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Modeling forest floor contribution to phosphorus supply to maritime pine seedlings in two-layered forest soils

Mathieu Jonard[a,*], Laurent Augusto[c], Emmanuel Hanert[b], David L. Achat[d], Mark R. Bakker[d], Christian Morel[c], Alain Mollier[c], Sylvain Pellerin[c]

[a] Université catholique de Louvain, Faculté d'Ingénierie Biologique, Agronomique et Environnementale, Unité des Eaux et Forêts, Croix du sud 2/009, B-1348 Louvain-la-Neuve, Belgium
[b] Université catholique de Louvain, Faculté d'Ingénierie Biologique, Agronomique et Environnementale, Département des sciences du milieu et de l'aménagement du territoire, Place Croix du sud 2/016, B-1348 Louvain-la-Neuve, Belgium
[c] INRA, UMR 1220 TCEM (INRA-ENITA), avenue E. Bourlaux 71 BP81, 33883 Villenave d'Ornon, France
[d] ENITA de Bordeaux, UMR 1220 TCEM (INRA-ENITA), avenue E. Bourlaux 71 BP81, 33883 Villenave d'Ornon, France

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ABSTRACT

The quantitative contribution of the forest floor to P nutrition of maritime pine seedlings was experimentally determined by Jonard et al. (2009) in a greenhouse experiment using the radio-isotopic labeling. To extend the results of the experiment on a known mineral soil, a modeling approach was developed to predict P uptake of maritime pine seedlings growing in a mineral soil covered with a forest floor layer. The classical nutrient uptake model based on the diffusion/mass-flow theory was extended to take into account mineralization of P in dead organic matter, microbial P immobilization and re-mineralization and P leaching. In addition, the buffer power characterizing the P retention properties of the mineral soil was allowed to vary with time and with the P-ion concentration in solution. To account for increasing root competition with time, a moving boundary approach was implemented. According to the model, the forest floor contributed most of the P supply to the seedlings (99.3% after 130 days). Predicted P uptake was consistent with observed P uptake and modeling efficiency was 0.97. The uptake model was then used to evaluate the impact of the P retention properties of the mineral soil on the contribution of the forest floor to P uptake. Simulations showed that the contribution of the forest floor was much lower in the quasi non-reactive soil (45.7%) but rapidly increased with soil P reactivity.

1. Introduction

A series of field observations reported in the scientific literature led us to believe that phosphorus nutrition of forest trees could be favored by thick holorganic layers in forest ecosystems growing on acid soils (Carey et al., 1982; Paré and Bernier, 1989; Compton and Cole, 1998; Jonard et al., 2006; Merino et al., 2008). We hypothesized that the forest floor is much more efficient in supplying P to trees than the underlying mineral horizons given its low P retention capacity that allows close coupling of P mineralization and root uptake (Wood et al., 1984; Paré and Bernier, 1989; Northup et al., 1995). In the mineral horizons, most mineralized P is generally transferred to the solid phase; so, the P-ion concentration in solution is maintained at a much lower level than in the forest floor (Achat et al., 2009).

To better understand the role of the forest floor in P nutrition, maritime pine seedlings were grown in pots containing an organic and a mineral layer (Jonard et al., 2009). By labeling the isotopically exchangeable P ions in the mineral layer with ^{33}P, it was possible to estimate that 99.1% of the P taken up by the pine seedlings originated from the organic layer. However, it is difficult to generalize the results of this experiment conducted on one known mineral soil, since the contribution of the forest floor to P nutrition most probably depends on the properties of the mineral soil.

The objective of this paper is to develop a P uptake model adapted to our soil–plant system, to validate it by comparing the predictions of the model with the P uptake measurements and to use it in a wider range of soil conditions with the aim of extending the results of the greenhouse experiment.

Our model of P uptake by roots was elaborated classically by coupling the differential transport equations in soils with the absorption kinetics by roots (Nye and Tinker, 1977; Barber, 1995; Roose et al., 2001). The continuity equation derived for this type of problem can be solved analytically for specific boundary conditions or numerically. Analytical solutions can be found by supposing that

* Corresponding author. Tel.: +32 0 10 47 25 48; fax: +32 0 10 47 36 97.
E-mail address: Mathieu.jonard@uclouvain.be (M. Jonard).

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the concentration profile around the root is in a steady state (Nye and Tinker, 1977; Yanai, 1994; Comerford et al., 2006) or by considering that the root behaves as a zero sink, which means that the uptake rate equals the rate at which the nutrient arrives at the root surface (De Willigen and van Noordwijk, 1994). For the forest floor layer, the steady-state solution could be applied but the zero-sink assumption is not realistic since, given the high concentration of P ions in solution (Jonard et al., 2009), the P uptake was certainly regulated. For the mineral soil, given the very low concentration of P ions in solution and the strong buffer power (Jonard et al., 2009), the zero-sink approach is certainly more appropriate. Roose et al. (2001) proposed a more general analytical solution, which was however impossible to implement in our case since it depends on the concentration far from the root that varies with time in both growing media. To have the same solution for both growing media, we decided to solve the continuity equation numerically. The classical nutrient uptake model was extended to take into account mineralization of P in dead organic matter, microbial P immobilization and re-mineralization and P leaching (Appendix A). Using the SSAND model (steady-state approach), Kabba et al. (2009) showed the importance of the mineralization flux for the prediction of P uptake. To our knowledge, these P sources and sinks have never been considered with the numerical approach, possibly because it complicates the problem as new roots start growing in new boundary conditions (concentration). The classical uptake model assumes that the concentration of diffusive P ions at the solid/solution interface of the soil and the concentration in solution are linearly related and that the buffer power is constant. In our model, we allowed the buffer power to vary with time and with the concentration in solution by characterizing the P-ion transfer between the solid phase and the solution using the isotopic dilution method (Fardeau, 1996; Frossard and Sinaj, 1997). Finally, to account for increasing root competition with time, a moving boundary approach was implemented (Reginato et al., 2000). Since the development of ectomycorrhizal mycelium was very limited during the experiment (Jonard et al., 2009), it was not taken into account in the model.

