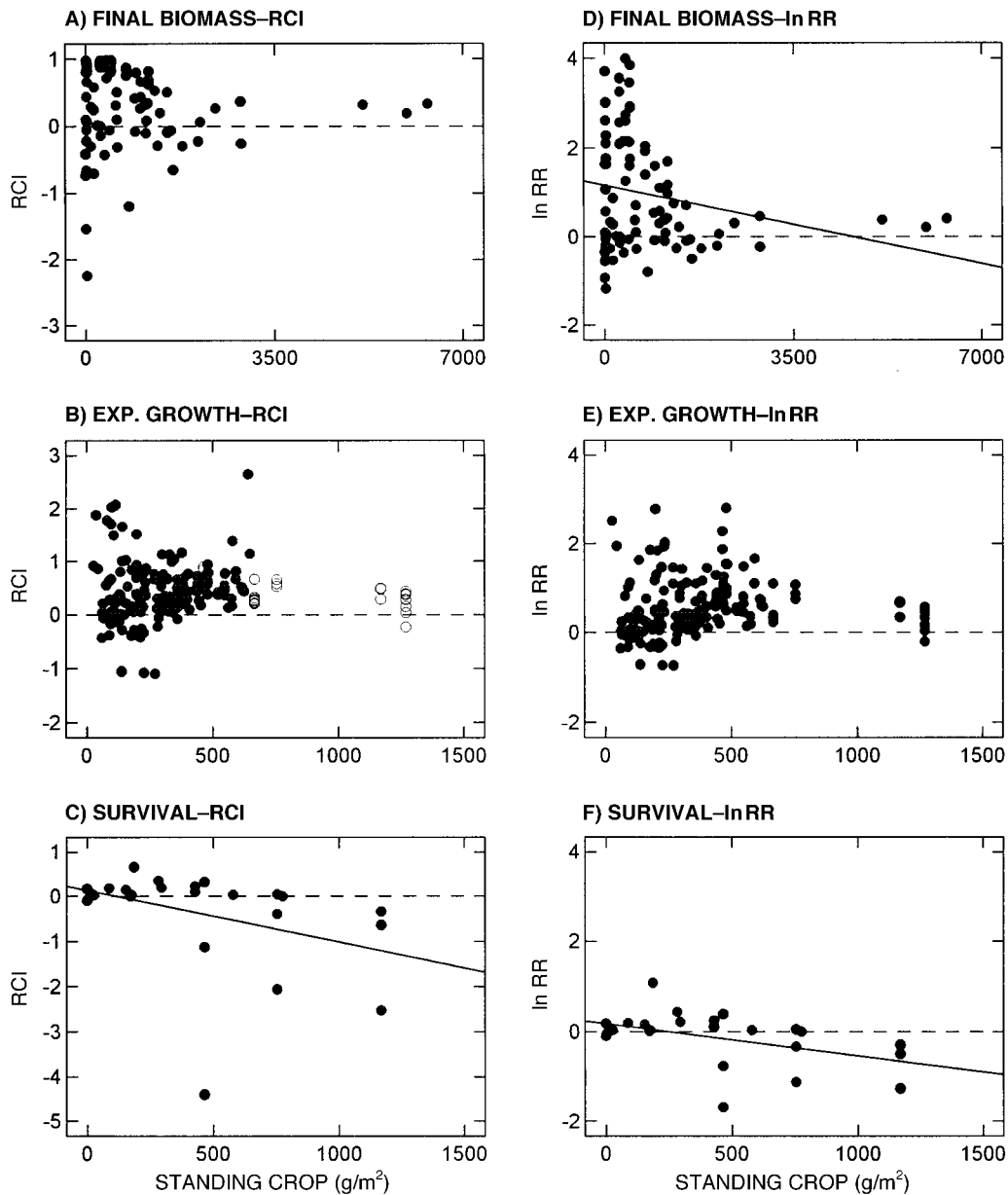


FIG. 1. (A–C) Relative competition intensity (RCI) and (D–F) the log response ratio (ln RR) as a function of standing crop for three response variables measured in 14 studies (see Table 1 for statistics on these relationships). Lines are shown only for significant regressions (see Table 1). Positive values of RCI or ln RR indicate competition, while negative values indicate facilitation. RCI has no minimum value for facilitation but has a maximum value of 1 indicating maximal competition, except when performances in the presence and absence of competitors are of opposite signs (e.g., negative growth only in control treatments). The ln RR has neither a minimum nor maximum value but cannot be calculated for cases of negative growth. The open circles in (B) are for 25 cases from Wilson and Tilman (1991, 1995) in which variance estimates for RCI were reported. Data sources for biomass are Whigham (1984), Wilson and Keddy (1986, 1991), Reichman (1988), Goldberg and Miller (1990), Wilson and Tilman (1991), and Belcher et al. (1995); data sources for exponential growth rate: Wilson and Tilman (1991, 1995), Twolan-Strutt and Keddy (1996), and Reader et al. (1994); and data sources for survival are Gurevitch (1986), Reichman (1988), Reader and Best (1989), Kadmon and Shmida (1990), Reader (1990), Wilson and Tilman (1991), and Kadmon (1995).

data on variance of RCI or ln RR were rarely available. Thus, we could not use parametric, weighted analyses and so could not take advantage of the fact that the sampling distribution of ln RR is approximately nor-

mal. Second, in the few cases where variance of treatment means was known, ~25% of the values were such that the normal approximation was unlikely to be correct (see Hedges et al. 1999). In addition, ln RR could

not be calculated in cases where one of the treatment means was zero or negative, e.g., if organisms shrink. This reduced the sample size for analyses of ln RR and may have biased the results because using ln RR eliminated only cases of very strong proportional competition ( $RCI > 1$ ). On the other hand, ln RR has two empirical advantages over RCI: it is symmetrical for competitive and facilitative interactions and it does not impose a ceiling on the maximum possible competition intensity. Given that neither index is ideal, we report results for both indices for all three response variables.

