

Tree effects on crop growth on a phosphorus-fixing Ferralsol

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Preface

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Abstract

In agroforestry systems trees affect crops. This study aimed at understanding how trees grown in lines for pole production affect maize on an unfertilized, P-fixing Ferralsol, in the agricultural area of Western Kenya. I hypothesized that, because maize production was primarily limited by P-deficiency, trees would affect maize growth by effects on P-uptake of maize, as determined by P-availability of the soil, soil water contents and root-length densities.

Field-based experiments were used to investigate 1) rhizosphere modifications by trees and maize roots and their effects on P-availability, 2) tree water-use and extraction from the soil profile, and 3) root distributions of trees and maize. The tree-crop interaction model WaNuLCAS was adjusted and used to compute the effects on maize production of soil drying and rhizosphere modifications as caused by the trees.

Soil drying occurs if water-use of trees is larger than water-inputs by rainfall. High water-use of trees in tree lines was mainly related to high leaf-area and low leaf-efficiency. Meteorological variables influenced water-use of tree lines less. The importance of leaf-area as determinant of water-use of tree lines was due to the large range over which water-use of tree-lines responds linearly to increases in leaf-area.

Water extraction from the soil declined with distance to the tree line (horizontal dimension) and was not clearly related to relative root length density. This was due to the decreasing water-potential gradient, between root and soil, with increasing distance to the stem-base. Vertically, root length densities decreased more strongly than water-potential gradient, and determined the water-extraction profile.

Through higher organic anion contents and pH increases in rhizosphere soil, *Cassia spectabilis* (syn. *Senna spectabilis*) and *Grevillea robusta* mobilized soil P, which was taken up by the trees themselves. Residual P-availability was not increased. The relatively long duration of pH-increases and organic anion exudation in the rhizosphere of *Cassia*, combined with the relatively high synlocation of *Cassia* and maize roots, suggests that maize can profit from P mobilized by *Cassia* roots.

Acid phosphatase activity was highest in the rhizosphere soil of *Grevillea* and probably caused the observed shift from organic to inorganic P-fractions in the soil. However, maize showing low acid phosphatase activity in the rhizosphere, depleted organic-P fractions in the rhizosphere soil similarly as *Grevillea*. Therefore, it is likely that uptake of organic P from soil is more limited by its availability in the rhizosphere than by hydrolysis catalyzed by phosphatase activity.

Model simulations revealed that a decrease in soil water content of 2.5 % (at high pF) decreased maize production by 30 - 40 %, due to 1) decreased P-diffusion due to soil drying, and 2) the cumulative effect of decreased P-diffusion on decreases in maize and maize-root growth. Maize yield increases of 12 % as measured near *Cassia* tree lines could only be simulated when organic anion and pH effects on P-availability in the rhizosphere of *Cassia* were included in the model. Without rhizosphere modifications, *Cassia* would compete with maize, due to its high demand for P. However, positive rhizosphere effects as exerted by *Cassia* were minimal if soil-drying induced P-deficiency occurred simultaneously.

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General Introduction

General Introduction

Agroforestry

Agroforestry is old as practice but relatively young as a branch of agricultural science. It differentiated from the main stream of agricultural sciences in the 70s-80s (Torquebiau, 2000). Agroforestry is any form of land use in which trees and crops and/or animals are combined. Some old existing types were; i) Slash and burn practices with tree-fallows, ii) parklands in large parts of sub-Sahara Africa, iii) use of shade trees for plantation crops, iv) tropical agroforestry homegardens, v) multistrata agroforests of South East Asia, vi) the “taungya” system in East Africa and vii) herding of animals in rangelands (Torquebiau, 2000). To order these types, different classifications were made, based on the agroforestry components; agrosilviculture (trees and crops), silvopastoralism (trees and animals) and agrosilvipastoralism (trees, crops and animals), or based on time-structure; simultaneous and sequential agroforestry systems, or on spatial structure; mixed or zonal arrangements. Functional criteria of the woody component added an extra classification; trees used for wood, fruits, fodder, shelter, shade, soil conservation and fertility or fencing (Torquebiau, 2000).

The complexity of classifications is reflected in the definitions of agroforestry. One extreme of the range of definitions is a purely physical and scientific definition: “Agroforestry is a form of multiple cropping which satisfies three basic conditions: 1) there exist at least two plant species that interact biologically, 2) at least one of the plant species is a woody perennial, and 3) at least one of the plant species is managed for forage, annual or perennial crop production” (Sommariba; 1992). The other side of the range contains more “political” definitions including aims of (ecological) sustainability and social and economical gains, e.g “Agroforestry is a dynamic, ecologically based natural resource management system that, through the integration of trees in farm- and rangeland, diversifies and sustains smallholder production for increased social, economic and environmental benefits” (Leakey; 1996). The risk of including aims in a definition is that non-successful tree-crop/animal systems cannot be called agroforestry, and therefore agroforestry is per definition “good”. The problem of the more political definitions is that aims change with politics and politics change with people at the top. This is especially clear in the International Center for Research in Agroforestry (ICRAF) as one of the Consultative Group of International Agricultural Research (CGIAR), where we see recently a shift in priority from increasing smallholder production and food-security to environmental issues. This shift is based on the interests of the donor community, and supported by economical calculations, which suggest that ecosystem support functions of land are about 300 times more in money-value than the money-value of the food-crop function of the same land (Izac and Sanchez, 2001). Remains the question whether the money value of 300 bags of maize in ecosystem

support functions (for whom?) is as valuable and necessary as one bag of maize for a nearly starving farm-family in e.g. Africa.

Agroforestry in Africa; expectations and disappointments

The original and successful long-fallow land-use systems (Nye and Greenland, 1960) became more and more impossible in 1970-1980 in Africa, due to population growth. This demanded for new alternatives. Alternatives should be low-cost (financially) due to the general poverty of the rural population in large parts of the tropics. Agroforestry was seen as one such alternative by combining fallow and production mechanisms at the same time and space (Kang et al, 1985). At the start of increasing interest in Agroforestry, many hypotheses were postulated, showing all possible advantages of tree-crop combinations in a qualitative way (Nair, 1984; Young, 1991). Trees would be able to supply nitrogen to the system by biological nitrogen fixation (BNF) from the air, and pump other nutrients from depth and recycle them to the surface soil through litter. Trees would minimize nutrient losses by erosion and leaching due to their always-present root-systems. They would restore soil organic matter content and temper microclimate (Nye and Greenland, 1960; Young, 1991). All these potential advantages caused high expectations for agroforestry systems.

