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Integrating resource heterogeneity and plant plasticity: modelling nitrate and phosphate uptake in a patchy soil environment

R.B. JACKSON and M.M. CALDWELL*

*Department of Botany, University of Texas at Austin, Austin, TX 78713 and *Department of Rangeland Resources and the Ecology Centre, Utah State University, Logan, UT 84322-5230, USA*

Summary

1 We used the Barber–Cushman model of nutrient uptake to simulate the importance of soil heterogeneity and root plasticity for nitrate (NO_3^-) and phosphate (P) uptake. Model inputs included root physiological parameters and soil characteristics obtained from five years of field studies in the sagebrush steppe. At an intensively sampled field site the average variation in soil P and NO_3^- around individual plants was 3-fold and 12-fold (3× and 12×, respectively), the range of soil variability used in our simulations.

2 In soil patches three-fold enriched in P (3×), simulated P uptake was three to four times greater than in soil of background P concentrations (1×). The importance of soil heterogeneity and root plasticity was even more pronounced for NO_3^-. In 12× soil patches, NO_3^- uptake was 7–20 times greater than at 1×, depending on simulation conditions. Plasticity (root proliferation and increased uptake kinetics) accounted for up to 75% of NO_3^- and over 50% of P acquired from enriched soil patches. Even without plasticity, nutrient uptake increased substantially in enriched patches because of higher soil-solution concentrations.

3 Using the same model we simulated P and NO_3^- uptake for an actual 0.25-m^2 soil area in the field. Plant acquisition of P in this area was 28% higher with root plasticity than without, equally attributable to root proliferation and increased uptake kinetics. Plant NO_3^- uptake was 61% greater with plasticity, due almost exclusively to increased uptake capacity of roots.

4 We also simulated P and NO_3^- uptake in hypothetical soil arrays containing an equivalent quantity of nutrient distributed homogeneously or heterogeneously. A plant without plasticity always acquired less P or NO_3^- in the heterogeneous arrays than in the homogeneous arrays. With plasticity, it acquired more nutrients in three of four cases compared to the homogeneous 'control'.

5 We present these simulations as a way to integrate field experiments, generate and test hypotheses, and stimulate discussion. Given that heterogeneity is the norm rather than the extreme, our simulations highlight the importance of soil heterogeneity and root plasticity for both nutrient acquisition and plant competition in the field.

Keywords: Barber–Cushman model, below-ground competition, nitrogen and phosphorus uptake, root proliferation, soil microsites, tussock grass

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Introduction

Plants acquire resources in environments that are decidedly patchy, both above and below-ground (e.g. Anderson 1964; Beckett & Webster 1971; Palmer & Dixon 1990). There is considerable evidence that many plants respond to this heterogeneity with phenotypic plasticity, i.e. 'behaviour' that can enhance their acquisition of essential resources (Robinson 1994; de Kroon & Hutchings 1995). For below-ground processes, potential responses include changes in root growth rates, demography, or architecture (e.g. Drew & Saker 1975; Pregitzer *et al.* 1993; Fitter 1994), nutrient uptake kinetics (e.g. Jackson *et*

al. 1990), mycorrhizal infection (e.g. St John *et al.* 1983), exudation (e.g. Jungk & Claassen 1989), and, most speculatively, the form or density of root hairs (e.g. Clarkson 1985; Meisner & Karnok 1991). Some analogous morphological and physiological adjustments exist for above-ground structures (e.g. Rincon & Grime 1989; Küppers 1989; Pearcy 1990).

Despite many excellent examples of heterogeneity and plasticity in the literature, quantifying and integrating their importance remains difficult. There are many reasons for this difficulty, but foremost is the need for detailed environmental data (at a scale relevant to individual plants) and physiological and morphological plant data, preferably from the same field system. For plant canopies, models exist for predicting light attenuation and sunfleck characteristics (see Baldocchi & Collineau 1994). A recent model has examined the importance of sunflecks and natural understorey light conditions for plant carbon gain of a tropical understorey herb (Pearcy *et al.* 1994). For below-ground systems, the issues are much less tractable. Predicting nutrient availability and movement in the soil is far more complicated than the already difficult task of predicting light availability above-ground, and differs for each respective nutrient (Nye & Tinker 1977). In addition, measuring below-ground parameters is simply more difficult than working above-ground.

In this study we drew upon five years of field experiments in the sagebrush-steppe (e.g. Jackson *et al.* 1990; Caldwell *et al.* 1991a; Jackson & Caldwell 1993a,b) to model the consequences of soil heterogeneity and root plasticity for nutrient uptake from soil. We used the Barber–Cushman model of nutrient uptake to examine acquisition of phosphate and nitrate (Barber & Cushman 1981; Oates & Barber 1987). We began by using comprehensive soil sampling in the field as a basis for setting the initial concentration and range of each nutrient for control and enriched soil patches (Jackson & Caldwell 1993a,b). We used physiological and morphological root data from the field for the tussock grass *Agropyron desertorum* to set the root parameters for control and enriched soil patches (e.g. Jackson *et al.* 1990; Caldwell *et al.* 1991a,b). These parameters, which included rooting density, root growth rates, and Michaelis–Menten parameters of nutrient uptake (I_{max} and K_m), often differed for control and enriched soil patches in our system (e.g. Jackson *et al.* 1990; Caldwell *et al.* 1991b). We then ran the model to address the following questions:

1 How important is soil heterogeneity for nutrient availability and uptake in a realistic field setting?
2 What is the relative importance of root morphological and physiological plasticity in exploiting resource heterogeneity?
3 Do conclusions depend on whether the nutrient is relatively mobile (NO_3^-) or immobile (P) in the soil?

Methods

MODEL DESCRIPTION

We used a mechanistic model of nutrient uptake for the simulations (Barber & Cushman 1981; Oates & Barber 1987). The model is based on diffusion and mass flow of nutrients to roots, where nutrient influx at the root surface is combined with root growth to describe nutrient uptake (Barber 1984). See Bouldin (1961) and Nye & Marriott (1969) for development of the theory that led to such models as Barber–Cushman.

The model is a three-step process, beginning with a description of nutrient flow to the roots. The first equation includes both radial diffusion and mass flow of nutrients to the root surface:

$$\frac{\partial C_l}{\partial t} = \frac{1}{r}\frac{\partial}{\partial r}\left(rD_e\frac{\partial C_l}{\partial r} + \frac{r_0 v_0 C_l}{b}\right) \quad (1)$$

where C_l is the nutrient concentration in the soil solution, r is the radial distance from the root axis, D_e is the effective diffusion coefficient in soil, r_0 is the root radius, v_0 is the flow of water to the root, b is the buffering capacity of the soil, and t is time. The first term in parentheses is the diffusional component; the second represents mass flow. The above equation allows C_l at $r = r_0$ to be evaluated numerically.

