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Source: *Journal of Ecology*, Mar., 2007, Vol. 95, No. 2 (Mar., 2007), pp. 301-308

Published by: British Ecological Society

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Measuring the components of competition along productivity gradients

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Summary

1 Controversy surrounds the measurement of competition intensity. Moreover, when biomass varies systematically along productivity and other environmental gradients, common indices of competitive outcome mask important ecological interactions.

2 This study presents two indices derived from how neighbours interact with target plants. The first, *relative crowding*, increases directly with the abundance of neighbours present and decreases inversely with the potential size and vigour of the target plant itself. The second, *interaction strength*, is the integral of suppression of the target by neighbours over the range of neighbour abundance. Relative crowding and interaction strength are derived independently, but when multiplied produce the commonly used relative competitive index, showing the biological underpinnings of the relative competition index in terms of crowding and strength of interaction. Since the new indices of relative crowding and interaction strength explicitly account for the amount of neighbour biomass, they serve as a valid method to track the effects of changing habitat conditions on the components of competition.

3 The new indices are applied to three published data sets. In each case, relative crowding increased with standing crop. In one case competition was reported as unchanged along a productivity gradient, whereas the new indices show that relative crowding and interaction strength both had significant patterns, but their effects were counteracting. These results do not fit current theories of competition. Further empirical studies are needed to see if competition theory needs revision.

4 Separating the mechanisms of competition into relative crowding and strength of interaction reveals previously hidden patterns that help bring to light underlying processes of competition along productivity gradients.

Key-words: competition indices, competition intensity, crowding, interaction strength, plant competition, productivity gradients, relative crowding

Journal of Ecology (2007) **95**, 301–308

doi: 10.1111/j.1365-2745.2007.01215.x

Introduction

As an inevitable consequence of organisms with overlapping resource requirements, competition has always held an important place among ecological concepts. Competition can be a key factor in structuring communities and determining ecosystem dynamics (Grace & Tilman 1990; Crawley 1997; Aerts 1999; Grace 1999; Ewanchuk & Bertness 2004). Conceptual and methodological developments of the last few decades, such as the distinction between effects and responses

(Goldberg 1990) and the value of phytometers (Gaudet & Keddy 1988), have focused attention on the changes that competition causes in a target organism. At the same time, controversy has dogged decisions regarding the proper index for measuring the outcomes of competition on organisms. Dozens of indices are available (Williams & McCarthy 2001; Weigelt & Jolliffe 2003); each emphasizes different aspects of competition. In plant ecology, two of the most widely used indices are the absolute competitive index (CI_a) and the relative competitive index (CI_r). Both compare the performance of a target plant grown mixed with neighbours (y_{mix}) and grown in isolation (y_{iso}) (Wilson & Keddy 1986; Miller 1996):

$$CI_a = y_{iso} - y_{mix} \text{ and } CI_r = \frac{y_{iso} - y_{mix}}{y_{iso}}.$$

These indices are now accepted as reflecting separate underlying aspects of competition (Grace 1993).

All available indices measure the outcome of competition without regard to habitat or environmental conditions. Because the world is heterogeneous, we need tools that advance understanding of how competition changes in varying environments (McGill *et al.* 2006). Recent research has focused particularly on productivity gradients, both in space (Peltzer *et al.* 1998; Goldberg *et al.* 1999; Van der Wal *et al.* 2000; Foster 2002; Kuijper *et al.* 2005) and in time (Foster 2000; Thompson *et al.* 2001; Fuhrer 2003). However, the interpretation of competition along gradients has been fraught with controversy. Therefore, it is important to re-examine the measurement of competition when growth, biomass and interactions shift from one location to another.

