

Root decisions

ANGELA HODGE

Department of Biology, Area 14, University of York, York, YO10 5YW, UK

ABSTRACT

Root systems have recognizable developmental plans when grown in solution or agar; however, these plans often must be modified to cope with the prevailing conditions in the soil environment such as the avoidance of obstacles and the exploitation of nutrient-rich patches or water zones. The modular structure of roots enables them to respond to their environment, and roots are very adaptive at modifying growth throughout the root system to concentrate their efforts in the areas that are the most profitable. Roots also form associations with microorganisms as a strategy to enhance resource capture. However, while the responses of roots in nutrient patches are well-recognized, overall ‘rules of response’ and variation in strategy among plant species that can be applied in a number of different environments are still lacking. Finally, there is increasing evidence that root–root interactions are much more sophisticated than previously thought, and the evidence for roots to identify self from non-self roots will be briefly discussed.

Key-words: mycorrhizas; root-released compounds; root response to heterogeneity; root–root interactions; root system coordination; Tragedy-of-the-Commons response.

Abbreviations: AM, arbuscular mycorrhiza; AMF, arbuscular mycorrhizal fungi; QTL, quantitative trait loci; RSA, root system architecture.

INTRODUCTION

It is well-established that plants are able to show considerable plasticity in their morphology and physiology in response to variability within their environment, particularly as regards foraging for resources (Hodge 2004, 2006; Valladares, Gianoli & Gómez 2007). Perhaps it was inevitable, therefore, that parallels between animal and plant behaviour would be drawn (see Gersani *et al.* 2001; Maina, Brown & Gersani 2002; Trewavas 2005). More recently, some researchers have even called for a new field of plant biological research, that of plant ‘neurobiology’ (Brenner *et al.* 2006; see also Baluška, Volkmann & Menzel 2005). The idea of plants having ‘brain-like’ control is nothing new and, as cited by Trewavas (2005, 2007), was first suggested by Charles Darwin in the late 19th century. However, while this new field does have some support (see Trewavas 2007), others have argued it adds very little to what could already

be described under the existing areas of plant cell biology, physiology or signalling (Alpi *et al.* 2007; Struik, Yin & Meinke 2008). The purpose of this review was not to be drawn into this debate of plant ‘neurobiology’ but, rather, to review the literature on how roots respond both to some key environmental problems they face as part of their normal growth and function, and how they respond to other plant roots. Thus, the debate on plant ‘neurobiology’ aside, **roots do respond in a number of remarkable and sophisticated ways** in which we are only just beginning to understand.

OBSTACLES TO ROOT GROWTH AND FUNCTION

Roots are modular structures, which makes them extremely flexible in detecting their environment and responding accordingly. Roots can respond to moisture gradients, and a novel gene, *miz1* (from *mizu-kussei* meaning ‘water’ and ‘tropism’, respectively, in Japanese) has recently been identified which appears to be important for hydrotropism in *Arabidopsis* (Kobayashi *et al.* 2007). Mutants had normal gravitropism and elongation, suggesting the hydrotropism response is independent of gravitropism but that the root cap is important for detecting signals from both tropic responses (Kobayashi *et al.* 2007). Recently, Dinneny *et al.* (2008) attempted to localize stress perception in roots of *Arabidopsis*. In response to salt stress radially, genes located in the epidermis, cortex and stele were highly responsive, while longitudinally, an increase in salt responsiveness correlated with the start of the elongation zone. Strikingly, however, in the few studies that have examined the response of multiple stresses, only a small proportion of the regulated genes appear to be ‘shared’ (see Rizhsky *et al.* 2004; Dinneny *et al.* 2008), thus suggesting much more complex pathways than investigations with only a single stress may otherwise imply.

The root cap has also been shown to be important in detecting obstacles via touch. Roots of various plant species (*Arabidopsis thaliana*, *Lepidium sativum* and *Phleum pratense*) were able to perceive touch stimuli upon encountering a glass rod obstacle, and modified their gravitropic growth to circumvent the physical obstacle (Massa & Gilroy 2003). Although other parts of the root also responded to touch, the root cap was more effective in down-regulating the gravitropic response to allow obstacle avoidance (Massa & Gilroy 2003). Growth of *Pisum sativum* roots were also modified by the presence of a physical barrier (in this case, nylon string), and while numbers of

Correspondence: A. Hodge. Fax: +44 1904 328505; e-mail: ah29@york.ac.uk

lateral roots produced remained relatively unaffected, their length, extent of withering and azimuth all changed at the side to which the barrier was placed compared to the opposite side of the root system with no physical barrier. An accumulation of unidentified root-released compounds because of the presence of the physical barrier was thought to be responsible for these changes in lateral root growth (Falik *et al.* 2005). Having such a mechanism presumably prevents roots developing in areas which are not profitable for exploration and thus conserve resources. Perhaps the most well-established (and most studied) response by roots, however, is their ability to respond to nutrient-rich zones or 'patches' by proliferation of roots; but here also, roots are faced with a number of decisions, if and how to respond to the patch, should growth elsewhere be modified and so forth as discussed below.

RESOURCE ALLOCATION TO ROOTS

All plants face a basic economic decision: where best to invest their resources. The costs associated with getting this wrong may lead to reduced nutrient capture, less resources for reproduction, hence reduced fitness, and at the extreme, competitive exclusion from the particular environment. Thus, the first decision the plant must make is how to allocate resources between above- and below-ground structures. So, how does the environment influence this allocation and are there any differences among plant species in biomass allocation above- and below-ground? The evidence available suggests that plants generally show the same adaptive response: when nutrient uptake from the soil is limiting, they invest more in their roots. For example, in a survey of the literature Reynolds & D'Antonio (1996) found that while the root weight ratio (RWR; the ratio of root weight to total plant weight) increased with decreased nitrogen (N) availability, there was no evidence that plasticity in the RWR was related to plant competitive ability. Thus, under low N all plants showed the same response and allocated more resources to their roots to enhance N capture.

Similarly, Campbell, Grime & Mackey (1991) found that when plants were grown in a nutrient heterogeneous or 'patchy' environment, generally both competitively dominant and inferior plant species responded in the same way by allocating 10–20% of their new dry matter production to their roots. Importantly, however, Campbell *et al.* (1991) also found that the manner in which plants allocated their biomass *within* the root system varied. The competitively dominant plants exploited the nutrient-rich patches to a greater extent simply because they were larger and had higher growth rates rather than because they had greater flexibility within their root system. In contrast, the competitively inferior plants, although smaller, allocated more of their *new* root growth to nutrient-rich areas, that is, they placed their new roots with greater precision. From their work, Campbell *et al.* (1991) concluded there was a trade-off between the scale and the precision of the response depending on the competitive ability of the plant species.

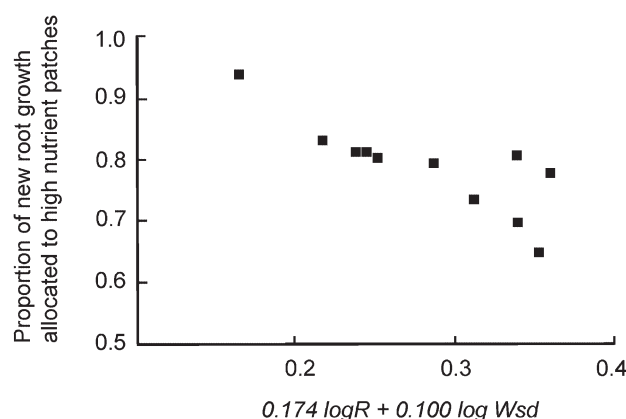


Figure 1. Precision of root foraging of the species used by Campbell *et al.* (1991) as a function of plant size. As size increases, precision decreases. Plant size has been expressed in terms of seed weight (*Wsd*) and growth rate (*R*) by means of a regression of root allocation on these two variables, and a new variable based on the regression coefficients constructed to display the relationship. This figure was originally published in Fitter (1994) *Exploitation of Environmental Heterogeneity by Plants* (eds M.M. Caldwell & R.W. Pearcy), pp. 305–323. Academic Press, San Diego, Copyright Elsevier (1994). Reproduced with kind permission from the author and the Elsevier.

Later, Fitter (1994), using Campbell *et al.*'s (1991) original data, demonstrated that precision was in fact a simple function of plant size (see Fig. 1) and thus, larger plants, rather unsurprisingly, behaved differently from small ones. Therefore, an interesting question arises from Fitter's analysis: how do small specimens of large plants (i.e. Campbell *et al.*'s competitively dominant species) respond? Do they show greater precision when starved or younger than they do when larger either by being older or well-fed?

