FORUM

What evidence is necessary in studies which separate root and shoot competition along productivity gradients?

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Introduction

The experimental study of plant competition has led to substantial disagreements on numerous issues (e.g. Keddy 1989; Grace & Tilman 1990; Grime et al. 2001). Resolution of the related methodological debates, with an emphasis on achieving better concordance between experimental design and the specific questions of interest, should allow for an improved understanding of the role of competition in natural communities (sensu Connolly et al. 2001). Field studies which isolate either or both of root and shoot competition are often initiated to determine whether the strength of the two competitive forms varies along an environmental gradient (e.g. Wilson & Tilman 1991, 1993; Belcher et al. 1995; Twolan-Strutt & Keddy 1996; Peltzer et al. 1998; Cahill 1999), and whether they interact in a non-additive manner (e.g. Dillenburg et al. 1993; Cahill 1999).

Among the issues raised in debate over appropriate methodologies for such studies (Grubb 1994; Cahill 1999; McLellan et al. 2000), are (i) whether we need full separation of above- and below-ground interactions between neighbouring plants to obtain accurate measures of the relative importance of root and shoot competition, and (ii) whether we must measure responses to such competition in both above- and below-ground plant parts. In other words, does the experimental act of separating root and shoot interactions necessitate a more complex approach and set of data than is considered adequate in studies that simply manipulate the presence of whole plant competitors?

If we are interested in root and shoot competition, our first reaction to both these issues might be ‘yes’, but are these obvious answers necessarily correct? Depending upon the specific questions being tested, using above-ground responses (e.g. shoot biomass) to measure root competition may be no worse than the common practice of using above-ground responses to measure the combined effects of root and shoot competition (e.g. Reader et al. 1994; Berkowitz et al. 1995; McLellan et al. 1997; Emery et al. 2001; Foster 2001; Howard & Goldberg, 2001). I will argue that, in some situations, using total plant biomass to estimate the effects of root competition may actually be less accurate than measures of shoot biomass alone.

Field studies that isolate root or shoot competition generally involve the manipulation of neighbours around focal individuals (e.g. root exclusion tubes and tying back neighbouring shoots Casper & Jackson 1997; McPhee & Aarsen 2001). The underlying idea is that differences in individual growth can represent either the intensity of competition in the community (e.g. Twolan-Strutt & Keddy 1996), or the competitive response of different species (e.g. Wilson & Tilman 1995; Cahill 1999; Howard & Goldberg 2001).

To obtain independent measures of root competition, shoot competition, and their combined effects (full competition), plants grown with the roots but not shoots of neighbours (RN), the shoots but not roots of neighbours (SN) and with both neighbour roots and shoots (AN – all neighbours) are compared with those grown with no neighbours (NN). The SN treatment is, however, omitted from most studies, with the strength of shoot competition estimated as the difference between full and root competition, i.e. assuming an additive interaction between competitive forms (e.g. Wilson & Tilman 1991, 1993; Belcher et al. 1995; Twolan-Strutt & Keddy 1996; Peltzer et al. 1998; Emery et al. 2001). In an alternative approach, the neighbouring canopy is left intact and focal plants are grown with and without soil partitions (or trenches), and any difference between treatments is assumed to represent a measure of root competition (e.g. Coomes & Grubb 1998; Gersani et al. 2001). These two latter designs assume root and shoot competition are discrete processes, with one not altering the strength of the other. However, root competition can increase the strength of shoot competition by compounding the negative effects of asymmetric competition for light (Dillenburg et al. 1993; Cahill 1999) and the combined effects of root and shoot competition can be less than the sum of their independent effects (see review of glasshouse studies by Wilson 1988). If root and shoot competition do interact in their effects on plant growth, then measuring the strength of one competitive form will require their experimental separation.

Insisting on such separation greatly increases the complexity of experimental designs and imposes serious logistic impediments. Assuming the number of plots used in a single field study is fixed (due to limitations of
WHAT DATA NEEDS TO BE COLLECTED FROM THE FOCAL PLANTS?

