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To compete or not to compete: an experimental study of interactions between plant species with contrasting root behaviour

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Abstract Game-theoretic models predict that plants with root systems that avoid belowground competition will be displaced by plants that overproduce roots in substrate shared with competitors. Despite this, both types of root response to neighbours have been documented. We used two co-occurring clonal species (*Glechoma hederacea* and *Fragaria vesca*) with contrasting root responses to neighbours (avoidance of competition and contesting of resources, respectively) to examine whether functional variation in other traits affected the success of each rooting strategy, leading to a different outcome from that predicted on the basis of root behaviour alone. Vegetative propagation rates, morphology and biomass allocation patterns were examined when each species was challenged with competition from physically separate ramets with either the same rooting strategy (intraclonal competition) or the contrasting rooting strategy (interspecific competition). Contrary to the predictions of game-theoretic models, the species that exhibits avoidance of root competition (*Glechoma*) was not competitively inferior to the species that does not (*Fragaria*). *Glechoma* achieved greater total mass in the interspecific treatment than in the intraclonal treatment. However, *Fragaria* did not experience more intense competition from *Glechoma* than it did in the intraclonal treatment. Strong interference between the two species appeared to be avoided because *Glechoma* invested preferentially in rapid exploitation of unoccupied space, whereas *Fragaria* invested in increasing the competitive ability and local persistence of established ramets. Our results suggest that interspecific trade-offs between traits related to competitive ability and resource exploitation can allow coexistence of species with contrasting rooting behaviours. Full assessment of the adaptive value of different root responses to neighbours therefore requires concurrent consideration of the combined effects of a wide array of functional traits.

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Introduction

Resource depletion has traditionally been regarded as the main mechanism determining belowground interactions between plants. However, other types of interaction between roots have been identified recently, and these have attracted considerable interest. Some studies have demonstrated the involvement of toxins in inhibiting the growth of neighbouring roots, but the basis of interactions in other cases, where neither resource depletion nor toxins are involved, remains largely unknown (Mahall and Callaway 1992, 1996; Bais et al. 2003; Falik et al. 2003; Holzapfel and Alpert 2003; Gruntman and Novoplansky 2004). In the few detailed studies that have been carried out to date, a variety of reactions to the roots of neighbours have been reported, including strong avoidance of root growth towards neighbours, no response, and even intensified root growth towards the roots of neighbours (Mahall and Callaway 1992, 1996; Falik et al. 2003; Holzapfel and Alpert 2003; de Kroon et al. 2003; Semchenko et al. 2007). However, the underlying causes of the evolution and coexistence of these different rooting behaviours remain unexplored.

While plant species differ in a variety of above-ground characteristics and life-history traits, previous theoretical models that have attempted to predict the adaptive value of different rooting strategies have assumed that, with the exception of their root responses to neighbours, plants possess identical characteristics. This simplification has led to the conclusion that the only evolutionarily stable strategy for plants lacking toxic exudates with which to suppress neighbours is to intensify root growth in the presence of neighbours rather than to avoid competition (Gersani et al. 2001; Maina et al. 2002; O’Brien et al. 2007). We suggest that consideration of functional variation in other plant traits that influence the competitive success of species could prompt the development of theoretical models that explain the range of root behaviours that have been observed.

To date, variation in functional traits has never been related to rooting behaviour in empirical studies because little information has been available about between-species differences in root responses to neighbours. However, a recent study by Semchenko et al. (2007) provides such information, reporting contrasting responses to neighbouring roots in two herbaceous clonal species, *Fragaria vesca* (wild strawberry) and *Glechoma hederacea* (ground ivy). *Fragaria* ramets expand their root systems in all directions irrespective of the presence and identity of neighbours and associated changes in resource availability. In contrast, *Glechoma* ramets tend to avoid belowground competition by limiting their root growth towards neighbours and by selective proliferation of roots in substrate that is free of competitors. Although Semchenko et al. (2007) addressed root responses to the presence of neighbours, the consequences of these contrasting rooting strategies under conditions of intense resource competition, and the role of other species traits, were not examined.