The disappointment came short after. Although the advantages were present, the main disadvantage, competition for resources between tree and crop, was overlooked, and this competition caused that the advantages mentioned above were largely off-set (Ong, 1995). Total primary production of trees and crops could still be larger than that of the crop alone, but the crop yield itself was often decreased. And in this case only a high value of the trees and a valid marketing infrastructure could make the system economically viable and attractive to farmers. This harsh landing of heavenly prospects caused on the one hand that interests of agroforestry research shifted to sequential systems (e.g. improved fallows) with no competition between trees and crops. On the other hand, in simultaneous systems, quantification of the balance between positive and negative effects of trees on crops became necessary.

Quantifying tree-effects on crops: Ong's equation

Ong (1995) developed an equation for alley-cropping systems, expressing the total effect of trees on the crop. This equation was simplified by Sanchez (1995) to $I = F - C$, in which C is the total negative competition effect on crop yield, F is the total positive effect on crop yield, supposed to come from increased soil fertility, and I (interaction) is the final balance of positive and negative effects on crop yield. I is positive if the fertility effect is larger than the competition effect and I is negative if $F < C$. Cannell et al (1996) attempted to clarify the resource base of this equation. They argued that part of the mulch effect of the tree is based on light, water and nutrient resources which the tree acquired in competition with the crop (F_{comp}). Another part may have been obtained in complement to resources

available for the crop (F_{noncomp}). Similarly, part of the resources acquired by the tree in competition with the crop is recycled within the system and may thus be used by a future crop (C_{recycl}). If F_{comp} is based on the same resources as C_{recycl} in the longer run the two terms would cancel. The question whether or not a tree-crop combination gives yield benefits then depends on, 1) the complementarity of the resource use, 2) the value of direct tree products, specifically those obtained in competition, $C_{\text{nonrecycl}}$, relative to the value of crop products that could have been produced with these resources and 3) the efficiency of recycling tree resources into crop products, specifically for the resources obtained in competition with the crop, C_{recycl} .

The main advantage of Ong's method is its simplicity in quantifying system performance as result of a few main effects, which can be easily measured with a relatively simple experimental setup. But there are disadvantages.

The first is the lack of a time-frame. The assumption of Cannell et al (1996) that $F_{\text{comp}} = C_{\text{recycl}}$ may be true once the system has reached equilibrium in the long term, but before that stage the fertility-effect is more prone to delays (due to slow or low liberation of available nutrients from recycled material) than the competition-effect. Thus, in the first years which are important for the assessment of the technology by the farmer, $F_{\text{comp}} < C_{\text{recycl}}$, and I has a large chance to be negative. The equation does not allow for delayed effects.

Another disadvantage is that the agroforestry system performance results of this equation can not be transferred from one environment to another.

Quantifying tree-effects on crops: Kho's equation

Kho (2000) developed a method to overcome the latter disadvantage of Ong's equation. His method allows for the transfer of performance results of a specified system from one environment to another and is based on a similar sum of positive and negative factors as used by Ong. The factors are tree-effects on crop production (t ha^{-1}) via the availability of different resources (light (L), water (W), Nitrogen (N), Phosphorus and bases¹ (P). These factors are multiplied by an environmental factor (l, w, n, p) indicating the degree of limitation of each resource in a specified environment. The sum of all environmental factors is one ($l+w+n+p=1$), and the size of single environmental factors is between 0-1. The largest factor indicates the main limitation of an environment, the lowest the least limiting resource. Thus the equation becomes:

$$I = l*L + w*W + n*N + p*P.$$

If the tree supplies N to a crop but competes with the crop for P to a similar but negative extent, and does not affect the other resources, it depends on the environmental factors n and p what the final effect I is. If $p > n$ then I is negative, because the negative effect $p*P$ is larger than the positive effect

¹ P and bases can be split up in separate nutrients if this fits the environment better

$n*N$. If $n > p$ then I is positive, because the negative effect $p*P$ is smaller than the positive effect $n*N$.

This method is meant to quantify system performance in different environments, but full quantitative use requires measurement of many response variables in sole-crop and tree-crop situations, which may not be available from existing experiments, and which would require a complex experimental setup.

Quantifying tree-effects on crops: Possibilities and impossibilities of both equations

However, Kho's method can be used quite easily in a qualitative way, and complements Ong's method in the transfer of performance results from one to another environment. The use of both methods together may give a reasonable idea of why tree-crop-interaction systems perform as they do. However, even if the two methods are used complementarily, there are still limitations to their usefulness. Kho (2000) mentioned already that his method is not applicable if pests and diseases or allelopathy caused by the tree component are important factors determining the performance.

Neither Ong's nor Kho's method has a time frame necessary for delayed effects like mentioned above and for long-term trends. Thus, an important aim of agroforestry in general is not addressed: the methods may show that a certain agroforestry system works better in certain environments than a sole crop, but this does not yet mean that such system is really sustainable over a longer period.

Another feature, which these methods do not cover, is when the performance of a tree-crop system is highly dependent on interactions between factors, and thus a simple sum of positive and negative factors is not going to give the right result. An example of this is the water-P interaction in P-fixing soils, in which P-transport to roots is decreased by decreases in soil water content. Decreases in soil water content by trees affects the environmental factor p , thus necessitating a $W*p$ term in the equation of Kho.

In cases where long-term performance and interaction of tree- and environmental factors are important, mechanistic research may be necessary to explain the functioning of the system, to understand its performance and to be able to extrapolate the system's performance over time or to other environments. However, mechanistic research suffers from its own pitfalls. An important one is the loss of overall understanding due to a focus on one or two details. Another related one is the risk of getting lost in a multitude of detailed processes, without realizing that only a few may really play an important role in determining 80-90 % of a systems performance in a certain environment. These pitfalls of mechanistic research in turn may be (partly) overcome by starting to look at the system from the perspective of Kho's method. The first question is, what are the main limiting factors of a certain environment (including pests and diseases) and the second question is, how do

trees and crops influence each other in general (including mechanisms like allelopathy) and particularly via the main resource limitation. Using Kho's method to look at main environmental resource limitations and tree-effects on the different resources it is possible to prioritize the mechanisms that need to be looked at in more detail.

