

Root–shoot growth responses during interspecific competition quantified using allometric modelling

David Robinson^{1,*}, Hazel Davidson¹, Clare Trinder¹ and Rob Brooker²

¹Institute of Biological and Environmental Sciences, School of Biological Sciences, University of Aberdeen, Aberdeen AB24 3UU, UK and ²The Macaulay Land Use Research Institute, Craigiebuckler, Aberdeen AB15 8QH, UK

* For correspondence. E-mail david.robinson@abdn.ac.uk

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- **Background and Aims** Plant competition studies are restricted by the difficulty of quantifying root systems of competitors. Analyses are usually limited to above-ground traits. Here, a new approach to address this issue is reported.
- **Methods** Root system weights of competing plants can be estimated from: shoot weights of competitors; combined root weights of competitors; and slopes (scaling exponents, α) and intercepts (allometric coefficients, β) of ln-regressions of root weight on shoot weight of isolated plants. If competition induces no change in root : shoot growth, α and β values of competing and isolated plants will be equal. Measured combined root weight of competitors will equal that estimated allometrically from measured shoot weights of each competing plant. Combined root weights can be partitioned directly among competitors. If, as will be more usual, competition changes relative root and shoot growth, the competitors' combined root weight will not equal that estimated allometrically and cannot be partitioned directly. However, if the isolated-plant α and β values are adjusted until the estimated combined root weight of competitors matches the measured combined root weight, the latter can be partitioned among competitors using their new α and β values. The approach is illustrated using two herbaceous species, *Dactylis glomerata* and *Plantago lanceolata*.
- **Key Results** Allometric modelling revealed a large and continuous increase in the root : shoot ratio by *Dactylis*, but not *Plantago*, during competition. This was associated with a superior whole-plant dry weight increase in *Dactylis*, which was ultimately 2.5-fold greater than that of *Plantago*. Whole-plant growth dominance of *Dactylis* over *Plantago*, as deduced from allometric modelling, occurred 14–24 d earlier than suggested by shoot data alone.
- **Conclusion** Given reasonable assumptions, allometric modelling can analyse competitive interactions in any species mixture, and overcomes a long-standing problem in studies of competition.

Key words: Allocation, allometry, competition, dry weight, *Dactylis glomerata*, growth, modelling, *Plantago lanceolata*, root, shoot, whole-plant.

INTRODUCTION

Adjustments in root and shoot growth are often assumed to be a fundamental facet of a plant's phenotypic plasticity in response to its environment. Such adjustments can be simple ontogenetic correlates of size or growth rate and do not necessarily represent adaptive responses to compensate for resource limitations imposed on a plant by its environment, including by its neighbours (Reich, 2002). An alternative view is that relatively greater root growth in response to shortages of nutrients or water could maximize a plant's probability of capturing those resources, especially if a competitor fails to respond to a comparable extent. Such responses will, therefore, be associated ultimately with increased fitness; likewise, greater leaf and/or stem growth would be expected to occur if light or CO₂ is limiting. This is the 'functional equilibrium' (Brouwer, 1962) or 'balanced growth' (Davidson, 1969) hypothesis, which is supported by some experiments (Shipley and Meziane, 2002; Berendse and Möller, 2009), but criticised elsewhere for being over-simplistic and failing to explain or predict many observed responses (Farrar and Gunn, 1998; Poorter and Nagel, 2000; Reich, 2002; Müller

et al., 2000). Yet another theory (Enquist and Niklas, 2002) considers the global biophysical constraints on biomass partitioning by individual plants within which the responses of all species are expected to fall. But whatever its detail, the general idea of shifts in growth allocation patterns remains embedded in standard explanations of how different plant species can compete and coexist.