Although the questions that arise from Fitter's (1994) further analysis remain to be tested, the original 'scale and precision trade-off' hypothesis for competitively dominant versus inferior plants has been widely investigated for a range of plant species from different environments. However, subsequent evidence to support this hypothesis has been, at best, weak (see Einsmann *et al.* 1999; Farley & Fitter 1999; Bliss *et al.* 2002; Kembel & Cahill 2005; de Kroon & Mommer 2006; Rajaniemi 2007; but see Wijesinghe *et al.* 2001). This, in turn, recently prompted Grime (2007) to clarify that in his and his coworkers' original work, they never proposed that such a scale-precision response occurred for all plant species, but rather, to those from communities in which intermittent disturbance (e.g. biomass removal) occurs such as mown meadows. Grime's (2007) clarification, however, has also sparked controversy in the literature (see Kembel *et al.* 2008) not least because the plant species originally used by Campbell *et al.* (1991) were extremely heterogeneous varying in morphology, life history, potential growth rate and ecology, and hence from a range of habitats varying in disturbance.

Thus, given the deliberate wide variation in species selection criteria employed by Campbell *et al.* (1991) as a test of

the predictive power of their foraging assays, it was inevitable in the desire to find general principles of root behaviour that others would test the generality of the scale-precision trade-off for other plant species and environments. Direct comparisons among these subsequent studies are complicated by variation among researchers in assessing 'scale' and 'precision', but it seems likely that scale and precision are simply not widespread plant attributes, at least in as far as explaining foraging differences between competitively dominant versus inferior species (see Kembel & Cahill 2005). Importantly, Wijesinghe *et al.* (2001), one of the few studies that did find support for smaller rooted species showing greater precision, also found that 'precision' was not a fixed attribute and varied within the plant species tested depending on the way the patches were presented. In other words, precision may also be a plastic response, and the extent to which this response is expressed may depend on the attributes of the nutrient patch encountered as well as the plant species.

Given the subsequent lack of evidence to support the original scale-precision hypothesis may lead one to conclude the study by Campbell *et al.* (1991) has only limited benefit. However, this would be far too harsh a judgement. Campbell *et al.* (1991) were among the first to try and tackle a difficult problem, one which we are still wrestling with today, and, as highlighted in this review, general rules of root behaviour are hard to predict. The more we examine roots, the more complex their responses and interactions prove to be. Moreover, the approach by Campbell *et al.* (1991) was novel. Their microcosm unit enabled nutrient-rich and nutrient-poor quadrants to be established without the use of barriers, thus allowing free root growth and the plant choice as to where they placed their roots within this patchy environment. Finally, and perhaps most importantly, Campbell *et al.* (1991) demonstrated that while the allocation below-ground may be similar, how this biomass is then distributed may differ among plant species or, rather may differ under the experimental conditions they employed. Thus, the *context* in which the response is observed is as important as the response itself, and one should not be measured without due consideration of the other, a topic that we will return to in the next section.

It is often true when interesting patterns of root responses to particular conditions are reported, it is often assumed that this is what all plants do. Take the findings by Malcolm Drew and coworkers in the 1970s (Drew, Saker & Ashley 1973; Drew 1975; Drew & Saker 1975, 1978), together with the spectacular images of barley roots proliferating in zones to which single inorganic nutrients of phosphate, nitrate or ammonium had been enriched published at the same time ensured that this work became a citation classic as far as root biologists were concerned. Yet, although less frequently reported, not all roots proliferate in nutrient patches (Jackson & Caldwell 1989; Hodge *et al.* 1998). Moreover, Drew *et al.*'s studies probably show root proliferation at its maximal as the concentrations of nutrients applied were large (100-fold), and only one part of the root system was exposed to such differing concentrations.

However, even with such large differences, shoot growth was only slightly depressed compared to controls receiving the high nutrient levels to all parts of their root system, showing that the increased numbers and length of lateral roots in the section receiving the high nutrients were largely able to compensate for the lack of nutrients elsewhere (Drew 1975). In soil, the root system will probably encounter a wide range of patches all of varying quality, in addition to other environmental stresses, and thus the roots must then 'decide' if to respond and the extent of the response. In any case, it will likely result in a dampening down of the proliferation response compared to that shown by Drew *et al.* as the root system interprets the different signals from the various root modules. However, this makes Drew *et al.*'s findings no less important, because they demonstrated the large capacity for proliferation at least in a crop species. That it was shown in a crop species is also important because these plants are ecologically distinct, characterized by high potential growth rates and nutrient demands. Campbell *et al.*'s (1991) study, on the other hand, clearly demonstrated that not all plant species respond to the nutrient-rich zones in the same way (see also Jackson & Caldwell 1989; Hodge *et al.* 1998).

WHICH ROOT TRAITS ARE IMPORTANT FOR FORAGING?

Although various root traits have been suggested to be important to explain the differences among various plant species in foraging ability including scale and precision, specific root length (SRL), physiological versus morphological responses, the problem is that evidence exists both to support and counter the relative importance of each of these traits (reviewed by Hodge 2004). Thus, while there is no definitive 'rule' to explain the differences among plant species in root proliferation, Hodge (2004) suggested that plant N concentration as a result of uptake from the patch may decide if root proliferation occurs or not. More recently, Kembel *et al.* (2008), using principal component analysis (PCA) based on correlations among leaf and root ecophysiological traits and root foraging traits, found that 'precision' of foraging was positively correlated with root nitrogen concentration and leaf/root respiration per unit mass. This finding is the more remarkable given that Kembel *et al.* (2008) used data from two different studies which had employed different growing conditions (i.e. leaf and root ecophysiological traits data came from Tjoelker *et al.* 2005, and the root foraging traits data from Johnson & Biondini 2001), resulting in data for a total of 16 species common to both studies. Strong relationships between respiration and N concentrations in fine roots have previously been reported (Reich *et al.* 1998; Tjoelker *et al.* 2005), so it is perhaps less surprising 'precision' was linked to both of these traits.

Interestingly Tjoelker *et al.* (2005) also found a decline in both respiration rates and N concentration with increased longevity of roots (and leaves). However, *Lolium perenne* roots showed a range of demographic responses to patches of L-lysine of varying concentration and size, although N

captured by the plant from these patches was a simple function of the amount added (Hodge *et al.* 1999a). If these demographic responses were optimal for the patch applied was unknown but, again, it does illustrate the range of responses (in this case, on root longevity) that a single plant root system can display in response to variation in patch dynamics. Therefore, as I have previously suggested (Hodge 2004) the *context* in which the response is expressed (prevailing environmental conditions, attributes of the patch, etc.) is as important as the actual response itself when interpreting why such a response has been evoked.

The importance of determining the context dependency of the response is perhaps best illustrated by the work on root proliferation responses to N-rich patches in soil. Essentially, while roots of several plant species could be shown to respond to N-rich patches by root proliferation, the actual benefit of this response in terms of increased N capture remained elusive (see van Vuuren, Robinson & Griffiths 1996; Fransen, de Kroon & Berendse 1998; Hodge *et al.* 1998). Robinson (1996) argued it made no sense for plants to proliferate roots in response to a mobile ion such as nitrate (a product of microbial decomposition of such N-rich organic patches), thus why had such a behavioral response not been lost through evolution? The situation became even complicated following the work of Zhang & Forde (1998) who clearly demonstrated that *Arabidopsis* roots responded specifically to NO_3^- ions and part revealed the genetic control of the response. The actual functional 'benefit' of a nitrate response, however, was still no clearer until it was demonstrated that when two plant species were grown together *competing* for a common organic N-patch, then root proliferation did confer a competitive advantage. The species which proliferated the most subsequently captured more N (Hodge *et al.* 1999b; Robinson *et al.* 1999). Thus, root proliferation even to mobile mineralized N sources such as NO_3^- did make sense providing: (1) plants with different capacities for root proliferation were competing for the N; (2) the N supply was both spatially and temporally available as it would be in a decomposing organic patch; and (3) the N supply was finite, again as it normally would be in the soil environment. Remove any of these factors, such as growing plants as individuals and not in competition as in previous studies (i.e. van Vuuren *et al.* 1996; Fransen *et al.* 1998; Hodge *et al.* 1998), and the importance of root proliferation became obscured because the available nitrate would diffuse to the roots of the individual plant regardless of its proliferation response. Thus, if the reasons for how roots behave in the way that they do are to be unearthed, we need to also understand the *environmental* context of the response. Add to this the fact that most plant species are mycorrhizal (which is often ignored in 'root' proliferation studies), and a further level of complexity must be taken into consideration.

ROOT SYSTEM COORDINATION

When roots encounter a nutrient-rich patch, enhanced growth in the patch zone is often accompanied by a

decrease in root growth elsewhere (i.e. in poorer resource areas) (Drew 1975; Granato & Raper 1989). Such a response makes a great deal of economic sense for the plant (i.e. invest in roots where they can provide the greater return and remove resources from areas where the returns are less). This root system coordination is perhaps best illustrated by the study of Gersani & Sachs (1992) using *P. sativum* (pea) plants with their roots split between two pots. The number of new lateral roots produced was correlated with the nutrient solution strength. In addition, removal of half of the root system led to a large increase in new primordial formation on the remaining roots such that overall number of primordia remained relatively constant in comparison to roots which had not been halved. Falik *et al.* (2003) also using pea, found plants appeared to be able to distinguish between self and non-self neighbours by producing fewer and shorter roots when in the presence of the same plant, which suggests there was physiological coordination among roots that developed on the same plant. In addition, Holzapfel & Alpert (2003) found that connected clones of *Fragaria chiloensis* (wild strawberry) with a high degree of physiological integration segregated their roots to avoid competition for resources between the connected clones. This root segregation enabled adult plants within connected pairs to accumulate as much biomass as singly grown adults, and more combined biomass than disconnected clones grown together. Collectively, these findings demonstrate that root system development can be closely regulated and coordinated *among* the whole root system and *between* related individuals suggesting a complex below-ground communication system. The challenge now is to examine the extent and role of this below-ground communication system under more natural conditions and with a greater number of plants.