It is widely recognised that behaviour leading to competition between roots of the same plant, or between roots of genetically identical plants, should be selected against and avoided wherever possible (Falik et al. 2003; Gruntman and Novoplansky 2004; Schenk 2006). In clonal species, the frequency of competition between genetically identical ramets can be strongly influenced by species growth form. *Glechoma* is likely to experience frequent contact between ramets of the same clone due to its relatively short stolon internodes, and could therefore benefit from avoiding competition with neighbouring ramets (Semchenko et al. 2007). However, when growing with ramets of a species that does not avoid competition, such as *Fragaria*, the avoidance strategy of *Glechoma* would be predicted to be competitively inferior (Zhang et al. 1999; Gersani et al. 2001). In contrast, *Fragaria* produces long stolon internodes and will commonly interact with unrelated individuals interspersed between its ramets. For *Fragaria*, a more aggressive rooting strategy, such as predicted by game-theoretic models of root competition (Gersani et al. 2001; Maina et al. 2002; O'Brien et al. 2007), could be advantageous. Unless other traits modify the adaptive value of the two rooting strategies, the following predictions would be made: (1) a species with an avoidance rooting strategy, such as *Glechoma*, should perform better in monoculture of the same clone than in mixture with a species having an unresponsive rooting behaviour, such as *Fragaria*; (2) in contrast, a species with unresponsive rooting behaviour should perform better in mixture with a species that avoids root competition than in monoculture; (3) in a mixture of the two species, *Glechoma* should be outcompeted by *Fragaria*. Despite these predictions, the two species can be found growing completely intermingled in some communities, showing that coexistence of species with contrasting rooting behaviour is possible. Spatial competition models predict that coexistence of species with different competitive abilities is possible if an apparently inferior competitor has characteristics such as greater fecundity, higher growth rate or greater dispersal range, allowing faster colonization and exploitation of unoccupied space (Pacala and Rees 1998; Bolker and Pacala 1999; Amarasekare 2003; Wildová et al. 2007). Important characteristics that show wide functional variation between clonal species include rate of vegetative propagation, ramet size, spatial distribution of ramets and biomass within a clone, degree of physiological integration between connected ramets, capacity to store resources, runner and ramet longevity, and plasticity in clonal morphology and resource allocation (Lovett Doust 1981; de Kroon and Schieving 1990; de Kroon and Hutchings 1995; Hutchings and Wijesinghe 1997; Stuefer et al. 2002).

The aim of this study was to determine the principal differences in functional traits between species with contrasting root behaviour, and to examine how these differences affect the intensity of interspecific competition and the potential for coexistence. Vegetative propagation, morphology and biomass allocation patterns of two such species, *Glechoma hederacea* and *Fragaria vesca*, were examined when ramets of each species were challenged with competitors possessing either the same rooting strategy (a treatment involving intraclonal competition), or a different rooting strategy (a treatment involving interspecific competition). We hypothesised that each rooting pattern would be associated with a distinct set of attributes that together comprise alternative growth strategies, making it difficult to predict from root behaviour alone the relative performance of the two species in monocultures and interspecific mixture. A treatment allowing root competition but excluding shoot competition was employed to confirm the importance of root interactions in competition between ramets. A treatment with full competition (i.e. competition between roots *and* shoots) was used additionally to assess the importance of differences between the aboveground morphologies of the species in modifying the intensity of competition.

Materials and methods

Study species

Fragaria vesca L. is a winter-green clonal perennial herb producing numerous rosettes of leaves connected by long arching stolons. Vigorous clonal spread is frequently observed.

Regeneration from seed is probably most important for colonizing new sites (Grime et al. 2007).

Glechoma hederacea L. is a winter-green clonal perennial herb. Ramets consist of two leaves and are borne on branching stolons that usually persist for up to one growing season (Slade and Hutchings 1989). It is a carpet-forming herb with fast vegetative spread; establishment from seed is rare in many habitats (Grime et al. 2007).

The two species can be found growing together at woodland margins, in hedgerows and in scrubby grassland (Hutchings and Price 1999; Grime et al. 2007). In these habitats, the distances between adjacent ramets on a stolon are 2–11 cm and 19–49 cm for *Glechoma* and *Fragaria*, respectively (average of 6 and 33 cm, respectively; M. Semchenko, unpublished data).

Experimental design

Ramets of three genotypes each of *Glechoma* and *Fragaria* were selected from a stock of genotypes collected from widely separated sites in East Sussex, UK (Semchenko et al. 2007). These ramets were propagated vegetatively in a greenhouse for several months. Unrooted stolons of *Glechoma* and *Fragaria* growing from rooted mother ramets were placed on moist perlite to initiate root growth. After 4 days, the second, third and fourth ramets counted back from the apex of each stolon were separated from each other and from the rest of the clone by severing stolons mid-way between adjacent nodes, and transplanted into trays 18 cm long, 6 cm wide and 9.5 cm deep, filled with pre-washed sand. Nutrients were supplied in the form of controlled release fertiliser pellets (16% N, 8% P, 11% K, 2% Mg and micronutrients; Osmocote Mini Plus, Scotts Professional Ltd., Nottingham, UK) which were thoroughly mixed with the sand at the rate of 800 mg l^{-1}. These pellets release nutrients at a constant rate over a period of 3–4 months.

In the following text, the terms "focal ramet" and "neighbouring ramets" refer respectively to the ramets in the central and flanking positions within a tray, whereas the terms "mother ramet" and "daughter ramets" are used respectively for the ramet that was initially planted in the tray at the start of the experiment, and all of the new ramets that were subsequently produced by it. Sixteen treatments were established that combined three factors: species identity of the focal ramet (a ramet of either *Glechoma* or *Fragaria* established in the centre of each of the trays), mode of competition (full (i.e. root *and* shoot) competition or only root competition) and planting pattern (focal ramet without neighbours; two neighbours without a central focal ramet; monoculture, in which the focal ramet and both of the neighbouring ramets came from the same clone; mixture, in which the focal ramet was located between two neighbouring ramets of the other species; Fig. 1). The neighbouring ramets were each planted 4.5 cm from the focal ramet. In all treatments, and regardless of the species represented, the neighbouring ramets were the second and the fourth ramets from the apex of the stolon from which they were derived, and the focal ramet was the third ramet from the apex of the stolon from which it was derived. Within each tray, all ramets of the same species originated from the same stolon. Each treatment was replicated 12 times, and all genotypes were represented in each treatment.