Many approaches to measuring competition are flawed because they fail to account for differences in organism size between species or between experiments (Freckleton & Watkinson 1997; Connolly *et al.* 2001; Lamb *et al.* 2006). The same problems arise when organism size varies along a productivity gradient. Existing indices of competition do not control for biomass. As such, they are misleading when compared across more than one set of habitat or environmental conditions. For example, CI_a and CI_r are often determined in field studies from removal experiments (e.g. Reader *et al.* 1994; Belcher *et al.* 1995; Kadmon 1995; Van der Wal *et al.* 2000; Foster 2002). The amount of biomass removed will vary depending on the capacity of each habitat to support growth, which means that the amount of experimental manipulation will also vary across the productivity, or biomass, gradient. Similar concerns arise in glasshouse studies (Gibson *et al.* 1999).

In addition, increased crowding can change the competitive influence of neighbours as a group without altering the competitive abilities of individual plants. Likewise, the competitive influence of neighbours can change with shifting strengths of plant–plant competitive interactions without any change in crowding. For example, even if the biomass removed is the same within each habitat of a field study, competition can vary because of shifts in the ability to take up and utilize resources that occur between neighbours and the target plant. This phenomenon is the ‘per-unit’ or ‘per-amount’ effect (Goldberg & Werner 1983), which, mysteriously, field competition studies have mostly ignored (cf. Howard 2001). When neighbour biomass is relatively constant, as when a competition study is conducted under uniform environmental conditions, indices such as CI_a , CI_r , $\log(RR)$ (Goldberg *et al.* 1999; Hedges *et al.* 1999), II (Markham & Chanway 1996), RII (Armas *et al.* 2004), or $RECI$ (Corcket *et al.* 2003; Brooker *et al.* 2005) respond only to the per-unit effect

because crowding does not vary systematically from location to location. However, when the objective is to understand how competition varies along productivity gradients, indices that do not distinguish between pure crowding and the actual strength of plant–plant interactions will mask many ecological interactions of interest.

Consider this situation in terms of four components that describe the response of an individual to neighbours:

$$y_{mix}(h) = f(y_{iso}(h), z_{mix}(h), I(h)),$$

where $y_{iso}(h)$ is the growth potential of the target plant without neighbours; $z_{mix}(h)$ is the abundance of neighbours, or crowding; and $I(h)$ is the interaction strength, the influence of an individual neighbour on the target plant. All these vary according to the habitat conditions, h . Studies that compare interactions across different habitat conditions ask the question, ‘How does the intensity of competition (or interaction) vary?’. Commonly, an index of competition is reported for each condition or location along a gradient. But when both z and I vary with h , as is true along a productivity gradient, then the response measure and the analysis should be capable of distinguishing between changing interaction strengths ($I(h)$) and simple changes in crowding ($z(h)$). Indices like CI_a , CI_r , $\log(RR)$, II , RII and $RECI$ cannot make this distinction.

This study has three objectives: (i) develop two new measures of the outcome of interspecific interaction that separate the effects of crowding from the strength of interaction; (ii) explain how the new indices can distinguish different patterns of competitive interactions along productivity gradients; and (iii) employ the new indices with previously published data sets to determine if the new approach provides new insight into plant interactions. Although the focus here is on plant–plant interactions, the concepts generalize to any organism where a target individual can be associated with a neighbourhood.

Derivation of the new indices

Most indices of the outcome of interspecific competition compare the performance of a target plant grown with neighbours (y_{mix}) with its performance grown in isolation (y_{iso}) or in monocultures (but see Miller 1996). Performance can be expressed as above-ground biomass, seed production, relative growth rate, or any other ecological measure that is meaningful in the context of the goals of a particular study. Likewise, neighbourhood size will vary from study to study, but should match distances at which individuals interact (Addicott *et al.* 1987; Casper *et al.* 2003).