2. Materials and methods

2.1. Greenhouse experiment

This greenhouse experiment is fully described in Jonard et al. (2009). In the following, we only mention the most important characteristics of the experiment. Three-week-old maritime pine seedlings were planted in pots containing a layer of mineral soil (MS) overlaid with a forest floor layer (FF). The pots were placed in a greenhouse and distributed in five blocks according to a randomized block design. Three pots were positioned within each block since the maritime pine seedlings were harvested at three different dates. In addition, a control pot without seedlings was included in three out of the five blocks.

The pots were filled with 1480 g of dry mineral soil and 236 g of dry forest floor materials (depth of MS: 10 cm + depth of FF: 6 cm). Twenty-three days after sowing, three seedlings of maritime pine (*Pinus pinaster* Aït.) were transplanted in each pot. At this stage, the seedlings had an average biomass of 0.028 g seedling^{-1}, a P content of 0.21 mg seedling^{-1} and a root length of 7.4 cm seedling^{-1}.

At each date (61, 95 and 130 days after planting), a third of the seedlings (five pots) were harvested. The seedling shoots were cut; the roots were extracted from the growing media and carefully washed with deionized water. The roots were then divided into two components corresponding to the two layers (MS and FF). For all seedlings, total root length and mean root diameter of both root components were measured with Winrhizo software (Ver. 2005.A; Regent Instruments, Quebec, Canada). For each seedling, shoot and root biomass were determined after drying at 105 °C until constant weight. The concentration of P in the shoot and roots was determined by inductively coupled plasma spectrometry after combustion in a muffle furnace at 450 °C for 12 h and acid digestion with HNO_3 (14 N).

During the pot experiment, the shoot and root biomasses of the pine seedlings increased exponentially and amounted to respectively 2.16 g and 0.55 g per seedling 130 days after planting. For all harvest dates, P uptake was calculated by subtracting the initial P content of the seedlings from the current P content. The relative contribution of the mineral soil and the forest floor to P uptake was estimated based on a parallel pot experiment using labeling of isotopically exchangeable phosphate ions of the mineral soil and applying the dilution principle (Jonard et al., 2009). The P uptake of the pine seedlings also increased exponentially with time and amounted to 1.81 mg per seedling 130 days after planting. During this period, the forest floor contribution to P uptake was estimated at 99.1%.

2.2. Model description

The main assumptions are:

1. The two growing media are homogeneous and isotropic.
2. Moisture conditions are constant throughout the simulation in both growing media.
3. Root segments are smooth cylinders of constant radius and length.
4. Roots are uniformly distributed and parallel in each growing medium.
5. Root growth is exponential.
6. P uptake occurs from P ions in solution at the root surface and is regulated according to a Michaelis–Menten equation.
7. Inward radial velocity of water at the root surface is constant.
8. The mineralization rate of dead organic matter is constant.
9. The amount of P transferred from the forest floor to the mineral soil is distributed homogeneously within the mineral soil.

The continuity equation for P-ion flux through a cylinder of soil around a root can be modeled as follow:

Transport equation:

$$(\theta + b)\frac{\partial c}{\partial t} = \frac{\theta D}{r}\frac{\partial}{\partial r}\left(r\frac{\partial c}{\partial r}\right) + \frac{aV}{r}\frac{\partial c}{\partial r} + \mathrm{Min} + \Delta \mathrm{P}_{\mu} - L \quad (1)$$

Boundary conditions:

$$\theta D\frac{\partial c}{\partial r} + Vc = \frac{I_{\max} c}{K_{\mathrm{m}} + c} \quad \text{on } r = a, \quad (2)$$

$$\theta D\frac{\partial c}{\partial r} + Vc = 0 \quad \text{on } r = R(t) \text{ and } 0 < t < T \quad (2')$$

Initial conditions:

$$c = c_0 \text{ at } t = 0 \text{ and } a < r < R(t)$$

where

(i) c is the P-ion concentration in solution per unit of soil volume (mol P m^{-3}) and c_0 is the initial concentration (mol P m^{-3});
(ii) t is the time elapsed since the beginning of the simulation (s) and T is the time elapsed between transplanting and harvest (s);
(iii) b is the buffer power:

$$b = \frac{\partial c_{\mathrm{s}}}{\partial c} \quad (3)$$

with c_s, the amount of diffusive P retained on the solid phase (mol P m^{-3}). The dynamics of c_s vs c and t is mathematically described by the kinetic Freundlich equation, which generally highly and closely fit experimental values in soils (Morel et al., 2000; Stroia et al., 2007):

$$c_s = vc^w t^p \quad (4)$$

where v, w and p are parameters fitted with the experimental dataset obtained during a short-term batch experiment (determination of the kinetics of isotopic dilution by radio-isotopic labeling of P ions with ^{32}P). Deriving Eq. (4) with respect to c gives

$$b = vwc^{w-1}t^p \quad (5)$$

Eq. (5) is valid for $t < t_{max}$ which is the time necessary to reach the isotopic equilibrium. According to Fardeau (1993), c_s increases with time (Eq. (4)) until a maximum value which is assumed to be equal to the total amount of soil inorganic P. In the forest floor, b is equal to zero since the solid phase is not reactive and all the P ions are in solution (Jonard et al., 2009).

(iv) D is the diffusion coefficient (m^2 s^{-1}) given by $D = D_0\theta f$ with D_0, the diffusion coefficient in free water (m^2 s^{-1}); θ, the volumetric water content (m^3 m^{-3}) and f, the tortuosity factor (m m^{-1}).