Although the majority of studies which have suggested a coordination of root development have been conducted under very artificial systems, Linkohr *et al.* (2002) also found enhanced lateral root length inside a soil patch, while suppression occurred outside the patch zone in the background sand medium. However, although the study by Linkohr *et al.* (2002) was more realistic, the contrast between nutrient status inside the patch compared to outside was large (i.e. soil versus sand). In other studies, where less extreme nutrient concentrations have been used, coordination of growth is not always observed (Robinson 1994; Hodge *et al.* 1998). Moreover, the ability of a root system to coordinate growth when exposed to multiple patches, and consequently experiencing numerous signals simultaneously, is lacking. Yet, roots must experience such conditions in the natural environment.

While information on actual coordination of growth upon experiencing numerous patches at the one time is lacking, Duke & Caldwell (2000) did investigate the impact on root *physiological* adjustments when part of a root system was first exposed to one patch (i.e. the 'primary' patch), followed by a number of other patches of varying sizes and concentrations applied to different parts of the root system. The addition of further patches did not reduce

the uptake capacity of roots in either the primary patch or control area (receiving no nutrient amendment), except at the highest level of patch amendment (four additional patches each of the same phosphate concentration as the original primary patch). Further, uptake rates of roots exposed to additional patches of low or medium concentration did not differ compared to control parts of the root system not experiencing a nutrient-patch, even though these patches probably contributed to reducing the P demand of the plant. Thus, the ability of the whole root system to interpret, and respond to, multiple signals at once may be more restricted (at least in terms of physiological adjustments) than studies using single treatments imply. In addition, the background nutrient status that the overall root system is experiencing probably determines if a coordinated response is evoked or not. Surprisingly, few studies have used realistic patches added to a realistic growth medium backgrounds; fewer still have considered the attributes of the patch itself (i.e. patch concentration, size, duration and so forth) in relation to the response obtained (but see Farley & Fitter 1999; Hodge *et al.* 2000a–c).

MORE DISCRETE CHANGES – ALTERED RSA

In addition to altering their biomass allocation, roots can also modify their architectural plans as a result of the prevailing soil conditions. Changes in the RSA, which is the spatial configuration of the root system, can occur without necessarily a change in overall root biomass (see Fitter 1994). Fitter and coworkers (Fitter & Stickland 1991; Fitter *et al.* 1991) demonstrated that a herringbone topology (where branching is predominantly on the main root axis), although associated with high construction costs, was best for soil exploration. However, although this topology may be best for locating nutrient-rich patches in the soil, it is not necessarily best to exploit those resources: Farley & Fitter (1999) showed that root topology was less herringbone in an encountered patch, thus RSA shifted from exploratory to exploitative when in the patch zone. RSA can be modified by a wide range of environmental conditions (see Robinson, Hodge & Fitter 2003; Malamy 2005), although only responses to phosphate availability will be considered here. The majority of this work has been conducted using the model plant *Arabidopsis* but, as discussed as follows, here too generalizations upon how roots will respond are hard to predict under all circumstances.

Williamson *et al.* (2001) demonstrated that phosphate availability had a marked effect on RSA of *Arabidopsis* plants (ecotype Columbia). Under low P, lateral root density and length increased while the growth of the primary root was reduced. This reduction in primary root growth was associated with reduced cell elongation (Williamson *et al.* 2001). Sánchez-Calderón *et al.* (2005) also reported a decrease in the mature epidermal cells of the primary root of *Arabidopsis* (also using ecotype Columbia) such that by 10 d, epidermal cell length was only 20% of that in plants grown on high phosphate medium. Sánchez-Calderón *et al.* (2005) further showed that low P

induced the *Arabidopsis* primary root to inhibit cell division and promote cell differentiation at the root tip via a shift from an indeterminate to a determinate developmental programme. More recently, Svistoonoff *et al.* (2007) demonstrated that actual physical contact of the *Arabidopsis* primary root tip with low-phosphate medium was required to arrest root growth, and that the root cap itself may be involved in sensing P limitation in the root environment, again highlighting the importance of the root cap in detecting and responding to environmental signals.

While a reduction in primary root growth of *Arabidopsis* under low P availability has been widely reported (e.g. Linkohr *et al.* 2002; López-Bucio *et al.* 2002; Jain *et al.* 2007), it is important to note not all *Arabidopsis* genotypes show such a response. Similarly, the impact on lateral root density is variable with both decreased (Al-Ghazi *et al.* 2003) or increased (Williamson *et al.* 2001; Linkohr *et al.* 2002; López-Bucio *et al.* 2002; Sánchez-Calderón *et al.* 2005) densities reported under low P. Some of these differences may be because of differences in experimental conditions including the ecotype or accession of *Arabidopsis* studied. For example, Chevalier *et al.* (2003) studied the effects of phosphate starvation on four commonly used accessions (i.e. Col, Cvi, Ler and Ws), and found in all four P starvation reduced the length of the primary root. Similarly, numbers of lateral roots were significantly reduced (at the $P=0.05$ level for Ler and Cvi, and at the $P=0.01$ level for Ws and Col) compared to corresponding control plants grown on normal P containing media. However, Chevalier *et al.* (2003) then examined 73 *Arabidopsis* accessions from a wider range of habitats and found that while 50%, the accessions showed reduced primary root growth and less lateral root production under P starvation; 25% were not responsive to P availability. In the remaining 25%, P starvation only affected either the primary or lateral roots, but not both. Thus, P starvation could have a null or negative effect on the primary root, and a positive, null or negative effect on lateral root number. There was, however, no correlation between geographical location and accession response (Chevalier *et al.* 2003). Thus, even using a well-investigated model plant such as *Arabidopsis*, responses varied significantly with the accession studied.

Although this only briefly discusses phosphate availability, as previously mentioned, RSA as a root trait shows plasticity to a wide range of environmental factors (Malamy 2005). Moreover, QTL mapping in roots suggests that QTL may play a role in nutrient and water capture through an effect on RSA (Zheng *et al.* 2003; MacMillan *et al.* 2006; Ochoa, Blair & Lynch 2006), in addition to explaining at least some of the phenotypic variation in RSA (Price & Tomos 1997; Giuliani *et al.* 2005). Thus, exploitation of QTL cloning and marker-assisted selection for RSA may lead to improved crop varieties in the future, although the very ability of RSA to respond so well to prevailing environmental conditions does make this research area more challenging (see de Dorlodot *et al.* 2007).

MYCORRHIZAS AND OTHER NUTRIENT ACQUISITION STRATEGIES

The majority of plants are capable of forming mycorrhiza associations with various soil fungi. Of the seven different types of mycorrhiza symbiosis which can form depending on the host plant–fungal combination (Smith & Read 2008), the most common is that of the AM association. The AM association is named after the ‘arbuscule’ (meaning ‘little tree’), a fungal structure that forms in the roots of the host and is believed to be the site of phosphate transfer to the host plant; hence, it is the diagnostic feature of a functioning AM symbiosis. The AM association is also the most ancient type of mycorrhiza with fossil evidence revealing structures remarkably similar to the modern-day arbuscule present in the underground stems or ‘rhizoids’ of Devonian plants [c. 400 million years ago (m.y.a.)] (Remy *et al.* 1994). Thus, mycorrhizal symbiosis evolved very early in the evolution of land plants.

Although all ions have similar diffusion coefficients in free solution, in soil phosphate interacts with aluminium, iron and calcium ions to form sparingly soluble complexes. Phosphate can also be tightly held on charged soil particles. All these factors mean that diffusion of phosphate through soil is slow, and depletion zones rapidly build up around the surface of absorbing roots. Furthermore, the first land plants had no real roots; thus, the acquisition of poorly soluble phosphate would have been a major challenge when the move from water to land was first made. The mycorrhizal fungal partner can extend outside this nutrient depletion zone around the root and acquire phosphate from a larger volume of soil. Although it is unknown how the symbiosis first started, the fungus may have initially been a pathogen, but the association then evolved to be beneficial to both: the plant receiving phosphate and other benefits; the fungus obtaining carbon from the host plant.

