

Indices of plant competition

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Summary

1 Mathematical indices, formed by combining several primary measures, can help researchers summarize, interpret and display results from plant competition experiments. This essay compiles and discusses more than 50 indices that have been used in studies of plant competition.

2 Indices allow researchers to quantify and express several attributes of plant competition, including competition intensity and importance, competitive effects and responses, and the outcome of competition.

3 Several qualities should be considered when selecting a competition index for use. These include specificity and clarity of meaning, mathematical and statistical properties, density dependence, versatility and freedom from size bias.

4 Many indices are based on comparisons of plant performance in mixtures compared with pure stands or control plots. Additional measures of competition are also available from yield-density functions, size distributions and neighbourhood analysis.

5 Indices reflect the consequences of competition. In order to appreciate competitive processes, indices have to be used in conjunction with studies of the chronology, circumstances and composition of plant associations.

Key-words: competition indices, competition intensity, competitive effects, competitive responses, outcome of competition

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Introduction

‘The interpretation of the outcome of competition can depend critically on the way competition is measured’ (Freckleton & Watkinson 1999, p. 286). This statement is applicable to several aspects of ‘measurement’, including experimental design, the selection of response variables and the quantification of competitive behaviour. In attempting to quantify plant competition it is a common practice to form indices by amalgamating several primary response variables, or by combining measures from different experimental subunits. The selection and use of indices by researchers has an important bearing on the way competition is assessed, which in turn may condition the inferences drawn from plant competition experiments.

Competition indices can help researchers in several ways. By condensing experimental data indices can

facilitate the presentation of results. By aggregating several different measures indices can express and quantify composite ideas that may better characterize competition than is possible through a simple primary measure (Hunt 1982). By condensing and organizing experimental results indices can help researchers interpret complex data, and the use of the same index by different researchers may help results from different studies to be compared.

Nevertheless, competition indices have possible shortcomings, and they can be flawed and misapplied; they need to be used appropriately and with care. Over time, different researchers have formulated indices that are relevant to the particular circumstances that they were attempting to assess. Somewhat independent streams of literature exist for quantifying plant interactions in ecology, agriculture and forestry, and this has contributed to the wide variety of competition indices currently available. It can be difficult for researchers to decide which index to use, and we hope this review will assist researchers by cataloguing and describing more than 50 plant competition indices that have been

introduced. Several more limited discussions of competition indices are available in the literature (Mead 1979; Aarssen 1985; Connolly 1986, 1987; Wilson 1988; Rejmanek *et al.* 1989; Snaydon 1991; Grace *et al.* 1992; Cousens & O'Neill 1993; Grace 1995; Garnier *et al.* 1997; Jolliffe 1997; Loreau 1998; Goldberg *et al.* 1999; Jolliffe & Wanjau 1999; Jolliffe 2000; Sackville Hamilton 2001).

Context

Competition is an important factor in biology and is being investigated in many settings and for many purposes. There is still debate about appropriate definitions, experimental designs, and methods for analysing and interpreting experimental results. After Begon *et al.* (1996), competition will here be defined as an interaction between individuals, brought about by a shared requirement for a resource in limited supply, and leading to a reduction of the performance (e.g. survival, growth, reproduction) of at least some of the competing individuals.

Competition has several attributes, and it can be examined from different perspectives, including: importance, intensity, effect, response and outcome (Gibson *et al.* 1999a; Connolly *et al.* 2001; Sackville Hamilton 2001). The use of this terminology has not been entirely consistent, but *intensity* and *importance of competition* are both terms used to describe the variation of plant performance caused by competition relative to that due to other ecological factors or sources of variation. The intensity of competition is defined as the amount by which competition reduces the optimal condition of an individual, while the importance of competition is the degree to which competition contributes to the overall decrease in fitness relative to other processes affecting the performance of the organism (Welden & Slauson 1986). In this context, for example, researchers might attempt to determine changes in competition intensity that occur along salinity or productivity gradients, or compare the importance of competition to other processes such as herbivory. In exploring the *effect of competition*, researchers evaluate how competition by companions influences target plants, while the *response to competition* entails the ability of target plants to avoid being suppressed by their companions (Goldberg & Werner 1983; Goldberg & Fleetwood 1987). In assessing competitive effects, the intra- and interspecific components of competition can be of interest, and a hierarchical ranking of competitive effects might be developed for the species and individuals present. Finally, the *outcome of competition* refers to the role of competition in directing long-term adjustments in composition of a mixture, i.e. it pertains to the determination of which species 'win' and 'lose' as a result of competition.

Experimental designs are another context for the use of competition indices. In addition to aspects of layout, sampling and replication, experimental designs

regularly incorporate factors that relate to variation in competition, including population density, plant species, resource levels and other aspects of the chronology and circumstances of growth. Some indices are tied to particular experimental designs, and several recent papers have reviewed the pros and cons of some designs used in plant competition research (Cousens 1996; Gibson *et al.* 1999a; Jolliffe 2000; Sackville Hamilton 2001). It is beyond the scope of this paper to discuss this aspect thoroughly for each of the indices presented here. Researchers should be aware, however, that inferences that might be drawn through the use of an index can be limited by the experimental design, and *vice versa* (Garnier *et al.* 1997; Jolliffe & Wanjau 1999; Connolly *et al.* 2001).

Evaluating indices

The utility of a competition index can be examined from several different standpoints. As indices are regularly used to characterize competition, they ought to be *clear, specific and consistent in meaning and relevant* to important themes and perspectives. Such qualities help indices to characterize competition, and can assume critical importance when researchers attempt to distinguish between subtly different alternative hypotheses. Because different competition indices are often built from similar primary measures, there are natural overlaps in meaning among them. In some instances confusion has arisen when the same index has been introduced more than once, under different names (e.g. *diffuse competition* and *relative competition intensity*). Also, confusion occurs because some indices exist in more than one form, having been modified to broaden their applicability or address mathematical or statistical shortcomings (e.g. *relative competition intensity* and *relative neighbour effect*). Occasionally, different standards have been used for what is ostensibly the same index (e.g. *relative yield*). Such inconsistency can block comparisons between studies and impede subsequent meta-analysis.

