Competitive Ability: Definitions, Contingency and Correlated Traits

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Competitive ability: definitions, contingency and correlated traits

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SUMMARY

Although the relationship between individual plant traits and competitive success in communities is an essential component of comprehensive models of the role of competition in structuring plant communities, three obstacles have stymied efforts to empirically examine such relationships. First, definitions of competitive ability are often inconsistent among bodies of theory and between theoretical predictions and empirical research. Much of the theoretical literature is for populations and often at equilibrium, while experimental work has been largely on individuals and short term. This situation is likely to continue, except for a few model systems, and therefore it is critical that individual-level surrogates for population-level phenomena be found. I suggest that competitive response of seedlings to established vegetation may be an effective surrogate for estimating competitive success of populations at equilibrium and that competitive response of individuals with more similar-sized neighbours may be an effective surrogate for competitive success of populations earlier in succession or in non-equilibrium systems. Second, competitive ability may be contingent on many factors, such that it may not be an identifiable characteristic of any particular taxon and thus no broadly applicable relationships between traits and competitive ability may exist. However, a literature survey shows that both competitive response and competitive effect are generally, but not always, consistent regardless of identity of competing species, making the search for relationships with traits reasonable, at least within environments. Among environments, both competitive effect and competitive response are consistent in only about half the studies, making it unreasonable to assume *a priori* that competitive hierarchies will be similar under different conditions. The third obstacle is logistical; competitive ability is necessarily measured experimentally, and preferably in the field, making it difficult to obtain sufficient sample sizes (numbers of taxa) for rigorous analysis of relationships with traits. I suggest several simplifying assumptions and experimental approaches that could enable much more efficient assaying of competitive abilities of many species.

1. INTRODUCTION

Ecologists generally agree that competition often has a major role in structuring communities, especially in plants (Begon *et al.* 1990; Crawley 1990; Goldberg & Barton 1992). However, there is much less agreement about the two necessary components of any comprehensive model to explore this role: patterns in variation in the importance of the process of competition and in the traits that lead to success given that competition is an important process. In this paper, I focus on the latter component and specifically, how to evaluate relationships between individual plant traits and competitive success.

Three major obstacles have stymied attempts to examine relationships between traits and competitive ability. First, competitive ability can be a rather vague concept that is defined in very different ways by different authors (Milne 1961; Abrams 1987; Goldberg 1990; Grace 1990). Therefore apparent contrasts or similarities between predictions from different bodies of theory or between theory and empirical observation are not necessarily valid. Second, even with consistent definitions of competitive ability, it is potentially a highly contingent trait, which could greatly restrict the domains in which consistent correlations between traits and competitive ability can be found. The third obstacle is logistical; competitive ability can be a very time-consuming property to measure compared to life history, morphological or physiological traits, resulting in an extremely limited database to test relationships. As a contribution towards an eventual synthesis of the relationship between individual plant traits and competitive ability, I devote most of this paper to 'clearing the decks' in preparation for eventual testing of predictions about these relationships by addressing each of these three obstacles.

2. DEFINITIONS OF COMPETITIVE ABILITY

How to define competitive ability has been a source of debate among ecologists for decades (Milne 1961; Abrams 1987; Thompson 1987; Thompson & Grime 1988; Tilman 1987) and, as discussed below, differences in definitions of competitive ability are at least partly responsible for different predictions of traits correlated with competitive ability (Goldberg 1990; Grace 1990). The key problem here is that much of formal theory is based on populations at equilibrium but the vast majority of experimental work on competition has been at the individual level and short term. Despite the many recent examples of changes in outcome of experiments over time (e.g. Tilman & Wedin 1991*a*; Grace *et al.* 1992; Heske *et al.* 1994; Inouye & Tilman 1995), logistical and temporal constraints will mean that long-term experiments are simply not possible except in a few model systems. The majority of experimental work on competition will likely continue to be individual level and short term. The value of such work in agronomy and forestry is apparent. However, if it is also to be profitable in understanding patterns in natural communities, it is incumbent on ecologists to (1) formulate reasonable individual-level definitions that are comparable among species and studies, and (2) investigate how individual-level measures of competitive ability relate to long-term population-level outcomes of competitive interactions.