One difficulty faced by any explanatory framework attempting to integrate the responses of root and shoot growth with a plant's competitiveness is the mundane but intractable one of estimating the root growth of competing individuals growing in soil (Cahill, 2002; Zobel and Zobel, 2002). It is difficult to separate the entangled roots of neighbouring plants unless they are very small or only a small portion of each root system is sampled (Robinson et al., 1999). If C₃ and C₄ species are grown together, there is the possibility of using the distinct ¹³C natural abundances of those species to partition the combined root mass of the competitors once it has been extracted from the soil (Wong and Osmond, 1991). An inert, porous material such as Turface, supplemented by frequent additions of nutrients and water (Gurevitch et al., 1990), can

act as a growth medium that minimizes entanglement of multiple root systems, allowing their relatively easy manual separation (J. Gurevitch, Stony Brook University, New York, pers. comm.). Species-specific biochemical (Roumet *et al.*, 2006) and molecular (Mommer *et al.*, 2008) markers have been used to quantify the relative amounts of material contributed by each species to multi-species root mixtures, but are expensive to apply routinely. Plant competition studies on soil-grown plants must otherwise restrict their analyses to above-ground data such as shoot growth or, where possible, seed production. Below-ground responses to competition, and their relationship to those above ground, have largely resisted detailed investigation.

Here, an allometric modelling approach is developed and used to estimate the root weights of competing individuals of two species. To do this, root and shoot growth of isolated plants is compared with that of competing plants. Measured species-specific root–shoot allometries of isolated plants are first applied to the competitors, the null hypothesis being that the presence of neighbours induces no allometric changes from those expressed when growing alone. If that null hypothesis is true, the combined root mass of the competing plants, which can be measured, will equal the combined root mass estimated allometrically from the separate shoot weights of each competitor, which can also be measured. Therefore, the combined root mass can then be partitioned directly among the competitors according to the allometries of the isolated plants.

If, however, the null hypothesis is rejected and the presence of neighbours causes shifts in relative root and shoot growth, the combined root mass of the competing plants will not equal that estimated allometrically from the shoot weights of the competitors and, obviously, the isolated-plant allometries cannot then be applied directly to competitors. The problem is then to estimate the allometries of the competing plants. This can be done by incrementally adjusting the isolated-plant allometries until the estimated combined root masses of competitors, obtained by again using their measured shoot weights, agrees with the measured combined root mass (hence ‘allometric modelling’). The resulting allometric parameters estimated for each competitor will then be consistent with the measured total amount of root produced. These parameters can then be used to explore the root–shoot interactions of the competitors.

This approach is illustrated using an experiment involving two herbaceous species common in the British Isles, *Dactylis glomerata* and *Plantago lanceolata*.

MATERIALS AND METHODS

Theory

For a young herbaceous plant, the allometric variation in its root weight (R) can be described as a simple power function of its shoot weight (S):

$$R = \beta S^\alpha \quad (1)$$

where α is the scaling exponent and β the allometric coefficient. A linear version of eqn (1) is obtained by

ln-transformation:

$$\ln R = \ln \beta + \alpha \ln S \quad (2)$$

(Niklas, 1994, p. 16). α is the ratio of root and shoot relative growth rates (Hunt and Nicholls, 1986). For isometric growth, $\alpha = 1$, and root and shoot weights increase in the same proportion. When $\alpha > 1$, root growth disproportionately exceeds that of the shoot, and when $\alpha < 1$, the opposite is true. The allometric coefficient (β) has no clear physiological definition, but variations in β can cause differences in root : shoot ratio even if α is constant (Farrar and Gunn, 1998). Instantaneous root : shoot ratio depends, therefore, on both α and β .

If two plants, A and B, compete, each will express its own root : shoot allometry as manifested in the α and β values it attains, and which may not necessarily be the same as those when A and B are grown alone. When A and B compete, their combined root weight (R_C) is the sum of their individual root weights ($R_A + R_B$) but, in practice, neither R_A nor R_B can be measured directly. But R_C should be resolvable into its allometric components since, from eqn (1),

$$R_C = R_A + R_B = \beta_A S_A^{\alpha_A} + \beta_B S_B^{\alpha_B} \quad (3)$$

where the subscripts A and B denote the two species. S_A and S_B are the measured shoot weights of the species when competing. R_C estimated by eqn (3) must equal the measured combined root weight (R_M) of A and B when competing. In R_C and $\ln R_M$ should therefore be related via a linear regression of the form

$$\begin{aligned} \ln R_C &= \ln(R_A + R_B) = \ln(\beta_A S_A^{\alpha_A} + \beta_B S_B^{\alpha_B}) \\ &= b + a \ln R_M + \varepsilon \end{aligned} \quad (4)$$

in which the slope (a) and intercept (b) should equal 1 and 0, respectively, and ε is the estimation error. The problem is to estimate α and β values of A and B to satisfy eqn (4) subject to this constraint. Once estimated, these α and β values can be used with measured values of S_A and S_B to derive corresponding estimates of R_A and R_B . The estimation procedure is described below under ‘Data analysis and allometric modelling’.

