

Root and shoot competition: a meta-analysis

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Summary

1. We review the effects of root and shoot competition on plant biomass by meta-analysis of 38 published studies, each reporting on the factorial effects of root-competition and shoot-competition on herbaceous plants.
2. There were significant differences in the overall effects of root, shoot and full competition. Root competition generally resulted in larger biomass reduction than shoot competition, particularly among the smaller of the two competitors. An interaction between root and shoot competition was observed in some experiments but was generally not significant.
3. While root competition was generally stronger than shoot competition at lower nutrient levels, there was no overall difference at higher nutrient levels due to much lower levels of root competition. In contrast, the overall effect of full competition increased considerably with nutrient level.
4. Root competition was generally more important when the neighbour was a grass as compared with a herb or a legume, and when domesticated plants competed with wild neighbours, suggesting that wild genotypes are stronger competitors for below-ground resources than are crop plants.
5. Effects of competition were generally stronger in experiments with additive designs than in those with substitutive designs. Also, experiments using single target individuals showed stronger effects of competition, root competition in particular, than did experiments using groups targets.
6. *Synthesis.* Despite large variation among experiments, some general patterns were supported: effects of root competition are generally stronger than shoot competition, particularly (i) for smaller competitors, (ii) at low fertility levels, (iii) when the competitor is a grass rather than an herb, (iv) when the competitor is a wild rather than a domesticated species, and (v) in additive design experiments. The effects of root and shoot competition appear to be additive under many conditions. Whereas root competition may often be the primary limitation on mean plant performance, shoot competition will influence the variation around this mean and may determine which individuals or species dominate.

Key-words: above-ground, below-ground, biomass, competitive interaction, experimental design, plant–plant interactions, soil nutrient level

Introduction

Competition for resources is one of the fundamental mechanisms determining the structure and development of natural and managed plant communities. In natural ecosystems, competition among plants is known to influence species composition (Goldberg 1990), population and community dynamics (Grime 1979; Tilman 1985; Thompson 1987) and diversity (Chesson 2000). In agro-ecosystems, intraspecific competition among crop plants affects vegetative growth and reproductive output (Weiner 1988), while competition between crops and weeds is the greatest single source of yield loss (Liebman 2001). Moreover, competition between crop species is

important for the growth and yield of components in multi-crop systems (Vandermeer 1989).

Given that roots and shoots are physically discrete and acquire different resources from the environment, numerous studies of plant competition have attempted to separate the effects of root and shoot competition (see Clements, Weaver & Hanson 1929; Donald 1958; Wilson 1988; Snaydon 1996; McPhee & Aarssen 2001). Above- and below-ground partitions between adjacent plants (Clements, Weaver & Hanson 1929) allow researchers to compare four possible competition treatments: (i) control, (ii) root competition only, (iii) shoot competition only and (iv) full (root and shoot) competition.

Numerous studies have evaluated the relative importance of root and shoot competition at different nutrient levels,

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and the results have varied greatly. Some studies support the hypotheses (i) that root competition is the dominant contributor to plant competition, and (ii) that there is no clear relationship between the effects of competition and environmental productivity (which is usually manipulated by adding nutrients, e.g. Belcher, Keddy & Twolan-Strutt 1995; Lamb, Shore & Cahill 2007). This is consistent with some studies concluding that the overall strength of competition generally remains unchanged along a productivity gradient (Tilman 1988; Wilson & Tilman 1991). Some studies have found increasing effects of both above- and below-ground competition as productivity increases (Nicotra & Rodenhouse 1995; Grime 2001), while others have found root competition to be more important than shoot competition at lower productivity sites (e.g. Satorre & Snaydon 1992; Acciaresi, Chidichimo & Sarandon 2003), and the importance of above-ground competition to be higher with increasing productivity (Tilman 1988; Wilson & Tilman 1991; Grime 2001; Keddy 2001). In view of these apparently contradictory results, a review of the available data may show if there are general trends.

There has been much recent interest in potential interactions between above- and below-ground competition, asking whether each mode of competition enhances or reduces the effect of the other. Again, experimental results vary substantially with some studies finding a positive interaction (e.g. Cahill 1999, 2002), while others find no interaction (e.g. Lamb, Shore & Cahill 2007; Bartelheimer, Gowing & Silvertown 2010). Cahill (1999) found that the level of interaction varied with productivity from no interaction in unfertilized sites to positive interaction in fertilized sites. Studies of plant roots are challenging because (i) several essential resources are involved (i.e., water, macro- and micronutrients), which (ii) are often heterogeneously distributed in three dimensions (Gibson 1986; Bliss *et al.* 2002), and not least, (iii) roots can rarely be observed directly. Accordingly, several researchers have used only above-ground partitions and deduced the marginal effect of shoot interaction by subtracting the effect of root competition from that of full plant competition, thus assuming that there is no interaction between the two modes of competition and that their effects are additive (e.g. Peltzer, Wilson & Gerry 1998).

A number of previous reviews have focused on various aspects of root and shoot competition. Wilson (1988) reviewed competitive effects in 23 studies separating root and shoot competition in a factorial design and concluded that (i) root competition is usually stronger than shoot competition, but (ii) shoot competition was most often stronger than root competition in studies of crop–weed interactions, (iii) the relative importance of root competition was found to increase with length of the study, (iv) root interactions were more important in monoculture than in species mixtures, and (v) added soil resources (fertilizer or water) rarely affected root competition in the absence of shoot competition. Snaydon (1996) reviewed 31 studies reporting competitive effects of root and shoot competition, paying particular attention to studies of

intercropping. A simple quantitative analysis of resource complementarity and competitive ability in different competition treatments supported the findings of Wilson (1988): resource complementarity was found to be greater above- than below-ground and competition accordingly weaker.

Despite significant debate on the importance of design and technique used in plant competition experiments, published studies often fail to acknowledge their importance for assessing the relative roles of root and shoot competition. In his review of experiments separating root and shoot competition (agricultural studies in particular), Snaydon (1996) evaluated the overall numeric effect of experimental design, particularly addressing the relative merits of additive and substitutive (replacement) designs. On this basis, he concluded that variation in results might reflect more the variation in designs than differences in the importance of root versus shoot competition. Likewise, McPhee & Aarssen (2001) reviewed the range of experimental techniques being used for the separation of root and shoot competition. Without quantitative analysis, they concluded that each technique is appropriate for testing only specific classes of hypotheses. The accumulation of studies since these reviews, along with the development of new statistical methods, offers new opportunities to reviewing results bearing on these questions.

Here, we perform a quantitative and systematic analysis of published studies on root and shoot competition. We look for underlying patterns and potential explanations for apparently contradictory results. Meta-analysis has become an important tool in ecology because it was first used to review the effects of overall competition in field experiments (Gurevitch *et al.* 1992). By reviewing within this rigid statistical framework, we aim to address the following questions:

- 1 What is the influence of competitor characteristics on the effects of root, shoot and full plant competition? For example, do niche differences among competitors above- and/or below-ground decrease the strength of interspecific competition?
- 2 Under what circumstances are root or shoot competition stronger, and specifically how does this change with the nutrients level?
- 3 When are the effects of root and shoot competition additive, and when is there an interaction between them, such that one makes the other stronger or weaker?
- 4 What is the influence of experimental designs and methods on observed effects?