In this way the use of system-performance analysis methods can be a first step to determine priorities for mechanistic research.

The Western Kenyan highlands

The research described in this thesis was done in the sub-humid highlands (alt. 1200-1600 m) of Western Kenya (figure 1).

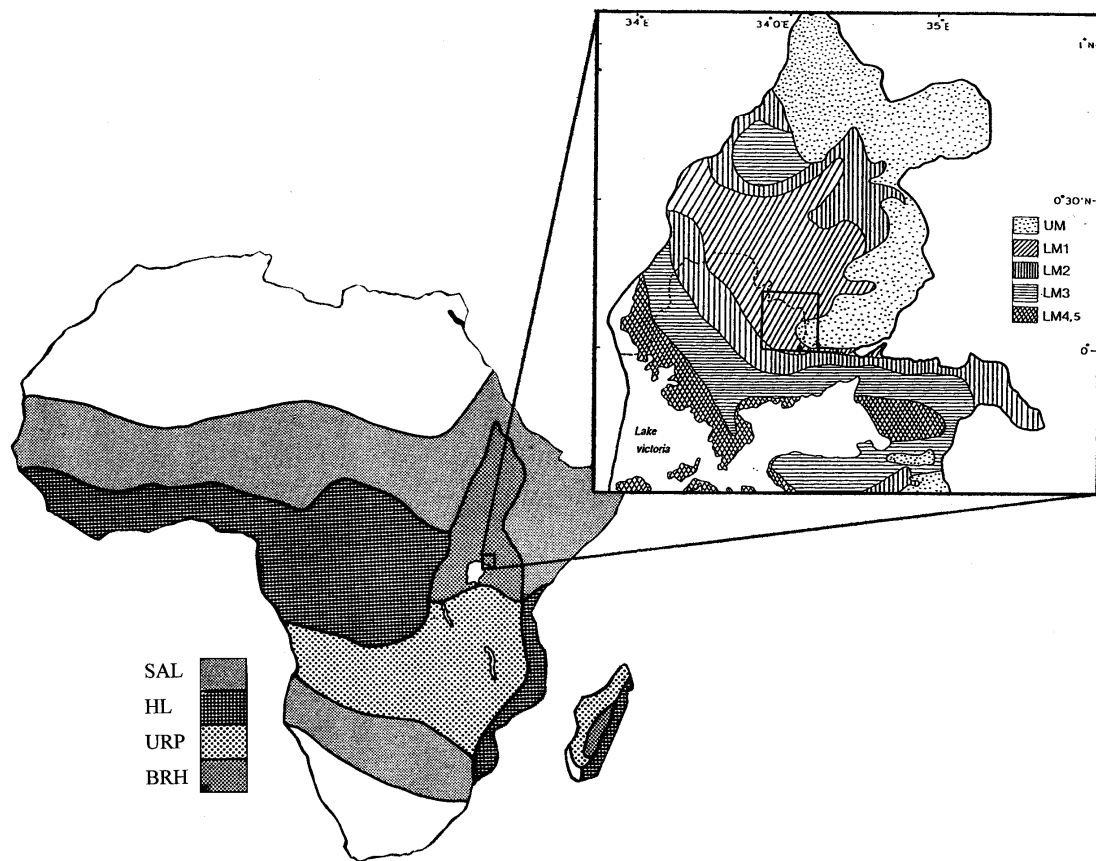


Figure 1. The study area in the sub-humid highlands of Western Kenya (small square within the inset), including landform and climate indications. SAL: semi arid lowlands, HL: humid lowlands, URP: uni-modal rainfall plateau, BRH: bimodal rainfall highlands. In the inset UM: upper midland zones with annual mean temperature 18-21 °C, LM: lower midland zones with annual mean temperature 21-24 °C, 1: humid, 2: subhumid, 3: semi-humid and 4,5: transitional to semi-arid.

Average temperature is 22⁰C with minimal fluctuation throughout the year. Daily short-wave radiation ranges generally from 17-22 MJ m⁻² d⁻¹, with only a few overcast days per year halving the incoming radiation. Due to the proximity of Lake Victoria, fluctuation in air humidity throughout the year is relatively small, 50-80%. Rainfall (1000-1600 mm yr⁻¹) occurs largely from March/April to November/December with a small dip in July/August. As a result there are two cropping seasons. Maize (mixed with beans) is the main crop.

A large part of the area (639 km²) is covered by deep dark reddish brown ferralsols/oxisols (Shepherd et al, 1992) containing 50-85% clay. Phosphorus is the first limitation to crop production, due to P-fixation (adsorption of native soil P) to soil particles (>300 ppm P in soil at 0.02 ppm soil solution concentration (Okalebo in: Shepherd et al, 1992)). Other evidence of high P-fixation in these ferralsols is given by Nziguheba et al. (1998). If P is applied, nitrogen and potassium become limiting.

Population densities increased from 150 p km⁻² before 1970 to >1000 p km⁻² in the densest areas around 1990 (Shepherd et al, 1992). Farm sizes are small (0.2-2.0 ha per family) and the agriculture consists of mainly continuous cropping with little use of fertilizers and insufficient manure, causing an estimated nutrient deficit of 100 kg N ha⁻¹ yr⁻¹ and 10 kg P ha⁻¹ yr⁻¹ in smallholder farms (Shepherd, 1993 unpublished data). Although potential crop yields are 4 t ha⁻¹, crop yields were 0.9-2.7 t ha⁻¹ around 1980, and may have declined since. The production levels on farms of less than 0.5 ha do not meet household demand, and a high proportion of food (52-71%) is purchased with cash (Shepherd et al, 1992), which is however scarce as well.

Farmer's management of trees has intensified over time. Especially in the densely populated (> 500 p km⁻²) areas with highly intensive farms, tree cover increased to 30% of the land (Shepherd et al, 1992).