The *mathematical properties* of indices are also of interest, in several ways. The merging of several primary variables into an index inevitably results in some loss of detail, compared with the original data (Hunt 1982; Gilliver & Pearce 1983; Jolliffe 2000). Moreover, the combination of several variables into an index tends to expand confidence limits and make the statistical qualities of an index difficult to comprehend (Firbank & Watkinson 1990; Jasienski & Bazzaz 1999). Many competition indices involve ratios, which obscure knowledge of relationships between the variables (Jasienski & Bazzaz 1999). Also, bias can occur due to the mathematical structure of an index. Problems related to mathematical properties of indices all tend to worsen with increasing number of variables and mathematical operations in an index. For this reason, in listing competition indices we will include information on their mathematical complexity as indicated by

the number of mathematical operations used for their calculation. Also, the *versatility* of an index can be restricted by its mathematical structure or connection to particular experimental designs. For example, some indices useful with two-species mixtures cannot easily be expanded to deal with multi-species associations (e.g. *aggressivity*), and some indices are only applicable to replacement (e.g. *relative yield total*) or additive series designs (e.g. *regression competition coefficient*). Partly because of problems relating to mathematical properties, some authors (Goldberg & Scheiner 1993; Freckleton & Watkinson 1997, 1999, 2000; Sackville Hamilton 2001) argue against the use of indices in general and recommend the use of yield density functions and regression analysis instead. Undoubtedly, these are valuable alternative approaches, but many experiments involve simpler designs, e.g. just 'with' and 'without competition', where regression analysis is not feasible.

Another possible bias of indices is *size bias*, where initial differences in species size confound the evaluation of competition. For example, indices based on yield per plant may tend to emphasize an intrinsic competitive advantage of large plants over small plants (de Wit 1960; Connolly 1986; Gibson *et al.* 1999a; Sackville Hamilton 2001). Size inequalities are commonplace, because species are non-uniform in stature, and size varies during the course of plant development. Size measures are regular elements of competition indices, so size bias may be present in most investigations of plant competition and in most competition indices.

Furthermore, plant competition can be conditioned by the abundance of plants and the relative frequencies of species, but competition indices themselves can also exhibit qualities of *density and frequency dependence*. Competition experiments often involve the use of different population densities and species proportions, and even when these factors are not directly visible they may underlie the variables built into a competition index. These dependencies can lead to spurious conclusions. Density and frequency dependencies can interfere with interpretation by confounding competition with the characteristics of the indices used to assess competition. As with size bias, problems of density and frequency dependence regularly occur in plant competition studies. They are not always of concern, however, especially some field and agronomic studies where no attempt is being made to normalize competitive circumstances or potentials (see also Sackville Hamilton 2001).

Finally, and very much related to density dependence, is the problem of *standardization* of an index. Many competition indices compare the performance of plants in mixture with their performance in pure stands (monoculture, e.g. 'relative physiological performance'). This means a measure of interspecific competition is standardized by an unknown and probably different amount of intraspecific competition. This approach can limit the generality of inferences drawn

from experiments, but for some studies these restrictions are unimportant to the main question of interest, as, for example, in some agricultural research where standard crop densities may be used. Alternatively, plants in mixture have been standardized by plant performance in the absence of competition (e.g. *log response ratio*), although this may introduce some non-competitive influences because plants growing in isolation may be exposed to risks of stresses, pests and diseases that are moderated if neighbours are present. Both monoculture and isolated plant controls, however, have been criticized, particularly in studies including environmental gradients (Freckleton & Watkinson 1997, 1999 and see discussion of RCI).

Indices and measures of plant competition

The competition indices that compare the performance of plants in pure stands, or some other experimental control, with their performance in mixture will be described first, followed by additional measures derived from yield-density functions and neighbourhood analysis.

Indices comparing plants in pure stands and mixtures are compiled in three tables according to different attributes of competition: the intensity of competition (Table 1), the effects of competition (Table 2) and the outcome of competition (Table 3). The segregation of indices among these tables is somewhat arbitrary, and reflects our impression of their main areas of application; it does not mean that an index listed in one table is forbidden to be used in other ways. Within each table the indices are listed according to similarities in their calculation.

These tables are based on an extensive literature study, and contain citations of the source papers that introduced the indices, some examples where the indices have been used to evaluate competition, and some cases where the indices have been compared with one another. Most of the formulae in the tables are in their original version, but in some cases the notation has been changed to match the definitions used here. Some indices have been defined in different ways. If this was due to a specialized experimental design, a version for general use is given. If indices have different frames of reference (e.g. monoculture vs. control treatment) these variations are cited. Also, if we found alternative versions of an index, we present either the older or more common version in the tables, while the other versions are mentioned in the text.

INDICES OF INTENSITY OF COMPETITION (TABLE 1)

Plant competition is only one of many ecological processes that shape the composition dynamics and productivity of vegetation, and several competition indices have been used to compare the influence of competition relative to other ecological factors. In

Table 1 Indices to quantify the intensity of competition. The following conventions and abbreviations refer to all three tables. Column C gives a measure of complexity, which sums the number of mathematical operations (* 100 = 0; +, -, *, log = 1, / = 2). P is performance per plant (yield, biomass, RGR, cover); A, B is performance per plant of species a, b; M is mean P of the most productive species m; Y is performance per unit area (with $Y = P \times d$); RY is relative yield (see nr. 25a); O is number of seeds produced per plant; d is density in general; d_a is density of species in monoculture; d_m is density in mixture; d_{ab} is total density of a and b in mixture and p is proportion of species a in mixture ($p = d_a/d_{ab}$); n is number of replicates. The subscripts are defined with: a, b for species a, b; x for all the species used in an experiment, contr for a plant growing alone; mono, mix for plants growing in monoculture or mixture; remov, non for target plant(s) in removed or control plots (of removal experiments); targ, neigh for the target or sum of neighbour plants; 0, 1, 2 for time intervals (0 = start, 1 = first harvest, 2 = second harvest)

