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REGULAR ARTICLE

Modelling facilitation or competition within a root system: importance of the overlap of root depletion and accumulation zones

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Abstract
Aims The concept of intra-plant, inter-root competition considers the overlap of nutrient depletion zones around roots, but neglects the spatial pattern of root exudates that can increase nutrient availability. We tested the hypothesis that interactions between nutrient accumulation zones due to exudation by different roots can lead to intra-plant inter-root facilitation.
Methods We used the PARIS model (Raynaud et al. 2008) to simulate phosphorus uptake by a population of roots that are able to increase phosphorus availability by exuding citrate. We carried out several simulations with the same parameters but with increasing root density in order to study out if changes in root densities would alter nutrient uptake per unit root.
Results Emerging relationships between root uptake efficiency and root length density indicated cases of inter-root competition or facilitation. The sizes of the accumulation and depletion zones were calculated to explain these results. Our simulations showed a continuum between cases of inter-root competition and facilitation. Facilitation occurred at low exudation rates, when phosphorus supply was not saturated within the phosphorus depletion zone surrounding roots. Low exudation systems led to a lower phosphorus uptake per unit root length, but minimized phosphorus losses in the process.
Conclusions Based on our model, we derived conditions that allowed predicting whether competition, facilitation or no interaction, is the dominant interaction between roots within a root system, based on the different distances to which an isolated root alters P concentration and supply.

Keywords Diffusion · Exudation · Modelling · Phosphorus · Rhizosphere · Spatial distribution

Introduction

Living roots contribute to plant mineral nutrition by two complementary processes: nutrient absorption and exudation. On the one hand, plants are able to adjust the location, surface and uptake rates of their roots to the local concentration in available nutrients (Hodge 2004). On the other hand, they are able to locally increase the availability of mineral nutrients by releasing various products (protons, carbohydrates, secondary metabolites) in the soil surrounding their roots (Dakora and Phillips 2002). For example, experiments and models

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have shown that local modifications of soil pH due to the release of organic acids by roots can alter the availability of phosphorus (Hinsinger 2001) and significantly increase plant P uptake at the level of individual plants (Kirk et al. 1999b) or plant community (Li et al. 2007). Root exudates can also boost microbial activities, leading to increased mineralization which can, in turn, increase nutrient availability locally (Dijkstra and Cheng 2007; Shahzad et al. 2015).

By taking up nutrients at their surface, roots create diffusion gradients leading to the formation of depletion zones around them (Tinker and Nye 2000). In the same way, exudates accumulate around roots to form accumulation zones. Nearby roots therefore compete with each other when their respective depletion zones overlap (Ge et al. 2000). Similarly, if exudates increase nutrient availability in the soil surrounding roots, nearby roots could also increase their respective nutrient uptake when exudate accumulation zones overlap. These zones of influence (i.e. depletion and accumulation zones around roots), from which competitive or facilitative interactions can arise, are therefore of fundamental importance for plant nutrition and soil functioning (York et al. 2016). Yet, the consequences of these zones of influence are still poorly understood due to their size which is restricted to short distances around roots (i.e. a few millimetres). In order to tackle these limits, several modelling approaches have been developed to explore how root activity can lead to the creation of these root zones of influence, and alter nutrient availability and plant nutrient uptake in the case of (1) single roots (Kirk et al. 1999a; Ptashnyk et al. 2011; Zygalakis and Roose 2012), (2) root systems of single plants (Rubio et al. 2001; Schnepf et al. 2012; Dunbabin et al. 2013) or (3) root systems of different plants in a community (Raynaud et al. 2008). All these studies found that the distance between roots, which results from root system characteristics (size, architecture, root density), could lead to the overlap of these accumulation and/or depletion zones. This could thus alter nutrient availability and plant nutrient uptake in a complex manner: intra-plant, inter-root facilitation adds to intra- and inter-plant competition as a constraint shaping root system architecture and root foraging strategies (Rubio et al. 2001). In this case, net facilitation between roots would occur when the synergistic effect of having a root neighbour is higher than its competitive effect, so that increasing root density increases the absorption of nutrient per unit of root length. Facilitation as a belowground interaction is a quite common concept (Lin et al. 2012). However, to our knowledge, it has never been used at the scale of roots within a single root-system and existing modelling studies have not yet studied how the simultaneous development of accumulation and depletion zones alters rhizosphere nutrient availability and nutrient uptake.

Models of solutes movements around roots indicate that the overlap of depletion or accumulation zones depends on factors controlling diffusion fluxes in soils such as soil physico-chemical characteristics, soil water content (Williams and Yanai 1996; Raynaud 2010), as well as the architecture of the root system (e.g. root density). Overlap increases with root density (Rubio et al. 2001; Schnepf et al. 2012) and the consequences of this overlap on plant nutrition depends on the process considered: overlap of nutrient depletion zones should decrease root uptake efficiency (i.e. the amount of nutrient taken up per unit root) whereas overlap of accumulation zones could increase root uptake efficiency if exudates increase nutrient availability. The distance between roots and the respective size of root accumulation and depletion zones should thus determine whether intra-plant, inter-root competition or intra-plant, inter-root facilitation occurs. This latter possibility has so far hardly been mentioned.

Using a simulation model, our objective was to test the above rationale, i.e. to determine whether inter-root facilitation is possible and if so, under which conditions. To do so, we considered the case of a small volume of soil explored by the roots of a single plant individual that takes up a mineral nutrient and can increase its availability through the exudation of solutes. In order to carry out realistic simulations, we have chosen to model the uptake of phosphorus (P) and the changes in its availability through the release of citrate (C) by roots (Hodge 2004; Fig. 1). The case of citrate is well documented and relatively simple to model as a direct effect of C concentration on soil physico-chemical properties (Hinsinger 2001). For example, in some soils, phosphorus can be found in the form of phosphate rocks (e.g. apatite) that can release soluble phosphate when in presence of plant-released citrate, due to lower pH conditions in the plant rhizosphere (Li et al. 2007). In the modelled soil volume, interactions between roots were assessed by calculating the relationships between plant P uptake and root length density, as well as P uptake efficiency (P uptake per unit of root length). As root length density increases, the mean distance between individual roots decreases, which should lead to more

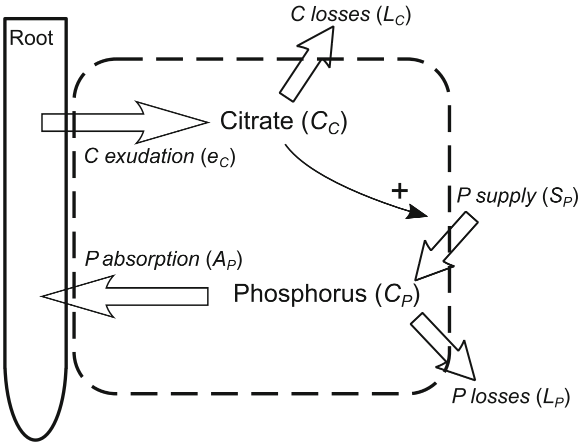

Fig. 1 Schematic representation of the modelled system. Two concentrations of solutes within the soil solution are quantified by C_P (phosphorus) and C_C (citrate) variables. Large white arrows represent fluxes for these soil solutes: the supply of phosphorus to the soil solution *(S_P)*, its losses *(L_P)* or absorption by roots *(A_P)*, citrate exudation from roots *(e_C)* and its losses *(L_C)*. The small arrow represents the modulation of phosphorus supply by citrate concentration C_C (see Eq. 6). All these processes are spatially explicitly quantified within a 2D grid (see Fig. 4)

overlap of the different accumulation and depletion zones. In this context, we distinguished inter-root competition from facilitation by negative and positive relationships between root length density and P uptake efficiency.

