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Plant root proliferation in nitrogen-rich patches confers competitive advantage

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Plants respond to environmental heterogeneity, particularly below ground, where spectacular root proliferations in nutrient-rich patches may occur. Such 'foraging' responses apparently maximize nutrient uptake and are now prominent in plant ecological theory. Proliferations in nitrogen-rich patches are difficult to explain adaptively, however. The high mobility of soil nitrate should limit the contribution of proliferation to N capture. Many experiments on isolated plants show only a weak relation between proliferation and N uptake. We show that N capture is associated strongly with proliferation during inter-specific competition for finite, locally available, mixed N sources, precisely the conditions under which N becomes available to plants on generally infertile soils. This explains why N-induced root proliferation is an important resource-capture mechanism in N-limited plant communities and suggests that increasing proliferation by crop breeding or genetic manipulation will have a limited impact on N capture by well-fertilized monocultures.

Keywords: morphological plasticity; nutrient patch; nutrient uptake; plant competition; root proliferation

1. INTRODUCTION

All soils are naturally heterogeneous and, consequently, nutrients are made available to plants in spatial patches and temporal pulses (Fitter 1994). This heterogeneity is determined by the distribution of soil organic matter (Van Noordwijk *et al.* 1993; Stark 1994) and the rate of its microbial decomposition (van Vuuren *et al.* 1996; Stark & Hart 1997; Hodge *et al.* 1998). In agricultural soils, this inherent patchiness is increased by granular fertilizers (at a fine scale) and fertilizer bands (at a coarser scale). Plants can respond to such heterogeneity by localized proliferation of roots, a presumed 'foraging' response allowing absorbing surfaces to be located preferentially in nutrient-rich patches where nutrient capture will be greatest. Such responses are taxonomically widespread (Robinson 1994; Robinson & van Vuuren 1998) and prominent in current plant ecological theory (Hutchings & de Kroon 1994; Robinson 1994; Casper & Jackson 1997; Grime *et al.* 1997). The recent discovery, in *Arabidopsis* of a gene, *ANRI* (Zhang & Forde 1998), which controls lateral root growth and is rapidly and specifically induced by nitrate (NO_3^-) in N-starved plants, shows that the response has a genetic basis and opens the possibility of genetically manipulating crops to maximize the proliferation response and NO_3^- uptake capacity.

This response will be genuinely adaptive, however, only if it does increase nutrient uptake relative to that of an unresponsive plant, and this depends on the mobility and degree of buffering of nutrient ions in soil (Nye &

Tinker 1977, p. 82). Large proliferative responses to phosphate patches (e.g. Drew & Saker 1978) are easy to explain by their effects on phosphorus (P) capture: phosphate is poorly mobile and well-buffered in soil, and most P acquired by a plant originates in soil less than 1 mm from the surface of a root or mycorrhizal hypha (Nye & Tinker 1977, p. 145). If roots (or associated hyphae) are, on average, greater than 2 mm apart, some soil will remain unexploited unless proliferation increases root length per unit soil volume (i.e. root-length density, L_v).

In contrast, NO_3^- diffuses in soil some three or four orders of magnitude faster than phosphate. Roots 1 cm apart will probably compete for NO_3^- after *ca.* 1 day (Nye & Tinker 1977, p. 225). To absorb all NO_3^- from a patch, roots should not have to proliferate as much as in a phosphate patch, yet they do (Drew *et al.* 1973; Drew & Saker 1978; Hutchings & de Kroon 1994; Robinson 1996). Equally puzzling is that roots may proliferate in an N-rich patch after most of that N has been taken up (van Vuuren *et al.* 1996). These observations are inconsistent with the idea that the proliferation response to N patches is 'adaptive' for N capture (Jackson & Caldwell 1996; Leyser & Fitter 1998), prompting the question 'Why do plants bother?' (Robinson 1996).