Once the concentration of the nutrient at the root surface has been determined, nutrient uptake is calculated by apparent Michaelis–Menten kinetics:

$$J_r = \frac{I_{max}(C_l - C_{min})}{K_m + (C_l - C_{min})} \quad (2)$$

where C_l is the nutrient concentration at the root surface, J_r is net nutrient uptake, I_{max} is the maximal net influx of ions into roots, C_{min} is the solution concentration where net uptake is zero (influx = efflux), and K_m is the soil solution concentration where influx equals $0.5 \times I_{max}$. Net nutrient uptake is then calculated based on local nutrient uptake for both new and existing roots:

$$T = 2\pi r_0 L_0 \int_0^{t_m} J_r(r_0, S)\,dS + 2\pi r_0 \int_0^{t_m} \frac{df}{dt}\int_0^{t_m - t} J_r(r_0, S)\,dS\,dt \quad (3)$$

T is the total net nutrient uptake at time t_m, L_0 is initial root length, df/dt is the rate of root growth, and $J_r(r_0,S)$ is net nutrient uptake for a given root diameter and surface area (see eqn 5.11 in Barber (1984) for more detail). Numerical solution includes a Crank–Nicholson approach for solving finite difference equations (Baldwin 1976; Barber 1984). All of the roots in the simulations are considered to be physiologically active for nutrient uptake.

MODEL PARAMETERS AND INDIVIDUAL PATCH SIMULATIONS

The inputs to the model were derived from a series of controlled-plot and natural field experiments in the sagebrush steppe (e.g. Jackson *et al.* 1990; Caldwell *et al.* 1991a,b; Jackson & Caldwell 1993a,b). We used data for the perennial tussock grass *Agropyron desertorum* (Fisch. ex Link) Schult., which has shown considerable root plasticity to nutrient heterogeneity in the soil (e.g. Jackson & Caldwell 1989; Jackson *et al.* 1990). The variables required to run the model and the specific values for the P and NO_3^- simulations are presented in Table 1. We used these parameters for 2- and 10-day simulations, to examine the importance of plasticity (as evidenced by root proliferation and/or increased uptake kinetics) in relatively short- and long-lived soil patches.

We used data from the field site of Jackson & Caldwell (1993a,b) to select the range of concentrations for P and NO_3^- in the simulations. Median $NaHCO_3$-extractable soil phosphate at the field site was 17 mg P kg^{-1} (soil dry-mass basis) and most values were between 10 and 50 mg P kg^{-1} (with individual values as high as 81 mg P kg^{-1}). The average variation of P in nine 0.25-m^2 areas around individual plants was threefold. Based on these typical values, the initial range of P concentrations selected for the model was 10, 30 and 50 mg kg^{-1} (1×, 3× and 5×, respectively). Concentrations at the root surface were not held at these levels, but generally declined as zones of depletion developed over time (e.g. Nye & Tinker 1977).

Soil-extractable P was converted to soil-solution P with the soil bulk density and soil water contents of Jackson & Caldwell (1993b) and the Freundlich equation developed in Caldwell *et al.* (1992):

$$P_s = 123.4P_l^{1.14} \quad \text{or} \quad P_l = (P_s/123.4)^{1/1.14} \qquad (4)$$

where P_s is solid-phase P and P_l is soil-solution P (with units of mg P kg^{-1} soil for both). The soil-

Table 1 The variables required to run the nutrient uptake model and their specific values for the phosphate and nitrate simulations (see Methods). The column of 'additional description' identifies in which simulations the values were used. Note that 'E' refers to scientific notation (e.g. 1.00E2 = 100)

Parameter/Definition		Units	P	NO_3^-	Additional description
Soil nutrient supply					
C_{li}	Initial nutrient concentration in soil solution (at $t = 0$)	μmol cm^{-3}	1.27E-2 3.33E-2 5.21E-2	1.00E-1 6.00E-1 1.20E0	1, 3, and 5× patches for P; 1, 6, and 12× patches for N; (Figs 1, 2 and 5)
D_e	Diffusion coefficient for nutrient movement through bulk soil	cm^2 s^{-1}	3.20E-9 1.18E-9	2.00E-6	wet simulations (Figs 1–5) dry simulations (Fig. 1)
b	Buffer power of nutrient on the solid phase for nutrient in solution	unitless	1.00E2	1.00E0	all simulations (Figs 1–5)
Root morphological characteristics					
L_0	Initial root length	cm	5.00E3	5.00E3	all simulations (Figs 1–5)
k	Rate of root growth	cm s^{-1}	0 2.32E-3 4.63E-3	0 2.32E-3 4.63E-3	no proliferation (Figs 1–5) intermed prolif (Figs 3 and 4) full proliferation (Figs 1–5)
r_0	Mean root radius	cm	8.33E-3	8.33E-3	all simulations (Figs 1–5)
r_1	Half-distance between root axes	cm	3.19E-1 2.72E-1	3.19E-1 2.72E-1	no proliferation (Figs 1–5) full proliferation (Figs 1–5)
Root uptake kinetics					
I_{max}	Maximum net influx	μmol cm^{-2} s^{-1}	9.52E-7 2.18E-6 3.41E-6	5.18E-6 1.18E-5 1.85E-5	control kinetics (Figs 1–5) intermed kinet (Figs 3 and 4) elevated kinetics (Figs 1–5)
K_m	Nutrient concentration in solution where net influx is 0.5 I_{max}	μmol cm^{-3}	1.65E-2 2.72E-2 3.78E-2	2.50E-2 2.50E-2 2.50E-2	control kinetics (Figs 1–5) intermed kinet (Figs 3 and 4) elevated kinetics (Figs 1–5)
C_{min}	Solution nutrient concentration where nutrient influx is zero	μmol cm^{-3}	2.00E-4	2.00E-3	all simulations (Figs 1–5)
v_0	Water uptake at the root surface	cm s^{-1}	1.00E-7 5.00E-8	1.00E-7	wet simulations (Figs 1–5) dry simulations (Fig. 1)

extractable *P*-values of 10, 30 and 50 mg kg^{-1} correspond to 12.7, 33.3 and 52.1-μM soil-solution P.

Soil-solution NO_3^- values were taken from Jackson & Caldwell (1993a,b). Median soil NO_3^- at the site was 1.1 mg NO_3^--N kg^{-1} soil, corresponding to $\approx$300-μM NO_3^- (Jackson & Caldwell 1993b). Most of the values were between 80 and 1500 μM NO_3^-. For the simulations, we selected 100, 600 and 1200 μM NO_3^- as the time-zero concentrations to represent 1×, 6× and 12× patches (with 12-fold being the average variation found around individual plants; Jackson & Caldwell 1993a). As in the P simulations, concentrations at the root surface were not held at these levels, but declined over time.