(*a*) *Individual-level definitions of competitive ability*

The magnitude of competition at the individual level can be quantified as the per unit effect of individuals of some neighbour taxon on the response of some target taxon, where 'unit' can refer to individuals, biomass or any other measure of abundance, and response is measured as some component of fitness of target individuals at different abundances of the neighbours. While this single value expresses competitive ability of both taxa in a particular interacting pair, comparisons of this value among taxa, i.e. comparisons of competitive ability, can be done in two distinct ways that have very different interpretations (Jacquard 1968; Goldberg & Werner 1983). Comparisons among neighbour species assess ability to suppress other plants or competitive effect, while comparisons among target species assess resistance to suppression or competitive response. These two measures of competitive ability are not necessarily positively correlated (e.g. Goldberg & Landa 1991; Keddy *et al.* 1994) and therefore it is critical that both predictions of the traits correlated with competitive ability and empirical tests of those predictions be explicitly separated.

To compare competitive response, target performance should be standardized to performance in the absence of neighbours to eliminate differences among target taxa due solely to differences in size or growth rate rather than in response to neighbours (Goldberg & Scheiner 1993; Grace 1995). While this seems obvious, its implications are not. Most importantly, it means that, in addition to their other well known problems, replacement series experiments cannot be used to quantify competitive response to other species of neighbours because they only provide a measure of the relative intensity of intra- to interspecific competition. This could vary among target species solely because of variation in intraspecific competition rather than in response to interspecific competition.

(*b*) *Relating theory to experimental results: predicting traits determining competitive ability*

Predicting which traits should be correlated with competitive ability has been one of the major goals of plant community ecology in recent years, with a wide variety of sometimes contrasting traits predicted (table 1). The most comprehensive set of predictions for plants are those of Tilman (1988, 1990*a*), Smith & Huston (1989), Grime (1977, 1979) and Colasanti & Grime (1993). These authors all make predictions of both short- and long-term outcomes (although they do not necessarily call patterns at both timescales reflective of competitive ability) and at both high and low productivity, where productivity is usually determined by a gradient in soil resources (nutrients and/or water). All are based at least in part on formal theory (usually simulation modelling, necessitated by the inclusion of size structure, which in turn is critical to include for biologically reasonable models in terrestrial plant communities). Table 1 also includes some predictions for sets of traits correlated with competitive ability for particular resources or in a more limited range of environments.

Because the models summarized in table 1 differ greatly in what is explicitly defined as competitive ability, their predictions are not directly comparable. For example, Tilman (1987) has defined competitive ability as the ability of a population to dominate at equilibrium and generated predictions about traits correlated with this measure of competitive ability from a simulation model of competition for nutrients and light along a nutrient supply gradient (Tilman 1988, 1990*a*). Similarly, Smith & Huston (1989) make predictions about competitively superior morphologies for populations at equilibrium over a water supply gradient (see their figure 7), although they consider only competition for light throughout the gradient. However, competitive ability for populations at equilibrium is clearly impractical to measure for many, if not most, plants and therefore testing these predictions about traits correlated with competitive ability will most often require a surrogate. Goldberg (1990) argued that response of individuals in strongly size-uneven situations could be an effective surrogate (see also Wilson & Tilman 1995). That is, the competitive response of seedlings or juveniles to established vegetation should reflect rankings of long-term response of populations at equilibrium, because in a population at equilibrium, seedlings must be able to tolerate the depleted resource levels imposed by surrounding adults. Consistent with this argument, using MacArthur's (1972) consumer-resource equations, J. H. Vandermeer & D. E. Goldberg (unpublished results) show that ability of individuals to deplete resources is irrelevant to the equilibrium outcome of competition for a single resource and only ability to tolerate low levels of the resource determines the outcome.