#### Statistical analysis

Conventional parametric meta-analysis techniques could mostly not be used in this data set, because these rely upon weighting of individual data points based on their reliability (sampling error) to carry out tests of hypotheses and to calculate confidence intervals around mean effect sizes (Gurevitch and Hedges 1999). However, only 26 cases in three studies provided variance estimates for each value of interaction intensity or its components. Further, these represented a biased subset; 25 of these 26 cases were from two studies in the same physical location (Wilson and Tilman 1991, 1995). Therefore, most of the analyses below used unweighted data (Gurevitch and Hedges 1999).

To test for an overall quantitative relationship between interaction intensity and standing crop, we analyzed the unweighted data in two ways: using standard unweighted least-squares regression analysis and, following the suggestions of Adams et al. (1997) and Gurevitch and Hedges (1999), using statistical tests based upon randomization procedures. The test involved randomly permuting values of standing crop for each value of interaction intensity and calculating the least-squares estimate of the slope for each of 2500 such simulations. The proportion of random slopes smaller than the observed least-squares slope was used to calculate significance levels. Results were identical using the unweighted data in parametric and in randomization tests; we report the results only from the randomization tests.

To test for qualitative similarity of patterns among studies, we calculated the slopes (and their standard errors) of regressions of interaction intensity on standing crop for each taxon within each study, using standard least-squares regressions. Sample size for each slope value ranged from 2 to 55; when only two standing-crop levels were available in a study, standard errors could not be calculated. For each of the three response variables for each index of interaction intensity, we used two procedures to calculate the mean and confidence interval of the slopes using MetaWin (Rosenberg et al. 1997, Gurevitch and Hedges 1999). We first included all the studies in an unweighted analysis and used a randomization procedure to calculate the bias-corrected 95% confidence intervals (Rosenberg et al. 1997). For the subset of slopes based on more than two

TABLE 1. Results of randomization tests of regressions of interaction intensity (RCI or ln RR) on standing crop for all 14 plant competition studies combined.

Response variable	Slope†	<i>t</i>	<i>P</i>	df
<b>RCI‡</b>				
Biomass (all)	-0.038	-0.699	0.243	84
Biomass (sc < 1500)	0.121	0.632	0.735	71
Exponential growth	-0.021	-0.118	0.453	180
Survival	-1.144	-1.953	0.031	26
<b>ln RR§</b>				
Biomass (all)	-0.252	-2.372	0.010	84
Biomass (sc < 1500)	-0.342	-0.934	0.177	71
Exponential growth	0.048	0.286	0.612	163
Survival	-0.716	-2.647	0.007	26

Notes: For biomass as the response variable, regressions were done separately for all data (range of standing crop up to 7000 g/m<sup>2</sup>) and using only data with standing crop (sc) < 1500 g/m<sup>2</sup> (similar to range of all data for exponential growth and survival; Fig. 1). Data are shown in Fig. 1.

† Slopes are reported multiplied by 10<sup>3</sup> for ease of comparison.

‡ RCI = relative competition intensity.

§ ln RR = log response ratio.

levels of standing crop, we also calculated means and confidence intervals for each response variable based on a parametric, mixed model, weighting by the variance of each slope (Hedges and Olkin 1985, Rosenberg et al. 1997). In both cases, we used the confidence intervals to test whether the mean slope across studies for each response variable was significantly greater than zero (Grime 1973, 1977) or not different from zero (Newman 1973, Tilman 1988).

#### Results

In testing for an overall quantitative relationship, the results were consistent with neither the Grime nor the Tilman hypotheses. Instead, all three response variables tended to show *decreasing* interaction intensity as productivity increases (Fig. 1). Using randomization tests, this surprising decrease was significant for survival for both metrics of interaction intensity, but only for ln RR for final biomass, and for neither for exponential growth rate (Table 1; these results are based on linear regressions because our question concerned the sign and existence of a relationship, rather than the actual magnitude of an increase or decline). The overall negative trends mask an interesting difference between the response variables. For biomass and growth there is a clear boundary effect: interaction intensity ranges from strongly facilitative (negative values of both RCI and ln RR) to strongly competitive at low standing crop but tends to have a narrow range at slightly competitive levels at high standing crop (Fig. 1a, b, d, and e). Statistical tests for this kind of boundary effect are just now being developed for primary analyses (Blackburn et al. 1992, Thomson et al. 1996, Garvey et al. 1998, Scharf et al. 1998; none exist for meta-analyses). Nevertheless, the consistent restriction of facilitation to less favorable environments for these two response vari-

ables agrees with other results reviewed by Bertness and Callaway (1994) and Callaway and Walker (1997) and with their model of interactions along productivity gradients. In contrast, for survival the results are again inconsistent with predictions from the literature: there is not a strong envelope effect and facilitative interactions are largely restricted to the relatively *more* productive environments (Fig. 1c and f).

Because the studies using biomass as the response variable were from a much wider range of standing crops than the other two variables, we also analyzed a subset of these data with a comparable range of standing crop to those for growth rate and survival (<1500 g/m<sup>2</sup>). In this case, neither RCI nor ln RR significantly varied with standing crop, although a negative upper boundary was still apparent (Table 1, Fig. 1a and d).