I_{max} and K_m values for P and NO_3^- uptake in control and enriched soil patches were taken from Jackson *et al.* (1990), Jackson & Caldwell (1991), and BassiriRad *et al.* (1993). Several potential uncertainties should be acknowledged with the ion uptake parameters, including possible uptake by microbes associated with excised roots from the field (e.g. Barber & Frankenburg 1971), the extrapolation of short-term assays to as long as 10 days in our simulations, and the use of data from both *Pseudoroegneria spicata* (formerly *Agropyron spicatum*) and *Agropyron desertorum*. Despite potential shortcomings, excised and attached roots often show quite comparable rates of nutrient uptake when the excised root assays are completed within a few hours, as in the studies above (e.g. Bloom & Caldwell 1988). In addition, BassiriRad *et al.* (1993) reported that estimates of I_{max} obtained from short-term NO_3^- assays with *Agropyron desertorum* compared well with estimates of whole-plant $^{15}NO_3^-$ uptake over 14 days. To compare responses for the two nutrients, the simulations assumed the same relative increase in I_{max} for NO_3^- and P in enriched patches (similar to the NH_4^+ and P response to N enrichment for *Agropyron spicatum*; Jackson & Caldwell 1991). K_m values increased slightly for P in enriched patches (Jackson *et al.* 1990), but were unchanged for NO_3^- (BassiriRad *et al.* 1993). The combined changes in I_{max} and K_m for P and NO_3^- are referred to as 'elevated kinetics' in this paper. C_{min} values for P and NO_3^- were taken from the model's default parameters because we lacked an experimental estimate. Sensitivity analyses showed the output to be quite insensitive to C_{min}, as shown previously by Barber (1984). D_e values for P were taken from Caldwell *et al.* (1992) for the wetter and drier soil simulations (volumetric water contents $\theta = 0.21$ and 0.16, respectively). In addition to the reduction in D_e, water flux to the roots (v_0) was reduced by 50% for the drier soil simulation, though this adjustment had little effect on P uptake. Buffering capacity (b), v_0, and D_e for NO_3^- were taken from the default parameters of the model (Oates & Barber 1987). We lacked the additional data necessary to simulate NO_3^- uptake in the drier soil.

Root morphological properties (half-distance between roots, mean root diameter, and root density) were taken from Caldwell *et al.* (1991b). In that study, root proliferation of 80% occurred during the sample period (i.e. there were 1.8-fold the number of roots after soil enrichment as before enrichment), though other studies have shown more pronounced proliferation for *A. desertorum* (e.g. Eissenstat & Caldwell 1988; Jackson & Caldwell 1989). To approximate this 80% proliferation, we assumed a linear rate of root growth resulting in 80% more root length at the end of 10-day simulations. For the 2-day simulations we assumed the same rate of new root growth, so the net proliferation was quite small (16% total proliferation at the end of the simulation). The assumption of linear root growth may in some cases underestimate the importance of root proliferation, particularly for the 2-day simulations, since *A. desertorum* may sometimes respond quite quickly to nutrient enrichment (Jackson & Caldwell 1989).

We examined two root-proliferation scenarios. In the first scenario the enriched patch of soil occurred in the presence of control root densities (control roots already present in the patch). Because Barber–Cushman does not allow competition between roots we approximated this scenario by reducing the spacing between roots in the simulation (from $r_1 = 0.319$ cm in 'no proliferation' to 0.272 cm in full proliferation, an average increase in root length density of 40% for the 10-day simulations; see Table 1). In the second scenario, the enriched patch was assumed to be a previously unexplored soil volume. For P uptake, the distinction between a new and existing soil patch was unimportant and is not presented, due to the relative immobility of P in soil (see Discussion).

NUTRIENT UPTAKE IN A 0.25-m^2 SOIL AREA FROM THE FIELD

After the above simulations of individual patches, we then modelled nutrient uptake for the actual pattern of nutrient availability observed in a 0.25-m^2 soil area in the field. Soil nutrient concentrations in the area were estimated with 25 soil samples spaced in a 5 × 5 array, 12.5 cm between adjacent samples (Jackson & Caldwell 1993a,b). In order to use the Barber–Cushman model, which assumes homogeneity for a given soil volume, 25 discrete cells were parameterized using the soil nutrient concentrations found in the 25 soil samples. The 0.25-m^2 soil area had fairly low soil variability (2.5- and 6.4-fold for the respective P and NO_3^- arrays), given the 3- and 12-fold average variation found for P and NO_3^- in areas of equal size (Jackson & Caldwell 1993a). The soil contained between 20% and 30% soil water, so we used the wetter soil parameters for the simulations ($\theta = 0.21$). Because we lacked a 'response surface' of relative root proliferation and kinetics across all nutrient concentrations, we allocated plasticity in a step-wise fashion. This does not mean that we expect the par-

ameters to change in a step-wise fashion in the field, we simply lacked more detailed information to make unequivocal estimates across the range of concentrations. For root proliferation at least, there is evidence that the degree of proliferation depends on the concentration of nutrients applied (Jackson & Caldwell 1989). In our current simulations, roots were assigned either control parameters (no plasticity), 50% (intermediate) plasticity, or 100% (full) plasticity (see definitions below and Table 1), with control parameters assigned until soil nutrient concentrations were a least a third greater than median values, and full plasticity when concentrations were at least twice median values (median values of 17 mg P kg^{-1} and 300 μM NO_3^-; Jackson & Caldwell 1993a). For P uptake, plants were assigned control parameters for soil values $\leqslant$26 mg P kg^{-1} ($k = 0$ cm s^{-1}, $K_m = 16.5$ nmol cm^{-3}, and $I_{max} = 9.52 \times 10^{-7}$ μmol cm^{-2} s^{-1}; see Table 1), intermediate plasticity between 27 and 33 mg P kg^{-1} ($k = 23.2$ μm s^{-1}, $K_m = 27.2$ nmol cm^{-3}, and $I_{max} = 2.18 \times 10^{-6}$ μmol cm^{-2} s^{-1}), and full plasticity for values $\geqslant$34 mg P kg^{-1} ($k = 46.3$ μm s^{-1}, $K_m = 37.8$ nmol cm^{-3}, and $I_{max} = 3.41 \times 10^{-6}$ μmol cm^{-2} s^{-1}). For NO_3^- uptake, plants were assigned control parameters for soil solution concentrations $\leqslant$400 μM NO_3^- ($k = 0$ cm s^{-1} and $I_{max} = 5.18 \times 10^{-6}$ μmol cm^{-2} s^{-1}; see Table 1), intermediate plasticity between 400 and 600 μM NO_3^- ($k = 23.2$ μm s^{-1} and $I_{max} = 1.18 \times 10^{-5}$ μmol cm^{-2} s^{-1}), and full plasticity for values $\geqslant$600 μM NO_3^- ($k = 46.3$ μm s^{-1} and $I_{max} = 1.85 \times 10^{-5}$ μmol cm^{-2} s^{-1}). For both P and NO_3^-, only 8 of the 25 cells in the 0.5-m $\times$ 0.5-m soil area had sufficient nutrients to 'induce' plasticity. We generated contour plots of P and NO_3^- uptake for plants with and without plasticity.