Nr	Index	Calculation	C	Introduced by
1a	Absolute competition intensity	$ACI = P_{mono} - P_{mix}$	1	Campbell & Grime (1992)
1b	Absolute competition intensity	$ACI = RGR_{remov} - RGR_{non} = P_{contr} - P_{mix}$	1	Reader <i>et al.</i> (1994)
2a	Relative competition intensity	$RCI = (P_{mono} - P_{mix})/P_{mono}$	3	Grace (1995)
2b	Relative competition intensity	$RCI = (P_{contr} - P_{mix})/P_{contr}$	3	Wilson & Keddy (1986a) as 'diffuse competition'
3	Relative competition intensity	$RCI = [(P_{mono} - P_{mix})/P_{mono}] * 100$	3	Campbell & Grime (1992) see Jolliffe <i>et al.</i> (1984)
4	Relative competitive performance	$Cpi = [(P_{contr} - P_{mix})/P_{contr}] * 100$	3	Keddy <i>et al.</i> (1998)
5	Relative neighbour effect	$RNE = (P_{contr} - P_{mix})/x$ $x = P_{contr}$ if $P_{contr} > P_{mix}$; $x = P_{mix}$ if $P_{mix} > P_{contr}$	3	Markham & Chanway (1996)
6	Total interaction index	$TII = (P_{mix} - P_{contr})/x = 1 - RNE$ (x see RNE)	3	Suding & Goldberg (1999)
7	Total effect of associate	$TE = (P_{non} - P_{remov})/P_{contr}$	3	Miller (1994)
8	Relative physiological performance	$Rx_a = A_{mono}/M_{mono}$	2	Austin (1982)
9	Normalized ecological performance	$Ex_a = A_{mix}/M_{mix}$	2	
10	Relative performance	$RP = P_{mix}/P_{mono}$ (standardized by P_{contr})	2	Parrish & Bazzaz (1982)
11	Relative increase per plant	$RIP = (P_{mix1} - P_{contr0})/(P_{mono1} - P_{contr0})$	4	Wilson & Keddy (1986b)
12	Competitive response	$Cr = P_{mix}/P_{contr}$	2	Goldberg & Fleetwood (1987)
13a	Mean competitive effect	$Ce_b = 1 - (1/n) \sum A_{mix}/A_{mono}$	7	McGilchrist (1965) as 'producer effect'
13b	Mean competitive effect	$Ce_b = 1 - (1/n) \sum A_{mix}/A_{contr}$	7	Goldberg & Fleetwood (1987)
14a	Mean competitive response	$Cr_a = 1/n \sum A_{mix}/A_{mono}$	6	McGilchrist (1965) as 'associate effect'
14b	Mean competitive response	$Cr_a = 1/n \sum A_{mix}/A_{contr}$	6	Goldberg & Fleetwood (1987)
15	Absolute severity of competition	$ASC_{mono} = \log_{10}(A_{contr}/A_{mono})$	3	Welden & Slauson (1986) modified by Snaydon & Satorre (1989)
16a	For monoculture and mixture	$ASC_{mix} = \log_{10}(A_{contr}/A_{mix})$	3	
16b	Relative severity of competition	$RSC = \log_{10}(A_{mono}/A_{mix})$	3	Snaydon (1991)
17	Log response ratio	$\ln RR = \ln(P_{mix}/P_{contr}) = \ln(1 - RCI)$	3	Hedges <i>et al.</i> (1999); Cahill (1999)
18	Log response ratio	$\ln RR = \ln(P_{contr}/P_{mix}) = -\ln(1 - RCI)$	3	Goldberg <i>et al.</i> (1999)
19	Aggressivity	$a = 1/2 [(A_{mix}/A_{mono}) - (B_{mix}/B_{mono})]$	6	McGilchrist & Trenbath (1971)
20	Simpler model of aggression	$a = 100 * A_{mix}/(A_{mix} + B_{mix})$	3	Yates & Dutton (1988)
21	Competitive ratio	$CR = (A_{mix}/A_{mono})/(B_{mix}/B_{mono})$	6	Willey & Rao (1980)
22	Competition intensity index	$CI = [(A_{mono} + B_{mono})/(A_{mix} + B_{mix})] - 1$	5	Wilson (1988)
23	Competitive balance index	$CB = \ln[(A_{mix}/A_{mono})/(B_{mix}/B_{mono})]$	7	Wilson (1988)
24	'Competition index'	$Ci = 2 * P_{mix}/(P_{contr} + P_{mix})$	4	Wilson (1988)

assessing competition intensity it is not essential to determine how competition varies with population density (Sackville Hamilton 2001). Therefore, one feature of all the formulae listed in Table 1 is the lack of density measures. This does not mean, however, that competition intensity is independent of density, because the variables in these indices are intrinsically frequency and density dependent.

As with many other indices, the *absolute competition intensity* (ACI, nr. 1a) exists in a version for use in monoculture (Campbell & Grime 1992; Turkington & Klein 1993; Grace 1995; Kadmon 1995; Davis *et al.* 1998) and in a version standardized by control plants growing alone (nr. 1b, Reader *et al.* 1994; Tielbörger & Kadmon 2000b; Fowler 2002). Where productivity varies in different habitats, it has been shown that absolute competition intensity is more sensitive to changes in productivity than relative competition intensity

(nr. 2 see below, Campbell & Grime 1992; Turkington & Klein 1993; Grace 1995; Kadmon 1995). ACI has been criticized as an index of the intensity of competition because it fails to reflect the proportional impacts on plant populations (Wilson & Tilman 1993; Goldberg & Scheiner 1993), but it might be useful in indicating the mechanisms controlling competition (Goldberg & Scheiner 1993).

Related to ACI is the most commonly used index, *relative competition intensity* (RCI, nr. 2). The name 'relative competition intensity' has been used first by Reader *et al.* (1994), though the index was introduced earlier (see below). RCI has been used in several ways. Based on monocultures, RCI has been calculated as a direct ratio of monoculture and mixture performance (nr. 2a, Grace 1995; Sammul *et al.* 2000; Greiner la Peyre *et al.* 2001) and as a percentage of monoculture vs. mixture performance (nr. 3, Campbell & Grime

Table 2 Indices to quantify the effect of competition. Abbreviations according to Table 1

Nr	Index	Calculation	C	Introduced by
25a	Relative yield	$RY_{a,b} = Y_{mix}/Y_{mono}$ with $d_A = d_a + d_b$ $= p(A_{mix}/A_{mono}) = (1-p)(B_{mix}/B_{mono})$	4	de Wit (1960); de Wit & Van den Bergh (1965)
25b	Relative yield	$RY = Y_{mix}/Y_{contr}$	4	Keddy <i>et al.</i> (1994)
26	Relative yield total	$RYT_{ab} = RY_a + RY_b$	7	de Wit (1960); de Wit & Van den Bergh (1965)
27	Relative crowding coefficient	$k_{ab} = [RY_a/(1 - RY_a)][RY_b/(1 - RY_b)]$	19	Cousens & O'Neill (1993) see de Wit (1960)
28	Land equivalent ratio	$LER = (Y_{a,mix}/Y_{a,mono}) + (Y_{b,mix}/Y_{b,mono})$	9	Willey & Osiru (1972)
29	Effective land equivalent ratio	$eff. LER = RY_b/[(1 - RY_a) + (LER - 1)p]$	21	Mead & Willey (1980)
30	Yield suppression coefficient	$YSC_a = (A_{mix}/A_{mono})$ with $d_A = d_{ab}/2$	2	Aarssen (1985)
31	Yield suppression ratio	$YSR = YSC_a/YSC_b$	5	
32	Relative monoculture response	$R_m = (Y_p - Y_{mono})/Y_p$ with $Y_p = Y_{contr} * d$	6	Jolliffe <i>et al.</i> (1984)
33	Relative mixture response	$R_x = (Y_{mono} - Y_{mix})/Y_{mono}$	6	
34	Relative resource total	$RRT = d_a/d_A + d_b/d_B$ ($A_{mono} = A_{mix}$ at d_A)	5	Connolly (1987)
35	Relative yield of mixtures	$RYM = (Y_{a,mix} + Y_{b,mix})/[(Y_{a,mono} + Y_{b,mono})/2]$	10	Wilson (1988)
36	Relative land output	$RLO = (Y_{a,mix} + Y_{b,mix})/(Y_{a,mono} + Y_{b,mono})$	8	Jolliffe (1997)
37	Total land output	$TLO = Y_a + Y_b$	3	Jolliffe & Wanjaw (1999)
38	'Proportional deviation from expected value'	$Di = (Y_{mix} - Y_{contr})/Y_{contr}$ $DT = (\sum Y_{mix} - \sum Y_{contr})/\sum Y_{contr}$	6 9	Loreau (1998) based on Wardle & Barker (1997)
39	'Index of competition'	$W_r = \sum Si/Di$ (where S cross-sectional tree area, D neighbour distance < 5 m)	3	Stoll <i>et al.</i> (1994) after Weiner (1984)
40	Response to neighbours	$p_{ab} = (A_{mix} - \text{mean } A_{mono})/\text{mean } P_{neigh}$	5	Bazzaz & Garbutt (1988)
41	Regression competition coefficient	$P_{targ} = P_{contr} - X * P_{neigh}$ (where X is the competition coefficient)	2	Goldberg & Werner (1983), Goldberg (1987)

