



Simulation of soil drying induced phosphorus deficiency and phosphorus mobilization as determinants of maize growth near tree lines on a Ferralsol

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Abstract

Understanding the effect trees have on the growth of crops requires an understanding of the multiple interacting processes that determine resource uptake by the crops. On a Ferralsol in sub-humid western Kenya maize (*Zea mays* L.) growth was primarily limited by phosphorus availability. We observed that maize growth near grevillea (*Grevillea robusta* A. Cunn.) tree lines was strongly reduced, while maize growth was slightly increased near cassia (*Cassia spectabilis* DC (syn. *Senna spectabilis*, DC, H.S. Irwin and R.C. Barneby). This was contrary to expectations because grevillea has a relatively low nutrient demand while Cassia has a relatively high nutrient demand.

We compared maize growth in an experiment with simulations using the mechanistic tree–crop interaction model WaNuLCAS. The model simulations showed that the measured 30–40% decrease in maize growth near the Grevillea tree line was due to 0.025 m³ m⁻³ lower soil water contents (at mean levels of 0.35 m³ m⁻³ and high pF). This was not due to direct water limitation. The lower soil water content caused decreased P diffusion to roots and a cumulative decrease in crop root-growth and a concomitant decrease in crop growth over time.

Measured maize yield near Cassia was 115%, unaffected by trees. Model simulations predicted it should be reduced to 80% due to direct competition for P between tree and crop. This suggests that rhizosphere modifications measured near Cassia roots probably supplied P to the tree itself and also to the maize crop.

On P-limiting tropical soils, it is important to prevent soil drying to avoid soil drying induced P deficiency. In these conditions tree species that are able to mobilize P can prevent competition with the crop and may even increase crop performance.

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1. Introduction

Trees are a common feature in the agricultural landscape of western Kenya and many other tropical areas with small-scale subsistence farming. The attractiveness of agroforestry systems to farmers depends on the combined value of the components, including both market and socio/cultural values. The biophysical performance of such a system may be taken as a starting point in assessing its feasibility (Cannell et al., 1996).

Relatively simple methods for analyzing the performance of alley-cropping systems were developed by Ong (1995) and Kho (2000). Ong's method is based on splitting the overall interaction term (I) into a fertility (F) and an additive competition (C) component, both expressed in terms of crop yields. Kho's method focuses on direct influences of trees on availability of resources to the crop, multiplied by a degree of limitation for each resource, which depends on the environment. These methods are relatively simple to use and give useful (qualitative) assessments of performance in many cases (Radersma et al., in press). Although they are usually applied on plot scale they can also be used for describing crop zones at increasing distance from trees.

One disadvantage of these methods is that the simple sum of the components used in the equations cannot cope with situations where two parameters interact. Mechanistic research into the processes is needed in situations where this interaction is important.

In an experiment on tree lines bordering maize fields on a P-fixing Ferralsol in western Kenya, we observed that maize growth was decreased near *Grevillea* (*Grevillea robusta* A. Cunn.) tree lines and increased near *Cassia* (*Cassia spectabilis* DC (syn. *Senna spectabilis*, DC, H.S. Irwin and R.C. Barneby) tree lines. *Grevillea* is known to have a relatively low nutrient demand (N, P, K), while *Cassia* is known to have a relatively high nutrient demand. Ong's method would predict that, because a fertility effect (F) is absent (all organic material from the trees was removed), only a competition effect (C) determines the interaction and the maize yield increase near *Cassia* cannot be explained. Kho's method would reason that, because the main limiting factor of the environment is phosphorus (P), the negative effect of

Grevillea on crop growth is likely due to its effect on P-availability. However, *Grevillea* is known to be a relatively P-efficient tree (high biomass production, low P use), compared with *Cassia*, hence direct competition for P would be more likely near *Cassia* than near *Grevillea*.

P is the first limitation to maize growth in western Kenya. Therefore, we assumed that trees affect crop growth primarily by their effects on crop P-uptake. Factors important for P uptake are; the available fraction of total soil P, root-length densities (including mycorrhiza) and soil water content. The last two factors are especially important for P uptake at low levels of available P, as in the depleted Ferralsols of western Kenya.

Trees decrease available P for crops because they use P themselves. On the other hand trees may increase available P for crops by root exudates or rhizosphere effects. Rhizosphere effects can increase P desorption and dissolution and may turn organic P into inorganic P, as demonstrated for *Cassia*, *Grevillea* and maize by Radersma and Grierson (2004).

Trees may also affect root length densities of crops by allelopathy (Ridenour and Callaway, 2001) or through increases in root: shoot ratio in response to competition (Marschner, 1995). However, an increase in root: shoot ratio may not lead to higher root length densities, because lower amounts of assimilates allocated to the shoot result in lower biomass production. Thus, above-ground crop growth may be positively or negatively affected by an increasing root: shoot ratio, the overall effect being small. Tree roots with their mycorrhizal associations may also increase the rate of mycorrhizal infection of crop roots growing in the same soil volume (Redhead, 1979), and thereby increase P uptake of the crop.

Trees often affect soil water contents, either increasing (Caldwell and Richards, 1989; Dawson, 1993) or decreasing them (Smith et al., 1999; Odhiambo et al., 2001), and thereby influence P transport to crop roots, and root growth.

In the study described below we used a mechanistic simulation model and results from a field experiment to explore the effects of trees on P availability, soil water content and crop root-growth, thus influencing crop growth. The mechanistic model of tree-crop interactions, WaNuLCAS (van Noordwijk et al.,

1999; van Noordwijk and Lusiana, 2000) was used to simulate crop growth near *Grevillea* and *Cassia* tree lines. The field experiment was set up to examine the effects of various tree species, grown as border line in maize fields, on soil water contents and maize yield on a P-limiting Ferralsol in western Kenya.

2. Materials and methods

2.1. The trial

The field trial with tree lines bordering maize fields was established in 1992 on a farmers' field in sub-humid western Kenya. A field depleted in nutrients through continuous cropping was selected.

The soil was a deep (>3 m), Oxisol/Ferralsol, with a pH of 5–5.5 and clay contents ranging from 500 g kg⁻¹ in the top soil to 800 g kg⁻¹ in the sub-soil.