These results are all from unweighted analyses and so do not take into account the great variability in reliability of the data points. We therefore also calculated a weighted meta-analytical regression (Hedges and Olkin 1985, Gurevitch and Hedges 1999) using the few data points that did have associated variance estimates for RCI, although these data are a clearly nonrandom subset of the larger data set (Fig. 1b: open circles, all data from Wilson and Tilman [1991, 1995]). In neither study was the variance on the separate treatment means reported so that the weights for ln RR could not be calculated. These limited data again show a significant negative relationship of interaction intensity (using RCI based on growth rates) with standing crop (slope = -0.38,  $n = 25$  cases,  $P = 0.009$ , slope multiplied by 10<sup>3</sup>).

We also tested the qualitative version of these hypotheses, i.e., that slopes within studies should be all positive (Grime 1973) or all flat (Newman 1973, Tilman 1988), but not necessarily to the same extent or with the same intercept. For all three response variables for both metrics, the confidence interval for mean slope across studies was large and overlapped zero (Fig. 2), although it is interesting that, for both RCI and ln RR, the mean slopes for biomass and growth rate were negative but for survival were positive. For RCI, results were identical using a parametric analysis on the subset of cases where parametric weights (derived from standard errors of the slopes) were available (D. E. Goldberg, T. Rajaniemi, J. Gurevitch, and A. Stewart-Oaten, *unpublished data*). However, for ln RR, the parametric results for weighted data show that the negative slopes for biomass (mean = -0.23, 95% CI from -0.74 to -0.11) and growth rate (mean = -1.07, 95% CI from -1.42 to -0.73) became significantly different from zero, although mean slope for survival remained not different from zero (mean = 0.06, 95% CI from -0.37 to 0.48).

#### Discussion

Individual studies of interaction intensity in plant communities can cover only a limited range of pro-

ductivity levels, providing limited power to assess how interactions vary with productivity. The meta-analyses reported in this paper suggest an important result that is not consistent with existing theory: total competition intensity declines with increasing productivity rather than increasing (Grime 1973, 1977) or staying similar (Newman 1973, Tilman 1988). The results thus provide a powerful illustration of the importance of quantitative synthesis—this trend was not apparent in previous narrative (e.g., Twolan-Strutt and Keddy 1996, Kadmon 1995) or vote-counting reviews (Goldberg and Barton 1992, Goldberg and Novoplansky 1997). Indeed, the possibility that competition might decline with productivity has not been discussed in the plant ecology literature.

One possible explanation for the negative relationship between competition intensity and productivity has to do with effects of herbivory. Several models have predicted that the importance of predation should increase with productivity or environmental favorability (e.g., Connell 1975, Menge and Sutherland 1987, Room et al. 1989, Price 1991, but see Louda et al. 1990). If herbivores maintain standing crop below a resource-determined equilibrium at higher productivity, the competitive effects on individual fitness could decline with productivity.

An alternative explanation is based on patterns of root vs. shoot competition. A consistent decline in total competition intensity (root + shoot) with productivity could come about if the relative magnitudes of root and shoot competition change consistently in particular ways. For example, if the overall intensity of root competition tends to be greater than that of shoot competition, but they have similar proportional changes with productivity, total magnitude of competition would decline with productivity. Consistent with this explanation, greater maximum competitive effects of root than shoot competition are typically found in greenhouse experiments (Donald 1958, Wilson 1988), although field results are more mixed (Wilson and Tilman 1991, 1995, Twolan-Strutt and Keddy 1996, Peltzer et al. 1998). On the other hand, shoot competition typically increases more with productivity than root competition declines; all else equal this would give an increase in competition intensity with productivity (Wilson and Tilman 1991, 1995, Twolan-Strutt and Keddy 1996, Peltzer et al. 1998). Studies of root vs. shoot competition are accumulating rapidly; a meta-analysis of these data is needed to explore the quantitative balance between the two and if this balance shifts in predictable ways.

In contrast to the overall trend towards decreasing competition intensity with increasing productivity, the pattern in *variation* of interaction intensity with productivity is more consistent with current hypotheses. Both growth and biomass data are consistent with the Bertness-Callaway (1994) hypothesis that positive effects of neighbors (negative RCI or ln RR) are most