Table 3 Indices to quantify the outcome of competition. Abbreviations according to Table 1

Nr	Index	Calculation	C	Introduced by
42	Relative reproductive rate	$RRR = O_a/O_b$	2	de Wit (1960); de Wit & Van den Bergh (1965)
43	Relative replacement rate	$RRR II = (RY_{a1}/RY_{a2})/(RY_{b1}/RY_{b2})$	22	
44	Relative efficiency index	$REI_{ab} = RGRa_{mix} - RGRb_{mix}$	1	Connolly (1987)
45	Cumulative relative effic. index	$REIc = (A_{mix1}/A_{mix0})/(B_{mix1}/B_{mix0})$	6	
46	Expected relative effic. index	$REI_{exp} = RGRa_{mono} - RGRb_{mono}$	1	Grace (1995)
47	Removal response coefficient	$C_{ab} = (B_{remov}a_1 - B_{non1})/A_{remov}a_0$	3	Silander & Antonovics (1982)
48a	Expected RA	$RAa_{mono} = A_{mono}/\sum Px_{mono}$	3	Goldberg (1994)
48b	Actual RA in mixture	$RAa_{mix} = A_{mix}/\sum Px_{mix}$	3	(for RA = relative abundance)
48c	Absolute difference in RA	$Da = RAa_{mix} - RAa_{mono}$	7	
48d	Proportional difference in RA	$PDa = (RAa_{mix} - RAa_{mono})/RAa_{mix}$	12	

1992; Turkington & Klein 1993 where it was called *proximal competitive effect*, Gibson *et al.* 1999b). More commonly, however, RCI has been calculated relative to the performance of control plants. This form of the index (RCI, nr. 2b) was introduced for removal experiments by Silander & Antonovics (1982) as the *removal response coefficient* (C_{ab} , nr. 47, Table 3), similar to the *diffuse competition* proposed by Wilson & Keddy (1986a). Another variant of RCI compares the performance of plants growing in mixture with control plants growing alone (nr. 2b, Wilson & Keddy 1986a; Wilson & Tilman 1991, 1993; Wilson 1993; Reader *et al.* 1994; Belcher *et al.* 1995; Berkowitz *et al.* 1995; Bonser & Reader 1995; Kadmon 1995; Wilson & Tilman 1995; Miller 1996; Twolan-Strutt & Keddy 1996; Cheplick 1997; Peltzer *et al.* 1998; Goldberg *et al.* 1999; Cheplick & Gutierrez 2000; Dormann *et al.* 2000; Foster 2000; Tielbörger & Kadmon 2000b; Zamfir & Goldberg 2000; Greiner la Peyre *et al.* 2001;

Peltzer & Köchy 2001; Peltzer 2001; Facelli & Facelli 2002; Fowler 2002), and when expressed as a percentage this index was termed *relative competitive performance* (C_{pi} , nr. 4, Keddy *et al.* 1998, 2000). Closely allied is the *relative neighbour effect* (RNE, nr. 5, Markham & Chanway 1996; Davis *et al.* 1998; Dormann *et al.* 2000; Howard 2001; and Howard & Goldberg 2001 as *relative interaction intensity*), which was suggested as an improvement of RCI to overcome its skewed distribution and facilitate statistical analysis (Markham & Chanway 1996). Related to RNE is the *total interaction index* (TII, nr. 6, Suding & Goldberg 1999), which is basically identical to the *total effect of associates* (TE, nr. 7) introduced earlier by Miller (1994). Miller, however, used a multispecies removal experiment in his approach and defined the removal plot as one with only four of the otherwise five associate species.

As mentioned above, the use of RCI based on monoculture yield (nr. 2a) can be criticized because

performance in mixture is standardized by an unknown and probably different amount of competition in monoculture. The standardization by plant performance in the absence of competition (Miller 1996), however, can also be a problem. Comparing isolated 'control' plants with a monoculture on the one hand and a mixture on the other hand (e.g. in target-neighbour experiments) may allow the separation of intra- and interspecific competitive effects. This possibility, together with some aspects of the usefulness of competition indices, has been critically discussed for RCI in a recent debate (Freckleton & Watkinson 1997; Markham 1997; Freckleton & Watkinson 1999; Peltzer 1999). A problem arises in quantifying competition using RCI (or other competition indices) under changing environments: changes in intra-specific interactions due to changed environmental conditions are likely to be attributed to changes in interspecific competition (Freckleton & Watkinson 1997, 1999). Particularly because RCI is often used for target-neighbour designs, Freckleton & Watkinson (1997, 1999) state that results obtained with RCI may be misleading. Markham (1997) and Peltzer (1999) disagree, arguing that indices such as RCI measure net neighbour effects and do not make assumptions about processes by which neighbours interact. Several researchers have concluded that RCI is an appropriate index of competition intensity (Goldberg & Scheiner 1993; Markham 1997; Peltzer 1999). This may be true when dealing with plant interactions in the more general sense of interference, but the points raised by Freckleton & Watkinson (1997, 1999) indicate that assumptions have to be made in order to interpret specific components of competition using RCI, especially under different environments.

In an earlier approach, Austin (1982) evaluated the *relative physiological performance* (R_{x_a} , nr. 8) and the *normalized ecological performance* (Ex_a , nr. 9) by means of a linear regression (Austin 1982; Grace 1988; Gurevitch *et al.* 1990). By comparing results from both these indices, Austin attempted to predict the performance of a multispecies mixture from monoculture yield.