NUTRIENT UPTAKE IN HYPOTHETICAL HOMOGENEOUS AND HETEROGENEOUS ARRAYS

We used the Barber–Cushman model to address one additional question. We modelled an equal quantity of nutrient (P or NO_3^-) distributed either homogeneously or heterogeneously in 25 soil cells (as in the 0.25-m^2 soil area above). The arrays were set up so that only 1 of the 25 cells had an enriched patch for the heterogeneous case, a conservative framework that would by definition be less dramatic than the individual patch simulations. For P, the homogeneous array contained 25 cells at 10.8 mg P kg^{-1} soil concentration. The heterogeneous array contained 24 cells at 10 mg kg^{-1} and one cell at 30 mg kg^{-1}, the same total 'quantity' of P as in the homogeneous case. The distributions for NO_3^- were 25 cells at 144 μM NO_3^- (homogeneous case) or 24 cells at 100 μM NO_3^- and one cell at 1200 μM NO_3^- (heterogeneous case). The single enriched cell for each nutrient was set at the average variability observed around individual plants in the field (Jackson & Caldwell 1993a; see above).

We ran six simulations for each nutrient: three 2-day simulations and three 10-day simulations with identical root and soil parameters for the two durations. The first simulation examined P or NO_3^- uptake in the homogeneous case with control root parameters (no plasticity, Table 1). The second examined nutrient uptake in the heterogeneous array with control root parameters (no plasticity, Table 1). The third examined uptake in the heterogeneous array with no plasticity in the 24 'control' cells and full plasticity (Table 1) in the single enriched cell. Thus, even in the case of heterogeneity + plasticity, roots in 24 of 25 cells were assigned no plasticity whatsoever.

Results

Phosphate uptake was 3.2- to 4.3-fold greater in 3$\times$ soil patches than in control patches for all model simulations (Fig. 1). In the 5$\times$ patches, P-uptake increased 4.9- to 6.6-fold with root proliferation and elevated kinetics, depending on water availability and the length of the simulations. On average, soil heterogeneity (the range in soil nutrient concentrations) was slightly more important for nutrient acquisition in 10-day than in 2-day simulations, and the relative contribution of plasticity (root proliferation and increased uptake kinetics) was more important in the wetter than in the drier soil.

For the wetter soil, approximately half of all P uptake in 3$\times$ and 5$\times$ patches was due to root plasticity. In the drier soil, the contribution of plasticity decreased, though even in the most conservative case (3$\times$ patches) the additional amount of P obtained by the plant solely from plasticity was 75% of the total amount obtained in a 1$\times$ control patch (Fig. 1c). In the absence of plasticity, P uptake was 2- to 4-fold greater in 3$\times$ and 5$\times$ patches compared with 1$\times$ patches for all model simulations (attributable solely to the increase in soil-solution P).

The importance of soil heterogeneity and root plasticity for nutrient uptake was even more pronounced for NO_3^- than for P (Fig. 2). In 12$\times$ soil patches, NO_3^- uptake was between 7- and 20-fold greater than in control patches, depending on simulation conditions. NO_3^- uptake in 6$\times$ patches was 6- to 10-fold greater with plasticity than in controls. The length of the simulations and how the nutrients became available in the soil had important consequences for NO_3^- uptake. For 10-day simulations, root plasticity contributed little to NO_3^- uptake in an existing soil patch (control roots already present) until the patch was relatively concentrated (12$\times$, where it comprised 45% of total NO_3^- uptake, Fig. 2d). The reason for this result was that the physiological uptake capacity of existing control roots was sufficient to take

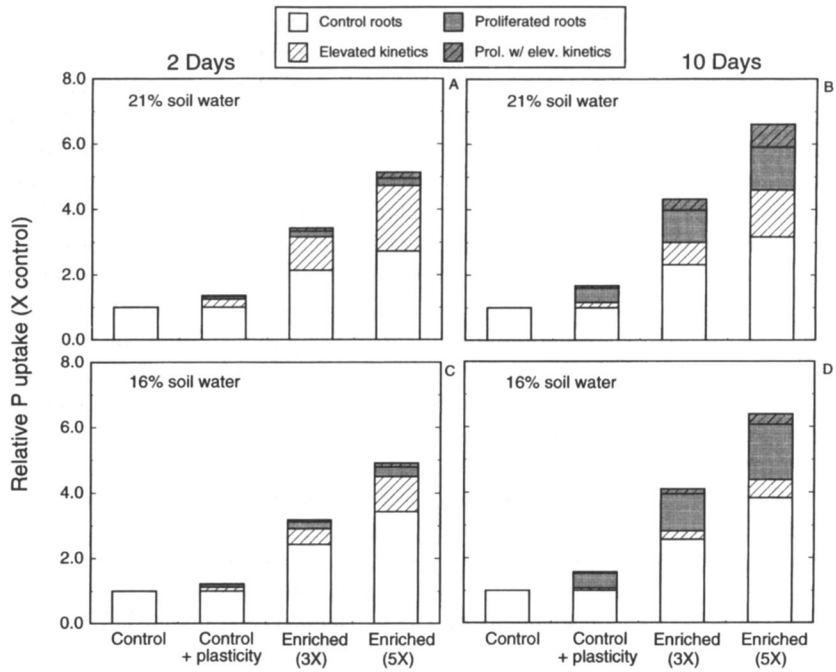

Fig. 1 Simulated relative phosphate uptake in control patches (10 mg P kg^{-1}), 3× patches (30 mg P kg^{-1}), and 5× patches (50 mg P kg^{-1}) by control roots, control roots with elevated kinetics, proliferated roots, and proliferated roots with elevated kinetics. (A) 21% soil water, 2-day simulations, (B) 21% soil water, 10-day simulations, (C) 16% soil water, 2-day simulations, and (D) 16% soil water, 10-day simulations. The values within each panel were set relative to their own respective controls (i.e. relative uptake for control patches always equals 1). The soil *P*-values were taken from the field studies of Jackson & Caldwell (1993a,b). The soil-extractable *P*-values of 10, 30 and 50 mg kg^{-1} correspond to 12.7, 33.3 and 52.1 μM soil-solution P.