Experiment

Seeds of *Dactylis glomerata* and *Plantago lanceolata* were germinated in plug trays of John Innes seedling compost in a controlled environment chamber at 16 °C with 12 h of supplementary lighting per day. After 3 weeks, seedling plugs were transferred to 10-cm-diameter pots containing sieved, low-nutrient agricultural topsoil (sandy loam, pH 5.5). One individual plant or two (one of each species) were planted in each pot. Pots were placed under supplementary lighting (12 h per day) in a glasshouse maintained at 16 °C. All pots were watered with Phostrogen all-purpose general fertilizer at regular intervals. No attempt was made to impose conditions favouring either above- or below-ground competition. Leaf canopies were not screened; nor were root systems separated

by barriers (cf. Donald, 1958). Twenty destructive harvests were taken at 3- or 4-d intervals from 10 to 76 d after sowing. Each plant combination was replicated three times. At each harvest, shoots were removed and roots washed from the soil. The intermingled roots of competing plants were not separated but treated as composite samples. All harvested material was oven-dried at 80 °C for 48 h prior to weighing.

Data analysis and allometric modelling

Reduced major axis (RMA) regressions (Niklas, 1994, p. 331) of ln-transformed root and shoot dry weights of isolated plants yielded estimates of α and β for *Dactylis* and *Plantago* when grown alone. (RMA, or Model II, regressions are identical to the first axis of a principal components analysis.) These values of α and β were substituted into eqn (3) along with corresponding measured shoot dry weights to derive initial estimates of R_A , R_B and, therefore, of R_C for competing plants.

In R_C was regressed on $\ln R_M$ (eqn 4) using data from all 60 plants. If the resulting slope (a) and intercept (b) of that regression differed from 1 and 0, respectively, the initial values of α and β (i.e. those estimated for isolated plants) for *Dactylis*, *Plantago* or both were adjusted incrementally and simultaneously until $a = 1.0 \pm 0.0001$ and $b = 0.0 \pm 0.0001$. The resulting α and β values of the two species were then, by necessity, consistent with those expressed by competing individuals of the two species in that the estimated combined root weights of the competitors (R_C) matched those measured in the experiment (R_M). Those allometries were then used to estimate the root dry weights of competitors at each harvest and, along with the measured shoot dry weights, the corresponding root : shoot ratios, using eqn (1).

RESULTS

The roots and shoots of both species grew approximately isometrically when in the absence of neighbours, increasing in dry weight by up to four orders of magnitude during the experiment. Confidence limits on the estimates of the scaling exponent (α) of *Dactylis* bracketed a value of 1, just below the lower 95 % confidence limit for the α estimate of *Plantago* (Table 1). Allometric coefficients (β) for the two species differed; β of *Dactylis* significantly exceeded that of *Plantago* ($P < 0.05$).

The linear regression of $\ln R_C$ on $\ln R_M$ had a slope (a) and intercept (b) significantly different from 1 and 0, respectively,

TABLE 1. Root : shoot allometries of *Dactylis glomerata* and *Plantago lanceolata* when growing alone

Species	α	β	n	R^2
<i>Dactylis glomerata</i>	0.989 (0.948–1.10)	0.544 (0.423–0.698)	60	0.974
<i>Plantago lanceolata</i>	1.05 (1.01–1.09)	0.349 (0.272–0.448)	60	0.978

α and β are the scaling exponent and allometric coefficient, respectively (eqn 1) estimated from RMA regressions of \ln root dry weight (mg) on \ln shoot dry weight (mg).