Many species form monospecific patches under natural conditions as a result of clonal propagation. Ramets of the same genotype were used in this study when establishing the intraspecific treatments to reflect the composition of natural monocultures. It is known that, although the root responses of the two species to the presence of neighbours differ, responses within the species to different types of neighbour, whether belonging to the same clone (either with intact or severed stolon connections between ramets) or to a different clone, are

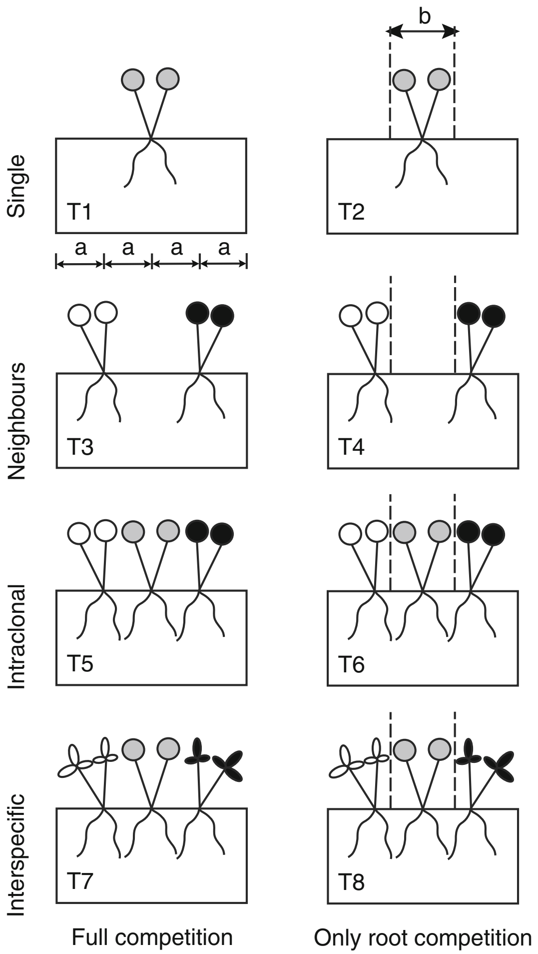

Fig. 1 Experimental design. Four planting combinations were crossed with two modes of competition (full competition and only root competition) and applied to two focal species (*Fragaria vesca* and *Glechoma hederacea*). The diagram illustrates the treatments for only one of the focal species; the same set of treatments was also implemented for the second species, giving a total of 16 treatments. In all treatments, neighbouring ramets were the second (shown in *white*) and the fourth (shown in *black*) ramets from the stolon's apex and the focal ramet (shown in *grey*) was the third from the stolon's apex. Distances between adjacent ramets and between neighbour ramets and tray walls are indicated by *arrows* and *letters* "a" ($a = 4.5$ cm). In treatments with root competition only (T2, T4, T6, T8), a white opaque plastic partition (12 cm high and 20 cm long) was placed vertically on each side of the focal ramet to prevent shoot competition with neighbours (distance between partitions indicated by *arrows*; $b = 6$ cm). Each treatment was replicated 12 times. See Sect. "Methods" for further detail

consistent (Semchenko et al. 2007). Therefore, the rooting behaviour of the study species is unlikely to be affected by the type of intraspecific interaction to which they are exposed.

To prevent aboveground competition in the "only root competition" treatment, white opaque plastic partitions 12 cm high and 20 cm wide were placed vertically and perpendicularly across the trays, between the focal ramet and its neighbours, at a distance of 3 cm from the rooting position of the focal ramet (Fig. 1). The inclusion of treatments with all combinations of the presence and absence of partitions, and the presence and absence of focal plants and neighbours, allowed us to test and control for possible confounding effects of partitions when assessing the effects of belowground competition (McPhee and Aarssen 2001).

The trays were placed in a glasshouse with a 16-h/8-h day/night cycle and a temperature of 18–20°C. Positions of trays were randomized within the glasshouse every 10 days. Trays were surface-watered to keep the substrate moist at all times. New ramets produced during the experiment (daughter ramets) were prevented from rooting.

After 8 weeks of growth, the roots and above-ground parts of each mother ramet, and all stolons and daughter ramets produced by buds emerging from its leaf axils, were harvested separately, dried at 75°C for 48 h and weighed. The height of each mother ramet, and the number of daughter ramets produced by it, were recorded. By the time of harvest, both species had produced numerous daughter ramets, some over a meter away from the mother ramet (Table 1). In addition, mother ramets of *Glechoma* started exhibiting signs of senescence. Therefore, we considered that the experiment had continued for long enough to fulfil our aim of analysing the outcome of local interactions between adjacent ramets.

Statistical analysis

One-way ANOVAs, applied to data on focal ramets grown without neighbours and without aboveground partitions, were used to assess general differences in growth characteristics between the studied species.

