

Competition for nutrients and optimal root allocation

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Abstract The allocation of resources among roots and shoots represents the largest flux of resources within a plant and therefore should have been selected to maximize benefits to plants. Yet, it is unclear why some species like temperate grasses have such high root length density (RLD). Either the slow rate of diffusion of inorganic N in soils or interplant competition could explain the high RLD of temperate grasses. Using a fine-scale model of nutrient dynamics in the soil and plant growth, a cost–benefit approach was used to assess optimal allocation rates for plants that accounted for value of both carbon and nitrogen. In the absence of interplant competition, resource benefits are maximized with very little root length except in extremely dry soils for ammonium. In the presence of a competitor, optimal allocation of N to roots is much greater and increases as ability of competitors to produce root length increase. Competition for inorganic nitrogen generates a classic aspect of the tragedy of the commons, the “race for fish”, where plants must

allocate more resources to acquisition of the limiting resource than is optimal for plants in the absence of competition. As such, nutrient competition needs to be directly addressed when understanding plant- and ecosystem-level resource fluxes as well as the evolution of root systems.

Keywords Allocation · Co-limitation · Competition · Nitrogen · Roots · SERMUN

Introduction

The allocation of resources among organs represents the largest transfer of resources a plant makes. For example, 75% of the N acquired by roots can be allocated aboveground (Poorter et al. 1990) while over 60% of the C fixed annually can be allocated belowground (Law et al. 1999). With such large quantities of resources being moved, allocation patterns among organs should be subject to strong natural selection in order to optimize growth and fitness (Bloom et al. 1985).

Whether plants allocate optimally is called into question with the observation that herbaceous species of North American temperate grasslands when growing in the absence of interspecific competition can have similar biomass production rates, but differ in fine root length density (RLD)

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by two orders of magnitude. In the upper depths of the soil in temperate grasslands, fine (<1 mm) RLD for C_3 and C_4 grasses can be 20–40 cm of root length per cm^{-3} soil (Craine et al. 2003c; Jackson et al. 1997) and exceed $800 \text{ g m}^{-2} \text{ year}^{-1}$ in the first meter of soil (Craine et al. 2003b). Although the production and maintenance of large root systems demands vast quantities of resources, the high RLD is not necessary for high biomass production. Temperate grassland legumes, like the non-mycorrhizal, cool-season *Lupinus perennis* can produce over $1300 \text{ g m}^{-2} \text{ year}^{-1}$ of biomass, which is at least the same if not greater to that of grasses. Yet, the fine RLD of productive stands of *L. perennis* can be less than 0.25 cm cm^{-3} (Craine et al. 2002).

It is not obvious if grasses would benefit from allocating less resources belowground if legumes can have such high production with so little root length. Legumes are associated with N_2 -fixing bacteria that allows them to grow independent of an external inorganic N supply, but they can acquire sufficient water and nutrients besides N with a low RLD. Hence, the reliance of grasses on an external N supply is likely a distal cause of their high RLD. Yet, it is uncertain why relying on an external N supply would cause plants to be selected to have a hundred times higher RLD than species that do not rely on an external N supply. Other factors such as competition for water and rooting depth might contribute to explaining the differences in RLD among species, but examining the role of differences in reliance on an external inorganic N supply is an appropriate starting point for assessing the role of competition in optimal allocation as it has long been hypothesized that competition for inorganic N might select for high RLD (Andrews and Newman 1979; Donald 1981).

There are two alternative sets of hypotheses that can explain the high RLD in plants that rely on an external N supply. First, in the absence of competition from other plants, acquiring inorganic N from the environment requires high RLD due to a slow rate of diffusion of inorganic N. Alternatively, the high RLD of plants such as prairie grasses could be due to competition among plants for N, similar to how competition for light causes increases the allocation of

resources to stems and leaves over what is optimal in the absence of competition (Anten and Hirose 2001; Falster and Westoby 2003). Experimental evidence is consistent with the hypothesis that plants increase allocation to roots in volumes of soil where the roots of competitors are present (Gersani et al. 2001). Yet, this work on competition and allocation focused exclusively on whether the presence of competitors would lead to increased proliferation and cannot assess what the optimal RLD would be in the absence of competition. By extension, their work was unable to test whether plants in the absence of competition allocate more to roots than is optimal.

My goal here is to determine whether competition for nutrients among plants should lead to greater allocation of resources to roots than would be expected in the absence of competition or whether high root length is necessary for acquisition of N when its supply is limiting. I use a raster-based model that simulates the movement and uptake of nutrients by roots as well as root respiration, growth, and mortality (Craine et al. 2005). With this approach, I first test the sensitivity of net resource benefit of plants in the absence of interplant competition to differences in RLD defined as the length of roots per unit soil volume. The optimal RLD is defined as the RLD that generates the highest net resource balance. Second, I test the sensitivity of net resource benefit of a plant in the absence of competition to changes in relative allocation rates of N to root growth ($\text{Alloc}_{\text{N,R}}$). Once the optimal allocation rate of N to roots is established for plants in the absence of competition, I test the hypothesis that interplant competition for N leads to an increase in the optimal $\text{Alloc}_{\text{N,R}}$.

Methods

Incorporating multiple currencies into cost-benefit analyses

Assessing optimality in allocation is difficult without being able to first determine the allocation rates that optimize growth or fitness. Cost-benefit analyses should be able to be used to assess optimality of allocation rates both in the

presence and absence of interplant competition. The most developed approach to quantifying optimality in root systems was the cost–benefit analyses by Yanai et al. (1995) where a solute transport model was used to assess the resource balance of plants and in turn optimal root longevity and root diameter. Yanai et al. and subsequent papers (Bouma et al. 2001; Eissenstat and Yanai 1997; Volder et al. 2005) hypothesized that plants adjust allocation and the traits of roots in order to optimize the efficiency of uptake relative to expenditures. Although the focus on cost–benefit analyses by Yanai et al. is appropriate, the focus on efficiency could be improved. Business firms that maximize profit or plants that maximize production do not necessarily maximize the ratio of benefits to costs. Firms that maximize profit continue to invest until the marginal revenue is offset by the marginal cost (Bloom et al. 1985). By analogy, plants would continue to invest in roots or alter its traits until there is no additional net benefit in their production.

Shifting the economic analysis from efficiencies to marginal revenues faces the difficulty of calculating costs and benefits with multiple currencies, which has long been a problem in ecology and economics (Craine et al. 2003a; Patterson 1998). Economic analyses of roots need to simultaneously compare costs and benefits where benefits are generally measured in nutrients and costs are measured in energy and nutrients. Past attempts to rectify this problem have attempted to reduce the value of N to its energy content (Skogsmyr and Fagerstrom 1992). Yet, this approach discounts all the resources that are spent to produce the root system that acquires the nutrients. The cost of N to a plant is more than just the energy required for reduction. For example, plants must spend large amounts of resources on a root system to obtain N.