Materials and methods

EXPERIMENTAL STUDIES

The main criterion for inclusion of studies in the meta-analysis was publication in a peer-reviewed journal listed in The Science Citation Index Expanded database in December 2011 (dating from 1900 to present). The data base was explored using the wide Boolean search [(shoot AND root) OR (above AND below)] AND competition (allow-

ing for lemmas, i.e., different words derived from the same root). The 5329 references thus obtained were filtered according to listed subject categories, keeping only references within environmental sciences and ecology, agriculture, plant sciences, biodiversity and conservation, genetics and heredity and evolutionary biology. The titles of the resulting 1898 references were then evaluated according to relevance, resulting in 400 references with a clear focus on plant competition. The abstracts of these were then scrutinized, resulting in 153 articles studying aspects of both root and shoot competition, including the reviews of Wilson (1988) and McPhee & Aarssen (2001). The reference lists of these articles were then used to identify further studies not obtained from the data base search, which were then filtered following the described identification procedure based on titles and abstracts. Due to the very limited number of studies on woody plants, and to ensure some degree of similarity in growth form, only studies on herbaceous species were retained. The resulting set of 75 studies was then filtered by excluding experiments that (i) did not report from all factorial combinations of root and shoot competition (control, root, shoot and full competition), (ii) deployed different sowing times between competing species, or (iii) reported only means of multiple treatments, for example, different neighbour species, densities or sowing dates. Previous reviews of root and shoot competition by Wilson (1988), Snaydon (1996) and McPhee & Aarssen (2001), provide no description of study identification and filtering.

DATA EXTRACTION

All remaining studies provided measurements of plant biomass, with 76% reporting above-ground biomass only and 24% reporting total biomass. Components of reproductive output were rarely reported and thus excluded. All studies reported dry weights except one (Irons & Burnside 1982), which reported only fresh weights. Estimates of competition effect were calculated for each experiment based on the reported biomass per plant (see below), which in some cases had to be derived from plant biomass per area and information on plant density, assuming 100% seed germination and survival (unless specified). Reported numbers of experimental replications as well as standard deviations or other measures of experimental variation were retrieved from each competition treatment and transformed to standard deviations of biomass per plant (see Kiær, Skovgaard & Østergård 2009) to estimate the variance of competition effects (see below). All data were extracted from tables or digitized from graphs using the software DigXY version 1.2 (www.thunderheadeng.com/digxy). In order to reduce non-independence, we retained only data from the last measurement when measurements were repeated over different growth stages, thus reflecting the longest period of interaction among competitors.

A total of 10 descriptive characteristics of plant competitors, growth environments and experimental partitioning of competitors were consistently available from each retrieved experiment (Table 1). In some studies, the lower nutrient level was reported as merely 'unfertilized', whereas in others, a fertilization level was reported. All fertilization treatments involved nitrogen-based (N) commercial fertilizers, and some treatments included phosphorous (P) and/or potassium (K) as well. When experiments reported competition results from more than two nutrient levels, only the lowest and the highest levels were used. As proxies for analysing apparatus effect, experimental partitions were (i) classified according to the materials used above- and below-ground, respectively, and (ii) recorded whether they were maintained in the set-up (in some other position) during competition while allowing for competitor interac-

Table 1. Characteristics obtained from each experiment

Characteristic	Levels
<i>Plant competitors</i>	
Functional group (targets and neighbours)	Grass, Herbaceous (non-leguminous), Leguminous
Domestication level (targets and neighbours)	Crop, Weedy, Wild
<i>Environment</i>	
Facility (control/naturalness)	Growth chamber, Glasshouse, Outdoor container, Field, Grassland
Substrate volume	Pot, Container, Unrestricted
Productivity level	Low, High
<i>Equipment</i>	
Above-ground partitions	Neighbour manipulation, Reflective, Transparent, Semi-transparent, Opaque
Peripheral shoot growth	Restricted, Unrestricted
Below-ground partitions	Solid, With mesh net
Partition presence	Removed at competition, Maintained at competition (in another position)
<i>Experimental</i>	
Technique	Divided pot, Target, Row
Design	Additive, Substitutive
Target type	Single, Group

tion, that is, whether any apparatus effects were consistent between the compared treatments.

EXPERIMENTAL DESIGNS AND TECHNIQUES

McPhee & Aarssen (2001) discriminated among (i) Divided pot, (ii) row-based and (iii) so-called Target techniques. In the Divided pot technique, competing plants are grown in glasshouse pots with vertical dividers placed perpendicularly above- and below-ground (Clements, Weaver & Hanson 1929; Donald 1958). It is among the most widely used techniques for studying root and shoot interactions in a factorial design. In the row technique, two genotypes are planted in parallel rows with and without above- and/or below-ground separators between rows, allowing a certain level of intraspecific competition within the rows. The row technique is often used to study competition effects between intercropped species. The target technique surrounds a single target plant by some number of neighbour plants, which are then completely removed in the no-competition control treatment or restrained using net or wire above-ground and solid or mesh partitions below-ground. It is the most widely used technique for studying root and shoot competition in natural settings.

From the point of view of meta-analysis, the categories devised by McPhee and Aarssen do not, by themselves, provide a sufficient basis for a comparative analysis. For example, some row technique experiments use an additive design, in which the average soil volume available to each individual is lower in competition treatments compared with the control treatment (e.g. Schreiber 1967), whereas other row techniques use a substitutive design, in which average resource space per individual in the competition and control treatments is the same (e.g. Snaydon 1971). Furthermore, while some divided pot experiments study target individuals, others study groups of target individuals, thereby implicating a certain level of intraspecific competition in the control treatment. None of the previous

quantitative reviews of above- and below-ground competition accounted for this distinction. Consequently, we used two basic distinctions to group and compare the extracted results, both of which can have profound influence on the competitive environments experienced by plant individuals: (i) Additive vs. substitutive experimental designs and (ii) experimental designs using single target plants vs. groups of target plants.

MEASURES OF COMPETITION EFFECT

Effects of full plant (F), root (R) and shoot (S) competition were estimated for each target in each retrieved experiment, using the log response ratio (Hedges, Gurevitch & Curtis 1999), so that

$$C_F = -\ln(\bar{x}_F/\bar{x}_C), \quad \text{eqn 1}$$

$$C_R = -\ln(\bar{x}_R/\bar{x}_C) \text{ and} \quad \text{eqn 2}$$

$$C_S = -\ln(\bar{x}_S/\bar{x}_C), \quad \text{eqn 3}$$

where \bar{x}_F denotes mean per-plant biomass following full (root and shoot) competition, \bar{x}_R the mean per-plant biomass following root competition only, \bar{x}_S the mean per-plant biomass following shoot competition only and \bar{x}_C the mean per-plant biomass following growth in the control treatment. When competition effects on plant biomass are relatively small, terms will become identical and $C_{F/R/S}$ will approximate zero, while due to the use of negation, larger biomass reductions from competition will cause larger values of $C_{F/R/S}$. Our use of sign is opposite to that of Cahill (1999) and Hedges, Gurevitch & Curtis (1999) but similar to that used in the meta-analysis of Goldberg *et al.* (1999). Among the competition indices in common use, the log response ratio has statistical properties that are best suited for linear analysis, because it is equal to the absolute difference between each log-transformed term (Hedges, Gurevitch & Curtis 1999; Weigelt & Jolliffe 2003; Lamb, Shore & Cahill 2007). In a few instances, biomass was reported to be larger in one of the competition treatments than in the control treatment, resulting in negative estimates of competition effect and indicating facilitation. The models used allow such values, and so they were maintained for analysis. Throughout, competition effects are reported as percentages biomass change, which are calculated by back-transformation of log response ratios.

Identified numbers of replication and standard deviation (SD) of measured per-plant biomass were used to approximate the variance of each log response ratio (Hedges, Gurevitch & Curtis 1999) as

$$\text{Var}(C_F) = \text{Var}(\ln(\bar{x}_F)) + \text{Var}(\ln(\bar{x}_C)) \approx \frac{(\text{SD}_F)^2}{n_F \bar{x}_F^2} + \frac{(\text{SD}_C)^2}{n_C \bar{x}_C^2}, \quad \text{eqn 4}$$

here using C_F as an example, where n_C denotes the number of replicated measurements behind the average per-plant biomass in control treatments, n_F denotes the number of replicated observations behind the average per-plant biomass in full competition treatments, and the rest are given above.