We expected the outcome of our model to depend on all factors that can affect the sizes of root accumulation and depletion zones, i.e. on any factor that affects the inputs, diffusion and losses of the solutes involved. Here, we mostly focused on C exudation rate. Our hypotheses were that: (i) both inter-root competition and facilitation can arise in our model system, (ii) the occurrence of each type of interaction can be explained by patterns of overlap of accumulation and depletion zones and especially (iii) inter-root facilitation should emerge from overlap of accumulation zones with no, or reduced, overlap of P depletion zones. A last hypothesis arising from (iii) is that (iv) inter-root facilitation should occur for intermediate values of root length density.

Material and methods

Model description

We modelled the case of a plant taking up P, and exuding C (Fig. 1), using a modified version (see below) of the PARIS model (Raynaud and Leadley 2004; Raynaud et al. 2008) which is an extension of the Barber-Cushman model (Barber and Cushman 1981) to a set of roots exploring a horizontal layer of soil. The model simulates different rhizosphere processes, including solutes (P and C) diffusion and losses, P absorption at the root surface, C exudation by roots, and the production of available P from a chemical reaction between C and soil (Kirk et al. 1999a; Kirk et al. 1999b). Model variables and parameters are summarized in Tables 1 and 2 and details of the model equations are given below.

All the modelled processes occur in a 1 cm thick (parameter z) layer of soil, having a surface of 2 × 2 cm. In contrast to the original PARIS model (Raynaud and Leadley 2004; Raynaud et al. 2008) that considered a hexagonal grid, the soil layer is organized as a 100 × 100 squared grid of voxels that can be either soil or root. Tests comparing squared and hexagonal geometries as well as the comparison between the diffusion fluxes calculated with these geometries and those obtained from the analytical solution around a single root indicate that, at steady state, results are very robust to the geometry of the grid. Voxel width ($h = 0.2$ mm) is equal to the diameter of roots and the modelled soil layer is 1 voxel high so that voxels have dimensions $h \times h \times z$. Solute fluxes through soil are thus only horizontal. Roots are assumed to grow vertically down into the soil, and no root branching occurs within the simulated soil volume. As we consider roots having the same geometry as voxels, one root has an exchange surface ($h \times z$) with the four orthogonal nearest voxel neighbours. We define d_R as the root length density within the soil volume (cm cm^{-3}). To eliminate boundary conditions problems and avoid edge effects, we consider the surface modelled as a torus in which top and bottom, as well as left and right edges are connected (periodic boundary condition; Haefner 2005).

Soil water content (parameter θ, cm^3 cm^{-3}) is constant and homogeneous over the modelled soil volume. The diffusion of solutes (phosphorus and citrate) only occurs within the soil liquid phase and is thus a function of θ. For a given solute i, the diffusion flux between two adjacent soil voxels v and w is:

$$F_{(i)v,w} = -D_{e,i}\frac{\Delta C_i}{h} \quad (1)$$

where $D_{e,i}$ (cm^2 s^{-1}) is the effective diffusion coefficient of solutes in the soil and ΔC_i (mmol cm^{-3}) is the

Table 1 Model variables: symbols, definitions and units

	Symbol	*Definition*	*Units*
Phosphorus	C_P	P concentration in soil solution	$\mathrm{mmol_P\ cm^{-3}}$
	S_P	P supply	$\mathrm{mmol_P\ s^{-1}}$
	L_P	Nutrient losses	$\mathrm{mmol_P\ s^{-1}}$
	A_P	Total plant absorption rate	$\mathrm{mmol_P\ s^{-1}}$
	UE_P	Plant uptake efficiency	$\mathrm{mmol_P\ cm^{-1}\ s^{-1}}$
	ε	Nutrient uptake efficiency	mol P/ mol C
Exudate	C_C	Citrate concentration in soil solution	$\mathrm{mmol_C\ cm^{-3}}$
	L_C	Exudate losses	$\mathrm{mmol_C\ s^{-1}}$
Root zone of influence	$r^1{}_C$	Extent of citrate accumulation zone around a single root	mm
	$r^1{}_{S05}$, $r^1{}_{S95}$	Extent of increased P supply zones around a single root	mm
	$r^1{}_P$	Extent of P depletion zone around a single root	mm
Territories	t_C	Extent of citrate accumulation when roots are in interaction	mm
	t_{S95}, t_{S05}	Extent of increased P supply when roots are in interaction	mm
	t_P	Extent of P depletion zone when roots are in interaction	mm

concentration difference between voxels v and w (O'Reilly and Beck 2006). $D_{e,i}$ is calculated from θ, the solute diffusion coefficient in pure water (D_i, $\mathrm{cm^2\ s^{-1}}$), an impedance factor related to the tortuous pathways of water films in the soil (also known as tortuosity factor, f_l; Olesen et al. 2001) and the soil buffer power for the solute considered (b_i; van Rees et al. 1990; Raynaud et al. 2008):

$$D_{e,i} = D_i \theta f_l \Big/ b_i \tag{2}$$

Table 2 Model parameter values used in simulations

Symbol	*Values*	*Ref.*
θ	$0.15\ \mathrm{cm^3\ cm^{-3}}$	7
θ_{th}	$0.1\ \mathrm{cm^3\ cm^{-3}}$	5
ρ	$1.16\ \mathrm{g\ cm^3}$	7
$D_{l,P}$	$8.2\ 10^{-6}\ \mathrm{cm^2\ s^{-1}}$	8
$k_{d,P}$	$82.6\ \mathrm{cm^3\ g^{-1}}$	5
μ_P	$10^{-3} – 10^{-7}\ \mathrm{mmol_P\ s^{-1}}$	
$D_{l,C}$	$6.2\ 10^{-6}\ \mathrm{cm^2\ s^{-1}}$	8
$K_{d,C}$	$4.4\ \mathrm{cm^3\ g^{-1}}$	1, 5
μ_C	$10^{-5}\ \mathrm{mmol_C\ s^{-1}}$	2, 3
K_S	$10^{-5}\ \mathrm{mmol_C\ cm^{-3}}$	7
S_{min}	$10^{-12} – 10^{-11}\ \mathrm{mmol_P\ cm^{-3}\ s^{-1}}$	7
S_{max}	$5\ 10^{-10}\ \mathrm{mmol_P\ cm^{-3}\ s^{-1}}$	7
n_R	1–600 unitless	
I_{max}	$2\ 10^{-8}\ \mathrm{mmol_P\ cm^{-2}\ s^{-1}}$	7
K_U	$10^{-4}\ \mathrm{mmol_P\ cm^{-3}}$	7
e_C	$10^{-10} – 10^{-8}\ \mathrm{mmol_C\ cm^{-2}\ s^{-1}}$	1,2,3,4

