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

3

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13

14

15 **Summary**

16 *Aims:* The concept of intra-plant, inter-root competition considers the overlap of nutrient depletion  
17 zones around roots, but neglects the spatial pattern of root exudates that can increase nutrient  
18 availability. We tested the hypothesis that interactions between nutrient accumulation zones due to  
19 exudation by different roots can lead to intra-plant inter-root facilitation.

20 *Methods:* We used the PARIS model (Raynaud et al 2008) to simulate phosphorus uptake by a  
21 population of roots that are able to increase phosphorus availability by exuding citrate. We carried  
22 out several simulations with the same parameters but with increasing root density in order to study  
23 out if changes in root densities would alter nutrient uptake per unit root.

24 *Results:* Emerging relationships between root uptake efficiency and root length density indicated  
25 cases of inter-root competition or facilitation. The sizes of the accumulation and depletion zones  
26 were calculated to explain these results. Our simulations showed a continuum between cases of  
27 inter-root competition and facilitation. Facilitation occurred at low exudation rates, when  
28 phosphorus supply was not saturated within the phosphorus depletion zone surrounding roots. Low

29 exudation systems led to a lower phosphorus uptake per unit root length, but minimized phosphorus  
30 losses in the process.

31 *Conclusions:* Based on our model, we derived conditions that allowed predicting whether  
32 competition, facilitation or no interaction, is the dominant interaction between roots within a root  
33 system, based on the different distances to which an isolated root alters P concentration and supply.

34

35 **Key-words:** diffusion, exudation, modelling, phosphorus, rhizosphere, spatial distribution

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37

## 38 Introduction

39 Living roots contribute to plant mineral nutrition by two complementary processes: nutrient  
40 absorption and exudation. On the one hand, plants are able to adjust the location, surface and uptake  
41 rates of their roots to the local concentration in available nutrients (Hodge 2004). On the other hand,  
42 they are able to locally increase the availability of mineral nutrients by releasing various products  
43 (protons, carbohydrates, secondary metabolites) in the soil surrounding their roots (Dakora and  
44 Phillips 2002). For example, experiments and models have shown that local modifications of soil  
45 pH due to the release of organic acids by roots can alter the availability of phosphorus (Hinsinger  
46 2001) and significantly increase plant P uptake at the level of individual plants (Kirk et al, 1999b)  
47 or plant community (Li et al, 2007). Root exudates can also boost microbial activities, leading to  
48 increased mineralization which can, in turn, increase nutrient availability locally (Dijkstra and  
49 Cheng 2007; Shahzad et al. 2015).

50 By taking up nutrients at their surface, roots create diffusion gradients leading to the  
51 formation of depletion zones around them (Tinker and Nye, 2000). In the same way, exudates  
52 accumulate around roots to form accumulation zones. Nearby roots therefore compete with each  
53 other when their respective depletion zones overlap (Ge et al. 2000). Similarly, if exudates increase  
54 nutrient availability in the soil surrounding roots, nearby roots could also increase their respective  
55 nutrient uptake when exudate accumulation zones overlap. These zones of influence (i.e. depletion  
56 and accumulation zones around roots), from which competitive or facilitative interactions can arise,  
57 are therefore of fundamental importance for plant nutrition and soil functioning (York et al. 2016).  
58 Yet, the consequences of these zones of influence are still poorly understood due to their size which  
59 is restricted to short distances around roots (i.e. a few millimetres). In order to tackle these limits,

60 several modelling approaches have been developed to explore how root activity can lead to the  
61 creation of these root zones of influence, and alter nutrient availability and plant nutrient uptake in  
62 the case of (1) single roots (Kirk et al, 1999a; Ptashnyk et al. 2011; Zygalkakis and Roose 2012), (2)  
63 root systems of single plants (Rubio et al. 2001; Schnepf et al. 2012; Dunbabin et al. 2013) or (3)  
64 root systems of different plants in a community (Raynaud et al. 2008). All these studies found that  
65 the distance between roots, which results from root system characteristics (size, architecture, root  
66 density), could lead to the overlap of these accumulation and/or depletion zones. This could thus  
67 alter nutrient availability and plant nutrient uptake in a complex manner: intra-plant, inter-root  
68 facilitation adds to intra- and inter-plant competition as a constraint shaping root system  
69 architecture and root foraging strategies (Rubio et al. 2001). In this case, net facilitation between  
70 roots would occur when the synergistic effect of having a root neighbour is higher than its  
71 competitive effect, so that increasing root density increases the absorption of nutrient per unit of  
72 root length. Facilitation as a belowground interaction is a quite common concept (Lin et al. 2012).  
73 However, to our knowledge, it has never been used at the scale of roots within a single root-system  
74 and existing modelling studies have not yet studied how the simultaneous development of  
75 accumulation and depletion zones alters rhizosphere nutrient availability and nutrient uptake.

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

87 Using a simulation model, our objective was to test the above rationale, i.e. to determine  
88 whether inter-root facilitation is possible and if so, under which conditions. To do so, we considered  
89 the case of a small volume of soil explored by the roots of a single plant individual that takes up a  
90 mineral nutrient and can increase its availability through the exudation of solutes. In order to carry  
91 out realistic simulations, we have chosen to model the uptake of phosphorus (P) and the changes in  
92 its availability through the release of citrate (C) by roots (Hodge, 2004; Fig. 1). The case of citrate

93 is well documented and relatively simple to model as a direct effect of C concentration on soil  
94 physico-chemical properties (Hinsinger 2001). For example, in some soils, phosphorus can be  
95 found in the form of phosphate rocks (e.g. apatite) that can release soluble phosphate when in  
96 presence of plant-released citrate, due to lower pH conditions in the plant rhizosphere (Li et al,  
97 2007). In the modelled soil volume, interactions between roots were assessed by calculating the  
98 relationships between plant P uptake and root length density, as well as P uptake efficiency (P  
99 uptake per unit of root length). As root length density increases, the mean distance between  
100 individual roots decreases, which should lead to more overlap of the different accumulation and  
101 depletion zones. In this context, we distinguished inter-root competition from facilitation by  
102 negative and positive relationships between root length density and P uptake efficiency.

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

111

## 112 Material and Methods

### 113 *Model description*

114 We modelled the case of a plant taking up P, and exuding C (Fig. 1), using a modified version (see  
115 below) of the PARIS model (Raynaud and Leadley 2004; Raynaud et al. 2008) which is an  
116 extension of the Barber-Cushman model (Barber and Cushman, 1981) to a set of roots exploring a  
117 horizontal layer of soil. The model simulates different rhizosphere processes, including solutes (P  
118 and C) diffusion and losses, P absorption at the root surface, C exudation by roots, and the  
119 production of available P from a chemical reaction between C and soil (Kirk et al 1999a; Kirk et al  
120 1999b). Model variables and parameters are summarized in Tables 1 and 2 and details of the model  
121 equations are given below.

122 All the modelled processes occur in a 1 cm thick (parameter  $z$ ) layer of soil, having a surface  
123 of 2x2 cm. In contrast to the original PARIS model (Raynaud and Leadley 2004; Raynaud et al.

124 2008) that considered a hexagonal grid, the soil layer is organized as a 100x100 squared grid of  
 125 voxels that can be either soil or root. Tests comparing squared and hexagonal geometries as well as  
 126 the comparison between the diffusion fluxes calculated with these geometries and those obtained  
 127 from the analytical solution around a single root indicate that, at steady state, results are very robust  
 128 to the geometry of the grid. Voxel width ( $h=0.2$  mm) is equal to the diameter of roots and the  
 129 modelled soil layer is 1 voxel high so that voxels have dimensions  $h \times h \times z$ . Solute fluxes through  
 130 soil are thus only horizontal. Roots are assumed to grow vertically down into the soil, and no root  
 131 branching occurs within the simulated soil volume. As we consider roots having the same geometry  
 132 as voxels, one root has an exchange surface ( $h \times z$ ) with the four orthogonal nearest voxel  
 133 neighbours. We define  $d_R$  as the root length density within the soil volume ( $\text{cm cm}^{-3}$ ). To eliminate  
 134 boundary conditions problems and avoid edge effects, we consider the surface modelled as a torus  
 135 in which top and bottom, as well as left and right edges are connected (periodic boundary condition;  
 136 Haefner 2012).

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

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

141 where  $D_{e,i}$  ( $\text{cm}^2 \text{s}^{-1}$ ) is the effective diffusion coefficient of solutes in the soil and  $\Delta C_i$  ( $\text{mmol cm}^{-3}$ )  
 142 is the concentration difference between voxels  $v$  and  $w$  (O'Reilly and Beck 2006).  $D_{e,i}$  is calculated  
 143 from  $\theta$ , the solute diffusion coefficient in pure water ( $D_i$ ,  $\text{cm}^2 \text{s}^{-1}$ ), an impedance factor related to the  
 144 tortuous pathways of water films in the soil (also known as tortuosity factor,  $f_i$ ; Olesen et al,  
 145 2001) and the soil buffer power for the solute considered ( $b_i$ ; van Rees et al. 1990; Raynaud et al.  
 146 2008):

$$D_{e,i} = D_i \theta f_i / b_i \quad (2)$$

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

$$b_i = \theta + \rho k_{d,i} \quad (3)$$

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

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

151 where  $\theta_{th}$  represents the soil water content threshold below which diffusion ceases due to  
152 discontinuous diffusion pathways.

153 Each voxel loses P ( $L_P$ ,  $\text{mmol}_P \text{ s}^{-1}$ ) and C ( $L_C$ ,  $\text{mmol}_C \text{ s}^{-1}$ ) at rates  $\mu_P$  ( $\text{s}^{-1}$ ),  $\mu_C$  ( $\text{s}^{-1}$ ) that  
154 express the disappearance of these solutes due to consumption by other organisms.

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

$$U_P = I_{max} \frac{C_{P,v}}{C_{P,v} + K_U} \quad (5)$$

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

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

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

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

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

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

$$\frac{dC_{C,v}}{dt} = (hz) \frac{e_c}{hhz} - \mu_C C_{C,v} + \frac{1}{h} \sum_{w=1}^4 F_{(C)v,w} \quad (7)$$

$$\frac{dC_{P,v}}{dt} = S_P - (hz) \frac{U_P}{hhz} - \mu_P C_{P,v} + \frac{1}{h} \sum_{w=1}^4 F_{(P)v,w} \quad \text{for voxels adjacent to roots}$$

$$\frac{dC_{C,v}}{dt} = -\mu_C C_{C,v} + \frac{1}{h} \sum_{w=1}^4 F_{(C)v,w} \quad (8)$$

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

171

## 172 *Numerical analysis*

173 Model equations were implemented in JAVA, within the 3Worlds modelling platform (Gignoux et  
 174 al., 2005; Gignoux et al. 2011). Individual roots were randomly distributed within a 2-dimensional  
 175 rectangular grid of cells representing the modelled layer of soil. Solutes diffusion and root-soil  
 176 interactions (absorption and exudation) were programmed as reusable sub-routines plugged into the  
 177 3Worlds core application.