Traditionally, it had been assumed because of the low number of described AM fungal species (around 200) together with the large number of host plant species (c. 2×10^5) that any AM fungus could colonize any host and provide a similar function for that host; however, the study by van der Heijden *et al.* (1998) meant that this assumption had to be rethought. Different members of a calcareous European grassland community were influenced in different ways by different AMF. Interestingly, the dominant plant species in the community (*Bromus erectus*) was not influenced by AMF, but the subordinate species were. In 8 out of 11 cases, these subordinate species were entirely dependant on the presence of AMF to be successful in that community. van der Heijden *et al.* (1998) further showed that different AMF had different impacts on members of the plant community, and that there was no ‘super-fungus’ present. Although there has been some work on how AMF may modify root foraging responses (Farley & Fitter 1999; Hodge, Robinson & Fitter 2000d; Hodge 2001a, 2003a,b; Wijesinghe *et al.* 2001), many questions remain including the importance of actual AM fungal foraging, the nutrients they are able to capture (see Hodge, Campbell & Fitter

2001), if this differs among AM fungal species (Hodge 2001a; Cavagnaro *et al.* 2005; Leigh, Hodge & Fitter 2008), and the consequences for different plants linked together by a common mycelial network (CMN) in soil as a means to possibly reduce the consequences of soil nutrient heterogeneity (Ozinga, Van Andel & McDonnell-Alexander 1997).

Root proliferation is often still observed when both roots and mycorrhizal hyphae are present in patches (Hodge 2001a,b), which may mean that there are risks associated with the plant relying on the fungus to acquire the nutrients (i.e. the fungus may acquire the nutrients for itself or pass them to another plant). Root proliferation (involving the construction of new laterals) often does take considerable time to occur (see Hodge *et al.* 1999b), and that delay may be a means for the plant of testing if the nutrient patch is durable or not. However, the time taken for substantial root proliferation (c. several weeks, see Hodge *et al.* 1999b) does suggest that roots are unlikely to compete directly with microorganisms that are involved in the decomposition process (at least in complex organic patches) for the resources released, until microbial turnover occurs. It has, however, recently been suggested that AMF may use this root proliferation mechanism as a means to obtain carbon from their host (Fitter 2006). The host detects increased phosphate uptake at the site of the fungal arbuscule, and thus allocates carbon to that area of the root. Instead of the carbon being used to construct new roots (as in the proliferation response), the AMF acquires the carbon instead. This is a win–win situation as the plant still acquires the phosphate while the fungus obtains the carbon it needs. If the enhanced P signal continues or increases in strength, then the flow of carbon becomes so intense that root proliferation begins (Fitter 2006). Whether such a mechanism operates is highly speculative, but it does have its attractions in explaining how AM fungal hyphae inside the root manage to acquire carbon without ‘cheating’ on their host.

As plants have evolved so has the type of mycorrhizal association, and in some cases, such as cluster rooted species, the association has been lost (but see Boulet & Lambers 2005). Although the morphology of cluster roots is variable, typically they comprise clusters of closely spaced, often hairy, rootlets of limited growth that develop along the main root axis and which have a bottlebrush appearance (Shane & Lambers 2005). Cluster roots are induced by low phosphate availability and develop in a range of species belonging to a number of different families (e.g. Proteaceae, Fabaceae, Casuarinaceae, Myricaceae and Leguminosae). The lack of mycorrhizal symbiosis in cluster rooted species may at first appear counterintuitive because these species tend to occur in extremely nutrient impoverished soils which are very low in phosphate. However, the large secretion of citrate by cluster roots as well as the release of other compounds including APases and isoflavonoids (Weisskopf *et al.* 2006a,b) is a much more effective strategy for exchanging for phosphate absorbed on soil particles (and possibly releasing phosphate from organic forms) intensively in a small soil volume than using mycorrhiza hyphae

to forage for the very low amounts of phosphate in a large soil volume (Lambers *et al.* 2008).

AVOIDING COMPETITION AND ROOT SEGREGATION

Plant roots also have the ability to avoid roots of other plants by root segregation. For example, Caldwell, Manwaring & Durham (1996) found that roots taken from soil cores although generally aggregated in distribution also appeared to be segregated with respect to individual species. Root biomass of *P. sativum* (pea) plants grown with their roots split between two pots (called 'fence-sitters') was proportional to the level of nutrients added to each pot (i.e. when nutrient levels were the same in both pots, the root biomass in these pots were equal; when one pot had twice the nutrients of the other, the root biomass in that pot was also double that of the other pot) (Gersani, Abramsky & Falik 1998). When an increasing number of competitor pea plants were added to one of the two pots, the fence-sitter plants showed no change in either their total root weight or fitness (determined as fruit dry weight); however, allocation of the fence-sitter roots *between* the two pots changed. The fence-sitter moved its root biomass away from the pot to which the competitors were added and into the pot to which it alone had access. For every competitor plant added, the fence-sitter shifted 0.12 g of its root biomass away from the competitor containing pot and into the competitor-free pot (Gersani *et al.* 1998). Root segregation has frequently been reported (reviewed by Schenk, Callaway & Mahall 1999) and may be because of a number of factors including avoidance of resource competition among different species. When the nutrient level in the pot to which the competitors were added was twice that of the fence-sitter's other pot, the fence-sitter again moved roots away from the competitor pot as increasing numbers of competitor plants were added. However, when only one competitor was present, the root biomass of the fence-sitter in the pot with the competitor and with double the nutrient concentration was similar to that in the other pot containing half the level of nutrients. The fence-sitter was again able to maintain both its total root biomass and more importantly, its fitness, irrespective of the number of competitors added to the second pot. In contrast, the fitness of the competitor plants declined (Gersani *et al.* 1998).

OTHER DECISIONS – COMPETING SINKS AND THE 'TRAGEDY OF THE COMMONS'

When two fence-sitter plants are grown together sharing two pots, however, an increased root biomass compared to that produced when plants are grown singly in individual pots (see Fig. 2) has been reported for a number of plant species including *P. sativum* (O'Brien, Gersani & Brown 2005), *Phaseolus variegatus* (Maina *et al.* 2002) and *Glycine max* (Gersani *et al.* 2001). Thus, while both fence-sitters had the option of segregating their roots away from the competitor plant (the option taken by the fence-sitter plant in

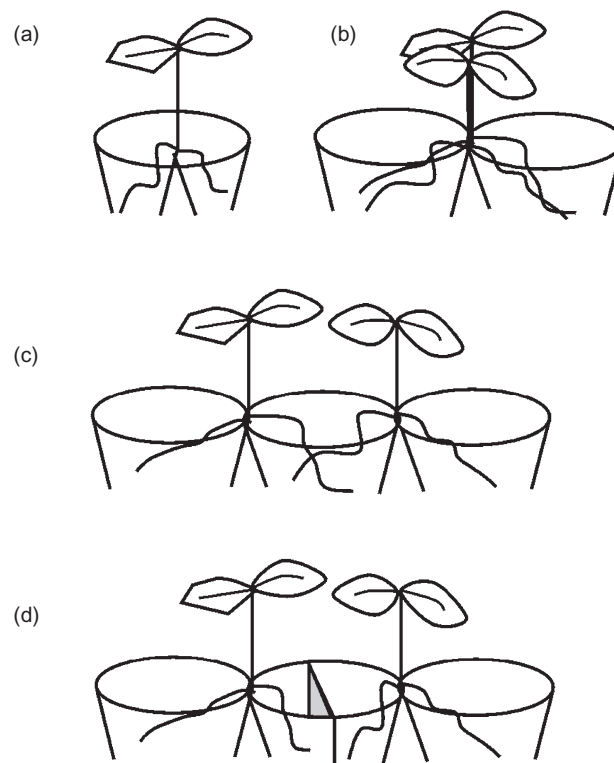


Figure 2. Comparisons made in many of the 'Tragedy of the Commons' root studies. (a) An individual plant grown in a single pot is used as a 'control' compared to (b) two 'fence-sitter' plants with their roots in both pots (see Gersani *et al.* 2001; Maina *et al.* 2002; O'Brien *et al.* 2005). In the three pot design of O'Brien *et al.* (2005), two fence-sitter plants each have access to the middle pot only where interaction between the two root systems is either permitted (see c) or denied by placement of a physical barrier (see d). In all cases, although the relative volumes the root systems have access to are the same, the absolute volumes differ between the experimental and 'control' pots. Adapted from O'Brien *et al.* (2005) with kind permission from the author and the trustees of the *New Phytologist*.

the study by Gersani *et al.* (1998), both instead increased their root production in the shared space. However, it should be noted that only the fence-sitter had access to additional space and nutrients in the study by Gersani *et al.* (1998), thus, only this plant could make any 'decision' regarding its root placement. It should also be emphasized that the decision made by the fence-sitter on root placement in that study enabled this plant to maintain fitness. In the two fence-sitter approaches, both plants had equal access to both pot volumes and the nutrients contained within them. The overproduction of roots observed by these fence-sitters has been referred to as a 'Tragedy of the Commons' scenario (Gersani *et al.* 2001; Maina *et al.* 2002) because the strategy that both fence-sitters engage in – to produce more roots than the other – comes at the expense of reduced reproductive biomass and, consequently, overall fitness (Gersani *et al.* 2001; Maina *et al.* 2002; O'Brien *et al.* 2005). The term 'Tragedy of the Commons', which involves individuals exploiting resources for their own gain, but

which comes at the expense of all, was first used by Hardin (1968) and has since been applied to a range of environmental (Dodds 2005; Lloyd 2007) and biological systems (Rankin, Bargum & Kokko 2007) including microbial populations (MacLean & Gudeli 2006; MacLean 2008) and plant competition for light (Schieving & Poorter 1999; Falster & Westoby 2003) and water (Zea-Cabrera *et al.* 2006) in addition to nutrient resources (Gersani *et al.* 2001; Maina *et al.* 2002; Craine 2006; O'Brien, Brown & Moll 2007).