The abundance of neighbours changes as habitat conditions change, especially along productivity gradients. Decreases in growth from competitive neighbours depend proportionally on the abundance of neighbours present (Ramseier & Weiner 2006). That is, D ,

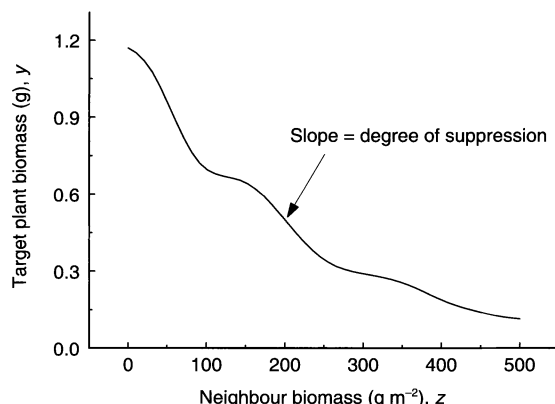


Fig. 1 Pictorial representation of the degree of suppression per neighbour biomass and overall interaction strength (I).

$$I = \frac{1}{z} \int - \frac{dy}{dz} dz.$$

$\propto z_{mix}$, where D_r is the effect of relative crowding and z_{mix} is the abundance of neighbours surrounding the target plant. However, the effects of crowding on the target plant also depend on its size and vigour (Keddy 2001). For example, a thick mixture of neighbours will impose a higher degree of crowding from the perspective of a small, weak plant than from the perspective of a large, vigorous plant. The most direct way to capture this relationship is $D_r \propto 1/y_{iso}$. Large size when grown in isolation is the result of vigorous growth so, presumably, y_{iso} might also reflect current vigour. Combining these arguments leads to a measure of the relative degree of crowding that is the ratio of the abundance of neighbours to the potential size of the target plant: $D_r = z_{mix}/y_{iso}$.

How neighbours interact with the target plant is also important in determining the outcome of the interaction. Being surrounded by neighbours that do not compete for shared limiting resources will cause little reduction in the performance of a target plant compared with being surrounded by fewer neighbours that have active and similar resource demands. One way to envision interaction strength is as the degree of suppression in a curve of target plant biomass vs. neighbour biomass (Fig. 1): the steeper the curve, the stronger the suppression. But suppression occurs throughout the range of actual neighbour abundance, so the average slope of the curve is an index of interaction strength. Because most cases of interaction in the literature are negative (suppression), following convention the index is the average of the negative of the slope:

$$I = \frac{1}{z} \int - \frac{dy}{dz} dz.$$

Evaluating I over the domain of neighbour abundance yields:

$$I = \frac{1}{z_{mix}} \int_0^{z_{mix}} - \frac{dy}{dz} dz = \frac{y_{iso} - y_{mix}}{z_{mix}}.$$

I is analogous to the per-unit effect of interacting with neighbours (Goldberg & Werner 1983), but the present derivation is conceptually distinct. Goldberg *et al.* (1999) and others express concerns that per-unit measures assume underlying models of target performance vs. neighbour biomass. However, the derivation of I from general suppression concepts shows that I is valid no matter the underlying model.

Degree of crowding and interaction strength combine to produce the net effect of neighbours on the performance of a target plant, as given by the mathematical expression

$$D_r \cdot I = \left(\frac{z_{mix}}{y_{iso}} \right) \cdot \left(\frac{y_{iso} - y_{mix}}{z_{mix}} \right) = \frac{y_{iso} - y_{mix}}{y_{iso}} \equiv CI_r.$$

In other words, the *independently derived* components D_r and I combine to produce CI_r , the widely used index of relative competition intensity. These direct relationships between D_r , I , and CI_r demonstrate the biological underpinnings of the relative competition intensity index in terms of crowding and strength of interaction.

An important advantage of using D_r and I is that they allow the effects of changing habitat conditions to be tracked. Habitat conditions influence the performance of the target plant (y_{iso} and y_{mix}) and the abundance of neighbours (z_{mix}). As a result, degree of crowding and interaction strength will also vary with habitat conditions:

$$D_r(h) = \frac{z_{mix}(h)}{y_{iso}(h)} \text{ and } I(h) = \frac{y_{iso}(h) - y_{mix}(h)}{z_{mix}(h)}.$$

The influence of z_{mix} can be safely ignored only if neighbour biomass is constant for each comparison, which is rarely true.

