Meine van Noordwijk, Simone Radersma and Betha Lusiana

Modelling root architecture and phosphorus uptake in agroforestry

A modified version of the WaNuLCAS model is outlined that includes a range of phosphorus (P) acquisition mechanisms of crops and trees and interactions via recycling and rhizosphere modification.

The benefits of combining plants with different P acquisition mechanisms are not directly obvious

Does agroforestry have a role to play on soils where P is the main nutrient constraint for plant growth? For N, complementarity can be achieved by combining plants with and without the ability to fix atmospheric N_2, but the benefits of combining plants with different P acquisition mechanisms are not directly obvious. Specialized P acquisition mechanisms include mycorrhizal associations (lacking in some plant families), excretion of phosphatases that mobilize (hydrolyse) organic P, and excretion of organic anions that modify rhizosphere pH and P sorption properties and/or mobilize P from strong chemical bonds. Whether these P acquisition mechanisms only accelerate P mining or really add to the available pools from which uptake can occur in the future depends on the soil and the size of less available pools. The total non-available pool in most soils (including tropical Oxisols or Ferralsols) is usually so large relative to the annual demand that P mobilization can indeed be significant, even if it affects only a small fraction of this pool.

P uptake models based on diffusion to a zero sink can treat mycorrhizal hyphae as very thin roots

A major question, however, is how the benefits of such P acquisition are shared in mixed plant communities. The degree of synlocation of tree and crop roots (the degree to which they occur together) probably determines how the direct benefits of rhizosphere modification are shared. Indirect benefits may consist of returns of P via root turnover and/or litterfall. Tree-crop interactions (positive or negative) that affect soil water balance affect availability, as P mobility (diffusion) in soil strongly depends on soil water content. It is certainly not an easy task to judge the net balance of positive and negative tree-crop interactions where P is the major nutrient constraint, and we may have to rely on models to predict the combined effects.

Most processes that affect P cycling in agroforestry systems are similar to those of N, but the parameter values and thus the relative importance of processes differ considerably. This applies to diffusion in soil solution towards roots, regulation of uptake by plant demand, reduction of plant growth if uptake cannot keep up with demand, shifts in shoot-root allocation under nutrient stress, adjustments of root distribution to the success of roots in different compartments in uptake of the currently limiting soil resource, and mineralization from organic pools.

Whereas root length density as low as 0.1 $cm\ cm^{-3}$ is sufficient to utilize all the nitrate available in a layer, increases of root length density up to 10 $cm\ cm^{-3}$ increase the opportunities for P uptake in nearly all soils. As such root length densities are rare outside the 'sod' in permanent grassland. Most plants have mycorrhizal hyphae to increase their effective root length density. Phosphorus uptake models based on diffusion to a zero sink can treat mycorrhizal hyphae as very thin roots (van Noordwijk and Brouwer, 1997). An effective root length density L_v^* can be defined as:

$$L_v^*=L_v(1+MycFrac*RHypL*(HypDia/RtDia)^{0.5}$$

where L_v is root length density ($cm\ cm^{-3}$), MycFrac indicates the fraction of root length that is mycorrhizal, RHypL represents the length of hyphae per unit length of mycorrhizal root, and HypDia and Rtdia are the diameter (mm) of hyphae and roots, respectively. The overall effect may be a five-fold increase of effective root length density by mycorrhizal associations (for example, 1 + 0.2 * 100 * 0.2). The largest uncertainty is in the RHypL parameter. Recent measurements of Boddington (1998) have confirmed values in the 50-100 range for trees and crops on an acid soil in Lampung, Indonesia.

This approach of including mycorrhizal hyphae as part of root architecture into models of P uptake and introducing a multiplier to the measured root length density is parallel to the way the fractal branching properties of roots can be exploited. Beyond the first diameter class reflecting secondary thickening of roots, the fractal properties change and an empirical ratio of fine root length per unit length above this critical diameter is needed (Van Noordwijk *et al.*, 1996a; 1996b), followed by an empirical multiplier for mycorrhizal hyphae per unit fine roots. The resulting uncertainty of the effective root length density is obviously considerable.