1: Jones and Darrah (1994), 2: Kirk et al. (1999a), 3: Kirk et al. (1999b), 4: Nielsen et al. (1994), 5: Oburger et al. (2011), 6: Olesen et al. (2001), 7: Raynaud et al. (2008), 8: Vanysek (2000)

Soil buffer power (b_i; which is related to adsorption/desorption of solute on the soil solid-phase; unitless) depends on soil density (ρ), θ and solute distribution coefficient $k_{d,i}$ following:

$$b_i = \theta + \rho k_{d,i} \tag{3}$$

and soil impedance factor f_l depends on soil water content and a threshold value below which diffusion ceases due to discontinuous pathways (Olesen et al. 2001):

$$f_l = 1.1(\theta - \theta_{\mathrm{th}}) \tag{4}$$

where θ_{th} represents the soil water content threshold below which diffusion ceases due to discontinuous diffusion pathways.

Each voxel loses P (L_P, $\mathrm{mmol_P\ s^{-1}}$) and C (L_C, $\mathrm{mmol_C\ s^{-1}}$) at rates μ_P ($\mathrm{s^{-1}}$), μ_C ($\mathrm{s^{-1}}$) that express the disappearance of these solutes due to consumption by other organisms.

All roots are assumed to be identical, except for their position in the soil volume. Roots take up P from adjacent soil voxels at a rate per unit root surface that follows a Michaëlis-Menten equation, with maximum uptake rate I_{max} (mmol$_P$ cm^{-2} s^{-1}) and half saturation constant for uptake K_U (mmol$_P$ cm^{-3}), where $C_{P,v}$ is P concentration in the adjacent soil voxel v (mmol$_P$ cm^{-3}):

$$U_P = I_{max} \frac{C_{P,v}}{C_{P,v} + K_U}. \tag{5}$$

Plant P uptake rate, A_P, is calculated as the sum of uptake rates of all roots present in the soil: $A_P = n_R\ U_P$ where n_R is the number of roots in the modelled soil volume.

Roots release C in adjacent voxels at constant rate e_c (mmol$_C$ cm^{-2} s^{-1}) per unit root surface.

To simulate P solubilization, available P is released into each soil voxel at the rate S_P (mmol$_P$ cm^{-3} s^{-1}) depending on C concentration in the soil voxel. When C is not present in a soil voxel, P supply rate is constant with $S_P = S_{min}$. When C is present, P supply is increased depending on C concentration ($C_{C,v}$) up to $S_P = S_{max}$ following the relationship:

$$S_P = S_{min} + (S_{max} - S_{min}) \frac{C_{C,v}}{C_{C,v} + K_S} \tag{6}$$

where S_{max} (mmol$_P$ cm^{-3} s^{-1}) is the soil maximal P supply rate, $C_{C,v}$ is the C concentration in the soil voxel v and K_S (mmol$_C$ cm^{-3}) is a half-saturation constant for P supply (Raynaud et al. 2008).

Overall, solute concentration changes across time in a soil voxel v can be summarized by the differential equations below (see Supplementary Material for the model equation in continuous form), where w corresponds to the four neighbouring soil voxels of v:

$$\begin{aligned} \frac{dC_{C,v}}{dt} &= (hz)\frac{e_C}{hhz} - \mu_C C_{C,v} + \frac{1}{h}\sum_{w=1}^{4} F_{(C)v,w} \\ \frac{dC_{P,v}}{dt} &= S_P - (hz)\frac{U_P}{hhz} - \mu_P C_{P,v} + \frac{1}{h}\sum_{w=1}^{4} F_{(P)v,w} \end{aligned} \quad \text{for voxels adjacent to roots} \tag{7}$$

$$\begin{aligned} \frac{dC_{C,v}}{dt} &= -\mu_C C_{C,v} + \frac{1}{h}\sum_{w=1}^{4} F_{(C)v,w} \\ \frac{dC_{P,v}}{dt} &= S_P - \mu_P C_{P,w} + \frac{1}{h}\sum_{w=1}^{4} F_{(P)v,w} \end{aligned} \quad \text{for all other voxels.} \tag{8}$$

Numerical analysis

Model equations were implemented in JAVA, within the 3Worlds modelling platform (Gignoux et al. 2005; Gignoux et al. 2011). Individual roots were randomly distributed within a 2-dimensional rectangular grid of cells representing the modelled layer of soil. Solutes diffusion and root-soil interactions (absorption and exudation) were programmed as reusable sub-routines plugged into the 3Worlds core application.

All parameter values used for simulations are given in Table 2. P and C parameters were taken from different literature sources (see Table 2 for details). We modelled rhizosphere processes for increasing number of roots (n_R), with values ranging from 1 to 600 roots in a 1x2x2 cm^3 soil volume (14 different values of n_R). This corresponds to root length densities d_R ranging from 0.25 cm cm^{-3} to 150 cm cm^{-3} (although unrealistic, this upper value was useful for the interpretation of our results). Because voxels can be either soil or root but not both, the increase in root density thus reduces the amount of soil modelled, and eventually the total P supply of soil. In the case where supply in all soil voxels is $S_P = S_{max}$, this reduction in P supply is at most 6% between the two extremes of the chosen range of root densities, and less than 1% for densities below 25 cm cm^{-3}. Roots were placed randomly within the 2 × 2 cm modelled surface. To avoid the risk that our results depend on a particular root spatial distribution, 5 different maps were used for each root length density value (e.g. 5 × 14 = 70 maps in total). The model outputs obtained from these different maps are shown as points in Figs. 3 and 5. As the exudation rate of C (e_C) affects the size of exudation rhizospheres (Raynaud 2010), our simulations were done for several values of this parameter (Table 2).

The kinetics and mass-transport equations were solved simultaneously. Model equations (Eqs. 7 and 8) were solved numerically using Forward Time Centered Space (FTCS) finite difference scheme (Press et al. 2007) until all fluxes of P and C reached steady-state (e.g., P supply (S_P) becomes equal to the sum of plant P uptake A_P and P losses L_P, and the rate of C liberated by all roots equals the rate of C lost from the soil). The time step for integration was 10 s. For each simulation, the influx, stocks and outflux of solutes were calculated for both P and C (Table 1). We defined P uptake efficiency UE_P as the quantity of P taken up by unit of root length:

$$UE_P = \frac{A_P}{d_R V} \tag{9}$$

where A_P represents total P absorption and V is the simulated soil volume.