178 All parameter values used for simulations are given in Table 2. P and C parameters were  
 179 taken from different literature sources (see Table 2 for details). We modelled rhizosphere processes  
 180 for increasing number of roots ( $n_R$ ), with values ranging from 1 to 600 roots in a  $1 \times 2 \times 2 \text{ cm}^3$  soil  
 181 volume (14 different values of  $n_R$ ). This corresponds to root length densities  $d_R$  ranging from 0.25  
 182  $\text{cm cm}^{-3}$  to 150  $\text{cm cm}^{-3}$  (although unrealistic, this upper value was useful for the interpretation of  
 183 our results). Because voxels can be either soil or root but not both, the increase in root density thus  
 184 reduces the amount of soil modelled, and eventually the total P supply of soil. In the case where  
 185 supply in all soil voxels is  $S_P = S_{max}$ , this reduction in P supply is at most 6% between the two  
 186 extremes of the chosen range of root densities, and less than 1% for densities below 25  $\text{cm cm}^{-3}$ .  
 187 Roots were placed randomly within the  $2 \times 2 \text{ cm}$  modelled surface. To avoid the risk that our results  
 188 depend on a particular root spatial distribution, 5 different maps were used for each root length  
 189 density value (e.g.  $5 \times 14 = 70$  maps in total). The model outputs obtained from these different maps  
 190 are shown as points in Figs. 3 and 5. As the exudation rate of C ( $e_C$ ) affects the size of exudation  
 191 rhizospheres (Raynaud 2010), our simulations were done for several values of this parameter (Table  
 192 2).

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



199 defined P uptake efficiency  $UE_P$  as the quantity of P taken up by unit of root length:

$$UE_P = \frac{A_P}{d_R V} \quad (9)$$

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

201

## 202 *Assessment of the sizes of root influence regions on soil properties*

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

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

224 When several roots are present, gradients around individual roots can overlap, so that all the  
225 simulated soil volume can be under the influence of one or more roots and the above limits cannot  
226 be used. Moreover, if the accumulation or depletion zones of two neighbouring roots overlap,  
227 concentrations and supply will not be monotonic along the line between these two roots (Fig. 2,  
228 right panels). We thus assumed that the “territory” of a root can be defined as the distance from that

229 root within which the gradient of concentration or supply was monotonic (e.g. citrate concentration  
230 decreases to a minimum with increasing distance from the root). This distance no longer measures  
231 the size of the zone of influence of a single root, but rather indicates the level of overlapping and  
232 interaction between the zones of influence of single roots. Because all roots have identical  
233 parameters in a simulation, if all neighbouring root zones of influence overlap, the average radius of  
234 the territory of a root is equal to the average half distance between 2 roots for a given root density  
235  $r_{max}(d_R) = \sqrt{1/(\pi d_R)}$ .

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

246

## 247 Results

### 248 *Phosphorus fluxes depend on root density and exudation rates*

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

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

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

266

### 267 *Patterns of accumulation and depletion zone sizes determine inter-root competition* 268 *or facilitation*

269 Figure 2 gives an example of a C concentration profile around a single root and the corresponding P  
270 supply profile, as well as the calculated influence zone radii  $r_C^I$ ,  $r_{SP05}^I$  and  $r_{SP95}^I$ . Due to the non-  
271 linearity of the relationship between C concentration  $C_C$  and P supply  $S_P$  (Eq. 6), the calculated C  
272 accumulation zone radius,  $r_C^I$ , was not a good descriptor of the volume upon which roots alter P  
273 supply in the soil. We thus focused on territory sizes of P supply ( $t_{S05}$ ), P supply saturation ( $t_{S95}$ )  
274 and P depletion ( $t_P$ ). In order to illustrate the links between nutrient concentration and territory  
275 sizes, Figure 4 maps the changes in P supply around roots, as well as the extent of P depletion zones  
276 in two maps differing in root length densities and for the three exudation rates tested. The chosen  
277 root length densities in these maps correspond to the two contrasted patterns observed for P root  
278 uptake efficiency in Figure 3d: a decrease of  $UE_P$  between low and high root length density for high  
279 exudation rate whereas  $UE_P$  increased between these two values at low exudation rate.

280 Figure 4 shows that for a citrate exudation rate of  $10^{-8}$  mmol cm<sup>-2</sup> s<sup>-1</sup>, the whole soil volume  
281 was influenced by roots for P supply, even at low  $d_R$ . At high  $d_R$ , P supply was maximized in the  
282 whole modelled soil volume. The pattern was similar for a C exudation rate of  $10^{-9}$  mmol cm<sup>-2</sup> s<sup>-1</sup>,  
283 although very small regions of bulk soil are still present at low  $d_R$  and P supply is not maximized  
284 over the whole soil volume. C exudation rates lower than  $10^{-9}$  mmol cm<sup>-2</sup> s<sup>-1</sup> yielded a slightly  
285 different pattern, leaving large part of the soil unaffected by roots at low  $d_R$ , whereas most soil was  
286 affected by roots at high  $d_R$  but with supply values  $< S_{max}$ . In particular, at low  $d_R$ , P depletion  
287 zones around roots were relatively isolated, whereas most P concentration were under the influence  
288 of roots at high  $d_R$  values.

289 Figure 5 shows the average territory radius around one root as a function of  $d_R$  and  $e_C$  and  
290 suggests that this extent followed a similar pattern for all three territory types along the gradient of

291 root length density  $d_R$ : whatever the territory considered, average territory radii was constant for  
292 low  $d_R$  values and then decreased with increasing  $d_R$ . (Fig. 5). A territory radius equal to  $r_{max}(d_R)$   
293 thus indicates that zones of influence of neighbouring roots overlap so that roots mutually influence  
294 the solute concentrations in each other's surroundings. The only exception for this general pattern  
295 was the radius of saturated P supply territory  $t_{S95}$ , which was slightly greater at intermediate  $d_R$   
296 values compared to low  $d_R$  values in the case of intermediate and low values of C exudation (barely  
297 visible on Fig. 5, but significant). This increase occurs because close roots increase the saturation of  
298 P supply between them, thus increasing the size of their saturation rhizosphere without necessarily  
299 merging or overlapping them (see Fig. 4, mid left panel).

300

## 301 Discussion

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

310 To our knowledge, our study is the first exploring the mechanisms through which  
311 facilitation within the root system of a single plant can occur. Our results suggest that the ability of  
312 a plant to increase P availability through exudation does not prevent inter-root competition, but  
313 rather creates a continuum between cases of inter-root competition and inter-root facilitation.  
314 Studies on root foraging strategies have not, to date, considered the consequence of root exudation  
315 on nutrient supply (Ge et al. 2000; Cahill and McNickle 2011; Pagès 2011; but see Schnepf et al.  
316 2012) and have not distinguished the respective scales of root exudation and nutrient uptake  
317 (McNickle et al. 2009). Our study suggests that exudation of solutes by neighbouring roots can  
318 dramatically alter nutrient availability near the root system so that increasing root density might not  
319 necessarily lead to a decrease in root uptake efficiency. Still, our study explored a relatively simple  
320 case and the robustness of our results and their implications for the understanding of root foraging  
321 strategies remain to be thoroughly studied both through modelling and experiments. Below, we  
322 focus on the mechanisms that lead to the emergence of inter-root facilitation and how they could be

323 generalized. Then, we analyse the implications of the variability of inter-root interactions for root  
324 foraging strategies.

### 325 *Mechanisms leading to the emergence of facilitation between roots*

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

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

$$344 \quad r_P^1 < d \text{ (condition 1).}$$

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

$$348 \quad r_{S05}^1 > d \quad \text{(condition 2).}$$

349 However, if the two roots increase C concentrations sufficiently enough to saturate P supply  
350 up to distance  $d$ , P supply is constant and equal to  $S_{max}$  across the whole distance  $2d$  and adding  
351 more exudate to the soil does not increase P supply (Fig. 4b). This becomes similar to a case where  
352 P supply is constant in the whole soil volume. In such case, P uptake of a root competing with  
353 others only depends on its uptake rate (Raynaud and Leadley 2004) and facilitation does not occur.

354 A necessary condition to observe facilitation is thus that the saturated P supply zones of both roots  
355 do not overlap, which corresponds to:

$$356 \quad r_{S95}^1 < d \quad (\text{condition 3}).$$

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

$$363 \quad r_P^1 > 2d - r_{S05}^1 \quad (\text{condition 4}).$$

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

$$368 \quad r_P^1 > r_{S95}^1 \quad (\text{condition 5})$$

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

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

383 Our results are consistent with the classical observation, usually at the plant community  
384 scale, that facilitative interactions are more frequent in resource-poor systems (Bruno et al. 2003;

385 Kéfi et al. 2008). In our model, the base level of P supply ( $S_{min}$ ) was very low compared to its  
386 saturation value so that exudation was the only way for roots to access to available P. If this base  
387 level was to increase (i.e. the share of directly available nutrients increases), facilitation should be  
388 less frequent. The shape of the relation between exudate concentration and P supply might also have  
389 some influence on our results. However, we believe that whenever P supply increases with exudate  
390 concentration and saturates above a given exudate concentration, qualitatively similar results should  
391 be obtained as the conditions described above should still hold. Moreover, as our model has shown  
392 that the relative size of root zones of influence is crucial in determining the type of root interaction,  
393 any parameter affecting their size (e.g., soil water content, diffusion of exudates, *etc.*, see Raynaud  
394 2010) should influence the type of interaction between roots within root systems. As some of these  
395 parameters vary a lot on the short term, e.g. soil water content (Loague 1992), the same root system  
396 should switch from facilitation to competition over short time-scales. The value we chose for soil  
397 water content in our analysis is an intermediate value, so that our simulations should reflect an  
398 intermediate case of root system functioning. Ultimately, studies on inter-root interactions  
399 (facilitation or competition) should articulate the different time-scales of root-soil interactions, from  
400 the short-time changes of soil properties and root activities to the long-term dynamic of root growth  
401 and demography (Hodge et al. 2009). For example, dauciform or cluster roots (Shane and Lambers  
402 2005, Shane et al. 2006) allow plants to increase their absorption of P. This is likely to arise because  
403 these roots have very high exudation rates and saturate the soil volume in carboxylates. However,  
404 the facilitation mechanism we suggest with our model could also be influential. Our rationale  
405 should also be tested for more complex patterns of root spatial distributions (e.g. aggregation) that  
406 emerge from dynamic root architecture models (e.g. Pagès 2011). In particular, such models should  
407 better take into account the fact that roots are not parallel and that portions of roots that exude and  
408 take up nutrients are not necessarily the same (Doussan et al. 2003).