In field experiments, it is often assumed that the reduced plant growth due to competition causes a reduction in reproduction, and thus recruitment, population size and, finally, relative abundance, so that the measured growth response of individual plants can be taken as a proxy for either the strength of competition in the community, or the competitive ability of a species. This is an awfully large set of extrapolations to take from simple growth measures. It is also important to keep separate the concepts of what we generally actually measure (short-term effects of species interactions) and what we hope to infer (long-term performance of a species) (Gibson et al. 1999). Nevertheless, there is evidence that short-term effects of competition can correlate with abundance in the field (Gaudet & Keddy 1992; Howard 2001; Howard & Goldberg, 2001). For example, when the effects of neighbouring plants on the germination, survival, seedling and adult growth of several plant species were measured in the field, changes in seedling shoot biomass (reflecting short-term effects of competition) were among the best predictors of a species’ relative abundance (Howard & Goldberg 2001). This raises the important question of whether the underlying logic of focal plant studies changes with the type of competition being measured, i.e. must one measure both root and shoot responses of focal plants in studies which separate root and shoot competition? I argue ‘no’, based upon both theoretical and practical considerations.

Practical considerations

Difficulty in extracting roots is often stated as a reason why only shoot growth is reported (e.g. Reader et al. 1994; McLellan et al. 1997). Roots regularly break as focal plants are dug out and washed from the soil, with the exact proportion of the root system recovered (‘extraction efficiency’) varying among soil types, root system morphologies (e.g. taproot vs fibrous), and researchers. It is unlikely that increased allocation of time and money to extraction will ever fully eliminate this loss. Similar loss does not exist for measures of shoot biomass, and thus measures of focal plant shoots are inherently more accurate than those of roots. It is important to note that harvesting plants at a single point in time excludes any tissues which have already senesced, and thus standing biomass is itself only a proxy for ‘true’ root biomass but, because their biomass is highly correlated with stem biomass (e.g. Casper et al. 1998), measuring focal plant roots may provide little additional information compared to shoot data alone. Furthermore, large roots are less important in terms of uptake than fine roots, most of which may be excluded from measures. The ecologically relevant information obtained is therefore reduced, particularly if a factor of interest (e.g. mycorrhizal infection) can differentially affect fine root abundance (Hodge et al. 2000).
A more substantial concern is the fact that the methods used to isolate root competition may themselves influence one’s ability to extract the root systems of focal plants. Measures of root competition require plants to be grown both with and without the roots of neighbours. Regardless of how neighbour roots are manipulated, some focal plants will have their root system in soil free from neighbouring roots, where extraction efficiencies will be higher than when roots are intertwined with those of neighbours, and are more likely to break off when removed from the soil. Even if the ‘true’ root biomasses were the same, we should recover less root biomass in plants grown with root competition than those grown without root competition. The degree of entanglement likely varies as a function of neighbour root density, and if this varies along the gradient of interest, measured root : shoot ratios may shift even if there is no biologically important basis.

Extraction efficiency may also vary due to the effects of neighbour roots on focal plant size. Neighbouring roots decrease target plant size (e.g. Jones et al. 1989; Cahill & Casper 2000), which is itself related to root system architecture. Larger plants tend to have thicker, heavier roots, reflected as decreased root length per unit root biomass and a decreased number of root tips per unit root biomass relative to smaller plants (Bernston et al. 1997; Casper et al. 1998). We will therefore have higher extraction efficiencies for the larger plants grown without competition (thicker roots) than from smaller plants grown with competition. Such recovery errors violate a primary assumption of the use of proxies to measure competition: that the relationship between proxy and process does not vary between treatments of interest.