The experimental design was a randomized complete block with four treatments and four replicates: sole maize (*Zea mays* L.), maize with a line of *Grevillea robusta* A. Cunn., maize with a line of *Cassia spectabilis* DC (syn. *Senna spectabilis*, DC, H.S. Irwin and R.C. Barneby) and maize with a line of *Calliandra calothyrsus* Meissn. Plot sizes were 16 m × 20 m with the tree lines in the center of the plot parallel to the 20 m side. Spacing of the trees in the line was 0.5 m for *Cassia* and *Calliandra* and 1 m for *Grevillea*. Spacing between maize rows was 0.75 m, parallel to the tree line with the first maize row 1.12 m away from the tree line. The within row spacing was 0.25 m. Plots were weeded once or twice per season, depending on weed pressure.

Where the trees bordered the plot edge, 2 m deep metal sheets were installed in trenches in the soil for 3 m on each side of the tree line to prevent tree-root penetration into neighboring plots. Further details of this trial are given in Radersma and Grierson (2004). In this paper, only the treatments of maize with *Cassia* and *Grevillea* tree lines are discussed.

Soil water measurements were taken during half a year in the short rainy season of 1995 at 3–4 week intervals using a neutron probe (Didcot Instruments, Wallingford, UK). Water measurements were done at five distances from the tree line (0.37, 1.12, 2.62, 4.87,

7.87 m), which coincided with maize rows, at six depths (0.35, 0.70, 1.05, 1.40, 1.75, 2.10 m) on both sides of the plot. Calibration of the neutron probe was done with eight access tubes in the experimental area; two at intermediate soil–water levels, three at the driest and three at the wettest time of the year. First, 10 water counts were taken by probe in an access tube in a barrel full of water. Then, 10 counts per depth were taken in the access tube for calibration, followed by again 10 water counts. Then, seven volume rings (100 cm³) per measurement depth were hammered vertically into soil planes around the pipe, in such a way that all rings came from within a globe with a 0.20 m radius around the measurement point. Rings were weighed wet, oven dried for 48 h (108 °C) and weighed dry to derive the volumetric water content. Bulk density was measured on the same rings.

Maize was harvested per row (rows 1–4 away from the tree line) or per two rows (rows 5–10 away from the tree line). Maize measurements from both sides of the tree line were combined as no differences between sides were visible. Fresh weights of cobs and stover were taken separately. A sub-sample of cobs and stover was taken per row or two rows, weighed fresh, dried in the oven and weighed dry to derive yield dry weights.

2.2. Brief description of the model, with special attention to phosphorus

The tree–crop interaction-model WaNuLCAS simulates crop and/or tree growth using daily time steps. It divides the area bordering a tree line in four parallel zones, one tree zone and three crop zones with increasing distance from the tree line, each with four soil layers (Fig. 1a). Zone width and layer depth are input values. The four layers and four zones define 16 cells from which uptake of resources is calculated every day.

The model for phosphorus uptake is shown in Fig. 1b. Estimating phosphorus uptake on each day starts with calculating the target P-content for the current biomass of the trees, broken down into leaf, wood, root and twigs, and the crop. The target P-contents are compared with the current nutrient content to derive the nutrient deficit, which is the P demand for that day. Next, potential nutrient uptake from each cell (zone x

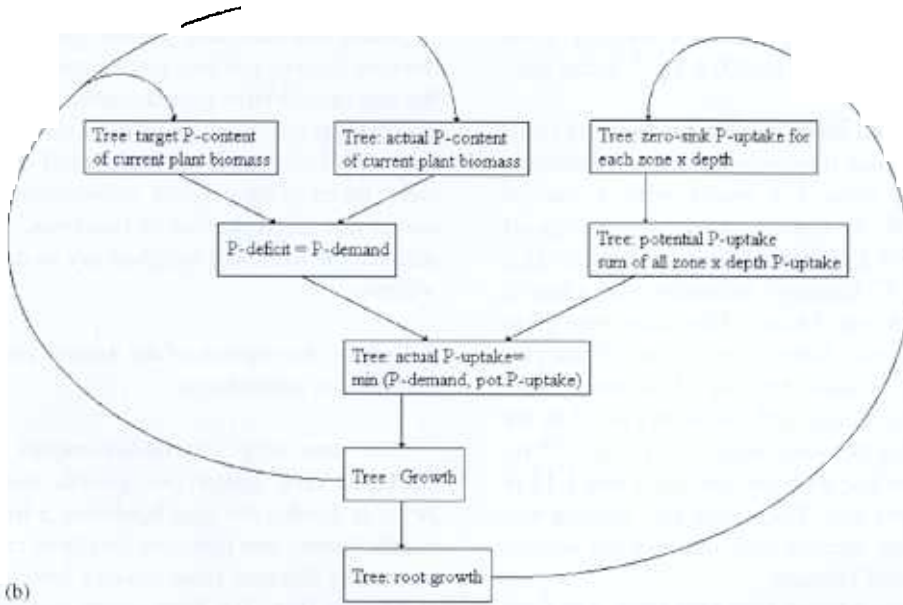
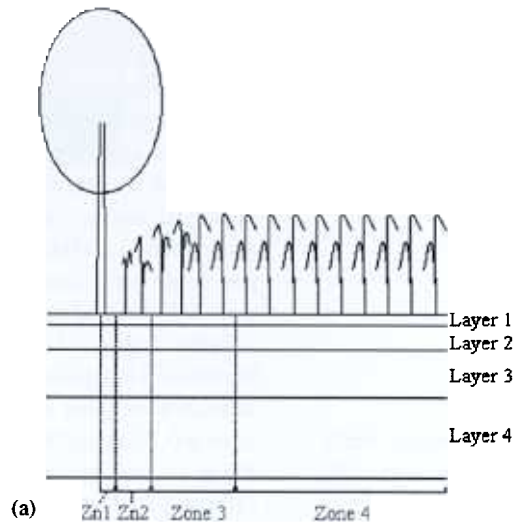