Solving the problem of mixed units for economic analyses of plants requires converting the value of one resource into terms of another. This requires determining the relative value of C and N. In economics, the market exchange rate between two units should reflect the relative value of the units. If the exchange rate is known, a common currency can be used to evaluate economic situations involving dual units. When ana-

lyzing the C and N economies of plants, the relative value of C and N should be indicated by the exchange rates of the two resources by whole plants or stands as long as both are limiting to production. For C and N, this would be stand-level photosynthesis and nutrient uptake (Craine et al. 2003a).

Model description

The model used for simulations in this paper is SERMUN, which is written in C++ and uses a raster-based approach to model the movement and uptake of nutrients in soil solution (Craine et al. 2005). In the model, a thin slice of soil is divided up into a grid. Although the model simulates dynamics in two dimensions, each grid cell (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. All voxels are the same size. Cells with roots contain no available nutrients. At the beginning of a simulation, a user-determined number of roots of up to two species are randomly assigned to grid cells. Roots are assumed to grow orthogonal to the plane. Soil solution nutrient concentrations are initially set to be the same for all cells in all simulations.

Roots of each species are assigned traits associated with their construction, e.g. root tissue density, nutrient concentration of root biomass, and the fraction of biomass that is C. Nutrient uptake kinetics, respiration rate parameters, and mortality rates are also assigned. At the whole-plant level, allocation of acquired N to further root growth and the marginal production of C relative to N allocation to shoot are designated. Soil and nutrient parameters include volumetric soil moisture, adsorption-desorption constants, and diffusion rate.

At the beginning of each time step, the nutrient content of each voxel is increased by a rate equivalent to the mineralization rate (Table 1). In this model, this mineralization rate, i.e. 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

Table 1 Parameter descriptions, base values used in simulations, units, and sources for the values

Parameter	Description	Value	Units	References
ρ_R	Root tissue density	2×10^{-4}	g mm^{-3}	Craine et al. (2002)
θ	Volumetric soil moisture	0.02 or 0.2	$\text{mm}^3 \text{H}_2\text{O mm}^{-3} \text{soil}$	
[C _R]	Concentration of C in root biomass	450	mg g^{-1}	Craine et al. (2002)
[N _R]	Concentration of nutrients in root biomass	10	mg g^{-1}	Craine et al. (2002)
Alloc _{N,R}	Fraction of acquired N allocated to roots	Varies	Unitless	
CCost _{Constr}	Cost of construction of C in new root relative to carbon content	1.33	$\text{mmol C mmol}^{-1} \text{C}$	Cannell and Thornley (2000)
CCost _{Maint}	Cost of maintenance of root based on root N content	2.03×10^{-5}	$\text{mmol C mmol}^{-1} \text{N s}^{-1}$	Tjoelker et al. (2005)
CCost _{MaintInt}	Intercept of relationship between N content and maintenance respiration	-7.44×10^{-8}	$\text{mmol C mmol N s}^{-1}$	Tjoelker et al. (2005)
CCost _{NUpt}	Cost of taking up N based on N acquisition rate	1	$\text{mmol C mmol}^{-1} \text{N}$	Scheurwater et al. (1998)
CCost _{Red}	Cost to reduce N to -3 state	2.01	$\text{mmol C mmol}^{-1} \text{N}$	Cannell and Thornley (2000)
C_{\min}	Concentration of nutrient in solution at root surface where uptake is zero	2×10^{-9}	$\text{mmol mm}^{-3} \text{H}_2\text{O}$	Kelly et al. (2001)
C_{Return}	Amount of C returned to roots per unit N allocated to shoots	300	$\text{mmol C mmol}^{-1} \text{N}$	
D_1	Diffusion constant for nutrient in solution	1.9×10^{-3}	$\text{mm}^2 \text{s}^{-1}$	Hunik et al. (1994)
I_{\max}	Maximum rate of uptake of nutrient per unit surface area of root	1×10^{-10}	$\text{mmol mm}^{-2} \text{s}^{-1}$	Kelly et al. (2001)
K_d	Partition coefficient of NH_4^+ between liquid and solid phase.	3300	$\text{mm}^3 \text{H}_2\text{O g}^{-1} \text{soil}$	Venterea and Rolston (2000)
K_m	Solution nutrient concentration at which uptake is half of maximum rate.	1.00×10^{-6}	$\text{mmol mm}^{-3} \text{H}_2\text{O}$	Kelly et al. (2001)
Mort _R	Probability of a given root dying each second	4.39×10^{-8}	s^{-1}	Craine et al. (2002)
N_{sup}	Rate of mineralization	1.13×10^{-13}	$\text{mmol mm}^{-3} \text{soil s}^{-1}$	
p_d	Thickness of voxel in model.	0.01	mm	
p_w	Width of voxel in model	0.2	mm	
Value _{CN}	Relative value of C and N	300	$\text{mmol C mmol}^{-1} \text{N}$	Craine et al. (2003a)

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.

Nutrient movement is controlled with two main functions. The first function controls diffusion among voxels. For a given voxel, diffusion is calculated between a cell and 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 equation 1, the amount of nutrient that moves between two cells is calculated according to Fick's first law (Van Rees et al. 1990):

$$F_d = D_1 \times \theta \times f \times \frac{\Delta C}{\Delta x} \times p_w \times p_d \quad (1)$$

In the diffusion equation, D_1 is the diffusion constant for a nutrient in liquid, 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, and Δx is the distance between the centers of the voxels and equal to p_w . f is the impedance and currently is set to be equal to the volumetric soil moisture. For Fick's first law, as soil moisture declines, so does diffusion. Diffusion is also proportional to the concentration gradient between adjacent cells. Mass flow of water is currently not included in the model.

The second equation controls the partitioning of nutrients between solid and liquid phases. Adsorption and desorption are determined by the Freundlich equation, which assumes a constant ratio between the content of nutrient in solid and liquid phases. At each time step, after diffusion, nutrients are partitioned between solid and liquid phases using the formula:

$$N_{\text{solid}} = N_{\text{total}} \times \frac{K_d}{1 + K_d} \quad (2)$$

where N_{solid} is the total amount of nutrient in the solid phase and N_{total} is the total amount of nutrient in both solid and liquid phases, and K_d is ratio of nutrients in solid and liquid phases. Thus, for example, when nutrients are depleted from the solution phase, a new equilibrium is established as adsorbed nutrients enter solution. Likewise, when nutrients are mineralized and enter into solution, some will become adsorbed depending on K_d and the amount in the solid phase.

In the model, there is no mass flow of water and therefore no supply of nutrients via this mechanism. Uptake (U) only occurs actively, is scaled to root surface area, and is controlled by the Michaelis–Menten equation:

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

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

voxels that do not have roots and share a full side with the root (maximum of four) 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. 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. In order to avoid edge effects, dynamics on opposite sides of the grid associated with uptake and diffusion are linked as if the cells were adjacent.

At the end of each time step, a fraction of the total amount of nutrient acquired during that time step is allocated to storage for root growth. The remainder of the nutrient is allocated to shoots. For each unit of nutrient allocated to shoots, a constant amount of C is allocated to roots for root processes (see below). As detailed below, this C is first used for maintenance and uptake respiratory processes and then the remainder is available for root growth.