Both Tilman (1988) and Smith & Huston (1989) also make predictions about traits leading to dominance earlier in succession, which also apply to disturbed sites. Translation to individual-level measures of competitive ability is again problematical and I

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Table 1. *Summary of predictions about traits correlated with competitive ability*

('high' (or 'low') indicates that competitive ability increases (or decreases) with increasing values of the trait. All predictions are for a measure of individual-level competitive ability as described in the text and not dominance *per se* to avoid confounding these predictions with the importance of the process of competition.)

trait	response size-uneven (low productivity)	response size-uneven (high productivity)	effect size-even or uneven (all environments?)	response size-even (all environments?)
allocation to roots	high[a,b]	low[a]		low[a]
allocation to leaves	low[a,b]	low[a]		low[a]
allocation to stems	low[a,b]	high[a]		low[a]
allocation to above ground	low[a,b,d]	high[a,d]		high[a]
allocation to reproductive output	low[a,b]	low[a]	low[c]	high[a]
plant or leaf height	low[a,b,d]	high[a,d]		low[a,g]
maxRGR	low[a,b,d]	low[a,d]	high[c]	high[a,d]
leaf size			high[c]	
biomass/plant			high[c]	
specific root length (length/mass)			high[f]	
leaf area ratio (leaf area/plant mass)			high[c]	
lateral spread			high[c]	
plant longevity	low[d]	high[d]		
tissue N, N productivity	low[b,e]	high[e]		
tissue longevity, nutrient retention	high[b,e]	low[e]	low[c]	
defence investment	high[b]			
maximal nutrient uptake/mass	low[b]		high[c]	
efficiency nutrient uptake	high[b]			
litter production			high[c]	
shade tolerance	low[b,d]	high[a,d]	low[c]	low[a,d]
drought tolerance	high[d]	low[d]	low[c]	low[d]
low nutrient tolerance	high[b,e]	low[a,e]	low[c]	low[a,e]

[a] From Tilman 1988.
[b] From Tilman 1990*b*.
[c] From Grime 1977.
[d] From Smith & Huston 1989.
[e] From Berendse & Elberse 1990.
[f] From Caldwell & Richards 1986.
[g] From Givnish 1982.

tentatively suggest that early successional dominance reflects individual-level response when plants are competing at roughly even sizes (table 1). That is, at the initiation of interactions among a group of individuals, resources have not yet been strongly depleted and resource preemption by any individual is possible (see also Goldberg 1990).

In contrast, Grime (1977) has defined competitive ability as the ability of individuals to take up resources rapidly and prevent their use by other organisms. This seems to correspond with short-term competitive effect, i.e. ability to suppress other plants (Goldberg 1990). Because Grime argues that competitive hierarchies are consistent between environments but that competition is relatively unimportant in unproductive environments, the predictions in table 1 hold for competitive ability in low and high productivity, but not for the traits of dominant species in low and high productivity.

The assignments of predictions from different sorts of models or components of models to the different ways of measuring individual-level competitive ability in table 1 are, of course, themselves hypotheses that should be tested both theoretically and empirically. To the extent that these assignments are correct, the apparently large differences in prediction among columns in table 1 are not necessarily contradictory because predictions are for different components of competitive ability and should be tested independently.

3. CONSISTENCY AND CONTINGENCY OF COMPETITIVE HIERARCHIES

Before attempting to evaluate the predictions in table 1, it is necessary to investigate to what extent competitive ability can be regarded as a characteristic of a particular taxon at all and the domains in which consistent correlations might occur.

The database for this investigation included both a quantitative component (all papers meeting the criteria from *Ecology* and *Journal of Ecology* over the 17-year period from 1979–1995) and a less objective and smaller selection of studies, mostly consisting of those cited in papers from the quantitative database as potentially relevant to the questions. I chose *Ecology* and *Journal of Ecology* for the quantitative survey because they included over 60% of the experiments found in an earlier survey of seven ecological journals of field competition experiments in plants for the first ten years of this period (Goldberg & Barton 1992).