Another index of *relative performance* (RP, nr. 10, Parrish & Bazzaz 1982) is a simple ratio, corresponding to *relative yield* (RY, nr. 25a, Table 2) except that RP does not take population density into account. RP is standardized by plants growing in monoculture. For comparisons between species, RP is standardized on the basis that the biomass of an individual growing alone is set to unity ($P_{\text{contr}} = 1$) and the biomass of plants of the same species growing with neighbours is expressed in proportion to P_{contr} . Similar to this is the *relative increase per plant* (RIP, nr. 11, Wilson & Keddy 1986b), which is calculated as a simple ratio of mixture to monoculture performance standardized by control plant biomass. Also similar is the index of *competitive response* (Cr, nr. 12, Goldberg & Fleetwood 1987; Goldberg 1987), which is calculated as a ratio of plants growing in mixture to control plants growing alone. Cr was not introduced as a competition index, but was

intended to standardize plant performance when comparing biomass reduction in different target species. Lepš (1999) and Moen & Meurk (2001) used this index to quantify competition intensity, but the original purpose of *competitive response* was to express the avoidance of competition by a target species.

After the introduction of *relative yield* (RY, nr. 25a, Table 2), McGilchrist (1965) suggested a procedure to average the relative yields for species mixtures. This led to indices intended to distinguish between the mean effect of a neighbouring species on a different target species (*producer effect*, nr. 13a) and the response of a target species to a different neighbour species (*associate effect*, nr. 14a). These indices have rarely been used (Miller & Werner 1987; Roxburgh & Wilson 2000). Based on a similar concept, however, Goldberg & Fleetwood (1987) proposed the use of a competitive response matrix to examine both *mean competitive effect* (Ce_b , nr. 13b) of different neighbour species on the same target species and *mean competitive response* (Cr_a , nr. 14b) of different target species grown with the same neighbour species (Goldberg & Fleetwood 1987; Goldberg 1990; Gurevitch *et al.* 1990; Goldberg & Landa 1991; Keddy *et al.* 1994; Rösch *et al.* 1997; Dietz *et al.* 1998; but see Goldberg & Werner 1983 for introduction of the names based on regression coefficient matrices). As these two indices can show different patterns of behaviour (Keddy *et al.* 1994), the distinction between them seems justified. A study by Keddy *et al.* (1998) evaluated what was termed 'competitive response' but that study actually addressed *relative competition intensity* (RCI, nr. 2) and not *competitive response* (Cr, nr. 12).

To evaluate the intensity of competition from adjacent plants on the performance of target plants, Welden & Slauson (1986) introduced a measure that was later modified (Snaydon & Satorre 1989) to be the *absolute severity of competition for monocultures* (ASC_{mono} , nr. 15) and *mixtures* (ASC_{mix} , nr. 16a). Again, the performance of plants growing without competitors is used in these indices. Because the performance of isolated control plants is rarely measured in applied agricultural studies, Snaydon (1991) subsequently proposed an index of *relative severity of competition* (RSC, nr. 16b). In the non-logarithmic scale this index has been used as a competition coefficient for pair-wise estimates of competitive ability (Warren *et al.* 2002). The ASC_{mix} is equal to the recently introduced *log response ratio* (nr. 18, see below).

The *log response ratio* ($\ln RR$, nr. 17, Hedges *et al.* 1999; Suding & Goldberg 2001; Weigelt *et al.* 2002) is one of two identical indices based on the calculation of *competitive response* (Cr, nr. 12). The other is the *total competitive response* (TCR, formula see $\ln RR$ Cahill 1999). These indices are related to RCI (nr. 2b) with $\ln RR = \ln(1 - RCI)$. Goldberg *et al.* (1999) used the inverse *competitive response* to calculate the *log response ratio* (nr. 18 = ASC_{mix} , nr. 16a), which changes the sign but not the value and presumably not the

statistical qualities of the index. The $\ln RR$ is suggested to provide a more suitable measure of competition intensity than RCI, because $\ln RR$ is symmetrical for competitive and facilitative interactions and it does not impose a ceiling on the maximum possible competition intensity (Goldberg *et al.* 1999). Hedges *et al.* (1999) favoured the logarithm of the response ratio, because the logarithm linearizes the metric – while the ratio is strongly affected by changes in the denominator, the log ratio is affected equally by changes in either nominator or denominator – and normalizes the sampling distribution that is originally skewed (Hedges *et al.* 1999).

Additional indices of the intensity of competition involve measures of plant biomass in monocultures and mixtures in more complex formulae. McGilchrist & Trenbath (1971) proposed the index of *aggressivity* (a, nr. 19; Willey & Rao 1980; Connolly 1986; Bazzaz & Garbutt 1988; Yates & Dutton 1988; Gurevitch *et al.* 1990; Snaydon 1991; Cousens & O'Neill 1993; Mynhardt 1994; Connolly *et al.* 2001). The formula given in Table 1 was devised for a replacement series, but can be modified for partial additive series (designs *sensu* Gibson *et al.* 1999a) by multiplying by two (Snaydon 1991). Connolly (1986) found *aggressivity* to be size biased if a replacement series design is used. Yates & Dutton (1988) suggested a way to simplify the index of *aggressivity* (nr. 20), but this simplification removes the standardization of the index by monoculture controls.

The *competitive ratio* (CR, nr. 21, Willey & Rao 1980; Connolly 1986; Cousens & O'Neill 1993; Connolly *et al.* 2001) was proposed in the context of agricultural intercrops as an index of relative aggressiveness of species (Connolly 1986). However, it exhibits size bias in favour of larger plants in replacement designs (Connolly 1986).

Wilson (1988) introduced several uncommonly used indices such as the *competition intensity index* (CI, nr. 22), which is useable with simple additive designs. According to Snaydon (1991), the calculation of this index is invalid. Also, Wilson (1988) introduced the *competitive balance index* (CB, nr. 23), which is the logarithm of the *competitive ratio* (nr. 21) and which corresponds to values of *aggressivity* (nr. 19) above zero (Wilson 1988). A *competition index* (Ci, nr. 24, Wilson 1988) includes measures of control plants. This index was introduced for a specialized experiment, but has not been used since.

INDICES OF COMPETITIVE EFFECTS (TABLE 2)

Indices used to quantify the effects of competition on growth, reproduction or survival of plants (Table 2) characteristically reflect how plant performance is influenced by some aspect of population density or neighbour size. Hence, all of these are subject to possible problems of frequency or density dependence. Some of these indices are based on species yield per land area, and thereby provide an assessment of the

collective behaviour of a species. A clearer interpretation of competitive effect, however, is possible if these indices use some measure of yield per plant. This is because yield per land area is not independent of population density (yield/area = yield/plant \times population density). Sackville Hamilton (2001) discussed some of these indices in detail, in conjunction with their specification by yield-density relationships.