Fig. 1. Spatial structure of WaNuLCAS as used in the simulations (a) and diagram of nutrient and water model (b)

layer) of each component (crop or tree) is calculated from Eq. (1) (van Noordwijk and Lusiana, 2000), assuming zero-sink uptake:

where U_{ijk} is the potential nutrient uptake from each cell (depth x zone) ij by each plant-component k (= tree or crop), Lrv is root length density, D_0 is the

$$U_{ijk} = \frac{Lrv_{ijk} \pi D_0 (a_1 \theta_{ij} + a_0) \theta_{ij} H_{ij} N_{stock,ij}}{\sum_k Lrv_{ijk} (K_a + \theta_{ij}) \left[-\frac{3}{8} + \frac{1}{2} \ln \frac{1}{R_0 \sqrt{(\pi \sum_k Lrv_{ijk})}} \right]} \quad (1)$$

diffusion constant for the P in water, θ is the volumetric soil water content, a_1 and a_0 are parameters relating effective diffusion constant to θ . H is the depth of the soil layer, N_{stock} is the available nutrient pool (for P this is the mobile P-pool) per volume of soil, K_a is the apparent adsorption constant and R_0 is the root radius. The apparent adsorption constant for P is not constant but depends on the concentration.

Actual uptake for each cell is derived after summing all potential uptake rates for each plant component and each cell in which it has roots and comparing it with P demand. If P demand is smaller than potential P-uptake, actual uptake in each cell is a factor (P-demand divided by potential P-uptake) smaller than potential uptake. If P demand exceeds potential P-uptake, actual P-uptake in each cell equals potential P-uptake. Finally, actual uptake has a feedback on plant growth (Fig. 1b).

Tree and crop root densities and distribution can be modeled as fixed measured Lrv values, as function of distance and depth (a function with elliptical isodensity lines) with fixed Lrv per cell or with Lrv responding to above ground plant-growth. Mycorrhizal hyphae are modeled as an extension of root length density using four parameters: possible mycorrhizal infection, actual fraction of infection, hyphal diameter and hyphal length per unit root length.

In the nutrient-uptake part of the model two inorganic P-pools are used. The mobile P-pool is derived from P-Bray or P-Olsen values and its availability depends on a chosen adsorption isotherm (an isotherm can be chosen from a list supplied by the model). The second pool is the immobile P-pool, which only feeds into the mobile P-pool by a weathering parameter. Further details on the structure of the model can be found in van Noordwijk and Lusiana (2000) and van Noordwijk et al. (1999).

In the model, P is only taken up from the mobile P pool. Rhizosphere effects on P-availability could be modeled through use of immobile-P. If easily available P-fractions (i.e. resin P) in the rhizosphere soil of the tree did not differ from measured P fractions in bulk soil, but the tree did not respond to fertilizer P (as for Cassia and Grevillea, Radersma and Grierson, 2004), we assumed that P mobilization (transfer from immobile P to mobile P) in the rhizosphere was adjusted to and equal to P uptake by the tree. In simulations with such P-mobilizing capacity, the P demand was

assumed to be satisfied from the immobile P-pool, and P demand (P content of all tree parts) was set at zero. The immobile P-pool is large compared to P uptake so depletion of the immobile P-pool through uptake can be ignored. On the other hand, if measured P fractions in rhizosphere soil did not differ from measured P fractions in bulk soil, but plant growth increased upon P application (as for maize Radersma and Grierson, 2004), we assumed that P-mobilization is negligible and P uptake and plant growth adjust to low available P in the mobile-P pool. In simulations without P-mobilizing capacity the plants kept their P demand as determined (= P-content \times growth rate), which is taken up from the mobile P-pool in the model.

2.3. Deriving the input parameters for WaNuLCAS

Key parameters for the simulations are shown in Table 1 and explained below.

2.3.1. Choice of P-parameters

A list of soils with known double-Langmuir¹ P-adsorption isotherm was provided by the WaNuLCAS model. We chose a strongly P-sorbing Indonesian soil (Sitiung²) for the three lower layers, and a somewhat less sorbing Indonesian soil (Lampung BMSF³) for the top layer. Alternatively, a more sorbing scenario was used with a higher sorbing Indonesian soil (RbujungU⁴) for the three deeper layers and Sitiung¹ as top layer.

P-Olsen values measured in the different layers of the trials described above were input values for initial mobile-P. The 3.5 years old tree lines had not had any effect on P-Olsen values in the different zones. Total P in the soil was about 500 mg kg⁻¹ (P. Smithson, personal communication) and this value was used to calculate initial immobile P in each cell.

¹ Double-Langmuir isotherm: $P\text{-sorbed} = \text{SorbMax1} \times \text{SorbAff1} \times \text{Conc} / (1 + \text{SorbAff1} \times \text{Conc}) + \text{SorbMax2} \times \text{SorbAff2} \times \text{Conc} / (1 + \text{SorbAff2} \times \text{Conc})$.

² Sitiung 1: $\text{SorbMax1} = 4.71 \text{ mg P cm}^{-3}$, $\text{SorbMax2} = 1.95 \text{ mg P cm}^{-3}$, $\text{SorbAff1} = 523 \text{ ml mg}^{-1}$, $\text{SorbAff2} = 666 \text{ ml mg}^{-1}$.

³ Lampung BMSF: $\text{SorbMax1} = 4.51 \text{ mg P cm}^{-3}$, $\text{SorbMax2} = 0.05 \text{ mg P cm}^{-3}$, $\text{SorbAff1} = 565 \text{ ml mg}^{-1}$, $\text{SorbAff2} = 725 \text{ ml mg}^{-1}$.

⁴ RbujungU: $\text{SorbMax1} = 9.9 \text{ mg P cm}^{-3}$, $\text{SorbMax2} = 0.02 \text{ mg P cm}^{-3}$, $\text{SorbAff1} = 700 \text{ ml mg}^{-1}$, $\text{SorbAff2} = 1884 \text{ ml mg}^{-1}$.