However, a number of issues with the studies upon root–root interactions have been highlighted that question if the roots are actually engaged in a ‘tragedy’ scenario. For example, Laird & Aarssen (2005) have highlighted potential problems with generally only taking the *average* response of both fence-sitter roots because of the difficulty of separating out intermingled root systems. An average value takes no account of one *individual* plant performing better than the other, resulting in asymmetric competition. This together with a decelerating relationship between plant biomass and the amount of nutrients actually available suggests that plants should, on average, be smaller than when plants are grown alone. Thus, by taking only average values, the results are mathematically biased towards a ‘Tragedy of the Commons’ response even though this may not have occurred at the level of the individual. Furthermore, a ‘Tragedy of the Commons’ response does not always occur even when average values are taken (see O'Brien *et al.* 2005; Murphy & Dudley 2007). When two fence-sitters pea plants were grown in a three-pot design such that only the middle pot was shared, root production in the middle pot increased compared to when the interaction was prevented (by placing a physical barrier between the two root systems in the middle pot). However, reproductive biomass (hence, fitness) was not significantly different if the root systems of the fence-sitters interacted or not (O'Brien *et al.* 2005), thus, no ‘Tragedy of the Commons’ response occurred in this case. Similarly, reproductive biomass was not adversely affected when soybean (*G. max*) plants were grown together in the study by Murphy & Dudley (2007) even though allocation to root biomass increased. This is in direct contrast to the results of Gersani *et al.* (2001) who did find a ‘Tragedy of the Commons’ response using soybean plants, but at a lower planting density in the competitor pots than that used by Murphy & Dudley (2007). Semchenko, Hutchings & John (2007a) also reported no ‘Tragedy of the Commons’ response occurred in their study using oat (*Avena sativa*) plants as root, shoot and total biomass were the same regardless if the two oat plants were separated by partitions or not. Reproductive biomass (i.e. fitness) was not measured directly in their study; instead, total plant mass was used as a surrogate.

Semchenko *et al.* (2007a) also investigated the effect of adding activated carbon, a strong absorber of organic compounds, to the growth media. When added to the pots of plants where the root systems were permitted to interact, the addition of activated carbon did not alter plant mass or root–shoot allocation. However, when plants were grown with either plastic or mesh partitions separating the roots of

the two plants, the addition of activated carbon increased plant performance. These results are consistent with the findings of Falik *et al.* (2005) discussed at the beginning of this review, who observed root growth was more restricted when obstacles to root growth were present. This root inhibition was also alleviated by the addition of activated carbon or potassium permanganate, a strong oxidizer of organic compounds (Falik *et al.* 2005). The surprising aspect of Semchenko *et al.*'s (2007a) findings, however, is that these root inhibitory compounds were seemingly unable to diffuse through the mesh partitions and disperse into a larger soil volume. An obvious area of future research is to identify these root-released compounds, as well as investigating their function and persistence under more realistic and complex environments where they may be subject to degradation or utilized as substrates by the microbial biomass.

Another major problem with many of the studies that have been conducted on competing root systems is that *absolute* soil volume, hence physical space, varied when competitors were added. This variation in pot volume (and often total nutrient resources available) to the plants among the comparisons used has been a major criticism of such studies (see Schenk 2006; Hess & de Kroon 2007; but see also O'Brien & Brown 2008). An increase in pot volume has been demonstrated to enhance vegetative growth even when equal amounts of nutrients are supplied (McConaughay & Bazzaz 1991). Reproductive biomass also varied with increased space, but in a more complex manner depending on the plant species grown (McConaughay & Bazzaz 1991). This suggests that roots are able to perceive the volume of space available to them and respond accordingly although if plants actually *compete* for space has been questioned (see Wilson, Steel & Steel 2007). Therefore, as the fence-sitters had access to both pots, hence twice the space and nutrients of the individual plant grown in a single pot, increased root growth may have simply been because of increased space and access to nutrients. Indeed, Schenk (2006) recently demonstrated using the data from the ‘Tragedy of the Commons’ experiments by Gersani *et al.* (2001) and Maina *et al.* (2002) that if soil volume was taken into account the roots responded to the extra soil volume and not to the presence of the competitor plant.

INFLUENCE OF NEIGHBOURS ON ROOT RESPONSES

Although it has been known for some time that at least some plant species respond differently to other plant species compared to when grown with an identical species as a neighbour (Mahall & Callaway 1991; Krannitz & Caldwell 1995; Huber-Sannwald, Pyke & Caldwell 1996), there is increasing evidence that root behaviour is much more sophisticated than this. Furthermore, not all root–root interactions are resource driven. Some may involve chemical signalling or production including allelopathy, the suppression of neighbouring roots by the release of toxic compounds. Allelopathy, however, remains a controversial area

in the literature, with one of the main arguments against the effectiveness of toxic compounds being that these must, by definition, be of greater concentration around the producer plant. Therefore, the producer must have evolved resistance to the toxin and consequently there would be strong selection pressure on the rest of the community to have also evolved resistance, thereby rendering the toxin ineffective in the longer term (see Fitter 2003). However, in the case of invasive plants, allelopathy may potentially be an effective mechanism to suppress native plants if the native population has not yet experienced the toxin, and thus the evolutionary pressure to have evolved resistance has been absent (see Bais *et al.* 2003). More recent evidence suggests that some invasive plants may release antifungal compounds that act by inhibiting the mycorrhizal fungi on which the native plant species rely (Stinson *et al.* 2006) and that these phytotoxins are more effective on mycorrhizal fungi present in invaded soils than the invading plants' native region (Callaway *et al.* 2008). Presumably the mycorrhizal fungi in the invaded region have not previously been exposed to the toxin and again the evolutionary pressure for resistance has not been present.

It has also been suggested that roots are able to identify 'self' (i.e. roots from the same plant) from those of another plant, even when the other plant is genetically identical (Falik *et al.* 2003; Falik, de Kroon & Novoplansky 2006). In fact, many of the 'Tragedy of the Commons' root studies discussed in the previous section have been reinterpreted as the plants showing self/non-self discrimination. However, in many cases where self/non-self interactions have been investigated, the same problems as those previously discussed remain (i.e. comparing plants that have been grown in different volumes of soil). One study in which the absolute volume of soil remained the same among comparisons was that by Gruntman & Novoplansky (2004). They demonstrated *Buchloe dactyloides* (buffalo grass) plants were able to differentiate between self and non-self neighbours, and produced fewer and shorter roots when grown in the presence of roots from the same individual. However, when cuttings from the same node were separated from each other by growing in different pots, they became increasingly alienated from each other and responded to each other's presence as if genetically and physiologically different clones.

Dudley & File (2007) also recently demonstrated that *Cakile edentula* (sea rocket) plants that shared the same mother allocated less biomass to their roots when grown together compared to when grown with plants that had different mothers. Importantly, however, reproductive biomass (a measure of plant fitness) did not differ among the groups over the experimental period. This reduction in root biomass among related individuals Dudley & File (2007) referred to as 'kin recognition', although to get actual 'kin selection' plant fitness would also have to differ among the treatments (see Callaway & Mahall 2007), but it did not. The role of such a self/non-self or 'kin' recognition mechanism intuitively makes sense for the plant as it reduces competition for resources between related root systems while increasing competition in response to

non-self individuals, thus potentially denying the other competitor plant of the said resources. In contrast, roots of *Glechoma hederacea* (ground ivy) tended to avoid below-ground competition with neighbouring plants irrespective of the genetic or specific identity of the neighbouring plants (Semchenko, John & Hutchings 2007b). Moreover, actual physical contact between roots was not required for this inhibition to occur. However, another clonal plant, *Fragaria vesca* (wild strawberry), grew roots equally towards and away from intraspecific ramet neighbours, and their elongation was stimulated by contact with roots of *G. hederacea* ramets. Importantly, *F. vesca* also showed increased root growth towards neighbouring ramets in units where frequent applications of fertilizer were applied and therefore suggesting against resource depletion being the driving force in the observed root growth (Semchenko *et al.* 2007b). These results are important as they suggest that not all plants respond in the same way when challenged with self or non-self. Thus, as with the root proliferation work, the quest to find general principles or rules of root behaviour continues.

