

Supply pre-emption, not concentration reduction, is the mechanism of competition for nutrients

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Summary

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- Concentration reduction theory is the leading theory regarding the mechanism of competition for nutrients in soils among plants, yet it has not been rigorously tested.
- Here we used a spatially explicit, fine-scale grid-based model that simulated diffusion and plant uptake of nutrients by plants in soil to test whether concentration reduction theory was appropriate for terrestrial plant competition for nutrients.
- In the absence of competition, increasing the rate of diffusion allows a plant to maintain positive growth rates below the lowest average concentration to which it can reduce nutrients in soil solution (R^*). As such, differences among plants in the reduction of soil moisture, which here primarily affects nutrient diffusion, can cause R^* to predict competitive success incorrectly. The stronger competitor for nutrients captures the largest proportion of the nutrient supply by ensuring nutrients contact its roots before those of a competitor.
- Although the metric derived from concentration reduction theory, R^* , might have predictive power for competitive outcomes in terrestrial ecosystems, this evidence suggests that plants outcompete other plants for nutrients by pre-empting the supply, not reducing the average concentration.

Key words: concentration reduction, nitrate, resource competition, SERMUN, supply pre-emption.

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Introduction

Resource competition among terrestrial plants is central to ecological theory. Yet, the concentration reduction theory (Tilman, 1982; Tilman, 1987) has been the theory that almost exclusively has been used to address the mechanisms by which terrestrial plants compete for nutrients over long time-scales. The concentration reduction theory was originally developed with respect to the dynamics of competition among phytoplankton for nutrients (Tilman, 1976; Tilman, 1977). The theory states that when populations of two plant species are competing for a common limiting nutrient, the species that can reduce the average concentration of nutrient in solution to the lowest level and persist at that level will be competitively superior for that nutrient (Tilman, 1980). In equations of nutrient supply, nutrient uptake, and plant

growth, the concentration of nutrient in solution is known as R and the lowest concentration at which a population can persist is known as R^* . The essence of the concentration reduction theory is that it is the average concentration of a limiting nutrient in soil solution that determines growth of individuals and therefore the reduction of this concentration is the mechanism of competition for resources. Concentration reduction theory generates the hypothesis that the outcome of competition for a single limiting resource can be predicted by measuring each species' R^* for that resource.

However, concentration reduction may not be an appropriate theory for competition for nutrients by terrestrial plants because it does not take into account the diffusion of nutrients in soils (Huston & DeAngelis, 1994). Several of the assumptions of the concentration reduction theory are less applicable to terrestrial systems than they are to the aquatic systems for which

the equations were developed. The model from which the R^* hypothesis was derived assumes that plant nutrient uptake is a function of the average concentration of the nutrient in solution (Tilman, 1982). Diffusion in aquatic systems might be high enough to assume that concentrations are relatively uniform in a given volume of water and therefore uptake by any individual can be considered a function of the average concentration. In terrestrial systems, diffusion of nutrients in soil solution often limits uptake (Chapin, 1980; Raynaud & Leadley, 2004) and nutrient concentration gradients are created around roots (Tinker & Nye, 2000). This diffusion limitation differs among nutrients and among soils, but consistently becomes greater with declining soil moisture as impedance increases and the effective diffusion rate declines (Tinker & Nye, 2000).

In addition, there is little empirical evidence to support resource reduction theory for terrestrial plants. For predicting empirical competitive outcomes among terrestrial plants, the R^* hypothesis has not been used outside of Cedar Creek Natural History Area (CCNHA), Minnesota, USA. At CCNHA, it has only been tested in two experiments with a small number of grasses (Tilman & Wedin, 1991; Wedin & Tilman, 1993). Although the concentration reduction theory as applied to nutrients is based on resource concentrations in soil solution (e.g. mg nutrient l^{-1}), empirical research has used content in an equivalent amount of dry soil as a measure of R^* (e.g. mg nutrient kg^{-1} dry soil). In expressing R^* as content in dry soil, any differences in soil moisture among stands of different species are ignored, potentially misrepresenting the concentration of resources in the soil solution.

Not incorporating diffusion limitation nor accounting for differences in soil moisture among stands does not necessarily invalidate the concentration reduction theory. In general, theories are not rejected because they have not been applied precisely or contain assumptions that simplify the mathematics of models. Theories are typically maintained until their explanatory power is lower than another theory. Yet, it is important to separate the hypotheses or metrics that a theory generates from the assumptions it makes about how a system functions. To invalidate a theory such as concentration reduction, the assumptions of the theory must be tested and shown to be incorrect, these incorrect assumptions must cause incorrect predictions, and an alternative, more appropriate model must be offered.