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

417 Finally, although our model is based on a very simple case of an exudate that directly



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

### 433 *Implications for root foraging strategies*

434 The concept of intra-plant inter-root competition was originally formulated in a context where the  
435 carbon cost of nutrient acquisition was to be evaluated: inter-root competition within the root  
436 system decreases the benefits of a root when it is close to another one (Ge et al. 2000; Rubio et al.  
437 2001). When only root absorption is considered, a good proxy of the carbon cost of nutrient  
438 acquisition is root length density and we used it in our definition of P uptake efficiency. This  
439 approximation can be used when comparing root systems differing by their root length density but  
440 not by their levels of root exudation rates (Lynch and Ho 2005). In this context, our results suggest  
441 that cases of intra-plant, inter-root facilitation should favour local root proliferation where root  
442 length density increases nutrient uptake efficiency. By contrast, inter-root competition should  
443 favour sparser root systems that limit competitive interactions between roots (Ge et al. 2000). The  
444 building of root systems thus not only depends on the presence of other plant competitors but also  
445 on plant-created heterogeneity, that can both can lead to an increase (due to facilitation) or decrease  
446 (due to competition) of root length density (Rubio et al. 2001). Similarly, facilitation between roots  
447 of the same plant individual could favour dense root systems limiting their exploration of the soil  
448 volume (de Parseval et al. 2016).

449 In our simulations, the case of inter-root facilitation occurred at low exudation rates, where



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

465 Rationales based on the carbon cost of nutrient acquisition do not always account well for  
466 root foraging strategies. In the context of competition between roots, the use of game theory has  
467 proved useful (O'Brien and Brown 2008). For example, even if the proliferation of roots implies a  
468 high carbon cost relative to the benefits (increase in nutrient absorption), this behaviour also leads  
469 to a competitive advantage for the root system with higher root length density (Robinson et al.,  
470 1999; Raynaud and Leadley 2004; Craine et al. 2005). Although our results focus on interactions  
471 between roots from a single root system, they could easily be generalized to interactions between  
472 roots from different root systems and suggest that roots of one species could benefit from the  
473 proximity of roots of another species that would increase nutrient supply in their vicinity (Raynaud  
474 et al. 2008). The possibility of positive interactions between root systems or individual plants could  
475 be taken into account through new game theory root models, especially if one takes into account the  
476 ability of self/non self-recognition by roots (Gruntman and Novoplansky 2004). Somehow, our  
477 model suggests a mechanism that could account for some of the predicted and documented cases of  
478 inter-plant facilitation (Callaway et al. 2002).

479 One important application of root foraging studies is the identification of roots traits that  
480 could be selected to enhance crop yields and/or sustainability (Lynch 2011). However, the study of  
481 crop species often neglected the role of exudation (Pagès 2011), whose importance seems to be  
482 minimised when nutrients are brought in high concentration and in a highly available form, as it is

483 often the case in agroecosystems. Studies about mechanisms by which plants increase the  
484 availability of nutrients (Chapman et al. 2006) have mainly focused on wild species from nutrient-  
485 poor environment. Agroecosystems are high yielded but lead to huge losses of mineral nutrients.  
486 One reason for that is the massive use of mineral fertilizers. Another reason is that high yield  
487 varieties have been selected and that these varieties are probably able to quickly absorb available  
488 nutrients but do not impede losses of nutrient. Our results suggest that selecting species that limit  
489 nutrient losses and foster root facilitation either intra- or inter-plants could reduce the need of  
490 fertilizers while maintaining high yields (Loeuille et al. 2013).

491

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497

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629 Tables

630 **Table 1:** Model variables: symbols, definitions and units

631 **Table 2:** Model parameter values used in simulations

## 632 Figures Legend

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

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

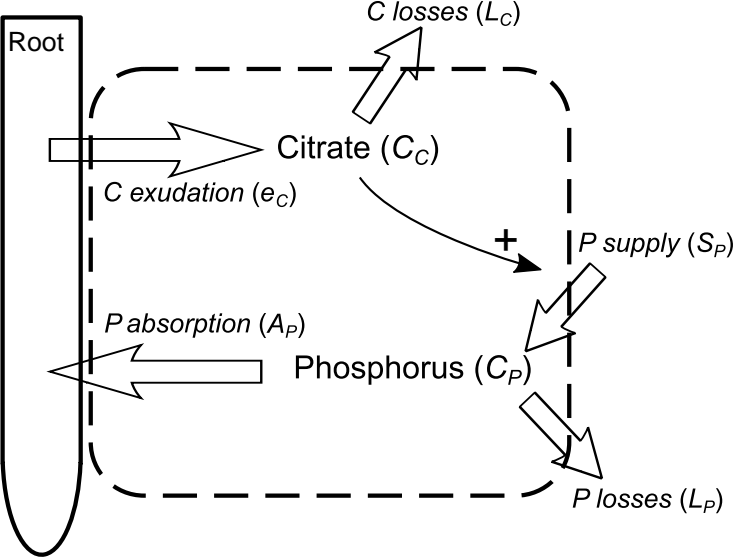
648 **Figure 3:** Relationships between root density ( $d_R$ , log scale) and different variables quantifying  
649 phosphorus fluxes in the root-soil system: average soil phosphorus supply ( $S_P$ , panel a) and losses  
650 ( $L_P$ , panel b), the ratio of phosphorus absorbed relative to its supply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

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

663 **Figure 5:** Estimation of average zone of influence diameters of single roots for phosphorus



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



# Single Root

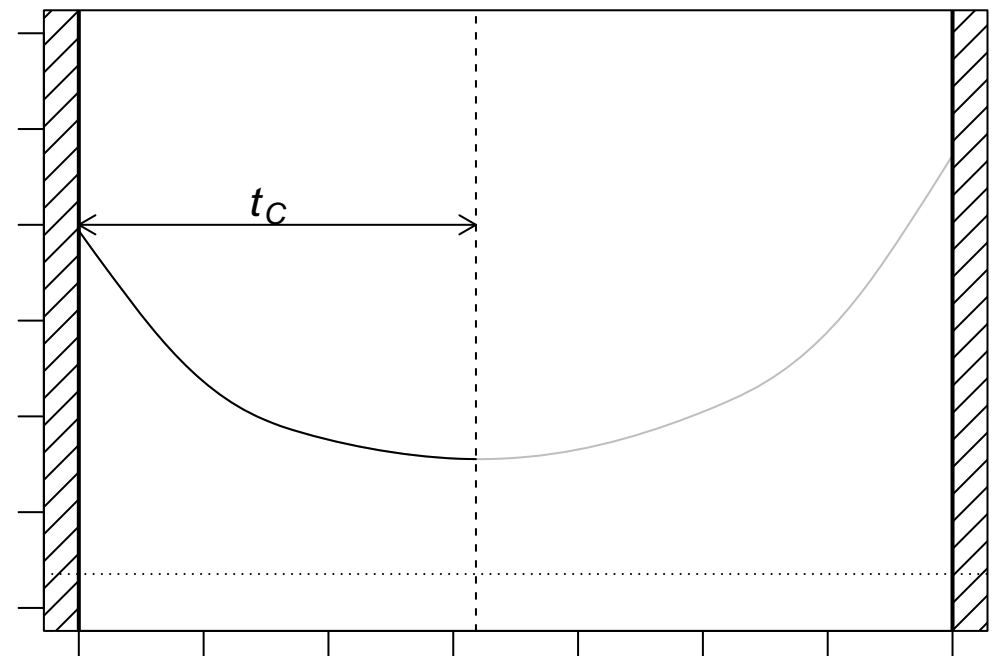
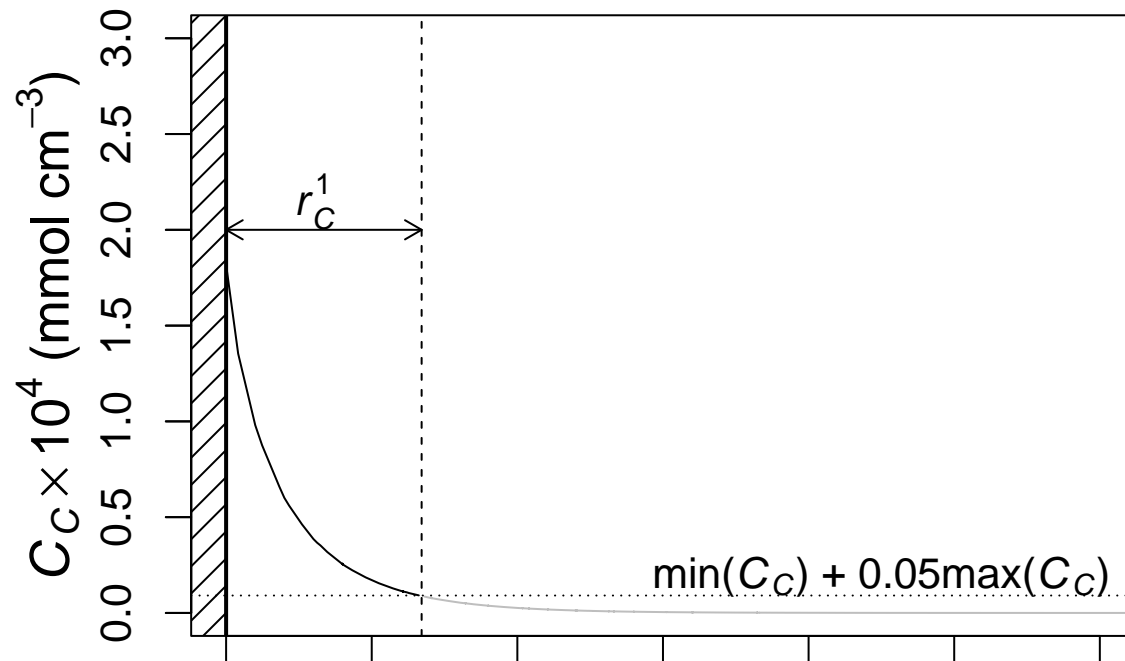
# Two Root

