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Plant root proliferation in nitrogen-rich patches confers competitive advantage

David Robinson¹, Angela Hodge², Bryan S. Griffiths¹ and Alastair H. Fitter²

¹Cellular and Environmental Physiology Department, Scottish Crop Research Institute, Dundee DD2 5DA, UK (d.robinson@SCRI.scri.ac.uk)
²Department of Biology, University of York, PO Box 373, York YO10 5YW, UK

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 interspecific 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 (NO³⁻) 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 NO³⁻ 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_r).

In contrast, NO³⁻ diffuses in soil so three or four orders of magnitude faster than phosphate. Roots 1 cm apart will probably compete for NO³⁻ after ca. 1 day (Nye & Tinker 1977, p. 225). To absorb all NO³⁻ 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; Schwinghamer & Weiner 1998) because previous studies have involved isolated plants or...
Seed萌 were supplied by Johnson Seeds, Lincolnshire, UK. Plants were grown in an N-poor soil:sand mix in 40 cm x 28 cm x 0.3 cm Perspex microcosm units (figure 1) in which 15N-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 15N-labelled N source; van Vuuren et al. 1996; Hodge et al. 1998, 1999) contained 1.6% N (28.2 atom% 15N) with a C:N mass ratio of 3:1. A 7.5 cm x 20 cm x 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 Conviron(TM) model E15 controlled-laboratory cabinet (Conviron, Winnipeg, Canada), where fluorescent tubes and incandescent bulbs provided a photon flux density of ca. 450 µmol m⁻² 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 outwith the patches measured (Magiscan(TM) Joyce-Loebel 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 15N 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 L₁ during N uptake by two species, X and Y, during competition for a common N supply were explored using a simple model

\[
\frac{dU_X}{dt} = \frac{dU_{\infty,X}}{dt} + \frac{dU_{\infty,Y}}{dt} = \left( \phi_X \frac{dC_x}{dt} + \phi_Y \frac{dC_y}{dt} \right) \frac{dL_{\infty}}{dt},
\]

\[
\frac{dU_Y}{dt} = \frac{dU_{\infty,X}}{dt} + \frac{dU_{\infty,Y}}{dt} = \left( \phi_X \frac{dC_x}{dt} + \phi_Y \frac{dC_y}{dt} \right) \frac{dL_{\infty}}{dt},
\]

where \( t \) is time (in days), \( U_X \) and \( U_Y \) are the uptake rates per unit soil volume (µg cm⁻³) by X and Y of NO₃⁻ (subscript ‘a’) plus NH₄⁺ (subscript ‘a’); \( C_x \) and \( C_y \) are, respectively, soil NO₃⁻ and NH₄⁺ concentrations (µg cm⁻³); and \( \phi_X \) and \( \phi_Y \) are coefficients (cm² d⁻¹) expressing the rates at which roots absorb NO₃⁻ and NH₄⁺ from soil. \( \phi \) is equivalent to the term ‘2 sorption’ in Nye & Tinker’s (1977, p. 215) notation, where \( \alpha \) is the ‘root absorbing power’ (cm d⁻¹) and \( a \) is the mean root radius (cm). \( \phi \) is assumed constant and the same for X and Y, but different for NO₃⁻ and NH₄⁺, reflecting the relative

2. METHODS

(a) Experimental

Two grass species, Loliwm perenne L. (perennial ryegrass) and P. 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 a N-poor medium containing a 15N-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.
Figure 2. Mean (+ s.e.) root-length densities ($L_r$) 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 $L_r$ on time ($t$, days), from which absolute growth rates of $L_r$ were derived (inset). For *L. perenne*, $L_r = \exp(-2.42+0.209t-0.0016t^2)$; for *P. pratensis*, $L_r = \exp(-2.52+0.20t-0.0017t^2)$.

diffusivities of these ions in soil. Typically, $\phi_0$ is one-tenth of $\phi_a$ (Clarke & Barley 1968).

In equation (1), $C_0$ and $C_x$ 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 $C_0$ and $C_x$

$$U_N(t) = U_{\infty}(t) + U_{\infty}(t) = \phi_0 C_0(t) + \phi_0 C_x(t) L_N(t);$$

$$U_X(t) = U_{\infty}(t) + U_{\infty}(t) = \phi_x C_0(t) + \phi_x C_x(t) L_N(t),$$

$$C_0(t+1) = C_0(t) - [U_{\infty}(t) + U_{\infty}(t)],$$

$$C_x(t+1) = C_x(t) - [U_{\infty}(t) + U_{\infty}(t)],$$

$L_N$ is also time dependent (see below). For simplicity, we assume no additions of $\text{NO}_3^-$ or $\text{NH}_4^+$ 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, *L. perenne* roots in the patch were packed twice as densely as those of *P. pratensis*. In both species, an increase in $L_n$ 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 ($U$, $\mu g$ per plant) on root-length density in the patch ($L_n$, cm cm$^{-2}$) was $U = 0.90L_n$ ($R^2 = 0.951$) 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 $\mu g$ captured by *P. pratensis*, *L. perenne* captured 1.8 $\mu g$ linear regression of patch N uptake ($\mu g$) 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 $L_n$ 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 $L_n$ as inputs (figure 2), the explicitly competitive model predicted the observed pattern of N uptake by *L. perenne* and *P. pratensis*.
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 $L_s$ 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 (*Nasholm et al.* 1997). Further, NH$_4^+$ is the first inorganic product of organic-N decomposition; NO$_3^-$ is produced later, from NH$_4^+$-N. 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 $L_s$, 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 $L_s$ 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 $L_s$ 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. 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

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 interspecific competition for mineralized N are greatest.

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