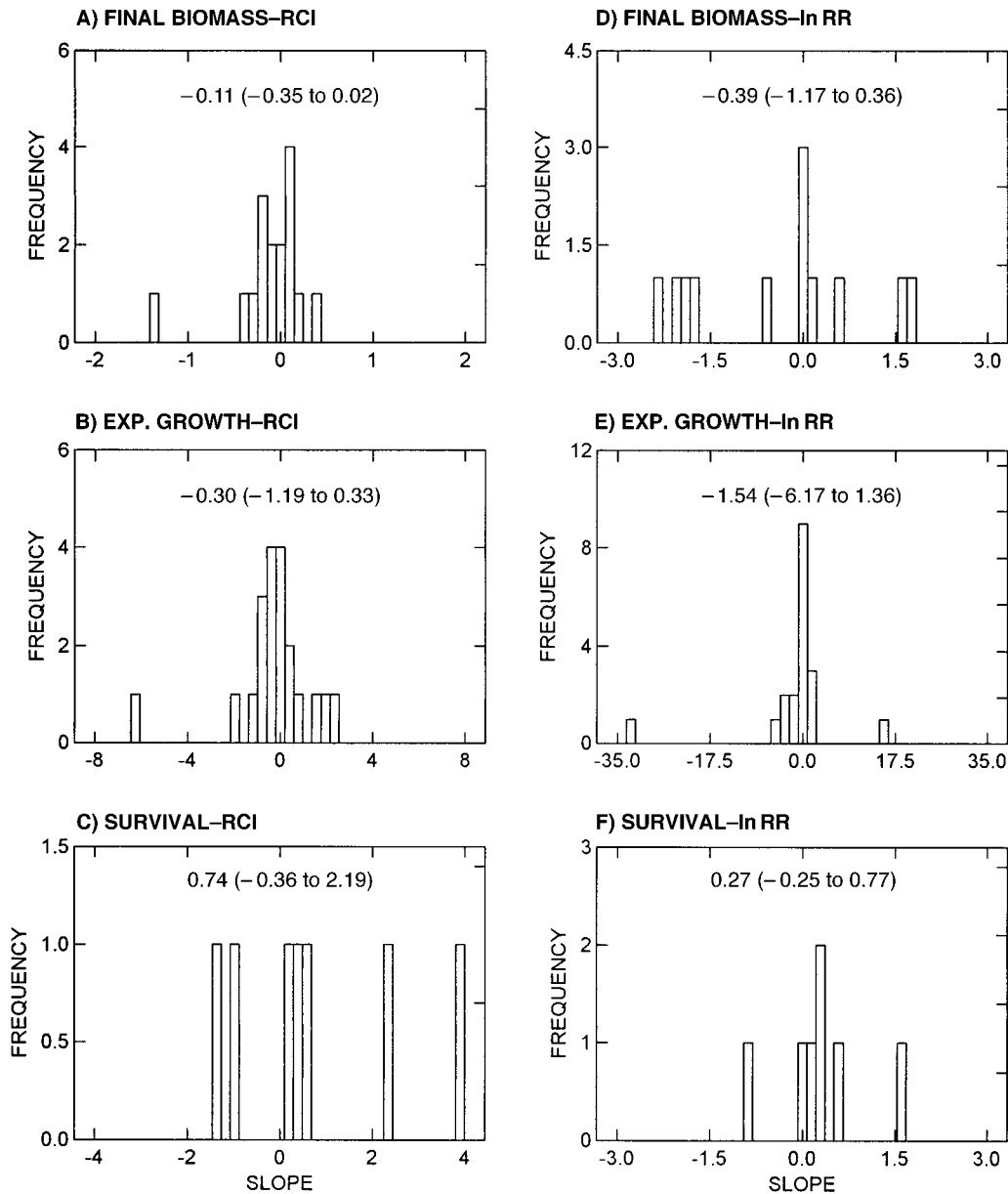


FIG. 2. Frequency distribution of slopes from least-squares regressions of (A–C) relative competition intensity (RCI) and (D–F) log response ratio (ln RR) on standing crop for each taxon in each site in each study. Slopes are shown multiplied by  $10^3$  for ease of comparison; negative slopes indicate that competition decreases with productivity. Numbers are the mean and, in parentheses, the 95% bias-corrected confidence interval using randomization procedures on unweighted data in MetaWin (Rosenberg et al. 1997). Note that confidence intervals overlap zero in all cases (but see *Example: plant competition and . . . : Results* for parametric, weighted analyses with a subset of the data). Analyses excluded three outlier slopes calculated over very narrow ranges of standing crop ( $<50$  g/m<sup>2</sup>). Data sources are the same as in Fig. 1 except that two studies with only a single level of standing crop were excluded (Reichman 1988, Reader 1990).

common at low productivity (Fig. 1a, b, d, and e). The result for survival, however, is more consistent with the overall negative trend—the frequency of facilitative interactions increases with productivity (Fig. 1c and f). The reason for this is unclear, especially in light of the fact that facilitative effects are more common for survival overall (47%) than for biomass (36%) or exponential growth rate (14%) (Fig. 1).

Although most of the analyses show at least hints of negative relationships between competition intensity and productivity, there are some important differences in results between the three response variables and the two metrics of interaction intensity. First, the statistical inferences tended to be much stronger for ln RR than for RCI, although ln RR is almost never used in the plant-competition literature. The reason appears to be

that RCI has a ceiling at 1 (unless plants shrink). The absence of this ceiling in lnRR revealed a great deal of variation in the magnitude of interaction among the RCI values close to 1, making an overall negative trend more detectable (compare Fig. 1a and d). Second, while it is encouraging that the overall trends were mostly similar, results depended on the choice of response variable. Although choice of a response variable appears to be arbitrary in the literature, ecological interpretations can differ greatly. For example, if, within studies, competitive effects on survival really do not generally differ with productivity, while effects on biomass and growth decline with productivity (Fig. 2), it becomes critical to know the relative importance of individual survival and growth to population dynamics to make sensible interpretations about effects of competition on distribution and abundance (cf. McPeck and Peckarsky 1998).

Patterns of response also varied depending on whether the analysis focused on quantitative vs. qualitative consistency among studies. For tests of an overall quantitative relationship, the trend towards declining competition with productivity was clearest for survival. However, the mean of within-study slopes was actually slightly (nonsignificantly) positive for survival, while negative for biomass and growth rate (significantly so for the weighted analyses). The reason for this result is unclear, although it suggests strong differences in dynamics between taxa and/or habitats (i.e., strong parametric or functional variation, *sensu* Osenberg et al. 1999).

#### *Caveats*

These conclusions should be tempered by several cautions that arise due to limitations of the available data. First, the difference in results between weighted and unweighted (or weighted by sample size) analyses is troubling. While the fact that results are more often significant using weighted data is consistent with the typical greater power of these tests, the data in these analyses could also be biased subsets (as in Fig. 1b). This emphasizes the importance of providing estimates of error in primary studies; this is not yet as standard in ecology as we might expect or hope (Gurevitch et al. 1992). Second, in no case, do the authors explicitly justify use of a particular response variable in terms of contributions to population growth, and so the results for some or all cases may not reflect effects on population growth rates. Third, all of the data included in the analysis reflect only an initial response (first growing season) to the experimental manipulations. To relate these results to effects on distribution and abundance, we have to assume that patterns in the effects of interactions on response during the first growing season are directly correlated with effects at steady state; this may not be generally true. Fourth, response variables are often not justified at a more detailed level and may produce misleading results. For example,

while individual plant growth rates based on exponential growth models are the single most common response variable in the data set, it is unlikely that most plants grow exponentially over entire seasons. The appropriate metric of interaction strength can differ depending on whether growth is exponential or additive and therefore the interpretation of RCI and lnRR of growth rates can depend on the shape of the growth function (Osenberg et al. 1999).