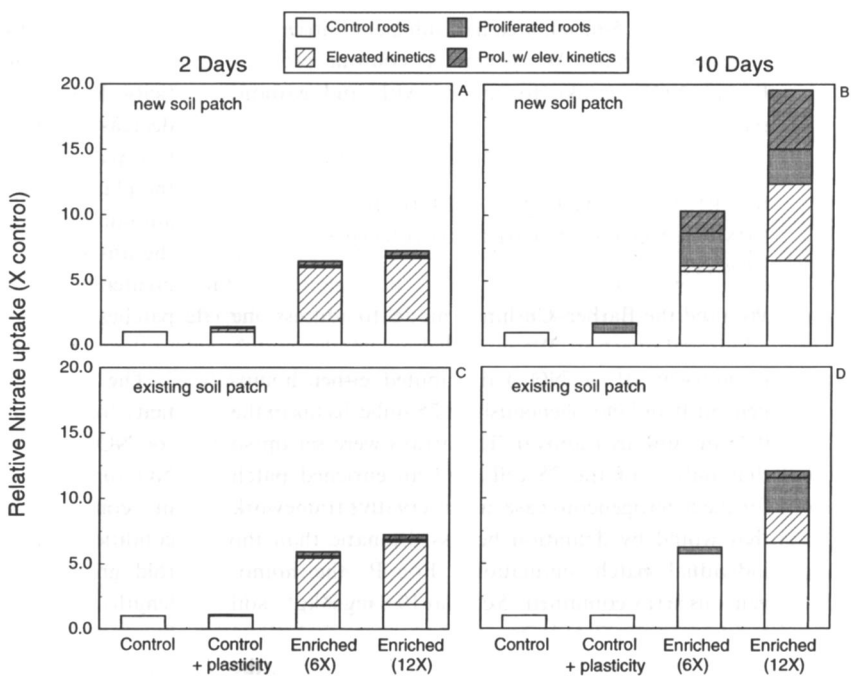

Fig. 2 Simulated relative nitrate uptake in control patches (100 μM NO_3^-), 6× patches (600 μM NO_3^-), and 12× patches (1200 μM NO_3^-) by control roots, control roots with elevated kinetics, proliferated roots, and proliferated roots with elevated kinetics. (A) 2-day simulations for a new soil patch, (B) 10-day simulations for a new soil patch, (C) 2-day simulations for an existing soil patch, and (D) 10-day simulations for an existing soil patch. The values within each panel were set relative to their own respective controls (i.e. relative uptake for control patches always equals 1). Additional root growth occurred 'outside' the control patch for new soil patches (A,B) and 'inside' the control patch for existing soil patches (C,D). The soil-solution NO_3^- values for the simulations were taken from the field studies of Jackson & Caldwell (1993a,b).

up the relatively mobile NO_3^- ion in 1× and 6× patches. When the soil patch was in a previously unexplored volume of soil, plasticity was quite important for both 6× and 12× patches (contributing 44% and 66% of total NO_3^- uptake; Fig. 2b). In these 12× patches, root plasticity contributed 13 times the NO_3^- taken up in an individual control patch (1×). This distinction, whether the patch came available in the presence of roots or in previously unexplored soil, was relatively unimportant for the 2-day simulations (Fig. 2a,c). For 2-day simulations, increased uptake kinetics were by far the most important factor for NO_3^- uptake.

With these simulations as background, we then modelled P and NO_3^- uptake for an actual 0.25-m^2 soil area in the field (Jackson & Caldwell 1993a,b). Relative P availability in the 0.25-m^2 soil area varied approximately threefold, with 38 mg P kg^{-1} as the highest value in the array (Fig. 3d). Plant uptake of P in the region was 28% higher with root plasticity than without (Fig. 3a–c; based on 10-day simulations). This 28% increase in P uptake was fairly evenly distributed between root proliferation and elevated kinetics (Fig. 3c). For 2-day simulations of the same soil region, plasticity increased nutrient uptake by 21%, due almost exclusively to elevated kinetics (data not shown).

Soil heterogeneity and root plasticity were much more important for NO_3^- uptake in the 0.25-m^2 soil area than for P uptake (Fig. 4a–c). Plant NO_3^- uptake in the region was 61% greater with plasticity than without (Fig. 4c), primarily because of a few hotspots of NO_3^- availability in the lower half of the soil area (Fig. 4d). The increase in NO_3^- uptake was due almost exclusively to elevated kinetics in these 2-day simulations.

The hypothetical homogeneous and heterogeneous arrays also provided valuable insights into the importance of heterogeneity and plasticity (Fig. 5). One of the most interesting results was that without plasticity, plants always acquired less nutrients in the heterogeneous arrays than in the homogeneous arrays (albeit only slightly so for P), even though the same total quantity of nutrients was available. For the 10-day simulations, a plant with plasticity (heterogeneity + plasticity) took up 20% more NO_3^- than in the homogeneous array and over 40% more than in the heterogeneous array without plasticity (Fig. 5a). In contrast for the 2-day simulations, a plant with plasticity took up slightly less NO_3^- in the heterogeneous array than in the homogeneous array (though still 20% more than in the heterogeneous array without plasticity). For phosphate, the plant took up the most P in the heterogeneous case with plasticity, though increases were less than 10% (Fig. 5b). Clearly heterogeneity does not always lead to increased nutrient uptake, but the plant without plasticity growing in a heterogeneous soil always acquired the smallest quantity of nutrients in these simulations.