The relative effect of root and shoot competition, that is, the relative reduction in biomass due to root as opposed to shoot competition, was estimated as $C_{R-S} = C_R - C_S$. This measure is close to zero when strength of the two modes are equal; positive values indicate that root competition is stronger than shoot competition, while negative values indicate the opposite. The variance of C_{R-S} was derived as $\text{Var}(C_{R-S}) = \text{Var}(C_R - C_S) = \text{Var}(C_R) + \text{Var}(C_S)$, which is given from eqn 4. Similar equations were used to calculate differences of competition effect in reciprocal competitor combinations (see below).

The estimated mean and approximated variance of the interaction between shoot and root competition were obtained following Morris *et al.* (2007) as

$$C_{R \times S} = \ln(\bar{x}_F/\bar{x}_R) - \ln(\bar{x}_S/\bar{x}_C), \quad \text{eqn 5}$$

$$\text{Var}(C_{R \times S}) \approx \frac{(\text{SD}_F)^2}{n_F \bar{x}_F^2} + \frac{(\text{SD}_R)^2}{n_R \bar{x}_R^2} + \frac{(\text{SD}_S)^2}{n_S \bar{x}_S^2} + \frac{(\text{SD}_C)^2}{n_C \bar{x}_C^2}, \quad \text{eqn 6}$$

respectively, where all terms are defined above. In this formulation, negative values of $C_{R \times S}$ indicate that the effect of full competition is smaller than the additive effect of root and shoot competition, and positive values indicate that the effect of full competition is larger than additive.

STATISTICAL ANALYSES

Overall meta-estimates of competition effect and root–shoot interaction were derived from random effects models in which the original estimates of competition effect were weighted with the inverse of their respective variances (Hedges & Olkin 1985), considering original estimates as independent and approximately unbiased samples with assumed known variances (see Viechtbauer 2010 for details). The influence of each extracted characteristic on the effect of each measured type of competition was tested in a mixed effects meta-regression model against the null-hypothesis that regression coefficients equal zero (see Viechtbauer 2010 for details). Characteristics were treated as factor variables and coded as sets of dummy (0/1) variables in order to model each factor level. Analyses showed a significant effect of two aspects of experimental design: additive versus substitutive designs and individual plant targets versus group targets (see Results). To account for the possible confounding effect of experimental design, these two aspects of experiment design were included as an additional four-level explanatory factor in all comparisons between factor levels, as presented below. The level of random variation between competition effects, known as the residual heterogeneity, was used to estimate the degree to which the tested factors could explain differences among experiments, applying restricted maximum-likelihood (REML) estimation of a Q statistic (Viechtbauer 2007).

From a subset of experiments, measures of variation were either not reported or irretrievable. In order to include all such experiments in the meta-analysis, their missing standard deviations were imputed for each meta-regression model by sampling with replacement from the set of standard deviations from experiments with the same level of the tested characteristic (Wiebe *et al.* 2006). Each model was analysed 1000 times, each based on resampled standard deviations, and values for each test statistic were derived as the average across samples. This so-called multiple imputation is the only available method that accounts for the uncertainty from the missing standard deviations and has been recommended over other imputation methods (Wiebe *et al.* 2006; see also Furukawa *et al.* 2006).

All calculations and analyses were made in the R environment (version 2.14.0; R Development Core Team 2012), using the *metafor* package version 1.6-0 (Viechtbauer 2010).

Results

A total of 152 factorial experiments met our criteria, deriving from 38 studies published between 1958 and 2010 (data available from Appendix S1 in Supporting Information). A total of 102 experimental combinations reported a number of

replicates and measures of experimental variation, as required for traditional meta-analysis. Across all studies reviewed, full competition reduced plant biomass by 55% overall, root competition alone reduced by 45%, and shoot competition alone reduced by 23% (all $P < 0.001$). Root competition was stronger than shoot competition in 96 (63%) of the experiments (see Appendix S1) and 23% larger overall ($P < 0.001$). Negative interaction effects between root and shoot competition, in which the presence of one mode of competition reduced the effect of the other, were found in about half (56%) of the experiments, and the overall meta-estimate of this interaction was far from significant ($P = 0.382$). Among the 102 values of root and shoot interaction associated with a variance, 16 were significantly positive, while 16 were significantly negative. Non-significant overall levels of interaction were found in all groups of studies, unless specified below. These results were stable across experiments, as estimated from a 'leave-one-out' procedure (not shown). Residual variation (heterogeneity) among experimental results was signifi-

cant for all modes of competition (not shown), indicating significant underlying structures in the data set due to biological and experimental differences among studies.

COMPETITOR CHARACTERISTICS

Functional group

Competitor plants were classified into three functional groups: grasses, non-leguminous herbs and legumes. While the effects of full, root and shoot competition were overall highly significant for target plants from all of these groups (effect of shoot competition on grass targets $P < 0.01$, all others $P < 0.001$), some between-group differences were found (Fig. 1a). Herbs were generally more sensitive to competition than the other two functional groups: the overall effect of full competition was 43% larger among herbs than among grasses and 42% larger than among legumes (both $P < 0.05$), while the overall effect of root competition was 39% larger among herbs than