Research aim and its context

In the densely populated areas with small farms, trees have become more and more incorporated in the use of land because farmers realized that growing food crops alone cannot reach their demands. Trees are a source of cash. Because of the small land holdings, trees are especially planted on borders along fields.

My main research aim is, to increase the understanding of how trees affect crops on the common P-fixing soils, where crop production is mainly limited by P-availability. The results of my study, i.e. increased understanding of tree-effects on the maize-crop should be translated to farmers or should

be used to develop guidelines to farmers on how to manage the trees and how to choose the tree-species with minimal competition to crops.

Evidently, this is an attempt to push the limits of a marginal situation up to their ends, optimizing tree-crop systems on depleted phosphorus fixing soils of small land holdings in Western Kenya, or any other similar place in the tropics. This research will not solve the large problem of nutrient depletion in Western Kenya or sub-Saharan Africa. Much effort is and has been given to the fertility depletion problem by many other scientists of ICRAF, the Dutch-Kenyan Nutmon-group, IFDC, TSBF and many others. I agree with their perspective that in general fertility replenishment is necessary in Africa. However, as long as the farmers, who have an interest in replenishing soil fertility, do not have enough money to buy fertilizers, and the people having the money (donor countries and to a lesser extent local governments) do not see fertility replenishment as their interest and therefore do not pay, the situation is stuck. In this situation supplying the knowledge to optimize the marginal situation is all my work can do.

Trees effects on crop growth in a P-limiting environment

To understand how trees affect crops on our P-fixing soils, where phosphorus is the first limitation to crop growth, the logic of Kho's "environmental factors", indicating the degree of limitation of the different resources to crop growth in this environment is a first step. The light-factor (l) is small, because radiation is high and shading by most tree lines is light, indicating that maize-growth in this level of shade is not limited by lack of light. Gacheru (pers. comm.) found that maize growth was not reduced as long as artificial shading reduced less than 50 % of incoming radiation. The water-factor (w) is small as well, because rainfall is sufficiently high to grow two crops, the deep clayey soils have a good water-holding capacity, and signs of water-stress in the crop were limited to relatively long dry spells, which do not occur often. The nitrogen-factor (n) is low as long as phosphorus is not applied, as shown by large soil-nitrate reserves (N-bulge) below 30-50 cm, sorbed on positively charged soil particles (Hartemink et al, 1996) and absence of N-deficiency symptoms in the crop. Phosphorus is the main limitation to crop-production on these soils in the area, shown by large growth response to P-application (Jama et al, 1998) and visible deficiency symptoms in maize plants (purpling). Therefore the phosphorus-factor (p) is the largest.

This analysis leads to the general hypothesis that trees are most likely to affect the crop via their effect on P-uptake by the crop. This focus on "tree-effects on crop-P-uptake" includes the more commonly investigated "effect on soil-P-availability" as well as the less commonly studied "effect on P-transport to crop-uptake-sites".

The questions following from this hypothesis were, 1) what are important determinants of crop-P-uptake and, 2) how and to which extent do trees influence these determinants.

P-uptake determinants

Uptake by a root system of any nutrient from soil depends on the availability of the nutrient in soil and on transport to the roots.

P-availability

Phosphorus is the macronutrient, which is most strongly adsorbed on soil particles, especially in soils with high contents of clay and variable charge materials like in tropical Ferralsols / Oxisols. In these soils P-availability is low. Total phosphorus in the Ferralsols of Western Kenya is about 500 mg kg⁻¹ (Smithson, pers. comm.), while resin-P (measure of available-P) is ~1-2 mg kg⁻¹. This level is usually insufficient for high crop yields.

In natural ecosystems, with low availability of nitrogen and phosphorus, species mainly adjust by decreasing growth rate, because this answers best to the aim of species survival in sub-optimal conditions (Chapin, 1980). In addition to this main strategy, some plants in low nutrient situations show specific adaptations to increase nutrient availability. Although there are no ways in which plants can add phosphorus to the soil-plant system, some plant species from environments with low levels of available-P show mechanisms to overcome natural P-deficiency (Marschner, 1991a). One group of strategies is directed towards increasing the availability of organic-P (which usually needs to be transformed into inorganic-P before it can be taken up) and P adsorbed to soil-particles. Increased phosphatase activity at the root-wall or in the rhizosphere catalyzes the hydrolysis of organic P-ester-forms into inorganic-P (Tarafdar and Chhonkar, 1978). Organic anions, exuded by the roots, exchange with both inorganic and organic phosphate at the adsorption complex (Nagarajah et al. 1970), thus decreasing P-sorption and increasing P-availability. In most Ferralsols, desorption of P is also enhanced upon an increase in pH (Tiessen and Moir, 1993), which may occur in the rhizosphere, caused by proton exudation of roots. Microbial populations in the rhizosphere may have influence on organic P decomposition and (im)mobilization, but this is not known to affect P-nutrition of plants significantly (Bowen and Rovira, 1999).

So far, it is unknown which mechanisms may play a dominant role in the interactions between trees and crops in simultaneous agroforestry systems.

P-transport in soil

Because of its strong adsorption to soil particles, phosphorus is also the macronutrient of lowest mobility in soil. Only 5% of P-transport to the roots is due to mass-flow with the water taken-up and 2% of P is directly intercepted by roots from the soil (Barber, 1995). The largest part (93%) of soil

P is transported by diffusion². Diffusion is highly dependent on soil water content, because volumetric soil water content determines diffusion directly and determines the impedance factor, which is a determinant of diffusion³ itself. Thus soil water content is an important determinant of P-transport to roots, which is the rate-limiting step of P-uptake in soils with low P-availability. Because of the low mobility of phosphorus in soils, short transport distances favor P-uptake. This infers that in P-limiting soils, high root densities are important for plant-P-uptake. However, production of roots costs assimilates, so although the plant increases its root mass in relation to shoot mass, it needs to find a functional balance between the production of roots, which increase P-uptake, and production of shoot for carbon assimilation and growth. Therefore, except for a higher root:shoot ratio, plants adjust to P-limitations by strategies maximizing uptake-surface at minimum assimilate cost. This happens through production of finer roots (Marschner, 1995) and root hairs (Hendriks et al. 1981), association with mycorrhizae⁴ (Redhead, 1979), and adjustment of root-system architecture (Fitter et al. 1991).