Numbers in parenthesis are 95 % confidence limits on the estimates of α and β .

these values falling outside the 95 % confidence limits of each parameter (Fig. 1). Therefore, the combined root dry weights of competitors could not be predicted simply by applying the allometric statistics obtained for *Dactylis* and *Plantago* growing alone. It follows that the root : shoot allometries of *Dactylis*, *Plantago* or both were not necessarily the same when these plants competed as when they grew alone.

The α and β estimates for competing *Dactylis* and *Plantago* were adjusted from their initially assumed values – those obtained from Table 1 for isolated plants – in three ways. (1) Only *Dactylis* was assumed to respond to competition, *Plantago*'s α and β values remaining unchanged from those it expressed when growing alone. Consistency between R_C and R_M was possible if *Dactylis* increased its β value significantly in response to competition (Table 2); no significant change in α was necessary. (2) When only *Plantago* was assumed to respond to competition, a significant increase in its α and a significant decrease in β were required to match R_C with R_M . (3) When both species were assumed to respond allometrically to competition, the changes in α and β required for R_C and R_M to agree were all within the 95 % confidence limits of those of isolated plants (cf. Table 1). This assumption predicted the smallest allometric responses to competition and, on that basis, is the most conservative of the three. Therefore, attention is here confined to the implications of that assumption.

α and β values derived for competing plants (Table 2), together with measured shoot weights of those plants, were used to estimate root dry weights of plants at each harvest. From these, harvest-specific values of the root : shoot ratio ($R:S$) were derived. When grown in isolation, *Dactylis* maintained a mean measured $R:S$ of 0.544 (0.471–0.618, 95 % CL) and *Plantago* of 0.504 (0.442–0.566). Although α and β values were not statistically different between isolated and competing plants (Table 2), they were nevertheless sufficient to generate contrasting $R:S$ responses of the competitors as

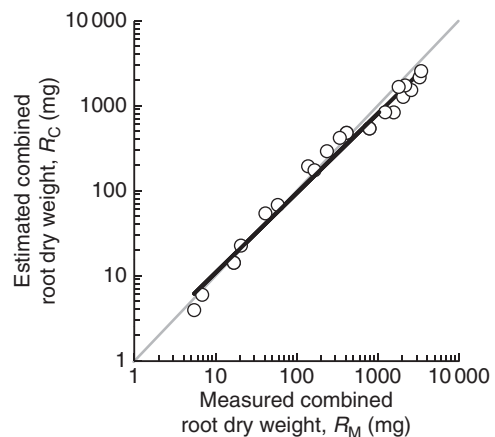


FIG. 1. Combined root dry weights (R_C) of competing *Dactylis glomerata* and *Plantago lanceolata* estimated from the allometries obtained for isolated plants (Table 1) and the measured combined root weights of the two species when growing together (R_M). Each symbol represents a separate harvest and is the mean of three replicates. The bold line is the linear regression of \ln -transformed data (cf. eqn 4): slope = 0.935 (0.874–0.996, 95 % CL), intercept 1.26 (0.875–1.82), $R^2 = 0.982$, $n = 20$. The grey line is the 1 : 1 relationship (slope = 1, intercept = 0).

TABLE 2. Root : shoot allometries of *Dactylis glomerata* and *Plantago lanceolata* when growing together

Responding species	Species	α	β	n	R^2
<i>Dactylis glomerata</i> only	<i>Dactylis glomerata</i>	1.027	0.822*	60	0.977
<i>Plantago lanceolata</i> only	<i>Plantago lanceolata</i>	1.222*	0.167*	60	0.973
Both	<i>Dactylis glomerata</i>	1.077 (1.076–1.078)	0.543 (0.540–0.545)	60	0.976
	<i>Plantago lanceolata</i>	1.035 (1.031–1.040)	0.286 (0.283–0.290)		

α and β values are the adjusted scaling exponents and allometric coefficients, respectively (eqn 1). These were derived by adjusting α and β from their initial values measured in isolated plants (Table 1) until linear regressions of ln-transformed estimated combined root weights (R_C , mg) on measured ln-transformed combined root weights (R_M , mg) produced values of $a = 1.0 \pm 0.0001$ and $b = 0.0 \pm 0.0001$ (eqn 4); the resulting R^2 values of those regressions are also shown.