Table 1
Key parameters used in the WaNuLCAS simulations

Soil-P parameters	Layer 1	Layer 2	Layer 3	Layer 4	Comments
	Lampung BMSF	Sitiung 1			Sorbing scenario
	Sitiung 1	Rbujung U			Strongly sorbing scenario
Initial immobile-P (mg kg ⁻¹)	500	500			
Initial Olsen-P (mg kg ⁻¹)	1.3	0.5			
Pmob (d ⁻¹)	1.6 × 10 ⁻⁵	8 × 10 ⁻⁶			
Tree and crop parameters	Cassia	Grevillea		Maize	Comments
Potential growth rate (kg m ⁻²)					
P demand parameters					
P-content leaves (mg g ⁻¹)	1.00	0.60		5.00	P-content of young maize (mg g ⁻¹)
P-content twigs (mg g ⁻¹)	0.70	0.40		1.00	P-content of maize (mg g ⁻¹)
P-content wood (mg g ⁻¹)	0.35	0.10		–	
P-content roots (mg g ⁻¹)	0.60	0.20			
Roots					
Type	1	1		1/2	
X0 (cm cm ⁻²)	15.0	10.1		50.0	
DD (m ⁻¹)	1	3.41		4.98	
DS (m m ⁻¹)	0.045	0.04		–	
Mycorrhiza					
Infection (%)	40	40		25	
Actual infection	0.4	0.4		1.0	
Hyphal diameter (cm)	0.01	0.01		0.01	
Hyphal length per unit root length	100	100		100	

Root type 1 describes the root distribution throughout the soil as elliptical function with fixed Lrv, type 2 similar but with root density dependent on above ground biomass growth. The elliptical function root parameter X0 is the total root length per unit surface at distance 0 from the tree line, DD governs the decrease with depth of the root length density and DS governs the decrease of the root length density with horizontal distance as relative measure to DD (van Noordwijk and Lusiana, 2000). Pmob is the overall transfer from immobile to mobile P by weathering and mineralization of soil organic matter.

To allow available-P levels to change minimally over time and over distance to the tree line, as observed in P-Olsen values in the experiment, overall mobilization of immobile P (P-mob in Table 1) accounts for P additions to the mobile pool derived from native SOM mineralization and weathering. Further organic matter dynamics were switched off, because organic material was removed from the plots.

2.3.2. Tree and crop parameters

For tree root densities over distance and depth, root type 1 was chosen. Root type 1 describes the root distribution as function of distance and depth. The chosen function has elliptical isodensity lines. For Grevillea the parameters of root type 1 were derived from measured root length densities of the trees by a non-linear fitting procedure (Radersma and Ong,

2004). For Cassia the parameters were derived from root measurement figures (Livesley et al., 2000; Livesley, unpublished data). The tree-root density distribution of the trees remained fixed during the simulation.

For maize root length densities over depth root type 2 was used except for the first simulations of the first and second series in which root type 1 was used. Root type 2 has a similar density function as root type 1, Lrv is not fixed (like in type 1) but a function of above ground biomass growth.

Mycorrhizal infection rates were measured in both pot- and field-trials (unpublished data). Differences existed between the species, but infection of maize roots did not seem to change with change of coexisting tree or distance to tree line. Therefore, although the parameters used (Table 1) may not be exact, they do not change the relative performance of zones at different distances from the tree.

Most other input values were derived from measurements in field trials in western Kenya (the described trial plus a similar one in the same area on a very similar soil) (unpublished data).

2.3.3. Soil water content and rainfall distribution

Instead of simulating soil water distribution near the *Grevillea* and *Cassia*, we used the measured soil water contents throughout the profile for the layers 2–4, because the soil water extraction close to *Grevillea* was not simulated well by WaNuLCAS (Radersma and Ong, 2004). For layer 1 (0–0.15 m), zone 4 we simulated the soil water contents using the rainfall distribution of Fig. 2. Then for layer 1, zone 2 the day-to-day simulated water content of layer 1 zone 4 was used, but every days' soil water content was diminished by the average difference ($\sim 0.02\text{--}0.025\text{ m}^3\text{ m}^{-3}$) in soil water content between zones 4 and 2 of deeper layers (as measured in the field). Similarly the soil water content of layer 1 zone 3 was derived from the simulated soil water contents of layer 1 zone 4.

2.4. Model simulations

The first series of simulations examined the effect of small decreases in soil water contents, as measured in the field trial near the *Grevillea* tree line, on maize biomass yield. These simulations were done for maize without trees, using the varying soil water contents in the different zones as measured with distance to the *Grevillea* line. Initially we tested two different P-isotherm scenarios.

In the second series of simulations, we repeated the simulations of the first series, but now in presence of a *Grevillea* tree line with its nutrient demand and uptake.

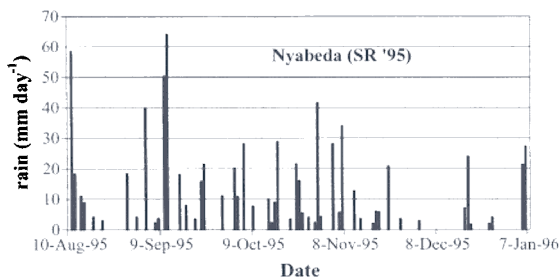


Fig. 2. Rainfall distribution in Nyabeda/Kenya in the short rainy season of 1995, during the measurements in the experiment and used in the model simulations.

The third series of simulations investigated the effects of a *Cassia* tree line on the maize yield in the zones with distance to the tree. We tested the effects of *Cassia* on maize production due to the slightly different soil water contents as measured in the field trial near the *Cassia* tree line and presence or absence of P-mobilization by *Cassia*.

3. Results

3.1. Maize yield and soil water contents in the field trial

Maize biomass at different distances to the lines of *Cassia* and *Grevillea* are shown in Fig. 3. Yields were slightly but significantly higher near the *Cassia* tree line. In contrast, maize yields decreased strongly and significantly approaching the *Grevillea* tree line. If P was applied, there were only small or no decreases in maize growth near the *Grevillea* tree line (Livesley et al., 2002).

Soil water contents are given in Fig. 4, and shows a similar pattern to maize yields. Soil water contents close to the *Cassia* tree line are slightly higher closer to the tree, and soil water contents near *Grevillea* decreased significantly with $0.025\text{ m}^3\text{ m}^{-3}$ less soil water close to the tree line than far from the tree line.