C is used by the root system for respiration and construction of new roots. Respiration costs include maintenance, growth, uptake, and the reduction of N. Maintenance respiration rate increases linearly with the N content of a root. Growth respiration occurs when a new root is produced and scales with the C content of the root. Uptake respiration scales with the amount of N taken up. The reduction of N is the cost of reducing N to its final -3 state and is only assessed when examining the dynamics of nitrate.

The production of new roots is dependent on the stores of N and C in the root system, which captures the basic resource control over root growth (Scheible et al. 1997) by the minimum number of roots that can be produced based on the C and N stores. The amount of C required to produce a root is the carbon content of the root, the C required for growth respiration, and the C required to reduce the N in roots. 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 the nutrient concentration of roots, root tissue density, and the volume of the voxel. When the cumulative store of nutrients exceeds this value, a new root of the species can be produced provided there is sufficient C stored for production. There is no limit to the amount of C or N that can be stored. When a root is produced, the stores of N are reduced by the nutrient content of the new root. New roots are located randomly in the soil volume. The nutrients that were present in the voxel are divided up among the adjacent non-root containing cells.

At each time step, the probability of mortality for the root 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 nutrient supply rate, the N content of a root, the allocation rate of acquired N to root growth, and the mortality rate.

Parameters

We parameterized the model to simulate the dynamics of nitrate or ammonium in a sandy soil (Table 1). The grid size was set to 100×100 voxels with each voxel $0.2 \times 0.2 \times 0.01$ mm for a total volume of 4 mm^3 . For sandy soil, we set $f = \theta$ (Tinker and Nye 2000). Nutrient supply was set to the equivalent of 5 g N m^{-2} to a 10 cm depth. When simulating nitrate, K_d was set to 0 so that there was no adsorption into the solid phase, but adsorption did occur for ammonium ($K_d = 3,300 \text{ mm}^3 \text{ H}_2\text{O g}^{-1} \text{ soil}$) (Venterea and Rolston 2000). Root 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 year. As described below $\text{Alloc}_{N,R}$ varied from 0.01 to 0.9. Measurements of nitrate uptake kinetics of grasses are rare and we based our values on measurements of *Acer rubrum* (Kelly et al. 2000; Kelly and Kelly 2001). I_{\max} , K_m , and C_{\min} were set to $1 \times 10^{-10} \text{ mmol mm}^{-2} \text{ s}^{-1}$, $1 \times 10^{-6} \text{ mmol mm}^{-3}$, and $2 \times 10^{-9} \text{ mmol mm}^{-3}$, respectively. Relation-

ships between root parameters and respiration rates were based on published relationships (Table 1).

C and N economics

Evaluating the economics of a process requires separately quantifying costs and benefits. Here, we quantify the costs and benefits of the initial root system, the root system during the simulation, and the root system at the end of the simulation (Fig. 1). The C costs of the root system include the initial costs and the running costs. The initial C costs include the C in the root structure, equivalent to the C content of the roots, and the growth respiration associated with production of the roots. For C, the running costs include the C cost of construction of additional roots, maintenance respiration, respiration associated with uptake, and any costs of reducing N for use in constructing new roots. The N costs of the system include the initial N costs of the root system at the beginning of the simulation and the running costs. For N, running costs include only the N associated with the production of new roots. When roots die, the C and N contained in the structure is not considered a cost as these resources were already charged at the time of production.

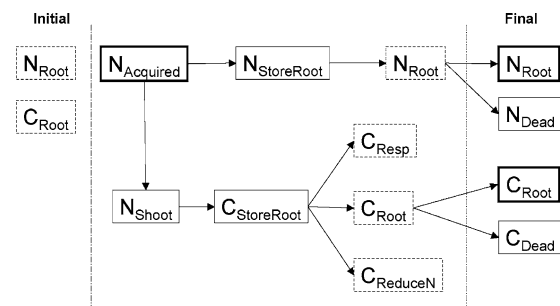


Fig. 1 Pathways for C and N used in calculating cost-benefit analyses. Pools that are considered benefits over a given period of integration are denoted by boxes with thick lines. Benefits include the N acquired over the period of integration and the C and N required to produce the roots at the end of the simulation. Pools that are considered costs are denoted by boxes with dotted lines. Costs include the C and N required to produce roots both at the beginning of and during the simulation as well as the C respired by the root system during the simulation. Boxes with thin solid lines are neither costs nor benefits

The main benefit of the root system is the N that is acquired. Although the model assumes that resources contained in roots cannot be reallocated, roots present at the end of the simulation are also considered benefits since there would be costs incurred to replace them. The C benefit of a root is equal to its cost of production (construction + growth respiration). The N benefit of the root is equal to its N content and the amount of energy needed (if any) to reduce the N to a -3 state. As the function of roots does not decrease with time and mortality is probabilistic and as such are not “scheduled” for removal, the value of a root is not depreciated with time. Neither the C that is fixed via photosynthesis nor stored for further root growth is considered a benefit at the end of the simulation as the N acquired that was used to acquire the C will be counted at full value with respects to C (see below).

Once the total C and N costs and benefits are calculated for a simulation, the net C and N benefits need to be combined into a common currency. Using a scalar, all N costs and benefits are converted in C units. Relying on the relationships between simulated stand-level C and N budgets (Craine et al. 2003a), we use a standard Value_{CN} of 300, where 1 mmol of N is equivalent to 300 mmol of C. This is the simulated Value_{CN} that was calculated at $4.3 \text{ g N m}^{-2} \text{ year}^{-1}$.

Runs

The sensitivity of uptake and net resource balance to RLD is examined first. The dynamics of individual plants in the absence of competitors were simulated for 1 year. The initial number of roots was varied from 1 to 90 roots per 100×100 grid, which is the equivalent of 0.25–22.5 cm root length cm^{-3} soil. To hold the number of roots constant over time, the probability of mortality was set to zero and root production was eliminated by setting the fractional allocation of N to root growth at zero. Separate simulations were run for nitrate and ammonium at 20 and 2% soil moisture. For these simulations, the fraction of the total N supply that was acquired over 1 year was calculated. Also calculated were the net resource costs, which were just maintenance and uptake respiration since there was no root pro-

duction or mortality. Net benefits were the difference between the benefits of the N acquired (converted to units of C) and respiratory costs.

To examine the sensitivity of growth and resource balance to variation in allocation rates in the absence of competition, 5 replicates of 18 levels of allocation were simulated for 1 year. Fractional allocation of N to roots varied from 0.01 to 0.9. Separate simulations were run for nitrate and ammonium. For each simulation, the initial number of roots set to 5 per grid (1.25 cm cm^{-3}). In these simulations, root systems were allowed to vary in size with production dependent on C and N stores and mortality probabilistic. C and N costs included initial, running, and final costs as root system size varied (Fig. 1). Net benefits were the differences between the gross benefits and costs. Here, we examine the consequences of varying soil moisture, Value_{CN} , and the length of the integration period.