To test whether the assumptions of concentration reduction theory are appropriate for terrestrial plant nutrient competition, we test its predictions with a more realistic, spatially explicit model of soil nutrient dynamics that does not assume that the soil solution is well mixed. In this paper we focus on nitrate, which readily diffuses in soil solution, with negligible adsorption or desorption. Nitrate thus is the nutrient most likely to adhere to the assumptions of resource reduction theory and is the nutrient focused on in empirical tests of R^* (Tilman & Wedin, 1991).

Using a spatially explicit, raster-based model that simulates the diffusion and uptake of nutrients in soil, we test two pre-

dictions of the concentration reduction hypothesis. First, we test whether it is the average soil solution nutrient concentration that determines the growth of plants in the absence of competitors and whether species would be able to grow at soil solution concentrations that are below its R^* . This allows us to test whether the decline of competitively inferior species is necessarily caused by the reduction by competitors of the average concentrations of nutrients in solution.

Second, we run simulations to test whether species with the same R^* for nitrate might have different competitive abilities for nitrate. To test this, we rely on the fact that diffusion of nutrients in soil solution is faster at higher soil moisture. As such, a plant could have a low R^* either because of a faster rate of uptake or because it leaves more water in soil solution (e.g. it transpires less). Yet, higher residual soil moisture should not confer competitive superiority and therefore differences in soil moisture could confound the predictive ability of R^* . We simulate competition between two species that differ in their ability to reduce soil moisture and maximum rates of uptake to test whether two species with the same R^* for nitrate can have different competitive abilities for nitrate.

Materials and Methods

Model description

SERMUN (Spatially Explicit Representation of the Movement and Uptake of Nutrients) uses a raster-based approach to model nutrient dynamics in soil rather than the numerical solutions to analytical equations (Silberbush & Barber, 1983). It is programmed in C++. A vertical slice of soil is represented by the model and divided up into a grid of voxels (volumetric pixels). Although the model simulates dynamics in two dimensions, each voxel has depth in order to quantify pools and fluxes. A voxel can either contain one root, which fills the entire voxel, or a mixture of soil, air, and water, of which only the volumetric water content (θ) is a model parameter. In order to avoid edge effects, dynamics on opposite sides of the grid are linked as if the cells were adjacent. At the beginning of a simulation, a user-determined number of roots of up to two species are randomly assigned to grid cells. Soil solution nutrient concentrations are initially set to be the same for all cells in all simulations. Cells with roots contain no available nutrients.

Roots of each species are assigned the following traits: root tissue density (ρ_R), nutrient concentration ($[N]_R$), allocation of acquired nitrogen (N) to further root growth ($Alloc_R$), and a fractional mortality rate of roots ($Mort_R$). Roots of each species also have characteristic nutrient uptake kinetics (I_{max} , C_{min} , K_m). See Table 1 for the standard values and sources of data. Roots are assumed to grow orthogonal to the plane.

Nitrate movement among cells is characterized by an effective diffusion constant (D_e), which is a product of the liquid diffusion constant (D_l) and impedance (f):

Table 1 Parameter values and their sources, as used in the model

Parameter	Units	Value	Reference
ρ_R	g mm^{-3}	2.00×10^{-4}	Craine <i>et al.</i> (2002)
$[N]_R$	mmol g^{-1}	0.714	Craine <i>et al.</i> (2002)
$Alloc_R$	mmol mmol^{-1}	0.5	Craine <i>et al.</i> (2002)
$Mort_R$		4.39×10^{-8}	Craine <i>et al.</i> (2002)
C_{\min}	$\text{mmol mm}^{-3} \text{H}_2\text{O}$	2.00×10^{-9}	Kelly <i>et al.</i> (2000)
I_{\max}	$\text{mmol mm}^{-2} \text{root area s}^{-1}$	100×10^{-12}	Kelly <i>et al.</i> (2000)
K_m	$\text{mmol mm}^{-3} \text{H}_2\text{O}$	1.0×10^{-6}	Kelly <i>et al.</i> (2000, 2001)
θ	$\text{mm}^3 \text{H}_2\text{O mm}^{-3} \text{soil}$	0.05–0.2	
N_{sup}	$\text{mmol mm}^{-3} \text{soil s}^{-1}$	1.13×10^{-13}	
D_l	$\text{mm}^2 \text{s}^{-1}$	1.90×10^{-3}	Hunik <i>et al.</i> (1994)
p_w	mm	0.2	
p_d	mm	0.01	
t_{step}	s	10	
t_{max}	(dimensionless)	1×10^6	

$$D_e = (D_l \times f) \quad \text{Eqn 1}$$

(f is inversely related to the resistance to diffusion of a nutrient: i.e. a larger f means faster diffusion). f is strictly a function of θ , although the parameters of this function can be unique to a given soil (Tinker & Nye, 2000).