Growth parameters and resource allocation patterns in competition treatments were analysed using general linear models that included four factors: ramet position within a tray (repeated measures factor with three levels: focal ramet and each of the two neighbouring ramet positions), identity of the focal ramet (fixed factor with two levels: *Glechoma* or *Fragaria*), mode of competition (fixed factor with two levels: full competition or only root competition), and planting pattern (fixed factor with two levels: intraclonal monoculture or interspecific mixture). All interactions between these factors were included in the model. Genotype identity nested within species was not included in the final analysis as it did not have a significant effect on any of the traits.

Examination of treatments with focal ramets grown without neighbours and neighbouring ramets grown without a focal ramet showed that aboveground partitions, which were used in other treatments to prevent shoot competition, had a significant direct effect

Table 1 Mean trait values measured for *Fragaria vesca* and *Glechoma hederacea* ramets grown without neighbours and without aboveground partitions

Trait	Species	
	Fragaria	*Glechoma*
Total mass (g)	2.47 (0.11)	3.63 (0.20)*
Aboveground mass of mother ramet (g)	1.05 (0.04)	0.13 (0.02)*
Height of mother ramet (cm)	10.4 (0.4)	3.3 (0.2)*
Mass of daughter ramets (g)	1.21 (0.07)	3.27 (0.18)*
No. of daughter ramets	11.2 (0.8)	37.3 (2.8)*
Root mass (g)	0.21 (0.02)	0.23 (0.03) NS

Standard errors of the means are shown in parentheses

$N = 12$. Differences between means of the two species: * $P < 0.0001$; NS, $P > 0.05$ (one-way ANOVA). Untransformed data are shown. When necessary, variables were ln-transformed before analysis to improve normality of residuals and homogeneity of variances on the growth of focal ramets, but no significant effect on the growth of neighbouring ramets. Therefore, to correct for the confounding effect of partitions on the growth of focal ramets, the competitive response to full competition versus only root competition was estimated using a standardised variable expressed as ln (mean dry mass of the focal ramet in a competition treatment/mean dry mass of the focal ramet in an appropriate control). Treatments with single ramets and no partitions were used as the control for full competition treatments, and treatments with single ramets and partitions present were used as the control for only root competition treatments (McPhee and Aarssen 2001). This metric is equivalent to the log response ratio used in previous studies (Cahill 1999; Hedges et al. 1999; Weigelt and Jolliffe 2003) except that different control treatments are used to calculate full and belowground competitive response.

Statistical analyses were performed using STATISTICA 7 (StatSoft Inc., Tulsa, OK, USA) and R 2.8.0 (R Development Core Team 2008).

Results

General growth characteristics

Ramets of *Glechoma* grown without neighbours exhibited significantly faster growth (demonstrated by greater total mass after the same growth period despite smaller initial size), and produced a greater mass of daughter ramets, than those of *Fragaria* (Table 1). At harvest, mother ramets accounted for 46% of aboveground mass in *Fragaria*, but only 4% of aboveground mass in *Glechoma*. Mother ramets of *Fragaria* were also significantly taller, and only produced one-third as many daughter ramets as did mother ramets of *Glechoma* (Table 1). No significant differences in root mass were found between the two species. The observed interspecific differences in biomass production and allocation between mother ramet and vegetative offspring followed similar patterns in the competition treatments (Fig. 2).

Growth responses to intraclonal and interspecific competition

For all measured traits except root mass, there were significant three-way interactions between the position of a ramet within a tray (i.e. focal ramet or neighbouring ramet), the identity of the focal ramet (*Fragaria* or *Glechoma*) and the planting pattern (intraclonal or interspecific; $P < 0.0001$; Fig. 2; Appendix—Table 2). No significant four-way interactions (between the factors mentioned above and the mode of competition, i.e. full competition or only root competition) were observed (Appendix—Table 2).

Focal plants of *Glechoma* exhibited greater growth in the interspecific competition treatment than in the intraclonal competition treatment (mean difference in total mass = 35%; $P = 0.0002$, Tukey test; Fig. 2a). The increase in growth was manifested as an increase in the number of daughter ramets (21% difference, $P = 0.0991$, Tukey test) and their total mass (40% difference, $P = 0.0001$, Tukey test; Fig. 2b). The root mass and the height and shoot mass of mother ramets of *Glechoma* did not differ significantly between intraclonal and interspecific competition treatments ($P > 0.05$, Tukey test; see Fig. 2c, d for shoot and root mass; height data not shown). There were no significant differences in any growth parameters between the intraclonal and interspecific treatments for focal ramets of *Fragaria* ($P > 0.05$, Tukey test; Fig. 2). As a result of the significant increase in mass of *Glechoma* and no significant difference in mass of *Fragaria* between