(v) r is the radial distance from the root axis (m);

(vi) R is the average radial distance from the center of the root to the next root's zone of influence

$$R(t) = \frac{1}{\sqrt{\pi((L_r(t))/\mathrm{Vol})}} \quad (6)$$

with L_r, the root length which increases exponentially with time $L_r = e^{kt}$ and Vol, the volume of soil (m^3);

(vii) a is the root radius (m);

(viii) V is the inward radial velocity of water at the root surface (m s^{-1});

(ix) Min is the mineralization rate of the dead organic matter (mol P m^{-3} s^{-1});

(x) ΔP_μ is the microbial re-mineralization rate (mol P m^{-3} s^{-1}), which is obtained by deriving the exponential equation describing the decrease in microbial P with time (Achat, 2009):

$$P_\mu(t) = P_{\mu 0}e^{-gt} \quad (7)$$

$$\Delta P_\mu = -\frac{dP_\mu}{dt} = P_{\mu 0}ge^{-gt} \quad (8)$$

where $P_{\mu 0}$ is the initial microbial P (mol P m^{-3}) and g is the decrease coefficient;

(xi) L is the rate of P transferred by leaching (mol P m^{-3} s^{-1});

For a root segment in the forest floor, the rate of P transferred by leaching (L_{FF}) is calculated by multiplying the average P-ion concentration of the forest floor solution (c_{av_FF} in mol P m^{-3}) by the rate of water transfer from the forest floor to the mineral soil (T_{water_FF} in m^3 m^{-3} s^{-1}), which is obtained from the rate of water uptake by roots in the mineral soil since the water content was maintained constant in the pot:

$$L_{FF} = T_{water\_FF}c_{av\_FF} \quad (9)$$

with

$$T_{water\_FF} = \frac{VL_{r\_MS}2\pi a}{\mathrm{vol}_{FF}} \quad (10)$$

where L_{r_MS} is the root length in the mineral soil (m) and vol_{FF} is the volume of the forest floor layer (m^3). The initial value of c_{av_FF} is known and its temporal change is obtained by taking into account all the sinks and sources of P ions in solution:

$$\frac{dc_{av\_FF}}{dt} = \mathrm{Min} - \frac{\mathrm{Up}_p}{\mathrm{vol}_{FF}} + \Delta P_\mu - L_{FF} \quad (11)$$

where Up_p is the P uptake rate in the forest floor (mol P s^{-1}) and vol_{FF} is the volume of the forest floor layer (m^3).

For a root segment in the mineral soil, the rate of P leaching from the forest floor (L_{MS}) is obtained by multiplying L_{FF} by the ratio between the volume of the forest floor and the volume of the mineral soil. As the leaching corresponds to an input of P in the mineral soil, a negative sign is thus affected to the value obtained.

$$L_{MS} = -L_{FF}\frac{\mathrm{vol}_{FF}}{\mathrm{vol}_{MS}} \quad (12)$$

where vol_{MS} is the volume of the mineral soil layer (m^3).

(xii) I_{max} is the maximal P influx rate (mol P m^{-2} s^{-1}) and K_m is the half-saturation constant for uptake (mol P m^{-3}).

The P uptake rate (Up_P in mol P s^{-1}) of a root segment of length l (m) is calculated as follows:

$$\mathrm{Up}_P = \frac{I_{max}c}{K_m + c}2\pi al \quad (13)$$

Our model considers that a new root segment appears every x days in each growing medium. In a growing medium, the length of the root segments (l in m) is determined based on an exponential growth function. The P uptake in a growing medium is calculated by integrating the P uptake rate over the time and by summing the contributions of the different root segments. The total P uptake of the three seedlings in the same pot is the sum of the P uptake in the forest floor and in the mineral soil. The initial P-ion concentration encountered by the different root segments that appear at different times is determined by solving Eq. (1) considering no P uptake by roots until the appearance of the root segment concerned.

2.3. Input variable

Aside from the simulation duration, the only input variable for our model is the exponential coefficient (k) describing root growth. Based on the root length measured at the three harvest dates, we observed that root length increased exponentially with time (Fig. 1). As we have only root length measurements at the beginning of the experiment and at harvest for a given pot, the coefficient (k) of the exponential equation ($L_r = e^{kt}$) is obtained by:

$$k = \frac{\ln(L_{r\_harvest}) - \ln(L_{r\_init})}{T} \quad (14)$$

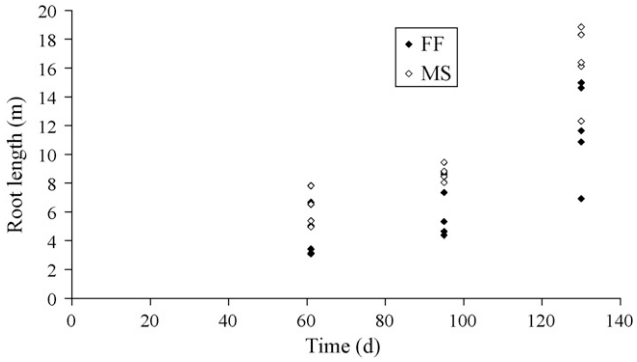

Fig. 1. Root length per pot at the three harvest dates for both growing media.

Table 1
Parameters of the P uptake model used for the forest floor and the mineral soil layers.

	FF	MS
Soil parameters		
c_0, initial P-ion concentration in solution (mol P m^{-3})	1.27E−02	5.74E−05
b, soil buffer power for P	0.00E+00	
v, parameter of the Freundlich kinetic equation		2.66E+01
w, parameter of the Freundlich kinetic equation		8.10E−01
p, parameter of the Freundlich kinetic equation		3.30E−01
t_{max}, time to reach the isotopic equilibrium (s)		2.07E+06
D_0, P-ion diffusion coefficient in free water (m^2 s^{-1})	8.91E−10	8.91E−10
f, tortuosity factor (m m^{-1})	1.55E−01	1.03E−03
θ, volumetric water content (m^3 m^{-3})	3.36E−01	2.17E−01
Min, P mineralization rate of the dead organic matter (mol P m^{-3} s^{-1})	5.51E−09	7.09E−09
$P_{\mu 0}$, initial microbial P (mol P m^{-3})	6.49E−01	2.45E−01
g, coefficient of the exponential equation describing P_μ decrease	3.70E−08	5.31E−08
vol, volume of the layer in the pot (m^3)	1.31E−03	1.48E−03
Plant parameters		
a, root radius (m)	3.50E−04	3.50E−04
L_{r0}, initial root length (m)	1.80E−01	4.20E−02
K_m, half-saturation constant for P uptake (mol P m^{-3})	1.21E−02	1.21E−02
I_{max}, maximal P influx rate (mol P m^{-2} s^{-1})	1.74E−09	1.74E−09
V, inward radial velocity of water at the root surface (m s^{-1})	5.67E−09	5.67E−09

where L_{r_init} and $L_{r\_harvest}$ are the initial and final root length (m pot^{-1}) and T is the time elapsed between transplanting and harvest. The initial root length is 0.18 m per pot in the forest floor and 0.042 m in the mineral soil.