Nutrient dynamics are controlled with three main functions. First, diffusion is calculated between all of the four orthogonally adjacent cells that do not contain roots. Diffusion is scaled by the surface area of the interface of two voxels. At each time step, the amount of nutrient that diffuses to or from each voxel is calculated and then concentrations are reset simultaneously for all voxels at the end of the time step. Using Eqn 1, the amount of nutrient that moves between two cells is calculated according to Fick's First Law (van Rees *et al.*, 1990):

$$F_d = D_l \times \theta \times f \times \frac{\Delta C}{\Delta x} \times p_w \times p_d \quad \text{Eqn 2}$$

(p_w and p_d are the voxel width and depth, respectively; ΔC is the difference in nutrient concentrations of the soil solution between two voxels; Δx is the distance between the centers of the voxels and equal to p_w). In nature, nutrients are supplied to roots via mass flow, but mass flow is relatively unimportant for highly mobile nutrients such as nitrate when availability is low (Chapin, 1991).

The second equation that controls the dynamics of nutrients in soil is nutrient uptake by roots. In the model, there is no mass flow of water and therefore no supply of nutrients via this mechanism. Uptake (U , in mmol s^{-1}) only occurs actively and is controlled by the Michaelis-Menten equation:

$$U = p_w \times p_d \times I_{\max} \times \frac{(C_j - C_{\min})}{K_m + (C_j - C_{\min})} \quad \text{Eqn 3}$$

(I_{\max} is the maximum inflow rate; K_m is the half-saturation constant, i.e. the concentration at which $I = I_{\max}/2$; C_j is the concentration of nutrient in the soil solution of the adjacent voxel; C_{\min} is the concentration of nutrient in the soil solution at which $U = 0$). At each time step, after diffusion occurs,

uptake is calculated for each root. SERMUN includes a limit function so that uptake can not deplete the nutrient concentration of a cell below C_{\min} , a condition that can be a problem in this discrete approach to modeling uptake only when the time steps are relatively long and/or I_{\max} is high and a root has just been produced. In addition, efflux of nutrients from roots is not permitted. If soil solution concentrations are below the C_{\min} of a species, no nutrients are lost from the roots of that species. This limit is put in effect to avoid the model pathology in which one plant becomes an infinite source of nutrients. This does not build in a function that prevents concentration reduction from becoming a mechanism of competitive dominance. Whether a plant takes up no nutrients or effluxes nutrients should not have any long-term impact on the outcome of competition, and only impacts how on rapidly the population of an inferior competitor declines. After nutrients are acquired by a plant, a constant fraction of nutrients are stored for later root growth depending on the fractional allocation rate.

The last equation that controls the dynamics of nutrients is nutrient supply. In this model, nutrient supply (N_{sup}) is assumed to be constant for the entire soil volume. At each time step, the nutrient content of the soil solution is increased by the nutrient supply scaled to the voxel volume and is adjusted by the fraction of cells occupied by roots at a given time point so that it is invariant for the soil volume across different root densities. The new nutrient concentration for a voxel is determined by calculating the ratio of solution nutrient content and θ .

At the end of each time-step, a fraction ($Alloc_R$) of the total amount of nutrient acquired during that time-step is allocated to storage for root growth. The cumulative store of nutrients needed for a species to produce a new root is equivalent to the nutrient content of a root, which is the product of $[N]_R$, ρ_R and the volume of the pixel. When the cumulative store of nutrients exceeds this value, a new root of the species is produced and the stores are reduced by the nutrient content of the root. New roots are located randomly in the soil volume.

At each time step, the probability of mortality for the root ($Mort_R$) of a species is a constant equivalent to a set median longevity. When a root dies, the cell is considered to contain soil again and the soil solution nutrient content of the cell remains at zero. The equilibrium number of roots in the grid is almost entirely determined by N_{sup} , the N content of a root, $Alloc_R$ and $Mort_R$. For these simulations, the equilibrium number of roots in the grid is 90 roots.