Assessment of the sizes of root influence regions on soil properties

Our modelling framework produces concentration maps for available P and C (C_P, C_C), as well as maps of P supply (S_P) that can be used to measure the spatial influence of roots on soil concentrations and supply. In order to get a simpler description of the size of the region upon which roots have some influence, we have used these calculated maps to assess the sizes of root zones of influence. We considered that (i) the distance to which a root can alter soil properties depended on the process considered (i.e. different distances were calculated for C_P, C_C, and S_P) and (ii) the result of root influence on soil properties was the creation of gradients that could be used to estimate these distances.

In the case of a single root, defining a "limit" between the volume of soil influenced by the root and bulk soil has to be drawn arbitrarily from the gradient (Hinsinger et al. 2009). For citrate concentrations C_C, this limit was set to a modification by roots >5% compared to bulk soil values (C accumulation zone, Fig. 2, top left). In the case of P supply S_P, we considered two distinct limits: the first corresponding to an increase >5% of the bulk soil supply (total supply zone), similar to C_C, the second corresponding to 95% of soil maximum supply S_P ("saturated zone", Fig. 2, middle left). Considering these two limits for P supply allowed a better description of soil supply heterogeneity. Finally, the size of the P depletion zone was calculated as the distance to the maximum P concentration from each root (Fig. 2, bottom left). These different limits calculated from simulations with a single root were used to calculate the radii of the citrate accumulation zone ($r^1{}_C$), the total supply zone ($r^1{}_{S05}$), the saturated zone ($r^1{}_{S95}$) and the P depletion zone ($r^1{}_P$) for an isolated root. Considering different values for these limits (e.g. 1% instead of 5%) modified the sizes of the different zones considered but did not qualitatively changed the results.

When several roots are present, gradients around individual roots can overlap, so that all the simulated soil volume can be under the influence of one or more roots and the above limits cannot be used. Moreover, if the accumulation or depletion zones of two neighbouring roots overlap, concentrations and supply will not be monotonic along the line between these two roots (Fig. 2, right panels). We thus assumed that the "territory" of a root can be defined as the distance from that root within which the gradient of concentration or supply was monotonic (e.g. citrate concentration decreases to a minimum with increasing distance from the root). This distance no longer measures the size of the zone of influence of a single root, but rather indicates the level of overlapping and interaction between the zones of influence of single roots. Because all roots have identical parameters in a simulation, if all neighbouring root zones of influence overlap, the average radius of the territory of a root is equal to the average half distance between 2 roots for a given root density $r_{max}(d_R) = \sqrt{1/(\pi d_R)}$.

In each simulated map, because root positions were drawn randomly, some roots could be isolated from others and thus develop full concentration gradients, whereas others would interact with each other. We thus calculated the average radius of root territory as the distance from a root within which (1) the concentration (or supply flux) was above the limits defined for the isolated root rhizosphere (see above) or (2) the gradient of concentration or supply from that root was monotonic. The corresponding variables, t_C (citrate exudation), t_{S05} (P supply), t_{S95} (saturated P supply) and t_P (P depletion) thus quantify the radius of these territories. Depending on the spatial distribution of roots and the root density in the simulated maps, these distances can take any values between the zone of influence size for a single root when a root is isolated from others ($r^1{}_C$, $r^1{}_{S05}$, $r^1{}_{S95}$, $r^1{}_P$), and $r_{max}(d_R)$ when all neighbouring roots interact.

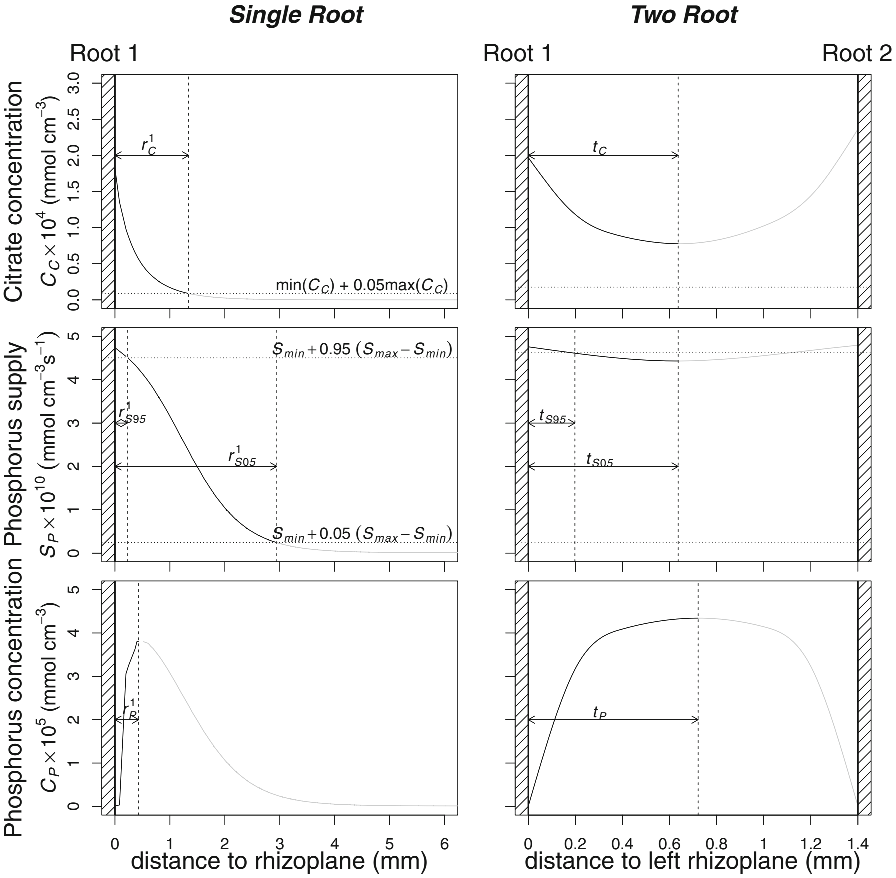

Fig. 2 Description of the gradients around a root. Hatched zones indicate the position of root rhizoplanes. **Left**: Zone of influence limits for citrate accumulation C_C (top), P supply S_P (mid) and P depletion C_P (bottom) around a root isolated from interaction with neighbours. Vertical dashed lines show the respective rhizosphere sizes ($r^1{}_C$, $r^1{}_{S05}$, $r^1{}_{S95}$, and $r^1{}_P$) and horizontal dashed lines show the threshold values used to calculate them (see text). **Right**: Territory for citrate concentration C_C (top), P supply S_P (mid) and P concentration C_P (bottom) when rhizospheres overlap. Note the difference in the x-axis scales between the left and right panels. Vertical dashed lines show the respective territory sizes (t_C, t_{S05}, t_{S95}, and t_P) and horizontal dashed lines indicate the threshold values used to calculate the rhizosphere sizes

Results

Phosphorus fluxes depend on root density and exudation rates

Soil P supply In all simulations, total P supply S_P increased with root length density d_R up to a maximum value that depended on S_{max} (Fig. 3a). The slight decrease observed for very high d_R values was due to the absence of P supply in the voxels occupied by roots, which reduced the total amount of soil voxels that can supply P (see Methods). The relationship between S_P and d_R also depended on C exudation rate e_C, with overall lower values for low C exudation rate e_C.

