Plant and Soil **232:** 41–50, 2001.

Root proliferation, nitrate inflow and their carbon costs during nitrogen capture by competing plants in patchy soil

David Robinson*
Department of Plant and Soil Science, University of Aberdeen, Aberdeen AB24 3UU, UK

Key words: carbon, heterogeneity, inflow, localised root proliferation, model, nitrate, respiration, soil

Abstract

The responses of roots to nitrogen- and phosphorus-rich patches of soil include proliferation of laterals and stimulation of nutrient inflow (uptake rate per unit root length) within the patch. Nitrate uptake from an N-rich patch is thereby maximised and, perhaps, compensates for an uneven supply of nitrate to the whole root system. Paradoxically, the often weak correlation between root length density and N uptake found in experiments on single plants and crop monocultures suggests that root proliferation in patches has only a minor compensatory influence on N capture. This paradox was resolved when it was realised that localised root proliferation during inter-specific competition for nitrate can lead to a strong association between root length density and nitrate capture. Here, a simple model of inter-specific competition is used to estimate the stimulation in inflow required in one plant to match the N capture of a competitor that responds only by root proliferation, and to estimate associated carbon costs. The model predicts that nitrate inflow must increase proportionally more than root length density to achieve the same N capture. For example, the N capture possible with a 10% increase in root length density can be matched by increasing N inflow by anything from 20% to 20-fold, depending on the initial conditions: the faster the rate of change in root length density, the greater the required relative increase in inflow. In those terms, proliferation would seem the better option, but one that may be more costly in terms of its carbon requirement.

Introduction

The responses of roots to nitrogen- and phosphorus-rich patches of soil include proliferation of laterals within the patch and a transient stimulation of nutrient inflow (uptake rate per unit root length) in those roots (Robinson, 1994; Robinson and Van Vuuren, 1998). Such responses will, logically, maximise N or P uptake from a N- or P-rich patch and, perhaps, compensate for the uneven supply of these nutrients to the whole root system. The potential magnitude of these responses to N and P has been demonstrated most dramatically in barley by the classic and much-cited work of Drew and Saker (1975, 1978). The range, diversity, control and ecological relevance of these 'foraging' responses have become the subject of close and growing scrutiny ever since.

* Fax No: +44-1224-272-703;
E-mail: david.robinson@abdn.ac.uk

Usually (but not always: Otani and Ae, 1996) there is a strong association between root length and P uptake. Root proliferation in P-rich patches is, therefore, easy to interpret in terms of a 'foraging' response. It is difficult to make the same statement about nitrate, however, despite the unmistakable strength and specificity of root proliferation in nitrate-rich patches. There is often only a weak correlation between a plant's root length density and nitrate uptake. This has been found in experiments on single plants (Van Vuuren et al., 1996) and crop monocultures (Wiesler and Horst, 1994). Root proliferation in patches may, therefore, have only a small compensatory influence on nitrate capture.

This is an uncomfortable conclusion to reach, and it is one that makes little sense in the light of Zhang and Forde's (1998) discovery that, in *Arabidopsis*, the extension of lateral roots in nitrate-rich patches is partly under genetic control. It is not coincidental that roots respond to nitrate patches in the way that

they do, but why do they do it? This question was answered by Hodge et al. (1999) and Robinson et al. (1999) who showed that localised root proliferation during competition for N between two perennial grasses (*Poa pratensis* and *Lolium perenne*) did lead to a strong association between root length density and nitrate capture in both species. *L. perenne* produced more roots in the patch and captured more N from it. This finding emphasised that the functional significance of any particular response to soil heterogeneity or any other factor cannot necessarily be predicted from experiments conducted in an inappropriate context (Robinson et al., 1999). While the genetics, molecular biology and physiology of plants' responses to nitrate can be investigated on plants isolated from their neighbours and from soil, the actual contributions of these responses to N capture and their influence on plant–plant interactions cannot.

The analysis by Robinson et al. (1999) ignored the influence of the stimulation in N inflow in roots in N-rich patches that often precedes the proliferation of those roots (Van Vuuren et al., 1996); this paper attempts to rectify that deficiency. If most of a plant's roots are in N-deficient soil, a demand for N is created within the plant. This demand 'primes' roots for high-affinity transport. Should the N supply be restored, e.g., if some roots grow into a nitrate-rich patch, nitrate is absorbed by those roots faster would have been possible at the same external concentration had no demand-induced priming occurred (see Robinson, 1996a). Precisely how this is achieved in molecular terms in unknown. If the nitrate transport system is analogous to that for sulphate (in molecular terms probably the most well characterised ion transport system in plants), starvation is manifested by a decreased phloem-mobile signal (probably shoot-derived glutathione in the case of S: Lappartient et al., 1999). Once translocated to roots, this signal represses the transcription of genes encoding high-affinity sulphate transporters (Vidmar et al., 2000). This implies that an increased whole-plant demand for S up-regulates sulphate inflow by increasing the density of sulphate transporters in root plasma membranes. Similar, but unknown, mechanisms might exist for the regulation of nitrate and ammonium transporters (Forde, 2000; Forde and Clarkson, 1999; Howitt and Udvardi, 2000).