Parameterization

We parameterized the model to simulate the dynamics of nitrate in a sandy soil. The model was set to simulate a 2×2 cm vertical slice of soil divided up into a 100×100 square grid. Each voxel is set to be 0.2 mm wide (p_w), 0.01 mm deep (p_d) and represents 0.0004 mm^3 of soil volume. Roots were set to occupy only 1 voxel. For sandy soil, we set $f = \theta$ (Tinker & Nye, 2000). Nutrient supply was set to the equivalent of 5 g N m^{-2} to a 10 cm depth. Plant morphological parameters were taken from measurements of field-grown grasses (Craine *et al.*, 2002). For the traits of our base species, we set root N concentration to 10 mg N g^{-1} biomass, root tissue density to $2 \times 10^{-4} \text{ g mm}^{-3}$ and median longevity to 0.5 yr. Consequently, equilibrium below-ground productivity was equivalent to $250 \text{ g m}^{-2} \text{ yr}^{-1}$ to 10 cm depth and equilibrium biomass was 180 g m^{-2} , which is the equivalent of 90 roots per 100×100 grid. Measurements of nitrate uptake kinetics of grasses are rare and we used values measured on *Acer rubrum* (Kelly *et al.*, 2000, 2001). I_{max} , K_m and C_{min} were set to $100 \times 10^{-12} \text{ mmol mm}^{-2} \text{ s}^{-1}$, $1.0 \times 10^{-6} \text{ mmol mm}^{-3}$ and $2.0 \times 10^{-9} \text{ mmol mm}^{-3}$, respectively.

Simulations and results

We ran our first set of simulations to determine the equilibrium soil solution concentrations of nitrate (R^*) for plants growing in soil at 20% volumetric moisture. We used the base species trait set, but varied I_{max} from 100×10^{-12} to $10 \times 10^{-12} \text{ mmol mm}^{-2} \text{ s}^{-1}$ at steps of $10 \times 10^{-12} \text{ mmol mm}^{-2} \text{ s}^{-1}$. Ten replicates were run for each species with a random initial root distribution for each replicate. R^* was determined after 115 d of simulation time, at which time concentrations were near steady-state. The R^* value was calculated by summing the nutrient contents of each voxel in the grid and then dividing by the total soil water content in the grid. With diffusion limitation explicit in the model, faster uptake rates (I_{max}) led to lower R^* (at 20% soil moisture, $R^* = 3.94 + 6.87 \times 10^{-10}/I_{max}$; $r^2 = 0.99$). The lowest R^* belonged to the species with the highest I_{max} ($100 \times 10^{-12} \text{ mmol mm}^{-2} \text{ s}^{-1}$).

If soil solution concentrations *per se* determine growth, then plants with lower I_{max} should not be able to grow at the R^* of the species with the highest I_{max} , since it would be below their own R^* . For each species across the I_{max} gradient, we calculated what its growth rate would be if it grew in a well-

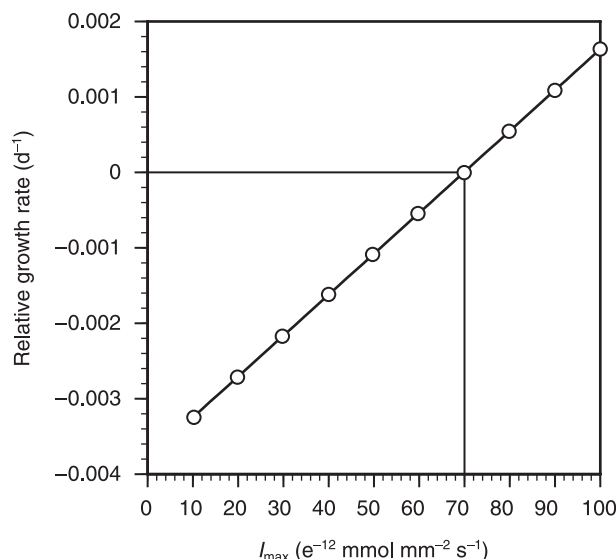


Fig. 1 The relationship between the maximum inflow rate (I_{max}) and relative growth rate at a single soil solution concentration when soil solutions are well-mixed. The soil solution concentration was set to the equivalent of the R^* (see text) of the species with the highest I_{max} when grown at 20% soil moisture and diffusion limitation in place. Initial biomass was the same for all plants. Vertical and horizontal lines indicate the I_{max} at which a plant had zero growth.

mixed solution of nitrate that was set to the lowest R^* of the species we examined, that of the species with the highest I_{max} ($100 \times 10^{-12} \text{ mmol mm}^{-2} \text{ s}^{-1}$). When grown in well-mixed solutions that were equivalent to the lowest R^* , species with an I_{max} of greater than $70 \times 10^{-12} \text{ mmol mm}^{-2} \text{ s}^{-1}$ still had a positive relative growth rate ($\text{RGR} = (\delta N/N)\delta t$) (Fig. 1).