This approach undoubtedly excludes a large number of relevant studies, especially in agronomic journals, but is likely to be reasonably representative for plants in naturally occurring communities. To enable comparisons of competitive response as well as effect and because of their other limitations, substitutive experiments conducted at a single density were excluded. With this exception, all experiments on interspecific interactions between living plants (i.e. purely litter effects were excluded) that met at least one of the following three criteria were included: (1) a minimum of two neighbour and two target taxa for testing contingency of hierarchies among species, (2) a minimum of two environments (experimental or natural) and two neighbour or two target taxa for testing contingency of effect or response hierarchies among environments, or (3) a minimum of three targets or three neighbours and quantitative estimation of at least one trait to be related to competitive ability. Taxa were usually species but sometimes genotypes within species and sometimes groups of species. An abbreviated listing of studies is given in Appendix I and a more complete listing can be found in Goldberg (1996*a*).

(*a*) *Consistency vs contingency of competitive hierarchies among species*

The whole notion of testing correlations between traits and competitive ability assumes that competitive ability is a property of a particular taxon and not of a particular *combination* of taxa. If this assumption is correct, rankings of competitive effects of neighbours would be similar among targets and/or rankings of competitive responses of targets would be similar among neighbours, i.e. both effect and response competitive hierarchies would be transitive within a given environment. The assumption is most likely to be correct if all the taxa involved in a comparison are competing for the same resources, which a number of authors have argued is more likely to be true for plants (and sessile animals) than for other organisms (Goldberg & Werner 1983; Shmida & Ellner 1984; Hubbell & Foster 1986; Mahdi *et al.* 1989).

Keddy & Shipley (1989) and Shipley (1993) tested this assumption and found generally consistent hierarchies; however their database and analytical approach have two limitations. First, they relied on matrices of substitutive experiments, for the good reason that these were the main source of available data. Herben & Krahulec (1990) and Silvertown & Dale (1991) have aptly critiqued the use of substitutive experiments in this context because of the sensitivity of their results to density and to plant size (but see Shipley & Keddy 1994). In addition, as already noted, it is impossible to compare competitive responses with this design. Second, the analytical approach they use does not separate consistency of competitive effect and of competitive response hierarchies; it is entirely possible in principle that one but not the other is consistent.

The database included 21 experiments that could be used to test the consistency of either effect and/or response hierachies among species within a single environment (table 2*a*). This excludes many studies that appeared to have gathered such data but the results were not analysed to test directly for transitivity or were not presented in such a way that I could reconstruct the competitive matrix. Two statistical approaches were used. Where ANOVAS testing explicitly for the appropriate interaction term (see Goldberg & Scheiner 1993) were provided, the absence of a significant interaction term was taken as evidence for consistency. Where a competition matrix was provided or could be reconstructed easily, I used Kendall's coefficient of concordance to test for consistency of rankings of competitive effect of neighbours among different targets or of competitive response of targets among different neighbours. Significant concordance was taken as evidence of consistency. Thus, in neither case, was an absolute criterion of complete transitivity used. In addition, for some studies in which neither ANOVAS nor concordance were provided or could be calculated, I used the author's interpretations or my own inspection of the data to infer consistency or contingency – these studies are counted separately in table 2.

Hierarchies are almost entirely consistent for competitive response and largely consistent (approximately 2:1) for competitive effect (table 2*a*). This contrast between effect and response is the exact opposite of that predicted by Goldberg (1990) on the basis of traits predicted to be correlated with effect and response. One possible explanation is that competitive responses are more similar among species and therefore analysis of changes in rankings is meaningless because species with different ranks are identical in statistical terms. This seems to be the case in the matrix analysed by Goldberg & Landa (1991), but it is clear in some other cases that rankings are still consistent even when differences in magnitude of response are large.