Parallel to the sensitivity analysis of $\text{Alloc}_{\text{N,R}}$ in the absence of competition, the sensitivity of growth and resource balance to variation in $\text{Alloc}_{\text{N,R}}$ (18 levels) was also determined in the presence of a competitor. Due to the similarity of results for nitrate and ammonium in the absence of competition, only the dynamics associated with a nitrate supply are examined here. Three sets of runs were conducted where the second plant had an $\text{Alloc}_{\text{N,R}}$ of 0.1, 0.25, or 0.4. Each plant started with RLD equal to 6.25 cm cm^{-3} . For the target species, fractional allocation of N to roots varied from 0.01 to 0.9. Dynamics were simulated for the equivalent of 1 year with five replicates at each level.

Results

The first set of simulations examined the resource economics of plants with a constant number of roots over time in the absence of interplant competition. With volumetric soil moisture set to 20% and plants supplied nitrate exclusively, the plant with a RLD of 0.75 cm cm^{-3} had the highest net benefit (Fig. 2c). The plant acquired 98.05% of the total nitrate supplied (Fig. 2a) but had low running costs for its root system compared to

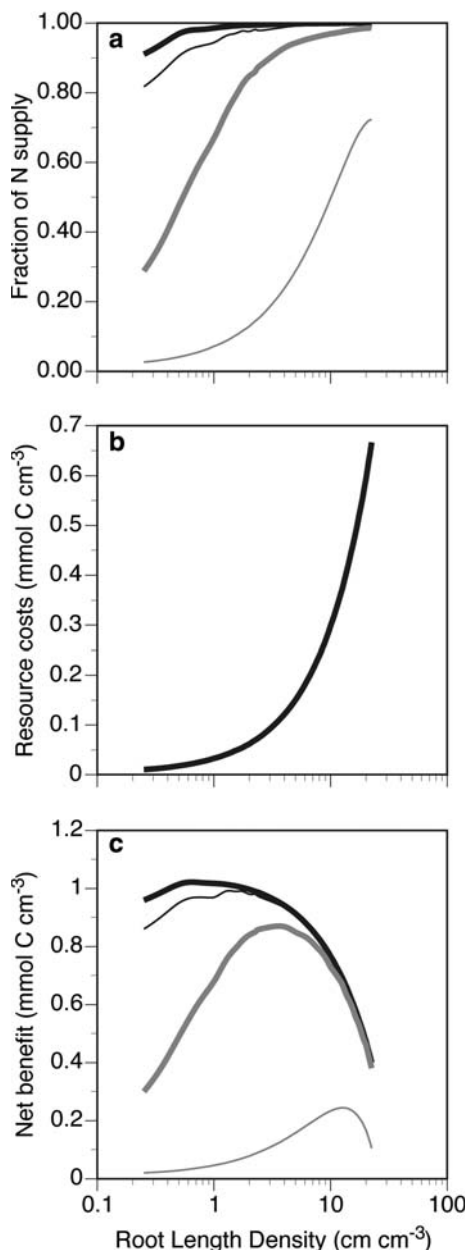


Fig. 2 Sensitivity to root length density over 1 year in the absence of competition of (a) the fraction of the N supply acquired by a plant, (b) respiratory costs (maintenance and uptake respiration), and (c) net resource benefit (value of N acquired—C costs of root system). For net benefit, N acquired is scaled by the relative value of N in terms of C ($300 \text{ mmol C mmol}^{-1} \text{ N}$). Simulations were run at 20% soil moisture (thick line) and 2% soil moisture (thin line) for a 10-fold difference in effective diffusion rates. Plants were supplied either nitrate (black lines) or ammonium (gray lines). Respiratory costs for the four cases are almost identical and differences cannot be discerned visually here

plants with higher RLD (Fig. 2b). The marginal return of increasing RLD beyond 0.75 cm cm^{-3} was lower than the marginal cost of supporting the larger root system leading to a declining net benefit (Fig. 2c). For ammonium, the plant with a RLD of 3.75 cm cm^{-3} had the highest net benefit, acquiring 92.21% of the total ammonium supply.

Decreasing diffusion by a factor of 10 by lowering soil moisture to 2% increased the optimal root density of a plant supplied nitrate to just 1.5 cm cm^{-3} and 13.75 cm cm^{-3} for plants supplied ammonium (Fig. 2c). With lower rates of diffusion, plants acquired a smaller fraction of the N supply due to increased diffusion limitation, but acquisition rates did not decrease much when RLD was high (Fig. 2a). The optimum number of roots increased with increasing Value_{CN} as the marginal return of the additional N acquired was weighted greater than the relative costs (largely C) of maintaining a larger root system. For example, at 20% soil moisture, if the Value_{CN} was 500, the optimum RLD for a plant supplied nitrate was 1 cm cm^{-3} , but only 0.5 cm cm^{-3} if the Value_{CN} was 100 (data not shown). Decreasing the integration period from 1 to 0.5 year had little effect on the optimum number of roots (data not shown).

The patterns of resource economics associated with variation in $\text{Alloc}_{\text{N,R}}$ paralleled those seen for plants that varied in the number of roots maintained. In the absence of competition, plants with 1% allocation rate and supplied nitrate had a RLD of 0.5 cm cm^{-3} after 1 year. The highest RLD after 1 year was for the plant with an $\text{Alloc}_{\text{N,R}}$ of 60% (20.75 cm cm^{-3} ; Fig. 3a). RLD declined with $\text{Alloc}_{\text{N,R}}$ greater than 60% as N accumulated in storage and root growth became C limited instead of N limited (data not shown). C storage was greatest at the lowest allocation rates and very little C was stored at an $\text{Alloc}_{\text{N,R}}$ of 60%, the point at which N allocation and C allocation were more or less in balance (data not shown). Although allocation rates differed by almost two orders of magnitude and final RLD by 40-fold, over the course of a year almost all of the N is acquired independent of allocation rates (Fig. 3b). A plant with a 60% allocation rate had the highest N recovery rate (99.94%), but a plant