Finally, all the analyses potentially have some problems of nonindependence (see Gurevitch and Hedges 1999). For the quantitative comparisons, many studies contribute multiple data points, e.g., from multiple productivity levels for a given taxon. Even for the qualitative comparisons of patterns, many studies include more than one taxon or repeated an entire productivity gradient in different sites or years. In addition, a few species are included in several different studies. The database was not big enough (maximum of seven studies for a given response variable) to test rigorously for such nonindependence. However, in the one study with >4 sites (Reader et al. 1994), the variation in interaction intensity within a single species among sites covered almost the full range of values in the entire database. The single study with >4 taxa also showed considerable variation (Wilson and Tilman 1995), although not as drastic as the comparisons in Reader et al. (1994). Therefore, it is unlikely that these sources of confounding have a significant impact on the results.

#### FUTURE DEVELOPMENTS: QUANTIFYING THE CONSEQUENCES OF INTERACTIONS FOR ENTIRE COMMUNITIES

All of the types of indices of interaction intensity described above quantify response of only a single taxon, the target. Such "single-taxon" indices of interaction intensity are relevant to many questions in ecology (see above, Wootton 1997, Laska and Wootton 1998). However, many of the long-standing debates on the "importance" of competition have also been concerned with community structure, i.e., involve the concurrent responses of several taxa to competition (Strong et al. 1984, Diamond and Case 1986). For example, Grime's (1973) original argument for why competition is more important at high productivity was actually an attempt to explain patterns of species diversity rather than patterns in distribution of particular species. Similarly, Tilman's (1982; Tilman and Pacala 1993) mechanistic models of competition in plants along productivity gradients predict effects of competition on diversity along productivity gradients, as well as on abundance of particular taxa.

To address such hypotheses about community consequences of interactions, it will be necessary to develop indices to quantify such effects directly; the intensity of individual-level effects will not necessarily translate directly to intensity of community-level effects (Abrams 1987, Goldberg 1994, Pacala and Levin

1997). Goldberg (1994) suggested and illustrated several such community indices based on change in relative abundances of all the species in a community in the presence vs. absence of interspecific competition (see also Goldberg et al. 1995, Goldberg and Estabrook 1998). Using relative abundance of each species as the response variables requires experiments that manipulate densities of entire communities; these are often logistically difficult in terrestrial communities and consequently rare (but see Campbell and Grime 1992, Turkington et al. 1993, Goldberg and Estabrook 1998). Therefore, an important future step will be to develop indices that use the more abundant individual-level data. For example, one simple index conceptually would be to examine the variation in single-taxon interaction intensity among taxa within a community because the more species differ in competitive ability, the greater the potential for competitive suppression or exclusion of some of the species. The statistical properties of indices such as the variance or coefficient of variation have not yet been explored for their use as effect sizes in meta-analysis. As emphasized by Gurevitch and Hedges (1999) in this Special Feature, understanding the statistical properties of effect sizes used in a meta-analysis is critical for rigorous interpretation of results.

#### CONCLUSIONS AND RECOMMENDATIONS

As with any primary study, numerous aspects of the design and analysis of a meta-analysis can influence the results. Much of this Special Feature on meta-analysis in ecology has focused on how to make appropriate choices at various stages of conducting a meta-analysis so that results are both biologically meaningful (Downing et al. 1999, Englund et al. 1999, Osenberg et al. 1999) and statistically valid (Gurevitch and Hedges 1999, Hedges et al. 1999). In this paper we focused on choices at three of the stages of conducting a meta-analysis: choosing a response variable, choosing the index to compare the response variable between treatment and controls, and choosing the mode of comparison of this index among studies. We found that choices at all three stages influenced details of the outcome of the meta-analysis.

These results and the caveats imposed on them due to limitations of the available data suggest several recommendations both for primary studies of interaction intensity in ecology and for synthesizing results of these primary studies. These recommendations include making advances on several fronts: more complete reporting of data, modifications of experimental designs and especially the kinds of response variables monitored, development of new indices rooted in ecological concepts, and statistical explorations of these indices for their use in meta-analysis.

1) As frequently noted by ecological meta-analysts, the lack of estimates of variance in the effect size for many studies makes it impossible to use standard meta-

analytical techniques (Gurevitch et al. 1992; see other papers in the Special Feature); more complete reporting would greatly increase the statistical power of meta-analyses. In addition, many studies report only an effect size (e.g. competition intensity), rather than the means of the treatments used to calculate the effect size. This can preclude using the data to calculate other estimates of effect size (e.g., ones developed subsequent to the study) and thus unduly restrict the database for meta-analysis.

2) The response variables and time scales used in primary studies should be better matched to the ecological hypotheses being tested. In particular, given that many of the hypotheses being tested derive from models at the population and community level, more response variables at these levels should be used. Where logistics preclude experiments to quantify effects of competition on populations, one alternative is to use multiple individual-level response variables so that demographic models of density-dependent population growth and abundance can be parameterized (McPeck and Peckarsky 1998). Expanding the types of response variables used will also mean developing new indices of interaction intensity that have clear conceptual meanings and whose statistical properties make them amenable to meta-analysis. Especially important are indices that quantify effects at the community level.