With species being able to grow at soil solution concentrations below their own R^* , we tested whether the plant with the highest I_{max} was competitively superior. For this purpose, we simulated competition between the base species and a species with a lower I_{max} of $80 \times 10^{-12} \text{ mmol mm}^{-2} \text{ s}^{-1}$. From our previous results, when soils are not well-mixed and soil moisture is set to 20%, the species with an I_{max} of $80 \times 10^{-12} \text{ mmol mm}^{-2} \text{ s}^{-1}$ has an R^* that is 18% greater than the base species ($12.92 \pm 0.27 \mu\text{M}$ vs $10.95 \pm 0.21 \mu\text{M}$). At the beginning of the simulation, half of the roots are assigned to each species with a total root density equal to the equilibrium root density of the species (90 roots per grid). We set soil moisture to 20%, explicitly included diffusion at this soil moisture, and 10 replicates of the simulation were run for the equivalent of 3 yr each. There are many metrics that can be applied for relative competitive success (Weigelt & Jolliffe, 2003). For simplicity sake, we consider a plant to be a superior competitor if it acquires the majority of the nitrate supply as well as an increasingly greater fraction of the nitrate supply over time, if not, exclude the other plant.

As predicted by concentration reduction theory, the low I_{max} , high R^* species is able to outcompete the high I_{max} , low R^* species. The low I_{max} species declined in biomass by

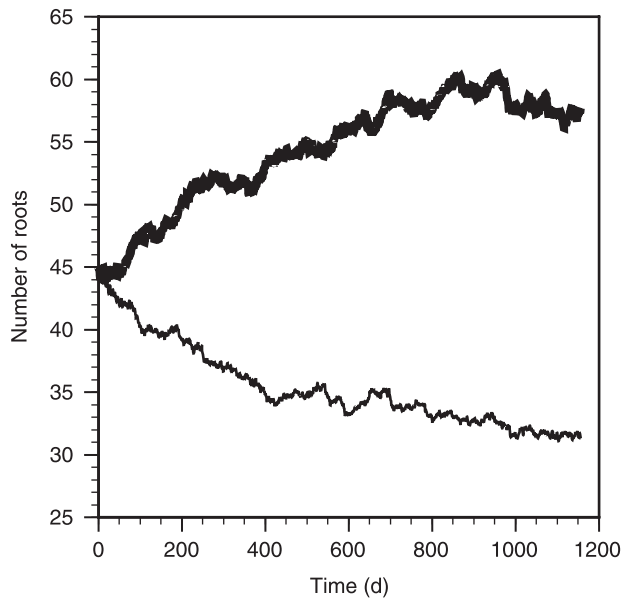


Fig. 2 Change in the number of roots per 100×100 voxel grid for base species (thick line) and species with a maximum inflow rate (I_{\max}) of 80×10^{-12} (thin line) when growing in the same soil volume at 20% soil moisture. Curves represent the average of 10 replicate simulations.

$30.4 \pm 6.8\%$ after 3 yr of competition with the high I_{\max} species, which increased by the same amount ($28.7 \pm 7.6\%$) (Fig. 2). Extending the timescale of interaction beyond 3 yr increased the dominance of the high I_{\max} , low R^* species and no indication of stable coexistence was observed. After 10 yr, the low I_{\max} species had been reduced to 4% of the total root biomass (data not shown). By contrast, when the poorer competitor was grown in the absence of interspecific competition in a well-mixed solution of nitrate, with concentrations set at the level of its competitor's R^* , its biomass increased at $0.055\% \text{ d}^{-1}$ (Fig. 1) and would have increased in biomass by 83% after 3 yr.

Having established that a species can grow in solutions that are below its own R^* and below the R^* of competitively superior species, our next objective was to explore whether there could be a case where equilibrium soil solution concentrations determined for two species grown with diffusion limitation would not predict competitive outcomes. We first established the R^* of a species growing at 5% soil moisture. At 5% soil moisture, a species with an I_{\max} of $100 \times 10^{-12} \text{ mmol mm}^{-2} \text{ s}^{-1}$ had an R^* of $46.2 \pm 1.1 \mu\text{M}$, 4.2 times higher than that at 20% volumetric soil moisture. Using the previously established relationship between I_{\max} and R^* at 20% soil moisture, we found that a species with an I_{\max} of $16.5 \times 10^{-12} \text{ mmol mm}^{-2} \text{ s}^{-1}$ growing at 20% soil moisture has an R^* equivalent to the R^* of the base species growing at 5% soil moisture.