Allometric responses to competition were assumed for *Dactylis* alone, *Plantago* alone, or both species. When no response was assumed, the α and β values were those shown in Table 1 for isolated plants.

Asterisked α and β values are those that differed significantly ($P < 0.05$) from those expressed by isolated plants (Table 1); other values were not significantly different from those in Table 1.

Numbers in parenthesis are the 95 % confidence limits of repeated ($n = 10$) independent estimates of α and β when both *Dactylis* and *Plantago* were assumed to respond, to illustrate the accuracy of the numerical estimation procedure.

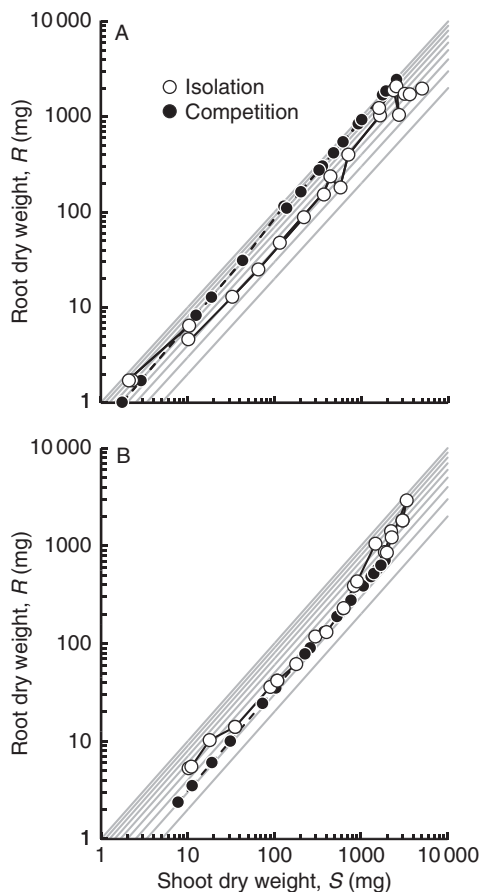


FIG. 2. Root and shoot dry weights of (A) *Dactylis glomerata* and (B) *Plantago lanceolata* grown in isolation or competing with each other, as indicated. Root weights of competitors were derived from the allometric modelling of combined root weights measured in the experiment, assuming that both species responded allometrically to competition (Table 2). Each symbol represents a separate harvest and is the mean of three replicates. α and β values for isolated plants are given in Table 1; those for competitors, in Table 2. Diagonal grey lines show constant root : shoot ($R:S$) ratios from $R:S = 0.2$ (the lowermost) to $R:S = 1$, in 0.1 increments.

growth progressed (Fig. 2). The mean $R:S$ of competing *Dactylis* was estimated to have been 0.846 (0.786–0.906, 95 % CL), whereas for *Plantago* the corresponding $R:S$ was

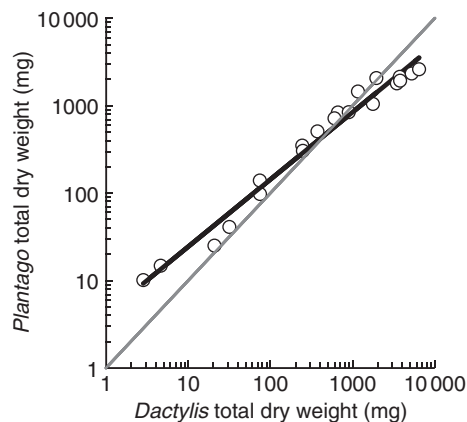


FIG. 3. Total dry weights (i.e. the sum of shoot and root weights) of *Dactylis glomerata* and *Plantago lanceolata* when competing with one another. Shoot weights were measured. Root weights were derived from the allometric modelling of combined root weights measured in the experiment (Fig. 2). Each symbol represents a separate harvest and is the mean of three replicates. The bold line is the RMA regression of ln-transformed data: slope = 0.778 (0.724–0.832, 95 % CL), intercept 3.93 (2.79–5.53), $R^2 = 0.977$, $n = 20$. The grey line is the 1 : 1 relationship (slope = 1, intercept = 0).