Root 1

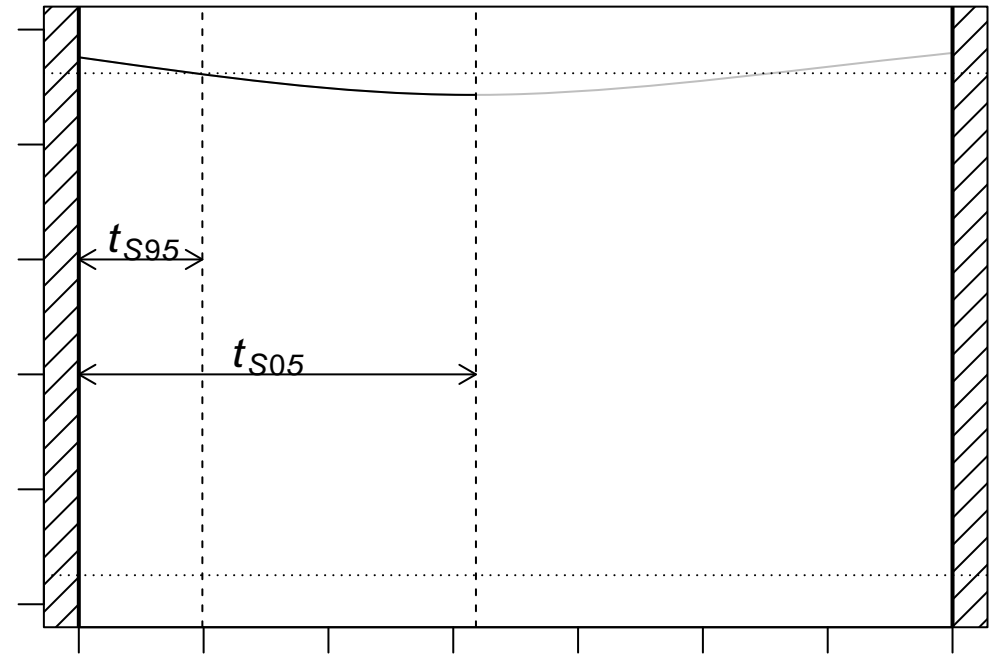
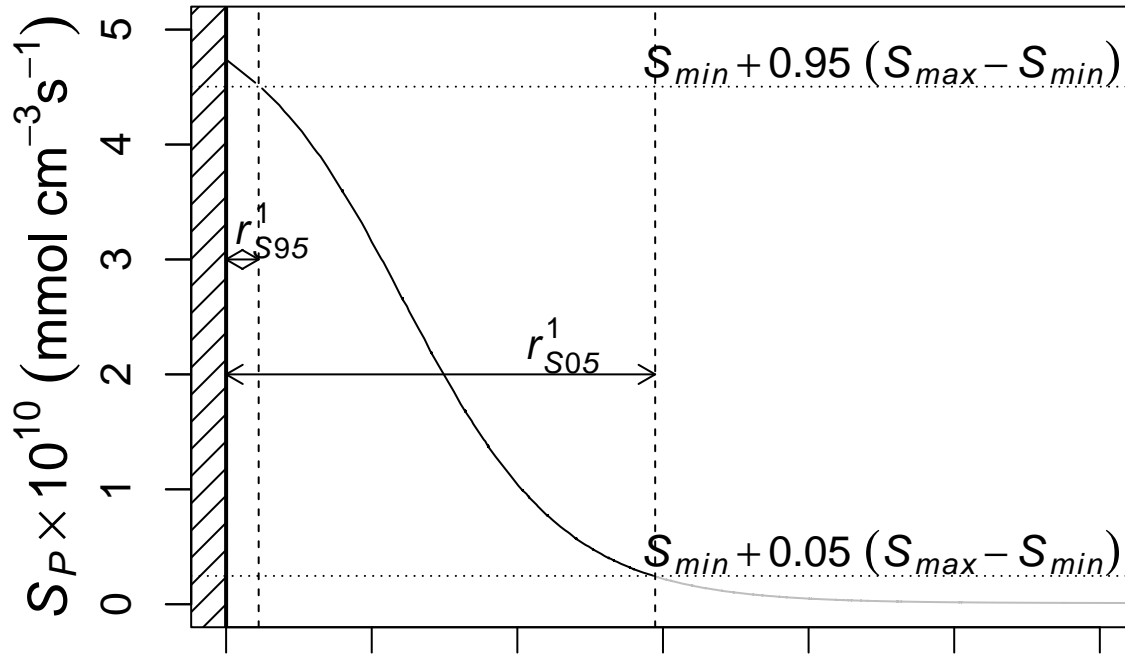
Root 1

Root 2

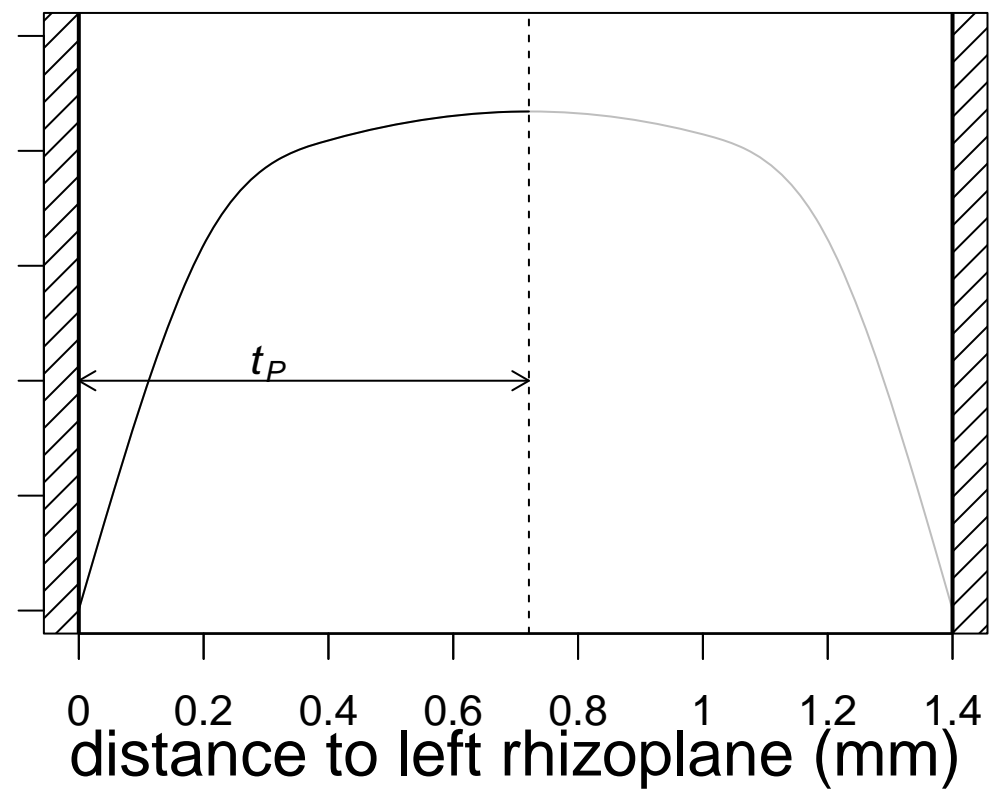
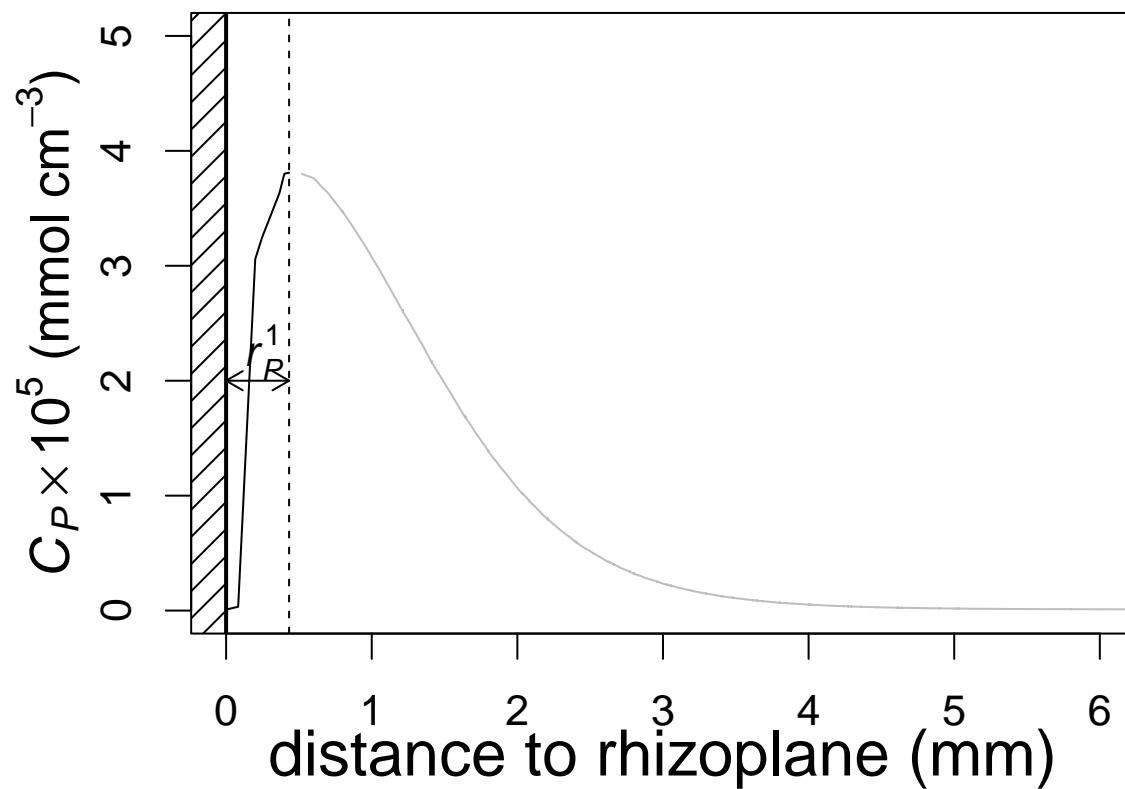
Citrate concentration