Plant P uptake and P losses from soil Total P uptake A_P always increased with root length density d_R and exudation rates e_C, without reaching saturation (*not shown*). On the contrary, P losses L_P displayed a unimodal shape (Fig. 3b): an increase from low to intermediate d_R as a direct consequence of higher P supply and a decrease once the maximum supply is reached while P uptake A_P carries on increasing.

P uptake efficiency Because available P can be taken up by roots or lost through microbial consumption, roots could not take all available P. With the chosen values for P loss rate μ_P, the relative proportion of absorbed P by all roots (A_P) over P supply (S_P) increased with root length density d_R from 0.015 to 0.5, and was higher for smaller e_C values (Fig. 3c). The efficiency of P uptake by single roots (UE_P, Eq. 9) varied depending on C exudation rate e_C (Fig. 3d): for high exudation rates, UE_P always decreased with root density whereas in the case of the lower exudation rate tested, UE_P first increased and then decreased.

Patterns of accumulation and depletion zone sizes determine inter-root competition or facilitation

Figure 2 gives an example of a C concentration profile around a single root and the corresponding P supply

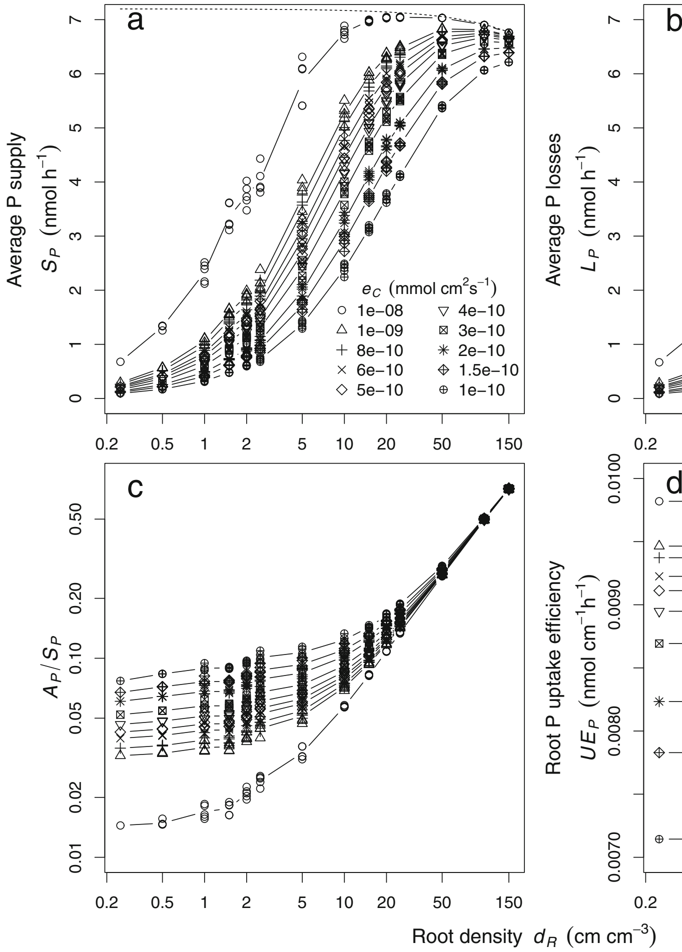

Fig. 3 Relationships between root density (d_R, log scale) and different variables quantifying phosphorus fluxes in the root-soil system: average soil phosphorus supply (S_P, panel a) and losses (L_P, panel b), the ratio of phosphorus absorbed relative to its supply (A_P/S_P, panel c, log scale) and phosphorus root uptake efficiency (UE_P, panel d). We focus here on the effect of the variation of exudation rates e_C (see legend panel a). In panel a, the dashed line at the top of the graphic corresponds to the maximum value of P supply (S_{max}) in the whole modelled soil volume. The decrease at high root density is due to the reduction in soil volume (see Methods). In all panels, points correspond to model outputs for different spatial distribution of roots with a given root density and exudation rate. Solid lines represent the means of simulations for a given root density and exudation rate

profile, as well as the calculated influence zone radii $r_C{}^1$, $r_{SP05}{}^1$ and $r_{SP95}{}^1$. Due to the non-linearity of the relationship between C concentration C_C and P supply S_P (Eq. 6), the calculated C accumulation zone radius, $r_C{}^1$, was not a good descriptor of the volume upon which roots alter P supply in the soil. We thus focused on territory sizes of P supply (t_{S05}), P supply saturation (t_{S95}) and P depletion (t_P). In order to illustrate the links between nutrient concentration and territory sizes, Fig. 4 maps the changes in P supply around roots, as well as the extent of P depletion zones in two maps differing in root length densities and for the three exudation rates tested. The chosen root length densities in these maps correspond to the two contrasted patterns observed for P root uptake efficiency in Fig. 3d: a decrease of UE_P between low and high root length density for high exudation rate whereas UE_P increased between these two values at low exudation rate.

Figure 4 shows that for a citrate exudation rate of 10^{-8} mmol cm^{-2} s^{-1}, the whole soil volume was influenced by roots for P supply, even at low d_R. At high d_R, P supply was maximized in the whole modelled soil volume. The pattern was similar for a C exudation rate of 10^{-9} mmol cm^{-2} s^{-1}, although very small regions of