If P-availability, soil water content and root density are all important determinants for P-uptake, the main question remains, which of these determinants can be affected by trees, and to which extent the effects of trees on these determinants affect crop growth.

It has been shown that P-availability is marginally increased by litter production and decomposition (Palm, 1995), especially in the tree-border systems, in which trees are grown for production of poles and not for mulch-production. However, if the tree is adapted to low P-availability by P-mobilizing strategies as mentioned above, its rhizosphere may increase P-availability. If the tree roots do not repel crop roots, the crop may accidentally cross or even colonize the tree-root rhizosphere-soil gaining from increased available-P levels. In this way, the tree would transfer P from unavailable to available forms, to the advantage of the crop.

This leads to my first research question: Do tree roots increase P-availability by root exudate effects, and can the crop benefit from this increased P-availability.

² Diffusion is movement of P from a higher concentration (in soil) to a lower concentration (at root surface) through water

³ With as equation to calculate diffusion: $D_e = f_i * \theta * D_l * C_l / C_s$ (Barber, 1995) and $f_i = 0.97 * \theta - 0.17$ (derived for clay soils from (De Willigen & Van Noordwijk, 1987)). With D_e [$\text{cm}^2 \text{s}^{-1}$] as effective diffusion coefficient, f_i [] as impedance factor, dependant on volumetric soil water content (θ) [] and soil-type, D_l [$\text{cm}^2 \text{s}^{-1}$] as diffusion coefficient of the specific nutrient through water, and C_l [mmol L^{-1}] as concentration of the nutrient in solution, while C_s [mmol/1000cc] was the amount of nutrient adsorbed, and thus C_l / C_s [] as measure of adsorption/buffering.

⁴ Mycorrhizal hyphae are about 10 times thinner than fine roots and have therefore more surface per unit assimilate, and take-up P like roots do.

Root-length density of trees and crops is an important factor for P-uptake in P-limiting soils where $P\text{-demand} > P\text{-uptake}$.

There is some evidence (e.g. chapter 3) that the root:shoot ratio of a crop increases if the crop is in competition with the tree. A higher root:shoot ratio on the one hand decreases the amount of carbohydrates allocated to the above ground plant parts, on the other hand increases the capacity of the plant to satisfy the demand for below ground resources as determined by above-ground growth. Thus, increases in root : shoot ratio affect the above ground crop growth in two opposite directions. Another possible effect of trees on the root-density of a crop is through an increase of mycorrhization of the crop-roots. However, there is no experimental evidence in literature yet and my preliminary tests did not show increases in mycorrhizal infections of maize roots in the presence of trees.

I assumed that the effect of trees on crop rooting densities via changes in root : shoot ratio and mycorrhization were too small to affect crop growth significantly, and did not examine this possibility further.

Soil-water-content can be affected by trees. Water transpired by the tree is extracted from the soil; trees intercept rainfall and decrease evaporation under their canopies by shading. But the largest effect is likely that single trees and tree-lines are relatively large water-users, because of their close coupling to the atmosphere (Mc Naughton and Jarvis, 1983), which is increased by advection. Atmospheric demand depends on meteorological variables, but tree-water-use is mainly controlled by the trees' own characteristics, leaf-area, crown-configuration (open/closed), and stomatal behavior. As soon as the tree extracts more water from a certain soil volume than the amount, which is replenished by rainfall, soil drying occurs. This affects P-transport and P-uptake negatively, as described above.

This leads to my second research question: What determines total water-use by tree lines and how is the spatial distribution of water extraction throughout the soil volume in the field bordering the tree-lines.

The third research question is: How do decreases in soil water content, as caused by tree-water-use, affect P-mobility and transport of P to crop-roots, and subsequent crop-growth.

I hypothesized that decreases in soil water content affect crop-P-uptake and crop-growth in a cumulative way. During the first time step after a small plant has used all its seed-resources, a lower soil water content causes that less P reaches each unit root length of the small plants. Less P is taken up, causing a decreased growth of the plant, above and belowground, compared with the plant in moist soil. The following time step, again less P reaches any unit of root length of this plant

compared with the control, but also the root length of this plant is slightly lower due to the reduced plant growth in the former time-step. In this way, the soil drying effect on P-diffusion translates into an exponential and cumulative effect on plant growth over time.

Such a hypothetical cumulative effect of ‘soil-drying-induced P-deficiency’ can be quantified using a mechanistic computer model of nutrient-uptake and plant growth, below and aboveground. The tree-crop-interaction model WaNuLCAS (van Noordwijk and Lusiana, 2000) is such a mechanistic model with daily time steps, which allows simulation of this water-induced P-deficiency hypothesis. Moreover, this model is made for (simultaneous) agroforestry systems, and could therefore be used to crosscheck field measurements of crop yield near the tree lines with the simulated crop-growth.

Model-simulations were also used to examine the balance between positive root-exudate effects on crop-P-uptake and growth against negative soil-drying induced P-deficiency effects of trees on crop-P-uptake and growth.

Choice of crop and tree species

Maize is the main staple-crop grown in the research area and was therefore chosen as test crop. In the short rainy seasons we grew sorghum, which is less common in the area, but not unusual, and which is better able to cope with the unpredictable rainfall-pattern.

The tree species were from a trial established to compare the performance of tree-line arrangements of different trees grown for pole-production (*Grevillea robusta* A. Cunn., *Eucalyptus grandis* W. Hill ex Maiden, *Cedrella serrata* Royle and *Markhamia Lutea* K. Schum.), or from another trial established for mixed agroforestry purposes (fertility, wood-production): *Cassia spectabilis* DC. (syn. *Senna spectabilis* (DC.) H.S. Irwin & R.C. Barneby), *Grevillea robusta*. The *Tithonia diversifolia* (Hemsl.) A. Gray used in the pot-trial was another “fertility species” high in P-content, popular at the time of my research.

Outline of the thesis

In Chapter 2 the usefulness of Ong’s and Kho’s performance analysis equations are tested in an alley-cropping trial. The understanding of the outcomes of their equations with the help of some mechanistic research is described in Chapters 3.