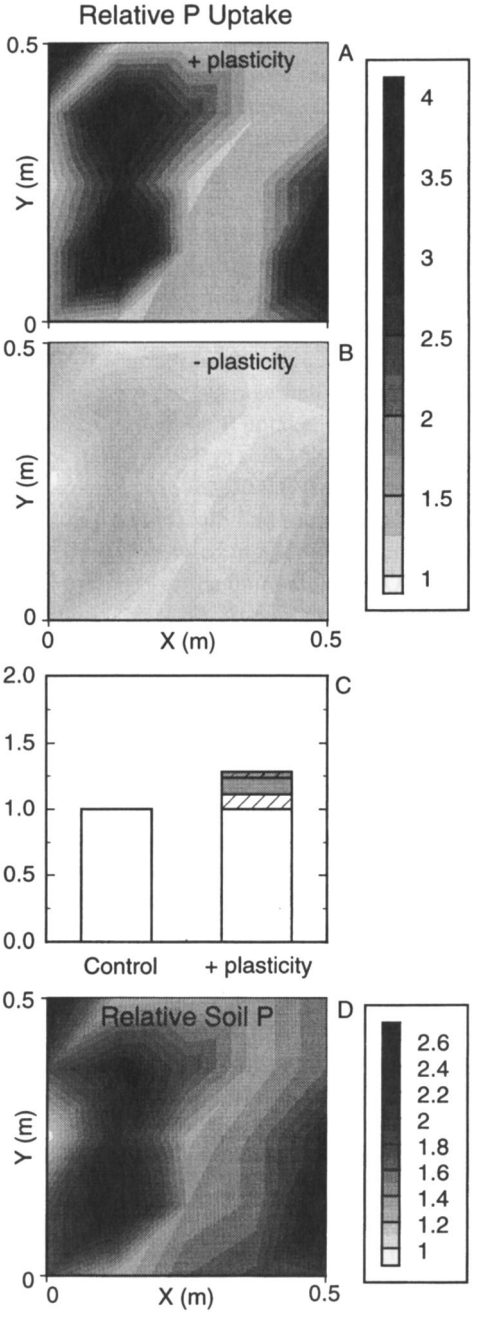

Fig. 3 Simulated relative phosphate uptake and measured soil availability from a 0.5-m × 0.5-m soil area in the field. (A) Simulated P uptake for a plant with plasticity in the 0.5-m × 0.5-m soil area (see Table 1 and the Methods for the specifics of plasticity). (B) Simulated P uptake for a plant without plasticity in the same soil area. (C) Phosphate uptake integrated over the entire soil area for the plants in A and B (open bar – contribution of control roots; hatched bar – elevated kinetics in control roots; filled bar – proliferated roots; filled and hatched bar – elevated kinetics in proliferated roots). (D) Relative P availability in the 0.5-m × 0.5-m soil area (actual field data from Jackson & Caldwell 1993a,b). For this 10-day simulation, P uptake in the soil was 28% greater with root plasticity than without.

Discussion

In our system, the consequences of soil heterogeneity and root plasticity for nutrient uptake were much

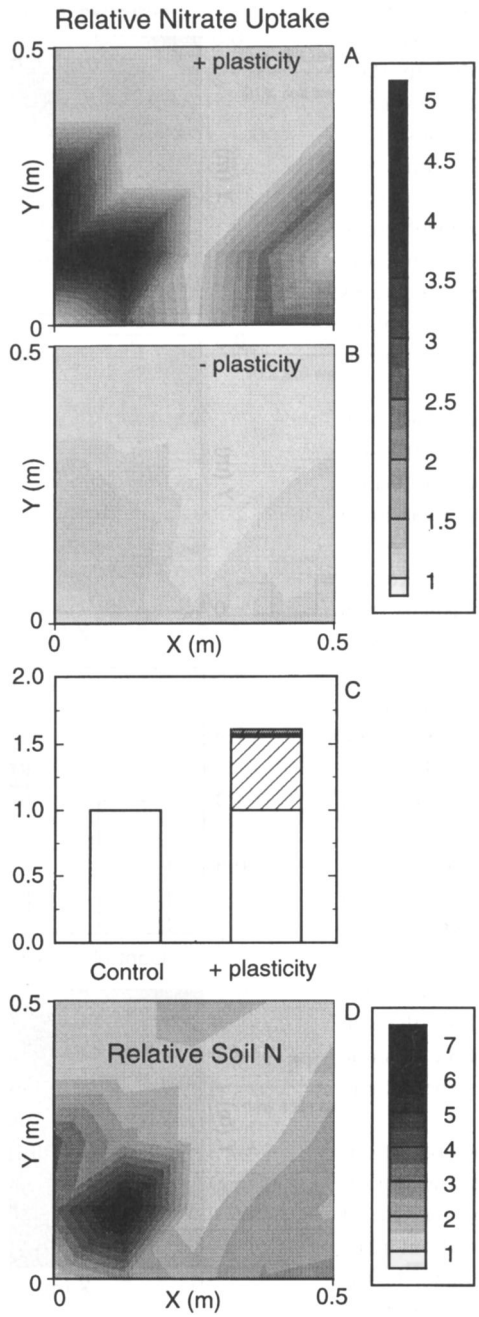

Fig. 4 Simulated relative nitrate uptake and measured soil availability from a 0.5-m × 0.5-m soil area in the field. (A) Simulated NO_3^- uptake for a plant with plasticity in the 0.5-m × 0.5-m soil area (see Table 1 and Methods for the specifics of plasticity). (B) Simulated NO_3^- uptake for a plant without plasticity in the same soil area. (C) NO_3^- uptake integrated over the entire soil area for the plants in A and B (open bar – contribution of control roots; hatched bar – elevated kinetics in control roots; filled bar – proliferated roots; filled and hatched bar – elevated kinetics in proliferated roots). (D) Relative NO_3^- availability in the 0.5-m × 0.5-m soil area (actual field data from Jackson & Caldwell 1993a,b). For this 2-day simulation, NO_3^- uptake in the soil was 61% greater with root plasticity than without.

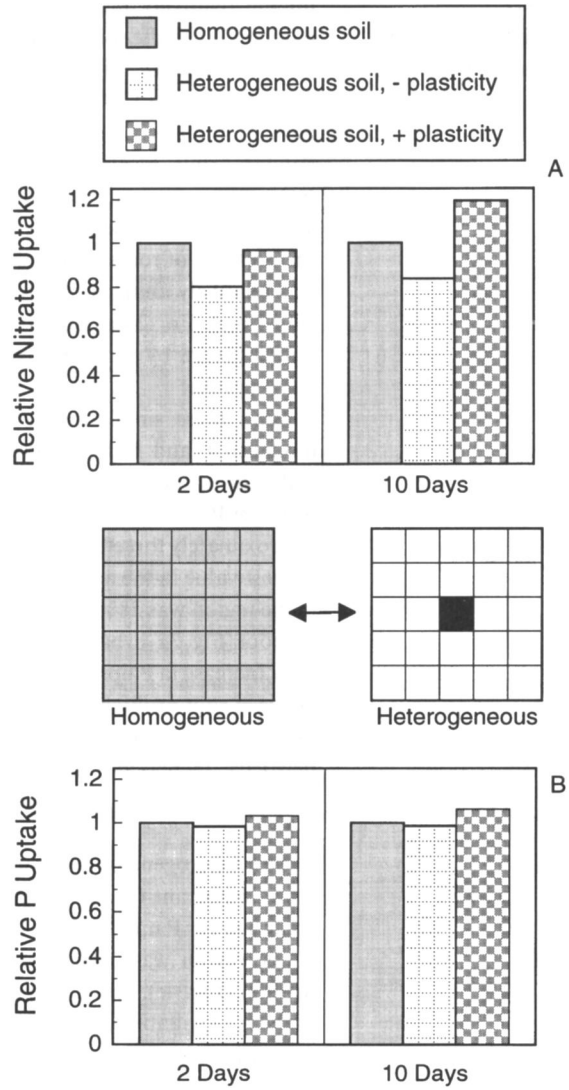

Fig. 5 Simulated relative nitrate uptake (A) and phosphate uptake (B) in hypothetical homogeneous and heterogenous arrays of the same total amount of nutrient. The arrays were set up so that only 1 of the 25 cells had an enriched patch in the heterogeneous case, a conservative framework that would, by definition, show much less dramatic effects than in Figs 1 and 2. For P, there were 25 cells at 10.8 mg P kg^{-1} soil (homogeneous), or 24 cells at 10 mg kg^{-1} and one cell at 30 mg kg^{-1} (heterogeneous); for NO_3^-, there were 25 cells at 144 μM NO_3^- (homogeneous) or 24 cells at 100 μM NO_3^- and one cell at 1200 μM NO_3^- (heterogeneous). For the homogeneous simulations, roots were modelled with no plasticity (Table 1). For the heterogeneous cases, roots were modelled either without plasticity (heterogeneous soil, – plasticity) or with plasticity in only the one enriched cell out of the 25 cell array (heterogeneous soil, + plasticity). Even in the case of heterogeneity + plasticity, roots in 24 of 25 cells had no plasticity whatsoever.