3.2. Step-wise simulation of tree effects on maize growth

The two P-sorption scenarios, a strong sorbing and a very strong sorbing scenario, gave similar results when comparing the relative maize biomass yields of zones at different distances from the tree lines, although absolute yield levels changed. In all simulations we used relative biomass yields (yield of zone (x)/yield of zone 4) to compare with measured yields so the choice of sorbing scenario did not affect the outcomes described below.

3.2.1. First series: effects of decreasing soil water contents as measured near *Grevillea* on maize

The results of the first series of model simulations investigating effects of soil–water content on P transport, P uptake and crop growth are shown in Fig. 5.

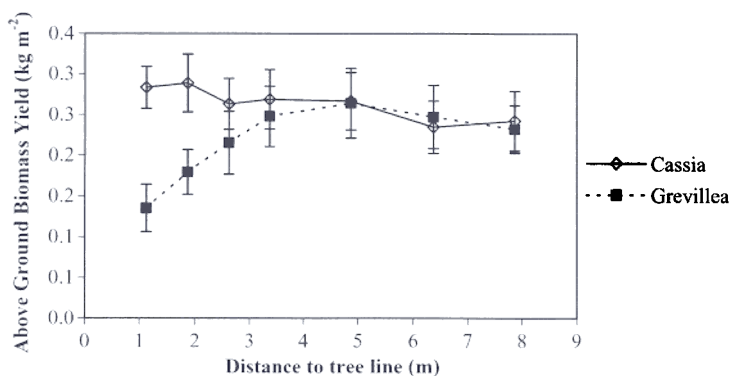


Fig. 3. Maize biomass yield (with standard error bars) in the short rainy season (September–December) 1995, with distance to tree lines of Cassia and Grevillea in the field experiment at Nyabeda/Kenya.

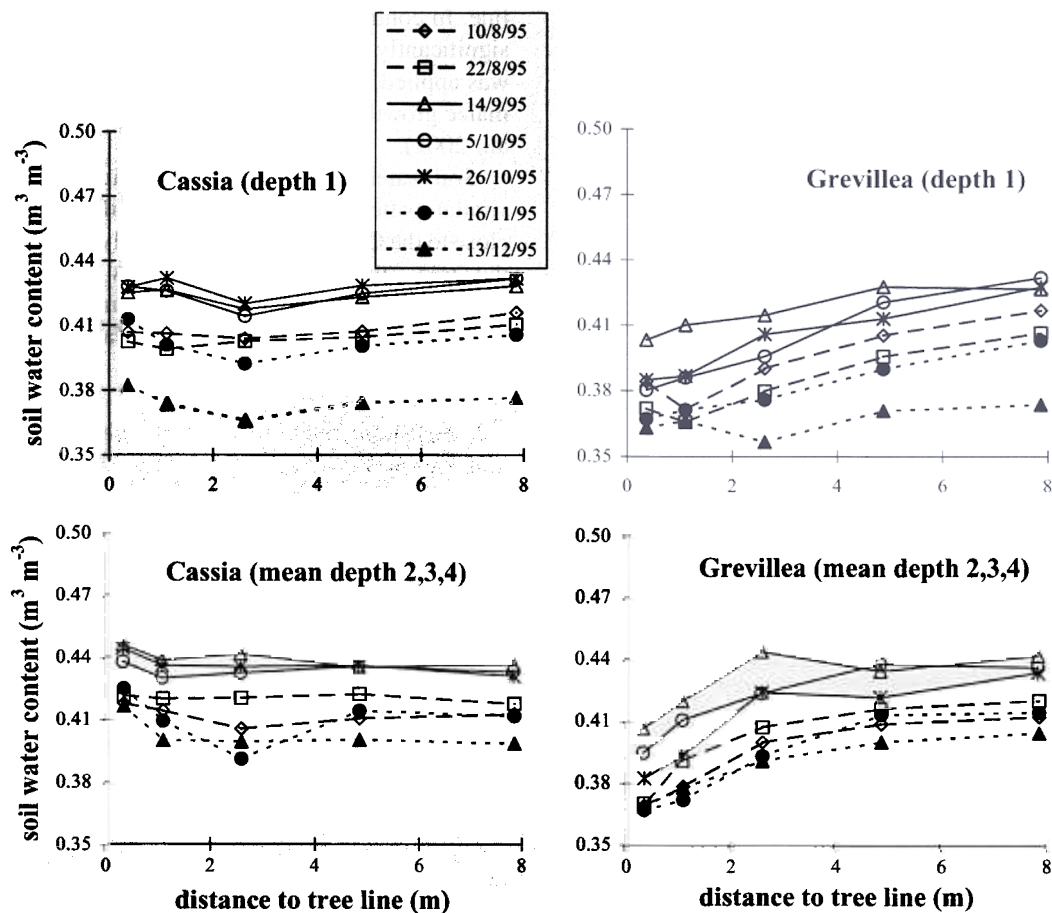


Fig. 4. Soil water contents with distance to Cassia and Grevillea tree lines as measured in the field experiment at Nyabeda/Kenya. Depth 1 is at neutron-source/neutron-counter depth of 0.35 m. Depth 2–4 were at 0.7, 1.05 and 1.40 m depth.

