

# Modelling the effect of arbuscular mycorrhizal fungi on plant phosphate uptake

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## Introduction

Phosphate (P) is an essential nutrient for plants which is sparingly soluble in most soils. Arbuscular mycorrhizal fungi may enhance plant P uptake by increasing the soil volume accessible for plants. Therefore, this ubiquitous symbiosis between many crop plants and soil fungi is currently viewed as a promising alternative to the excessive use of mineral fertilisers in agricultural management (FROSSARD et al. 2000). For applying this form of plant P nutrition in agricultural systems, mathematical modelling can help to estimate how much of P fertiliser could be substituted through mycorrhizal-enhanced P uptake. In this paper, we demonstrate how to quantify the growth of external fungal hyphae in soil, soil P depletion and P influx into a plant root colonised by arbuscular mycorrhizal fungi. We focus on a single mycorrhizal root and therefore use cylindrical coordinates as described in SCHNEPF et al. (2011).

## Modelling the growth of arbuscular mycorrhizal hyphae

Three arbuscular mycorrhizal fungi with different growth strategies are considered as described by SCHNEPF et al. (2008a): firstly, the linear branching strategy, secondly the nonlinear branching strategy, and thirdly the anastomosis strategy. The first two strategies assume that branching is linearly or nonlinearly proportional to the hyphal tip density in soil while the third strategy allows for the fusion of

external hyphae. All of these strategies are included in the model described in the following paragraph. *Figure 1* shows a 2-dimensional visualisation of the colony shapes resulting from the different fungal growth strategies.

The hyphal length density,  $\rho$ , is calculated with a continuous and spatially explicit hyphal population growth model (SCHNEPF et al. 2008a). It calculates hyphal tip and length densities based on elongation of the region just behind the hyphal tip, branching due to tip splitting, anastomosis and tip and hyphal death. Calibration of this model to experimental data (JAKOBSEN et al. 1992) gave evidence that all three growth strategies mentioned above occurred. The parameters we found in this calibration study (SCHNEPF et al. 2008a) are used in the following simulations. Model equations for the hyphal tip density  $n$  and the hyphal length density  $\rho$  are given by

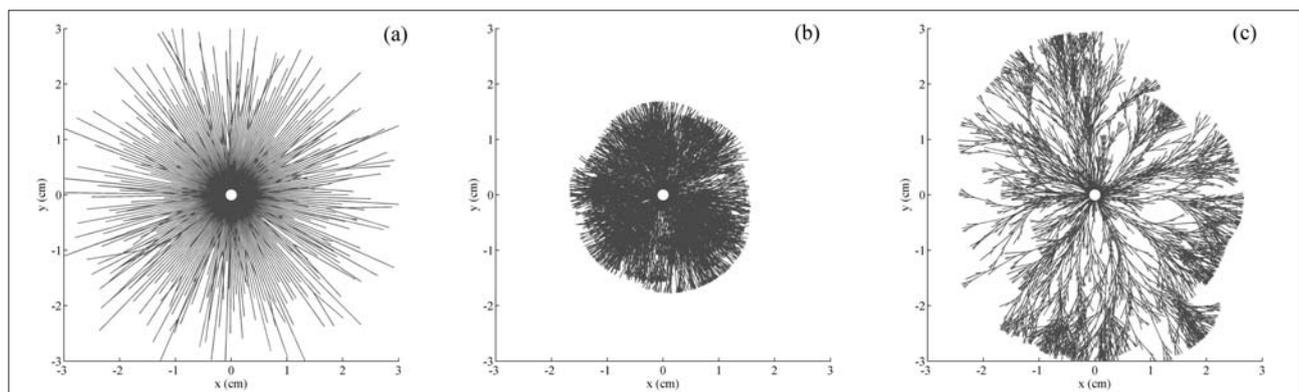
$$\frac{\partial n}{\partial t} = -\frac{1}{r} \frac{\partial}{\partial r} (r n v) + f \quad \text{Equation 1}$$

$$\frac{\partial \rho}{\partial t} = n v - d \rho \quad \text{Equation 2}$$

$$f = \underbrace{b_n n \left(1 - \frac{n}{n_{\max}}\right)}_{\text{branching}} - \underbrace{a_1 n^2 - a_2 n \rho}_{\text{anastomosis}} - \underbrace{d_n n}_{\text{tipdeath}} \quad \text{Equation 3}$$

$$n = 0, \quad \rho = 0 \quad \text{at } t = 0 \quad \text{Equation 4}$$

$$n = f_b(t) \quad \text{at } r = r_0 \quad \text{Equation 5}$$



**Figure 1: Visualisation of (a) linear branching, (b) nonlinear branching and (c) anastomosis growth strategies of arbuscular mycorrhizal fungi after 14 days (after SCHNEPF et al. 2011). Simulations are based on a discrete L-System model (LEITNER et al. 2010) which approximates the continuous model given by Eqs. (1)-(5).**

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( $n$  hyphal tip density,  $\rho$  hyphal length density,  $d$  hyphal death rate,  $b_n$  branching rate,  $n_{max}$  maximal tip density,  $a_1$  and  $a_2$  tip-tip and tip-side anastomosis rates,  $d_n$  tip death rate,  $f_b$  tip density at the root interface). This hyperbolic system of equations given by Eqs. (1)-(5) was solved numerically using a Lax-Wendroff-scheme (MORTON and MAYERS 1994).