3) In cases where the ideal measure of effect size is not known (e.g., where the underlying model describing the interactions is not known or is likely to vary among studies), we recommend use of multiple indices of effect size to determine robustness of patterns (see also Englund et al. 1999). In this study, we used two indices that are similar conceptually (both isolate effects of total abundance of associates on relative target performance) but that can have different biases depending on the underlying model (Osenberg et al. 1999). Although they often differed in statistical outcomes, the overall trends were similar, reinforcing our conclusion that competition often tends to decline with productivity. Further, theoretical explorations of the biases of indices of interaction intensity under different assumptions about the underlying dynamics of the systems will be critical for rigorous evaluation of patterns (Osenberg et al. 1999).

4) Because ecologists often do not know the exact functional form of models describing, for example, individual or population growth (let alone are able to parameterize those models), meta-analyses of qualitative, rather than quantitative relationships may often be more suitable. Such analyses require multiple taxa or environments within single studies so that patterns in interaction intensity *within* particular systems can be quantified. Despite the very large number of experiments on plant competition (Goldberg and Barton 1992, Gurevitch et al. 1992), field experiments rarely include more than three or four taxa or two or three environments so that our current ability to explore

within-system patterns is limited. Meta-analyses of multi-taxa or multi-environment experiments will often involve fairly complex effect sizes that summarize results of experiments at several different levels (e.g., the slopes of regressions of interaction intensity on standing crop in Fig. 2). The statistical issues surrounding such layers of analysis for different kinds of indices is an important area for future research.

#### ACKNOWLEDGMENTS

This work was conducted as part of the Meta-analysis Working Group (Meta-analysis, interaction strength and effect size: application of biological models to the synthesis of experimental data) supported by the National Center for Ecological Analysis and Synthesis, a Center funded by NSF (DEB-94-21535), the University of California–Santa Barbara, and the State of California. Additional support was provided to D. Goldberg by NSF grant DEB 9629723. We are grateful to the entire Working Group for stimulating discussion of these ideas, and to Ace Sarnelle, two anonymous reviewers, and, especially, Craig Osenberg for their helpful comments on the manuscript.

#### LITERATURE CITED

- Abrams, P. A. 1987. On classifying interactions between populations. *Oecologia* **73**:272–281.
- Adams, D. C., J. Gurevitch, and M. S. Rosenberg. 1997. Resampling tests for meta-analysis of ecological data. *Ecology* **78**:1277–1283.
- Belcher, J. W., P. A. Keddy, and L. Twolan-Strutt. 1995. Root and shoot competition intensity along a soil depth gradient. *Journal of Ecology* **83**:673–682.
- Bertness, M. D., and R. Callaway. 1994. Positive interactions in communities. *Trends in Ecology and Evolution* **9**:191–193.
- Billick, I., and T. J. Case. 1994. Higher-order interactions in ecological communities: what are they and how can they be detected? *Ecology* **75**:1529–1543.
- Blackburn, T. M., J. H. Lawton, and J. N. Perry. 1992. A method of estimating the slope of upper bounds of plots of body size and abundance in natural animal assemblages. *Oikos* **65**:107–112.
- Callaway, R. M., and L. R. Walker. 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology* **78**:1958–1965.
- Campbell, B. D., and J. P. Grime. 1992. An experimental test of plant strategy theory. *Ecology* **73**:15–29.
- Connell, J. H. 1975. Some mechanisms producing structure in natural communities: a model and evidence from field experiments. Pages 460–490 in M. L. Cody and J. M. Diamond, editors. *Ecology and evolution of communities*. The Belknap Press of Harvard University Press, Cambridge, Massachusetts, USA.
- . 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. *American Naturalist* **122**:661–696.
- DeSteven, D. 1991a. Experiments on mechanisms of tree establishment in old-field succession: seedling emergence. *Ecology* **72**:1066–1075.
- . 1991b. Experiments on mechanisms of tree establishment in old-field succession: seedling survival and growth. *Ecology* **72**:1076–1089.
- Diamond, J., and T. J. Case, editors. 1986. *Community ecology*. Harper & Row, New York, New York, USA.
- Donald, C. M. 1958. The interaction of competition for light and for nutrients. *Australian Journal of Agricultural Research* **5**:585–597.
- Downing, J. A., C. W. Osenberg, and O. Sarnelle. 1999. Meta-analysis of marine nutrient-enrichment experiments: variation in the magnitude of nutrient limitation. *Ecology* **80**:1157–1167.
- Englund, G., O. Sarnelle, and S. D. Cooper. 1999. The importance of data-selection criteria: meta-analyses of stream predation experiments. *Ecology* **80**:1132–1141.
- Franco, M., and J. Silvertown. 1996. Life history variation in plants: an exploration of the fast–slow continuum hypothesis. *Philosophical Transactions of the Royal Society of London B* **351**:1341–1348.
- Garvey, J. E., E. A. Marschall, and R. A. Wright. 1998. Detecting relationships in continuous bivariate data. *Ecology* **79**:442–447.
- Goldberg, D. E. 1987. Neighborhood competition in an old-field plant community. *Ecology* **68**:1211–1223.
- . 1994. Influence of competition at the community level: an experimental version of the null models approach. *Ecology* **75**:1503–1506.
- . 1996. Simplifying the study of competition at the individual plant level: the consequences of distinguishing between effect and response for forest vegetation management. *New Zealand Journal of Forestry Science* **26**:19–38.
- Goldberg, D. E., and A. M. Barton. 1992. Patterns and consequences of interspecific competition in natural communities: a review of field experiments with plants. *American Naturalist* **139**:771–801.
- Goldberg, D. E., and G. Estabrook. 1998. A method for comparing diversity and species abundances among samples of different sizes and an experimental example with desert annuals. *Journal of Ecology* **86**:983–988.
- Goldberg, D. E., and T. E. Miller. 1990. Effects of different resource additions on species diversity in an annual plant community. *Ecology* **71**:213–225.
- Goldberg, D. E., and A. Novoplansky. 1997. On the relative importance of competition in unproductive environments. *Journal of Ecology* **85**:409–418.
- Goldberg, D. E., and S. M. Scheiner. 1993. ANOVA and ANCOVA: field competition experiments. Pages 69–93 in S. Scheiner and J. Gurevitch, editors. *Design and analysis of ecological experiments*. Chapman & Hall, New York, New York, USA.
- Goldberg, D. E., R. Turkington, and L. Olsvig-Whittaker. 1995. Quantifying the community-level consequences of competition. *Folia Geobotanica Phytotaxonomica* **30**:231–242.
- Grace, J. B. 1995. On the measurement of plant competition intensity. *Ecology* **76**:305–308.
- Grime, J. P. 1973. Competitive exclusion in herbaceous vegetation. *Nature* **242**:344–347.
- . 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist* **111**:1169–1194.
- Gurevitch, J. 1986. Competition and the local distribution of the grass *Stipa neomexicana*. *Ecology* **67**:46–57.
- Gurevitch, J., and L. V. Hedges. 1993. Meta-analysis: combining the results of independent experiments. Pages 378–425 in S. M. Scheiner and J. Gurevitch, editors. *Design and analysis of ecological experiments*. Chapman & Hall, New York, New York, USA.
- Gurevitch, J., and L. V. Hedges. 1999. Statistical issues in ecological meta-analysis. *Ecology* **80**:1142–1149.
- Gurevitch, J., L. L. Morrow, A. Wallace, and J. S. Walsh. 1992. A meta-analysis of competition in field experiments. *American Naturalist* **140**:539–572.
- Hedges, L. V., J. Gurevitch, and P. Curtis. 1999. The meta-analysis of response ratios in experimental ecology. *Ecology* **80**:1150–1156.
- Hedges, L. V., and I. Olkin. 1985. *Statistical methods for meta-analysis*. Academic Press, Orlando, Florida, USA.
- Howard, T. G. 1998. The relationship of competitive hierarchies for germination, growth, and survivorship to rel-