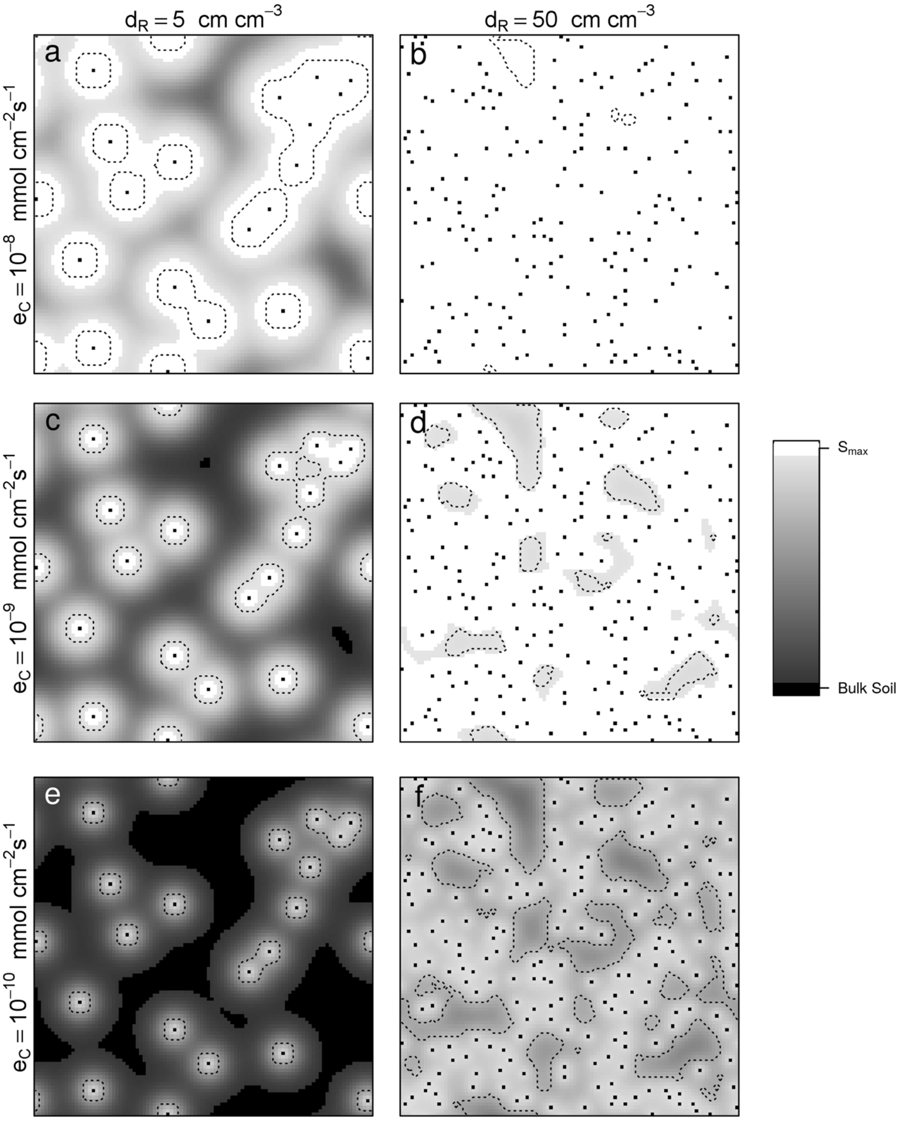

Fig. 4 Maps of rhizospheres calculated from simulations for the three exudation rates e_c tested and two root length densities d_R. Bulk soil is shown in black and the saturation territory (t_{SP95}) is shown in white. The light gray/dark gray gradient illustrates the variation in supply within the supply territory (t_{S05}). Dotted lines delimit phosphorus depletion territories *(t_P)*. Roots are figured by a black dot. See Fig. 2 for the criteria chosen to determine the border of each territory

bulk soil are still present at low d_R and P supply is not maximized over the whole soil volume. C exudation rates lower than 10^{-9} mmol cm^{-2} s^{-1} yielded a slightly different pattern, leaving large part of the soil unaffected by roots at low d_R, whereas most soil was affected by roots at high d_R but with supply values < S_{max}. In particular, at low d_R, P depletion zones around roots were relatively isolated, whereas most P concentration were under the influence of roots at high d_R values.

Figure 5 shows the average territory radius around one root as a function of d_R and e_C and suggests that this extent followed a similar pattern for all three territory types along the gradient of root length density d_R: whatever the territory considered, average territory radii was constant for low d_R values and then decreased with increasing d_R. (Fig. 5). A territory radius equal to $r_{max}(d_R)$ thus indicates that zones of influence of neighbouring roots overlap so that roots mutually influence the solute concentrations in each other's surroundings. The only exception for this general pattern was the radius of saturated P supply territory t_{S95}, which was slightly greater at intermediate d_R values compared to low d_R values in the case of intermediate and low values of C exudation (barely visible on Fig. 5, but significant). This increase occurs because close roots increase the saturation of P supply between them, thus increasing the size of their saturation rhizosphere without necessarily merging or overlapping them (see Fig. 4, mid left panel).

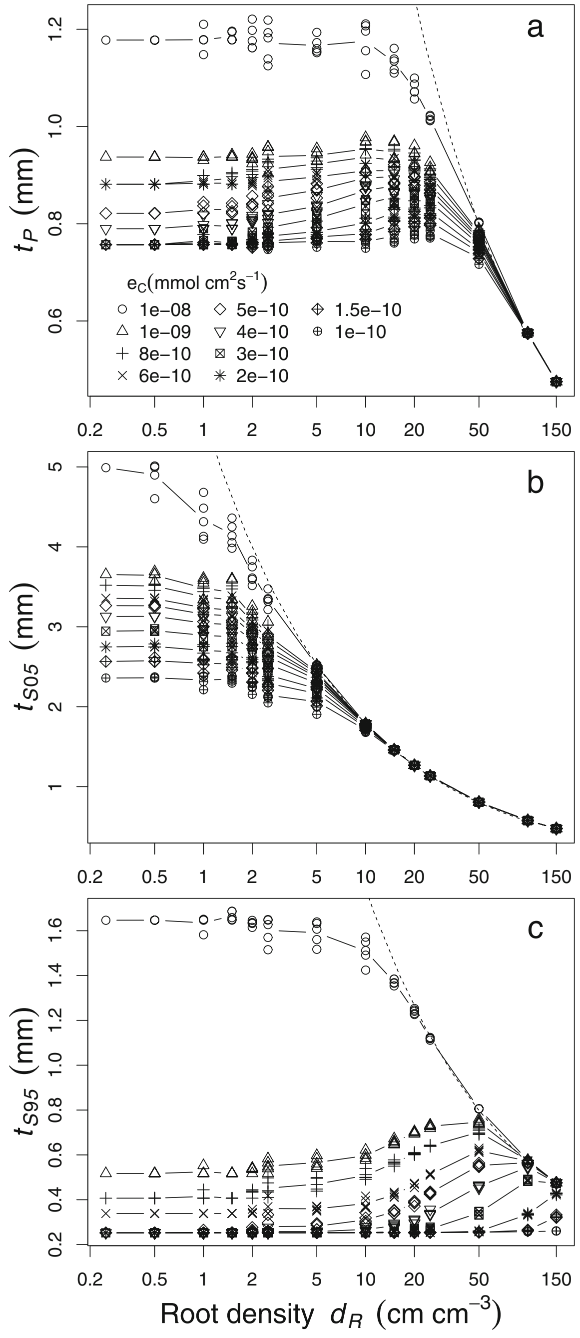

Fig. 5 Estimation of average zone of influence diameters of single roots for phosphorus depletion (**a**), phosphorus supply (**b**) and phosphorus supply saturation (**c**) as a function of root length density d_R. Cases of intra-plant, inter-root competition are presented by open circles and squares, and the case of inter-root facilitation by filled triangles. Dashed lines correspond to the maximum rhizosphere size ($r_{max} = \sqrt{(1/(d_R\pi))}$) as a function of d_R. In all panels, points correspond to the calculated diameter of zones of influence for different spatial distribution of roots with a given root density and exudation rate. Solid lines represent the means of these diameters for a given root density and exudation rate

Discussion

Most of our hypotheses were confirmed by our study: (i) facilitation between roots of the same root system can occur when the availability of a nutrient (e.g. phosphorus) depends on the exudation of a chemical factor (e.g. citrate) by roots; (ii) facilitation or competition depend on the degree of overlap between the rhizospheres of individual roots; (iv) facilitation occurs at intermediate levels of root density above which P uptake efficiency decreases, i.e. inter-root competition increases. Hypothesis (iii) was only partly confirmed: the overlap of P depletion zones around roots accounted well for the emergence of inter-root competition, but the overlap of C accumulation zones was not relevant to fully explain the emergence of inter-root facilitation.