While advocating the replacement series as an experimental design for measuring competition in two species mixtures, de Wit (1960) and de Wit & Van den Bergh (1965) introduced the indices *relative yield* (RY; nr. 25a) and *relative yield total* (RYT; nr. 26). Moreover, they suggested the use of replacement diagrams as a graphic tool for the analysis of those experiments. These methods compare plant performances in mixtures and monoculture and have since been widely used (McGilchrist & Trenbath 1971; Trenbath 1976; Harper 1977; Elberse & Kruyf 1979; Mead 1979; Berendse 1982; Fowler 1982; Berendse 1983; Aarssen 1985; Firbank & Watkinson 1985; Grace 1985; Connolly 1986, 1987; Austin *et al.* 1988; Wilson 1988; Firbank & Watkinson 1990; Gurevitch *et al.* 1990; Taylor & Aarssen 1990; Snaydon 1991; Grace *et al.* 1992; Cousens & O'Neill 1993; Mynhardt 1994; Jolliffe 1997; Rösch *et al.* 1997; Hooper 1998; Loreau 1998; Wetzel & Van der Valk 1998; Jolliffe & Wanjau 1999; Jolliffe 2000; Rebele 2000; Roxburgh & Wilson 2000; Weigelt *et al.* 2000; Connolly *et al.* 2001). Keddy *et al.* (1994) used RY based on control plants (nr. 25b). Again, these approaches have been criticized (Jolliffe 2000), although the criticisms have focused more on the replacement series design than on the indices related to it.

De Wit & Van den Bergh (1965) proposed RYT (nr. 26) as an index for evaluating complementary resource use by associated species. Connolly (1987), however, described RYT as an index to quantify the extent to which species in mixture capture more resources or use the available resources more effectively than pure stands. Also, in Connolly's (1986) view, RYT can only be so interpreted when the pure stand crop yields are independent of density. Jolliffe (2000) also raised doubts as to whether RYT is an appropriate measure of complementary resource use or niche differentiation, as a single density replacement series does not specify the levels of competition present in the association. Moreover, RY is biased in favour of larger plants (e.g. Connolly 1986), although, if a plant association is given sufficient time, this bias may be overcome (Grace *et al.* 1992). RYT has often been interpreted using replacement diagrams. These may reveal (in)equality of intra- and interspecific interference, and may indicate the directions of the imbalances, but they are inadequate for the quantitative assessment of interference (Jolliffe 2000).

Two more indices were introduced by de Wit (1960) and de Wit & Van den Bergh (1965): the *relative crowding coefficient* and the *relative replacement rate* (nr. 43, Table 3), because the *relative crowding coefficient* (k_{ab} ,

nr. 27, Willey & Rao 1980; Firbank & Watkinson 1985; Connolly 1986; Rejmanek *et al.* 1989; Firbank & Watkinson 1990; Snaydon 1991; Cousens & O'Neill 1993; Connolly *et al.* 2001; Fransen *et al.* 2001) was not clearly defined by de Wit (Snaydon 1991). Several descriptions exist and the one given in Table 2 is a more general form. *Relative crowding coefficient* was thought to be a useful index for weed control planning in case the results were not dependent on overall density (Rejmanek *et al.* 1989). Others also concluded that, for density-dependent results, this index is an inappropriate measure (Harper 1977) and of limited use for intercropping (Willey & Rao 1980).

Land equivalent ratio (LER, nr. 28; Willey & Osiru 1972; Trenbath 1976; Mead 1979; Mead & Willey 1980) was introduced as an index for agricultural intercropping experiments. Its first appearance seems to be an anonymous contribution in the 1974 annual report of the International Rice Research Institute, but the study by Willey & Osiru (1972) is a clear antecedent. This index is intended to measure the amount of land required for an intercrop to be as productive as the same crop grown in monoculture (Mead & Willey 1980). As a measure of yield advantage in intercrop systems, LER is often identical to RYT, but can sometimes differ from it depending on the monoculture basis LER is calculated on (Mead & Willey 1980; Jolliffe 2000). Mead & Willey (1980) extended this concept to *effective LER* (eff. LER nr. 29), a measure of the proportions in which species can be combined to give greatest productive efficiency. Chetty & Reddy (1984) also extended the concept of LER by defining *staple LER*, in which the yield of a main component species is not allowed to drop below a minimum, and Riley (1985) further discussed the standardization of *effective* and *staple* LERs. As with some other indices (e.g. RCI discussed above) therefore, LER has been defined in several ways. This can be looked upon as a positive, in that it gives flexibility of use to an index (Mead & Willey 1980). However, it can also be argued that inconsistency in definition of an index diffuses its meaning and impedes the comparison of different studies (Jolliffe 2000).

In 1985, Aarssen proposed the *yield suppression coefficient* (YSC, nr. 30) and the corresponding ratio of two competing species, the *yield suppression ratio* (YSR, nr. 31, Aarssen 1985; Gurevitch *et al.* 1990; Taylor & Aarssen 1990; Cousens & O'Neill 1993). The difference between YSC and *relative yield* (RY, nr. 25a) lies in the density of the monoculture. For YSC the density of one species in monoculture (d_A) corresponds to the density of that species in mixture ($d_A = d_a$), while for RY the density of one species in monoculture is the same as the total mixture density ($d_A = d_a + d_b$). YSR is density dependent and will only be an accurate estimate of relative competitive ability if the yield in monoculture at density d_a approximates monoculture yield at total mixture density ($d_a + d_b$) (Aarssen 1985). In this case, however, the RY would also be applicable.

Relative monoculture response (R_m , nr. 32) and *relative mixture response* (R_x , nr. 33, Jolliffe *et al.* 1984) were introduced to separate the effects of intra- and inter-specific interference. The *relative mixture response* is the same as the RCI based on monoculture yield (nr. 2a). Jolliffe *et al.* (1984) supposed this index could be used for all species, proportions and densities, unlike, for example, the *relative crowding coefficient* (nr. 27) that was only valid for two species mixed in equal proportions. As Roush *et al.* (1989) pointed out, however, these indices assumed that density effects are direct and non-interactive.

Connolly (1987) introduced *relative resource total* (RRT, nr. 34, Connolly *et al.* 1990). It is defined as the total pure stand area required to produce the same output as the unit area of the mixture. RRT and RYT (nr. 26) both aim to measure the same thing, with the same restrictions as already discussed for RYT. However, according to Connolly (1987, 1997) RRT is not subject to the size biases that can arise in the calculation of RYT.