The focus of this derivation is on plant competitive interactions involving resource acquisition and use, but the concepts and applications generalize easily to other types of interactions, such as influences over non-resource growing conditions, as well as to positive outcomes and other organisms. For example, species interactions can be facilitative (positive), as well as competitive, and facilitation is more likely in unproductive habitats (Bertness & Callaway 1994; Brooker & Callaghan 1998; Pugnaire & Luque 2001; Foster 2002; but see Maestre *et al.* 2005 and Lortie & Callaway 2006). Generalizing the index of relative competition intensity (CI_r) to accommodate the possibility of facilitation is straightforward. Relative interaction intensity (II_r , also called *RNE*) is defined (Markham & Chanway 1996; Suding & Goldberg 1999) as

$$II_r = \frac{y_{iso} - y_{mix}}{\max(y_{iso}, y_{mix})}.$$

Therefore, the adjustment in relative crowding (D_r) to accommodate positive interactions is

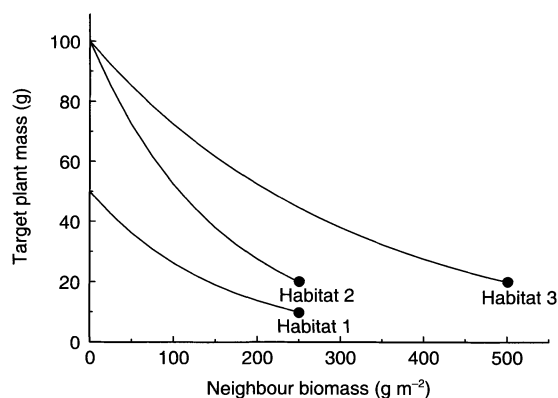


Fig. 2 Performance of the target plant vs. neighbour biomass in three hypothetical habitats, as shown in Table 1. Relative competition intensity (CI_r) is the same in all three habitats, even though they differ in position along the productivity gradient (the filled circles) and in the growth potential of the target plant in the absence of competitors.

$$D'_r = \frac{z_{mix}}{\max(y_{iso}, y_{mix})}$$

Interaction strength (I) remains defined as before. Similar adjustments are possible for the relative interaction index (RII) of Armas *et al.* (2004).

With any experimental examination of competitive outcome, treatments and controls must be properly designed. The emphasis has been on single target plants grown in isolation and grown with mixtures of neighbours using a removal design, an additive design, or a more complete version of these (Gibson *et al.* 1999; Silvertown & Charlesworth 2001). Another common design is to follow a group of target plants with and without neighbours. If the target plants are sparse enough, growing in groups is essentially like growing singly. If plants are dense enough to interact in groups, then the differences between the performances of target plants in monoculture vs. mixture result from a combination of added interspecific competition and reduced intraspecific competition. This flaw is inherent in all such designs. In the case of the indices D_r and I , y_{iso} will be underestimated, leading to an overestimate of D_r and an underestimate of I . Mis-estimation will be low if intraspecific competition among target plants is low.

Likewise, z_{mix} should be ideally determined independently of the influences of the target species. In most studies, $z_{mix} \gg y_{mix}$, so the influence of the target species on neighbours will be slight.

Habitat and the components of competition

Consider a hypothetical landscape with three habitats differing in productivity (Fig. 2). Competition experiments are conducted in each habitat, with target plants grown in isolation (neighbour biomass = 0) and grown with neighbours in either a removal or additive design. The habitats differ in the abundance of neighbours they support (z_{mix}) and in their suitability for the target plant

Table 1 Performance of the target plant (y_{iso} and y_{mix}) and neighbours (z_{mix}) in the three hypothetical habitats shown in Fig. 2. Relative competition intensity (CI_r) is the same in all three habitats, but the new indices of relative crowding (D_r) and interaction strength (I) reflect changes along the productivity gradients represented by the three habitats. See text for details

Habitat	y_{iso} (g)	y_{mix} (g)	z_{mix} (g m ⁻²)	CI_r	D_r	I
Habitat 1	50	10	250	0.8	5.0	0.16
Habitat 2	100	20	250	0.8	2.5	0.32
Habitat 3	100	20	500	0.8	5.0	0.16

(y_{iso}). Habitat 3, with the highest overall biomass (500 g m⁻²), is more productive than the other two; habitat 1 is least suitable for the target plant (10 g).