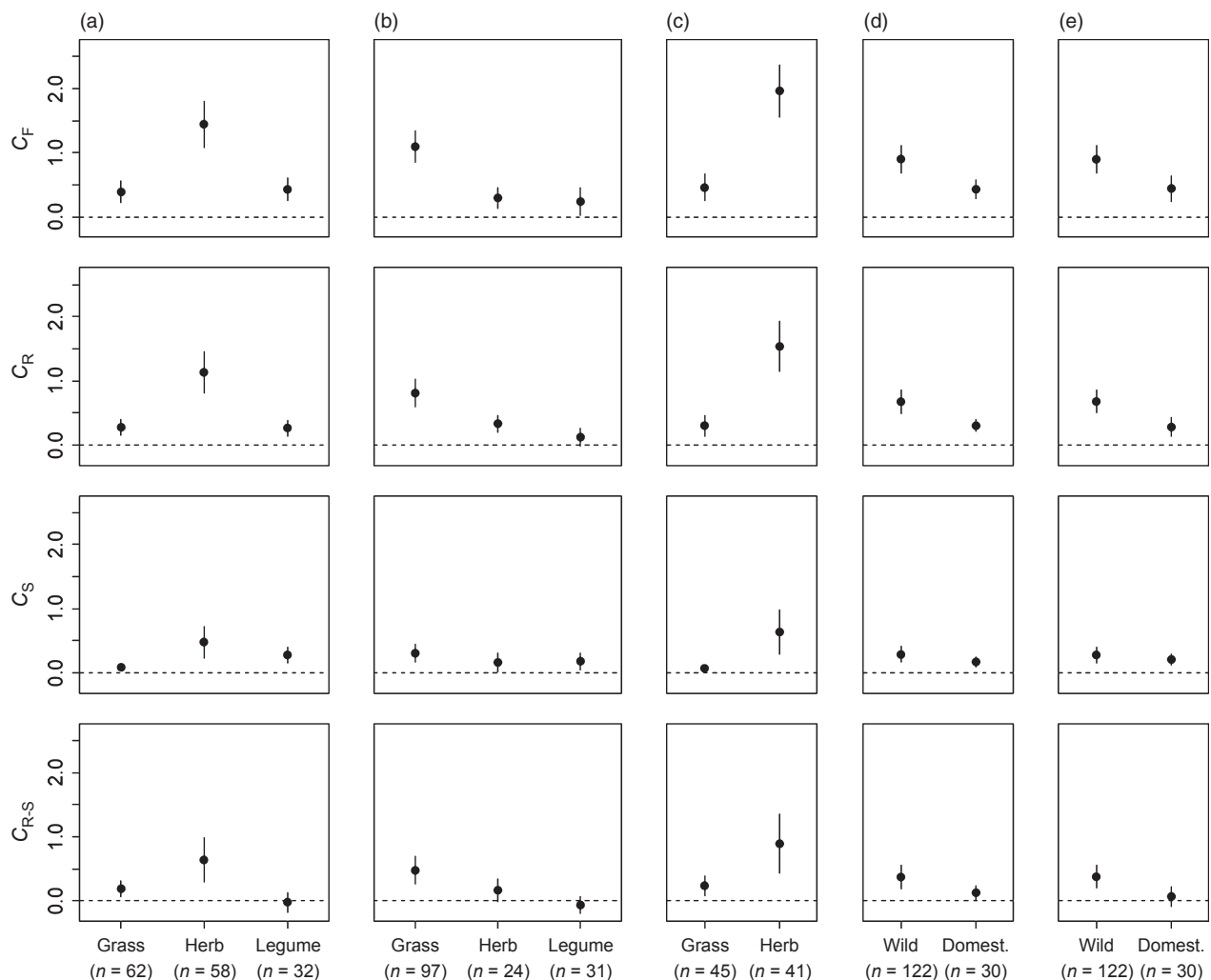


Fig. 1. Overall meta-estimates (closed circles) and confidence intervals (vertical lines) of effects of full (C_F), root (C_R) and shoot (C_S) competition, and root relative to shoot competition (C_{R-S}), for different levels of (a) target functional group, (b) neighbour functional group (c) functional group of targets competing with grass neighbours, (d) target domestication level and (e) neighbour domestication level. Scale is logarithmic. Sample sizes for each factor level provided in parentheses.

among grasses and 41% larger than among legumes (both $P < 0.01$). The overall effect of shoot competition was 23% larger for herb targets than for grasses ($P < 0.05$), whereas for legumes, the overall effect of shoot competition was intermediate and not significantly different from either. Root competition was significantly stronger than shoot competition among herb ($P < 0.001$) and grass targets ($P < 0.01$) but not among legume targets ($P = 0.720$), and this relationship was marginally larger for herbs compared with legumes ($P = 0.054$).

Grass plants were used as competitor neighbours in the majority of experimental combinations (97); fewer used legumes (31) or herbs (24; see Appendix S1). Each group of neighbours generally caused significant overall biomass reduction in the target plants following full, root or shoot competition (all $P < 0.05$; Fig. 1b), except when neighbouring roots were from a legume ($P = 0.081$). Effects of root competition from grass neighbours were generally only marginally higher than effects of root competition from legume neighbours ($P = 0.066$). The presence of grass roots generally reduced target plant biomass by 38% more than the presence of grass shoots ($P < 0.001$), while such a difference was only suggested for herbs ($P = 0.083$) and unsupported for legumes ($P = 0.330$). The relative importance of root competition from grass neighbours was slightly higher than for legume neighbours ($P = 0.087$). The effect of full competition with herb neighbours was 17% larger overall than the additive effect of root and shoot competition, suggestive of positive interaction between root and shoot competition ($P < 0.05$).

Two target-neighbour combinations of functional groups were sufficiently represented for meta-analysis: 45 experiments from 13 studies of grass targets and 41 experiments from 11 studies of herb targets, all competing with grass neighbours (see Appendix S1). The overall effects of full, root and shoot competition with grass neighbours were 65%, 60% and 34% larger among herbs than among grasses, respectively (all $P < 0.01$; Fig. 1c). Accordingly, the effect of competition from grass roots was larger than from grass shoots in both groups (both $P < 0.01$), the relative dominance of grass root competition being 37% larger among herb targets than among grass targets ($P < 0.05$). When grasses competed with grasses, the overall effect of full competition was 9% smaller than the additive effect of root and shoot competition, suggestive of negative interaction between root and shoot competition ($P < 0.05$).

Domesticated vs. wild species

Overall effects of full, root and shoot competition on domesticated as well as wild target plants were highly significant (all $P < 0.001$; Fig. 1d) and not significantly different between the two groups (not shown). The same was true for competition effects imposed by crop and wild neighbours (not shown; Fig. 1e). For wild target plants, the overall effect of root competition was 31% larger than that of shoot competition ($P < 0.001$), while this difference was only 12% for crop plants ($P < 0.05$; difference not significant). Reciprocal competitive effects between crop and wild species were available

from a subset of 21 experiments from 10 studies (42 experimental results in total). These did not suggest any overall differences in the competitiveness of crop plants and wild competitors (not shown). Root competition was generally more important than shoot competition when crops plants competed with wild neighbours ($P < 0.05$), but not when wild plants competed with crop neighbours ($P = 0.341$).

Plant size

A subset of 47 experiments (see Appendix S1) reported per-plant biomass of both competitors (94 experimental results in total). None of these studies used single target plants in an additive design. Using per-plant biomass in control treatments as a proxy for plant size, we were able to evaluate the general importance of relative plant size for competitive interaction. The relative reductions in plant biomass (competition effects) among the smaller competitors were overall 36% and 24% larger compared with the larger competitors following full and root competition, respectively ($P < 0.001$ and $P < 0.01$),

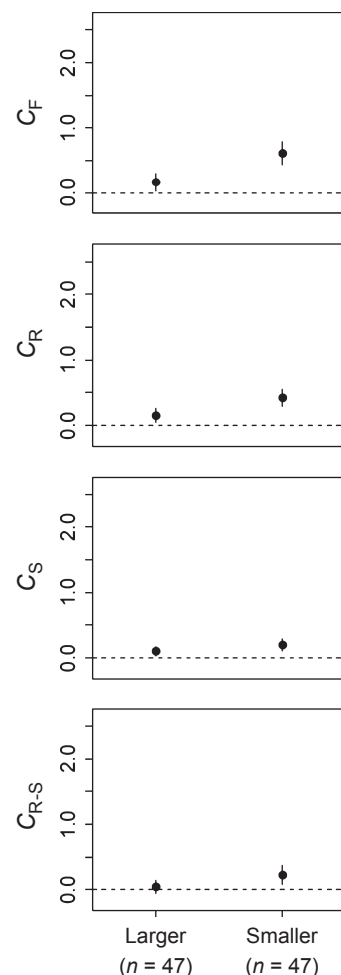


Fig. 2. Overall meta-estimates (closed circles) and confidence intervals (vertical lines) of effects of full (C_F), root (C_R) and shoot (C_S) competition, and root relative to shoot competition (C_{R-S}), depending on relative size of competitors from pairwise competition experiments. Scale is logarithmic. Sample sizes for each factor level provided in parentheses.

but not following shoot competition ($P = 0.099$; Fig. 2). Accordingly, the relative biomass reduction of smaller competitors was generally higher following root competition compared with shoot competition ($P < 0.05$), which differed significantly ($P < 0.05$) from the pattern among the larger competitors ($P = 0.368$; Fig. 2).

GROWTH ENVIRONMENT

Experiment type

We classified experiments on a five-level scale ranging from natural conditions to extensive control of the experimental environment. In increasing order, these were grassland, field (agricultural field or experimental garden), outdoor container, glasshouse and growth chamber. Overall competition effects generally decreased with increasing level of environmental control (Fig. 3a). Overall effects of full, root and shoot com-

petition were found in all environment classes (all $P < 0.001$) except growth chamber ($P > 0.28$ in all cases). Grassland experiments all employed the Target technique and generally resulted in larger effects of full, root and shoot competition compared with other environment types (all $P < 0.05$; except shoot competition in grassland experiments compared with agricultural field experiments, $P = 0.070$). In experiments using outdoor containers, overall competition effects were 9% smaller than the additive effect of root and shoot competition, indicative of negative interaction between root and shoot competition ($P = 0.071$).