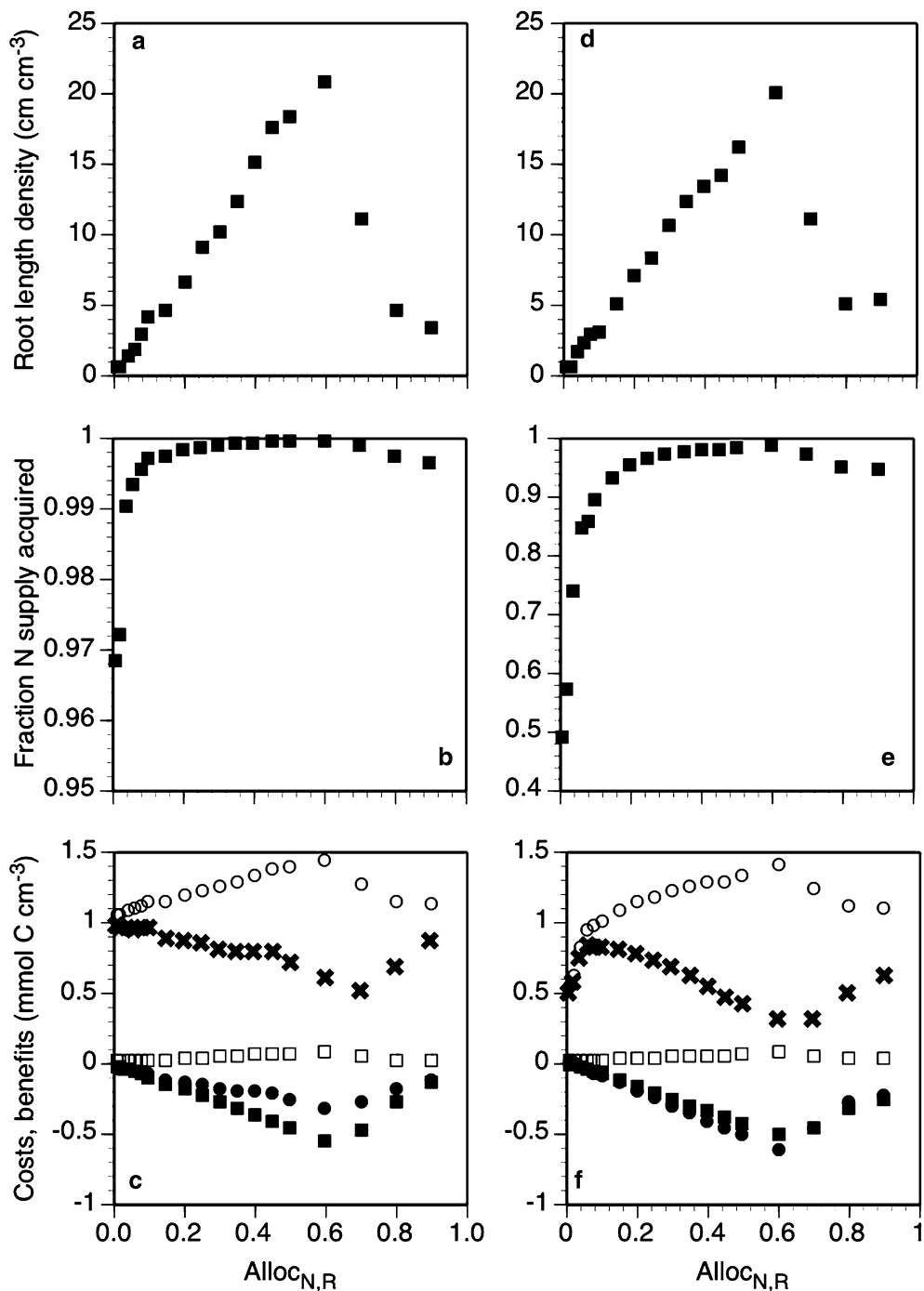


Fig. 3 Sensitivity of components of economics of root systems to differences in fractional allocation of N to roots in the absence of competition when supplied nitrate. Simulations were run for 1 year. Responses include root length density (**a, d**) fraction of the cumulative N supply acquired after 1 year (**b, e**), and cumulative C and N costs

and benefits (**c, f**). For **a–c**, plants were supplied nitrate and **d–f**, ammonium. For **c** and **f**, open circles are net N benefits, open squares are net C benefits, closed circles are net N costs, and closed squares are net C costs. The “x” indicates the net resource benefit accounting for net C and N benefits and costs

with 1% allocation rate still acquired 96.85% of the N supply with the rest left in soil solution.

The slightly lower acquisition rate of the plant with an $\text{Alloc}_{\text{N,R}}$ of 1% was offset with much lower root system costs. Total gross C costs for the root system of the plant with 1% allocation rate was 18 times lower than the plant with 60% allocation rate (Fig. 3c), while the total gross N costs were 8 times lower (Fig. 3c). As a result of the lower costs and similar cumulative N acquisition, the greatest net resource balance was the plant with the lowest allocation rates (Fig. 3c). The N acquired that represented the greater benefit for the plants with lower allocation rates was used to support the respiratory and turnover costs of the larger root system, leading to a reduced net benefit for the plant with a 60% allocation rate. The plant that allocated 70% of its N to roots had the lowest net benefit as a result of lower N uptake and similar costs compared to the plant with a 60% allocation rate. Increases in allocation beyond 70% were associated with smaller root systems that accumulated N in storage, which represents a net gain since the N is not converted into C to be spent on support for the root system.

For plants that varied in allocation rates in the absence of competition but supplied ammonium, results were much the same as with nitrate (Fig. 3d–f). The major differences were that plants with $\text{Alloc}_{\text{N,R}}$ less than 10% acquired a much lower fraction of the ammonium supply than the same plants supplied nitrate. For example, the plant with a 1% allocation rate of N to roots only acquired 49% (Fig. 3e) of the N supply as opposed to almost twice that for nitrate. As such, plants with very low allocation rates of N to roots were more N-limited as evidenced by the lower relative C storage of these plants (data not shown). When supplied ammonium, optimal $\text{Alloc}_{\text{N,R}}$ was still only 6%.

When supplied nitrate and competing against a plant with an $\text{Alloc}_{\text{N,R}}$ of 10%, the plant with a 1% allocation rate had declined to 28% of its original biomass (Fig. 4a). In general, the fraction of the N acquired at a given point in time was determined by the fraction of the total root length possessed by a plant. For example, at the end of the 1 year simulation, the fraction of the N

acquired over the last 1 day by each of the two species was proportional to its fraction of root length in the soil volume (Fig. 5). As the fraction of total root length and fractional uptake for a plant are proportional, even though the plant with 1% allocation had started with 50% of the root length, the decrease in the relative amount of root length over time caused the plant to acquire only 29% of the cumulative N supply after 1 year (Fig. 4b). Competition lowered the net benefit for a plant with 1% allocation rate of N to roots drastically in comparison to the same plant in the absence of competition. At the end of 1 year, the plant with a 60% allocation rate had the highest RLD (Fig. 4a), 17.45 cm cm^{-3} , and had acquired the second highest fraction of the N supply (86.90%, Fig. 4b). Beyond an allocation rate of 60%, net benefits increased, but this was due to the restriction of root biomass by C limitation as opposed to N limitation (data not shown).

Although in the absence of competition the plant with the greatest net resource benefit was the one with a 1% allocation rate of N to roots, when competing against a plant with a 10% allocation rate, the greatest net benefit was for the plant with a 25% allocation rate (Fig. 4c). The greatest root biomass and the greatest fraction of the N supply was for a plant with an $\text{Alloc}_{\text{N,R}}$ of 60% (Fig. 4a), but above the optimal allocation rate of 25%, the marginal benefit associated with increased N acquisition was lower than the marginal costs of supporting the larger root system. This led to a decline in net resource benefit (Fig. 4c). For example, the net benefit to the plant with 25% allocation rate of N to roots was $0.62 \text{ mmol C cm}^{-3}$, but 8% less for the plant with an allocation rate of N to roots of 45%. The allocation rate that maximized net resource benefit for the target species (25%) did not lead to the greatest net benefit for the two plants combined (Fig. 4c). As with a single plant in the absence of competition, net resource benefit for the two plants was optimized at low allocation rates.