0.343 (0.335–0.350). *Dactylis* adjusted its $R:S$ from a value initially similar to that of isolated plants (approx. 0.5; Fig. 2), gradually increasing it to a maximum of approx. 1.0 by the end of the experiment. It achieved this by the most subtle of adjustments in α with hardly any detectable change in β from that it expressed when growing alone (Table 2). Competing *Plantago*, by contrast, barely changed its $R:S$ during the experiment, maintaining a constant α value while reducing β only slightly.

These adjustments (or the lack of them) in root : shoot allocation had implications for the outcome of competition in terms of dry matter production. The total dry weight of *Plantago* initially exceeded that of its competitor (Fig. 3). Above about 450 mg total dry weight (after growing for 38–41 d), however, the growth of *Dactylis* outstripped that of *Plantago*. By the end of the experiment, the total dry weight of *Dactylis* was 2.5-fold greater than that of *Plantago*. This superiority occurred after *Dactylis* had established a significantly larger $R:S$ than that of *Plantago* (Fig. 2). Had only

shoot weights been used to analyse growth, however, the apparent competitive dynamics of *Dactylis* and *Plantago* would have been substantially different. Although the initial shoot growth of *Plantago* was still greater than that of *Dactylis*, *Dactylis* did not become dominant above ground until its shoot dry weight exceeded 1104 mg, after growing for 55–62 d (data not shown). Including the total root dry weights derived from allometric modelling revealed that the growth superiority of *Dactylis* over *Plantago* occurred 14–24 d earlier than suggested by shoot data alone.

DISCUSSION

Allometric modelling allowed the otherwise unquantifiable root weights of competing plants to be estimated over an extended period of growth. The patterns of root growth derived from those estimates suggested that the eventual superiority of *Dactylis* over *Plantago* in terms of its total dry weight production (Fig. 3) was associated with a continual and potentially decisive increase in its root : shoot dry weight ratio ($R:S$; Fig. 2A). *Plantago*'s considerable capacity to vary its $R:S$ when growing alone (Fig. 2B) or when competing intraspecifically (Berendse and Möller, 2009) was apparently suppressed when in competition with *Dactylis*. This effect was perhaps exacerbated by eventual over-topping by the taller *Dactylis* leading to some growth inhibition by partial shading.

The large increases in $R:S$ estimated for *Dactylis* when competing with *Plantago*, from 0.54 to 1.03, are physiologically unexceptional. In response to defined supplies of N or CO₂, hydroponically grown *Dactylis* can vary its $R:S$ from 0.3 to 1.5 (Harmens *et al.*, 2000). In response to inter- and intraspecific neighbours and to different sizes of pots containing an inert rooting medium, *Dactylis* increased its $R:S$ from 0.6 to 1.3 (Gurevitch *et al.*, 1990). More surprising is the apparent lack of $R:S$ response in *Plantago* when competing with *Dactylis*. In response to N and to changes in intraspecific neighbour density, *Plantago* can vary its $R:S$ 4-fold, from 0.5 to 2.0 (Berendse and Möller, 2009). This scale of response was not evident in the present experiment when *Plantago* competed with *Dactylis* (Fig. 2). The root : shoot growth response of any species is regulated genetically and by local environmental conditions, such that $R:S$ can vary widely but within limits set ultimately by biophysical constraints (Enquist and Niklas, 2002; Robinson, 2004). Nevertheless, it is difficult to predict precisely the $R:S$ that a plant will express in a certain context, whether predictions are based primarily on physiological, environmental or ecological inputs (Hunt and Nicholls, 1986; Cheeseman, 1993; Reynolds and Pacala, 1992).

This is the first report of plant competition that is able to use total root system weights of individuals growing in the same volume of soil. Conclusions drawn from our analyses can, therefore, be based on the growth of whole plants, and are not limited to the responses of above-ground parts (Cahill, 2002). However, the growth responses of neighbours are outcomes of many processes, including competition. Growth responses are not, therefore, direct measures of 'competition', although they undoubtedly influence the future competitive potential of individuals. A better mechanistic understanding of competitive processes, and of their interactions with

growth, will be possible by combining allometric modelling with direct measurements of competitive resource capture (C. Trinder *et al.*, unpub. res.).