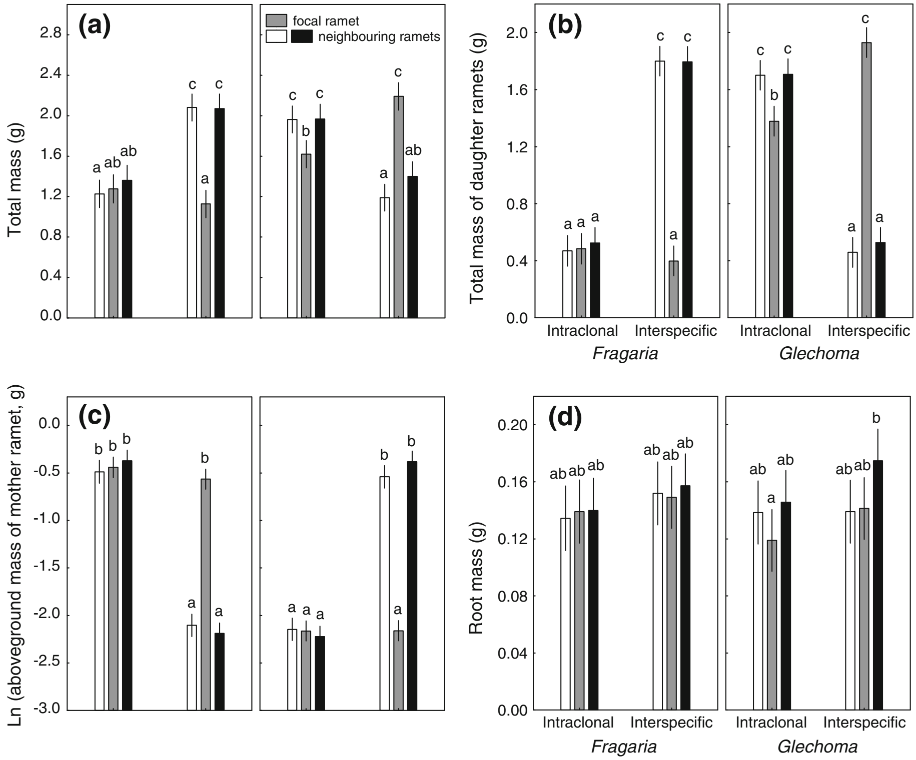

Fig. 2 The effects of the identity of neighbouring ramets (the same clone or a different species) on **a** total dry mass, **b** total mass of daughter ramets produced by each mother ramet, **c** aboveground mass of mother ramet and **d** root mass. Two species were used to provide the focal ramets: *Fragaria vesca* (graphs on the *left*) and *Glechoma hederacea* (graphs on the *right*). The shading used in this figure corresponds with the shading used in Fig. 1 to distinguish ramet positions within a tray. The figure demonstrates the significant interaction ($P < 0.05$) between focal species, planting pattern (intraclonal or interspecific) and ramet position within a tray for all traits except root mass. Data from treatments with full competition and only root competition were combined as the four-way interaction with the mode of competition was not significant for any of the traits ($P > 0.05$). *Error bars* denote 95% confidence intervals for the mean. *Different letters* indicate significant differences between means within each trait ($P < 0.05$, Tukey test)

the interspecific and intraclonal treatments, the total combined mass of the two interspecific mixtures was significantly greater than that of the two monocultures (the main effect of planting pattern significant at $F_{1,87} = 5.9$, $P = 0.0171$).

Effects of the mode of competition

When corrected for the effects of partitions, analysis of competitive responses showed that focal ramets of *Fragaria* experienced intense competition from neighbouring ramets in the intraclonal treatment with full competition, whereas little effect of neighbours was detected in the intraclonal treatment with root competition only (no significant difference in total mass between plants grown alone and in the presence of neighbours' roots, $P > 0.05$; Fig. 3). In contrast, focal ramets of *Glechoma* exhibited a similar response to competition from neighbours in the two intraclonal treatments (full competition or only root competition; Fig. 3). In the interspecific treatments, the intensity of competition was reduced by

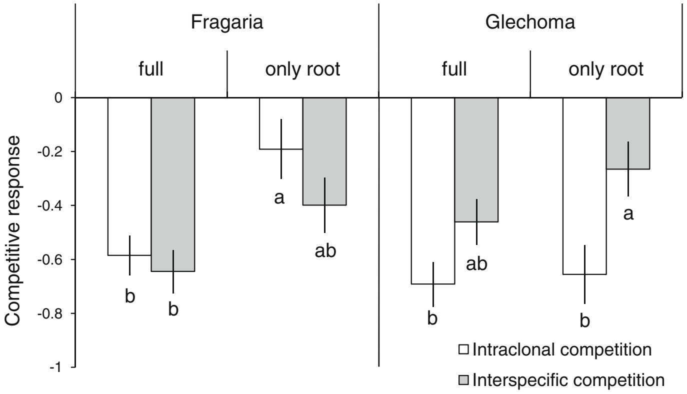

Fig. 3 Competitive responses exhibited by focal ramets of *Fragaria vesca* and *Glechoma hederacea* in treatments with either full competition or only root competition, and either intraclonal or interspecific competition. Competitive response was calculated as the natural logarithm of (mean dry mass of the focal ramet in a competition treatment/mean dry mass of the focal ramet in an appropriate control treatment). To remove possible confounding effects of partitions, a treatment with plants grown without neighbours and without partitions was used as control for full competition treatments, and a treatment with plants grown without neighbours and with aboveground partitions was used as control for "root only" competition treatments. Greater negative values mean that the focal ramet experienced more intense competition. *Error bars* denote 1SE of the mean. *Different letters* indicate significant differences between means within each species ($P < 0.05$; Tukey test)

the exclusion of aboveground competition for both species, but the reduction was not statistically significant.