After this preliminary assessment, I come to the main research, which is an attempt to understand and quantify the mechanisms by which trees affect maize growth in a tropical environment with P-fixing Ferralsols.

The first question “Do tree roots increase P-availability by root exudate effects, and can the crop benefit from this increased P-availability” is the subject of chapter 4 and 5. Quantitative

measurements of exudates and their effects on P-fractions are described in chapter 4. The spatial and temporal aspects of exudation and tree and crop root-growth are the topic of chapter 5.

The second question “What determines total water-use by tree-lines and how is the spatial distribution of water extraction throughout the soil volume in the field bordering the tree-lines” is the subject of chapters 6 and 7. The above-ground tree-water-use and its determinants are described in chapter 6, and the belowground root and water-extraction distribution story in chapter 7.

The third question “How do decreases in soil water contents, as caused by tree-water-use, affect P-mobility and transport to crop-roots and subsequent crop-growth” is the subject of chapter 8, which includes also the assessment of the balance of positive root-exudate effects of trees on crop-P-uptake and growth against negative soil-drying induced P-deficiency effects of trees on crop-P-uptake and growth.

The general conclusions are given in chapter 9.

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Application of system performance analysis methods to evaluate an alley-cropping system.

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Abstract

Methods to evaluate the performance of alley-cropping systems have been developed recently to improve the understanding of the frequently disappointing performance of agroforestry systems. Here we examine the value of two of these performance analysis methods of agroforestry systems, the methods of Ong and Kho. We also examined some important aspects these methods do not yet cover.

An alley-cropping experiment of maize (*Zea mays* L.) – Calliandra (*Calliandra calothyrsus* Meissn.) in Western Kenya was used for this purpose. Its set-up allowed complete and quantitative use of Ong's performance-analysis method, which evaluates the effect of tree-hedges on the crop by splitting the overall-effect on crop-yield (I) in negative competition effects (C) and positive mulch effects (F).

Kho's performance analysis method splits tree-effects according to resources (light, water, nutrients), and their importance in specific environments based on the environmental-limitation of each resource. This second method was only examined qualitatively, because the trial set-up did not allow for its quantitative use.

Maize yields of alley-cropping maize-Calliandra and mono-crop maize declined to 50-20% over time. Such a trend is not evaluated by the methods of Ong or Kho.

The choice of how to calculate F and C in Ong's equation was crucial for their balance 'I'. In one season I varied from 485 % negative to 45 % positive due to the different ways of calculating F and C. This was caused by interactions and time lags between competition (C) and fertility (F) effects, and showed that the equation is not as straightforward and simple as it pretends. Kho's method clarified most of the differences in F, C and I occurring in Ong's method in terms of resources and environmental limitations.

We conclude that, if the most appropriate way to calculate F and C for the specific alley-cropping system is chosen, alley-cropping performance can be roughly assessed by Ong's method, especially if complemented by Kho's logic in a qualitative way. However, the methods do not cover long-term performance, and are less applicable if strong interactions or time lags between terms within the equations occur.

Introduction

Alley-cropping or hedgerow-inter-cropping is a simultaneous agroforestry system⁵ with a relatively well-established history in the field of agroforestry research (which itself is only a few decades old). Initially, expectations of alley-cropping were high, based on the assumptions that trees, grown within crop-fields could function as a 'fallow-component' in the combined system. Alley-cropping was meant to provide a sustainable alternative to traditional cropping systems with long fallows, which had given way to continuous production due to population pressure (Kang et al, 1985). The fallow functions referred to were; biological nitrogen fixation (BNF), pumping nutrients from the sub-soil and recycling them to the surface (Nye and Greenland, 1960), safety-net against leaching

⁵ Agroforestry systems can be roughly divided into simultaneous and sequential systems. In simultaneous agroforestry systems the trees and crops grow in the same space at the same time. In sequential agroforestry

(Van Noordwijk, 1996), restoring soil organic matter and –in case of sloping land- erosion control (Nye and Greenland, 1960). The last function is obviously an advantage per se. However, on non-sloping land, the positive effects were often offset by competition-effects between the tree and the crop, with the tree as the stronger competitor, due to its established root system (Ong and Black, 1995; Garrity et al., 1995).

This disappointment turned the initial hype for alley-cropping dramatically into a near discarding of the system (and probably explains the shift to research of non-simultaneous agroforestry systems). However, revolutions in agriculture are more exception than rule, and although alley-cropping was not the ideal system, it could be a step-wise improvement compared to continuous mono-crops in environments where the advantages would outweigh the disadvantages. Thus, methods to evaluate and extrapolate alley-cropping performance were needed.

One branch of research meant to increase the understanding of the biophysical/technological possibilities of alley-cropping is a system-performance analysis approach.

Two methods of the system performance analysis approach are evaluated in this paper. The first method is by Ong (1995), described below. We used yield-data from an alley-cropping experiment in Western Kenya, which was designed to fit Ong's method. The results of Ong's method are then complemented with the possibilities of the second method by Kho (2000), described below. We applied Kho's method qualitatively, because it would need a different and complex experimental set-up to be used quantitatively. We examined the additional value of the two methods, their shortcomings and the premises for their use.

At the start of the experiment *Calliandra* was a promising hedge-species, because it improved maize yield most in an earlier trial in the same environment but on-station (Akyeampong et al, 1995). *Calliandra* was known to have less problems with pests and diseases than *Gliricidia sepium* (Jacq.) Steud. and *Leucaena leucocephala* (Lam.) de Wit, while producing about the same amount of biomass. *Calliandra* coppiced easily, was able to withstand continuous pruning, and showed easy nodulation and infection with VAM. It was known to be adapted to nutrient poor soils, to improve soil physical properties and increase top-soil-C (Gichuru and Kang, 1989).

Maize was chosen as crop because it is the most common staple food crop in Kenya.

Because many Western Kenyan soils suffer primarily from P-limitation and alley-cropping performance is dependent on soil P status for its success (Woomer et al, 1995), the experiment was conducted on a P-limiting soil on-farm, and included treatments with and without P application.