We then ran simulations that competed the species with the I_{\max} of $100 \times 10^{-12} \text{ mmol mm}^{-2} \text{ s}^{-1}$ with the one that had an I_{\max} of $16.5 \times 10^{-12} \text{ mmol mm}^{-2} \text{ s}^{-1}$. Each species started

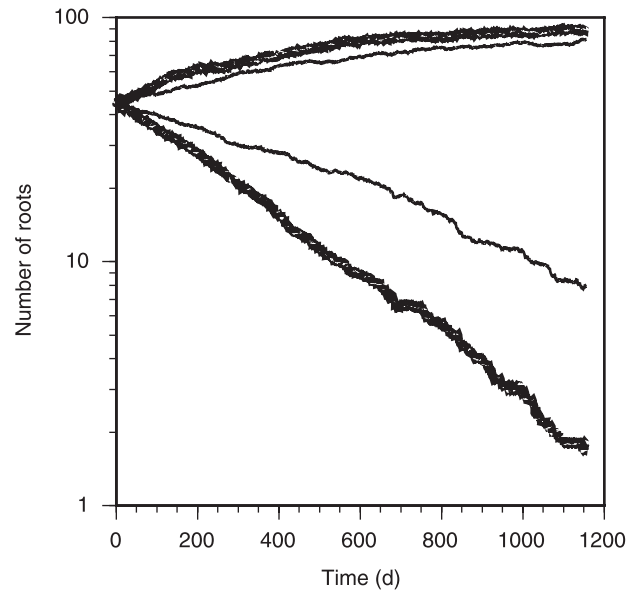


Fig. 3 Temporal trends in the number of roots per 100×100 voxel grid for base species (top two lines) and species with a lower maximum inflow rate (I_{\max}) of 16.5×10^{-12} (bottom two lines) when competing at soil moistures of 5% (thin lines) and 20% (thick lines). The base species growing at 5% soil moisture has the same R^* (see text) for nitrate as the lower I_{\max} species when growing in 20% soil moisture. Curves represent the average of 10 replicate simulations.

with 45 roots in the soil grid – half the equilibrium number of roots for a species growing at the standard conditions. Ten simulations were run for the equivalent of 3 yr at each of two volumetric soil moistures (5% and 20%). At both soil moistures, the high I_{\max} species outcompetes the low I_{\max} species when grown together. When these two species competed for 3 yr at 5% and 20% soil moisture, the low I_{\max} species was reduced to 17.4% and 3.8% of its initial biomass, respectively (Fig. 3).

Having established that the inclusion of diffusion causes the concentration reduction theory to incorrectly predict competitive outcomes, we examined the pattern of nutrients that surround roots that differ in their I_{\max} when diffusion limitation is present. We ran three simulations of two roots competing under the previously used conditions. For a 20×10 voxel grid, one root of each species was present and they were separated by 2 mm. In the first simulation, both roots had the same parameters. In the second and third simulation, the I_{\max} of one root was reduced by 30% and 70%, to 70×10^{-12} and 30×10^{-12} , respectively. Simulations were run for 1 yr. We determined the final soil solution concentrations in each voxel of the soil grid, as well as the position of the zero net transfer boundary. The zero net transfer boundary is the edge between depletion zones of roots where nitrate is equally likely to diffuse to either root. We calculated the position of the zero net transfer boundary by fitting a second-order equation to the nutrient concentrations distribution between roots and solving the equation's first derivative for the local maximum.