As $\text{Alloc}_{\text{N,R}}$ of the competitor increased, the optimal $\text{Alloc}_{\text{N,R}}$ of the target species increased. Against a competitor that allocated 25% of acquired N to roots, the plant that allocated 40% of its N to roots had the greatest net benefit

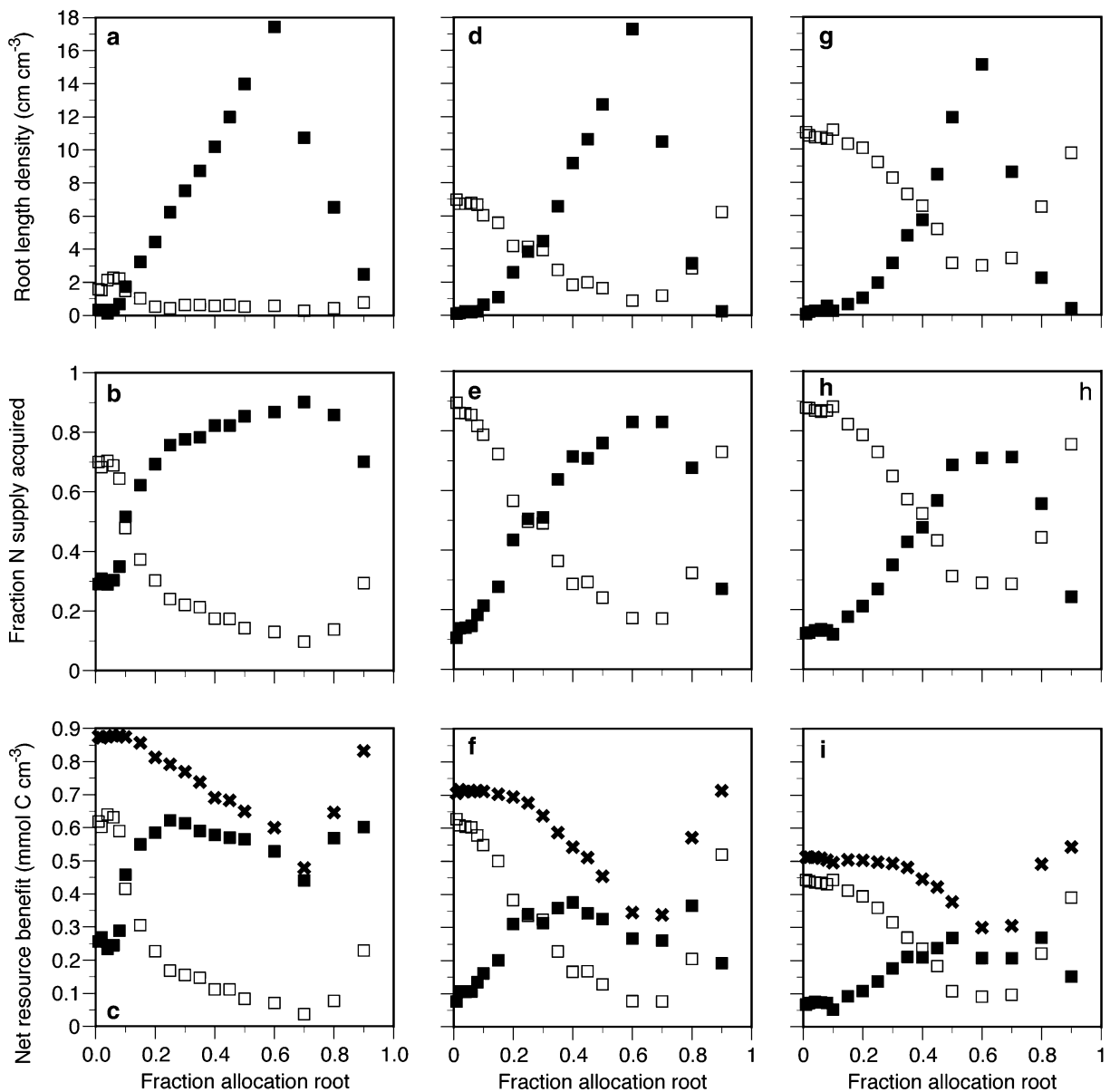


Fig. 4 Sensitivity of root system characteristics to differences in fractional allocation of N to roots in the presence of a competitor. Responses include root length density (**a**, **d**, **g**), fraction of the cumulative N supply acquired by species for which $\text{Alloc}_{N,R}$ varies (closed square) and its

competitor (open square) (**b**, **e**, **h**), and net resource benefit where “x” indicates the sum of the resource benefits (**c**, **f**, **i**). The $\text{Alloc}_{N,R}$ of the competitor was constant over time and set to 0.1 (**a–c**), 0.25 (**d–f**), or 0.4 (**g–i**)

(Fig. 4f). Increasing the competitor’s allocation rate to 40% increased the optimal allocation rate to 50%.

Optimal allocation rates decreased with increasing time of competition (Fig. 6). For the scenario where plants began with a RLD of 1.25 cm cm^{-3} and the competitor had an alloca-

tion rate of 10%, the optimal allocation rate was initially 60% and declined to 25% by 1 year. Similar patterns occurred when the competitor had higher allocation rates as optimal allocation rates early in the simulation were 60%, and declined with time. Also with increasing allocation rates of N to roots for competitors, the initial

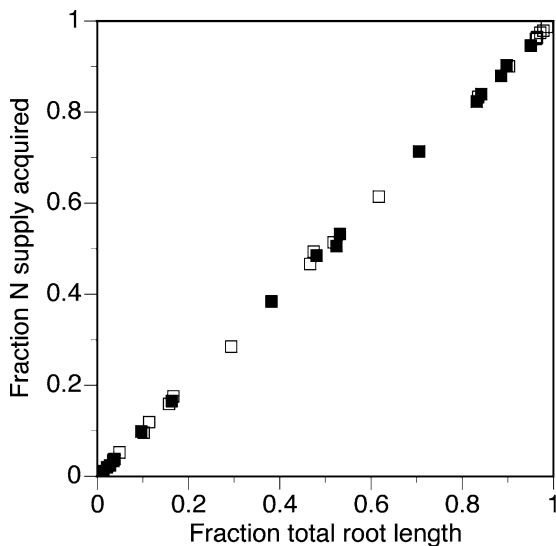


Fig. 5 Fraction of root length possessed by competing species at the end of 1 year of competition and the fraction of the N supply during the last 1 day that it had acquired. Plants either had a fractional allocation of N to roots of 0.1 (closed squares) or varied from 0.01 to 0.9 (open squares). The differences in allocation rates generated the variation in the fraction of the total root length at the end of 1 year

rate of decline of the optimal allocation rate was faster although optimal allocation rate at 1 year was higher.

Discussion

In the absence of competitors, the optimal resource balance for a plant supplied nitrate was obtained with a very low allocation rate of N to roots. The lack of adsorption of nitrate increases its effective diffusion rate and little root length was required to acquire most of the nitrate supply. When supplied nitrate, decreasing soil moisture or increasing the relative value of N increased the optimal allocation rate of N to roots, but only slightly on an absolute scale. For plants supplied ammonium, more root length was necessary to achieve optimal resource balance, but not much more so than nitrate when soil moisture was intermediate. Soil moisture would have to be extremely low for optimal RLD to begin to approach those of grasses in the field.