In this hypothetical example, relative competition intensity for the target plant (CI_r) is the same in all three habitats along the productivity gradient (Table 1), even though the relationships between neighbours and target plant differ. Habitats 1 and 2 have the same capacity to support neighbour biomass, but relative crowding (D_r) is higher in habitat 1, and interaction strength (I) is higher in habitat 2. In contrast, D_r and I are identical in habitats 1 and 3, which represent different positions along the productivity gradient. Thus, the new indices of relative crowding and interaction strength can reveal differences that CI_r cannot, as well as reflect similarities in the components of competition across differing habitat conditions.

Analysis with published data

METHODS

A 1999 meta-analysis of the intensity of plant competition and facilitation along productivity gradients (Goldberg *et al.* 1999) provides an objective and comprehensive source of data sets with which to analyse the effectiveness of the new indices of crowding (D_r) and interaction strength (I). To qualify for analysis, a study needed data at three or more levels of biomass, either across habitats or manipulated experimentally, plus data on plant performance with and without neighbours (rather than just report CI_r). Three data sets qualified for further analysis. Belcher *et al.* (1995) examined total, root and shoot competition along a gradient of biomass caused by changes in soil depth in alvar lands of Ontario, Canada. Phytometers of *Trichostema brachiatum* L. were grown without neighbours, with neighbour roots, and with neighbour roots and shoots. Only growth with and without neighbour roots and shoots have been analysed. Growth response was measured as above-ground biomass. Kadmon (1995) examined competition along a combined natural and experimental productivity gradient in an extremely dry mediterranean climate in Israel. Seedlings of *Stipa capensis* Thunb. were either allowed to

Table 2 Product-moment correlation coefficients (r) of relative competition intensity (CI_r), relative crowding (D_r), and strength of interaction (I) vs. standing crop for three data sets. r_{null} and the probability (P) that $|r| > |r_{\text{null}}|$ by chance were determined by a randomization procedure. Significant patterns ($\alpha = 0.05$) are shown in bold

Study	Variable	Trans- formation	Relationship with standing crop								
			CI_r			D_r			I		
			r	r_{null}	P	r	r_{null}	P	r	r_{null}	P
Belcher <i>et al.</i> (1995)	Above-ground biomass	Rank	+0.24	0.00	0.27	+0.57	0.00	< 0.01	0.13	0.00	0.55
Kadmon (1995)	Seed production	Log(SC)	+0.78	-0.05	< 0.01	+0.70	0.00	< 0.01	-0.62	-0.07	0.03
Reader <i>et al.</i> (1994)	Relative growth rate	None	-0.06	0.00	0.72	+0.44	-0.01	< 0.01	-0.48	-0.02	< 0.01

grow with neighbours or had all neighbours removed. Growth response was measured as number of seeds per individual. Reader *et al.* (1994) examined plant competition in *Poa pratensis* L. across 12 grassland or old-field communities on three continents. Seedlings were transplanted into plots in which neighbours were either left alone or removed. Growth response was measured as relative growth rate.

These three data sets were downloaded from the Ecological Society of America's Electronic Data Archive. The data available for the Kadmon (1995) and Reader *et al.* (1994) studies are plot averages. For each study, the indices CI_r , D_r , and I were calculated for each level of standing crop (that is, plot above-ground biomass, Goldberg *et al.* 1999). The relationship between these indices and standing crop was measured with Pearson correlation coefficients. Variables were transformed for analysis only when transformations were used in the original study.