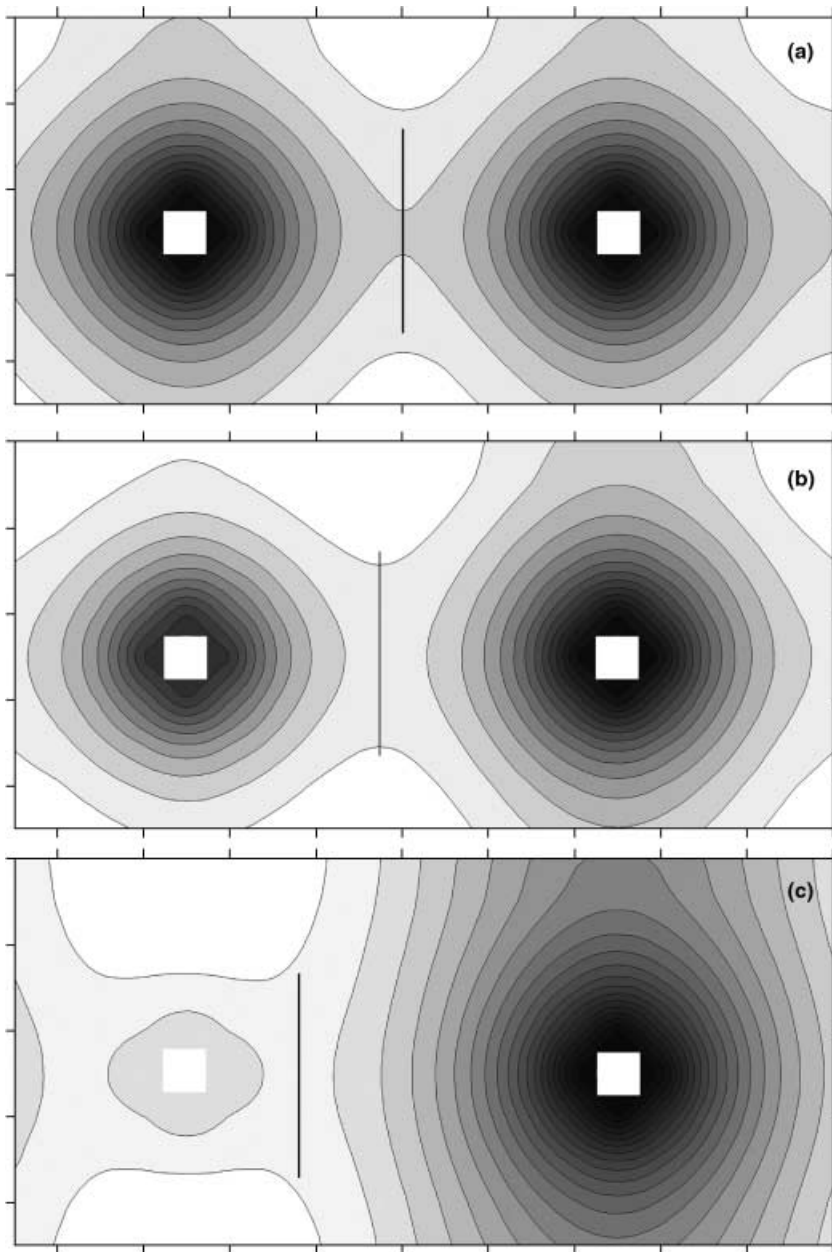


Fig. 4 Nutrient concentration gradients between the roots of two plants with a maximum inflow rate (I_{\max}) of 100×10^{-12} $\text{mmol mm}^{-2} \text{s}^{-1}$ (a) and between a root with an I_{\max} of 100×10^{-12} and 70×10^{-12} (b) or 30×10^{-12} $\text{mmol mm}^{-2} \text{s}^{-1}$ (c). The vertical line denotes the location of the zero net transfer boundary between the two roots.

Whereas the zero net transfer boundary was equidistant between the two roots when the roots had the same I_{\max} (Fig. 4a), reducing the I_{\max} of one species by 30%, brought the zero net transfer boundary 7% closer to the low I_{\max} root (Fig. 4b). Reducing the I_{\max} by 70% brought it 39% closer to the low I_{\max} root (Fig. 4c). In these cases, it appears that species that have higher I_{\max} outcompete species with lower I_{\max} because nutrients are more likely to diffuse to the roots of high I_{\max} species than low I_{\max} species. The competitively superior species pre-empt the nutrient supply from the competitively inferior species and it is the reduced supply that likely causes its biomass to decline.

Discussion

The concentration reduction theory assumes that terrestrial plants gain competitive dominance by reducing the concentration of the limiting nutrient in soil solution to levels below which are necessary to sustain populations of competitors. If this was true, then the biomass of species should decline at the average soil solution nutrient concentration of a superior competitor's R^* , and should not have a positive growth rate at their own R^* . However, when soil solutions are well-mixed, species can grow at concentrations that are below their R^* soil solution nutrient concentrations and therefore below that of

some superior competitors. Thus, it is not the average soil solution concentrations *per se* that cause species to decline when competing for nutrients. Assuming that the average soil solution nutrient concentrations determine competitive outcomes when nutrients are limiting might lead to incorrect predictions of competitive outcomes in situations where soil moisture differs between species. Soil moisture affects not just the relationships between soil solution nutrient content and concentration, but also the diffusion of nutrients in soil via impedance. Although it is possible to standardize the average soil solution concentrations across soil moistures to a standard soil moisture, the differences in the rate of diffusion need to be accounted for when predicting competitive superiority.