The intensity of competition experienced by focal *Fragaria* ramets was not significantly different between intraclonal and interspecific treatments, regardless of the mode of competition (Fig. 3). In contrast, focal ramets of *Glechoma* experienced less intense competition in the interspecific treatments than in the intraclonal treatments. The reduction in intensity of competition was more pronounced when shoot competition was prevented (Fig. 3).

Discussion

The results of the experiment did not support the predictions that *Glechoma*, the species exhibiting avoidance of root competition, should perform better in monoculture than in mixture with *Fragaria*, the species exhibiting unresponsive root behaviour, or that the opposite should be true for the performance of *Fragaria*. Instead, *Glechoma* achieved greater growth in the mixture with *Fragaria* than in intraclonal monoculture. However, *Fragaria* ramets did not show significant reductions in growth in mixture with *Glechoma*, compared with their growth in intraclonal monoculture. Consequently, neither of the species was clearly outcompeted by the other, and the two interspecific mixtures produced more biomass in total than the two monocultures. Our results suggest that differences between the species in other functional traits overcame the expected disadvantage of avoidance behaviour in interspecific competition and led to the performance of plants in monocultures and mixture being different from that predicted on the basis of root behaviour alone. *Glechoma* ramets, which grow fast and forage efficiently for soil-based resources (Birch and Hutchings 1994; Wijesinghe and Hutchings 1999), presumably increased their resource uptake in the interspecific mixture by avoiding *Fragaria* roots and by rapidly exploiting substrate that *Fragaria* roots had not occupied because of their slow growth (Semchenko et al. 2007). However, the additional mass obtained in the interspecific treatment was invested in production of vegetative offspring, rather than in enhancement of the capacity of the mother ramet for localised competition with neighbouring *Fragaria* ramets. No additional root production or increase in the aboveground size of mother ramets of *Glechoma* was observed (Fig. 2). As a result, *Fragaria* ramets did not experience more intense competition from *Glechoma*, even though *Glechoma* exhibited greater growth in the interspecific treatment.

The results of some previous empirical studies have suggested that a trade-off in resource allocation between clonal spread (colonization ability) and individual ramet size (ramet-level competitive ability) could serve as a mechanism by which species coexistence could be achieved (Wildová et al. 2007; Moora et al. 2009). The ability of weaker competitors to rapidly exploit unoccupied, resource-rich habitat patches could also promote species coexistence, but this mechanism has been largely overlooked or confounded with colonization ability in previous studies (Pacala and Rees 1998; Bolker and Pacala 1999; Amarasekare 2003). Our results indicate that a trade-off between the competitive ability of individual ramets and an ability to exploit unoccupied habitat rapidly for resources may allow the coexistence of species with contrasting rooting behaviours. In our study, *Fragaria* invested heavily in promoting the competitive ability and persistence of established ramets at the expense of high rates of growth and vegetative propagation. It allocated a high proportion of its resources into enhancing the capacity of established ramets to shade competing vegetation (i.e. it invested in greater height and aboveground mass of the mother ramet, Table 1) and to contest belowground resources (i.e. it displayed no tendency to avoid substrate occupied by the roots of neighbours). The strong competitive ability of *Fragaria* for aboveground resources was demonstrated by the fact that the impact of neighbours on the growth of *Glechoma* ramets in the interspecific treatment compared with the intraclonal treatment was reduced more when aboveground competition was prevented (Fig. 3). In contrast, *Glechoma* exhibited low competitive ability at the individual ramet level—it is characterised by small ramet size and avoidance of belowground competition. The success of *Glechoma* lies in its capacity for rapid exploitation of unoccupied space through fast growth and clonal propagation. Therefore, the rooting behaviour of the two species can be viewed as an integral part of their contrasting growth strategies: contesting belowground resources contributes to the competitive ability of *Fragaria*, which invests in long-term persistence in occupied patches, while avoidance of root competition with neighbours ensures efficient exploitation of unoccupied space by *Glechoma*.

Growth responses to intraclonal competition reinforce the conclusions about different capacities for aboveground competition in the two species. Focal ramets of *Glechoma* experienced similar reductions in growth in the “only root competition” treatment and in the “full competition” treatment. *Glechoma* has limited potential to exert intense competition aboveground as each ramet consists of only two small leaves. The limited growth of focal ramets in the presence of intraclonal neighbours was mainly due to partitioning of belowground space between neighbouring ramets. In contrast, belowground competition was not very intense in the intraclonal monoculture of *Fragaria* ramets (Fig. 3). However, the intense competition observed in the full competition treatment suggests that *Fragaria* ramets competed strongly for light.

In addition to the findings of this experiment, previous studies have shown that the two species exhibit considerable differences in other traits that reflect the fundamental trade-off between relative growth rate and life span (Lambers and Poorter 1992; Poorter and Garnier 2007). For example, the longevity of *Fragaria* ramets can be up to 6 years, whereas

Glechoma ramets generally survive no longer than a year (Angevine 1983; Slade and Hutchings 1989; Tamm et al. 2002). Conversely, specific root length, which is related to the potential resource uptake rate per unit root construction cost (Eissenstat 1991; Wright and Westoby 1999; Eissenstat et al. 2000), is 38% lower for *Fragaria* than for *Glechoma* (M. Semchenko, unpublished data).