Table 2. *Numbers of studies showing consistency and contingency of competitive effect and response among different competitors within a single environment* (*a*) *and among environments for a given competitor* (*b*)

(Individual studies and their results are listed in Appendix I. Values in parentheses are the number of studies with conclusions on consistency or contingency confirmed by statistical analyses while values outside of parentheses include studies where the conclusions are reached by data inspection. 'Variable' results indicate that more than one test could be conducted within a study and results differ among tests (e.g. more than one environment for consistency with respect to identity of competitors or more than one type of environment for consistency with respect to environments).)

	consistent	contingent	variable
(A) Identity of competitor			
effect	14 (13)	6 (6)	1 (1)
respons	12 (10)	1 (1)	2 (2)
(B) Environment			
effect	6 (5)	7 (6)	1 (1)
response	11 (7)	9 (6)	2 (2)

Potentially important caveats for this analysis are that the majority of the 22 experiments with appropriate data were conducted in glasshouses or common gardens (16), were short-term (16 less than 1 year), and were for even-sized interactions among seedlings (17) (Goldberg 1996*a*). However, the limited data available do not show any consistent relationships between these variables and the consistency or contingency of hierarchies (Goldberg 1996*a*). Thus, the search for correlations of traits with competitive ability in plants seems reasonable, especially for response.

(*b*) *Consistency and contingency of competitive hierarchies among environments*

Unlike the case of consistent hierarchies among species, consistency of hierachies among environments is not a necessary assumption for the entire approach of looking for correlations of traits with competitive ability. But it is critical for deciding the level at which to look for such correlations and how complicated or general any correlation structure will be. In addition, whether or not competitive ability is consistent among environments is at the centre of a major controversy in plant ecology. Grime (1977) has argued for a 'unified concept of competitive ability', i.e. positive correlations in competitive ability for different resources and therefore in different environments when different resources are likely to be limiting, while Tilman (1988, 1990*b*) has argued that trade-offs in competitive ability for different resources is a fundamental principle underlying patterns of plant distribution. These two positions may not be as different as they sound if the earlier arguments are correct that Tilman's definition of competitive ability corresponds to competitive response in size-uneven situations while Grime's definition of competitive ability corresponds to competitive effect. Consistency of competitive effect hierarchies but contingency of competitive response hierarchies among environments could be viewed as consistent with both sides of this divisive issue (Goldberg 1990).

The database includes 30 studies that allow comparisons of competitive effect and/or response hierarchies among environments and no clear answer emerges for either one (table 2*b*). About half of experiments testing for both competitive effect and competitive response were consistent between environments and about half were contingent. Again, many of the available experiments were in a glasshouse or common garden (11), short-term (10 less than 1 year) and involved only seedling–seedling interactions (14), but the limited data available do not suggest any patterns in consistency vs contingency with respect to these variables (Goldberg 1996*a*).

Clearly, there will be no simple answer to whether competitive ability is consistent among environments or hierarchies change and there is currently neither sufficient theory nor empirical work to guide us as to when hierarchies are likely to be consistent and when not. However, sufficient data do exist that both effect and response hierarchies can differ between environments that it is probably unreasonable to assume *a priori* consistency in any particular case.

4. CORRELATIONS OF TRAITS WITH COMPETITIVE ABILITY

A minimum of three species is needed to even begin to relate traits to competitive ability and this is clearly statistically insufficient to establish relationships. Unless species are carefully chosen, even statistically reasonable numbers of taxa will often be insufficient because of possible phylogenetic effects. In the context of understanding the consequences of traits, phylogenetic relationships may be important if apparent relationships between a trait and competitive ability are actually due to some other, shared trait that has not been measured. The distribution of numbers of targets or neighbours in the database is strongly skewed towards very few taxa with a median value between three and four taxa for both response and effect (Goldberg 1996*a*). This is despite a strong bias towards inclusion of larger numbers of taxa because of the criteria used (see above). Further, most of those with three or more taxa do not also include explicit relationships with traits and those few that do only use a single environment, most often a relatively productive one (Gross 1984; Goldberg 1987; Gaudet & Keddy 1988; Popma & Bongers 1988; Goldberg & Landa 1991; Reader 1993). Finally, the set of studies listed above that have three or more species and trait information do not, in any case, incorporate phylogenetic effects in the analyses, making it impossible to separate if the similarities in competitive ability are because of the shared trait values or because of other traits that might also be in common due to common ancestry.