greater for N than for P, primarily because of the greater variation for N in the field (Jackson & Caldwell 1993a,b). While P varied on average 3-fold around individual plants, NH_4^+ and NO_3^- varied by more than an order of magnitude. It may at first appear counterintuitive that the more mobile NO_3^- would show greater variation in the soil than the less-mobile P, but N cycling in the soil is more complicated than is P cycling. Phosphate is unlikely to be lost to

the atmosphere and is much less likely to be leached than is NO_3^-. In addition, competition with microbes may be greater for N (even NO_3^-) than for P (Davidson *et al.* 1992). In arid and semiarid systems where water limitation can limit nutrient movement, large variation in N availability may be the norm rather than the extreme.

A number of previous analyses concluded that plasticity may be relatively unimportant for NO_3^-, particularly compared to P uptake (e.g. Cornforth 1968; Robinson & Rorison 1983; Wiesler & Horst 1994). NO_3^- is more mobile in the soil than P, and existing root densities may sometimes be adequate for capturing NO_3^-. In an interesting analysis, Robinson (1996) modelled NO_3^- uptake for the laboratory experiments of Drew & Saker (1975), concluding that root proliferation did not necessarily lead to increased NO_3^- uptake. Our results for NO_3^- in an existing soil patch (the relevant comparison for Drew & Saker 1975) showed a similar result, with little benefit from root proliferation in most cases (Fig. 2c,d). Does this mean that heterogeneity and plasticity are unimportant for NO_3^-? Not necessarily. Increased uptake kinetics (greater I_{max}) led to substantially more NO_3^- uptake in most of our scenarios (Fig. 2), a factor not included in the analysis of Robinson (1996). It is also important to keep in mind the role of temporal factors in all such analyses. If our simulations continued indefinitely, much of the benefit of increased I_{max} in an existing soil patch would disappear, since the same finite pool of nutrients would eventually be taken up in all scenarios (given equivalent C_{min}). In a field setting, however, nutrients do not remain available indefinitely. NO_3^- may be taken up by a competitor, immobilized by microbes, or lost from the system through leaching or denitrification. An example of the potential importance of competition and spatial heterogeneity is provided by the hypothetical NO_3^- arrays in Fig. 5. If two plants shared one of the arrays for 10 days, one plant could take up almost as much N by focusing entirely on the single enriched cell as its competitor could extract from the remaining 24 control cells. If the plants split uptake in the 24 control cells, the relative 'value' of the enriched patch would be even greater. A new soil patch (Fig. 2a,b) obviously represents a separate case, providing a new pool of resources to a plant. The finer the scale of variation for a given nutrient, the greater is the likelihood that a soil patch will be uncolonized.

The importance of root plasticity, both in respect of uptake kinetics and proliferation, differed for the various nutrients and environmental scenarios. In general, the relative importance of elevated kinetics tended to be greater for NO_3^- than for P, as predicted from theory (Nye & Tinker 1977; Barber 1984). Elevated kinetics were relatively more important in 2-day than in 10-day simulations, partly because soil-solution concentrations of P and NO_3^- were usually reduced by the end of the 10-day simulations. Not surprisingly, root proliferation was less important in 2-day simulations, since less root growth had occurred. Clearly the ability of the soil to replenish nutrients to a patch will influence the patch longevity and its total pool of nutrients. Relatively faster responses of plasticity, such as elevated kinetics, may be especially important in patches that are ephemeral. Detailed sensitivity analyses for P and NO_3^- in the Barber–Cushman model are found in Barber & Cushman (1981) and Silberbush & Barber (1983).

The difference in mobility between P and NO_3^- had a number of important consequences for model results. Reducing the average half-distance between roots had little effect on P uptake, primarily because of the low mobility of P in soils (Nye & Tinker 1977). In consequence, for the 10-day simulations (where substantial proliferation had occurred) root proliferation always resulted in additional net uptake of P (Figs 1 and 3). For the more mobile NO_3^- ion, this was not always the case. At concentrations of 600 μM (6 ×) or less, root proliferation and increased uptake kinetics in the 10-day simulations resulted in little or no additional net NO_3^- uptake if the nutrient patch already contained control roots (Fig. 2d). In this case existing roots were sufficient to take up the available NO_3^-, and increasing the root density (decreasing their average spacing) decreased NO_3^- uptake by control roots (i.e. proliferating roots were effectively 'competing' with existing roots for NO_3^-). This is not obvious from Fig. 2, which presents the *net* increase in NO_3^- uptake due to plasticity. When the enriched patch was in previously unexplored soil, however, plasticity had a much larger relative effect, contributing to increased NO_3^- uptake even at 100 μM NO_3^- (Fig. 2b). The distinction of whether nutrients become available in soil patches already 'colonized' by roots or in unexplored patches of soil is potentially quite important for NO_3^- uptake in the field. The same distinction is less important for P at the root densities evaluated here, since each root, whether new or old, experienced little 'competition' for P by neighbouring roots.

As shown in these simulations, nutrient acquisition from a relatively rich soil patch is often greater than the magnitude of the difference between nutrient concentrations in the patch and the background soil (e.g. P uptake increases 4.3-fold in a 3 × patch relative to that from 1 × soil). For phosphate, the relationship between soil-solution and solid-phase nutrient concentrations is usually exponential rather than linear (Nye & Tinker 1977; Kovar & Barber 1988). Kovar & Barber (1988) surveyed 33 soils and showed on average that soil-solution P increases proportionally much more than solid-phase P when P is added to the soil. In simulations with the model used here, Kovar & Barber (1989) also showed that maximum phosphate uptake for crop plants occurs not when P is added evenly throughout the rooting zone, but when concentrated in as little as a few percentage of the total

rooting volume. The apparent reason was that concentrating the P in a relatively small soil area resulted in proportionally less P adsorbed by the soil in unavailable forms, and proportionally more in the soil solution immediately available to the plant (Kovar & Barber 1988).

Mycorrhizal fungi could be quite important for the capture of patchy soil nutrients (St. John *et al.* 1983), particularly the acquisition of relatively immobile nutrients such as P (Nye & Tinker 1977). One could, in principle, use the Barber–Cushman model to simulate hyphal uptake of nutrients by incorporating additional roots of a very fine diameter to the simulations. We chose not to do this since we lacked information on the abundance of extramatrical hyphae in the soil. Preliminary field studies in our system also showed no evidence of any increase in mycorrhizal infection for roots in enriched patches compared to control patches (Duke *et al.* 1994).