Previous theoretical studies have predicted that avoidance of belowground competition is not an evolutionarily stable strategy, and that it will be supplanted by a strategy of root proliferation in the presence of competitors (Zhang et al. 1999; Gersani et al. 2001; Maina et al. 2002). However, a variety of root responses to neighbours, including numerous cases of avoidance of root growth towards neighbours, have been documented (Mahall and Callaway 1992, 1996; Schenk et al. 1999; Holzapfel and Alpert 2003; Semchenko et al. 2007). We propose that consideration of root behaviour in conjunction with other functional traits may reveal mechanisms that permit the co-existence of species with different rooting patterns and may reconcile the discrepancy between theoretical predictions and empirical observations. The results of this study clearly demonstrate that, in the case of *Glechoma* and *Fragaria*, avoidance of root competition with neighbours is not inferior to contesting resources. The outcome of competition, and the capacity for species with different rooting strategies to coexist, appear to be contingent upon differences in additional characteristics such as growth rate, ramet size, biomass allocation to clonal spread, and the spatial distribution of ramets within a clone. Valid conclusions about the adaptive value of different root responses to neighbours can therefore only be reached if a broad array of functional traits is considered in combination.

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Appendix

See Table 2.

Table 2 The results of ANOVA for six plant traits

	df	Total mass	ln (mass of mother ramet)	Height of mother ramet	Mass of daughter ramets	Number of ramets	Root mass
Species	1	20.3***	170.4***	141.9***	130.5***	70.8***	0.1
Pattern	1	5.9*	0.2	1.9	10.9**	2.0	3.3
Mode of competition	1	4.1*	3.4	2.0	3.5	1.6	5.2*
Species*pattern	1	68.3***	701.1***	560.6***	504.2***	339.3***	0.02
Species*mode	1	0.9	2.1	0.4	1.5	0.02	0.1
Pattern*mode	1	2.4	1.0	1.5	4.0*	0.9	0.01
Species*pattern*mode	1	0.5	2.4	2.6	0.1	0.3	0.2
Error	87						
Position	2	4.9**	1.0	4.4*	3.2*	3.3*	4.7**
Position*species	2	43.5***	472.8***	299.9***	198.8***	169.5***	2.4
Position*pattern	2	1.9	0.8	0.9	4.4*	1.9	0.7
Position*mode	2	7.8**	5.4**	0.3	6.9**	4.4*	6.0**

Table 2 continued

	df	Total mass	ln (mass of mother ramet)	Height of mother ramet	Mass of daughter ramets	Number of ramets	Root mass
Position*species*pattern	2	90.9***	497.5***	280.9***	310.0***	242.0***	1.0
Position*species*mode	2	0.7	1.2	3.6*	0.3	0.5	1.0
Position*pattern*mode	2	1.1	0.4	0.9	0.9	0.4	0.01
Position*species*pattern*mode	2	0.5	0.05	0.1	0.8	1.2	0.1
Error	174						

F-values and the statistical significance of focal species (fixed factor with two levels: *Glechoma* or *Fragaria*), planting pattern (fixed factor with two levels: intraclonal monoculture or interspecific mixture), mode of competition (fixed factor with two levels: full competition or only root competition) and ramet position within a tray (repeated measures factor with three levels: focal ramet and each of the two neighbouring ramet positions) are presented

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.0001$

References

Amarasekare P (2003) Competitive coexistence in spatially structured environments: a synthesis. Ecol Lett 6:1109–1122

Angevine MW (1983) Variations in the demography of natural populations of the wild strawberries *Fragaria vesca* and *Fragaria virginiana.* J Ecol 71:959–974

Bais HP, Vepachedu R, Gilroy S, Callaway RM, Vivanco JM (2003) Allelopathy and exotic plant invasion: from molecules and genes to species interactions. Science 301:1377–1380

Birch CPD, Hutchings MJ (1994) Exploitation of patchily distributed soil resources by the clonal herb *Glechoma hederacea.* J Ecol 82:653–664

Bolker BM, Pacala SW (1999) Spatial moment equations for plant competition: understanding spatial strategies and the advantages of short dispersal. Am Nat 153:575–602

Cahill JF (1999) Fertilization effects on interactions between above- and belowground competition in an old field. Ecology 80:466–480

de Kroon H, Hutchings MJ (1995) Morphological plasticity in clonal plants: the foraging concept reconsidered. J Ecol 83:143–152

de Kroon H, Schieving F (1990) Resource partitioning in relation to clonal growth strategy. In: van Groenendael J, de Kroon H (eds) Clonal growth in plants: regulation and function. SPB Academic Publishing, The Hague, pp 113–130

de Kroon H, Mommer L, Nishiwaki A (2003) Root competition: towards a mechanistic understanding. In: de Kroon H, Visser EJW (eds) Root ecology, vol 168. Springer, Berlin, pp 215–234