Whether the slow diffusion of ammonium in extremely dry soils in the absence of interplant

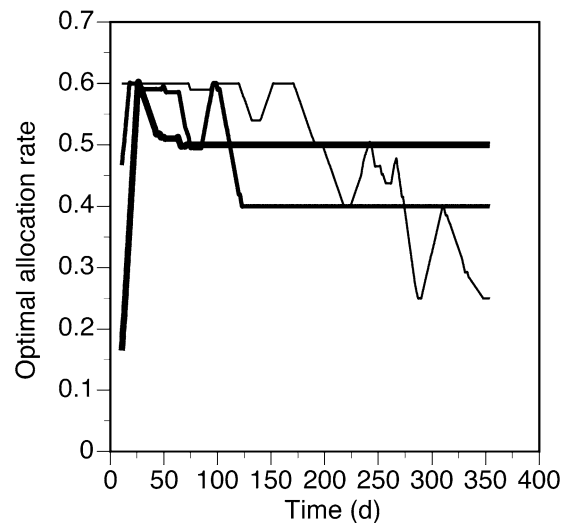


Fig. 6 Allocation rate that generated the greatest net resource benefit over 1 days for plants in competition against a plant that had an allocation rate of N to roots of 0.1, 0.25, or 0.4 (thin, medium, and thick lines respectively). Optimal allocation rates were calculated each day for 1 year and lines represent 20-days moving average

competition can explain observed high root length densities of species such as the grasses of North American humid grasslands would require that plants are selected to acquire ammonium at very low soil moisture. Although for example, plants in cold ecosystems where nitrification is inhibited by low soil temperatures can rely more heavily on ammonium than nitrate (Kielland 1994), net nitrification rates are often high in the North American humid grasslands and as such nitrate is often considered the dominant form of N supplied to plants in these ecosystems (Wedin and Tilman 1990). That said, although the affinities of different plant species for ammonium and nitrate differ among habitats and are considered to represent the relative supplies of the two forms of N (Aerts and Chapin 2000; Atkin et al. 1996), the relative contribution of ammonium and nitrate to actual uptake is poorly known. In part this is due to uncertainty on whether net mineralization adequately represents the N supply to plants or whether plants compete against microbes for gross N mineralization (Leadley et al. 1997; Schimel and Bennett 2004). If plants do compete with microbes for N that is part of gross, but not net, mineralization, the importance of ammonium might be higher than generally

thought and high RLD may have been selected for to increase the competitive ability of plants relative to microbes. In nature, nutrients are also supplied to roots via mass flow, but mass flow is relatively unimportant for highly mobile nutrients like nitrate when availability is low (Chapin 1991). If mass flow were important, it would likely be when soils are driest and moreso for NH_4^+ than NO_3^- .

Independent of whether these hypotheses could explain some of the higher root length found in grasses as compared to legumes, the presence of roots of another plant consistently increased the optimal allocation rates of N to roots. In the presence of a competitor, allocating more N to root growth allowed a plant to have a higher fraction of the total root length. This decreased the fraction of the N supply that was acquired by the competitor and consequently increased the target plant's net resource balance. This benefit to the individual of increased allocation comes at the expense of the other plant, as well as to the net benefit of the two plants together. With individuals prospering at the expense of the group, competition for nutrients follows the "race for fish" with over-capitalization in roots representing a tragedy of the commons. This is consistent with the predictions of ESS models (Gersani et al. 2001) that predict that as the number of competitors increases, optimal root biomass for an individual will increase. It should be noted that Gersani et al. state that from ESS theory, optimal allocation shifts from determining marginal benefits of additional units of root to average benefits of the entire root system. More insights into the role of competition are likely as the mechanistic models of nutrient dynamics such as SERMUN are combined with ESS approaches.

With respect to the range of allocation rates possible, plants must balance the short-term acquisition of nitrogen in the face of competition with the long-term costs of maintaining a large root system after competition has diminished. When assessed over relatively short time scales, regardless of the allocation rate of the competitor, the target plant always maximized net resource benefit with an allocation rate that

maximized root growth. Optimal $\text{Alloc}_{\text{N,R}}$ decreased with increasing time of integration. If the allocation rates remain high, plants more quickly acquire a larger fraction of the N supply and drive down root length of competitor, but long-term are left with an excess of root length to maintain. The long-term optimal allocation rate of N to roots increased with increasing allocation rate of competitors. As the ability to generate root length of competitors increases, so does the minimum allocation rate needed to preempt the majority of the N supply and maximize net resource benefit. By extension, plants should also allocate more to roots when competing against plants with greater longevity or thinner roots, as it is the ability to generate root length of competitors that influences the allocation rate of the target plant since uptake for a plant is proportional to its fraction of the total root length.

The best solution to optimizing allocation in the face of uncertain competitive pressure would be to alter allocation rates in proportion to the RLD of competitors. In this case, allocation to root growth would depend on the relative abundance of roots of competitors in a given volume of soil. This is the dynamic suggested by Gersani et al (2001) where plants that have their root systems split among two volumes of soil proliferate roots preferentially in volumes of soil that contain the roots of competitors.

Even if plants can adjust their allocation to the presence of competitors per se, the evolutionary stable strategy for plants that consistently experience intense competition for nutrients is to maximize root length with high allocation to roots. In an assemblage of species of different allocation rates, all other things equal, the species with the allocation rate that maximized root length would displace the others. Hence, even though it would be optimal to have long-term allocation rates only slightly above those of competitors, high $\text{Alloc}_{\text{N,R}}$ would become fixed quickly when competition for nutrients was the primary factor that determined the relative abundance of species. Other factors such as a lower Value_{CN} that would accompany greater light limitation and disturbances would decrease the relative importance of competition

for nutrients and would lead to a lower optimal allocation rate of N to roots.

With this in mind, the paradox of the differences in RLD of grasses and legumes can be explained easily. When growing in habitats where water and nutrients besides N are not limiting to growth, legumes can have high productivity with a low RLD. As opposed to legumes that can fix N₂, grasses must compete with other plants for nitrogen. Therefore, one would expect grasses to allocate resources to roots at a rate that maximized standing root length. Grasses also have roots that are of greater longevity and lower diameter than legumes, which would increase standing root length (Craine et al. 2002). Regardless of what the allocation rate of N to roots in grasses was, the high standing root length observed in grasses suggests that in the absence of competition, net resource benefit would be increased by decreasing the allocation rate until RLD was closer to the optima that were estimated here.

Resource competition is an important factor to accommodate when evaluating ecosystem resource fluxes as well as the evolution of plant species. Considering the collective work on allocation to leaf, stem, and root for competing plants, in general, competition causes individuals to allocate a greater fraction of resources to the acquisition of the most limiting resource compared to plants in the absence of competition. None of the findings observed here refutes the Equal Limitation hypothesis of Bloom et al. (1985). The race-for-fish aspect of the tragedy of the commons for plants competing for nutrients described here only states that the economic choices made by individuals in the absence of competition would differ from the choices made by individuals in the presence of competition. What maximizes net resource benefit for an individual plant in the presence of competition, does not lead to maximization of net resource benefit of the stand. Hence, one may not be able to easily extrapolate resource dynamics of individuals to the stand-level.