2.4. Determination of model parameters

The model parameters were not adjusted by inverse modeling based on the observed P uptake but were determined by complementary experiments or taken from the literature (Table 1).

2.4.1. Soil parameters

For both growing media, the initial P-ion concentration in solution was determined by colorimetry (Van Veldhoven and Mannaerts, 1987) on filtered solutions of mineral soil and forest floor suspensions (solid phase:solution ratio: 1:1.5 and 1:10, respectively) after gently shaking for 16 h overnight at 4 °C.

The parameters of the Freundlich kinetics that characterize the dynamics of retention and release of P ions between the solid and liquid phases of the mineral soil were obtained by determining the kinetics of isotopic dilution using the radio-isotopic labeling of P ions (with ^{32}P) during a short-term batch experiment (Stroia et al., 2007). The theoretical basis of this method is explained in Fardeau (1993, 1996) and in Frossard and Sinaj (1997).

The gross amount of P ions exchanged between the solution and the solid phase varies greatly both with time and with the concentration of P ions in solution, it was therefore determined for three time periods (4, 40 and 400 min) and several levels of P supply (0, 1, 2, 4, 6 and 10 μg P g^{-1}).

Soil suspensions were prepared by mixing 10 g of mineral soil (previously kept in a fresh state at 4 °C) with the appropriate volume of a KH_2PO_4 solution (100 mg L^{-1}), with 0.2 mL of biocide (toluene) and with distilled water to obtain a final ratio of solution to substrate of 1:1.5.

All suspensions were pre-equilibrated for 16 h on a shaking table. Carrier-free ^{32}P ions were added to the different suspensions at time zero. After 4, 40 and 400 min, approximately 4 mL were removed from all suspensions and filtered (0.2 μm). The radioactivity introduced (R) and that remaining in the filtered solution was counted in a liquid scintillation cocktail (Insta-gel Plus Packard), using a liquid scintillation counter (TriCarb TR Packard). The P-ion concentration in the filtered solution was determined by the molybdate and green malachite colorimetric method (Van Veldhoven and Mannaerts, 1987).

To estimate the mineralization rate in the pots during the experiment, samples of mineral soil and forest floor were incubated in containers placed in the greenhouse, assuming that the absence of seedlings did not bias our mineralization estimates. The incubation and pot experiments were conducted in parallel during the same period. Five containers were used for each kind of material, plus three control containers without any material. Incubation containers were made from plastic tubing (length 30 cm, Ø 15.5 cm). The bottom end was covered with a fine plastic mesh (30 μm) and supported by a perforated plate extended by a piece of small rubber tubing closed with Mohr pliers. The containers were filled with either 200 g of dry mineral soil or 30 g of dry forest floor material. Before starting incubation, the moisture of the mineral soil and the forest floor was adjusted to maximum water holding capacity.

Given the P retention properties of the mineral soil, the P flux resulting from the mineralization of dead organic matter cannot be obtained by measuring the increase in P ions in solution (Achat, 2009). Assuming that C and P are mineralized from dead soil organic matter in the same proportion (Achat, 2009) and that CO_2 is the main C mineralization product in our system, we estimated the proportion of P mineralized per unit of time as the ratio between the soil respiration rate (SR in mol C m^{-3} s^{-1}) and the total carbon content of the mineral soil (C_{tot} in mol C m^{-3}). This value was then multiplied by the organic P content of the mineral soil (P_{org} in mol P m^{-3}) to obtain the net P mineralization rate (Min in mol P m^{-3} s^{-1}):

$$\mathrm{Min} = \frac{\mathrm{SR}}{C_{tot}} P_{org} \quad (15)$$

CO_2 release from the mineral soil samples was measured with the absorption alkali method. Two open dishes (one with 20 mL of 1 M NaOH and the other with 50 mL of water) were placed in the mineral soil containers, which were then closed and made airtight. Every two weeks, the containers were opened for titration and replacement of the NaOH solutions and for adjustment of moisture content. As the net P mineralization rate decreased with time before stabilizing after two months of incubation, we considered that the net P mineralization rate measured after two months was equal to the gross P mineralization rate.

In the forest floor layer, the mineralized P is not retained on the solid phase but remains in the soil solution or is incorporated in the microbial biomass. On the other hand, the P-ion concentration in solution can increase due to re-mineralization of microbial P. To avoid any interference with the microorganisms (immobilization and re-mineralization of P), we estimated the P flux resulting from the forest floor mineralization as the difference between the amount of P ions in solution after fumigation obtained at the beginning and at the end of the incubation experiment. The chloroform fumigation method (Morel et al., 1996) was used as it kills the microbes and results in the release of inorganic P. We assumed that the fumigation efficiency was 100% (Achat, 2009). The fumigation method also allowed us to estimate the microbial P (P_μ in mol P m^{-3}) at the beginning and at the end of the incubation experiment; it was obtained by the difference between the inorganic P in

Table 2
Selected soil properties and characterization of the dynamics of retention and release of P ions (Freundlich kinetic equation) of different mineral soils.