A second mechanism by which N inflow might be up-regulated is the reduction of nitrate efflux from the roots of N-deprived plants. That mechanism could have a significant up-regulatory effect on N inflow only if nitrate efflux is a large fraction of the influx in N-rich plants (inflow = influx − efflux). If efflux were 10% of influx, totally eliminating efflux could increase the inflow by only 11%, whereas if efflux comprised 50% of influx, the elimination of efflux could double the inflow. It is not known how nitrate efflux varies with external nitrate supply (Scheurwater et al., 1999), so it is not yet possible to assess the importance of this mechanism.

Whatever the underlying mechanisms, the respective merits of localised proliferation versus up-regulated inflow for N capture from nitrate-rich patches have yet to be assessed experimentally, one reason being that genotypes that do one but not the other have yet to be identified (or created). Jackson and Caldwell (1996) used a simulation model of nutrient uptake to illustrate the relative importance of root proliferation and up-regulated nitrate inflow for N capture by single plants. Here I use a model developed by Robinson et al. (1999) to explore the consequences of root proliferation and up-regulated inflow for nitrate capture by competing plants.

Another aspect that has been overlooked until now is the carbon cost of proliferation and maintenance of roots within a nitrate-rich patch compared with the carbon required to transport nitrate across root membranes (see Lambers et al., 1998, p. 124). I have speculated previously (Robinson, 1996b) that, while the carbon costs of nitrate-induced root proliferation could be physiologically significant, the evolutionary penalties associated with (what seemed then) a poor investment might well be trivial and, therefore, of no selective disadvantage. Here, I focus on the possible differences in carbon cost associated with nitrate-induced root proliferation and an up-regulated inflow of nitrate.

Theoretical

The following equations and parameter values were used to simulate competition for nitrate between two contrasting species, and to estimate the associated carbon costs. Calculations were performed using Microsoft Excel 97.

Nitrate supply

In this model, nitrate is the only source of N available to plants. It is present at a defined initial concentration (100 μg cm^{-3}) and is gradually depleted to zero by plant uptake. No other processes of nitrate loss

(e.g., denitrification or immobilisation by microbes) are considered. Nitrification is similarly disregarded in the interests of simplicity. To explore particular questions, these processes could be incorporated easily within the framework of the existing model.

It is important to emphasise that this pattern of nitrate supply has a major influence on the model's predictions. Had a near-constant nitrate concentration been assumed, notions that plants compete for nitrate are as meaningless as the idea of plants 'competing' for atmospheric CO_2. Then, nitrate capture by one species would be independent of that by a neighbouring plant and nitrate capture at one time would have no effect on future nitrate availability. The same would apply at the opposite extreme, at the vanishingly small nitrate supplies characteristic of many uncultivated soils.

The basic spatial scale of the model is a unit of soil volume, envisaged as 1 cm^3. (For this reason, cm is the preferred unit of length measurement rather than the SI unit m). The nitrate concentration (C, μg cm^{-3}) at the end of the time interval t (days) to $t + 1$ is the concentration at the start of the interval minus the amount taken up by the plants from that volume of soil (U, μg cm^{-3}):

$$C_{t+1} = C_t - U_t \tag{1}$$

N uptake

N uptake (U, μg cm^{-3}) by a species from unit volume of soil during the time interval to $t + 1$ (i.e., Δt) is assumed to be the product of root length density (L, cm cm^{-3}) in that volume and the N inflow (I, μg cm^{-1} day^{-1}):

$$U_t = L_t I_t \Delta t \tag{2}$$

Root length density and inflow each varies independently with time, as defined below. (NB: to minimise typographical clutter, root length density is symbolised here as L rather than the more conventional L_v: Tinker and Nye, 2000).

The total amount (M, μg cm^{-3}) of N captured by a species is the sum of the amounts taken up in each time interval:

$$M = \sum_{t=0}^{t=t_{\max}} U_t \tag{3}$$

where $t_{\max}$ is the duration of the 'experiment' which may exceed the time taken for nitrate concentration to reach zero.

Root proliferation

Expressed in terms of root length density, a localised proliferation of roots has two essential variables. First, a rate of increase (r, day^{-1}) in root length density. Second, a maximum attainable root length density ($L_{\max}$, cm cm^{-3}). The data presented by Robinson et al. (1999) for *L. perenne* and *P. pratensis* illustrate these features nicely. A logistic equation is a convenient description of the change in root length density over the time interval Δt, a discrete form of which is:

$$L_{t+1} = L_t \Delta t \left[1 + r\left(1 - \frac{L_t}{L_{\max}}\right)\right] \tag{4}$$

An initial root length density of 0.01 cm cm^{-3} is specified for $t = 0$. Both r and $L_{\max}$ are allowed to vary in response to localised nitrate (see below).

Nitrate inflow

Ion uptake per unit of root is conventionally and conveniently described as a function of external ion concentration by Michaelis–Menten kinetics and this is adopted here. Inflow (I) at time t is described in terms of a maximum ($I_{\max}$) and a concentration (K_m) at which $I_t = I_{\max}/2$ (Tinker and Nye, 2000, p. 254):

$$I_t = \frac{C_t I_{\max}}{K_m + C_t} \tag{5}$$

Again, for simplicity, a minimum, positive value of C_t at which net inflow is zero (a 'compensation point': Lambers et al., 1998, p. 248) is omitted. $I_{\max}$ is assumed to vary as part of one plant's response to localised nitrate (see below), but K_m is here assumed constant (0.7 μg cm^{-3}, i.e., 50 μM: Forde and Clarkson, 1999). K_m concentrations for nitrate uptake tend to be so small compared with nitrate concentrations in soil solutions (e.g., >5 mM: Yanai et al., 1996) that adjustments to them have negligible influence on net N capture.