## Modelling soil P depletion and P influx into the plant root

We model P transport in soil based on the diffusion equation as described in SCHNEPF and ROOSE (2006) and SCHNEPF et al. (2008b). Furthermore, we assume that P is taken up by both root and fungal hyphae according to Michaelis Menten kinetics. The classical single root model (BARBER 1995, TINKER and NYE 2000) is extended by a sink term for P uptake from soil due to arbuscular mycorrhizal hyphae (see last term in Eq. (6)). The model is given by the following equations,

$$(\theta + b) \frac{\partial c}{\partial t} = \frac{1}{r} \frac{\partial}{\partial r} \left( D \theta f r \frac{\partial c}{\partial r} \right) - 2r_h \pi \rho(r, t) \frac{F_m c}{K_m + c}, \quad \text{Equation 6}$$

$$c = c_0, \quad \text{at } t = 0, \quad \text{Equation 7}$$

$$D \theta f \frac{\partial c}{\partial r} = \frac{F_m c}{K_m + c}, \quad \text{at } r = r_0, \quad \text{Equation 8}$$

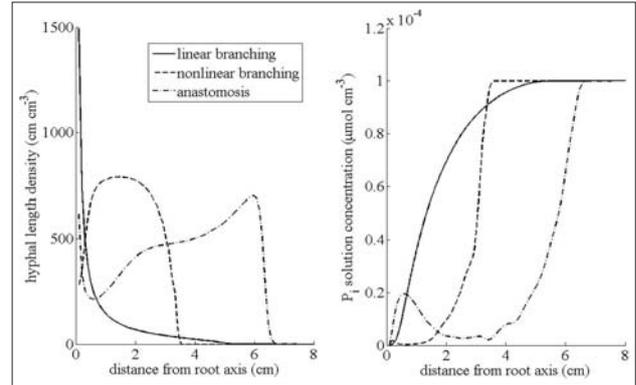
$$D \theta f \frac{\partial c}{\partial r} = 0, \quad \text{at } r = r_1, \quad \text{Equation 9}$$

( $c$  concentration of P in soil solution,  $t$  time,  $r$  radial distance from root axis,  $\theta$  volumetric water content,  $b$  buffer power,  $f$  impedance factor,  $D$  diffusion coefficient in water,  $c_0$  initial P concentration in soil solution,  $r_h$  hyphal radius,  $r_0$  root radius,  $r_1$  mean half distance between roots,  $\rho$  hyphal length density). Eqs. (6)-(9) were solved numerically with the finite element method using Comsol Multiphysics.

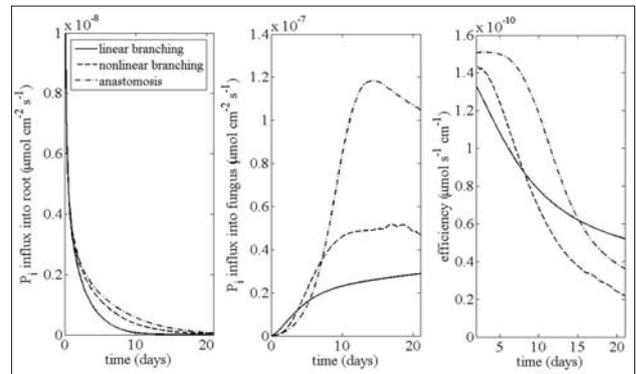
## Results

The hyphal length densities and P depletion at different distances from the root after 21 days are shown in *Figure 2*. The linear branching strategy produces the highest root length density at the root surface, then the hyphal length density declines exponentially with increasing distance from the root surface. Thus, P is strongly depleted within a radius of 1.5 cm around the root. The fungus with the nonlinear branching strategy has a peak in hyphal length density at about 1.7 cm distance from the root axis and the radius of P depletion is 3 cm. The anastomosis strategy produces a peak in hyphal length density at the front of the colony and results in the largest radius of P depletion of 6 cm. In this scenario, the soil is less depleted in the vicinity of the root itself. *Figure 3* shows the resulting influx of P into root (a) and hyphae (b). In all cases, P influx into root decreases quickly with time and influx into fungus becomes dominant. The most effective strategy with respect to P uptake per unit hyphal length is the anastomosis strategy (see *Figure 3c*).