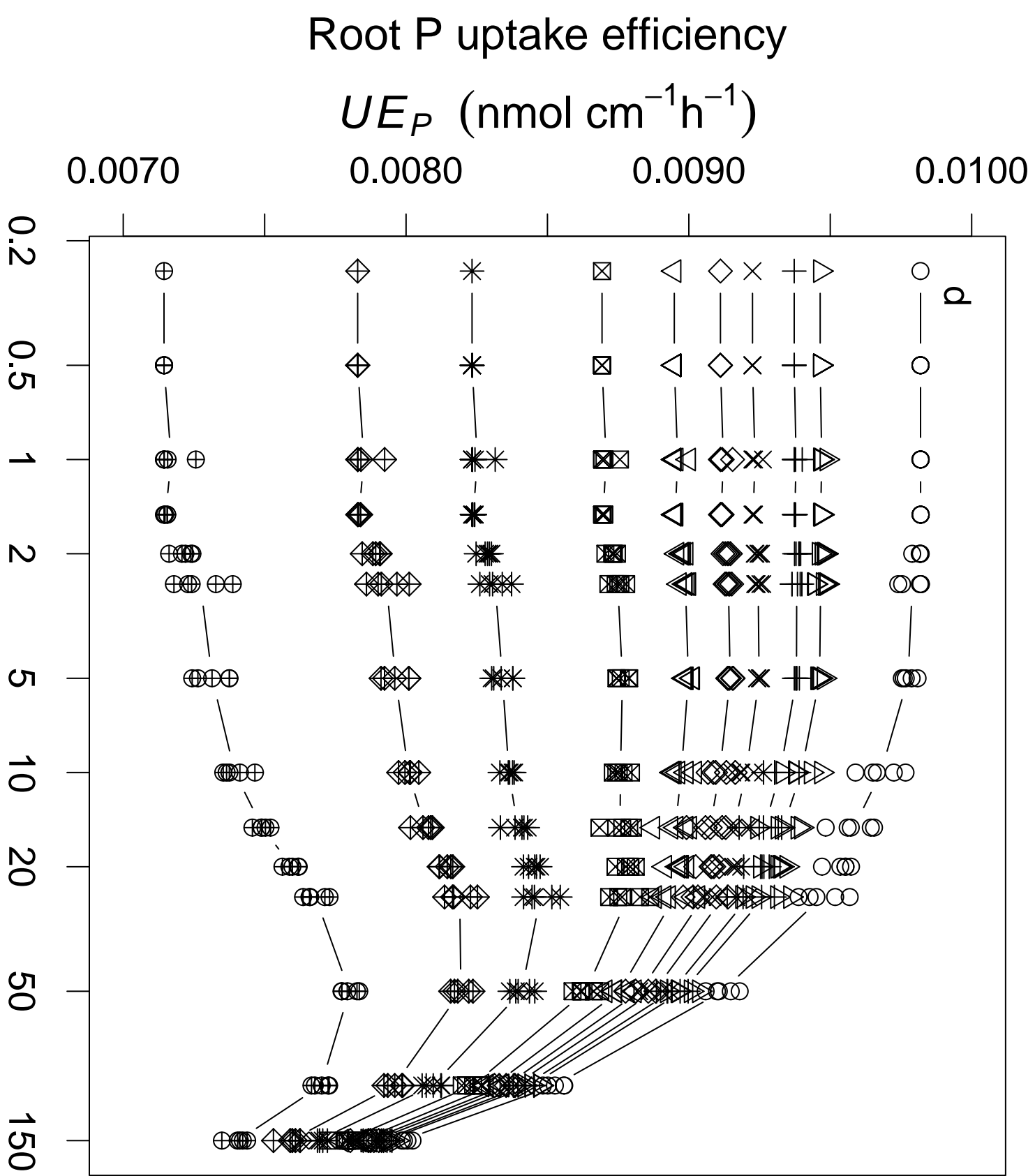
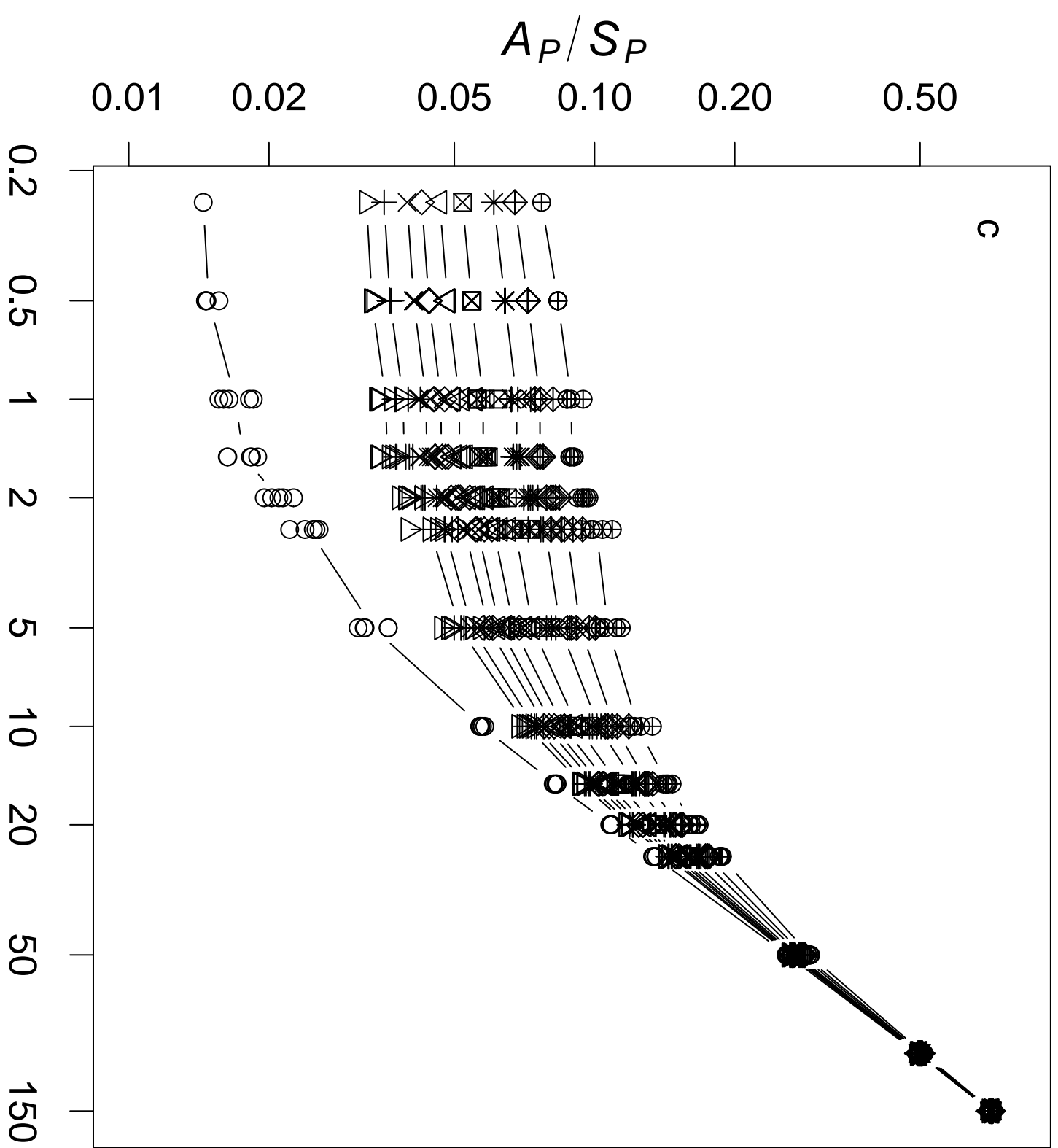
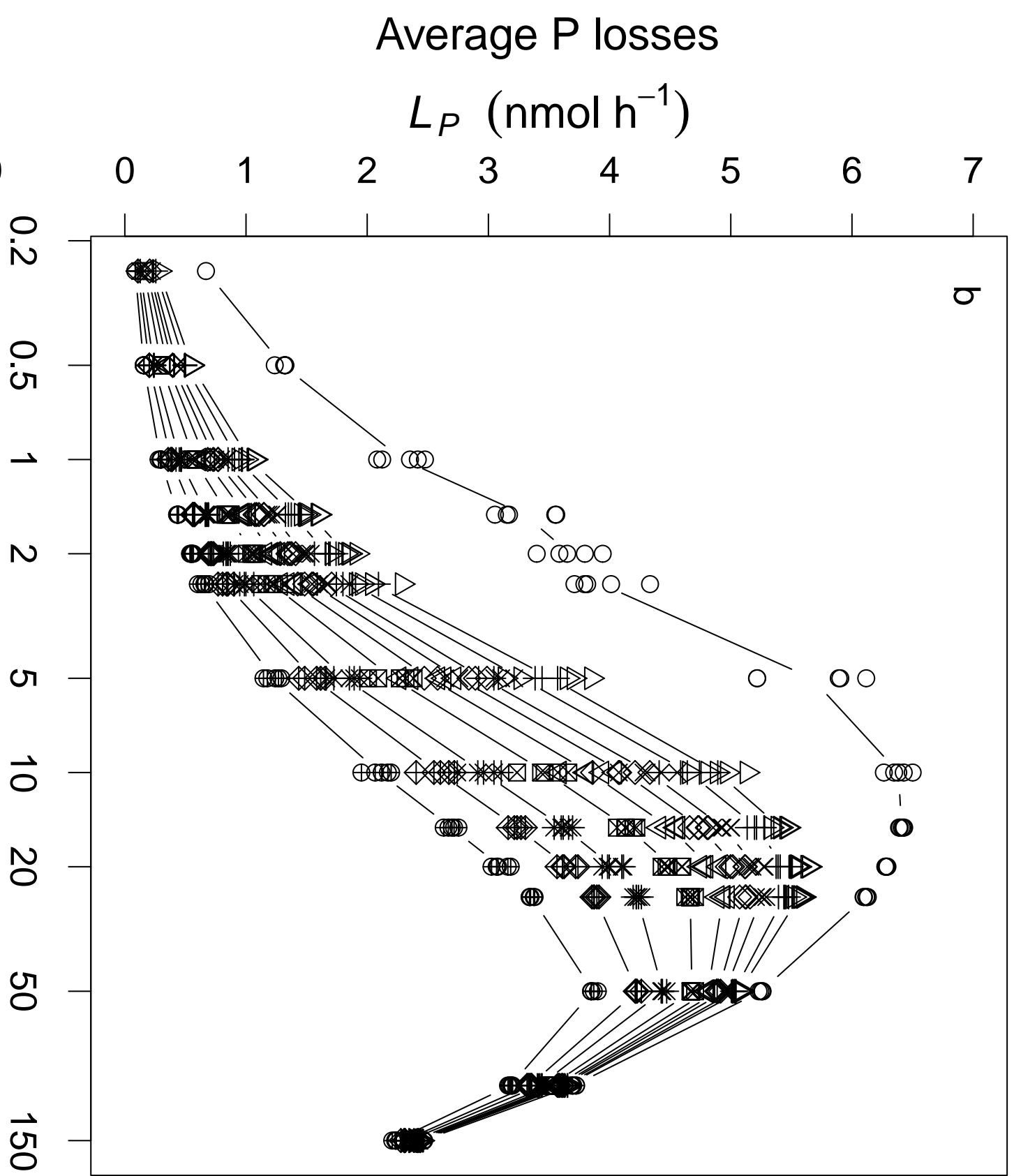
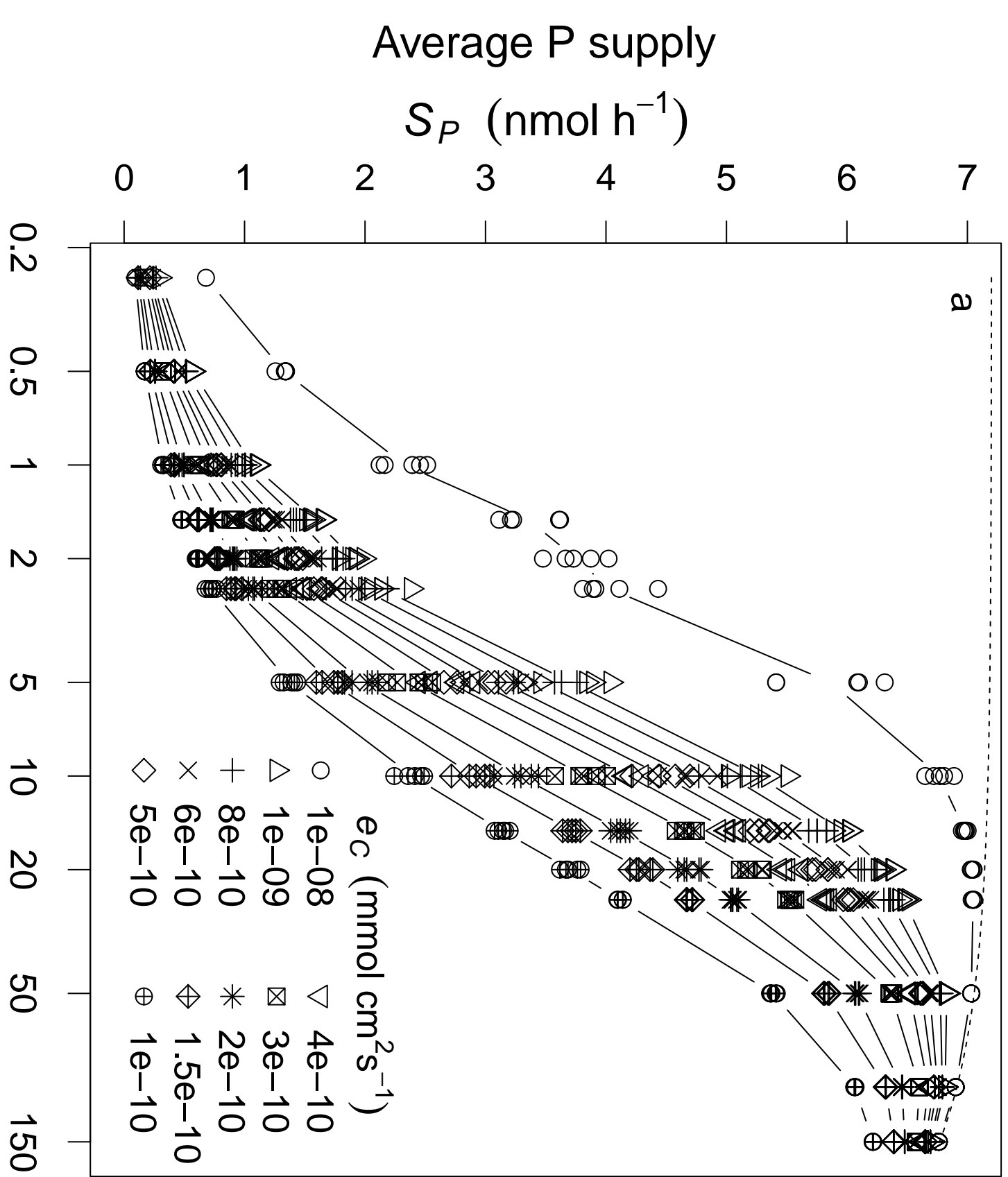