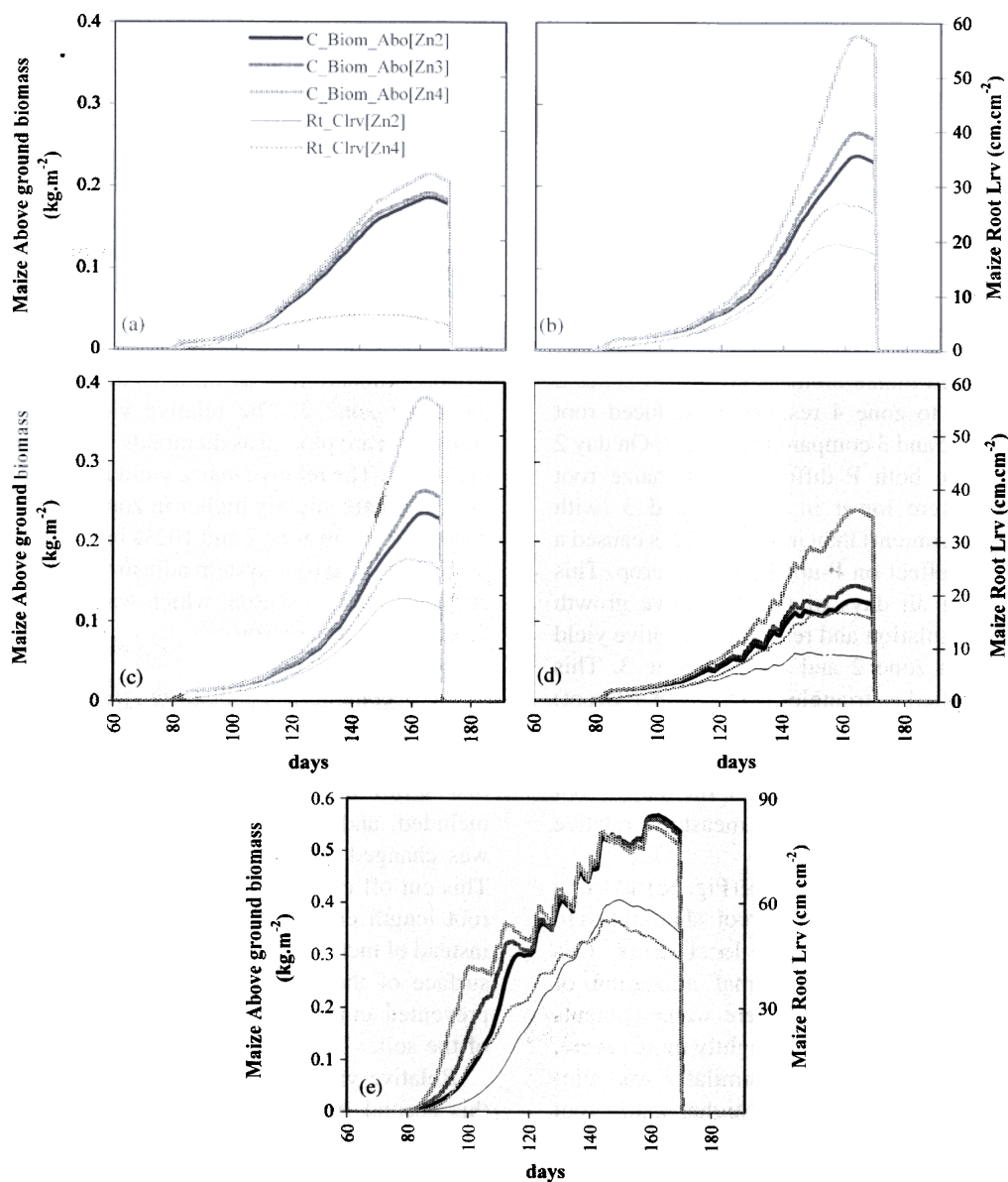


Fig. 5. Simulated maize above-ground biomass production (C_Biom_Abo) and root length per unit surface area (Rt_Clrv) of the second soil layer (0.10–0.5 m) at soil water contents (rather high pF range), as measured with distance to the Grevillea tree line given in Fig. 4. Zone 2 [Zn2] is closest to tree line to zone 4 [Zn4] furthest from tree line. (a) is a simulation with fixed crop-root profile (root type 1 = same crop root length density profile in all zones), (b) is a simulation with maize root growth dependent on above ground biomass growth (root type 2), (c) is a simulation similar to (b) but including flexible root: shoot ratio, responding to local resource availability, (d) is a simulation similar to c but including water-deficiency per se, (e) including water-deficiency and root responses as in c but excluding P deficiency.

In the first simulation of the first series (Fig. 5a) lower soil water contents in zone 2 decreased P diffusion to roots. This was the cause of decreases in biomass yield in zone 2 (87% of zone 4) and zone 3

(89% of zone 4). Root length densities per unit surface area of maize (Lrv in Fig. 5a) were kept the same in all zones in this simulation, independent of above-ground biomass growth. The relative yield levels of this

simulation are also plotted as squares (Mod.Pwat) in Fig. 6A. This shows clearly that the relative yield levels reached by only simulating the differences in P diffusion did not yet come close to the measured relative yield levels.

The second simulation of the first series (Fig. 5b), differed from the first simulation by simulating maize root growth dependent on maize above ground biomass growth. On day 1 in the simulation, lower soil water contents caused less P-uptake (through hampered diffusion) and caused decreased maize biomass growth. Decreased maize biomass growth in zones 2 and 3 compared to zone 4 resulted in reduced root growth in zones 2 and 3 compared to zone 4. On day 2 of the simulation both P diffusion and maize root length density were lower in zones 2 and 3 (with lower soil water-content) than in zone 4. This caused a double negative effect on P-uptake by the crop. This continued during all days of the vegetative growth period of this simulation and resulted in relative yield levels of 62% in zone 2 and 69% in zone 3. This simulation is plotted as triangles (Mod.Pwat + Croot) in Fig. 6A. This shows that relative yield levels reached by simulating differences in P diffusion together with the cumulative effect on maize root growth comes much closer to the measured relative yield levels.

The third simulation of this series (Fig. 5c) added to the second simulation by allowing root: shoot ratios to vary as a response of the crop to local stress. This response allowed for more optimal allocation of assimilates. In zones 2 and 3 where water contents were lower and thus P stress was slightly more severe, a somewhat higher fraction of assimilates was allocated to roots resulting in slightly higher maize root length density: biomass ratio (model output data not shown). The relative yield levels of this simulation are plotted as dashes (Mod.Pwat, Croot2) in Fig. 6A. The relative maize yield levels (62% in zone 2 and 69% in zone 3) including this stress response do not differ from those in the second simulation.

The fourth simulation of the first series (Fig. 5d) added the direct water limitation effect to the processes described in the previous three simulations. The direct effect of water deficiency increased the difference between final crop biomass in the different zones. The relative yield levels of this simulation are plotted as circles (Mod.Pwat, Croot2, wat) in Fig. 6A.