Experiments were also stratified according to three levels of soil volume, namely pots, containers and fields. Overall effects of full, root and shoot competition were larger in field experiments (field and grassland environments) than in experiments using pots or containers, respectively (all $P < 0.01$; Fig. 3b), and shoot competition was not significant overall for pot experiments ($P = 0.173$). Root competition effects in

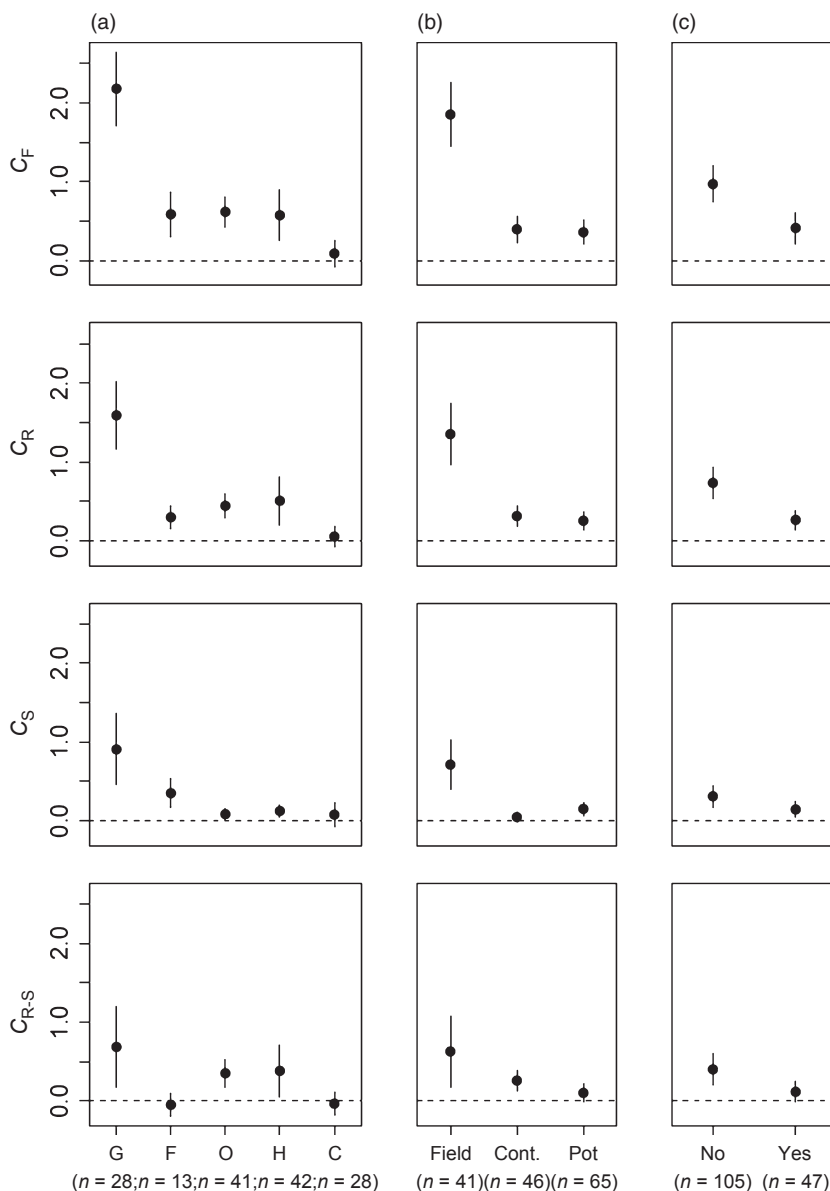


Fig. 3. Overall meta-estimates (closed circles) and confidence intervals (vertical lines) of effects of effects of full (C_F), root (C_R) and shoot (C_S) competition, and root relative to shoot competition (C_{R-S}), for different levels of (a) experimental environment (G: grassland; F: field; O: outdoor container; H: glasshouse; C: growth chamber), (b) soil volume and (c) partitions maintained (in another position) during competition. Scale is logarithmic. Sample sizes for each factor level provided in parentheses.

these smaller soil volumes were comparable to larger soil volumes (not shown).

Soil nutrient level

Ten studies used soil nutrient level as an experimental factor, providing 19 combinations of higher and lower nutrient levels (Table 2). Five studies used single target plants and five used multiple-target plants (see Appendix S1). High-nutrient conditions resulted in a large (269%, $P < 0.001$) overall increase in biomass per plant in the absence of competition, compared with low-nutrient conditions (meta-analysis based on pooled variance estimates of nutrient level pairs). Overall effects of competition were affected by nutrient level (Fig. 4). The overall effect of root competition decreased by 22% at higher compared with lower nutrient levels, although not signifi-

cantly, while the effect of shoot competition increased slightly. Accordingly, effects of root competition were overall 42% larger than effects of shoot competition at lower nutrient levels ($P < 0.01$), whereas a similar dominance of root competition was not found at higher nutrient levels ($P = 0.847$). This difference between nutrient levels in the dominance of root competition was not significant ($P = 0.130$), however. The relative biomass reduction following full plant competition was 22% lower at lower compared to higher nutrient levels, and even lower than following root competition alone, but this difference was not significant (not shown). Overall, effects of full competition were suggested to be smaller than the additive effects of root and shoot competition ($C_{R \times S} = -0.30$; $P = 0.174$) or absent ($P = 0.734$) at lower and higher nutrient levels, respectively. This difference was not significant ($P = 0.372$).

Table 2. Relative intensity of root and shoot competition (C_{R-S}) for studies with different levels of fertilization. Providing target species and fertilizer type used at high-nutrient levels. As indications of productivity increase, reported plant biomass from the no competition treatments are provided along with the relative increase in biomass at fertilization

Study	Target species	Fertilizer	Biomass (g/plant)	Biomass change (%)	C_F	C_{R-S}
Aerts, Boot & van der Aart (1991)*	<i>Molinia caerulea</i>	NPK	24.80	188	0.12	0.84
			8.60		-0.19	1.14
Bartelheimer, Gowing & Silvertown (2010)*	<i>Senecio aquaticus</i>	N	9.91	293	1.27	2.21
			2.52		0.40	1.71
	<i>Senecio jacobaea</i>	N	9.76	226	0.55	2.16
			2.99		1.04	1.13
Cahill (1999)*	<i>Abutilon theophrasti</i>	NPK	1.74	164	2.40	1.68
Cahill (2002)*	<i>Abutilon theophrasti</i>	NPK	0.66		2.83	1.74
			1.09	-31	4.05	-1.40
	<i>Amaranthus retroflexus</i>	NPK	1.56		3.29	0.56
			0.84	175	3.15	3.00
	<i>Plantago lanceolata</i>	NPK	0.31		3.52	2.39
			0.44	375	2.47	2.34
	<i>Rumex crispus</i>	NPK	0.09		3.14	1.98
			0.13	568	3.75	-2.38
Donald (1958)	<i>Lolium perenne</i>	N	0.02		1.85	2.39
			4.71	92	0.00	1.08
	<i>Phalaris tuberosa</i>	N	2.45		-0.12	1.25
			4.67	134	2.68	2.00
	<i>Rumex obtusifolius</i>	N	2.00		2.41	2.54
			0.38	41	3.87	1.60
Jeangros & Nösberger (1990)	<i>Rumex obtusifolius</i>	N	0.27		3.41	3.06
			0.04	347	1.05	1.45
	<i>Festuca rubra</i>	NP	0.01		0.56	1.48
			0.12	419	0.11	0.98
	<i>Lolium perenne</i>	NP	0.02		0.09	1.34
Kitamura, Whitney & Guevarra (1981)	<i>Desmodium intortum</i>	N	0.32	27	0.41	1.59
			0.25		0.41	1.85
	<i>Setaria anceps</i>	N	0.80	77	-0.32	0.75
			0.45		-0.59	0.48
	<i>Artemisia frigida</i>	N	0.13	41	2.41	2.76
Lamb, Shore & Cahill (2007)*	<i>Artemisia frigida</i>	N	0.09		2.15	2.59
			0.14	44	1.65	1.87
	<i>Chenopodium leptophyllum</i>	N	0.09		1.55	2.67
Wilson & Newman (1987)	<i>Deschampsia flexuosa</i>	PK	2.99	10	0.29	1.08
			2.72		0.30	0.93
	<i>Festuca ovina</i>	PK	3.32	12	-0.40	0.70
			2.95		-0.33	0.80

*Study providing measure of variation and number of replicates, enabling calculation of competition effect variances used in meta-analysis.