Eissenstat DM (1991) On the relationship between specific root length and the rate of root proliferation: a field study using citrus rootstocks. New Phytol 118:63–68

Eissenstat DM, Wells CE, Yanai RD, Whitbeck JL (2000) Building roots in a changing environment: implications for root longevity. New Phytol 147:33–42

Falik O, Reides P, Gersani M, Novoplansky A (2003) Self/non-self discrimination in roots. J Ecol 91:525–531

Gersani M, Brown JS, O'Brien EE, Maina GM, Abramsky Z (2001) Tragedy of the commons as a result of root competition. J Ecol 89:660–669

Grime JP, Hodgson JG, Hunt R (2007) Comparative plant ecology: a functional approach to common british species. Castlepoint Press, Colvend

Gruntman M, Novoplansky A (2004) Physiologically mediated self/non-self discrimination in roots. Proc Natl Acad Sci USA 101:3863–3867

Hedges LV, Gurevitch J, Curtis PS (1999) The meta-analysis of response ratios in experimental ecology. Ecology 80:1150–1156

Holzapfel C, Alpert P (2003) Root cooperation in a clonal plant: connected strawberries segregate roots. Oecologia 134:72–77

Hutchings MJ, Price EAC (1999) *Glechoma hederacea* L. (Nepeta glechoma Benth., *N. hederacea* (L.) Trev.). J Ecol 87:347–364

Hutchings MJ, Wijesinghe DK (1997) Patchy habitats, division of labour and growth dividends in clonal plants. Trends Ecol Evol 12:390–394

Lambers H, Poorter H (1992) Inherent variation in growth rate between higher plants: a search for physiological causes and ecological consequences. Adv Ecol Res 23:187–261

Lovett Doust L (1981) Population dynamics and local specialization in a clonal perennial (*Ranunculus repens*). I. The dynamics of ramets in contrasting habitats. J Ecol 69:743–755

Mahall BE, Callaway RM (1992) Root communication mechanisms and intracommunity distributions of two Mojave Desert shrubs. Ecology 73:2145–2151

Mahall BE, Callaway RM (1996) Effects of regional origin and genotype on intraspecific root communication in the desert shrub *Ambrosia dumosa* (Asteraceae). Am J Bot 83:93–98

Maina GG, Brown JS, Gersani M (2002) Intra-plant versus inter-plant root competition in beans: avoidance, resource matching or tragedy of the commons. Plant Ecol 160:235–247

McPhee CS, Aarssen LW (2001) The separation of above- and below-ground competition in plants—a review and critique of methodology. Plant Ecol 152:119–136

Moora M, Öpik M, Zobel K, Zobel M (2009) Understory plant diversity is related to higher variability of vegetative mobility of coexisting species. Oecologia 159:355–361

O'Brien EE, Brown JS, Moll JD (2007) Roots in space: a spatially explicit model for below-ground competition in plants. Proc R Soc Lond B Biol Sci 274:929–934

Pacala SW, Rees M (1998) Models suggesting field experiments to test two hypotheses explaining successional diversity. Am Nat 152:729–737

Poorter H, Garnier E (2007) Ecological significance of inherent variation in relative growth rate and its components. In: Pugnaire FI, Valladares F (eds) Handbook of functional plant ecology. CRC Press, Boca Raton, pp 67–100

R Development Core Team (2008) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Schenk HJ (2006) Root competition: beyond resource depletion. J Ecol 94:725–739

Schenk HJ, Callaway RM, Mahall BE (1999) Spatial root segregation: are plants territorial? Adv Ecol Res 28:145–180

Semchenko M, John EA, Hutchings MJ (2007) Effects of physical connection and genetic identity of neighbouring ramets on root-placement patterns in two clonal species. New Phytol 176:644–654

Slade AJ, Hutchings MJ (1989) Within-population and between-population variation in ramet behavior in the gynodioecious clonal herb, *Glechoma hederacea* (Labiatae). Can J Bot 67:633–639

Stuefer JF, Van Hulzen JB, During HJ (2002) A genotypic trade-off between the number and size of clonal offspring in the stoloniferous herb *Potentilla reptans*. J Evol Biol 15:880–884

Tamm A, Kull K, Sammul M (2002) Classifying clonal growth forms based on vegetative mobility and ramet longevity: a whole community analysis. Evol Ecol 15:383–401

Weigelt A, Jolliffe P (2003) Indices of plant competition. J Ecol 91:707–720

Wijesinghe DK, Hutchings MJ (1999) The effects of environmental heterogeneity on the performance of *Glechoma hederacea*: the interactions between patch contrast and patch scale. J Ecol 87:860–872

Wildová R, Wild J, Herben T (2007) Fine-scale dynamics of rhizomes in a grassland community. Ecography 30:264–276

Wright IJ, Westoby M (1999) Differences in seedling growth behaviour among species: trait correlations across species, and trait shifts along nutrient compared to rainfall gradients. J Ecol 87:85–97

Zhang DY, Sun GJ, Jiang XH (1999) Donald's ideotype and growth redundancy: a game theoretical analysis. Field Crop Res 61:179–187