Phosphorus supply



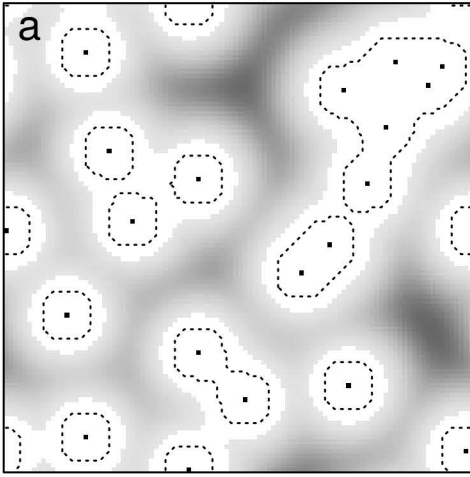
Phosphorus concentration



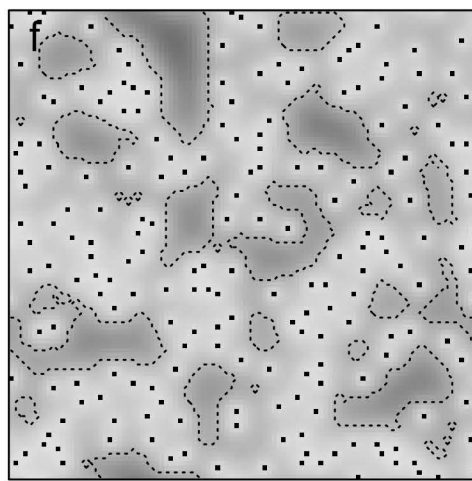
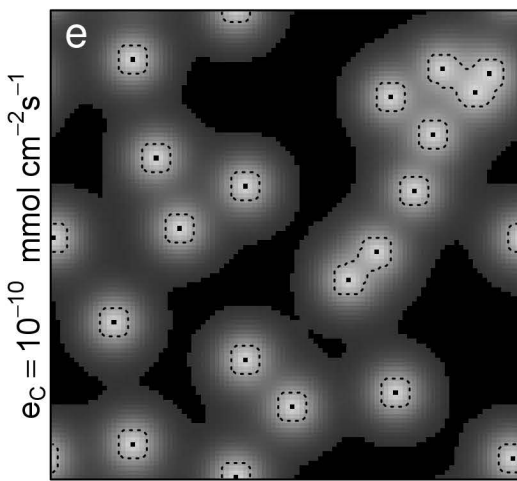
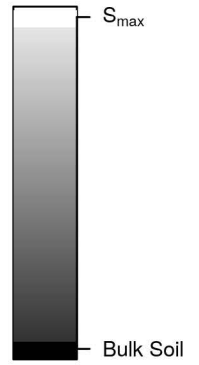
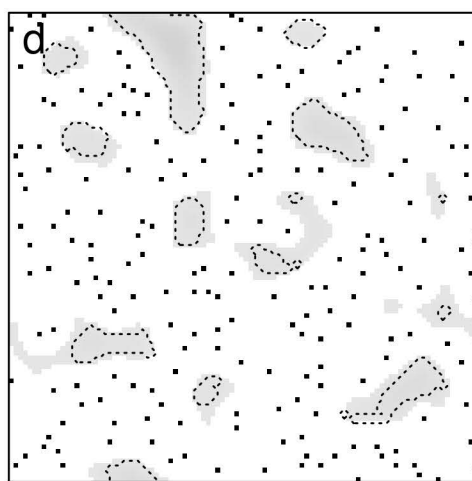
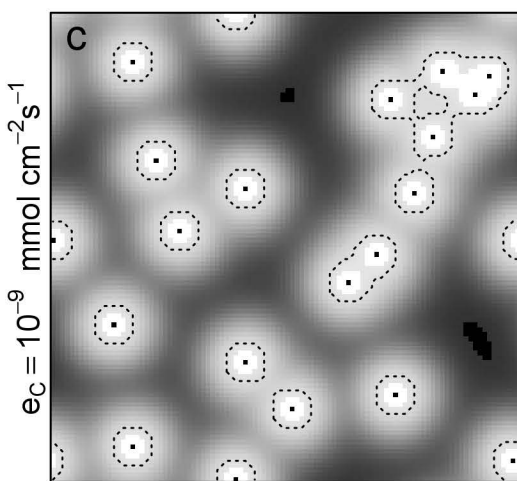
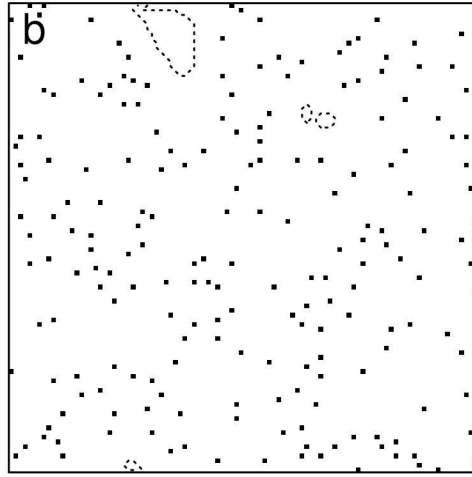