Inter-specific competition

Two potential competitors are defined, species A and B. Each has the same initial rate of increase in root length density (r), maximum root length density ($L_{\max}$) and maximum nitrate inflow ($I_{\max}$). Both species absorb nitrate from the same pool, so that their *joint* uptake in one time interval determines, via Eq. (1), the nitrate concentration in the next.

One species, A, responds to localised nitrate only by changing r and $L_{\max}$ so as to adjust its root length density (Eq. (4)). Its inflow remains unaltered. By contrast, species B retains its original rate of increase in root length density and $L_{\max}$, but increases its $I_{\max}$ in response to localised nitrate (Eq. (5)). A responds morphologically to localised nitrate, B physiologically.

The question that I ask is: to what extent must $I_{\max}$ in species B change to match the N capture afforded by species A's adjustment in root length density? This question is answered by increasing r and $L_{\max}$ for A by defined amounts from their initial values to simulate proliferation. $I_{\max}$ of B is then adjusted incrementally (using the Goal Seek tool in Microsoft Excel 97) to simulate an up-regulation of inflow until, at the end of the 'experiment', the two species have captured the same amount of nitrate.

For both A and B, the initial values of r, $L_{\max}$ and $I_{\max}$ were set to 0.2 day^{-1}, 20 cm cm^{-3} and 1.2 μg cm^{-1} day^{-1}, respectively. This value of I_{max} is equivalent to 1 pmol cm^{-1} s^{-1}, a typical measurement for roots in nitrate-rich solutions (Robinson, 1986).

Carbon costs

The amounts of carbon required for root proliferation, maintenance and nitrate transport were estimated for species A and B as follows.

Root dry weight (W, g cm^{-3}) per unit soil volume was estimated from root length density by assuming constant specific gravity (ρ, g cm^{-3}), dry:fresh weight ratio (ϕ) and mean radius (a, cm) of roots. Assuming cylindrical geometry, W at time t is given by:

$$W_t = \pi a^2 \rho \phi L_t \tag{6}$$

The constants ρ, ϕ and a were set to 1 g cm^{-3}, 0.1 and 0.01 cm, respectively. L_t/W_t is the specific root length (cm g^{-1}), which increases in response to localised nitrate (Hodge et al., 1998; Robinson and Rorison, 1983), implying that a, ρ and ϕ are not necessarily constant (Eissenstat and Yanai, 1997). Eq. (6) is, therefore, a gross simplification. More realistic models should use measured root diameter distributions (cf. Boot and Mensink, 1990) to derive W_t for named species (as opposed to the anonymous A and B).

The specific carbon requirements (χ_t, g C g^{-1} day wt.) for root growth, maintenance and nitrate uptake were calculated separately for A and B for each time interval as:

$$\chi_t = W_t(\chi_g + \chi_m \Delta t + \chi_u U_t) \tag{7}$$

χ_g is the specific carbon requirement for root growth. It is the sum of the carbon incorporated into structural material and that used in associated respiration. The carbon fraction of root dry matter was assumed to be 0.4 g C g^{-1} dry wt. Respiratory consumptions of O_2 in root growth of ~10 mmol g^{-1} day wt. were quoted by Lambers et al. (1998, p. 132). A 2:1 C:O stoichiometry during respiratory electron flow (Nobel 1991, p. 328) gives a specific respiratory C cost of root growth of 0.24 g C g^{-1} dry wt. Therefore, χ_g ~0.64 g C g^{-1} dry wt.

$\chi_m \Delta t$ is the carbon consumption in maintenance respiration. Lambers et al. (1998, p. 132) quoted a maintenance respiration rate (χ_m) for roots of ~10 nmol O_2 g^{-1} dry wt. s^{-1}. Using similar logic as in the previous paragraphs, a χ_m value of ~0.02 g C g^{-1} dry wt. day^{-1} was derived.

$\chi_u U_t$ is the respiratory carbon cost associated with transporting nitrate ions into roots and this varies with the amount of nitrate absorbed during a time interval. Lambers et al. (1998, p. 132) quoted respiratory costs per mol nitrate transported of ~1 mol O_2 mol^{-1} nitrate, so that χ_u ~1.7 g C g^{-1} nitrate absorbed. U_t is calculated using Eq. (2).

The values of χ_g, χ_m and χ_u were assumed to be the same for species A and B. Again, if species-specific information were available this could easily be substituted.

Finally, cumulative carbon costs (X) were calculated as:

$$X = \sum_{t=0}^{t=t_{\max}} \tag{8}$$

In all simulations, $t_{\max}$ was set to 50 days. Carbon costs were expressed as the difference in total cost between A and B.

Results

To illustrate the nature of the model's output, Fig. 1 shows the trajectory of N capture of species A when it is competing for nitrate with species B. A is assumed to proliferate roots in response to nitrate by changing the rate at which its root length density increases. B, in contrast, does not respond — it maintains its initial rate of increase in root length density and nitrate inflow. Predictably, A always obtains more nitrate than B and eventually out-competes it by wide margins. How should B respond if it is to match the N capture of its competitor?