Since the indices are themselves related, the 'spectre of spurious correlations' (Jackson & Somers 1991) prevents the use of standard normal theory for determining both the size and significance of correlation. Instead, in each case a randomization test was used to compare the observed correlation against distributions generated from the data set (Manly 2006). The randomization approach provides two types of information. First, it supplies the expected value of the correlation coefficient between variables under the null hypothesis of no relationship (r_{null}). If r_{null} is far from 0, then interpretation of the observed correlation coefficient is problematic (Jackson & Somers 1991). Second, the randomization test supplies a distribution-free significance level for the observed correlation coefficient.

RESULTS

The randomization test proved suitable for analysing the relationships between the interrelated indices of relative competition intensity (CI_r), crowding (D_r) and interaction strength (I) against neighbour biomass. Because the r_{null} values were all close to 0.00 ($|r_{\text{null}}| \leq 0.07$), the magnitudes of the observed correlation coefficients can be interpreted as usual.

All three studies reported relative competition intensity (CI_r). Belcher *et al.* (1995) and Reader *et al.* (1994)

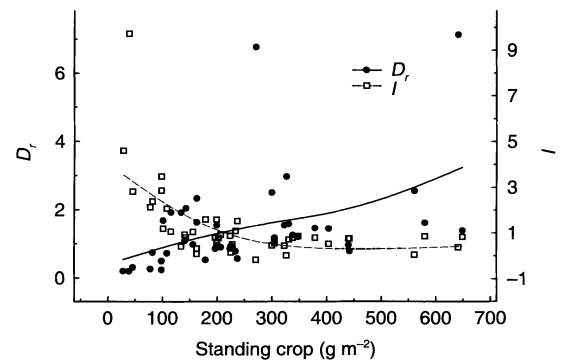


Fig. 3 Relative crowding (D_r) and interaction strength (I) vs. standing crop with *Poa pratensis* as the target plant (Reader *et al.* 1994). The lines are smoothing splines with 3 degrees of freedom. Because the response variable, relative growth rate, is very small compared with neighbour biomass, D_r and I have been rescaled by 10^{-4} and 10^4 , respectively. The significant relationships of D_r and I (Table 2) cancel each other, giving the false impression that competition is unaffected by the productivity gradient.

found no significant relationship between CI_r and standing crop, whereas Kadmon (1995) found a significant positive relationship. The randomization test results are consistent with these findings (Table 2).

The correlation of relative crowding (D_r) with standing crop was large and significantly positive in all three data sets (Table 2). That is, the effects of crowding by neighbours increased as the productive capacity of the habitats increased. In both the Kadmon and Reader data sets, the correlation of interaction strength (I) with standing crop was significantly negative. That is, the per-unit influence of a neighbour on the target plant diminished as standing crop increased. The results were virtually identical when II_r and D'_r were used instead of CI_r and D_r .

How D_r and I interacted determined the net outcome of interaction, as measured by CI_r . With the Belcher data set, only relative crowding was important, and crowding was not intense enough to overcome the variability present elsewhere in the data set (Belcher *et al.* 1995). This led to a weak and non-significant correlation between CI_r and standing crop. With the Reader data set, the individually significant influences of D_r and I countered each other (Fig. 3), causing a non-significant

net correlation of CI_r with standing crop. With the Kadmon data set, the statistically significant D_r was stronger than the statistically significant I , producing a positive correlation between CI_r and standing crop.

Discussion

Treatments of plant species interactions along habitat gradients have focused on the effect of productivity or biomass changes on patterns of competition intensity (reviewed by Grace 1991; Keddy 2001; Pierce *et al.* 2005). One school of thought holds that competition increases as productivity increases; another believes that although the type of resource shifts along the productivity gradient, competition intensity remains unchanged (Grace 1991). The method of measuring competition intensity – for example, absolute competition intensity (CI_a) vs. relative competition intensity (CI_r) – can influence which view is supported (Campbell & Grime 1992; Grace 1993). The more biologically meaningful indices of relative crowding (D_r) and interaction strength (I) shed new light on these conflicting views.