To our knowledge, our study is the first exploring the mechanisms through which facilitation within the root system of a single plant can occur. Our results suggest that the ability of a plant to increase P availability through exudation does not prevent inter-root competition, but rather creates a continuum between cases of inter-root competition and inter-root facilitation. Studies on root foraging strategies have not, to date, considered the consequence of root exudation on nutrient supply (Ge et al. 2000; Cahill and McNickle 2011; Pagès 2011; but see Schnepf et al. 2012) and have not distinguished the respective scales of root exudation and nutrient uptake (McNickle et al. 2009). Our study suggests that exudation of solutes by neighbouring roots can dramatically alter nutrient availability near the root system so that increasing root density might not necessarily lead to a decrease in root uptake efficiency. Still, our study explored a relatively simple case and the robustness of our results and their implications for the understanding of root foraging strategies remain to be thoroughly studied both through modelling and experiments. Below, we focus on the mechanisms that lead to the emergence of inter-root facilitation and how they could be generalized. Then, we analyse the implications of the variability of inter-root interactions for root foraging strategies.

Mechanisms leading to the emergence of facilitation between roots

Above all, the possibility of facilitation between roots depends on the mechanisms by which roots are able to locally increase the availability of nutrients. Our model allows tracking the creation of spatial heterogeneity in nutrient stocks and fluxes from individual root activity. In particular, the model allows distinguishing gradients of P supply from the gradients of C concentration that created them. The model thus allows extrapolation of the concept of root zone of influence to fluxes of P whereas it is more often applied to stocks (concentrations of solutes, partial pressure of gas etc.; Hinsinger et al. 2009). Because the model assumes that P supply is a saturating function of C concentration, we distinguished two different territories for P supply: the "saturated territory" (t_{S95}), i.e. the volume of soil in which the effect of a root is maximum and in which an increase of exudate concentration has no effect, and the total P supply territory (t_{S05}) that corresponds to the whole volume in which roots increase P supply.

We first discuss how facilitation and competition can occur in the case of two neighbouring roots and then extend this discussion to a population of roots randomly distributed on a 2D plane. First, consider two identical roots separated by the distance 2*d*, with root zones of influence radii r^1_P, r^1_{S05} *and,* r^1_{S95} (see Supporting information Fig. S1 for an illustration). Because these radii are those of the zones of influence of single roots (see Material and Method section), they do not depend on the distance *d*. These two roots compete for P if their P depletion zones overlap so that they do not compete for P if:

$$r^1_P < d \quad (condition\ 1).$$

Because exudates are released from roots and diffuse into the soil, P supply can change along the distance 2*d*. Both roots mutually alter soil P supply in their vicinity if their total supply zones overlap, which occurs when:

$$r^1_{S05} > d \quad (condition\ 2).$$

However, if the two roots increase C concentrations sufficiently enough to saturate P supply up to distance *d*, P supply is constant and equal to S_{max} across the whole distance 2*d* and adding more exudate to the soil does not increase P supply (Fig. 4b). This becomes similar to a case where P supply is constant in the whole soil volume. In such case, P uptake of a root competing with others only depends on its uptake rate (Raynaud and Leadley 2004) and facilitation does not occur. A necessary condition to observe facilitation is thus that the saturated P supply zones of both roots do not overlap, which corresponds to:

$$r^1_{S95} < d \quad (condition\ 3).$$

If conditions 2 and 3 allow identifying cases in which facilitation can occur, the intensity of the facilitation depends on the degree to which total P supply zones of the two roots overlap, as the benefits of root proximity only occurs in the overlapping region. This yields two more conditions on P depletion zones and total P supply zones. First, in order for the root to benefit from the increase in supply, the P depletion zones must include parts of the region where supply is increased (i.e. where total supply zones overlap), which corresponds to:

$$r^1_P > 2d - r^1_{S05} \quad (condition\ 4).$$

Second, if the P depletion zone of a root (r^1_P) is smaller than the zone over which this root brings P supply to its maximum value (r^1_{S95}), part of the P made available by exudates is out of reach for this particular root, and changes in exudate concentration near this root do not lead to changes in P supply (Fig. 4a). Thus, the condition:

$$r^1_P > r^1_{S95} \quad (condition\ 5)$$

is necessary for facilitation to occur. However, even when condition 5 is met, if $r^1_P \approx r^1_{S95}$ an increase in root density only leads to a limited increase in supply because increase in supply only occurs in the region between r^1_{S95} and r^1_P. Thus, facilitation is important only if $r^1_P >> r^1_{S95}$ and the greater the ratio r_P^1/r^1_{S95}, the greater the facilitation.

In the case of a population of roots randomly distributed on a 2D plane, the half distance between 2 neighbouring roots is, on average, $r_{max}(d_R)$ but can be larger or smaller for some roots. Replacing *d* by $r_{max}(d_R)$ thus gives average conditions for facilitation to occur. However, because half distances between 2 neighbouring roots vary around this mean, facilitation can occur before the above conditions are met. In our simulations, we found that facilitation started for $r^1_{S05} > r_{max}(d_R)/2$ at low exudation rates (see Supporting Information Fig. S2). Overall, because citrate concentration gradient around roots depends on exudation rates (Raynaud 2010), these different conditions explain why facilitation only occurs at low exudation rates (where P maximum supply only occur in the immediate vicinity of roots) whereas only competition occurs for higher exudation rates (because the whole soil is at maximum supply).