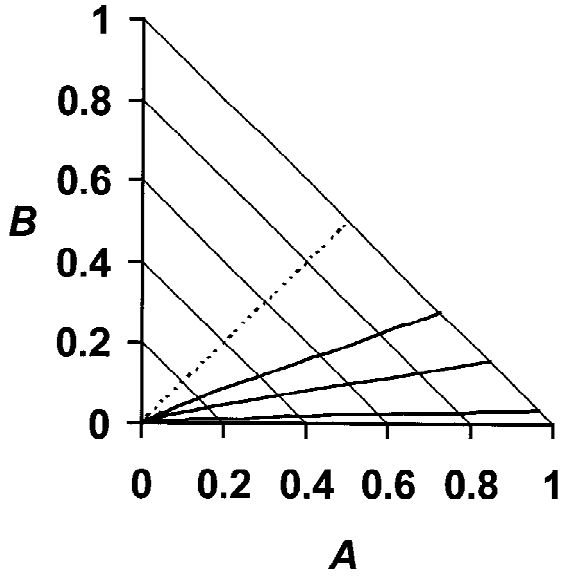

Figure 1. Simulated capture of N, as a fraction of that initially available, from unit volume of soil by species *A* and *B* during competition for nitrate. Diagonal lines represent different total N capture by *A* + *B*, with the uppermost line representing complete N capture. The broken line represents equal N capture by *A* and *B*. Capture starts at the origin and proceeds towards the uppermost total capture line on a trajectory dependent on the species' attributes. The solid curves represent trajectories of N capture for species *A* and *B* when *A* successively adjusts its rate of increase (*r*) in root length density from its initial value (0.2 day^{-1}, as in species *B*) to 0.25 (upper curve), 0.3 (middle curve) or 0.5 day^{-1} (lower curve). *B* does not respond by increasing its inflow which remains at 1.2 μg cm^{-1} day^{-1} throughout. L_{max} was set to 20 cm cm^{-3} in both species.

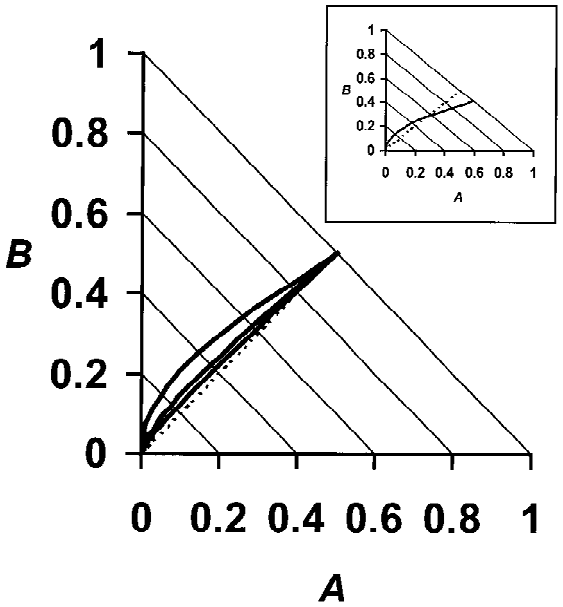

Figure 2. As for Fig. 1, but here species *B* responds by increasing I_{max} from its initial value (1.2 μg cm^{-1} d^{-1}) such that it ultimately captures the same fraction of N (0.5) as *A*. The solid curves represent trajectories of N capture for *A* and *B* when *r* in *A* is 0.5 (upper curve), 0.3 (middle curve) or 0.25 day^{-1} (lower curve), and when I_{max} in *B* is 29 (upper), 6.3 (middle) or 3.1 μg cm^{-1} day^{-1} (lower). Inset: The trajectory possible when I_{max} of *B* is limited to 22 instead of 29 μg cm^{-1} day^{-1} such that *A* (r = 0.5 day^{-1}) is the ultimate winner (fractional capture by *A* = 0.59; fractional capture by *B* = 0.41).

Figure 2 provides the answer. If *B* increases its I_{max} by between 2.6- and 24-fold, it could eventually capture as much nitrate as *A*. Interestingly, the predicted trajectories show that it is species *B* with its superior inflow that initially wins the contest for nitrate. However, as nitrate is depleted and *B*'s inflow reduced according to Eq. (5), and as *A*'s root proliferation increases, equality is eventually restored.

A fuller picture of the response required from *B* to match those of *A* is given by Figure 3. Increases in the maximum root length density (L_{max}) of *A* have hardly any effect compared with those in the rate of increase in root length density (*r*); it is the latter that, in this model, is the major determinant of the effectiveness of root proliferation in nitrate capture.

The difference in the carbon cost of *A* and *B*'s responses shown in Fig. 3 are presented in Fig. 4. There is a clear and steep increase in the carbon cost of root proliferation compared with the corresponding increases in inflow.

Discussion

The above analysis is an extreme simplification of what are, in reality, complex processes that contain large elements of uncertainty. Nevertheless, it does provide some new insights into the functional significance of plants' alternative responses to locally available nitrate. These insights are in the form of predictions that future experiments might be designed to test, should appropriately distinct genotypes become available for the purpose. Each is now discussed in turn.