Relative land output (RLO, nr. 36, Jolliffe 1997; Loreau 1998; Jolliffe & Wanjau 1999; Jolliffe 2000) was developed based on an earlier, but more restricted, version, the so called *relative yield of mixtures* index (RYM, nr. 35, Wilson 1988; Garnier *et al.* 1997). Like RYT (nr. 26) and LER (nr. 28), RLO compares productivity of mixtures and monocultures. However, while RYT is calculated with constant total density in monocultures and mixtures, RLO is based on the presumption that the same land area and species populations exist in mixtures and monocultures. In contrast to RYT, RLO (and LER) were not developed to interpret interference, but simply to quantify mixture productivity (Jolliffe 2000). However, for studies that used RLO instead of RYT (or LER) it seems likely that similar interpretations of experimental findings would often have been made, because both values usually differ only by a small percentage (Jolliffe & Wanjau 1999). Contrary to relative measures (RYT, LER, RLO) the *total land output* (TLO, nr. 37, Jolliffe & Wanjau 1999) simply assesses total production by a mixture, irrespective of densities or species combinations. As relative and absolute productions are not linked, species mixtures with highest RYT, LER or RLO values do not necessarily have highest absolute productivity (Garnier *et al.* 1997; Jolliffe & Wanjau 1999). Even more than RYT and RLO, TLO is not a direct measure of competitive processes, although it may reflect, to some extent, the outcome of competition.

The *proportional deviation from an expected value* (D_i , nr. 38, Wardle & Barker 1997; Loreau 1998; Tielbörger & Kadmon 2000a) is not a single index, but rather a composite of calculations of observed and expected values that are compared. Loreau (1998) argued that, given the multitude of potential interspecific effects in mixed communities, no single measure is likely to be satisfactory for all purposes. He proposed this index as being more generally applicable than RYT

(nr. 26) and it is supposed to have equivalent properties to RLO (nr. 36).

Weiner (1982, 1984) introduced a measure of interference as part of a density-dependent model to investigate the influence of local competition on tree growth. Later, Stoll *et al.* (1994) used a similar interference measure alone as an *index of competition* (W_r , nr. 39). This index, however, is restricted to studies of competition between trees.

Bazzaz & Garbutt (1988) estimated the equivalence of *response to neighbours* (p_{ab} , nr. 40) as the difference between a species' mass in mixture and monoculture relative to the mass of their neighbours. It should be noted, however, that the denominator in this index need not be in the same units as the numerator; it can be any measure of individual performance. An unusual thing about this index is that it includes neighbour biomass, which is usually a feature of yield-density relationships or competition models. The last index in Table 2 (nr. 41, Goldberg & Werner 1983; Goldberg 1987) is a simple example of a *competition coefficient* determined from a regression of target plant performance on neighbouring plant performance, and this is related to bivariate analysis, which will be discussed later.

INDICES OF THE OUTCOME OF COMPETITION (TABLE 3)

Indices of the outcome of competition attempt to provide information on the long-term changes of the composition of plant associations. Reduced to a two-species mixture the basic question would be 'Which species gains (wins) over time?' (Connolly *et al.* 2001). The element of time is therefore an important feature, and all the indices presented in Table 3 include time as part of the calculation. It should be noted, however, that indices in Table 1 or 2 could equally follow the progress of competition if multiple determinations were made over periods of time.

Relative reproductive rate (RRR, nr. 42, de Wit 1960; de Wit & Van den Bergh 1965), the ratio of seed numbers produced by two species in mixture, was an early index introduced to describe progressive changes in mixture composition. It was developed to study interference of annual species in pastures and has not been used extensively in recent times. Subsequently, de Wit & Van den Bergh (1965) introduced *relative replacement rate* (RRR II, nr. 43, de Wit & Van den Bergh 1965; Harper 1977; Elberse & Kruyf 1979), an index compounded from the relative yields of the associated species, that was intended to account for changes occurring across a sequence of multiple harvests.

Based on a similar idea, Connolly (1987) introduced *relative efficiency index* (REI, nr. 44) and *cumulative efficiency index* (REIc, nr. 45) to study the efficiency of one species relative to another in a mixture over a time interval (Connolly 1987; Grace *et al.* 1992; Grace 1995; Jolliffe 2000). Adding to this concept, Grace (1995)

proposed the *expected relative efficiency index* (REI_{exp} , nr. 46), and took the comparison of expected REI to normal REI to indicate effects of competition on mixture dynamics.

According to Sackville Hamilton (2001), both RRR and REI are effectively the same, except that they are based on different response variables. Moreover, both indices vary with density and frequency of the species in the mixture, which must be taken into account when interpreting the results. At least REI, however, has been shown to be size independent, thus eliminating the bias occurring when interpreting species of different sizes that occurs with RY and RYT (nr. 25a, 26; Grace *et al.* 1992; Jolliffe 2000).

The *removal response coefficient* (C_{ab} , nr. 47, Silander & Antonovics 1982) used control plants, growing without or with only few competitors, for the calculation of competitive outcome. It was designed for removal experiments in the field and is used to compare a series of measurements over time.

Other measures were developed for community level processes. These are the *relative abundance* of species in monocultures (RA_{mono} , nr. 48a) and mixtures (RA_{mix} , nr. 48b), and their subsequent combination to *absolute* (D, 48c) or *proportional differences in relative abundance* (PD, nr. 48d, Goldberg 1994; Greiner la Peyre *et al.* 2001). To obtain an overall index of change in community composition due to interspecific interactions, the absolute values of the difference or proportional difference in relative abundance over all species have to be summed. Apart from the monocultures, this approach requires an additive mixture of all the species grown together.

OTHER MEASURES

Additional measures of plant competition are available through the functional analysis of yield-density relationships and neighbourhood analysis. These two approaches directly assess how plants respond to crowding, or proximity of neighbours. Here, we will briefly outline the measures these approaches provide, but will not consider broader aspects of these approaches or their applications.

At the population level, competition can be measured through the coefficients of yield-density relationships. Efforts to develop these relationships began with Kira and his associates in the 1950s and early research was reviewed by Willey & Heath (1969). Papers by Wright (1981) and Spitters (1983) provide early examples of their use with species mixtures and explain the principles of how these relationships can be used to quantify intraspecific and interspecific components of plant competition. Since then different types of relationships have been used and compared (e.g. Cousens 1985; Firbank & Watkinson 1985; Law & Watkinson 1987; Turkington & Jolliffe 1996; Jolliffe 1997; Inouye 2001). Yield-density relationships require experimental designs where species population densities are

independently varied. Monoculture control plots are not required in such designs, but have commonly been included. The models express how plant performance declines with crowding; the coefficients on the density terms are indices of competitive effect because they measure the effect of crowding. These relationships have usually been used for two-species associations, but can be expanded to address multispecies systems.