The Barber–Cushman model has a number of limitations. The model does not characterize three-dimensional root architecture, as does the architectural model of Diggle (1988) or the soil-water model of Clausnitzer & Hopmans (1994). In order to do spatial analysis with Barber–Cushman the soil must be parceled into discrete sections as we did for the 0.25-m^2 soil area from the field and the hypothetical homogeneous and heterogeneous arrays. Excellent recent models of Huston & DeAngelis (1994) and Biondini & Grygiel (1994) are much more spatially explicit than Barber–Cushman, but they lack its physiological basis. Yanai (1994) developed a steady-state model of nutrient uptake that accepts time-varying input, but neither that model nor Barber–Cushman includes a cost function. Finally, the model does not include nutrient inputs and outputs, such as mineralization of organic matter, weathering of parent material, or leaching of nutrients.

Soil heterogeneity can be potentially important to plants even in the absence of plasticity. As our simulations show, nutrient uptake can be dramatically greater in an enriched patch of soil without any morphological or physiological adjustment (Figs 1 and 2). On the other hand, soil heterogeneity in the absence of plasticity may sometimes be unimportant. An illustration is provided by Michaelis–Menten uptake of nutrients at a root surface (Fig. 6). At low soil-solution concentrations (relative to K_m), net nutrient uptake increases approximately linearly with increasing soil-solution concentration, and nutrient uptake increases in the absence of plasticity (Fig. 6a, Case 1). At concentrations substantially higher than K_m, an identical increase in soil-solution concentration may result in little additional nutrient uptake (Fig. 6a, Case 2). When physiological adjustment occurs, the situation can be quite different (Fig. 6b). With a 50% increase in I_{max}, nutrient uptake increases dramatically with soil heterogeneity at both low and high soil-solution concentrations. Interestingly, an examination of soil-solution concentrations in the literature shows, for nitrate at least, that concentrations are usually much greater than apparent K_m values. For example, Reisenauer (1964) summarized almost 1000 samples from agricultural soils and found 95% of the soil solution samples to be $>400\ \mu M\ NO_3^-$, well above typically reported K_m values of 10–40 $\mu M\ NO_3^-$ (e.g. Smart & Bloom 1988; Bowman *et al.* 1989; Siddiqi *et al.* 1990). Values for unamended soils in natural plant communities are probably lower on average than Reisenauer's data.

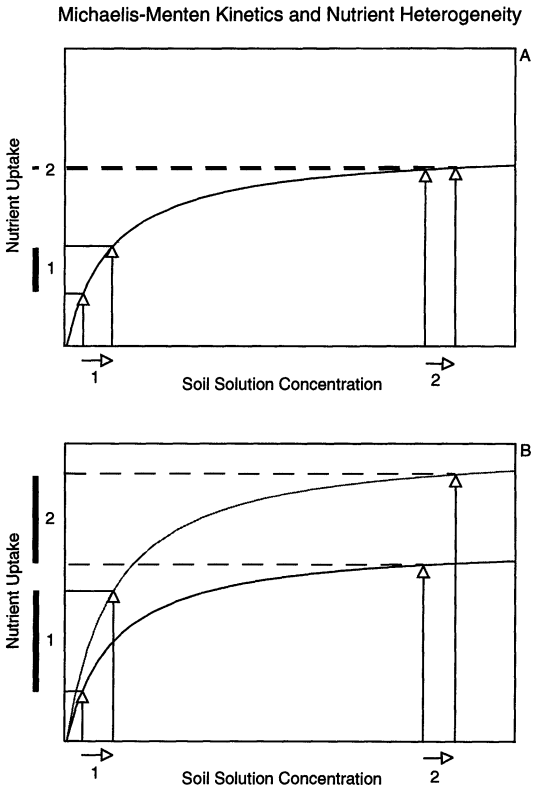

Fig. 6 The net increase in nutrient uptake at low and high nutrient availability (case 1 and 2, respectively) with a unit increase in nutrient availability. (A) Increased nutrient availability at low nutrients provides a doubling of nutrient uptake (case 1), whereas at high nutrients it provides essentially no net gain to the plant (case 2). (B) With a plasticity response to the nutrient heterogeneity (in this example a 50% increase in I_{max}), the plant gains substantially more nutrients in both cases.

What information, then, is needed to assess the importance of soil heterogeneity and physiological plasticity for a given system? At a minimum, we believe the following criteria must be addressed:

1 What are the amount of and type of variation observed, both spatial and temporal?

2 What is the 'grain' of the variability (*sensu* Gross *et al.* 1993)? Is the spatial or temporal scale of the process relevant to the physical scale of the plant?

3 Does the variability occur in a range where physiological or morphological adjustments by the plant can be meaningful?

4 Does the plant show morphological or physiological response to resource variability?

5 Do sympatric plant species, or individuals within species, show different levels of plasticity? Is plasticity of one species influenced by the presence of another? **6** Are there significant nonlinearities in the processes important for resource acquisition (Stark 1994)?

Items 1–5 are important for the potential importance of heterogeneity alone, or heterogeneity accompanied by plasticity. Item 6, linearity within the system, sets some potential limits to the importance of heterogeneity. For example, if nutrient uptake is strictly linearly related to nutrient availability, then the distribution of a given quantity of nutrients may not matter. In reality, the presence of plant competition for nutrients, and the likelihood of nonlinearity in most ecological processes, make point 6 largely academic.

Our previous field experiments and this modelling study provide some information on all of the above six points. Many of these points warrant further study. Temporal variation in soil resources is likely to be quite important in many systems, particularly those such as the Great Basin that experience a flush of water and nutrients with spring snowmelt or after rain. A better understanding of what functional groups or types of species are most likely to show plasticity is also needed (Tilman 1988; Friend *et al.* 1990; Campbell *et al.* 1991; Biondini & Grygiel 1994; Fitter 1994; Jackson *et al.* 1996), with an accompanying analysis of the costs and limitations of plasticity (e.g. Eissenstat 1992; Hutchings & de Kroon 1994). Understanding the influence of one species on the plasticity of another is a third factor deserving further study. This influence may be either 'direct' (e.g. Mahall & Callaway 1991) or 'indirect', mediated through other resources such as light availability (Jackson & Caldwell 1992). Such research may help explain why plasticity responses are not always consistent (e.g. N uptake in Jackson & Caldwell 1991, 1992). The consequences of heterogeneity and plasticity also need to be integrated at the scale of populations (e.g. Casper & Cahill 1996). We plan to use models to address some of these issues, including NH_4^+ heterogeneity in the soil, net nitrification (the conversion of NH_4^+ to NO_3^-), and competition between two or more plants of varying plasticity in a patchy soil environment.

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