The experiment was not designed with the aim of isolating effects of above- and below-ground competition using barriers between canopies or root systems (Donald, 1958). The root : shoot responses of *Dactylis* and *Plantago* deduced from the allometric modelling of their growth patterns cannot be attributed unequivocally to a greater influence of conditions in the soil versus those above ground. The increase in $R:S$ seen in *Dactylis* is, however, qualitatively consistent with the balanced growth hypothesis (Davidson, 1969): greater root growth when nutrients or water are in short supply relative to supplies of light or carbon. Hydroponically grown *Dactylis* increases its root : shoot scaling exponent (α) as the concentration of nitrate in the growth medium decreases (Harmens *et al.*, 2000). But it is difficult to attribute definitively a given change in $R:S$ to a given environmental stimulus, even when that stimulus is in the form of a well-defined experimental treatment (Poorter and Nagel, 2000).

The adjustments in root and shoot growth in response to competition inferred by allometric modelling were too small to be judged statistically different from those of isolated plants (Tables 1 and 2). Reliance on a purely allometric theory of plant allocation might have concluded, therefore, that root : shoot responses were unimportant to the interactions between *Dactylis* and *Plantago*. However, using the modelled allometries with the measured shoot weights of the competitors to derive their likely instantaneous root : shoot ratios revealed evidence for a strikingly divergent and functionally important response between the two species (Fig. 2). Contrasting approaches to analysing plant biomass allocation can generate substantial differences in the inferences that can be drawn from them, as highlighted previously by Poorter and Nagel (2000). While acknowledging the statistical problems of using ratios such as $R:S$ [or its equivalent, root mass fraction, $R/(R + S)$; Reich, 2002] that are but snapshots of continually changing ontogenetic, size-dependent, processes (Hunt and Nicholls, 1986; Farrar and Gunn, 1998), they remain useful metrics with which to quantify plants' responses to their local environment, provided that they are estimated at multiple time-points and across wide ranges in plant size, as here.

Many values of α and β other than those reported in Table 2 would satisfy eqn (4). But using the α and β values measured in isolated plants as initial estimates significantly reduced the range of possible solutions to eqn (4) that were found; the values reported in Table 2 are effectively unique solutions, as judged by the narrow 95 % confidence limits of the α and β estimates. This approach also makes biological sense. When small, a plant is essentially isolated, at least if growing in an even-aged stand. It is safe then to assume that its initial root : shoot allometry matches that of a truly isolated plant growing in the same environment. When the effects of competition begin to be manifested and allometric responses initiated, plants would be expected to alter α and β from their initial values, and not from other arbitrary allometries that could nevertheless generate mathematically correct solutions to eqn (4). That assumption might not apply to a small plant growing with larger neighbours and the application

of this approach to such circumstances should be done cautiously. As with all numerical procedures, it is advisable to confirm the apparent uniqueness of a solution for any dataset by conducting repeated, independent estimations.

The requirements for using this approach are to grow isolated plants as well as competitors, and to harvest plants frequently over a period sufficient to measure large dry weight changes from which reliable allometric statistics can be obtained for the isolated individuals. Its extension to more than two species would demand larger experiments. Including multiple competing species would also increase the number of ways in which allometric modelling could partition total combined root biomasses among the competitors. The latter issue could be handled using maximum likelihood techniques to generate probability distributions of α and β , the subsequent interpretation and selection of which would depend on applying species-specific information.

Extending the approach to the field is a more difficult step to envisage. Even if the required monoculture and mixed-species plots were established, or comparable areas of natural vegetation found, the perennial problem of quantitatively extracting roots from field soil would remain (Cahill, 2002; Zobel and Zobel, 2002). Underestimating root weight is inevitable in the field, especially for large plants (Robinson, 2004). If these practical problems can be accommodated, allometric modelling could be a powerful way to study the growth responses of neighbouring plants in the field. Including competitive root:shoot responses in trait-based analyses of community assembly (Shipley, 2010) could then be possible.

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