Thus, the database to actually test the predictions in table 1 in any kind of rigorous and general way is just about non-existent. This is not to say that excellent data on the traits determining competitive ability do not exist for particular ecological systems. Much is known about the mechanisms of competitive interaction from a few exceptionally detailed research programmes on specific systems that cannot be reviewed here for lack of space (e.g. Eissenstat & Caldwell 1987, 1988, 1989; Aerts *et al.* 1990, 1991; Berendse & Elberse 1990; Tilman 1990*a*; Tilman & Wedin 1991*a*, *b*; Wedin & Tilman 1993). Nevertheless, the ability to generalize from this detailed knowledge will also require studies that cover much broader ranges of species, albeit with the cost of much less mechanistic detail.

5. EXPANDING THE DATASET: PROBLEMS AND POSSIBLE SOLUTIONS

The lack of large numbers of species within studies on competitive ability is not because plant ecologists have not recognized the importance of doing so but because the logistics of such experiments in even a single simple glasshouse environment are nightmarish, with the number of necessary experiments going up exponentially with the number of species for a complete matrix of pairwise interactions. Therefore expanding the sample sizes for analysing relationships between traits and the outcome of interactions and rankings of competitive ability is going to require making some assumptions to reduce the dimensionality of the systems. One such simplifying assumption is to study competitive response to diffuse competition from all vegetation, or at most, particular growth forms, reducing a huge matrix of possible interactions to a single column vector of multiple target species with a single neighbour 'taxon'. This is, in fact, the most common approach to studying competitive interactions in the field (Goldberg & Barton 1992), which may reflect the intuition of biologists that the simplifying assumptions it entails are reasonable. Specifically, this approach assumes that relative competitive response is more important than effect to persistence and abundance of a taxon within a community, and that competitive effects are equivalent among neighbour taxa. The first assumption was discussed earlier but clearly needs to be tested explicitly. While the second assumption is clearly not correct under highly controlled conditions, it may not be too awful on a per unit size basis under field conditions (review in Goldberg 1996*b*). It may also be reasonable to lump neighbours if effects are not equivalent but rankings of neighbours are consistent among targets, which was true in approximately 2/3 of the cases in the quantitative survey (table 2*a*).

Within this set of simplifying assumptions, at least two primarily field-oriented approaches are possible to garner data on competitive ability on large numbers of species within a single study. The more conventional approach is to compare response of individuals in the presence vs absence of existing vegetation. The advantage of this approach is that it is directly 'field-relevant' to the particular system under study and is relatively simple in principle, if time consuming to actually carry out. There are, however, at least two disadvantages. First, it is best to use separate plots for each target species to avoid interactions among targets that could confound the results, requiring a linear (but at least not exponential) increase in number of plots with number of target species. Second, because only a single abundance of the neighbour (total vegetation or growth forms) is used, extrapolation to other sites or times with different neighbour abundances is limited, given the typical non-linearity of competitive interactions in plants.

An alternative approach to studying competitive ability for large numbers of species provides potential solutions to both these limitations. Goldberg *et al.* (1995) suggested a design called the community density series that is a simple extension of the classic yield-density experiment in agronomy. If density of the total community is varied, while holding initial relative abundances constant, subsequent changes in relative abundances along the community density gradient should reflect effects of plant–plant interactions. Specifically, the slope of a regression of eventual relative abundance on initial community density for a particular species is a measure of its community-context competitive ability. A single experiment thus yields estimates of competitive ability for all the species in a community over a gradient in density from much below to above naturally occurring abundances. Preliminary results using relatively simple communities of annual plants on stabilized sand dunes suggest that the method is feasible (D. E. Goldberg, R. Turkington and L. Olsvig-Whittaker, unpublished data).

6. CONCLUSIONS

For ecologists, the primary motivation behind understanding the links between individual plant traits and competitive ability is as a component of a larger programme that links competitive ability to relative abundances and dynamics in natural communities. Two broad types of approaches to this general programme can be caricatured as follows. One extreme is primarily experimental with detailed and long-term study of the mechanisms of interaction among few species. The other extreme is observational and based on broad surveys of large numbers of species with relatively easily measured traits, often garnered from the literature or from floras.