- ative abundance in an old field community. Dissertation. University of Michigan, Ann Arbor, Michigan, USA.
- Kadmon, R. 1995. Plant competition along soil moisture gradients: a field experiment with the desert annual *Stipa capensis*. *Journal of Ecology* **83**:253–262.
- Kadmon, R., and A. Schmid. 1990. Competition in a variable environment: an experimental study in a desert annual plant population. *Israel Journal of Botany* **39**:403–412.
- Keddy, P. A. 1990. Competition hierarchies and centrifugal organization in plant communities. Pages 265–290 in J. Grace and D. Tilman, editors. *Perspectives on plant competition*. Academic Press, San Diego, California, USA.
- Krueckberg, A. R. 1969. Soil diversity and the distribution of plants, with examples from western North America. *Madrono* **20**:129–154.
- Laska, M. S., and J. T. Wootton. 1998. Theoretical concepts and empirical approaches to measuring interaction strength. *Ecology* **79**:461–476.
- Louda, S. M., K. H. Keeler, and R. D. Holt. 1990. Herbivore influences on plant performance and competitive interactions. Pages 413–444 in J. Grace and D. Tilman, editors. *Perspectives on plant competition*. Academic Press, San Diego, California, USA.
- MacArthur, R. A. 1972. *Geographical ecology: patterns in the distribution of species*. Harper & Row, New York, New York, USA.
- Markham, J. H., and C. P. Chanway. 1996. Measuring plant neighbour effects. *Functional Ecology* **10**:548–549.
- McPeck, M. A., and B. L. Peckarsky. 1998. Life histories and the strengths of species interactions: combining mortality, growth, and fecundity effects. *Ecology* **79**:867–879.
- Menge, B. A., and J. P. Sutherland. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *American Naturalist* **130**:731–757.
- Miller, R. S. 1967. Pattern and process in competition. *Advances in Ecological Research* **4**:1–74.
- Miller, T. E. 1996. On quantifying the intensity of competition across gradients. *Ecology* **77**:978–981.
- Miller, T. E., and P. A. Werner. 1987. Competitive effects and responses between plant species in a first-year old-field community. *Ecology* **68**:1224–1233.
- Navarrete, S. A., and B. A. Menge. 1996. Keystone predation and interaction strength: interactive effects of predators on their main prey. *Ecological Monographs* **66**:409–430.
- Newman, E. I. 1973. Competition and diversity in herbaceous vegetation. *Nature* **244**:310.
- Osenberg, C. W., O. Sarnelle, and S. D. Cooper. 1997. Effect size in ecological experiments: the application of biological models in meta-analysis. *American Naturalist* **150**:798–812.
- Osenberg, C. W., O. Sarnelle, S. D. Cooper, and R. D. Holt. 1999. Resolving ecological questions through meta-analysis: goals, metrics, and models. *Ecology* **80**:1105–1117.
- Pacala, S. W., and S. A. Levin. 1997. Biologically generated spatial pattern and the coexistence of competing species. Pages 204–232 in D. Tilman and P. Kareiva, editors. *Spatial ecology: the role of space in population dynamics and interspecific interactions*. Princeton University Press, Princeton, New Jersey, USA.
- Paine, R. T. 1992. Food-web analysis through field measurement of per-capita interaction strength. *Nature* **355**:73–75.
- Peltzer, D. A., S. D. Wilson, and A. K. Gerry. 1998. Competition intensity along a productivity gradient in a low-diversity grassland. *American Naturalist* **151**:465–476.
- Price, P. W. 1991. The plant vigor hypothesis and herbivore attack. *Oikos* **62**:244–51.
- Reader, R. J. 1990. Competition constrained by low nutrient supply: an example involving *Hieracium floribundum* Wimm & Grab. (Compositae). *Functional Ecology* **4**:573–577.
- Reader, R. J., and B. J. Best. 1989. Variation in competition along an environmental gradient: *Hieracium floribundum* in an abandoned pasture. *Journal of Ecology* **77**:673–684.
- Reader, R. J. et al. 1994. Plant competition in relation to neighbour biomass: an intercontinental study with *Poa pratensis*. *Ecology* **75**:1753–1760.
- Reichman, O. J. 1988. Comparison of the effects of crowding and pocket gopher disturbance on mortality, growth and seed production of *Berteroa incana*. *American Midland Naturalist* **120**:58–69.
- Room, P. M., M. H. Julien, and I. W. Forno. 1989. Vigorous plants suffer most from herbivores: latitude, nitrogen, and biological control of the weed *Salvinia molesta*. *Oikos* **54**:92–100.
- Rosenberg, M. S., D. C. Adams, and J. Gurevitch. 1997. *MetaWin: statistical software for meta-analysis with resampling tests*. Version 1.0. Sinauer Associates, Sunderland, Massachusetts, USA.
- Rosenzweig, M. L., and Z. Abramsky. 1986. Centrifugal community organization. *Oikos* **46**:339–348.
- Scharf, F. S., F. Juanes, and M. Sutherland. 1998. Inferring ecological relationships from the edges of scatter diagrams: comparison of regression techniques. *Ecology* **79**:448–460.
- Schoener, T. W. 1983. Field experiments on interspecific competition. *American Naturalist* **122**:240–285.
- . 1986. Mechanistic approaches to community ecology: a new reductionism? *American Zoologist* **26**:81–106.
- Sih, A., P. Crowley, M. McPeck, J. Petranka, and K. Strohmeier. 1985. Predation, competition, and prey communities: a review of field experiments. *Annual Review of Ecology and Systematics* **16**:269–311.
- Silvertown, J., M. Franco, I. Pisanty, and A. Mendoza. 1993. Comparative plant demography—relative importance of life-cycle components to the finite rate of increase in woody and herbaceous perennials. *Journal of Ecology* **81**:465–476.
- Strong, D. R., D. Simberloff, L. G. Abele, and A. B. Thistle, editors. 1984. *Ecological communities: conceptual issues and the evidence*. Princeton University Press, Princeton, New Jersey, USA.
- Suding, K. N., and D. E. Goldberg. 1999. Variation in the effects of vegetation and litter on recruitment across productivity gradients. *Journal of Ecology*, in press.
- Thompson, K. 1987. The resource ratio hypothesis and the meaning of competition. *Functional Ecology* **1**:297–303.
- Thompson, K., and J. P. Grime. 1988. Competition reconsidered—a reply to Tilman. *Functional Ecology* **2**:114–116.
- Thomson, J. D., G. Weiblen, B. A. Thomson, S. Alfaro, and P. Legendre. 1996. Untangling multiple factors in spatial distributions: lilies, gophers, and rocks. *Ecology* **77**:1698–1715.
- Tilman, D. 1987. On the meaning of competition and the mechanisms of competitive superiority. *Functional Ecology* **1**:304–315.
- . 1988. *Plant strategies and the dynamics and structure of plant communities*. Princeton University Press, Princeton, New Jersey, USA.
- Tilman, D., and S. W. Pacala. 1993. The maintenance of species richness in plant communities. Pages 13–25 in R. Ricklefs and D. Schluter, editors. *Species diversity in ecological communities*. University of Chicago Press, Chicago, Illinois, USA.
- Turkington, R., E. Klein, and C. Chanway. 1993. Interactive effects of nutrients and disturbance: an experimental test of plant strategy theory. *Ecology* **74**:863–878.
- Twolan-Strutt, L., and P. A. Keddy. 1996. Above- and belowground competition intensity in two contrasting wetland plant communities. *Ecology* **77**:259–270.
- Whigham, D. F. 1984. The effect of competition and nutrient