	S1	S2	S3	S4[a]
Locality	Tagon	Pierroton	Blagon	Tagon
Coordinates	44°41′01″N 00°57′36″W	44°42′00″N 00°46′00″W	44°48′56″N 00°56′02″W	44°40′36″N 00°56′49″W
Total P (mol P m^{-3})	1.00	1.84	3.00	2.71
Organic P (mol P m^{-3})	0.75	0.98	0.74	1.55
Al oxide (mol Al m^{-3})[b]	7.41E−06	2.59E−05	8.15E−05	8.52E−05
Fe oxide (mol Fe m^{-3})[b]	1.79E−06	5.37E−06	1.43E−05	4.66E−05
c (mol P m^{-3})	0.04	6.03E−04	1.19E−04	5.74E−05
c of P-enriched soils (mol P m^{-3})[c]	0.68	3.76E−03	2.22E−04	1.24E−04
v	0.059	0.343	1.507	26.580
w	0.93	0.46	0.65	0.81
p	0.13	0.31	0.48	0.33
t_{max} (s)	1.92E+08	9.60E+05	4.42E+05	2.07E+06
R^2	0.955	0.920	0.996	0.980
n	68	59	14	18

[a] Mineral soil used for the greenhouse experiment.
[b] Extracted by the Tamm method.
[c] Predicted concentration of the mineral soil if it was enriched with all the P contained in the forest floor layer (1.12 mol P m^{-3}).

the solution of fumigated and non-fumigated forest floor samples. Inorganic P was determined by colorimetry (Van Veldhoven and Mannaerts, 1987) on filtered solutions of forest floor suspensions (solid phase:solution ratio, 1:10) after shaking overnight at 4 °C. The microbial P in the forest floor was higher at the beginning of the experiment than at the end. The high microbial P content at the beginning of the experiment was probably due to a flush of microbial biomass associated with disturbance of the forest floor during collection and grinding. We assume that this microbial biomass decreased exponentially with time (Achat, 2009) and we used the initial and final microbial P content to fit Eq. (7).

The initial microbial P was not determined for the mineral soil, but taken as the mean value of 11 similar soils from the same forest (Achat, 2009). The coefficient characterizing the decrease with time (Eq. (7)) was provided by the same author.

The maximum water holding capacity of the mineral soil and of the forest floor was determined by a gravimetric method on soil samples first saturated with water and then drained for 24 h while avoiding soil water evaporation.

The bulk density of the two growing media was measured on undisturbed soil samples taken from the control pots at the end of the pot experiment.

The tortuosity factor of the mineral soil was computed from soil texture and bulk density using the model of Olesen et al. (2001) and that of the forest floor was determined according the French standard method (AFNOR X31-508) using ^{32}P.

2.4.2. Plant parameters

The mean root radius was obtained from the pot experiment (Jonard et al., 2009). The parameters of the Michaelis–Menten kinetics (the maximal P influx rate and the half-saturation constant for P uptake) were obtained from Van Tichelen and Colpaert (2000).

The inward radial velocity of water at the root surface was taken from Kelly et al. (1992). To check the plausibility of this value, it was used to estimate the water use efficiency of the pine seedlings based on the root length estimated at a daily time step and on the seedling biomass (Jonard et al., 2009). Water use efficiency amounted to 0.005 g g^{-1}, which was in accordance with the values reported by Guehl et al. (1995) for maritime pine seedlings.

2.5. Model operation and evaluation

The model equations were discretized in space by means of a first-order, upwind finite difference scheme. For time integration, a third-order Adams–Bashforth scheme was used. Since such a scheme is not self-starting, a forward Euler and a second-order Adams–Bashforth scheme were used to compute the solution at the first and second time steps, respectively. Such a time integration scheme is conditionally stable. For the problem we considered, typical time step values are of the order of 1 min. The model was implemented in Matlab (The Mathworks inc., 2008, version 7.7.0).

The P uptake per horizon was predicted for different periods (61, 95 or 130 days) and was then compared with observed P uptake using different statistical methods: normalized average error (NAE), paired t-test, normalized root mean square error (NRMSE), modeling efficiency and regression test. NAE evaluates the extent of the bias between the average prediction and observation; the paired t-test indicates whether the mean difference between predictions and observations is significantly different from zero; NRMSE is a measure of predictive accuracy (Janssen and Heuberger, 1995); the modeling efficiency (EF) provides an index of performance on a relative scale (Vanclay and Skovsgaard, 1997); regression analysis enables to test simultaneously if the intercept and the slope of the linear relationship between observations and predictions differ significantly from 0 and 1, respectively (Mayer et al., 1994). Given the large range of P uptake values, a logarithmic transformation (base 10) was used for the calculation of EF and for the regression analysis to avoid residual heteroscedasticity. For each harvest date and each treatment, observed P uptake was calculated as described in Jonard et al. (2009).

2.6. Model use

For the greenhouse experiment, the growing media were collected in the forest of the *Landes de Gascogne*. Al- and Fe-oxihydroxide contents in the collected mineral soil, assessed using the ammonium oxalate method, were at the upper ends of the ranges observed for the sandy podzols in this region (Jonard et al., 2009); we thus assumed that the collected mineral soil was part of the more P-retentive soils (Achat, 2009). As the results of the greenhouse experiment most probably depended on the properties of the mineral soil, three other mineral soils covering the whole range of P reactivity encountered in the *Landes de Gascogne* were selected and characterized according to the methods described in Section 2.4 (Table 2). The P uptake model was then run for the different sets of mineral soil parameters over a period of 130 days, which allowed us to extend our results.