Incorporating phosphorus as a second nutrient in WaNuLCAS

The WaNuLCAS model (version 1.1 released in September 1998 and version 2.0 released in May 1999) considered only N as a nutrient (van Noordwijk and Lusiana, 1999). A working version can be obtained from b.lusiana@cgiar.org. The STELLA modelling environment, in which WaNuLCAS was written, however, allowed for a relatively easy incorporation of P as a second nutrient, and extension to K or any further nutrient will be even easier. By setting up an array 'nutrients' with N as the first and P as the second level, the equations originally developed for N can be applied to the broader class. Interactions between N and P are only indirect, based on the interaction of both nutrients with plant dry matter production.

The main adjustments and additions to the model are listed below.

- The apparent adsorption constant (the ratio of the desorbable pool of P and P concentration in soil solution) is not constant but depends on the concentration. Parameters for a range of soils are included in the parameter spreadsheet.
- The N:P ratios may differ between the various compartments in the organic matter section of the model, leading to different patterns of P immobilization and mineralization.
- An 'immobile pool' was added to the model, reflecting the difference between total P and available P, and equations were added for a potential mobilizing effect of crop or tree roots on this pool. In the current version there is no provision for the reverse process when the roots disappear.
- Roots may (temporarily) influence the adsorption constant in their vicinity by modifying pH and/or excreting organic anions competing for P sorption sites. Equations were added for such effects in proportion to the root length density of crop and tree roots. The benefits of a higher potential P uptake are shared over tree and crop on the basis of a 'root synlocation' parameter, reflecting whether the spatial distribution of crop roots in a soil compartment are such that they are mixed with tree roots or occur in separate clusters. This determines the part of the benefits of rhizosphere modification that will accrue to the species directly influencing the adsorption constant.