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References

- Aerts R, Chapin FS III (2000) The mineral nutrition of wild plants revisited: re-evaluation of processes and patterns. *Adv Ecol Res* 30:1–67
- Andrews R, Newman EI (1979) Root density and competition for nutrients. *Oecologia Plantar* 5:319–334
- Anten NPR, Hirose T (2001) Limitations on photosynthesis of competing individuals in stands and the consequences for canopy structure. *Oecologia* 129:186–196
- Atkin OK, Botman B, Lambers H (1996) The causes of inherently slow growth in alpine plants: an analysis based on the underlying carbon economies of alpine and lowland *Poa* species. *Funct Ecol* 10:698–707
- Bloom AJ, Chapin FS III, Mooney HA (1985) Resource limitation in plants – an economic analogy. *Annu Rev Ecol Syst* 16:363–392
- Bouma TJ, Yanai RD, Elkin AD, Hartmond U, Flores-Alva DE, Eissenstat DM (2001) Estimating age-dependent costs and benefits of roots with contrasting life span: comparing apples and oranges. *New Phytol* 150:685–695
- Cannell MGR, Thornley JHM (2000) Modelling the components of plant respiration: some guiding principles. *Ann Bot* 85:45–54
- Chapin FS III (1991) Effects of multiple environmental stresses on nutrient availability and use. In: Mooney HA, Winner WE, Pell EJ (eds) *Response of plants to multiple stresses*. Academic Press, San Diego, pp 67–88
- Craine J, Bond W, Lee W, Reich P, Ollinger S (2003a) The resource economics of chemical and structural defenses across nitrogen supply gradients. *Oecologia* 144:547–556
- Craine JM, Fargione J, Sugita S (2005) Supply pre-emption, not concentration reduction, is the mechanism of competition for nutrients. *New Phytol* 166:933–940
- Craine JM, Tilman DG, Wedin DA, Reich PB, Tjoelker MJ, Knops JMH (2002) Functional traits, productivity and effects on nitrogen cycling of 33 grassland species. *Funct Ecol* 16:563–574
- Craine JM, Wedin DA, Chapin FS III, Reich PB (2003b) Development of grassland root systems and their effects on ecosystem properties. *Plant Soil* 250:39–47
- Craine JM, Wedin DA, Chapin FS III, Reich PB (2003c) Relationship between the structure of root systems and resource use for 11 North American grassland plants. *Plant Ecol* 165:85–100
- Donald CM (1981) Competitive plants, communal plants, and yield in wheat crops. In: Evans LT, Peacock WJ (eds) *Wheat science – today and tomorrow*. Cambridge University Press, pp 223–247
- Eissenstat D, Yanai R (1997) The ecology of root lifespan. *Adv Ecol Res* 27:2–60

- Falster DS, Westoby M (2003) Plant height and evolutionary games. *Trends Ecol Evol* 18:337–343
- Gersani M, Brown JS, O'Brien EE, Maina GM, Abramsky Z (2001) Tragedy of the commons as a result of root competition. *J Ecol* 89:660–669
- Hunik J, Bos C, van den Hoogen M, De Gooijer C, Tramper J (1994) Co-immobilized *Nitrosomonas europaea* and *Nitrobacter agilis* cells: validation of a dynamic model for simultaneous substrate conversion and growth in k-carrageenan gel beads. *Biotechnol Bioeng* 43:1153–1163
- Jackson RB, Mooney HA, Schulze ED (1997) A global budget for fine root biomass, surface area, and nutrient contents. *Proc Natl Acad Sci USA* 94:7362–7366
- Kelly JM, Graves WR, Aiello A (2000) Nitrate uptake kinetics for rooted cuttings of *Acer rubrum* L. *Plant Soil* 221:221–230
- Kelly JM, Kelly JK (2001) Phosphorus and potassium uptake kinetics in red maple seedlings. *For Sci* 47:397–402
- Kelly JM, Scarbrough JD, Mays PA (2001) Hardwood seedling root and nutrient parameters for a model of nutrient uptake. *J Environ Qual* 30:427–439
- Kielland K (1994) Amino acid absorption by arctic plants: implications for plant nutrition and nitrogen cycling. *Ecology* 75:2373–2383
- Law BE, Ryan MG, Anthoni PM (1999) Seasonal and annual respiration of a ponderosa pine ecosystem. *Glob Change Biol* 5:169–182
- Leadley PW, Reynolds JF, Chapin FS III (1997) A model of nitrogen uptake by *Eriophorum vaginatum* roots in the field: ecological implications. *Ecol Monogr* 67:1–22
- Patterson M (1998) Commensuration and theories of value in ecological economics. *Ecol Econ* 25:105–125
- Poorter H, Remkes C, Lambers H (1990) Carbon and nitrogen economy of 24 wild species differing in relative growth rate. *Plant Physiol* 94:621–627
- Scheible WR, Lauerer M, Schulze ED, Caboche M, Stitt M (1997) Accumulation of nitrate in the shoot acts as a signal to regulate shoot–root allocation in tobacco. *Plant J* 11:671–691
- Scheurwater I, Cornelissen C, Dictus F, Welschen R, Lambers H (1998) Why do fast- and slow-growing grass species differ so little in their rate of root respiration, considering the large differences in rate of growth and ion uptake? *Plant Cell Environ* 21:995–1005
- Schimel JP, Bennett J (2004) Nitrogen mineralization: challenges of a changing paradigm. *Ecology* 85:591–602
- Skogsmyr I, Fagerstrom T (1992) The cost of anti-herbivory defence: an evaluation of some ecological and physiological factors. *Oikos* 64:451–457
- Tinker PB, Nye PH (2000) Solute movement in the rhizosphere. Oxford University Press, Oxford, 444 p
- Tjoelker MG, Craine JM, Wedin D, Reich PB, Tilman D (2005) Linking leaf and root trait syndromes among 39 grassland and savannah species. *New Phytol* 167:493–508
- Van Rees KCJ, Comerford NB, Rao PSC (1990) Defining soil buffer power: implications for ion diffusion and nutrient uptake modeling. *Soil Sci Soc Am J* 54:1505–1507
- Venterea RT, Rolston DE (2000) Mechanistic modeling of nitrite accumulation and nitrogen oxide gas emissions during nitrification. *J Environ Qual* 29:1741–1751
- Volder A, Smart DR, Bloom AJ, Eissenstat DM (2005) Rapid decline in nitrate uptake and respiration with age in fine lateral roots of grape: implications for root efficiency and competitive effectiveness. *New Phytol* 165:493–501
- Wedin DA, Tilman D (1990) Species effects on nitrogen cycling: a test with perennial grasses. *Oecologia* 84:433–441
- Yanai RD, Fahey TJ, Miller SL (1995) Efficiency of nutrient acquisition by fine roots and mycorrhizae. In: Smith WK, Hickley TM (eds) *Resource physiology of conifers*. Academic Press, San Diego, pp 75–103