As litter accumulation in the forest floor has two opposite effects on P availability (on one hand, sequestrating P in decomposing

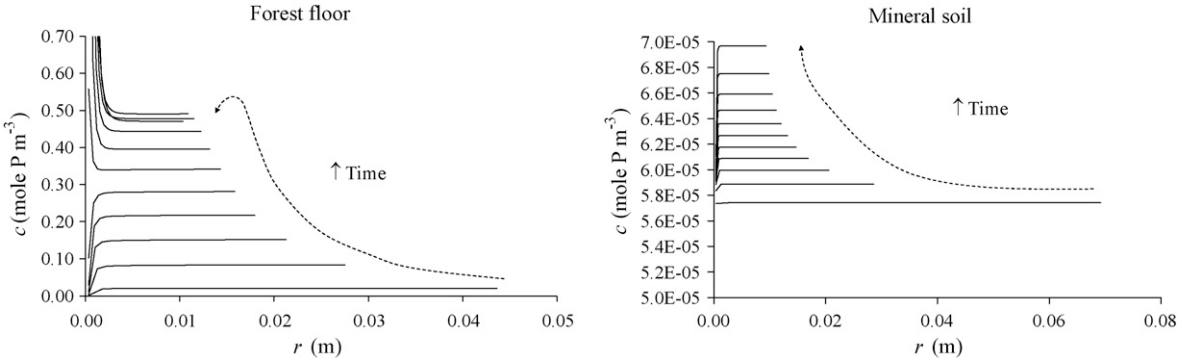

Fig. 2. Predicted P-ion concentration profiles around a root segment after 1, 13, 26, 39, 52, 65, 78, 91, 104, 117 and 130 days in the forest floor and mineral soil layers. The distance from the center of the root to the next root's zone of influence (R) decreases with time as root density increases.

and recalcitrant organic matter and on the other hand, creating a medium favorable for P uptake), we used our P uptake model to evaluate its global effect on the P nutrition of pine seedlings over the 130-day period. The P uptake model was run for soil–plant systems containing only mineral soil enriched with all the P contained in the forest floor. This allowed us to create virtual soil–plant systems in which litter decomposition is so fast that no litter accumulates (no forest floor develops). We assumed that the organic P of the mineral soil was not affected by this fast litter turnover. In these systems, an amount of P ions equivalent to the total P contained in the forest floor was added to the mineral soil (1.12 mol P m^{-3} of mineral soil) and partitioned between the solution and the solid phase using Eq. (4) at t_{max}. Table 2 shows the concentration of P ions in solution in the different P-enriched mineral soils. It should be noted that the volume of the mineral soil in these simulated systems was equal to the sum of the volumes of both growing media in the greenhouse experiment. The total P uptake predicted in these systems was then compared with that of the corresponding two-layer systems.

3. Results

3.1. P-ion concentration in solution

When the P uptake model was running, the P-ion concentration profile around the root was represented for both media (Fig. 2). In the forest floor, the P depletion zone quickly grew and could rapidly have reached steady state for a given P-ion concentration far from the root. However, the concentration changed from day to day since the soil solution in this layer was not buffered by physico-chemical processes. During the first 110 days, the model predicted a marked increase in the P-ion concentration in solution due to microbial P release and then a progressive decrease due to the fact that P mineralization was not able to compensate for P losses (uptake by roots, leaching). When the P-ion concentration in solution reached values near 0.3 mol P m^{-3}, the depletion zone was progressively replaced by an accumulation zone since P transport by mass flow was greater than maximum P uptake by roots (Fig. 2). In the mineral soil, the P depletion zone grew very slowly while the average P-ion concentration in solution, which was much lower than in the forest floor, remained quite stable given the strong buffer power in this layer (Fig. 2). During the greenhouse experiment, P ions in the mineral soil solution increased slightly since P inputs from organic matter mineralization and from the forest floor (leaching) were greater than P uptake (Fig. 2).

3.2. Observed and predicted P uptake

In both layers and for all harvest dates, observed and predicted P uptakes were of the same order of magnitude (Table 3). The contribution of the forest floor to P uptake was satisfactorily predicted; the model predicted a forest floor contribution of 99.3% after 130 days while this contribution was estimated at 99.1% based on the greenhouse experiment (Jonard et al., 2009). When analyzing the predictions layer by layer and date by date, we observed that the difference between the mean prediction and the mean observation in the forest floor ranged between −3% and −20% of the mean observation (NAE) and was never significantly different from zero (Paired t-test, $\alpha = 0.05$). In the mineral soil, this difference was greater at the first harvest date (73%) but was not significantly different from zero; at the second and third harvest dates, it amounted to −1% and −24%, respectively, and was not significantly different from zero (Table 3). The predictive accuracy estimated based on the NRMSE ranged between 28% and 35% of the mean observation and was similar for the forest floor and for the mineral soil, except for a higher value in the mineral soil at the first harvest date (98%). The model was also globally evaluated based on EF and on regression analysis (Fig. 3). EF amounted to 0.97, which is quite high knowing that EF = 1 means a perfect model and EF = 0 a model whose predictions are not better than the mean. The regression of observations on predictions showed a linear relationship with an intercept of 0.15 and a slope of 1.07. Both parameters were tested simultaneously with

Table 3
Statistical evaluation of predicted vs observed uptake.

Layer	Growing period (days)	n	Observed uptake (mmol P pot^{-1})	Predicted uptake (mmol P pot^{-1})	NAE[a] (mmol P mmol P^{-1})	Paired t test P	NRMSE[b] (mmol P mmol P^{-1})
FF	61	5	0.03489	0.02806	−0.20	0.2341	0.34
	95	5	0.08191	0.06745	−0.18	0.1716	0.28
	130	5	0.17353	0.16804	−0.03	0.8661	0.35
MS	61	5	0.00011	0.00019	0.73	0.0887	0.98
	95	5	0.00044	0.00044	−0.01	0.9312	0.29
	130	5	0.00152	0.00115	−0.24	0.1775	0.38

[a] Normalized average error.
[b] Normalized root mean square error.

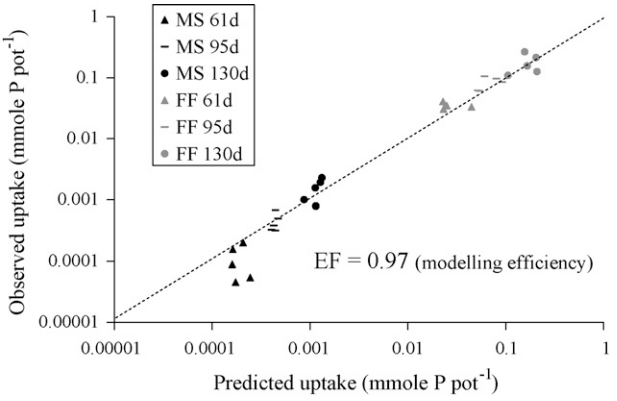

Fig. 3. Comparison between observed and predicted P uptake (MS: mineral soil, FF: forest floor). The dotted line represents the 1:1 relationship.

an *F* test, which led us to accept the null hypothesis (intercept = 0 and slope = 1, $P = 0.1199$).