The pre-emption of the nutrient supply from competitively inferior species can be seen in the diagrams of the concentration gradients around competing roots (Fig. 4). Here, the position of the zero net transfer boundary between two roots measures the relative ability of each root to 'pre-empt' the uptake of nitrate by its competitor, through increasing the area of its own depletion zone at the expense of the competing root's depletion zone. The competitively superior species captures nitrate from a larger volume of soil by shifting the zero net transfer boundary towards the roots of competitively inferior species. This occurred because the competitively superior species with the greater I_{\max} created steeper concentration gradients around the roots. This shifts the zero net transfer boundary away from the competitively superior species, securing it a greater fraction of the total nitrate supply. It was this ability to capture a larger fraction of the total available resource, not the ability to reduce soil solution concentrations, that conferred competitive ability in our simulations.

Although not formalized, the concept of supply pre-emption was clearly illustrated by Theissen maps that illustrated the zero net transfer boundaries among roots in a soil volume (Barley, 1970; Comerford *et al.*, 1994). To examine the sensitivity of uptake among competing roots to changes in soil and root properties, Smethurst & Comerford (1993) used analytical solutions to models of solute movement and uptake. With their model, they tested the sensitivity of nutrient uptake by two competing root systems where mass flow and diffusion of nutrients were explicit. Species with higher rates of nutrient uptake or root production effectively captured a larger fraction of the nutrient supply, reducing the supply to the competing root system. Pre-empting nutrient supply can be thought of as leading to 'space occupation', as described by Raynaud and Leadley (2004). As such, it should not be assumed that plants that have higher I_{\max} necessarily will be better competitors for N. For example, as shown by Smethurst & Comerford (1993), plants that produce and maintain more root length per unit nutrient acquired pre-empt a greater fraction of the nutrient supply from competitors. More research will be necessary to understand the relative importance of root length, the positioning of roots relative to supply, and uptake kinetics in determining partitioning of nutrient supplies.

In the equations used to represent the concentration reduction theory and that the R^* hypothesis is derived from (Tilman, 1982), there are no explicit concentration gradients around roots. The original formulations of the concentration reduction theory assume that solutions are well-mixed and it could be argued that it violates the assumptions of the model to include concentration gradients. If so, then it is clear that the theory's assumptions are incompatible with the dynamics of nutrients in soils and the theory should not be applied to terrestrial plants. It also could be argued that the nutrient content of the soil solution should be used in place of the soil solution concentration, as it has been when the theory was tested empirically. Yet, the concentration reduction theory is derived in part from equations of nutrient uptake, which are dependent on soil solution concentrations, not soil solution content. Similarly, it could be argued that the concentration reduction theory was never meant to apply to situations where soil moisture differed among species. Although this issue addresses the utility of the R^* hypothesis, a more useful theory not only describes the dynamics when plants are at the same soil moisture, but also accommodates different soil moistures.

We conclude that concentration reduction theory does not accurately describe the mechanism of competition for limiting nutrients in soils, although there is no reason to believe that it is not appropriate when diffusion is high enough to consider the solution well-mixed (Raynaud & Leadley, 2004). Concentration reduction theory works for well-mixed systems because, under these conditions, uptake can accurately be described as a function of average resource concentrations. However, in terrestrial systems, nutrient uptake rates are determined by concentrations at the root surface, which are not equivalent to average resource concentrations. Diffusion limitation decouples average soil solution concentrations and concentrations at the root surface. Concentrations at the root surface are influenced by nutrient supply, diffusion, and distance to nearest roots, along with uptake rates. All of these factors together determine actual plant uptake, necessitating a spatially explicit approach to accurately describe the mechanisms of competition among terrestrial plants. Parameterizing SERMUN with nitrate in a sandy soil is a conservative test of concentration reduction theory as it does not include the role of adsorption–desorption dynamics that would decrease diffusion, increase concentration gradients and make the soil less well-mixed.

Compared with concentration reduction, supply pre-emption should more adequately describe the dynamics of competition for nutrients in soils. In soils, it is the supply of nutrients to roots, as influenced by diffusion, that determines uptake rather than the average concentration in a given soil volume. Consequently, it is the pre-emption of the supply that leads to competitive dominance rather than the reduction of soil solution concentrations. The role of supply pre-emption as a theory does not invalidate the utility of the metric R^* . Indeed, species that pre-empt a greater fraction of

the nutrient supply might also have lower R^* in many situations. However, the development of a more realistic supply pre-emption model should lead to novel predictions about resource competition and potentially better metrics for predicting the outcomes of plant competition.

More research is required to further develop the supply pre-emption theory and examine what additional metrics for predicting competitive outcomes it might generate. A more thorough sensitivity analysis is required to better understand the factors that allow species to pre-empt nutrient supplies. Future empirical and theoretical research regarding competition should examine other nutrients and environmental conditions, and should recognize that plants can affect nutrient supplies in various ways.

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