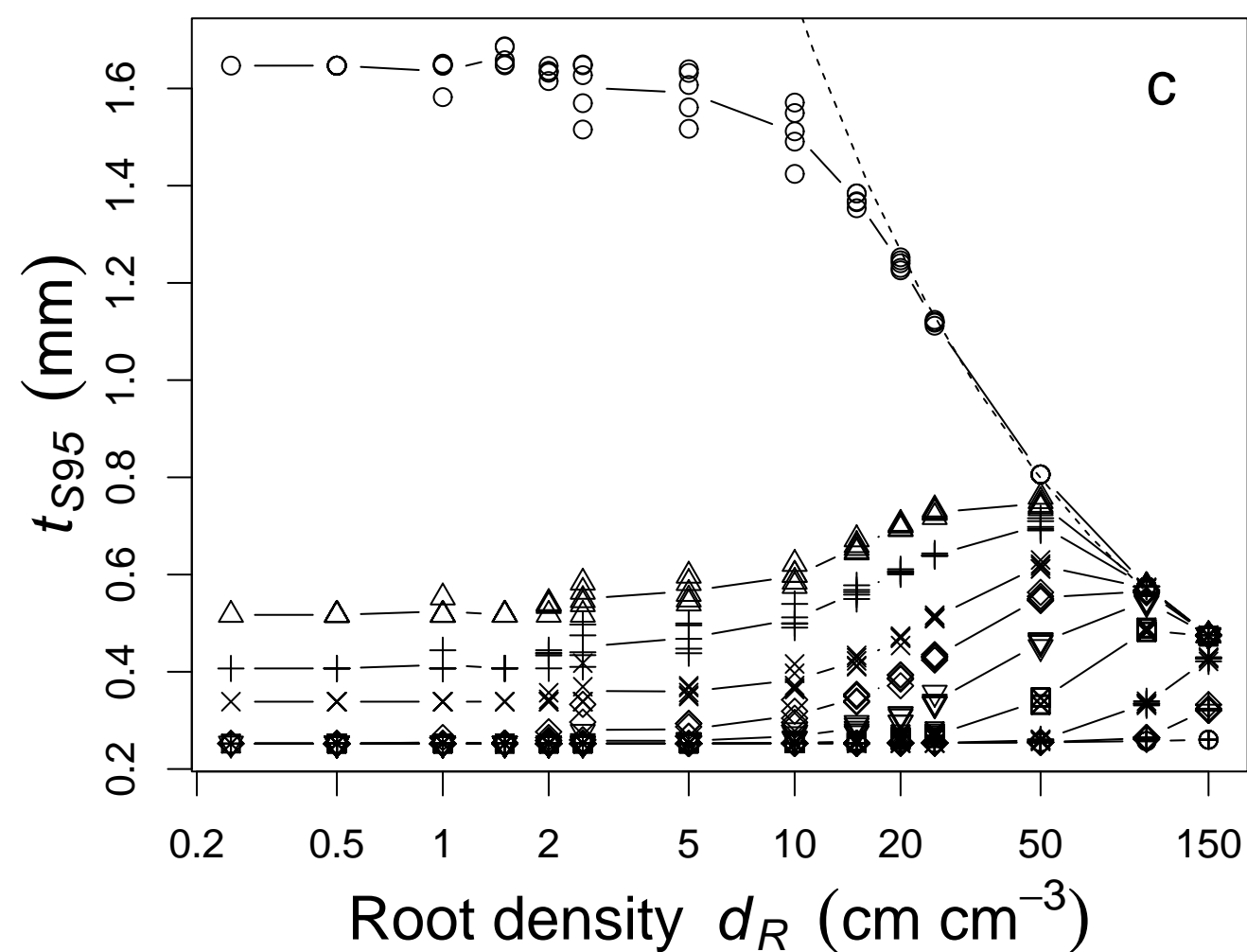
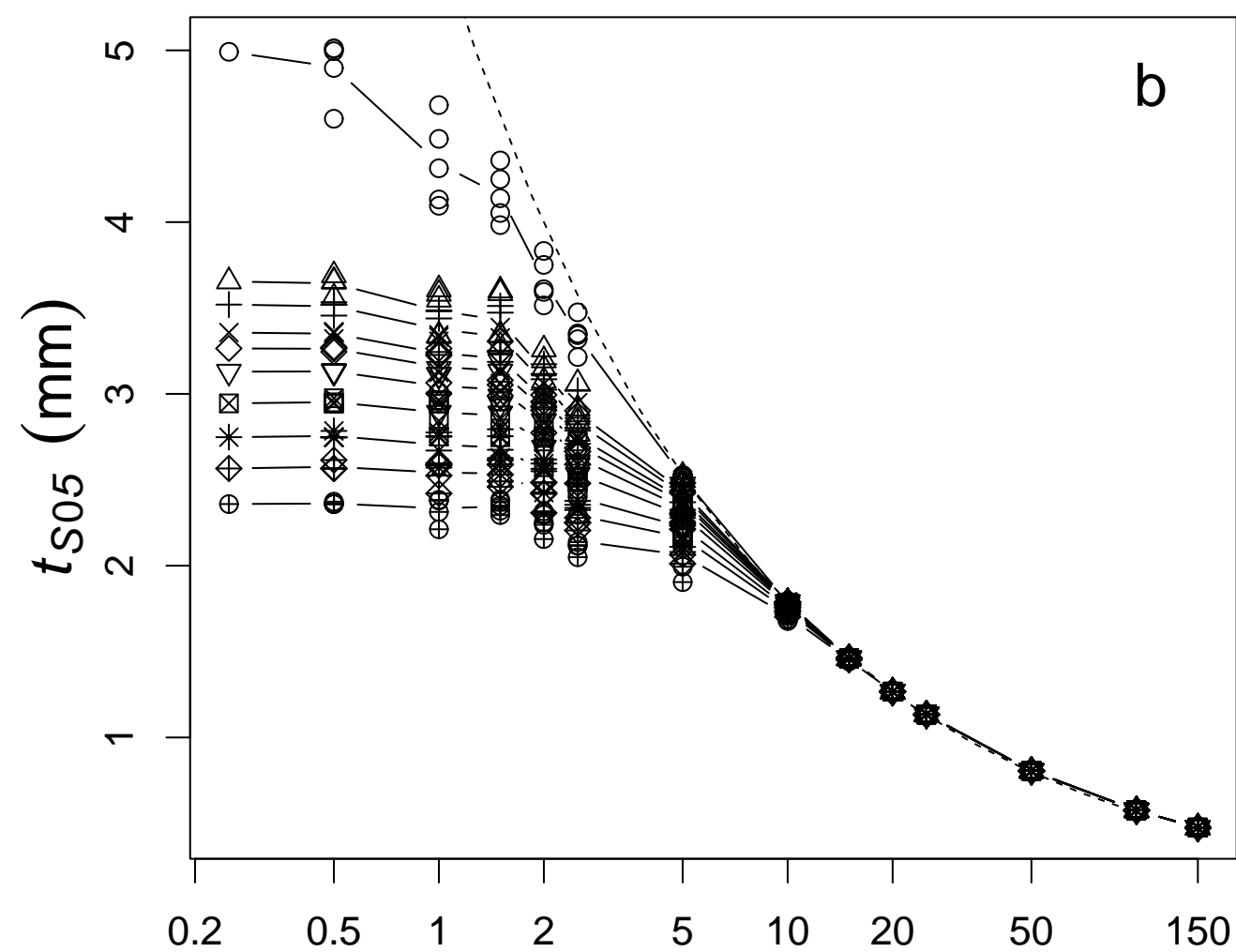
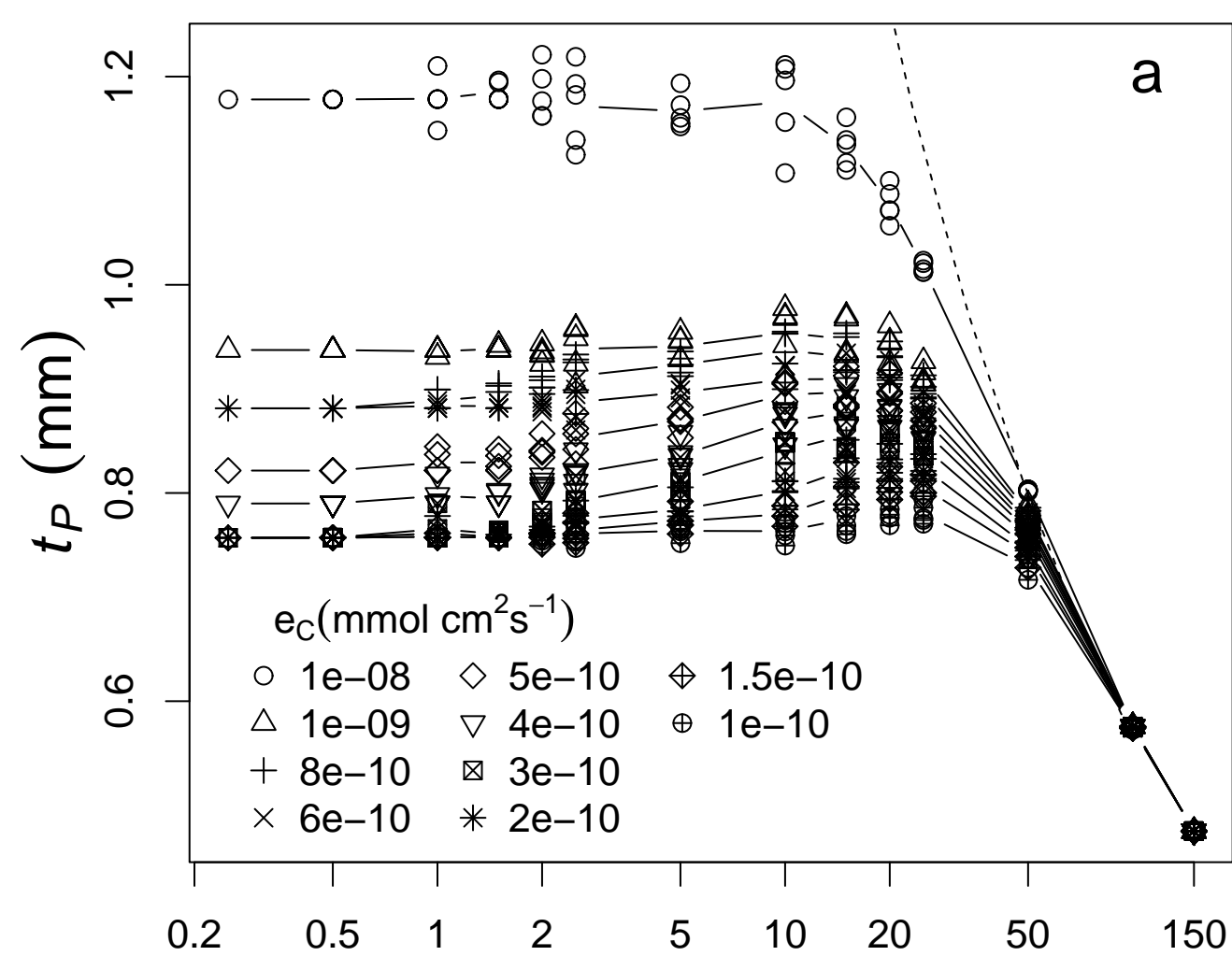
Root density  $d_R$  ( $\text{cm cm}^{-3}$ )

$d_R = 5 \text{ cm cm}^{-3}$



$d_R = 50 \text{ cm cm}^{-3}$





## **Supporting Information**

Article title: **Facilitation or competition within a root system depends on the overlap of root depletion and accumulation zones: a mechanistic model**

Authors: H. de Parseval, S. Barot, J. Gignoux, J.-C. Lata and X. Raynaud\*

## Mathematical development of the PARIS model:

The model considers the diffusion of citrate (C) and phosphate (P) in soil with effective diffusion coefficients  $D_{e,C}$  and  $D_{e,P}$  (Eq. 2). When C is present in the soil, it increases the concentration of P by  $S_P$  following Eq. 6. We assume that C and P disappear from the soil at rates  $\mu_C$  and  $\mu_P$ , respectively. The rate of change in C and P with time is then expressed as:

$$\frac{\partial C_C}{\partial t} = D_{e,C} \nabla^2 \cdot C_C - \mu_C C_C \quad (1)$$

$$\frac{\partial C_P}{\partial t} = D_{e,P} \nabla^2 \cdot C_P - \mu_P C_P + S_P \quad (2)$$

where  $C_P$  and  $C_C$  correspond to the concentration of P and C in the soil solution.