Root proliferation can be matched by increased inflow — within limits

Figure 3 illustrated the extent to which nitrate inflow must increase for it to match the N capture afforded by a certain root proliferation. The more vigorous the proliferation, the greater the inflow must increase to match it — it is obvious that this would be so.

The increases in root length density implied in Fig. 3 for species *A* are realistic, at least for plants

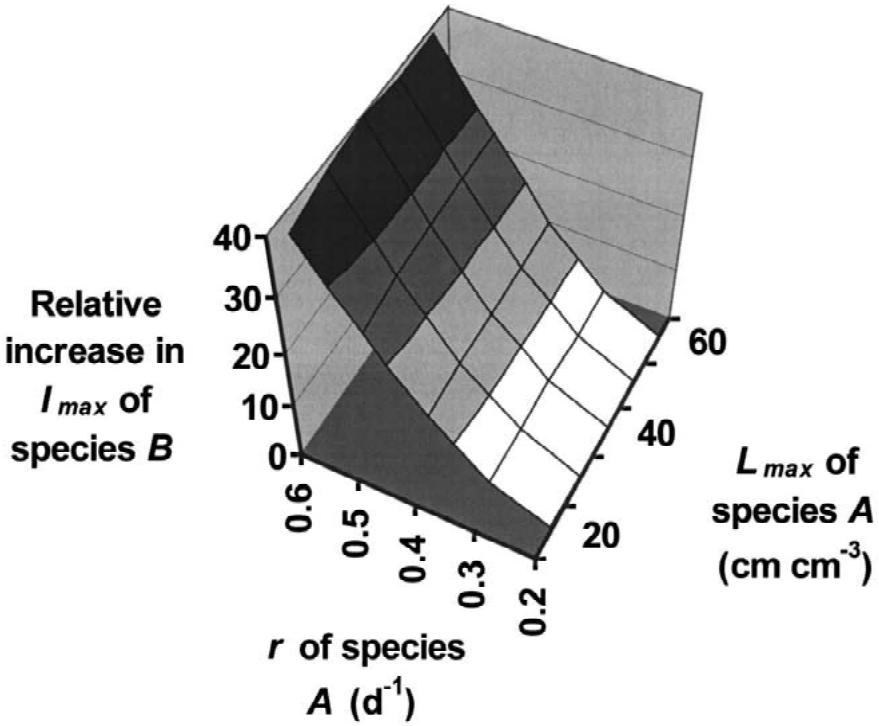

Figure 3. Increases in I_{max} relative to the initial value (1.2 μg cm^{-1} day^{-1}) of species *B* required to match the N capture of species *A*. The maximum root length density (L_{max}, cm cm^{-3}) and rate of increase in root length density (r, day^{-1}) of *A* vary as shown on the horizontal axes.

with finely branched, extensive root systems such as grasses (see e.g., Tinker and Nye, 2000, p. 260). However, inflow cannot increase in response to a transient increase in local nitrate as much as the model assumes. If I_{max} is increased by alterations in the density of transporters in root plasma membranes (see Introduction), >10-fold increases in I_{max} in real plants seem highly unlikely. Measured increases in local N inflows in N-rich patches of 2–3-fold are common (Robinson, 1994) and there is one report (Robinson et al., 1994) of an 11-fold increase in wheat. These correspond to cases where $r \leq 0.35$ day^{-1}, i.e., at the bottom end of the range of root proliferations shown in Fig. 3. Therefore, most of the calculated increases in inflow for our hypothetical species *B* are beyond the physiological capacity of existing genotypes.

This limitation on I_{max} means that proliferation could always be the superior response to maximise a competitor's nitrate capture, as illustrated in the inset to Fig. 2. That is especially true if the nitrate concentration becomes depleted towards zero since inflow is a function of concentration (Eq. (5)), whereas changes in root length density are not, apart from an initial concentration-dependent rate of lateral extension (Zhang et al., 1999). A plant with a modest nitrate inflow coupled to vigorous root proliferation would probably always capture a greater share of a finite nitrate supply than one expressing strong up-regulation of inflow but weak proliferation in response to nitrate.

Figure 2 shows that an up-regulation of nitrate inflow could allow greater initial nitrate capture than could root proliferation. The resulting time lags in N capture by individuals expressing such distinctly different responses might have important implications for plant–plant interactions in communities comprising a mixture of species, some capable of rapid up-regulation of inflow but slow proliferation, and others (probably fast-growing species) that tend to do the opposite. The former type of response would be more appropriate to exploit very transient pulses, whereas the latter type would allow greater access to more durable patches (cf. Campbell and Grime, 1989). A physiological response could, in some circumstances, be a better option than a morphological response.