- availability on the growth and reproduction of *Ipomoea hederacea* in an abandoned old field. *Journal of Ecology* **72**:721–730.
- Wilson, J. B. 1988. Shoot competition and root competition. *Journal of Applied Ecology* **25**:279–296.
- Wilson, S. D., and P. A. Keddy. 1986. Measuring diffuse competition along an environmental gradient: results from a shoreline plant community. *American Naturalist* **127**: 862–869.
- Wilson, S. D., and P. A. Keddy. 1991. Competition, survivorship and growth in macrophyte communities. *Freshwater Biology* **25**:331–337.
- Wilson, S. D., and D. Tilman. 1991. Components of plant competition along an experimental gradient of nitrogen availability. *Ecology* **72**:1050–1065.
- Wilson, S. D., and D. Tilman. 1995. Competitive responses of eight old-field plant species in four environments. *Ecology* **76**:1159–1180.
- Wootton, J. T. 1997. Estimates and tests of per capita interaction strength: diet, abundance, and impact of intertidally foraging birds. *Ecological Monographs* **67**:45–64.

#### APPENDIX

The database from 14 field experimental studies of competition in herbaceous plants is available in digital form from ESA's Electronic Data Archive: *Ecological Archives* E080-006. The database is restricted to studies that (1) eliminate both above- and belowground material of neighboring plants around individual target plants and compare these targets to plants with the naturally occurring abundance of neighbors, (2) provide data on response of target plants to manipulation of neighbors after one growing season, (3) provide data on standing crop, and (4) provide an index of competition intensity (either relative competition intensity or the log response ratio) or sufficient data to calculate an index.