One possible answer is that the response to N evolved in N-poor environments in which N-rich patches occur unpredictably from localized inputs of decomposable organic matter, e.g. dung or detritus, and in which plants were likely to compete for that N. We do not know how root proliferation influences competitive N capture from patches (Casper & Jackson 1997; Schwinning & Weiner 1998) because previous studies have involved isolated plants or

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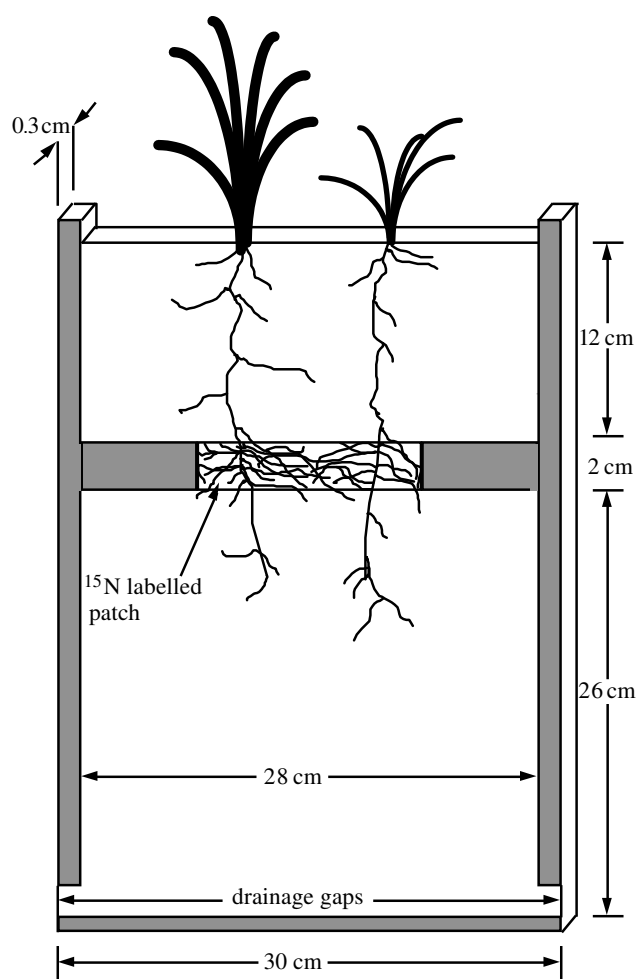


Figure 1. Microcosm unit in which the roots of *Lolium perenne* and *Poa pratensis* exploited a common N-rich patch of ^{15}N -labelled organic matter. Shaded areas are Perspex barriers to root growth.

monocultures of similar individuals supplied continually with N at near-constant concentrations (Robinson 1994).

Here we test the hypothesis that root proliferation in a decomposing organic patch will increase N capture when species with contrasting proliferation responses compete for that N. We show experimentally that N capture by two grass species is associated strongly with proliferation during interspecific competition for finite, locally available, mixed N sources. We also show, using a simulation model, that the weak association between proliferation and N uptake found in monocultures has a theoretical basis.

2. METHODS

(a) Experimental

Two grass species, *Lolium perenne* L. (perennial rye-grass) and *Poa pratensis* L. (smooth meadow-grass), potential competitors in pastures and differing in their capacities to proliferate roots in N-rich patches when grown in isolation (Hodge *et al.* 1998), were grown together in an N-poor medium containing a ^{15}N -labelled patch of organic matter. N from this patch was gradually made available to the plants via microbial mineralization of the organic N, and its capture by the plants was determined from isotopic analysis of sequentially harvested plants.

Seeds were supplied by Johnson Seeds, Lincolnshire, UK. Plants were grown in an N-poor soil:sand mix in 40 cm \times 28 cm \times 0.3 cm Perspex microcosm units (figure 1) in which ^{15}N -labelled organic matter was confined to part of the rooting zone. The organic matter (dried, chopped shoot material of *L. perenne* grown hydroponically on a ^{15}N -labelled N source: van Vuuren *et al.* 1996; Hodge *et al.* 1998, 1999) contained 1.6% N (28.2 atom % ^{15}N) with a C:N mass ratio of 31:1. A 7.5 cm \times 2.0 cm \times 0.3 cm band of this material was placed 12 cm below the surface of the soil-sand mix. Control 'patches' consisting of soil-sand mix were created in otherwise identical units. Monoculture controls were not used because responses to N-rich patches by isolated plants have already been demonstrated (Hodge *et al.* 1998).

Each unit contained one plant of *L. perenne* and one of *P. pratensis*. Day 0 of the experiment was designated as that when roots of both species were allowed access to the patch by removing Perspex strips which, until then, had isolated the patches from the rooting zone for 18 days. Units were maintained in a ConvironTM model E15 controlled-environment cabinet (Conviron, Winnipeg, Canada), where fluorescent tubes and incandescent bulbs provided a photon flux density of *ca.* 450 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at plant height. Relative humidity was set at 80% with a 16 h, 25 °C day and 8 h, 15 °C night. Four experimental units were harvested on 0, 7, 14, 21, 28, 35, 42, 49 and 56 days. Four control units were harvested on 0, 14, 28, 42 and 56 days.