To varying extents, real plants up-regulate inflow *and* proliferate roots if the external nitrate stimulus is strong enough (Robinson, 1994; Van Vuuren and Robinson, 1998; Zhang et al., 1999). Figure 2 im-

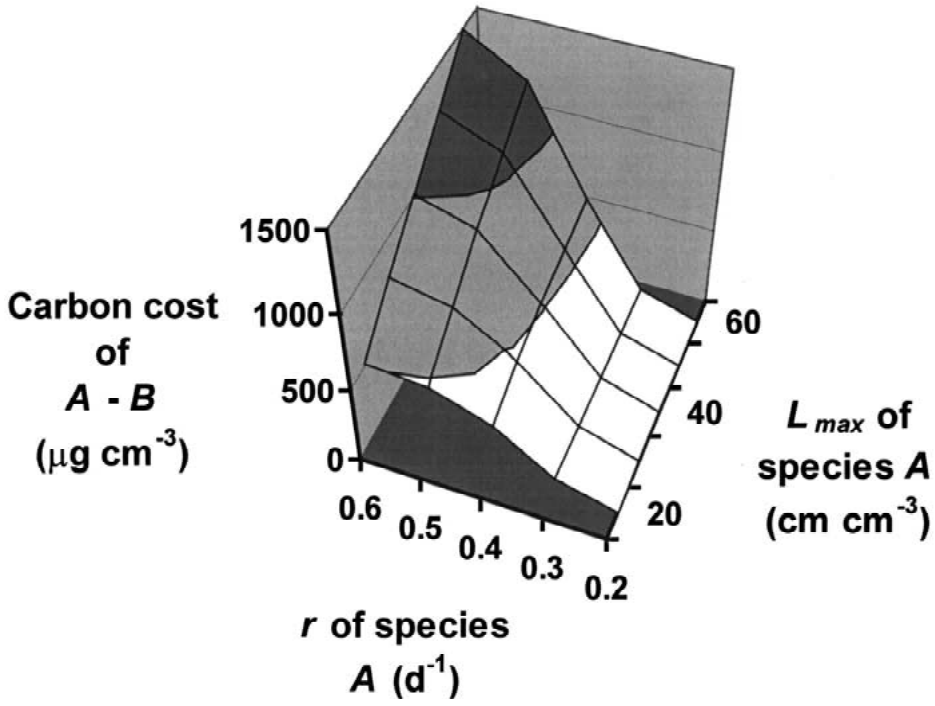

Figure 4. Differences in carbon cost per unit soil volume between species *A* and *B* for the responses shown in Fig. 3.

plies that N capture from a nitrate-rich patch would be maximised by an initial up-regulation of nitrate inflow followed by a phase of root proliferation during which inflow declines. This is seen in barley (Drew and Saker, 1975) and wheat (Van Vuuren et al., 1996), and is consistent with the expression of *NRT2* genes (which code for nitrate transporters) in previously N-starved roots of *Arabidopsis* following the re-supply of nitrate (Forde, 2000).

Root proliferation requires more carbon than does an increase in inflow

Figure 4 shows that the potential carbon cost of vigorous root proliferation can be considerably greater than for an up-regulation of nitrate inflow, per unit volume of soil. One penalty of producing many roots rapidly is that, once produced, roots have to be maintained even if there is no nitrate left to capture. In contrast, carbon is needed for nitrate transport only as long as any nitrate is available to be transported.

Remember, however, that the largest differences in cost shown in Fig. 4 correspond to cases where inflow must increase by physiologically unrealistic amounts to match the nitrate capture resulting from proliferation. The model's prediction is that real plants may need to invest $\sim$500 μg C cm^{-3} soil more to support a proliferation response than they would to up-regulate nitrate inflow over a notional 50-day period, i.e., an average of up to 10 μg C cm^{-3} day^{-1}. Whether this extra carbon cost is functionally significant will depend on many factors. These will include the total rooting volume of the plant, the fraction of that volume in which root proliferation occurs, the fraction of photosynthesis required daily for proliferation, and whether there is a corresponding reduction in root growth outside the nitrate-rich patch (cf. Drew et al., 1973). If the last of these occurs to a sufficient extent, the net carbon cost of root proliferation in a nitrate-rich patch could be zero to the whole plant.

Suppose that a plant has a rooting volume of 1000 cm^3 and a leaf area of 1000 cm^2, and that root proliferation occurs in a nitrate-rich patch comprising 10% of its rooting volume. The plant would therefore require an extra 1000 μg C day^{-1} to support that proliferation so as to compete effectively with a plant capable of strong up-regulation of nitrate inflow. If it fixes carbon at the modest net rate of 10 μmol m^{-2} s^{-1} (Nobel, 1991, p. 449; Lambers et al., 1998, p. 27), this is equivalent to a net carbon gain of 0.52 g C day^{-1} for a 12-h daily photoperiod. The extra carbon required for root proliferation is then only 0.2%

of the plant's daily carbon gain. This seems hardly a potentially ruinous burden, especially if compared with the often-quoted 10% of photosynthetic fixation taken by symbiotic mycorrhizal fungi, and if growth elsewhere in the root system is reduced (see above). Photosynthesis in this hypothetical plant would have to be reduced by 98% for the carbon requirement for root proliferation to be 10% of daily fixation. If this estimate is reasonable, root proliferation per se does not appear to present a major problem in terms of balancing a plant's carbon budget.