The relative maize yield levels (53% in zone 2 and 60% in zone 3) obtained by simulating indirect plus direct water deficiency effects came even closer to the measured relative yield level for zone 2, but was below the measured relative yield level for zone 3.

The fifth simulation of the first series (Fig. 5e) shows that when limitation of P is switched off, water limitation per se does not cause the strong reduction in biomass yield. Water limitation delays the start of maize growth in the dryer zones 2 and 3 at the start of the season, but catches up towards the end of the season. Allocation of assimilates to roots is higher in the dryer zone 2. The relative yield levels of this simulation are plotted as diamonds (Mod.wat, Croot2) in Fig. 6A. The relative maize yield levels at the end of the season are slightly higher in zones 2 and 3 than in zone 4 (104% in zone 2 and 102% in zone 3). This was probably due to root-system adjustment to water stress at the start of the season, which was beneficial at the dryer end of the season.

3.2.2. *Second series: including effect of P-demand of Grevillea on maize*

The second series of simulations were similar to the first series but a growing Grevillea tree line was included, and the exponential root-profile of maize was changed into a cut-off exponential root-profile. This cut-off exponential root-profile had a maximum root length density (Lrv) at 0.1 m depth and above instead of increasing Lrv towards infinity values at the surface of the soil. This adjustment of root profile prevented an unrealistically high Lrv in the top 0.1 m of the soil.

Relative yield levels derived from simulations of this second series are shown in Fig. 6B. The first simulation included only the direct P diffusion effect on relative maize yield. The relative maize yield levels (76% in zone 2 and 82% in zone 3), shown as squares in Fig. 6B are lower than the relative yield levels caused by the P diffusion effect alone of the first series of simulations (squares in Fig. 6A). The second simulation included P-diffusion, maize root growth dependent on maize above ground biomass growth and root-growth adjustment to stress. The effect of cumulative root growth reduced relative maize yield levels by about 10% extra (to 67% in zone 2 and 75% in zone 3), shown as dashes in Fig. 6B. The third simulation added the direct competition for P by the tree to the

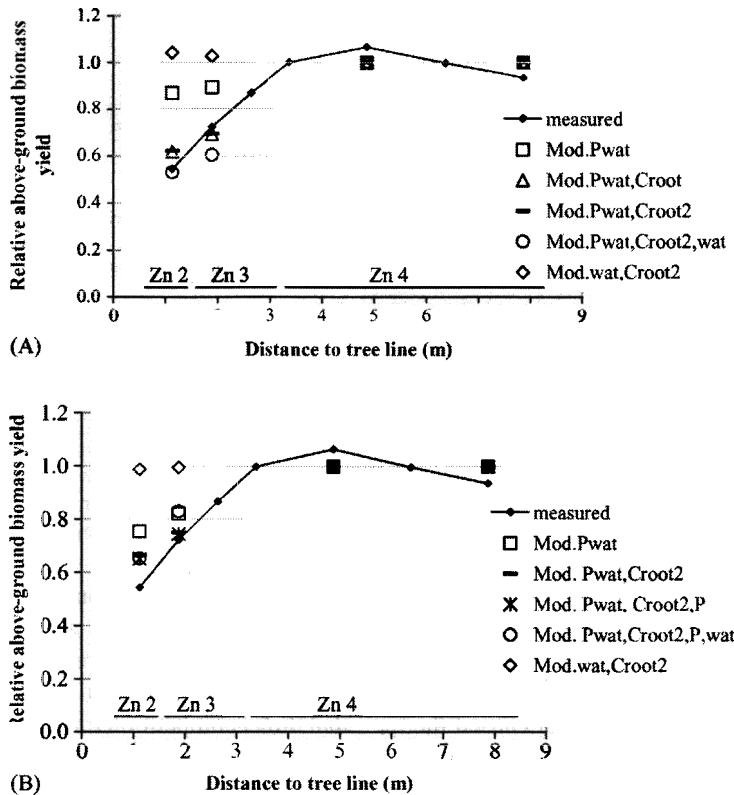


Fig. 6. Measured and simulated relative maize biomass yields, (A) without tree line but with soil water contents as measured near Grevillea, and (B) with a Grevillea tree line, its soil water profile and P demand, but with cut-off exponential crop-root system. The line with the small diamonds represents the measured biomass yield. In the descriptions of the other symbols, (Mod.) infers that the relative yield levels are model simulations, (Pwat) is the effect of soil water content on P diffusion, P uptake and concomitant crop growth, (Croot) means when crop root-growth depends on shoot growth, (Croot2) is like Croot but including that root: shoot ratio adjusts to availability of the most limiting resource (P or water), (wat) is the effect of direct water deficiency and (P) is the effect of direct P competition by the tree.

effects in the former two simulations. This is shown as stars (Mod.Pwat, Croot2, P) in Fig. 6B. Direct competition for P by Grevillea did not decrease relative maize yield levels further compared with the former simulation. The fourth simulation included direct water-limitation to the effects in the former simulations. This is shown as circles (Mod.Pwat, Croot2, P, wat) in Fig. 6B. The additive effect of direct water limitation on crop growth did not change relative maize yield level in zone 2 and even increased relative maize yield level in zone 3 back to 83%. The fifth simulation of this series includes water limitation per se, and switched off the limitation for P. This is shown as diamonds (Mod.wat, Croot2) in Fig. 6B. The effect of water limitation per se was negligible, decreasing relative maize yield level to 99% in zone 2.

3.2.3. Third series: effects of Cassia's soil water profile and P-demand on maize

The third series of simulations investigated the effects of a Cassia tree line on the maize yield. Relative yield levels derived from simulations of this third series are shown in Fig. 7.

The first simulation of this series, at soil water contents as measured near Cassia tree lines in the field, included the effects of soil water content on P diffusion and maize root growth. The P demand of Cassia was set at zero. The results are shown by the triangles (Mod.Pwat) in Fig. 7. The relative maize yield levels (102% in zone 2 and 90% in zone 3) follow the soil water contents shown in Fig. 4, but are still below the measured maize yield levels shown by the continuous line.