At harvest, the root systems were separated by careful manual dissection (possible because of the near two-dimensional geometry of the microcosm units) and their lengths within and without the patches measured (MagiscanTM (Joyce-Loebl) Image Analysis System, program FIBRE v. 4.4). Roots and shoots were oven-dried at 60 °C, weighed, and subsamples analysed for total N and ^{15}N by continuous-flow isotope ratio mass spectrometry (Tracermass, Europa Scientific, Crewe, UK). Data were analysed using anova (Genstat v. 5 release 3.2; Genstat 5 Committee 1993) and stepwise regressions (Hunt & Parsons 1974).

(b) Theoretical

The interrelationships among N uptake, inorganic N concentrations and L_v during N uptake by two species, X and Y, during competition for a common N supply were explored using a simple model

$$\begin{aligned} \frac{dU_X}{dt} &= \frac{dU_{nX}}{dt} + \frac{dU_{aX}}{dt} = \left(\phi_n \frac{dC_n}{dt} + \phi_a \frac{dC_a}{dt} \right) \frac{dL_{vX}}{dt}, \\ \frac{dU_Y}{dt} &= \frac{dU_{nY}}{dt} + \frac{dU_{aY}}{dt} = \left(\phi_n \frac{dC_n}{dt} + \phi_a \frac{dC_a}{dt} \right) \frac{dL_{vY}}{dt}, \end{aligned} \quad (1)$$

where t is time (in days), U_X and U_Y are the uptakes per unit soil volume ($\mu\text{g cm}^{-3}$) by X and Y of NO_3^- (subscript 'n') plus NH_4^+ (subscript 'a'; ' NH_4^+ ' in this model includes low molecular weight organic-N compounds, e.g. amino acids of similar diffusivity to NH_4^+ ions: Jones *et al.* 1994), C_n and C_a are, respectively, soil NO_3^- and NH_4^+ concentrations ($\mu\text{g cm}^{-3}$), and ϕ_n and ϕ_a are coefficients ($\text{cm}^2 \text{d}^{-1}$) expressing the rates at which roots absorb NO_3^- and NH_4^+ from soil. ϕ is equivalent to the term ' $2\pi\alpha a$ ' in Nye & Tinker's (1977, p. 215) notation, where α is the 'root absorbing power' (cm d^{-1}) and a is the mean root radius (cm). ϕ is assumed constant and the same for X and Y, but different for NO_3^- and NH_4^+ , reflecting the relative