CONCLUDING REMARKS

Roots are very effective at responding to their environment. Perhaps this very responsiveness and plasticity go some way in explaining why it has proved so troublesome to find universal 'rules' on how species will respond to various nutrient patches. In addition, most of the information on root responses come from studies that have changed only one factor at a time and often using extreme contrasts. Although this often results in impressive root responses (see Drew 1975), it does not reflect the constantly fluctuating soil environment. Rather, in soil, a more subdued response may be more cost effective in the longer term (Ho *et al.* 2005). In addition, in a complex environment such as soil, the root system will have to perceive and interpret multiple, and perhaps, conflicting signals at the same time from different parts of the root system. This also may be expected to result in more subdued responses than those measured under rather artificial experimental conditions, and may go some way in explaining why there are ecological limits to plant plasticity (see Valladares *et al.* 2007). In any case, the root cap region appears to be a key control centre for detection of the environment and the responses made, although much more work is required to understand the genetic and molecular controls using a range of environmental stresses together before we can even begin to exploit these traits.

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REFERENCES

- Al-Ghazi Y., Muller B., Pinloche S., Tranbarger T.J., Nacry P., Rosignol M., Tardieu F. & Doumas P. (2003) Temporal responses of *Arabidopsis* root architecture to phosphate starvation: evidence for the involvement of auxin signaling. *Plant, Cell & Environment* **26**, 1053–1066.
- Alpi A., Amrhein N., Bertl A., *et al.* (2007) Plant neurobiology: no brain, no gain? *Trends in Plant Science* **12**, 135–136.
- Bais H.P., Vepachedu R., Gilroy S., Callaway R.M. & Vivanco J.M. (2003) Allelopathy and exotic plant invasion: from molecules and genes to species interactions. *Science* **301**, 1377–1380.
- Baluška F., Volkmann D. & Menzel D. (2005) Plant synapses: actin-based domains for cell-to-cell communication. *Trends in Plant Science* **10**, 106–111.
- Bliss K.M., Jones R.H., Mitchell R.J. & Mou P.P. (2002) Are competitive interactions influenced by spatial nutrient heterogeneity and root foraging behavior? *New Phytologist* **154**, 409–417.
- Boulet F.M. & Lambers H. (2005) Characterisation of arbuscular mycorrhizal fungi colonisation in cluster roots of *Hakea verrucosa* F. Muell. (Proteaceae), and its effect on growth and nutrient acquisition in ultramafic soil. *Plant and Soil* **269**, 357–367.
- Brenner E.D., Stahlberg R., Mancuso S., Vivanco J., Baluška F. & Van Volkenburgh E. (2006) Plant neurobiology: an integrated view of plant signaling. *Trends in Plant Science* **11**, 413–419.
- Caldwell M.M., Manwaring J.H. & Durham S.L. (1996) Species interactions at the level of fine roots in the field: influence of soil nutrient heterogeneity and plant size. *Oecologia* **106**, 440–447.
- Callaway R.M. & Mahall B.E. (2007) Family roots. *Nature* **448**, 145–147.
- Callaway R.M., Cipollini D., Barto K., Thelen G.C., Hallett S.G., Prati D., Stinson K. & Klironomos J. (2008) Novel weapons: invasive plant suppresses fungal mutualists in America but not in its native Europe. *Ecology* **89**, 1043–1055.
- Campbell B.D., Grime J.P. & Mackey J.M.L. (1991) A trade-off between scale and precision in resource foraging. *Oecologia* **87**, 532–538.
- Cavagnaro T.R., Smith F.A., Smith S.E. & Jakobsen I. (2005) Functional diversity in arbuscular mycorrhizas: exploitation of soil patches with different phosphate enrichment differs among fungal species. *Plant, Cell & Environment* **28**, 642–650.
- Chevalier F., Pata M., Nacry P., Doumas P. & Rosignol M. (2003) Effects of phosphate availability on the root system architecture: large-scale analysis of the natural variation between *Arabidopsis* accessions. *Plant, Cell & Environment* **26**, 1839–1850.
- Craine J.M. (2006) Competition for nutrients and optimal root allocation. *Plant and Soil* **285**, 171–185.
- Dinneny J.R., Long T.A., Wang J.Y., Jung J.Y., Mace D., Pointer S., Barron C., Brady S.M., Schiefelbein J. & Benfey P.N. (2008) Cell identity mediates the response of *Arabidopsis* roots to abiotic stress. *Science* **320**, 942–945.
- Dodds W.K. (2005) The commons, game theory and aspects of human nature that may allow conservation of global resources. *Environmental Values* **14**, 411–425.
- de Dorlodot S., Forster B., Pagès L., Price A., Tuberosa R. & Draye X. (2007) Root system architecture: opportunities and constraints for genetic improvement. *Trends in Plant Science* **12**, 474–481.
- Drew M.C. (1975) Comparison of the effects of a localized supply of phosphate, nitrate, ammonium and potassium on the growth of the seminal root system, and the shoot, in barley. *New Phytologist* **75**, 479–490.
- Drew M.C. & Saker L.R. (1975) Nutrient supply and the growth of the seminal root system in barley. II. Localized, compensatory increases in lateral root growth and rates of nitrate uptake when nitrate supply is restricted to only part of the root system. *Journal of Experimental Botany* **26**, 79–90.
- Drew M.C. & Saker L.R. (1978) Nutrient supply and the growth of the seminal root system in barley. III. Compensatory increases in growth of lateral roots, and in rates of phosphate uptake in response to a localised supply of phosphate. *Journal of Experimental Botany* **29**, 435–451.
- Drew M.C., Saker L.R. & Ashley T.W. (1973) Nutrient supply and the growth of the seminal root system in barley. I. The effect of nitrate concentration on the growth of axes and laterals. *Journal of Experimental Botany* **24**, 1189–1202.
- Dudley S.A. & File A.L. (2007) Kin recognition in an annual plant. *Biology Letters* **3**, 435–438.
- Duke S.E. & Caldwell M.M. (2000) Phosphate uptake kinetics of *Artemisia tridentata* roots exposed to multiple soil enriched-nutrient patches. *Flora* **195**, 154–164.
- Einsmann J.C., Jones R.H., Mou P. & Mitchell R.J. (1999) Nutrient foraging traits in 10 co-occurring plant species of contrasting life forms. *Journal of Ecology* **87**, 609–619.
- Falik O., Reides P., Gersani M. & Novoplansky A. (2003) Self/non-self discrimination in roots. *Journal of Ecology* **91**, 525–531.
- Falik O., Reides P., Gersani M. & Novoplansky A. (2005) Root navigation by self inhibition. *Plant, Cell & Environment* **28**, 562–569.
- Falik O., de Kroon H. & Novoplansky A. (2006) Physiologically-mediated self/nonself root discrimination in *Trifolium repens* has mixed effects on plant performance. *Plant Signaling & Behavior* **1**, 116–121.
- Falster D.S. & Westoby M. (2003) Plant height and evolutionary games. *Trends in Ecology & Evolution* **18**, 337–343.
- Farley R.A. & Fitter A.H. (1999) The responses of seven co-occurring woodland herbaceous perennials to localized nutrient-rich patches. *Journal of Ecology* **87**, 849–859.
- Fitter A.H. (1994) Architecture and biomass allocation as components of the plastic response of root systems to soil heterogeneity. In *Exploitation of Environmental Heterogeneity by Plants* (eds M.M. Caldwell & R.W. Pearcy), pp. 305–323. Academic Press, San Diego, CA, USA.
- Fitter A.H. (2003) Making allelopathy respectable. *Science* **301**, 1337–1338.
- Fitter A.H. (2006) What is the link between carbon and phosphorus fluxes in arbuscular mycorrhiza? A null hypothesis for symbiotic function. *New Phytologist* **172**, 3–6.
- Fitter A.H. & Stickland T.R. (1991) Architectural analysis of plant root systems. 2. Influence of nutrient supply on architecture in contrasting plant species. *New Phytologist* **118**, 383–389.
- Fitter A.H., Stickland T.R., Harvey M.L. & Wilson G.W. (1991) Architectural analysis of plant root systems. 1. Architectural correlates of exploitation efficiency. *New Phytologist* **118**, 375–382.
- Fransen B., de Kroon H. & Berendse F. (1998) Root morphological plasticity and nutrient acquisition of perennial grass species from habitats of different nutrient availability. *Oecologia* **115**, 351–358.
- Gersani M. & Sachs T. (1992) Development correlations between roots in heterogeneous environments. *Plant, Cell & Environment* **15**, 463–469.
- Gersani M., Abramsky Z. & Falik O. (1998) Density-dependent habitat selection in plants. *Evolutionary Ecology* **12**, 223–234.
- Gersani M., Brown J.S., O'Brien E.E., Maina G.M. & Abramsky Z. (2001) Tragedy of the commons as a result of root competition. *Journal of Ecology* **89**, 660–669.
- Giuliani S., Sanguineti M.C., Tuberosa R., Bellotti M., Salvi S. & Landi P. (2005) *Root-ABA1*, a major constitutive QTL, affects