A physiological response might be a better option if carbon supply is limited

If the carbon supply from photosynthesis is less than generous, however, the conclusion reached in the previous section might not apply. Experiments with the perennial grass *Agropyron desertorum* (Bilborough and Caldwell, 1995; Cui and Caldwell, 1997) demonstrated a reduction in root proliferation in N-rich patches when plants were shaded, the magnitude of which was disproportionate to the effect of shading on plant size. Repeated defoliation by herbivores might be expected to have a similar effect. If either shading or defoliation was severe, and internal stores of carbohydrate limited, root proliferation might become an unaffordable response to nitrate patches compared with an up-regulation of inflow. Then, nitrate inflow might be expected to be even greater, albeit transiently, in plants experiencing a carbon shortage compared with those enjoying a surfeit of carbon and able to proliferate roots. Inflows have not yet been measured in experiments where shading or defoliation treatments have been applied. Cui and Caldwell's (1997) data can be used to show that over 60 days, the mean inflows of N from a localised nitrate patch were probably about the same ($\sim$7.5 μg cm^{-1} day^{-1} per cm^3 soil) whether *A. desertorum* was shaded or not. Any temporary up-regulation in inflow is unlikely to be detected over such a long interval, however, for which frequent sequential measurements are needed (Van Vuuren et al., 1996).

A large carbon cost associated with root proliferation within a nitrate-rich patch could be mitigated if, outside the patch, root turnover should increase or root production decrease, so reducing the total carbon requirement for the whole root system. Unfortunately, simultaneous measurements of root demography within and outside nutrient-rich patches required to test this possibility do not seem to have been made. The data that come closest to this are those of Pregitzer et al. (1993). They found that localised additions of ammonium and nitrate to soil supporting a mixed hardwood forest extended the average lifespan of fine roots within the patches compared with roots in untreated soil. If that observation reflects a difference among roots of the same plants (uncertain in Pregitzer et al.'s study because roots of individuals could not be distinguished), it would be consistent with them shedding roots faster outside a nutrient-rich patch. Savings in the carbon requirements of the whole root system would then follow. Far more data are needed before this hypothesis can be properly tested.

Missing pieces of the puzzle

No discussion of a plant's carbon budget is complete without including mycorrhizas. Tibbett (2000) argued that the localised growth and activity of hyphae of mycorrhiza-forming fungi could supplement root proliferation in nutrient-rich patches. However, the evidence for such an effect is scanty (St. John et al., 1983); to test it rigorously will demand information about the size, rate of growth and spatial distribution of hyphae within and outside patches. Mycorrhizal colonisation can stimulate root proliferation, as Hodge et al. (2000) found when *Plantago lanceolata* was colonised by the arbuscular mycorrhiza-forming fungus *Glomus mossae*, but there was no effect on the capacity of *P. lanceolata* to capture N from a patch of decomposing organic matter. We are just beginning to unearth the role of mycorrhizas in patch exploitation, and the cost and benefits that might accrue to plant and fungal partners.

Attention in this paper has focused on nitrate. There are several reasons for this deliberate myopia. First, the functional significance of root proliferation in response to nitrate had become all the more inexplicable since evidence for its genetic control appeared (Zhang and Forde, 1998; Zhang et al., 1999); the 'nitrate paradox' was ripe for resolution. Second, no data seem to exist for the respiratory costs of ammonium transport. The intrinsic cost will be half that for nitrate (I. Scheurwater, personal communication), but the net cost could be greater given the ubiquity of ammonium efflux from roots (Forde and Clarkson, 1999) which will reduce the energetic efficiency of ammonium capture. Third, even less is known of the transport costs associated with absorbing other forms of soluble N such as amino acids.

Ammonium and amino acids differ from nitrate in an important respect: mobility. Nitrate is one of the most mobile ions in soil. Its concentration is not buffered against depletion (other than by the concentration-independent microbial processes such as nitrification) and it diffuses rapidly through moist soil down concentration gradients. This means that it is reasonable to assume that the nitrate concentration at uptake sites approximates that which can be measured in the bulk soil. That assumption would be unreasonable for ammonium and amino acids. These diffuse through soil at least an order or magnitude more slowly than nitrate, are adsorbed onto negatively charged surfaces, and suffer significant drawdowns in concentration between bulk soil and absorbing roots (or hyphae). Nevertheless, it would be instructive to perform a similar analysis for these other forms of N to see to what extent the conclusions reached (or predictions made) for nitrate apply to them.

Acknowledgements

I am grateful to Brian Forde, Angela Hodge, Hans de Kroon, Jim McDonald, Dominic Standing, Margret van Vuuren and an anonymous reviewer for their helpful comments about earlier drafts of this paper.

References

Bilborough C J and Caldwell M M 1995 The effects of shading and N status on root proliferation in nutrient patches by the perennial grass *Agropyron desertorum*. Oecologia 103, 19–16.

Boot R G A and Mensink M (1990) Size and morphology of root systems of perennial grasses from contrasting habitats as affected by nitrogen supply Plant Soil 129, 291–299.

Campbell B D and Grime J P 1989 A comparative study of plant responsiveness to the duration of episodes of mineral nutrient enrichment. New Phytol. 112, 261–267.

Cui M and Caldwell M M 1997 Shading reduces exploitation of soil nitrate and phosphate by *Agropyron desertorum* and *Artemisia tridentata* from soils with patchy and uniform nutrient distributions. Oecologia 109, 177–183.

Drew M C and 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. J. Exp. Bot. 26, 79–90.

Drew M C and 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 localized supply of phosphate. J. Exp. Bot. 29, 435–451.

Drew M C, Saker L R and 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. J. Exp. Bot. 24, 1189–1202.

Eissenstat D M and Yanai R D 1997 The ecology of root lifespan. Adv. Ecol. Res. 27, 1–60.

Forde B G 2000 Nitrate transporters in plants: structure, function and regulation. Biochim. Biophys. Acta Biomembranes 1465, 219–235.