The results in *Figures 2* and *3* are based on the common assumption that external hyphae are able to take up P along their entire length. However, it has been shown by SCHNEPF et al. (2008b) that this is bound to overestimate hyphal P uptake from soil. In a theoretical case study, the



*Figure 2: Hyphal length densities and P solution concentration around the root corresponding to the linear branching, nonlinear branching and anastomosis growth strategies of arbuscular mycorrhizal fungi assuming that root and fungi have the same P uptake parameters (after SCHNEPF et al., 2011).*



*Figure 3: P influx per unit root surface area due to (a) root and (b) hyphae corresponding to the linear branching, nonlinear branching and anastomosis growth strategies of arbuscular mycorrhizal fungi. (c) P influx per unit hyphal length (after SCHNEPF et al. 2011).*

compared the differences with regard to the sites of P uptake along the individual hyphae and simulated, in addition to the full length scenario, two other scenarios that were based on the assumption that only the metabolic active part of the mycelium is taking up P or that P uptake occurs only at the hyphal tips. These simulations suggest that P uptake occurs at parts of the mycelium which are metabolically active. *Figure 4* shows the effectiveness of the different P uptake scenarios under the three branching patterns considered. The anastomosis pattern is also the most effective in the half length uptake scenario.

## Discussion and Outlook

In view of future shortcomings in mineral phosphate supply (LAMBERS et al. 2006), applying arbuscular mycorrhizal symbioses can help to reduce the use of mineral fertilizers in agricultural management. Simulation results show that P influx into root due to external mycorrhizal fungi is up to an order of magnitude larger than P influx due to root uptake. This is particularly pronounced when the fungus follows the linear branching strategy where the fungal hyphae compete for P inside the root depletion zone. The

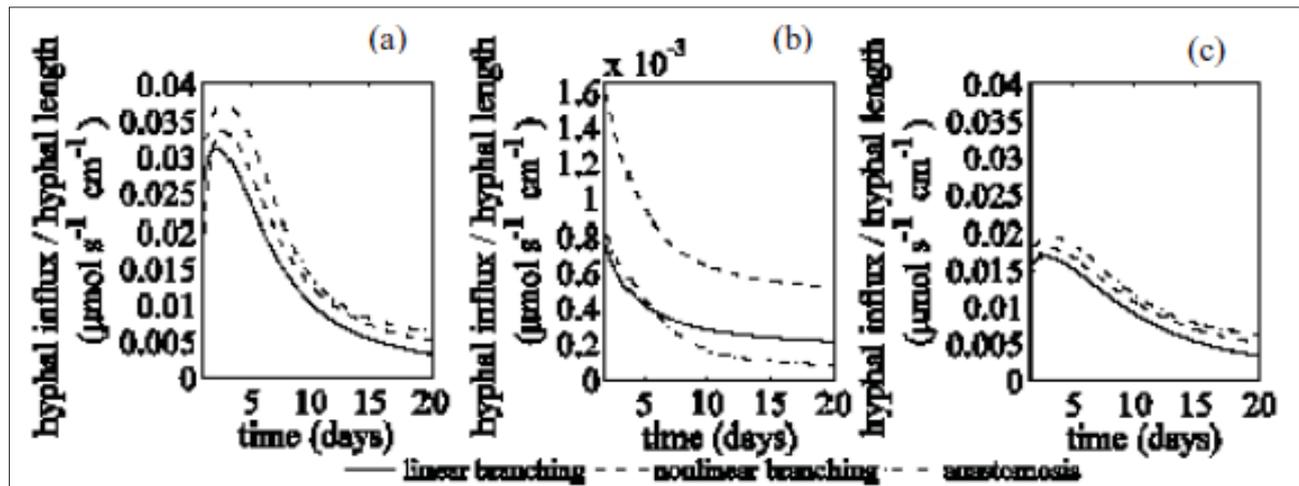


Figure 4: P uptake rate of the whole mycelium versus total hyphal length for three fungi with different growth patterns: (a) full length uptake scenario, (b) tip uptake scenario, (c) half length uptake scenario (after SCHNEPF et al., 2008b).

anastomosis strategy on the other hand makes more use of the soil volume near the front of the colony. Thus the competition between root and fungus inside the root depletion zone is less and the root contribution to overall uptake is higher. However, fungal P uptake dominates overall P uptake in all branching strategies. This supports the idea that roots can completely rely on the fungus for their P nutrition (SMITH et al. 2003).

A spatially explicit model for the spread of mycorrhizal mycelium and active parts is still missing. Assuming Michaelis-Menten kinetics for uptake may also oversimplify the actual uptake process. The molecular and biochemical characterisation of the corresponding P transport systems is currently studied (BUCHER 2007, RAGHOTHAMA and KARTHIKEYAN 2005). Thus, more experimental data for model parameterisation and validation are required.

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