Both of these approaches provide important and useful knowledge that cannot be gained otherwise. However, the main message of this paper is that an intermediate approach that links these two is equally important but currently largely missing: relatively short-term experiments that provide a link of inference missing in purely observational studies but that are designed to be applied to large numbers of species so results are rigorously generalizable. Westoby *et al.* (this issue) have provided an outstanding example of such an integration focusing on the consequences of seed size in terms of numerous processes, including competition. Keddy and his colleagues have pioneered this approach with respect to competitive ability, but so far largely applied it narrowly to only competitive effect among approximately equal-sized plants in productive environments (e.g. Gaudet & Keddy 1988, 1995; but see Keddy *et al.* 1994).

Applying this intermediate approach in a more general way is critical for broad testing of predictions about the traits determining ability to compete in natural vegetation and, from there, the relationship of competitive ability to abundance and dynamics in natural vegetation. Ecologists are increasingly being asked to make predictions about community dynamics in the face of anthropogenic environmental change. If more than a few species and systems are to be investigated to serve as a basis for assessing general models of community dynamics, it is essential that some way be found to scale up from short-term individual-level interactions to long-term population-level outcomes of competition and to circumvent the logistical constraints on studying competitive interactions in highly complex, diverse communities. The suggestions in this paper are meant to provoke discussion of such issues.

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APPENDIX

(List of studies summarized in table 2. For transitivity, 'n' indicates that rankings of competitive effect (or response) are not consistent among target (or neighbour) species, while 'y' indicates that results are consistent. For environments, 'n' or 'y' indicate contingency or consistency, respectively, of effect or response among environments. '?' indicates conclusions are not confirmed statistically. Two values within a cell indicate that results are variable among independent tests. Two rows for a given study indicate two independent experiments were performed. More information on each study can be found in Goldberg (1996*a*). An asterisk before a reference indicates the study is part of the quantitative database (see text).)

	transitivity		environment	
reference	effect	response	effect	response
Aarssen 1988	y	y	–	–
*Austin & Austin 1980	n	–	n	n
*Berkowitz *et al.* 1995	–	–	y?n	–
*Bertness & Yeh 1994	–	–	y?	–
*Bertness & Yeh 1994	–	–	–	n
*Campbell & Grime 1992	–	–	y	–
*de Steven 1991*a*, *b*	–	–	n?	–
*Fowler 1990	–	–	–	y
Gaudet & Keddy 1988	–	y	–	–
*Gaudet & Keddy 1995	–	y	–	–
*Goldberg & Fleetwood 1987	y	y	–	–
*Goldberg & Landa 1991	y	y	–	–
*Gurevitch 1986	–	–	y	–
*Gurevitch *et al.* 1990	yn	ny	n?	y?
Johansson & Keddy 1991	y	y	–	–
*Keddy *et al.* 1994	yn	n	n	yn
*Law & Watkinson 1987	y	y	–	–
Mahmoud & Grime 1976	y	y	y	y
*Marino 1991	–	n	–	n?
*Marino 1991	y	y	n	n
*McConnaughey & Bazzaz 1990	y?	y	y?	y
*McGraw & Chapin 1989	–	–	n	–
Mehroff and Turkington 1990	–	–	–	n
*Menchaca & Connolly 1990	–	n	–	–
*Miller & Werner 1987	y	y	–	–
*Pantastico-Caldas & Venable 1995	–	–	n?	y
*Peart 1989*a*	y	y	–	–
*Peart 1989*b*	–	n	–	–
Popma & Bongers 1988	–	–	n	–
*Reader 1993	–	–	n	–
*Rees & Brown 1992	–	–	y	–
Rice & Menke 1985	–	n	–	n
*Scandrett & Gimingham 1989	–	–	–	n
*Shainsky & Radosevich 1992	y?	y?	–	–
Shipley *et al.* 1991	–	–	y	–
*Turkington & Harper 1979	y	n	–	–
Welbank 1963	–	y	–	y
Wilson 1993*a*	–	–	y	–
*Wilson 1993*b*	–	–	y	–
*Wilson & Shay 1990	–	–	y?	–
*Wilson & Tilman 1991	–	–	y?	–
*Wilson & Tilman 1995	–	–	ny	–