- maize root architecture and leaf ABA concentration at different water regimes. *Journal of Experimental Botany* **56**, 3061–3070.
- Granato T.C. & Raper C.D. Jr. (1989) Proliferation of maize (*Zea mays* L.) roots in response to localized supply of nitrate. *Journal of Experimental Botany* **40**, 263–275.
- Grime J.P. (2007) The scale-precision trade-off in spacial resource foraging by plants: restoring perspective. *Annals of Botany* **99**, 1017–1021.
- Gruntman M. & Novoplansky A. (2004) Physiologically mediated self/non-self discrimination in roots. *Proceedings of the National Academy of Sciences of the United States of America* **101**, 3863–3867.
- Hardin G. (1968) The tragedy of the commons. *Science* **162**, 1243–1248.
- van der Heijden M.G.A., Klironomos J.N., Ursic M., Moutoglis P., Streitwolf-Engel R., Boller T., Wiemken A. & Sanders I.R. (1998) Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. *Nature* **396**, 69–72.
- Hess L. & de Kroon H. (2007) Effects of rooting volume and nutrient availability as an alternative explanation for root self/non-self discrimination. *Journal of Ecology* **95**, 241–251.
- Ho M.D., Rosas J.C., Brown K.M. & Lynch J.P. (2005) Root architectural tradeoffs for water and phosphorus acquisition. *Functional Plant Biology* **32**, 737–748.
- Hodge A. (2001a) Arbuscular mycorrhizal fungi influence decomposition of, but not plant nutrient capture from, glycine patches in soil. *New Phytologist* **151**, 725–734.
- Hodge A. (2001b) Foraging and the exploitation of soil nutrient patches: in defence of roots. *Functional Ecology* **15**, 416.
- Hodge A. (2003a) Plant nitrogen capture from organic matter as affected by spatial dispersion, interspecific competition and mycorrhizal colonisation. *New Phytologist* **157**, 303–314.
- Hodge A. (2003b) N capture by *Plantago lanceolata* and *Brassica napus* from organic material – the influence of spatial dispersion, plant competition and an arbuscular mycorrhizal fungus. *Journal of Experimental Botany* **54**, 2331–2342.
- Hodge A. (2004) The plastic plant: root responses to heterogeneous supplies of nutrients. *New Phytologist* **162**, 9–24.
- Hodge A. (2006) Plastic plants and patchy soils. *Journal of Experimental Botany* **57**, 401–411.
- Hodge A., Stewart J., Robinson D., Griffiths B.S. & Fitter A.H. (1998) Root proliferation, soil fauna and plant nitrogen capture from nutrient-rich patches in soil. *New Phytologist* **139**, 479–494.
- Hodge A., Robinson D., Griffiths B.S. & Fitter A.H. (1999a) Nitrogen capture by plants grown in N-rich organic patches of contrasting size and strength. *Journal of Experimental Botany* **50**, 1243–1252.
- Hodge A., Robinson D., Griffiths B.S. & Fitter A.H. (1999b) Why plants bother: root proliferation results in increased nitrogen capture from an organic patch when two grasses compete. *Plant, Cell & Environment* **22**, 811–820.
- Hodge A., Stewart J., Robinson D., Griffiths B.S. & Fitter A.H. (2000a) Spatial and physical heterogeneity of N supply from soil does not influence N capture by two grass species. *Functional Ecology* **14**, 645–653.
- Hodge A., Stewart J., Robinson D., Griffiths B.S. & Fitter A.H. (2000b) Competition between roots and soil micro-organisms for nutrients from nitrogen-rich patches of varying complexity. *Journal of Ecology* **88**, 150–164.
- Hodge A., Stewart J., Robinson D., Griffiths B.S. & Fitter A.H. (2000c) Plant N capture and microfaunal dynamics from decomposing grass and earthworm residues in soil. *Soil Biology & Biochemistry* **32**, 1763–1772.
- Hodge A., Robinson D. & Fitter A.H. (2000d) An arbuscular mycorrhizal inoculum enhances root proliferation in, but not nitrogen capture from, nutrient-rich patches in soil. *New Phytologist* **145**, 575–584.
- Hodge A., Campbell C.D. & Fitter A.H. (2001) An arbuscular mycorrhizal fungus accelerates decomposition and acquires nitrogen directly from organic material. *Nature* **413**, 297–299.
- Holzapfel C. & Alpert P. (2003) Root cooperation in a clonal plant: connected strawberries segregate roots. *Oecologia* **134**, 72–77.
- Huber-Sannwald E., Pyke D.A. & Caldwell M.M. (1996) Morphological plasticity following species-specific recognition and competition in two perennial grasses. *American Journal of Botany* **83**, 919–931.
- Jackson R.B. & Caldwell M.M. (1989) The timing and degree of root proliferation in fertile-soil microsites for three cold desert perennials. *Oecologia* **81**, 149–153.
- Jain A., Poling M.D., Karthikeyan A.S., Blakeslee J.J., Peer W.A., Titapiwatanakun B., Murphy A.S. & Raghothama K.G. (2007) Differential effects of sucrose and auxin on localised phosphate deficiency-induced modulation of different traits of root system architecture in *Arabidopsis*. *Plant Physiology* **144**, 232–247.
- Johnson H.A. & Biondini M.E. (2001) Root morphological plasticity and nitrogen uptake of 59 plant species from the Great Plains grasslands, U.S.A. *Basic and Applied Ecology* **2**, 127–143.
- Kemmel S.W. & Cahill J.F. Jr. (2005) Plant phenotypic plasticity belowground: a phylogenetic perspective on root foraging trade-offs. *American Naturalist* **166**, 216–230.
- Kemmel S.W., de Kroon H., Cahill J.F. Jr. & Mommer L. (2008) Improving the scale and precision of hypotheses to explain root foraging ability. *Annals of Botany* **101**, 1295–1301.
- Kobayashi A., Takahashi A., Kakimoto Y., Miyazawa Y., Fujii N., Higashitani A. & Takahashi H. (2007) A gene essential for hydrotropism in roots. *Proceedings of the National Academy of Sciences of the United States of America* **104**, 4724–4729.
- Krannitz P.G. & Caldwell M.M. (1995) Root growth responses of three Great Basin perennials to intra- and interspecific contact with other roots. *Flora* **190**, 161–167.
- de Kroon H. & Mommer L. (2006) Root foraging theory put to the test. *Trends in Ecology & Evolution* **21**, 113–116.
- Laird R.A. & Aarssen L.W. (2005) Size inequality and the tragedy of the commons phenomenon in plant competition. *Plant Ecology* **179**, 127–131.
- Lambers H., Raven J.A., Shaver G.R. & Smith S.E. (2008) Plant nutrient-acquisition strategies change with soil age. *Trends in Ecology & Evolution* **23**, 95–103.
- Leigh J., Hodge A. & Fitter A.H. (2008) Arbuscular mycorrhizal fungi can transfer substantial amounts of nitrogen to their host plant from organic material. *New Phytologist* 2008. doi: 10.1111/j.1469-8137.2008.02630.x.
- Linkohr B.I., Williamson L.C., Fitter A.H. & Leyser H.M.O. (2002) Nitrate and phosphate availability and distribution have different effects on root system architecture of *Arabidopsis*. *The Plant Journal* **29**, 751–760.
- Lloyd B. (2007) The commons revisited: the tragedy continues. *Energy Policy* **35**, 5806–5818.
- López-Bucio J., Hernández-Abreu E., Sánchez-Calderón L., Nieto-Jacobo M.F., Simpson J. & Herrera-Estrella L. (2002) Phosphate availability alters architecture and causes changes in hormone sensitivity in the *Arabidopsis* root system. *Plant Physiology* **129**, 244–256.
- McConnaughay K.D.M. & Bazzaz F.A. (1991) Is physical space a soil resource? *Ecology* **72**, 94–103.
- MacLean R.C. (2008) The tragedy of the commons in microbial populations: insights from theoretical, comparative and experimental studies. *Heredity* **100**, 233–239.