3.3. Predictions in other soil–plant systems

To evaluate the impact of the mineral soil P retention properties on the forest floor contribution to P uptake, the model was run using the parameters of the Freundlich kinetic equation and the initial P-ion concentration in solution measured in other mineral soils collected in the *Landes de Gascogne* forest (Table 2); the other soil and plant parameters were left unchanged. These mineral soils were chosen to cover the whole range of P reactivity in this forest. The model predicted that the less P-reactive mineral soil (S1) would enable a total P uptake more than two times higher than the other mineral soils (Fig. 4). The contribution of the forest floor amounted to 45.7% when associated with S1 and increased strongly with increasing P reactivity of the mineral soils (94.2%, 98.7% and 99.3% for S2, S3 and S4, respectively).

Another set of simulations was carried out to evaluate the impact of the forest floor on P uptake. The model was run for four soil–plant systems containing only mineral soil enriched with all the P contained in the forest floor. The soil and plant parameters used for these simulations were the same as above, except for P-ion concentration in solution, which was recalculated taking the P enrichment into account (Table 2). When comparing the soil–plant systems with and without the forest floor, we observed that the presence of the forest floor layer did not affect the total P uptake of S1 (low P reactivity of the mineral soil) and increased strongly the P uptake of S2, S3 and S4 (increasing P reactivity, Fig. 4).

4. Discussion

4.1. Model performance

Since the model parameters were not fitted but were independently determined by complementary experiments or taken from the literature, it was possible to evaluate the model based on all the P uptake measurements (Table 3, Fig. 3). The good overall agreement between observed and predicted P uptake indicates that the diffusion/mass-flow theory and the model assumptions are able to predict P uptake in the soil–plant system used for the greenhouse experiment. The remaining discrepancies can be ascribed to uncertainty in parameter estimates and in P uptake measurements. Some plant parameters (for water and P absorption by roots) were taken from other studies involving pine seedlings and were perhaps not perfectly appropriate for our situation. The biggest differences between measurements and predictions were observed for the mineral soil at the first harvest date and could be due to inaccurate measurement of P uptake. In this layer, P uptake was determined using radio-isotopic labeling (Jonard et al., 2009). As the amount of P taken up in the mineral soil during the first period was very small, the radioactivity measurements were close to the background noise and were therefore somewhat variable. This explanatory hypothesis is corroborated by the fact that the discrepancy decreased in the second and third periods (Fig. 3).

Good agreement between observed and predicted P uptake was also obtained by Kelly et al. (1992) who predicted P uptake by loblolly pine seedlings using the Barber–Cushman model (Barber, 1995). Reginato et al. (2000) further improved this result by developing a moving boundary approach to account for increasing root competition. On the other hand, the SSAND model based on an analytical solution (steady-state hypothesis) considerably underestimated P uptake by hybrid poplar seedlings (Kabba et al., 2009). These contrasted performances may partly be explained by differences in chemical fertility conditions. As P availability was high in the soil used by Kelly et al. (1992), predicted P uptake was mainly affected by plant parameters describing P absorption by roots. In contrast, in the soil used by Kabba et al. (2009), chemical fertility was low and therefore, the soil supply parameters probably played an important role in the prediction of P uptake. To explain their low model performance, Kabba et al. (2009) suggested that the processes regulating P supply were not adequately described in their model and that mycorrhizae possibly contributed to P uptake. An additional explanation for the disagreement between observed and predicted P uptake could be the inadequacy of the analytical solution due to non steady-state conditions. In our study, a numerical solution was retained as it had to be applied in the two layers (mineral soil and forest floor) whose properties were quite contrasted. Numerical solutions have the advantage of being correct in all sit-

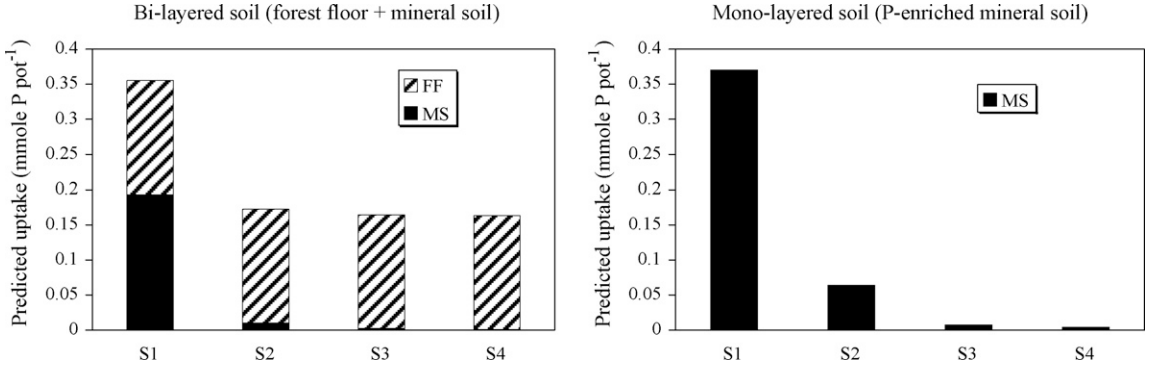

Fig. 4. Predicted P uptake in different soil–plant systems with increasing mineral soil P reactivity (S1–S4) and with or without forest floor layer (left and right) for a growing period of 130 days.

uations but they need much more calculation time to be resolved and the introduction of new processes in the model can be more complicated to implement. The good performance of our model can also be ascribed to the fact that the main processes regulating P-ion concentration in solution were taken into account.