EXPERIMENTAL DESIGN AND EQUIPMENT

Additive versus substitutive designs and single versus group targets

Competition effects were greatly influenced by experimental design: changes in overall density in competition treatments (i.e., additive vs. substitutive designs) and presence of intra-specific competitors in control treatments (single target versus group target designs). The overall effects of full, root and shoot competition were significantly larger for additive than for substitutive experiments (Table 3). The effects of root competition in additive experiments were significantly larger than those of shoot competition, whereas this was not the case for substitutive experiments. Similarly, meta-estimates of the effects of full, root and shoot competition were all significantly larger for single target compared with group target experiments, while the relatively larger effect of root competition compared with shoot competition was even larger among

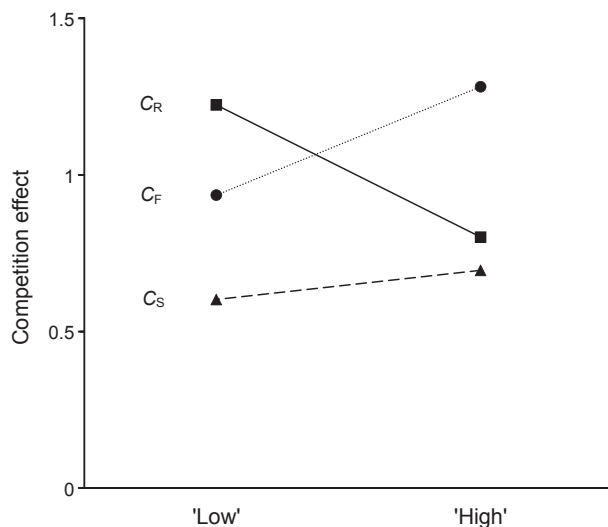


Fig. 4. Overall meta-estimates of the effects of full (C_F), root (C_R) and shoot (C_S) competition at lower and higher soil nutrient levels in the subset of experiments with pairwise treatments at each of both levels.

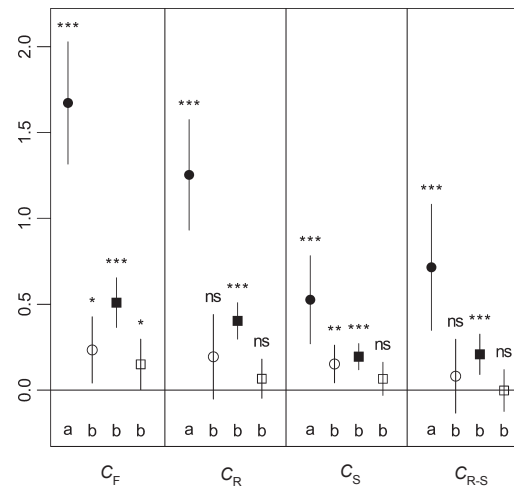


Fig. 5. Overall meta-estimates and confidence intervals (vertical lines) of effects of full (C_F), root (C_R) and shoot (C_S) competition, and root relative to shoot competition (C_{R-S}). Shown for each of four experimental designs being combinations of additive (solid), substitutive (open), single target (circle) and group target (square) designs. Scale is logarithmic. Indicating significance of meta-estimates (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns: non-significant). Meta-estimates with different letters are significantly different within each measure of competition effect.

single target experiments. No evidence of an overall interaction between root and shoot competition was found in any of the groups. A meta-analysis combining these two-level descriptors of experimental design into a single, four-level factor, confirmed that overall competition effects were largest in the group of experiments using additive designs and single target plants and smallest among experiments using substitutive designs and group targets (Fig. 5). The greatest influence of experimental design on competition effects was that of increased plant density in competition treatments (an attribute of additive but not substitutive designs), with overall non-significant effects of root competition for substitutive designs. Additionally, the overall effect of competition was significantly larger for root compared with shoot competition in both groups of experiments using additive designs but not in the groups of experiments using substitutive designs. The

Table 3. Relative changes in biomass following root, shoot and full (root + shoot) competition, root compared with shoot competition as well as interaction between root and shoot competition. Shown alongside number of experiments for each level of two features of experimental design along with levels of significance, as well as levels of significance of the stated difference in competition effect between levels

	Number of experiments	Full competition	Root (R) competition	Shoot (S) competition	R vs. S competition	R-S competitive interaction
<i>Change in resource space?</i>						
Additive	94	70%***	59%***	32%***	39%***	ns
Substitutive	58	15%*	9%(*)	7%(*)	ns	ns
Additive > Substitutive		***	***	**	**	ns
<i>Intraspecific competition?</i>						
Single target	67	75%***	65%***	36%***	45%***	ns
Group target	85	28%***	21%***	12%***	10%*	ns
Single > Group		***	***	**	**	ns

Levels of significance indicated as ***($P < 0.001$), **($P < 0.01$), *($P < 0.05$), (*) ($0.05 < P < 0.10$) and ns (not significant).

sharing of above-ground resources in additive competition treatments does not pose as large a restriction on the growth of individual plants as the sharing of below-ground resources.

Among the experiments using additive designs and single target plants (see Appendix S1), most (76%) employed the Target technique and a total of 35 (64%) studied competition between herb targets (poor competitors, see above) and grass neighbours (good competitors). This was confounded with the finding of extensive overall effects of full, root and shoot competition in this design group (81%, 71% and 41%, respectively), which were generally significantly larger ($P < 0.01$, $P < 0.01$ and $P = 0.061$, respectively) than in the subset of 13 experiments in this design group that employed the Divided pot technique (44%, 34% and 11%, respectively). Competition effects in this subset of experiments were still significantly larger than those found in the remaining design groups (Fig. 5), except for full competition in comparison with that of group targets in substitutive designs (not shown). While all other experiments studied competition between no more than two species, 30 of the 42 experiments employing the Target technique used a multispecies neighbour community. Experiments using substitutive designs and group targets used one of two experimental techniques: (i) experiments substituting intraspecific competitors in the control treatment by interspecific competitors in the competition treatments (Snaydon 1971; Scott & Lowther 1980; Kitamura, Whitney & Guevarra 1981; Martin & Field 1984, 1987, 1988; Bandula Premalal *et al.* 1998), and (ii) experiments using substitutive versions of the row technique, in which in-row intraspecific competitors were present in the competition treatments (Eagles 1972; Wilson & Newman 1987; Aerts, Boot & van der Aart 1991; Johnston & Pickering 2007). Effects of full and root competition did not differ significantly between these subgroups, whereas effects of shoot competition were larger overall in the former ($P = 0.079$).

Removal of partitions during the experiment

Within-study effects of apparatus used (cf. McPhee & Aarsen 2001) could not be evaluated, as this was reported for only four of the studies, whereas the effect of various experimental conditions related to experimental equipment and control could be assessed by meta-analysis.