- MacLean R.C. & Gudeli I. (2006) Resource competition and social conflict in experimental populations of yeast. *Nature* **441**, 498–501.
- MacMillan K., Emrich K., Piepho H.-P., Mullins C.E. & Price A.H. (2006) Assessing the importance of genotype \times environment interaction for root traits in rice using a mapping population II: conventional QTL analysis. *Theoretical and Applied Genetics* **113**, 953–964.
- Mahall B.E. & Callaway R.M. (1991) Root communication among desert shrubs. *Proceedings of the National Academy of Sciences of the United States of America* **88**, 874–876.
- Maina G.M., Brown J.S. & Gersani M. (2002) Intra-plant versus inter-plant root competition in beans: avoidance, resource matching or tragedy of the commons. *Plant Ecology* **160**, 235–247.
- Malamy J.E. (2005) Intrinsic and environmental response pathways that regulate root system architecture. *Plant, Cell & Environment* **28**, 67–77.
- Massa G.D. & Gilroy S. (2003) Touch modulates gravity sensing to regulate the growth of primary roots of *Arabidopsis thaliana*. *The Plant Journal* **33**, 435–445.
- Murphy G.P. & Dudley S.A. (2007) Above- and below-ground cues elicit independent responses. *Journal of Ecology* **95**, 261–272.
- O'Brien E.E. & Brown J.S. (2008) Games roots play: effects of soil volume and nutrients. *Journal of Ecology* **96**, 438–446.
- O'Brien E.E., Gersani M. & Brown J.S. (2005) Root proliferation and seed yield in response to spatial heterogeneity of below-ground competition. *New Phytologist* **168**, 401–412.
- O'Brien E.E., Brown J.S. & Moll J.D. (2007) Roots in space: a spatially explicit model for below-ground competition in plants. *Proceedings of the Royal Society Series B* **274**, 929–934.
- Ochoa I.E., Blair M.W. & Lynch J.P. (2006) QTL analysis of adventitious root formation in common bean under contrasting phosphorus availability. *Crop Science* **46**, 1609–1621.
- Ozinga W.A., Van Andel J. & McDonnell-Alexander M.P. (1997) Nutritional soil heterogeneity and mycorrhiza as determinants of plant species diversity. *Acta Botanica Neerlandica* **46**, 237–254.
- Price A.H. & Tomos A.D. (1997) Genetic dissection of root growth in rice (*Oryza sativa* L.). 2. Mapping quantitative trait loci using molecular markers. *Theoretical and Applied Genetics* **95**, 143–152.
- Rajaniemi T.K. (2007) Root foraging traits and competitive ability in heterogeneous soils. *Oecologia* **153**, 145–152.
- Rankin D.J., Bargum K. & Kokko H. (2007) The tragedy of the commons in evolutionary biology. *Trends in Ecology & Evolution* **22**, 643–651.
- Reich P.B., Walters M.B., Tjoelker M.G., Vanderklein D. & Buschena C. (1998) Photosynthesis and respiration rates depend on leaf and root morphology and nitrogen concentration in nine boreal tree species differing in relative growth rate. *Functional Ecology* **12**, 395–405.
- Remy W., Taylor T.N., Haas H. & Kerp H. (1994) Four hundred-million-year-old vesicular-arbuscular mycorrhizae. *Proceedings of the National Academy of Sciences of the United States of America* **91**, 11841–11843.
- Reynolds H.L. & D'Antonio C. (1996) The ecological significance of plasticity in root weight ratio in response to nitrogen: opinion. *Plant and Soil* **185**, 75–97.
- Rizhsky L., Liang H., Shuman J., Shulaev V., Davletova S. & Mittler R. (2004) When defense pathways collide. The response of *Arabidopsis* to a combination of drought and heat stress. *Plant Physiology* **134**, 1683–1696.
- Robinson D. (1994) The responses of plants to non-uniform supplies of nutrients. *New Phytologist* **127**, 635–674.
- Robinson D. (1996) Resource capture by localized root proliferation: why do plants bother? *Annals of Botany* **77**, 179–186.
- Robinson D., Hodge A., Griffiths B.S. & Fitter A.H. (1999) Plant root proliferation in nitrogen-rich patches confers competitive advantage. *Proceedings of the Royal Society of London. Series B. Biological Sciences* **265**, 431–435.
- Robinson D., Hodge A. & Fitter A.H. (2003) Constraints on the form and function of root systems. In *Root Ecology* (eds H. de Kroon & E.J.W. Visser), Ecological Studies, Vol. 168, pp. 1–31. Springer-Verlag, Berlin, Heidelberg, Germany.
- Sánchez-Calderón L., López-Bucio J., Chacón-López A., Cruz-Ramírez A., Nieto-Jacobo F., Dubrovsky J.G. & Herrera-Estrella L. (2005) Phosphate starvation induces a determinate developmental program in the roots of *Arabidopsis thaliana*. *Plant & Cell Physiology* **46**, 174–184.
- Schenk H.J. (2006) Root competition: beyond resource depletion. *Journal of Ecology* **94**, 725–739.
- Schenk H.J., Callaway R.M. & Mahall B.E. (1999) Spatial root segregation: are plants territorial? *Advances in Ecological Research* **28**, 145–180.
- Schieving F. & Poorter H. (1999) Carbon gain in a multispecies canopy: the role of specific leaf area and photosynthetic nitrogen-use efficiency in the tragedy of the commons. *New Phytologist* **143**, 201–211.
- Semchenko M., Hutchings M.J. & John E.A. (2007a) Challenging the tragedy of the commons in root competition: confounding effects of neighbour presence and substrate volume. *Journal of Ecology* **95**, 252–260.
- Semchenko M., John E.A. & Hutchings M.J. (2007b) Effects of physical connection and genetic identity of neighbouring ramets on root-placement patterns in two clonal species. *New Phytologist* **176**, 644–654.
- Shane M.W. & Lambers H. (2005) Cluster roots: a curiosity in context. *Plant and Soil* **274**, 101–125.
- Smith S.E. & Read D.J. (2008) *Mycorrhizal Symbiosis*, 3rd edn. Academic Press, London, UK.
- Stinson K.A., Campbell S.A., Powell J.R., Wolfe B.E., Callaway R.M., Thelen G.C., Hallett S.G., Prati D. & Klironomos J.N. (2006) Invasive plant suppresses the growth of native tree seedlings by disrupting belowground mutualisms. *Public Library of Science, Biology* **4**, e140. doi: 10.1371/journal.pbio.0040140.
- Struik P.C., Yin X. & Meinke H. (2008) Plant neurobiology and green plant intelligence: science, metaphors and nonsense. *Journal of the Science of Food and Agriculture* **88**, 363–370.
- Svistoonoff S., Creff A., Reymond M., Sigoillot-Claude C., Ricaud L., Blanchet A., Nussaume L. & Desnos T. (2007) Root tip contact with low-phosphate media reprograms plant root architecture. *Nature Genetics* **39**, 792–796.
- Tjoelker M.G., Craine J.M., Wedin D., Reich P.B. & Tilman D. (2005) Linking leaf and root trait syndromes among 39 grassland and savannah species. *New Phytologist* **167**, 915–919.
- Trewavas A. (2005) Green plants as intelligent organisms. *Trends in Plant Science* **10**, 413–419.
- Trewavas A. (2007) Response to Alpi *et al.*: plant neurobiology – all metaphors have value. *Trends in Plant Science* **12**, 231–233.
- Valladares F., Gianoli E. & Gómez J.M. (2007) Ecological limits to plant phenotypic plasticity. *New Phytologist* **176**, 749–763.
- van Vuuren M.M.I., Robinson D. & Griffiths B.S. (1996) Nutrient inflow and root proliferation during the exploitation of a temporally and spatially discrete source of nitrogen in soil. *Plant and Soil* **178**, 185–192.
- Weisskopf L., Tomasi N., Santelia D., Martinoia E., Langlade N.B., Tabacchi R. & Abou-Mansour E. (2006a) Isoflavonoid exudation from white lupin is influenced by phosphate supply, root type and cluster-root stage. *New Phytologist* **171**, 657–668.
- Weisskopf L., Abou-Mansour E., Fromin N., Tomasi N., Santelia D.,

- Edelkott I., Neumann G., Aragno M., Tabacchi R. & Martinoia E. (2006b) White lupin has developed a complex strategy to limit microbial degradation of secreted citrate required for phosphate acquisition. *Plant, Cell & Environment* **29**, 919–927.
- Wijesinghe D.K., John E.A., Beurskens S. & Hutchings M.J. (2001) Root system size and precision in nutrient foraging: responses to spatial pattern of nutrient supply in six herbaceous species. *Journal of Ecology* **89**, 972–983.
- Williamson L.C., Ribrioux S.P.C.P., Fitter A.H. & Leyser H.M.O. (2001) Phosphate availability regulates root system architecture in *Arabidopsis*. *Plant Physiology* **126**, 875–882.
- Wilson J.B., Steel J.B. & Steel S.-L.K. (2007) Do plants ever compete for space? *Folia Geobotanica* **42**, 431–436.
- Zea-Cabrera E., Iwasa Y., Levin S. & Rodriguez-Iturbe I. (2006) Tragedy of the commons in plant water use. *Water Resources Research* **42**, W06D02. doi: 10.1029/2005WR004514.
- Zhang H. & Forde B.G. (1998) An *Arabidopsis* MADS box gene that controls nutrient-induced changes in root architecture. *Science* **279**, 407–409.
- Zheng B.S., Yang L., Zhang W.P., Mao C.Z., Wu Y.R., Yi K.K., Liu F.Y. & Wu P. (2003) Mapping QTLs and candidate genes for rice root traits under different water-supply conditions and comparative analysis across three populations. *Theoretical and Applied Genetics* **107**, 1505–1515.

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