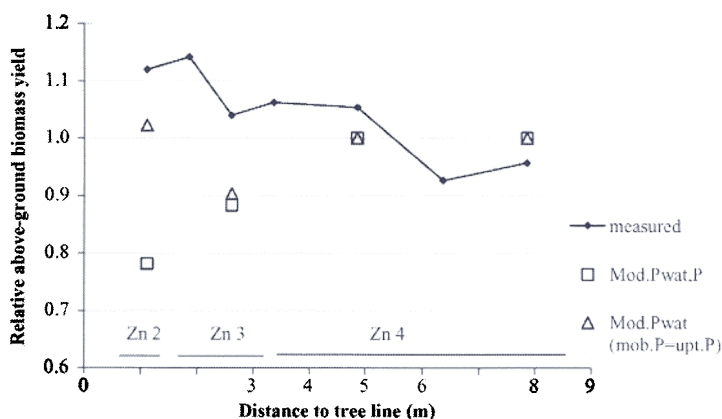


Fig. 7. Simulated and measured relative maize biomass yields with distance to Cassia tree line. The line with the small diamonds represents the measured biomass yield. In the descriptions of the other symbols, (Mod.) infers that the relative yield levels are model simulations, (Pwat) is the effect of soil water content on P-diffusion, P-uptake and concomitant crop growth, (Croot2) means when crop root-growth depends on shoot growth and that root: shoot ratio adjusts to P-availability and (P) is the effect of direct P-competition by the tree.

The second simulation of this series included P uptake from the mobile P-pool by Cassia. The relative maize yield levels of this simulation are shown by the squares (Mod.Pwat, P) in Fig. 7. Clearly including P uptake by Cassia from the mobile P-pool caused the relative maize yields of the zones near the tree line to decrease more than in the first simulation (78% in zone 2 and 88% in zone 3). This is even less in agreement with the measured maize biomass yields than the results from the first simulation.

4. Discussion and conclusions

Our model simulations showed that, on a clayey Ferralsol in western Kenya in which phosphorus is a main limitation to crop growth, a reduction of $0.020\text{--}0.025\text{ m}^3\text{ m}^{-3}$ soil water close to the tree line decreased above-ground biomass production of the maize crop by 30–40%. This was in agreement with measured maize yields near a Grevillea tree line in the field. Model simulations revealed that water limitation per se played a minor role in this effect. The main causes were two water-P-plant interaction mechanisms, (1) the decrease in soil water content decreases P diffusion, and thus P transport to the maize roots and P uptake, and (2) maize root-growth (and thus uptake of resources) is cumulatively reduced because of lower above ground biomass production caused by lower P uptake through decreased P diffusion. Such

decreased soil water contents of $0.02\text{--}0.025\text{ m}^3\text{ m}^{-3}$ had been measured near a Grevillea tree line. Including the Grevillea tree line in the model simulation, thus adding the nutrient demand of the tree, showed that direct competition for P by the Grevillea (with low P demand) had minimal effect on crop growth compared with the soil drying induced P deficiency effect.

In contrast, if soil drying near a tree line was minimal and the tree had a relatively high demand for P, like Cassia, the model simulations revealed that direct competition for P would reduce the relative maize yields near the tree line to less than 80%. However, this did not agree with the measurements of the maize yield in the field, which slightly increased near the Cassia. Several authors (Bhat et al., 1976; Marschner, 1991; Macklon et al., 1994; Barber, 1995) have mentioned that plant uptake of P from soils with low levels of available P cannot be calculated by physico-chemical equilibrium and transport equations alone. This is due to problems related to measuring P pools and their availability in P-fixing soils (Gijssman et al., 1996). It is also complex to include adaptations of plants to low P availability, such as symbiosis with mycorrhizal fungi and root exudation modifying the rhizosphere chemistry and P availability.

The increase in maize growth near Cassia tree lines can possibly be explained by including P-mobilization in the rhizosphere of Cassia as found by Radersma and Grierson (2004), because no other additions (e.g. litter) occurred near the tree lines, and there was no

evidence of decrease in mycorrhizal infection of maize roots with increasing distance from the tree line. Experimental evidence supports the idea that in the rhizosphere of Cassia P mobilization at least equals P uptake (Radersma and Grierson, 2004). The simplest way to add P mobilization in the model simulations was to shift the P uptake by Cassia from the mobile P-pool to the immobile P-pool. Shifting P uptake away from the mobile P-pool in the model was achieved by setting the P demand of the tree to zero. If the P demand of Cassia was set at zero, the relative maize yield levels approaching the tree line (90–102%) still did not reach the relative yield levels measured in the experiment near the Cassia line (104–114%). This may indicate that Cassia did not only mobilize P to satisfy its own demand, but also supplied some mobilized P to maize. This possibility is supported by the relatively high overlap between maize and Cassia roots in conjunction with pH increases and high oxalate concentrations in the rhizosphere of Cassia (Radersma, 2002).

Grevillea was also a species which seemed to be able to mobilize P to satisfy its own P demand (Radersma and Grierson, 2004). However, in the model simulations there was no difference in relative maize yields near the *Grevillea* line if P demand of the *Grevillea* is included or set at zero to simulate P mobilization. The soil drying induced P deficiency effect on relative maize yields near the tree line overwhelms the possible positive effect of P mobilization by *Grevillea*.

The mechanistic model WaNuLCAS was very useful in the investigation of the water-P interaction hypothesis. It is well known that P transport is largely by diffusion in P-fixing soils (Nye and Tinker, 1977; Barber, 1995), and that diffusion depends strongly on soil water contents (de Willigen and van Noordwijk, 1987; Barber, 1995). However, the large effect of small decreases in soil water content on crop growth on soils low in available P, mediated by the effect of a decrease in P diffusion and amplified by cumulative decreases in plant and root growth, has not been recognized on field scale. This soil drying induced P deficiency on P fixing soils can, in a wider context, explain crop performance features on such soils. It explains the importance of a good rainy season to maize production in an environment like western Kenya (in which water limitation per se is not

common). It may also explain why, with increasing soil-nutrient depletion, micro-variability of crop growth in a field increases. Soil water contents may vary by quite a few percent over small distances, and may cause large micro-variability in biomass production in situations with low levels of available nutrients, where diffusion becomes the most important transport mechanism.

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