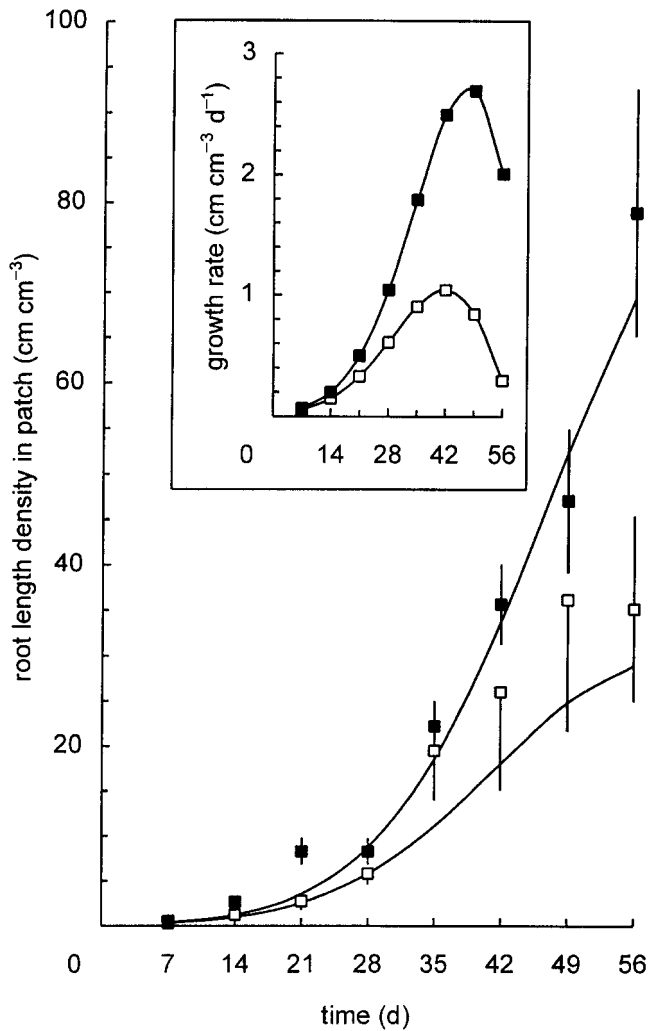


Figure 2. Mean (\pm s.e.) root-length densities (L_v) of *Lolium perenne* (filled squares) and *Poa pratensis* (open squares) in the N-rich patch. The curves are stepwise quadratic regressions (Hunt & Parsons 1974) of L_v on time (t , days), from which absolute growth rates of L_v were derived (inset). For *L. perenne*, $L_v = \exp(-2.42 + 0.209t - 0.0016t^2)$; for *P. pratensis*, $L_v = \exp(-2.52 + 0.20t - 0.0017t^2)$.

diffusivities of these ions in soil. Typically, ϕ_a is one-tenth of ϕ_n (Clarke & Barley 1968).

In equation (1), C_n and C_a are common to X and Y, which, therefore, compete for the same supply of N. Current uptake by both species then influences future values of C_n and C_a

$$\begin{aligned} U_X(t) &= U_{nX}(t) + U_{aX}(t) = [\phi_n C_n(t) + \phi_a C_a(t)] L_{vX}(t), \\ U_Y(t) &= U_{nY}(t) + U_{aY}(t) = [\phi_n C_n(t) + \phi_a C_a(t)] L_{vY}(t), \end{aligned} \quad (2)$$

$$\begin{aligned} C_n(t+1) &= C_n(t) - [U_{nX}(t) + U_{nY}(t)], \\ C_a(t+1) &= C_a(t) - [U_{aX}(t) + U_{aY}(t)], \end{aligned} \quad (3)$$

L_v is also time dependent (see below). For simplicity, we assume no additions of NO_3^- or NH_4^+ to the soil once uptake starts, nor any N removal from soil other than uptake (i.e. zero N mineralization or immobilization).

3. RESULTS

Proliferations of *L. perenne* roots in the N-rich patch exceeded those of *P. pratensis* (figure 2). After 56 days,

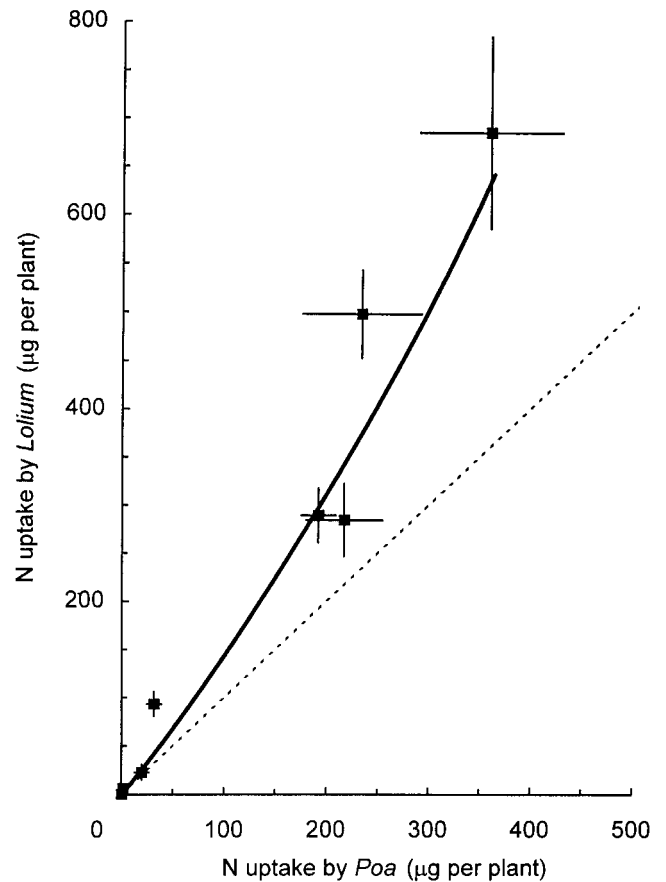


Figure 3. Patch N uptake by *Lolium perenne* compared with that by *Poa pratensis*. Symbols are measured means (\pm s.e.). The data are described by the quadratic equation $y = 10.9 + 1.23x + 0.0018x^2$ ($R^2 = 0.958$; curve not shown). The solid curve shows N uptake by these species simulated by equations (1)–(3). The simulation is described by the quadratic $y = -0.659 + 1.31x + 0.0012x^2$ ($R^2 = 1.0$). The $L_v(t)$ functions in figure 2 generated L_v values as model inputs; initial values of $C_n = C_a = 90 \mu\text{g cm}^{-3}$ and a constant ϕ_n of $0.002 \text{ cm}^2 \text{ d}^{-1}$ and ϕ_a of $0.0002 \text{ cm}^2 \text{ d}^{-1}$ were assumed (Clarke & Barley 1968). The broken line indicates equal N capture by the two species.