The theoretical development of both views emphasizes interaction strength when the interaction is over resources. For example, Grime & Hodgson (1987) describe high competitive ability of a plant in terms of broad resource foraging and rapid capture; they suggest that competition intensity is more likely under productive conditions. On the other hand, Tilman (1982, 1988) emphasizes morphologies that maximize plant resource capture under low resource conditions. Because the limiting resources shift from soil resources at low productivity to light at high productivity, the strength of this interaction is less likely to vary along productivity gradients.

In contrast to predictions based on the theoretical underpinnings of both views of competition, in two of the three sample data sets the strength of interaction per unit of neighbour biomass (I) decreased with standing crop. This pattern is consistent with a different mechanism, a decrease in per-mass rates of resource capture and use by neighbours relative to supply as productivity increased. Further empirical studies are needed to see if theories of competition require revision.

Relative crowding (D_r), the sheer force of neighbour mass, consistently increased with standing crop across the three sample data sets. When overall competition intensity increases with standing crop (Kadmon 1995; Foster 2000; Van der Wal *et al.* 2000), the cause might be relative crowding rather than changes in the competitive ability *per se* of neighbours. Overall indices of competition intensity cannot make this distinction.

In the Reader *et al.* (1994) data set, the declining strength of interaction with increasing productivity balanced the increase in relative crowding. The result, as reported by Reader *et al.* (1994), was unchanging relative competition intensity along the gradient. But to conclude that competition is unaffected by standing crop is a mistake. The pattern is consistent with the

prediction of unchanging relative competition intensity. However, the observed mechanism – balanced crowding and interaction strength – provides a new alternative to the theory of balanced competition arising from shifts from limiting soil resources to limiting light (Tilman 1982, 1986).

Interaction strength (I) is similar to other approaches that reflect proportional effects, such as per-gram or per-amount effects (Goldberg & Werner 1983; Goldberg & Landa 1991; Howard 2001). These indices directly measure competitive outcome, controlling for size. Goldberg *et al.* (1999) assert that using proportional effects, such as ‘per gram’, assumes that the proportion is constant over the range of data. As such, they prefer total effects. Howard (2001) relaxes the assumption of constant proportional effects by fitting per-unit competition intensity to a reciprocal model of neighbour biomass (Watkinson 1980). In this curve-fitting approach, the per-gram competitive effect is encapsulated within a single parameter describing the shape of the curve across the entire productivity gradient. This approach therefore cannot be used to examine changes in per-unit effects along habitat gradients. In contrast, the interaction strength index (I) proposed here requires no assumed mathematical models, does not assume constancy of interaction strength, and allows measurement of competition across productivity gradients.

The examination of competition components has been one of the fruitful developments in the study of competition during the past two decades. Competition has been split into responses and effects (Goldberg & Fleetwood 1987; Goldberg 1990; Keddy *et al.* 1994), above-ground and below-ground processes (Tilman 1982; Wilson 1988; Wilson & Tilman 1991; Peltzer *et al.* 1998), intensity and importance (Welden & Slauson 1986; Brooker *et al.* 2005), and indices of relative and absolute competition intensity (Campbell & Grime 1992; Grace 1993, 1995). Separating the mechanisms of competition into relative crowding (D_r) and strength of interaction (I) provides a new tool to advance the investigation of the patterns and processes of competition and how interactions vary along productivity gradients.

Acknowledgements

I thank Joyce Belcher, Ronen Kadmon and Richard Reader for kind permission to use their data sets. I thank Deborah Clark, Kimberly Davis, Linley Hall, Lora Perkins, Eric Seabloom, Paul Severns and anonymous reviewers for helpful discussions and comments on earlier versions of the manuscript.

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