4.2. Forest floor contribution to P uptake

The model predicted that the forest floor contributed 99.3% of P uptake after 130 days, which matches the proportion obtained in the greenhouse experiment. In a field study using radioisotope techniques (^{32}P and ^{33}P), Brandtberg et al. (2004) reported that the contribution of the forest floor to P uptake was 93% and 95% for spruce and birch trees, respectively. According to the model, which considers that roots absorb P ions from the soil solution, the much higher concentration of P ions in the forest floor solution than in the mineral soil solution (Fig. 2) explains why most of the P ions were taken up from the forest floor (Table 3). Compton and Cole (1998) also observed a much higher P-ion concentration in the forest floor solution than in that of the A and B mineral horizons. In our experiment, the high P-ion concentration in the forest floor can be ascribed to high rates of litter mineralization and of microbial re-mineralization and to the limited ability of the forest floor to retain P ions on its solid phase (low P reactivity). At the end of the experiment, the P-ion concentration in the forest floor solution began to decrease (Fig. 2). If the greenhouse experiment had been prolonged for several months or years, this concentration would probably have continued to decrease until P uptake was equilibrated with litter mineralization. In our experiment, the P released by litter mineralization was equivalent to half the P taken up by the pine seedlings over the 130-day period. Since the positive effect of the forest floor on P nutrition is linked to its low P reactivity, one can wonder if the forest floor contribution would not decrease when associated with a mineral soil with low reactivity. The model was therefore run with different soil parameters (Table 2) to cover the whole range of soil P reactivity found in the *Landes de Gascogne* forest. These simulations showed that the forest floor contribution was lower in the quasi non-reactive soil and increased with soil P reactivity (Fig. 4). When comparing predicted P uptake in systems with and without forest floor, we observed no effect of the presence of the forest floor on P uptake in the less P-reactive soil and a strong positive effect in all the other soils (Fig. 4). In P-reactive mineral soils, accumulation of litter in the forest floor creates a medium with low retention properties that makes P uptake easier. This positive effect of the forest floor on P nutrition largely compensates for P immobilization in the decaying litter of the forest floor. Conversely, the creation of a medium with low retention properties is not an advantage in non-reactive mineral soils. In both cases, the P return by litterfall is necessary to maintain P nutrition; however, the development of a forest floor layer is beneficial only on P-reactive soils. Although one would expect that the same processes occur in the field, it is not possible to quantify the forest floor contribution to P nutrition based on the results of the greenhouse and of the modeling approach since a lot of conditions change *in situ* (e.g. root vertical distribution and dynamics, horizon thickness, influence of meteorological conditions on mineralization, water movements, tree transpiration, mycorrhizae). The next step in the generalization of our results would be to adapt our model to field conditions. Several authors have mentioned better nutrient status in stands with thicker holorganic layers. In a study including 48 radiata pine stands in New Zealand, Carey et al. (1982) showed that P foliar concentration was positively correlated with forest floor mass. In the Quebec Appalachians, Paré and Bernier (1989) observed that sugar maple stands growing on soils with mor humus had higher P foliar concentrations than soils with mull humus. Using long-term thinning trials in Norway spruce stands, Jonard et al. (2006) showed that an increase in the forest floor mass with stand basal area was accompanied by a parallel increase in the foliar P concentration. Similar results were found by Merino et al. (2008) for beech in Spain. Comparing P cycling in Douglas fir and red alder stands, Compton and Cole (1998) observed that the higher P uptake in the red alder stand (4.3 vs 2.7 kg ha^{-1} year^{-1}) was associated with a larger amount of P in the O horizon (79 vs 24 kg ha^{-1}) and a lower amount of available P, as measured by Bray (NH_4F–HCl) extraction, in the mineral soil (4 vs 44 kg ha^{-1}).

5. Conclusion

Given the ability of the model to correctly predict P uptake by pine seedlings from different growing media, the results obtained in a particular case (greenhouse experiment) were extended to other soil conditions. According to our simulations, the accumulation of litter in the forest floor improves P nutrition by creating a medium with low P retention properties. This beneficial effect of the forest floor logically increases with the P reactivity of the underlying mineral soil.

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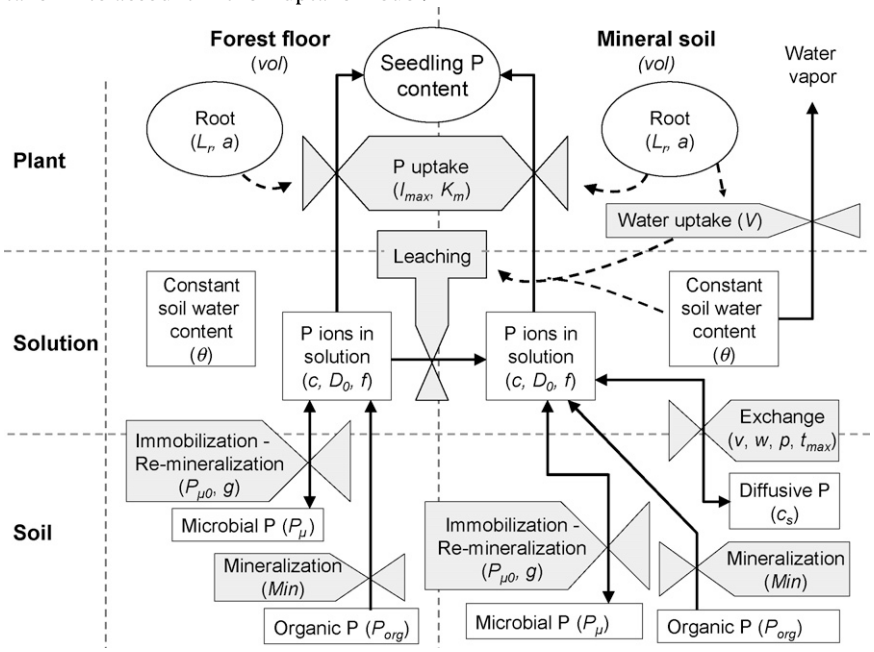
Appendix A.

Relational diagram describing the compartments and the fluxes taken into account in the P uptake model.



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