L. perenne roots in the patch were packed twice as densely as those of *P. pratensis*. In both species, an increase in L_v in the patch was associated with a proportional increase in N uptake from the patch, throughout the experiment. The zero-intercept regression of N uptake from the patch (U , $\mu\text{g per plant}$) on root-length density in the patch (L_v , cm cm^{-3}) was $U = 0.90L_v$ ($R^2 = 0.951$) for all data (regressions for *L. perenne* and *P. pratensis* separately were not significantly different from this common relation).

L. perenne captured progressively larger fractions of the patch N (figure 3): for every μg captured by *P. pratensis*, *L. perenne* captured $1.8 \mu\text{g}$ (linear regression of patch N uptake (μg) by *L. perenne* (y) on that by *P. pratensis* (x): $y = 1.81x - 3.91$, $R^2 = 0.949$). Patch N uptake by *L. perenne* exceeded that by *P. pratensis* at 28 days, the same time as the rate of increase in L_v by *L. perenne* became significantly faster than that by *P. pratensis* (figure 2). There were no significant interspecific differences in the rates of N uptake per unit root length (Hodge *et al.* 1999).

Using experimental data for L_v as inputs (figure 2), the explicitly competitive model predicted the observed pattern of N uptake by *L. perenne* and *P. pratensis*

(figure 3). There was no statistical difference between the measured and simulated N uptakes by *L. perenne* ($p=0.80$).

4. DISCUSSION

Figure 3 is, to our knowledge, the first experimental demonstration of an advantage (for N capture), which can be gained from a superior root proliferation in N-rich patches in otherwise N-deficient soil. Yet, how can this advantage be explained, given the arguments above that proliferation should make little difference to the exploitation of soil N? Our answer is threefold. First, the N patch was organic rather than inorganic, as occurs in natural soils. The roots of *L. perenne* and *P. pratensis* were, therefore, supplied with both NO_3^- - and NH_4^+ -N mineralized from the organic N by microbes. NH_4^+ is less mobile in the soil than NO_3^- , by about an order of magnitude (Clarke & Barley 1968). In theory, increases in L_v should increase significantly the capture of the less mobile NH_4^+ -N and low molecular weight organic-N molecules such as amino acids. The latter are also decomposition products and diffuse in soil approximately as fast as NH_4^+ (Jones *et al.* 1994) and may be absorbed by roots, especially if mycorrhizal (Näsholm *et al.* 1997). Further, NH_4^+ is the first inorganic product of organic-N decomposition; NO_3^- is produced later, from NH_4^+ . A plant that could 'intercept' NH_4^+ at its point of production in the decomposition pathway would be advantaged compared with a competitor able to exploit only NO_3^- (Kronzucker *et al.* 1997). It would also be able to compete effectively with soil microbes which themselves use NH_4^+ as an N source (Jackson *et al.* 1989).

Second, the chemical composition of the patch, and the microbial milieu in which it decomposed, were such that available N concentrations in the patch were maintained above zero throughout (Hodge *et al.* 1999). Changes in L_v , therefore, exerted a continual influence on N uptake from the patch, but did not exhaust the patch's available N (cf. van Vuuren *et al.* 1996).

Third, the faster increase in L_v by *L. perenne* exerted a continual influence on its own N uptake and on that of *P. pratensis*, i.e. there was interspecific competition for patch N. When plants capture N from a common supply, their capacity to attain root-length densities allowing maximum access to that supply is just one facet of resource acquisition: the speed at which they do this is also important. Other things being equal, the plant with the larger L_v in an N-rich patch at a given time (i.e. that with the fastest root proliferation) will capture more N from that patch (Nye & Tinker 1977, p. 281), provided that N is available to be taken up and is not replaced immediately by N mineralization (when competition for the N would be impossible). The agreement (figure 3) between our data and the model predictions in which inter-root competition for N was made explicit is strong evidence that *L. perenne* and *P. pratensis* did compete for patch N in the experiment.