Theory of the system performance methods

systems the trees and crops grow in the same area at different times.

The system-performance analysis approach compares the crop-performance of alley-cropping plots with a control of the crop alone, treating the exact mechanisms and differences within plots as a black box.

The first alley-cropping diagnosis method was developed by Ong (1995) and simplified by Sanchez (1995). In this method the alley-cropping effect on crop yield (= interaction effect) is expressed as the sum of negative competition effects and positive fertility effects as follows:

$$I = F - C$$

where:

I = interaction effect on maize yield.

F = fertility effect, i.e. the crop-yield increase caused by soil fertility improvements.

C = competition effect i.e. the crop-yield decrease caused by competition with trees for light, water and nutrients.

To apply this equation in alley-cropping a relatively simple experimental set-up is needed with 4 essential treatments; sole crop (M), sole crop with mulch from the hedge (Mm), crop + hedges without mulch (MH) and crop + hedges with mulch (MHm).

F can be calculated from measured crop-yields of Mm-M or MHm-MH, C can be calculated from measured crop-yields of M-MH or Mm-MHm. Thus all effects are expressed in the level of crop-yield.

If I is positive, there is a net complementarity.

If I is negative, there is a net competition to the detriment of crops.

Many existing trials could not be analyzed in this way, because of missing treatments (esp. alley-cropping without mulch and sole crop with mulch), or were flawed due to hedge root interference in control plots, or mistakes in hedge spacing and mulch application (Coe, 1994).

The main advantage of Ong's method is its simplicity; its main disadvantage is that the results are valid only for one location and cannot be extrapolated.

The diagnosis method developed by Kho (2000) tries to overcome the disadvantage of Ong's method. It is based on adding up positive and negative effects, similar to Ong, but it does not use a single competition and a single fertility effect, but positive or negative tree-effects on availability of different resources for crops: (light (L), water (W), nitrogen (N), phosphorus and bases⁶ (P)). These are multiplied by an environmental factor (l, w, n, p) indicating the degree of limitation of each resource. The sum of all environmental factors is one ($l+w+n+p=1$), and the size of single

⁶ P and bases can be split up in separate nutrients if this fits the environment better

environmental factors is between 0-1. The largest factor indicates the main limitation of an environment, the lowest the last limiting resource. Thus Kho's equation becomes:

$$I = l*L + w*W + n*N + p*P.$$

If the tree supplies nitrogen to a crop but competes with the crop for phosphorus and bases to a similar but negative extent, and does not affect the other resources, it depends on the environmental factors n and p what the final effect I is. If $p > n$, then I is negative, because the negative effect $p*P$ is larger than the positive effect $n*N$. If $n > p$, then I is positive, because the negative effect $p*P$ is smaller than the positive effect $n*N$.

Materials and methods

Site Description

The experiment was conducted at the Vet-farm in Maseno / Western Kenya, (Equator, Longitude 34°35 East, Altitude 1560m). The site is sub-humid with an annual rainfall of about 1750 mm, distributed over two main cropping seasons; the long-rainy season from March to June/July and the short-rainy season from September to December/January. Rainfall totals of the long rainy seasons from 1994 to 1997 were 1050 mm, 910 mm, 1230 mm and 550 mm respectively. Rainfall totals of the short rainy seasons from 1994 to 1996 were 800 mm, 550 mm and 750 mm respectively. The experiment was established on level land, formerly under pasture but cropped with maize for four seasons before the establishment of the experiment.

The soil has been classified as Oxisol/Ferralsol, a major soil type in the area (Shepherd et al, 1992). Initial soil characteristics in the top 0-15 cm were, pH (1:2.5 soil/water suspension) 4.9, exchangeable acidity 0.9 cmol_c kg⁻¹, soil organic C 1.33 %, exchangeable Mg 0.9 cmol_c kg⁻¹, exchangeable Ca 2.8 cmol_c kg⁻¹, exchangeable K 0.13 cmol_c kg⁻¹, bicarbonate-ethylene-diaminetetra-acetic acid (EDTA) extractable P 1.5 mg kg⁻¹, clay 34 %, sand 41% and silt 25%. Organic C was determined by wet oxidation with heated sulphuric acid-dichromate followed by colorimetric determination of Cr³⁺ (Anderson and Ingram, 1993). Exchangeable Ca, Mg, and acidity were determined by extraction with 1 M KCl. Extractable P and Exchangeable K were determined by extraction with 0.5 M NaHCO₃ + 0.01 M EDTA (pH 8.5). Towards depth (150 cm) clay contents increased up to 60 %, organic C and exchangeable bases decreased (except Ca) and EDTA extractable P increased up to 1.7 mg kg⁻¹.

Experimental Set-up and field layout

The treatments were a complete factorial combination of two land-use-systems; i) alley cropping and ii) sole maize, two P-levels; i) no P applied and ii) P-applied, and two mulch levels; i) hedge mulch applied and ii) hedge mulch exported. This resulted in the eight treatments shown in table 1.

Table 1. Treatments in experiment with set-up according to Ong's method, with and without P-application. M=maize, H=hedge, m=mulch and P= phosphorus.

MHm	Alley-cropping + mulch
MH	Alley-cropping without mulch
Mm	Maize alone + mulch
M (= control)	Maize alone without mulch
MHm + P	Alley-cropping + mulch + P
MH + P	Alley-cropping without mulch + P
Mm + P	Maize alone + mulch + P
M + P (= control+P)	Maize alone without mulch + P

The field layout was a completely randomised block design, with land-use-system and phosphate-level as main plots and a split for mulch-level.

In the +P treatments phosphorus was applied at a rate of 13 kg P ha^{-1} , as TSP, each season in the maize plant holes. Alley cropping treatments comprised of *Calliandra calothyrsus* Meissn. as the tree component and maize (*Zea mays* L.) as the inter-crop. Mulch quantities were determined by the hedge production.

The gross plot size was 7.4 m x 10.5 m. In alley cropping treatments, two hedges parallel to the 10.5 m side and spaced 4 m apart, bordered the alley in the middle of the plot as shown in figure 1. In this alley all measurements were taken.