It may seem that the only way to avoid these biases would be to dig up large volumes of soil around each plant, meticulously separating the entangled root systems. However, unless such accuracy in determining root biomasses is necessary to obtain a proxy measure of competitive outcome, we may find ourselves spending ever more effort to collect below ground data, only to reduce our accuracy in measuring the strength of competition. For example, suppose we have two experimental treatments, plants grown with no neighbours (NN) and plants grown with only the roots of neighbours (RN). Assuming that ‘true’ root biomass is directly proportional to shoot biomass and that entanglement and/or size bias reduces the extraction efficiency of the roots of RN plants (whose shoot biomass is smaller), then we would measure a lower proportion of the true total biomass of the RN than NN plants. The actual strength of root competition would thus be overestimated. No such bias would occur between the SN and NN treatments, neither of which has root interactions with neighbours, allowing for an accurate estimate of shoot competition. Our ability to determine how the relative importance of root and shoot competition varies with productivity is thus compromised.

Final comments

In a perfect world, such mundane practicalities would not be an issue. We would easily be able to separate root and shoot interactions fully and extract (or image) full root systems in the field. Even better, we would not need such proxy measures and could measure competitive outcomes directly. However, this is not a perfect world. I believe the current debate about these issues stems from not clearly differentiating between the data needed to answer a particular question, and what data would be wanted were we to address related questions. To measure how the strength of root competition varies along some gradient we need a measure of root competition – either direct or by proxy. To determine how plant allocation varies in response to competition along that gradient we also need detailed and accurate measures of root and shoot growth of the focal plants. Such data, although essential for addressing some very interesting questions, may be both unnecessary and impractical for productivity–competition studies that often have on the order of 500 focal plants.

Nonetheless, there do remain compelling reasons why one should measure root biomass in competition studies. For instance, if competition results in a shift in allocation within a plant, but not in total biomass, measuring only shoot biomass would give an equally inaccurate estimate of competition. However, it is important to note that even the long-standing assumption that plants exhibit the plastic response of increased allocation to roots under nutrient stress is being challenged (Muller et al. 2000). Current analyses suggest that the observed patterns are more a function of allometry (smaller plants have higher R:S ratios) than an example of plasticity (Muller et al. 2000). Understanding allometric and plastic responses to root competition is essential to a mechanistic understanding of plant–plant interactions, and will require an extremely precise set of root extractions. At this point we do not know how common below ground responses are, and are left needing to choose between a clear bias in extraction efficiency or a potential bias due to allocation shifts. Although this is not a particularly attractive situation, it is unlikely to have a universal or straightforward solution.

There are exceptions to these general problems of extraction efficiency. Focal species and community type will vary in ease and accuracy of extraction. Communities with low root biomass, either naturally or through manipulation (e.g. tillage), are likely to have higher extraction efficiencies than productive, grass-dominated systems. Similarly, species that tend to form larger roots should be more efficiently extracted than those with mostly fine roots. Although it should be left to the individual researcher to decide the validity of these concerns in their specific systems, it would be unreasonable to make a blanket assumption that they do not exist, particularly when research is conducted along gradients and/or with several species.
If we hope to understand the long-term effects of root and shoot competition on community structure, we should not hold these studies to a higher standard than we hold studies which simply document the full effects of neighbours on target plant growth. The issue of whether to accept the use of shoot biomass as a proxy for root competition should be dependent upon whether one believes that is a sufficient proxy for the overall effect being measured. If one rejects that idea, then one should rightly reject all studies that use short-term shoot measures as a proxy for long-term competitive outcomes, not only those which isolate above and below ground interactions.

My main goal in this paper was to present the argument that, for some studies involving roots, increasing the amount of data collected can decrease the accuracy of the results. The idea that increased data collection may decrease accuracy has not been widely discussed amongst ecologists, with the standard view appearing to be that more is better (but see Cahill et al. 2001). I have not attempted to provide a solution to our methodological problems, but instead have tried to raise several points to encourage a more public debate about what we as scientists believe constitutes sufficient evidence. I suggest here that the methodological limitations that can result in such trade-offs need to be carefully considered in the design of future studies, and in the interpretation of prior work.

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The necessary evidence of competition

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