Our results are consistent with the classical observation, usually at the plant community scale, that facilitative interactions are more frequent in resource-poor systems (Bruno et al. 2003; Kéfi et al. 2008). In our model, the base level of P supply (S_{min}) was very low compared to its saturation value so that exudation was the only way for roots to access to available P. If this base level was to increase (i.e. the share of directly available nutrients increases), facilitation should be less frequent. The shape of the relation between exudate concentration and P supply might also have some influence on our results. However, we believe that whenever P supply increases with exudate concentration and saturates above a given exudate concentration, qualitatively similar results should be obtained as the conditions described above should still hold. Moreover, as our model has shown that the relative size of root zones of influence is crucial in determining the type of root interaction, any parameter affecting their size (e.g., soil water content, diffusion of exudates, etc., see Raynaud 2010) should influence the type of interaction between roots within root systems. As some of these parameters vary a lot on the short term, e.g. soil water content (Loague 1992), the same root system should switch from facilitation to competition over short time-scales. The value we chose for soil water content in our analysis is an intermediate value, so that our simulations should reflect an intermediate case of root system functioning. Ultimately, studies on inter-root interactions (facilitation or competition) should articulate the different time-scales of root-soil interactions, from the short-time changes of soil properties and root activities to the long-term dynamic of root growth and demography (Hodge et al. 2009). For example, dauciform or cluster roots (Shane and Lambers 2005; Shane et al. 2006) allow plants to increase their absorption of P. This is likely to arise because these roots have very high exudation rates and saturate the soil volume in carboxylates. However, the facilitation mechanism we suggest with our model could also be influential. Our rationale should also be tested for more complex patterns of root spatial distributions (e.g. aggregation) that emerge from dynamic root architecture models (e.g. Pagès 2011). In particular, such models should better take into account the fact that roots are not parallel and that portions of roots that exude and take up nutrients are not necessarily the same (Doussan et al. 2003).

Whether these extended concepts of root zones of influence could be used in other studies and especially in the field has to be discussed. Much progress has been made in the in situ observation of gradients around roots (Hinsinger et al. 2009) but measuring supply and their degree of saturation would require a very fine knowledge of the stocks of unavailable nutrients and their potential of release. Still, our results suggest that the assessment of the P supply and saturated P supply zones is crucial to understand interactions within the root system, although the function that converts exudate concentration into a nutrient supply could strongly condition the outcome of root interactions.

Finally, although our model is based on a very simple case of an exudate that directly increases the availability of P by a chemical reaction (Hinsinger 2001), it is based on very general mechanisms (e.g. solute diffusion, nutrient uptake, etc.) and should apply to the roots of any plant in any soil. We used it here to highlight the existence of new possible interactions between neighbouring roots but the frequency of positive interactions between roots should be assessed by parametrizing the model for different case studies. Moreover, this theoretical approach could be generalized to other nutrients, whose availability depends on the release of molecules by roots, or on the interactions between roots and soil microorganisms. For example, mineralisation of organic nitrogen can depend on interactions between plant roots and soil micro-organisms, through the release of root exudates (Raynaud et al. 2006; Shahzad et al. 2015). Similarly, biological nitrification inhibition (Lata et al. 2004; Subbarao et al. 2006) by some grass species is due to the release by roots of molecules that inhibit microbial ammonium oxidation. However, to be generalized to such cases, a precise knowledge of the molecules involved and the processes and time scales that lead to the increase in nutrient availability is needed. Similarly in cases in which soil micro-organisms are involved, the spatial distribution of microorganisms with respect to root spatial distribution (Compant et al. 2010) could also influence interactions between roots.

Implications for root foraging strategies

The concept of intra-plant inter-root competition was originally formulated in a context where the carbon cost of nutrient acquisition was to be evaluated: inter-root competition within the root system decreases the benefits of a root when it is close to another one (Ge et al. 2000; Rubio et al. 2001). When only root absorption is considered, a good proxy of the carbon cost of nutrient acquisition is root length density and we used it in our definition of P uptake efficiency. This approximation can be used when comparing root systems differing by their root length density but not by their levels of root exudation rates (Lynch and Ho 2005). In this context, our results suggest that cases of intra-plant, inter-root facilitation should favour local root proliferation where root length density increases nutrient uptake efficiency. By contrast, inter-root competition should favour sparser root systems that limit competitive interactions between roots (Ge et al. 2000). The building of root systems thus not only depends on the presence of other plant competitors but also on plant-created heterogeneity, that can both can lead to an increase (due to facilitation) or decrease (due to competition) of root length density (Rubio et al. 2001). Similarly, facilitation between roots of the same plant individual could favour dense root systems limiting their exploration of the soil volume (de Parseval et al. 2016).

In our simulations, the case of inter-root facilitation occurred at low exudation rates, where the amount of P taken up by unit of root length was lowered (due to the low exudates concentration in soils), but where P losses were also minimised. Indeed, increasing exudation increases the availability of P which should also lead to an increase of losses through microbial immobilization. This suggests the existence of a gradient of strategies, in essence similar to the classical r/K gradient. This gradient would span from a very fast exploitation of the nutrient pool, associated to high exudation rates but also high losses, to a slow but more effective exploitation of the pool, associated with low exudation rates and low losses (Boudsocq et al. 2011; Reich 2014): indeed, more exudation leads to competition and a loss of efficiency, as measured by the amount of resource invested to absorb mineral nutrients. However, the different levels of root exudation tested in our model are not equivalent to the nutrient uptake efficiency as we have defined it. For a relevant comparison, the assessment of the relative cost of root construction and functioning is needed, as well as that of exudation to determine the total cost of P uptake (Lynch and Ho 2005). A low exudation strategy, that leads to inter-root facilitation, should be advantageous compared to a high exudation strategy only if the cost of exudation is high compared to that of root absorption, e.g. when complex molecules have to be synthesized.

Rationales based on the carbon cost of nutrient acquisition do not always account well for root foraging strategies. In the context of competition between roots, the use of game theory has proved useful (O'Brien and Brown 2008). For example, even if the proliferation of roots implies a high carbon cost relative to the benefits (increase in nutrient absorption), this behaviour also leads to a competitive advantage for the root system with higher root length density (Robinson et al. 1999; Raynaud and Leadley 2004; Craine et al. 2005). Although our results focus on interactions between roots from a single root system, they could easily be generalized to interactions between roots from different root systems and suggest that roots of one species could benefit from the proximity of roots of another species that would increase nutrient supply in their vicinity (Raynaud et al. 2008). The possibility of positive interactions between root systems or individual plants could be taken into account through new game theory root models, especially if one takes into account the ability of self/non self-recognition by roots (Gruntman and Novoplansky 2004). Somehow, our model suggests a mechanism that could account for some of the predicted and documented cases of inter-plant facilitation (Callaway et al. 2002).

One important application of root foraging studies is the identification of roots traits that could be selected to enhance crop yields and/or sustainability (Lynch 2011). However, the study of crop species often neglected the role of exudation (Pagès 2011), whose importance seems to be minimised when nutrients are brought in high concentration and in a highly available form, as it is often the case in agroecosystems. Studies about mechanisms by which plants increase the availability of nutrients (Chapman et al. 2006) have mainly focused on wild species from nutrient-poor environment. Agroecosystems are high yielded but lead to huge losses of mineral nutrients. One reason for that is the massive use of mineral fertilizers. Another reason is that high yield varieties have been selected and that these varieties are probably able to quickly absorb available nutrients but do not impede losses of nutrient. Our results suggest that selecting species that limit nutrient losses and foster root facilitation either intra- or inter-plants could reduce the need of fertilizers while maintaining high yields (Loeuille et al. 2013).

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