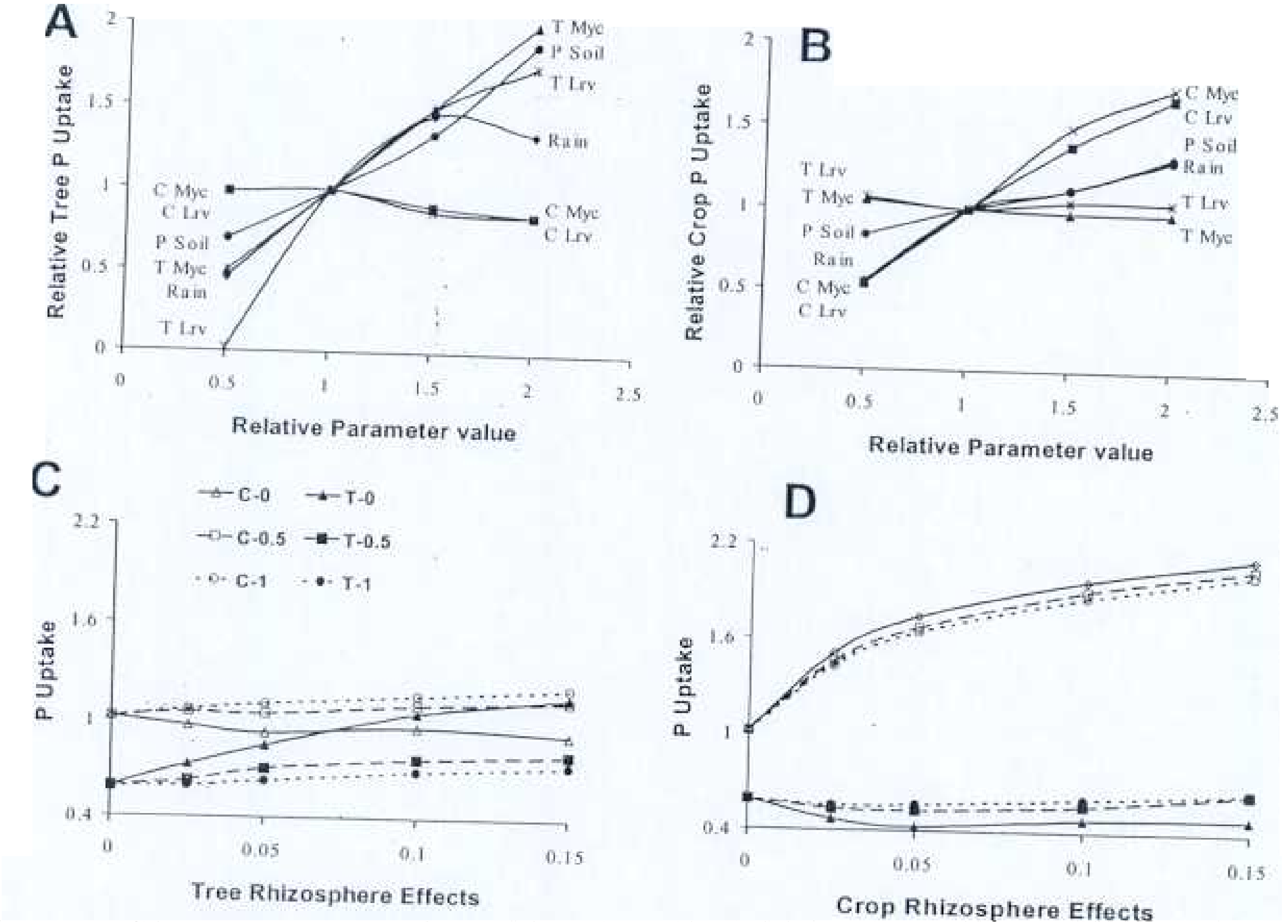

Figure 1. Preliminary calculations with the WaNuLCAS model after incorporating a P balance. A and B: Sensitivity of predicted P uptake by tree (A) and crop (B) to changes in parameters for root length density T Lrv and C Lrv, respectively), mycorrhiza (C Myc and T Myc), soil P content (P Soil) and rainfall. C and D: Effect of rhizosphere modification (% reduction in adsorption constant per unit root length density (cm cm-3)) by the tree (C) and crop (D), on P uptake by tree (T) and crop (C) depending on the synlocation parameter (0 = only plant modifying rhizosphere benefits, 1 = benefits shared on basis of root length density).

Synlocation of tree and crop roots determines how the benefits of rhizosphere modification are shared

As one might expect, the predicted P uptake by both tree and crop responds to changes in root length density (Lrv) and mycorrhizal parameters and initial soil P content, with mild negative responses to increased effective root length density by the other plant (Figure 1A and B). The sensitivity of the model indicates that reasonable estimates of effective root length density are essential for a 'process-based' model. When rhizosphere modification is included (Figure 1C and D), the results point out a clear effect of the synlocation parameter in deciding the net effect of trees on the crop in P mobilizing properties.

Concluding remarks

The model can provide a coherent hypothesis concerning how root architecture can influence root function, but there is substantial uncertainty on a number of key processes and parameter ranges. Future models may have to include P mobilizing effects of fires ('slash-and-burn') and specific effects of organic residues on P sorption, as such effects may be important especially in sequential agroforestry systems such as improved fallows.

Meine van Noordwijk[1], **Simone Radersma**[2] **and Betha Lusiana**[1]
[1]ICRAF S.E. Asia
PO Box 161
Bogor 16001
Indonesia
tel/fax +62 251 625415/6
email: M.van-noordwijk@cgiar.org
B.Lusiana@cgiar.org

[2]Maseno Agroforestry Research Centre
PO Box 25199
Kisumu, Kenya
tel +254 35 51245, 51163
email: afresmaseno@africaonline.co.ke

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