Forde B G and Clarkson D T 1999 Nitrate and ammonium nutrition of plants: physiological and molecular perspectives. Adv. Bot. Res. 30, 1–90.

Hodge A, Stewart J, Robinson D, Griffiths B S and Fitter A H 1998 Root proliferation, soil fauna and plant nitrogen capture from nutrient-rich patches in soil. New Phytol. 139, 479–494.

Hodge A, Robinson D, Griffiths B S and Fitter A H 1999 Why plants bother: root proliferation results in increased nitrogen capture from a nutrient-rich patch when two grasses compete. Plant Cell Environ. 22, 811–820.

Hodge A, Robinson D and Fitter A H 2000 An arbuscular mycorrhizal inoculum enhances root proliferation in, but not nitrogen capture from, nutrient-rich patches in soil. New Phytol. 145, 575–584.

Howitt S M and Udvardi M K 2000 Structure, function and regulation of ammonium transporters in plants. Biochim. Biophys. Acta Biomembranes 1465, 152–170.

Jackson R B and Caldwell M M 1996 Integrating resource heterogeneity and plant plasticity: modelling nitrate and phosphate uptake in a patchy soil environment. J. Ecol. 84, 891–903.

Lambers H, Chapin F S and Pons T L 1998 Plant Physiological Ecology. Springer, Berlin. 540 p.

Lappartient A G, Vidmar J J, Leustek T, Glass A D M and Touraine B 1999 Inter-organ signaling in plants: regulation of ATP sulfurylase and sulfate transporter genes expression in roots, mediated by pholem-translocated compound. Plant J. 18, 89–95.

Nobel P S 1991 Physicochemical and Environmental Plant Physiology. Academic Press, San Diego, CA 635 p.

Otani T and Ae N 1996 Sensitivity of phosphorus uptake to changes in root length and soil volume. Agron. J. 88, 371–375.

Pregitzer K S, Hendrick R L and Fogel R 1993 The demography of fine roots in response to patches of water and nitrogen. New Phytol. 125, 575–580.

Robinson D 1986 Limits to nutrient inflow rates in roots and root systems. Physiol. Plant. 68, 551–559.

Robinson D 1994 The responses of plants to non-uniform supplies of nutrients. New Phytol. 127, 635–674.

Robinson D 1996a Variation, co-ordination and compensation in root systems in relation to soil variability. Plant Soil 187, 57–66.

Robinson D 1996b Resource capture by localised root proliferation: why do plants bother? Ann. Bot. 77, 179-185.

Robinson D and Rorison I H 1983 A comparison between the responses of *Lolium perenne* L., *Holcus lanatus* L. and *Deschampsia flexuosa* (L.) Trin. to a localized supply of nitrogen. New Phytol. 94, 263–273.

Robinson D, Linehan D J and Gordon D C 1994 Capture of nitrate from soil by wheat in relation to root length, nitrogen inflow and availability. New Phytol. 128, 297–305.

Robinson D and Van Vuuren M M I 1998 Responses of wild plants to nutrient patches in relation to growth rate and life-form. *In* Inherent Variation in Plant Growth. Physiological Mechanisms and Ecological Consequences. Eds H Lambers, H Poorter and M M I Van Vuuren. pp. 237–257. Backhuys Publishers, Leiden.

Robinson D, Hodge A, Griffiths B S and Fitter A H 1999 Plant root proliferation in nitrogen-rich patches confers competitive advantage. Proc. R. Soc. London B 266: 431–435.

Scheurwater I, Clarkson D T, Purves J V, Van Rijt G, Saker L R, Welschen R and Lambers H 1999 Relatively large nitrate efflux can account for the high specific respiratory costs for nitrate transport in slow-growing grass species. Plant Soil 215, 123–134.

Tibbett M 2000 Roots, foraging and the exploitation of soil nutrient patches: the role of mycorrhizal symbiosis. Funct. Ecol. 14, 397–399.

Tinker P B, Nye P H 2000 Solute Movement in the Rhizosphere. Oxford University Press, Oxford. 444 pp.

Van Vuuren M M I, Robinson D and Griffiths B S 1996 Nutrient inflow and root proliferation during the exploitation of a temporally and spatially discrete source of nitrogen in soil. Plant Soil 178, 185–192.

Vidmar J J, Tagmount A, Cathala N, Touraine B and Davidian J C E 2000 Cloning and characterization of a root specific high-affinity sulfate transporter from *Arabidopsis thaliana*. FEBS Lett. 475, 65–69.

Wiesler F and Horst W J 1994 Root growth and nitrate utilization of maize cultivars under field conditions. Plant Soil 163, 267–277.

Yanai J, Linehan D J, Robinson D, Young I M, Hackett C A, Kyuma K and Kosaki T. 1995 Effects of inorganic nitrogen application on the dynamics of the soil solution composition in the root zone of maize in a Scottish soil. Plant Soil 180, 1–9.

Zhang H and Forde B G 1998 An *Arabidopsis* MADS box gene that controls nutrient-induced changes in root architecture. Science 279, 407–409.

Zhang H, Jennings A, Barlow P W and Forde B G 1999 Dual pathways for regulation of root branching by nitrate. Proc. Natl. Acad. Sci. USA 96, 6529–6534.