Above- and below-ground partitions of some form were used to separate the shoots and roots of competitors in all studies, except for the use of repeated clipping of shoots as above-ground separators in two studies (Jeangros & Nösberger 1990; Seager, Kemp & Chu 1992). In a subset of 47 experiments from 13 studies (see Appendix S1), those partitions were maintained in another position in competition treatments, thereby potentially affecting resource availability to competitors. Of these studies, all but one (Marvel, Beyrouy & Gbur 1992) used the additive single target design of Donald (1958), the substitutive multiple-target designs of Snaydon (1971), or similar. The effects of full and root competition were significantly smaller overall in those experiments maintaining partitions during competition rather

than fully removing them (both $P < 0.05$; Fig. 3c). The overall effect of root competition was not larger than that of shoot competition when partitions were maintained in competition treatments ($P = 0.102$), whereas this was clearly the case when partitions were removed ($P < 0.001$). Although this indicated that the presence of below-ground partitions reduces root interaction, one must consider the potential confounding effect from the fact that all but two experiments employing a target design removed partitions during competition. (cf. the previous section).

Above-ground partitions

The techniques used to separate competitor shoots could be classified according to five levels of reduction in target plant light availability (i.e., shading); in increasing order of shading, these were (i) neighbour manipulation (removal or repression), use of (ii) reflective, (iii) transparent, (iv) semi-transparent or (v) opaque partition materials. Opaque and reflective partitions were the only partition types to be applied more or less equally among experimental designs. When analysed as a separate subset, these partition types generally did not affect shoot competition or interaction of shoot and root competition differently (not shown). All experiments employing a Target design used neighbour repression.

Overall effects of full, root and shoot competition were 56–63% lower in experiments preventing lateral influx of ambient light in all treatments compared with experiments not doing so, and the interaction between root and shoot competition was 84% lower overall, but none of these differences were statistically significant (not shown).

Below-ground partitions

Most studies used a solid below-ground material (plastic, wood or metal) to partition the roots of potential competitors, while 12 experiments from three studies employing the Target technique used below-ground partitions consisting partly or fully of fine mesh net (Marvel, Beyrouy & Gbur 1992; Cahill 1999; Bartelheimer, Gowing & Silvertown 2010). The effect of root competition was lower overall in this subgroup compared with the 30 experiments from four studies also employing the Target technique but using solid below-ground partitions; however, this difference was not significant (not shown). The group of studies using net partitions were characterized by a negative interaction between root and shoot competition of -50% ($P = 0.058$), which was significantly smaller than the overall level of interaction among studies using solid partitions ($P < 0.05$).

Discussion

Conclusions from individual experiments on root and shoot competition are highly variable, depending on a wide range of experimental and environmental factors. With the overall aim of providing an overview of the influence of these factors,

we hope to move interpretations and discussions of plant competition experiments towards a more informed basis. Although limited by the information available for each experiment, a coherent picture of some contested aspects of root and shoot competition emerge from the data, and some previous results are reconfirmed.

ROOT AND SHOOT COMPETITION CHANGE WITH NUTRIENT LEVEL

Despite large variation in the meaning of 'higher' and 'lower' levels of soil nutrients among studies, our results provided pronounced support for a change in competition with soil nutrient level. First, while target plants in all but one experiment were larger at higher nutrient levels, the proportional loss of biomass due to shoot competition was also slightly higher at these nutrient levels. This supports the hypothesis that the strength of competitive interactions among plant shoots due to shading increases with plant size. Secondly, the proportional loss of biomass due to root competition was generally higher at lower productivity, so that root competition was more important than shoot competition at lower nutrient levels but was not the main determinant of biomass loss at all nutrient levels. Shoot competition was therefore relatively more important at higher nutrient levels. Thirdly, the effect of full competition increased markedly with nutrient level, opposite to the effect of root competition alone. Finally, our results suggest that the effects of root and shoot competition are increasingly additive with increasing nutrient levels. While this was not statistically supported, our results indicate that this was primarily due to an all-dominant effect of root competition at lower nutrient levels. Heterogeneous meanings of higher and lower nutrient levels in the dataset, combined with varying measures of competition effect and interaction, allude why these findings do not confirm those of Cahill (1999; see Fig. 4 therein).

These findings support ecological theory and the findings of Wilson (1988). At one extreme, when soil resources were abundant, plants would more likely have grown until the leaf area index reached its maximum, and asymmetric competition for light became prominent; if all resources are somehow unlimited, plants will end up competing for physical space (McConnaughay & Bazzaz 1991). At the other extreme, plants in more resource-poor environments were more likely to be affected by neighbouring roots while growing slower, thus delaying the onset of shoot interaction (Casper & Jackson 1997).

INTERACTION BETWEEN ROOT AND SHOOT COMPETITION IS NOT THE RULE

Although interaction between root and shoot competition was far from significant both overall and in most groups of studies, significant levels of interaction were found in approximately one-third of all experiments. Estimating effects of root competition by the use of above-ground but not below-ground dividers, assuming that effects are additive, therefore cannot be generally recommended, although interaction seems to be more promi-

nent in certain types of experiments. Negative interaction overall was indicated among the groups of experiments (i) studying competition between grasses (the most competitive group), (ii) using mesh-like below-ground partitions (represented only by Target design studies) or (iii) using outdoor containers (including many of the row studies [*sensu* Schreiber 1967]). These findings of negative interaction support Liebig's law of the minimum, which is the basis for many resource-based models of competition (e.g. Tilman 1985). According to this theory, one should expect one resource, and by implication one mode of competition, to be more limiting for plant growth when plants are competing. The other mode of competition would then end up having little additional effect, which would result in a negative interaction between root and shoot competition.

EFFECTS OF PLANT SIZE, FUNCTIONAL GROUP AND DOMESTICATION

Relative plant size

A general discussion on the role of size in plant competition is beyond the scope of this article, but the data provide an opportunity to ask about the effect of one clear and commonly used definition: the size of plants in the control treatment. Our results clearly show that the relative (per-unit-size) effects of competitor neighbours decrease with the size of the target plants when root competition is involved. Bigger seems better for target plants, whereby they may evade competition. However, this result must be interpreted with caution because none of the studies reporting the sizes of both targets and neighbours used single target plants in an additive design, which is perhaps the most relevant design for addressing this question. Furthermore, tempting as it is to interpret this in terms of size-asymmetric competition, such a deduction would require information on the relative sizes of targets and neighbours at the onset of competition, not simply the size of a target plant without competition (Schwinning & Weiner 1998).

Functional group

Competition effects differed significantly among the three functional plant groups. Grass plants, the most frequent group of neighbours, generally had larger competitive effects than legumes and other herbs, also when the target was a grass. Below-ground niche differentiation was indicated by studies involving legumes, which were generally much less sensitive to root competition and had smaller below-ground effects as neighbours, possibly due to legumes' alternative source of nitrogen.

Non-leguminous herbs were relatively poor competitors, having the largest overall biomass reduction of the three functional groups following competition. Herb targets were also more sensitive to competition from grass neighbours than were grass targets. This could be due to the different growth strategies of grasses and herbs. Most grasses form dense stands through tillering (clonal growth) and have fibrous root systems, whereas most herbs produce only one main stem,

have single (often tap-) root systems and do not as often grow clonally. However, these differences should be interpreted with caution because they are confounded with experimental methods among the studies reviewed. Almost all studies using the Target technique had a grass as neighbour, planting the target species into an existing grass sward (e.g. Jeangros & Nösberger 1990; Cahill 1999, 2002; Lamb, Shore & Cahill 2007). Therefore, those competition effects are expected to be larger than when target and neighbour plants start at the same growth stage, as in the Divided pot experiments.