Yield-density relationships have usually been found to have high coefficients of determination (R^2) when applied to data from plants growing in competitive situations (Jolliffe 1997). Coefficients of determination express the fraction of variation in plant performance that is related to variation in species population density, and therefore they measure the *importance of competition* (IC). This follows the concept introduced by Welden & Slauson (1986), who used the index $IC = SS_{\text{factor}} \times SS_{\text{total}}$ (after multivariate ANOVA with $SS =$ sums of squares; see also: McLellan *et al.* 1997; Sammul *et al.* 2000). Statistical measures were also exploited by Wagner & Radosevich (1998), who used the *relative mean squared residuals* ($RMSQR = 1 - \text{adj. } R^2$), as an index of competition intensity.

Instead of relating the performance of each species to population densities, interrelationships in the performances of target and companion species can be evaluated graphically, as in bivariate analysis (e.g. Mead 1979; Snaydon & Satorre 1989; Vandermeer 1989). Bivariate analysis has not been widely used, but it offers a way to assess how the biomass accumulation (or other measure of performance) of one species responds to biomass accumulation in a companion species.

Apart from these population level assessments, an understanding of competition is also achieved through the detail available from observations of individuals. Size hierarchy, as shown by the frequency distribution of plant size, is an indication of the tendency for individuals to be dominant or subordinate in a population. Large and small individuals may compete symmetrically or asymmetrically. In a model approach, Connolly & Wayne (1996) proposed an index of interspecific competitive asymmetry. Graphical analysis and measures of *skewness* and inequality of distribution as indicated by the *Gini coefficient*, have been used to distinguish between two modes of plant competition: resource pre-emption and resource depletion (e.g. Weiner & Thomas 1986; Weiner 1990; Newton & Jolliffe 1998).

Size distribution analysis is often coupled with neighbourhood analysis, which explores competition on the basis of the proximity, or size and spatial relations, of neighbouring plants. *Proximity indices* attempt to characterize the competitive neighbourhood of a target individual, on the basis of the nearness and sizes of neighbours in relation to the size of the target plant. They have proved particularly useful in long-lived, heterogeneous associations, such as forest associations, that can be difficult to address using

other techniques. We have not done a comprehensive search for proximity indices, but examples are found in Mack & Harper (1977), Ford & Diggle (1981), Weiner (1984), Silander & Pacala (1985), Biging & Dobbertin (1992), Newton & Jolliffe (1998) and Nienaber (1999), and the latter three papers compare several proximity indices.

In attempting to characterize both spatial relationships and plant densities, researchers are eventually challenged by complex issues of how to quantify the way plants occupy and exploit their environments. It is a simplification to use measures such as distances between stems, or areas per plant, in the many cases where neighbouring plants are largely mingled and growing in the same zones. Such simplification is commonly present, directly or indirectly, in most of the indices and approaches covered in this essay. Researchers have already worked towards greater sophistication in how plant presence is represented in both space and time, such as through the use of tessellation patterns, and this avenue of work needs to be advanced in the future. It is also important to appreciate that different approaches to the assessment of competition can often be combined. For example, Purves & Law (2002) recently developed models that combine aspects of bivariate analysis, neighbourhood analysis, proximity analysis and plant growth analysis, and tested their application in *Arabidopsis thaliana* monocultures.

Conclusion

Competition indices are widely used and have proved useful for interpreting and summarizing the intensity, effect and outcome of plant competition. We hope this essay will make researchers aware of the diversity of competition indices that are available and help them to choose indices that are suitable to their needs. In making such selections, researchers should be aware that indices have potential flaws, such as density dependence, size bias and dependence on experimental design.

Being derived from experimental observations, competition indices are primarily tools of analysis, not prediction. The existence of such a large number of competition indices begs the question as to whether all are necessary, and whether the list could be culled to a few indices that researchers might regularly rely upon. This would bring more coherence to the literature and simplify comparisons of different studies. In effect, such culling has already occurred as some indices have not been adopted into widespread use (e.g. *relative reproductive rate*, *relative monoculture* and *mixture responses*). Other indices, used more frequently in early studies of competition, are now seldom employed (e.g. *aggressivity*, *relative crowding coefficient*).

Apart from this 'natural' selection process, the recommendation of the 'best' indices will hardly find universal agreement, and we know of no index that is without some limitation. Clearly an ideal index would offer several potential benefits, be applicable to several

different aspects of competition, and possess a number of important qualities. We think it unlikely that any one index will be optimal for all of these properties. For example, an index that is an excellent but specialized measure is unlikely to be versatile.

Having said this, some indices might still be more appropriate to the majority of current studies than others. To quantify the intensity of competition, we listed a number of very similar indices (Table 1: 2a–18), of which the RCI (nr. 2b) is most widespread in use. In its modified versions, RNE (nr. 5) and ln RR (nr. 17), this type of index might often be a good choice depending on the experimental settings. For studies of the effect of competition, relative yield (nr. 25b) offers simple and easily interpretable comparisons of how a component species performs in mixtures and controls (e.g. mixtures vs. monocultures in agricultural settings). For binary mixtures RYT and LER (nr. 26 and 28) are similar and have been widely used. However, we suggest that RLO (nr. 34) should be used in their place, because it is applicable to multispecies associations and it compares mixtures with monocultures having similar populations and land areas. Additionally, RRT (nr. 34) provides a different type of assessment of the effect of competition, with less complexity than RYT, LER and RLO, and it is less subject to size bias. For studies aiming to quantify the outcome of competition, there don't seem to be convincing reasons to recommend one index over the others. Applying several related equations as REI or RA (Table 3: 43–45, 47a–d) might be one possibility to solve this problem, but yield-density models and neighbourhood analysis are more promising tools in this context.

It is certainly possible and sometimes desirable to use several indices in a study, particularly when more than one attribute of competition is being investigated. For example, Goldberg *et al.* (1999) recommended the use of multiple indices to determine the robustness and reproducibility of patterns. On the same theme, Jasienski & Bazzaz (1999) adopted multivariate analysis of variance of correlated variables as it is a more powerful approach than multiple univariate tests on ratios of the variables.

If existing competition indices have limitations and imperfections, then perhaps they might be improved upon. One approach that could be taken to do this is to develop indices that better represent competition as a process that occurs in space and time. At present, plant competition indices tend to be based on land area (population density) or interplant distances (proximity). The presence of environmental resources, the way plants occupy the environment, and the way plants compete for resources are, however, not usually one- and two-dimensional issues, and are not static over time. Hence, a more explicit consideration of how competition changes with environments, and the concept of resource supply and demand (Taylor *et al.* 1990; Davis *et al.* 1998), might form a theoretical framework to develop indices of broader applicability.

Despite the lengthy history of studies on plant competition, we know more of its consequences than its processes. It is revealing that the indices presented here tend to deal with plants as they stand at the end of some competitive episode. This does not directly evaluate the events, activities and mechanisms involved as plants compete for environmental resources. If we are to appreciate competition as a process, and learn its rules, we suggest that competition indices be used to track the progress and results of competition over time, in different kinds of plant associations, and under different environments.

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