For monocultures, the model predicts (figure 4) only small interspecific differences in N uptake before the N supply becomes exhausted (which did not occur in our experiment). Should N exhaustion occur, the model predicts no ultimate interspecific difference in N uptake by monocultures irrespective of their capacities to proliferate roots.

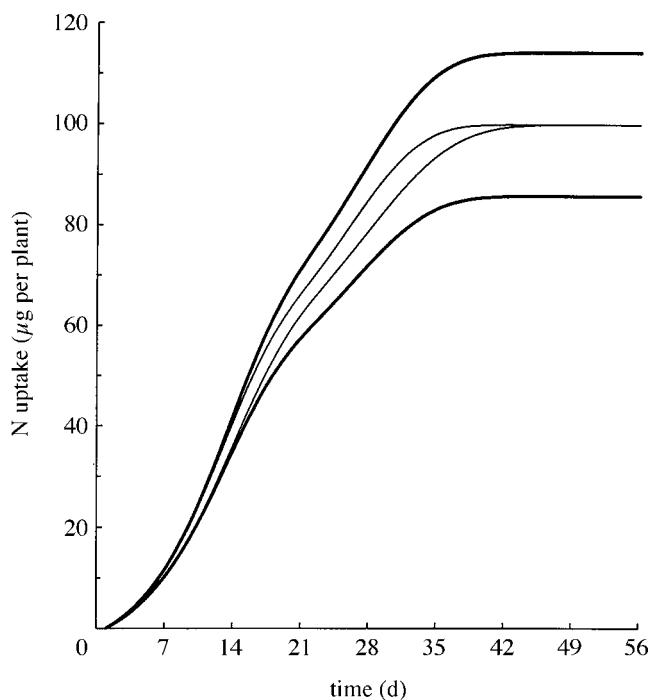


Figure 4. Simulations (equations (1)–(3)) of the effects of an interspecific difference in L_v on N uptake (μg per plant) by two species in monoculture (two plants of the same species growing together; fine curves), or in competition (one plant of each species growing together; bold curves), when N supply becomes exhausted ($C_n=C_a=0$). The $L_v(t)$ functions in figure 2 generated L_v values as model inputs, and the same values were used whether the plants were in competition or monoculture. Those for *L. perenne* produced the upper two simulations; those for *P. pratensis* the lower two. For illustration, $100 \mu\text{g}$ NO_3^- - and $100 \mu\text{g}$ NH_4^+ -N were assumed available to each pair of plants, giving initial values of $C_n=C_a=11 \mu\text{g cm}^{-3}$ in a 9 cm^3 patch; ϕ_n and ϕ_a values of, respectively, 0.1 and $0.01 \text{ cm}^2 \text{ d}^{-1}$ were used to simulate exhaustion of NO_3^- and NH_4^+ in <60 days.

erate roots. This agrees with experiments (Fransen *et al.* 1998; Hodge *et al.* 1998) and theory (Robinson 1996). Slow root growth and weak proliferation do not, apparently, impede eventual N capture by plants in monocultures. In contrast, the model predicts a large difference in ultimate N capture by competitors differing in their capacities to proliferate roots. It seems that interspecific competition for N drives a 'wedge' between species, progressively increasing N capture by the stronger root proliferator at the expense of the weaker, an effect absent from monocultures.

We conclude that the constraints that may have led to the widespread evolution (Robinson 1994; Robinson & van Vuuren 1998) of strong root proliferation in N-rich patches are interspecific competition for N and finite, local availabilities of mixed N sources. If either constraint is removed, the possible ecological and evolutionary advantages of root proliferation in response to N become obscured. This emphasizes the importance of environmental heterogeneity and plant phenotype in determining the outcome of interspecific competition (Tilman 1988, pp. 311–314; Huston & DeAngelis 1994), and that the functional significance of a particular phenotype (such as root proliferation) is highly context-dependent and

cannot necessarily be inferred from measurements made on isolated plants (Nye & Tinker 1977, pp. 281–282; McGraw & Chapin 1989).

Our findings imply that attempts to increase the morphological plasticity of crop root systems by genetic manipulation are unlikely to significantly increase N capture if those crops are grown as NO_3^- -fertilized monocultures (cf. figure 4). In contrast, interspecific differences in root-system plasticity may be important determinants of superior N capture—and eventual dominance—by certain individuals in mixed cropping systems and natural, N-limited communities. This would agree with observations (Tilman 1989; Tilman *et al.* 1996) that soil NO_3^- concentrations are least under the most diverse plant communities, i.e. where the opportunities for inter-specific competition for mineralized N are greatest.

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