Wild versus domesticated plant species

Our meta-analysis shows that crop species are generally not as competitive as wild and weedy species, especially below-ground. Thus, in contrast to the generalization of Wilson (1988), our result suggests that root competition, not shoot competition, is the stronger component when crops compete with wild or weedy species. This is compatible with the notion that domestication of crops has involved trading off competitive ability for higher yield under high-resource and weed-free conditions. Furthermore, weeds often have a better utilization of nutrients than do crop plants and are usually fast-growing species adapted to disturbed environments and therefore capable of reducing nutrient levels further and faster than the crop (Mohler 2001).

THE IMPORTANCE OF EXPERIMENTAL DESIGN

The methods and designs applied in plant competition experiments vary as much as the questions being addressed, and occasionally, the methods are not appropriate for the questions they are meant to address (Gibson *et al.* 1999; Connolly, Wayne & Bazzaz 2001). We recognized some of the major differences in experimental design and confirmed how these may have profound impacts on reported effects of competition.

The relative merits and weaknesses of additive and substitutive designs have been extensively debated in the literature on interspecific plant competition (e.g. Connolly 1986; Rejmánek, Robinson & Rejmánková 1989; Snaydon 1991, 1996; Cousens 1996; Gibson *et al.* 1999; Connolly, Wayne & Bazzaz 2001). Here, we assume that both can be useful for addressing certain questions (Cousens 1996) and thus merit equal consideration. Our meta-analysis supports previous conclusions that additive design experiments generally show substantially larger effects of competition than do substitutive designs. The advantages of the response surface design, in which the densities of competing species are varied independently, have become widely accepted (Rejmánek, Robinson & Rejmánková 1989; Snaydon 1996), even when the number of experimental combinations is limited (Inouye 2001). Unfortunately, we found no experiments separating root and shoot competition that employed a response surface design.

Another aspect of the design of plant competition experiments, which has not received the same level of attention, is whether the target is a single plant or a group of plants. Our meta-analytic review clearly shows that group targets gener-

ally suffered less from competition compared with control treatments, presumably because intraspecific competition within the control treatment reduced the relative effect of competition from neighbours. This is different from designs with single target plants, which provide the benefit of a simple and clearly interpretable meaning of the control treatment as 'no competition'. Niche theory and experimental evidence suggest that intraspecific competition may often be stronger than interspecific competition, potentially decreasing our ability to measure the effects of interspecific competition in the presence of intraspecific competition. When there is a group of target plants, a positive effect of interspecific competition may not be evidence for facilitation but rather that intraspecific competition is stronger than interspecific competition (e.g. Silvertown & Charlesworth 2001).

CAVEATS AND LIMITATIONS OF STUDIES TO DATE

Bias and confounding

Published studies of root and shoot competition do not represent a random sample of growing conditions and plant communities, but are biased towards model systems on which researchers have focused for scientific reasons or potential applications. Because bias and confounding of experimental factors may thus reduce the generality of our results, we discuss some of these briefly.

Overall effects of root and shoot competition were found to be smaller in more restricted soil volumes. This documents the concern of Wilson (1988) that the rooting volume in pots is typically unrealistically limited, such that contrasts between control and competition treatments become biased. This is not inconsistent with the hypothesis that root competition is stronger in smaller soil volumes due to resource limitation, which was not tested directly, but rather recognizes the limits of pot studies. Experiments in pots or small containers may further underestimate effects of shoot competition because (i) limited soil volume also limits shoot growth, including leaf area index, and thereby shoot competition and (ii) edge effects whereby plants near an unshielded edge (all plants if pots are small) can compensate for above-ground neighbour competition by access to light they would not obtain in a field stand. These artefacts of experimental set-ups may explain why competition effects seem to decrease with increasing levels of environmental control. Most glasshouse pot experiments use a substitutive design, especially for crop–weed interactions (Gibson *et al.* 1999). In our data set, however, additive designs were used as often as substitutive designs in glasshouse and growth chamber studies, and there was no distinct confounding with experimental design along the purported gradient of environments.

Above-ground partitions are known to reduce or alter the light quality to some extent. Reflective partitions appear to minimize such bias (e.g. Schreiber 1967), while transparent materials allow some competition for light to occur through the partition (e.g. Eagles 1972; Scott & Lowther 1980; Brede & Duich 1986). Partition types were unevenly distributed across experimental designs and most likely confounded with these.

For example, 42 of 46 experiments using neighbour manipulation rather than solid partitions employed the Target technique.

Finally, while the period of interaction varied substantially between studies (not shown), they suggest that the reviewed competition effects reflect the initial dynamics of competitive interaction, in which the roots of plants tend to start interacting before their shoots (Aspinall 1960; King 1971; Casper & Jackson 1997). It is unclear to what extent this may have affected the perceived dominance of root competition compared with shoot competition and the apparently low levels of interaction between root and shoot interaction.

Outcome of competition

Information on many aspects of competition was not available for comparison among studies, reducing our ability to detect overall trends and interactions.

All conclusions in this review are based on measurements of vegetative growth. While these are valuable in assessing immediate competition effects, surprisingly few studies reported on measurements of reproductive effect, as required to evaluate the long-term outcome of competitive interaction and its wider effect on plant populations and communities. While many studies of plant competition fail to make this distinction (Gibson *et al.* 1999), we acknowledge that such an evaluation is beyond the scope of this review.

Another obstacle to direct inferences from the types of experiments reviewed here is the distinction between the strength and the importance of competition (Welden & Slauson 1986). If competition is very strong, but reduces the performance of all species equally, such that species proportions do not change, it may not be important for community composition. Although root competition may often be stronger than shoot competition, shoot competition can affect the variation in performance and determine which individuals or species dominate. Root competition may tend to affect the rate of growth and therefore speed of stand development, while shoot competition has greater effects on outcome: who gains and who loses over time (Morris & Myerscough 1984).

Facilitation and competition

The observed outcome of plant–plant interactions is the sum of competitive and facilitative effects. The former are usually larger than the latter, and facilitation effects are often overlooked (Brooker *et al.* 2008), although there are numerous exceptions, especially in extreme environments.

In this review, several negative values of competition effect provide support for net facilitation, and significantly lower effects of root competition in experiments having legumes as targets and/or neighbours give strong indications of facilitation from nitrogen fixation. Studies investigating root and shoot competition have usually been performed when there was a presumption of or evidence for net competition, with the goal of investigating the mechanisms involved; these designs have rarely been used when there was evidence for net facilitation. Our data set was therefore

not suited for addressing questions on the general relationship between facilitation and competition. It would be valuable if researchers studying facilitation were to apply these methods.

Synthesis

The presented meta-analysis provides some quite clear implications for managed plant communities. For example, competition below-ground was generally stronger than above-ground in resource-poor soils, which may explain the common observation of higher yield losses to weeds in low-resource agricultural systems. Weeds are the largest source of yield loss in agriculture, and this problem is worst in nutrient- and water-limited environments, despite a low leaf area index, and, by implication, limited competition for light. Our findings suggest that gains may be achievable in low-resource agricultural systems under high weed pressure through the development of crop genotypes with more competitive root systems.

On the other hand, the implications of the results of our meta-analysis for natural plant communities require further investigation. One limit is that of scale: all experiments reviewed occur within one generation, yet it is well known that one cannot extrapolate from such experiments to vegetation dynamics. For example, competition over the course of succession often favours species that can tolerate low light levels in established vegetation, but such species do not usually compete well in single-generation experiments.

Finally, our meta-analysis highlights that studies on individuals cannot directly be applied to effects on populations, or vice versa, and confirms that additive and substitutive designs expose different attributes of competition. These problems could be largely overcome by the use of response surface designs, varying the densities of competitor groups independently across a given range when separating root and shoot competition.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Study references, characteristics and competition effects of all experiments included in the meta-analysis.