We consider the following boundary conditions:

*Inner boundary condition:* We assume that all roots in the model are identical, with surface  $s=4hz$ . Roots release C from the root surface at constant rate  $e_C$  and take up P at rate  $U_P$  that follows a Michaelis-Menten equation depending on P concentration at the root surface (Eq. 5).

*Outer boundary condition:* to limit border effects, we consider a periodic outer boundary condition, i.e., assume that diffusion in soil occurs on a torus in which top and bottom, as well as left and right edges of the soil volume are connected.

Due to the conservation of mass in the soil, at steady-state we thus have,

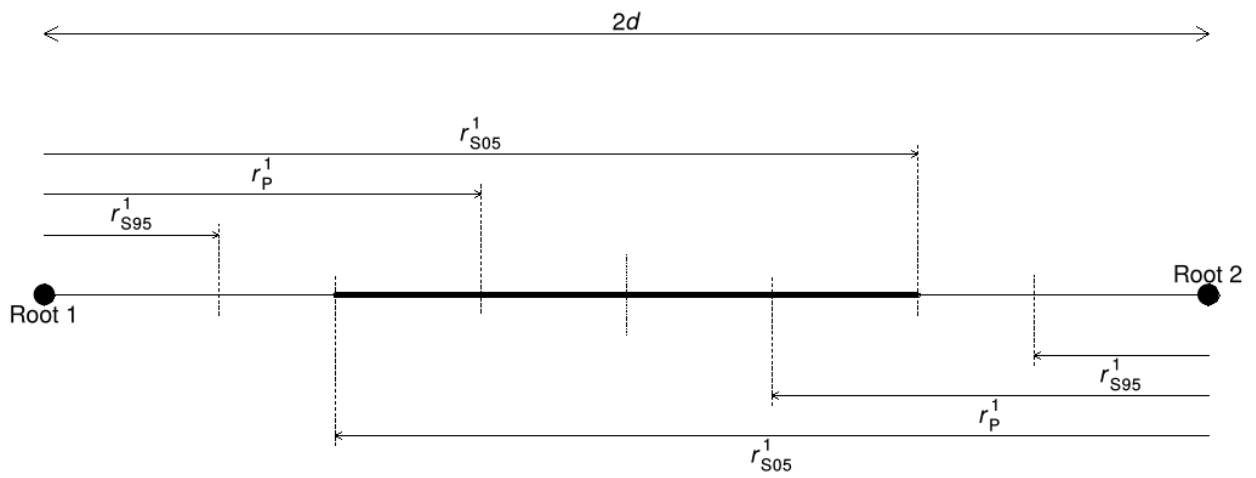
$$nsU_P = D_{e,P} \nabla^2 \cdot C_P - \mu_P C_C + S_P \quad (3)$$

$$nse_C = D_{e,C} \nabla^2 \cdot C_C - \mu_C C_C \quad (4)$$

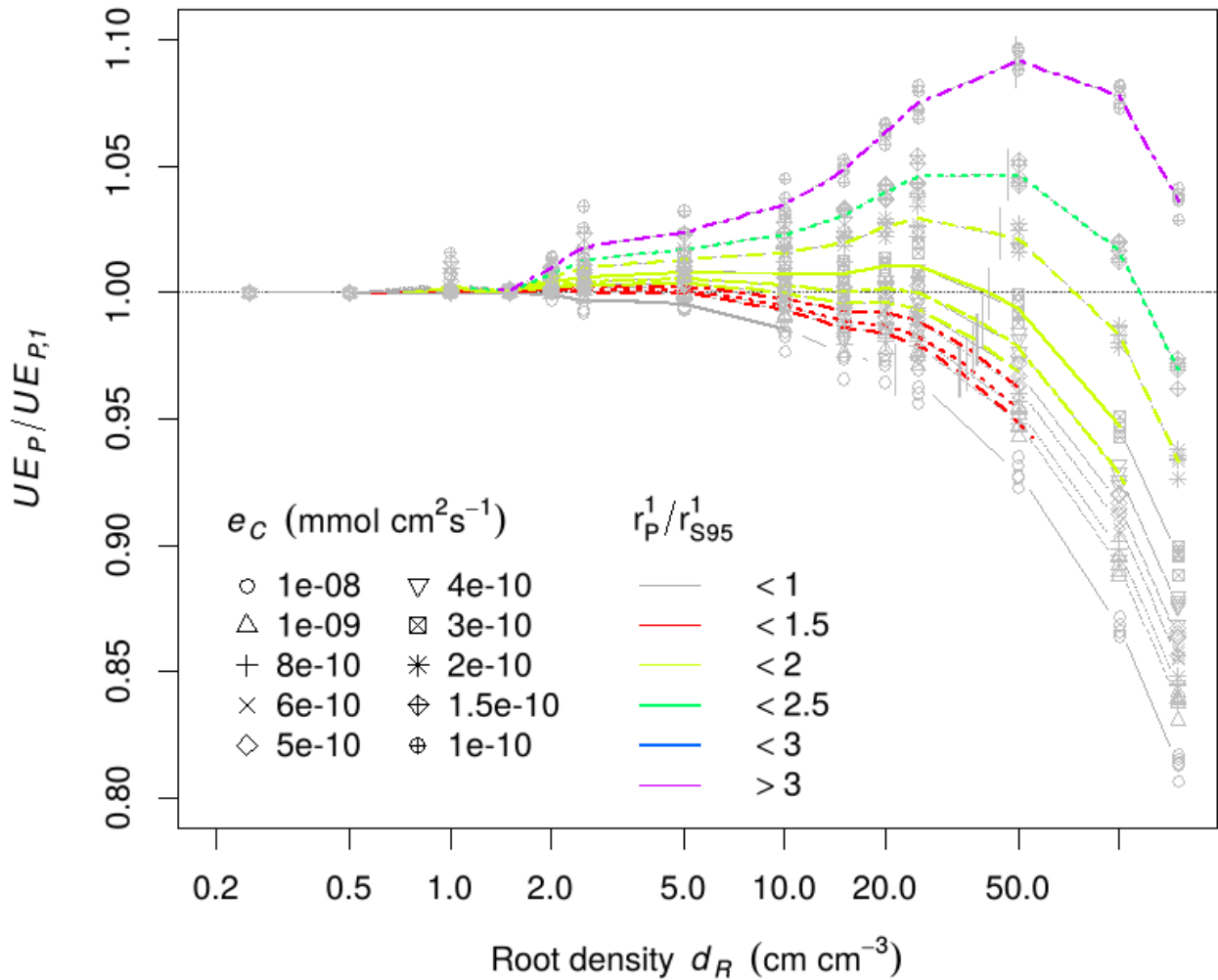
where  $s$  is the surface of a root and  $n$  is the number of roots in the modelled soil volume.



**Fig. S1:** Diagram illustrating interactions between two roots in one dimension. Roots are separated by distance  $2d$ . Horizontal arrows indicate the influences zones developed by root 1 and 2 while vertical dashed lines show their respective limits. In this diagram, the increase in supply occurs in the region shown as a thick horizontal line.



**Fig S2:** Phosphorus uptake efficiency (Eq. 9) relative to the uptake of a single root as a function of root density ( $d_R$ , log scale). Symbols follow the same convention as in Figure 3 and 5 of the main text. Lines are coloured for  $d_R$  values for which conditions  $r_{95}^l < r_{max}(d_R)$  (condition 2) and  $2*r_{05}^l > r_{max}(d_R)$  (condition 3) are met. Colours correspond to the value of  $r_P^1/r_{S95}^1$ . The vertical line indicates the density over which condition 1 is not met. See main text for details.



**Table 1**

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

**Table 2**

<i>Symbol</i>	<i>Values</i>	<i>Ref.</i>
$\theta$	0.15 cm <sup>3</sup> cm <sup>-3</sup>	7
$\theta_{th}$	0.1 cm <sup>3</sup> cm <sup>-3</sup>	5
$\rho$	1.16 g cm <sup>3</sup>	7
$D_{l,P}$	8.2 10 <sup>-6</sup> cm <sup>2</sup> s <sup>-1</sup>	8
$k_{d,P}$	82.6 cm <sup>3</sup> g <sup>-1</sup>	5
$\mu_P$	10 <sup>-3</sup> – 10 <sup>-7</sup> mmol <sub>P</sub> s <sup>-1</sup>	
$D_{l,C}$	6.2 10 <sup>-6</sup> cm <sup>2</sup> s <sup>-1</sup>	8
$K_{d,C}$	4.4 cm <sup>3</sup> g <sup>-1</sup>	1, 5
$\mu_C$	10 <sup>-5</sup> mmol <sub>C</sub> s <sup>-1</sup>	2, 3
$K_S$	10 <sup>-5</sup> mmol <sub>C</sub> cm <sup>-3</sup>	7
$S_{min}$	10 <sup>-12</sup> – 10 <sup>-11</sup> mmol <sub>P</sub> cm <sup>-3</sup> s <sup>-1</sup>	7
$S_{max}$	5 10 <sup>-10</sup> mmol <sub>P</sub> cm <sup>-3</sup> s <sup>-1</sup>	7
$n_R$	1 – 600 unitless	
$I_{max}$	2 10 <sup>-8</sup> mmol <sub>P</sub> cm <sup>-2</sup> s <sup>-1</sup>	7
$K_U$	10 <sup>-4</sup> mmol <sub>P</sub> cm <sup>-3</sup>	7
$e_C$	10 <sup>-10</sup> – 10 <sup>-8</sup> mmol <sub>C</sub> cm <sup>-2</sup> s <sup>-1</sup>	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).