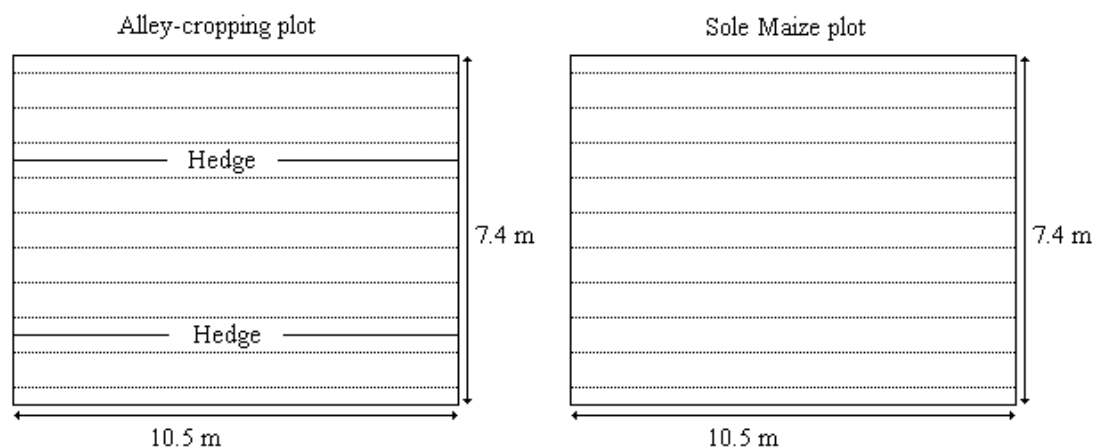


Figure 1. Field layout of alley-cropping plots and sole maize plots

Maize hybrid 512 was used for all the cropping seasons. Maize spacing was 80 cm x 30 cm (= 41666 plants ha⁻¹) in all treatments. Calliandra spacing within the hedge was 0.25 m. The distance between the hedge and the first maize row was 40 cm.

The experiment was continued for seven seasons (four long rainy seasons and three short rainy seasons) in the period 1994-1997.

Plant and plot management

Calliandra seedlings were inoculated with Rhizobium TAL 1145. Mycorrhizal infection was done by mixing nursery soils with soil from a healthy growing stand of Calliandra. Seedlings were transplanted in April 1994. Calliandra was cut back for the first time in November 1994, at a height of 0.3 m above ground level. Future hedge pruning was in February, May and September 1995, April, September, November 1996, March and June 1997. These dates coincided with land preparation time (Feb./March and Aug./Sept.) and times when the hedge was judged to start competing with the crop for above ground resources. During periods without crops (January-February) the hedge was allowed to grow unchecked. Leaves and twigs were used as mulch while all woody branches were removed. In the treatments plus mulch, half of the leafy biomass of the two hedges was spread in the alley, the remaining half being applied on the rest of the plot outside the hedges. Total leafy biomass from the hedges of MH and MH+P was applied on the Mm and Mm+P plots respectively.

During the cropping period, the plots were weeded twice.

Maize was harvested row by row. The central five rows were used to calculate the total yield. In hedgerow plots this was the whole area in between two hedges.

Maize stover (stem+leaf) and cobs were harvested and weighed separately, after which a sample of the stover and the whole row-yield of cobs were air dried and the cobs separated in core and grain, to calculate the total dry yields of stover and grain.

For the short rainy season of 1995, only the fresh weight data were available. Dry weight data were mislaid (due to different people being responsible for the experiment), so the dry weight : fresh weight ratio of other seasons was used to estimate total dry weight.

Plot interference was largely avoided by trenching (up to 1-1.5 m depth) all around the plots before the start of the long-rainy season of each year.

Statistical Analysis

Maize grain yield was analyzed by ANOVA, with a 2*2*2 factorial with split design, using GENSTAT 5.

Results

Maize yield

Maize grain yields for the 7 successive cropping seasons are shown in Table 2.

Yields in the long-rainy seasons were generally higher than in the short-rainy seasons. When comparing yields of the four *long* rainy seasons of 1994, 1995 and 1997 (LR96 is exceptionally poor), only the yields of sole maize +mulch +P did not decline. In the *short* rainy-seasons, the yields varied considerably from year to year and therefore the results were inconclusive with respect to trends over time.

Table 2. Maize Grain Yield in t ha⁻¹, as a function of combinations of maize with or without hedges (H) and with or without mulch (m) and phosphorus (P) applications, at Maseno, Western Kenya, in the period 1994-1997. LR: long rains (March-July), SR: short rains (Sept.-Dec.), MHm: +Hedge+mulch, Mm: sole maize+mulch, MH:+hedge no mulch, M: sole maize no mulch, +/-P: means of all +P or -P treatments, +/-hedge: means of all +hedge or sole maize treatments, +/- mulch: means of all +mulch or -mulch treatments.

Treatment	94LR	94SR	95LR	95SR	96LR	96SR	97LR	total
MHm	1.6	1.0	1.2	0.24	0.20	0.61	0.33	5.2
MH	1.9	0.9	1.0	0.15	0.23	0.21	0.10	4.5
Mm	2.5	1.3	1.9	0.29	1.16	0.77	1.67	9.6
M	2.2	1.1	1.3	0.17	0.44	0.30	0.23	5.8
MHm+P	3.1	1.8	2.6	0.59	1.31	0.91	1.32	11.6
MH+P	2.8	1.7	1.6	0.39	0.45	0.32	0.36	7.5
Mm+P	3.0	2.0	3.3	0.61	1.89	0.98	3.30	15.1
M+P	3.4	2.2	2.7	0.44	1.04	0.67	2.09	12.6
sed	0.35	0.26	0.33	0.080	0.321	0.137	0.345	1.39
sed same M/ MH*P	0.26	0.26	0.22	0.055	0.174	0.087	0.280	0.82
-P	2.1	1.1	1.3	0.21	0.51	0.47	0.58	6.3
+P	3.1	2.0	2.5	0.51	1.17	0.72	1.77	11.7
sed	0.21	0.13	0.20	0.049	0.209	0.087	0.200	0.90
-hedge	2.8	1.7	2.3	0.38	1.13	0.68	1.82	10.8
+hedge	2.4	1.4	1.6	0.34	0.55	0.51	0.53	7.2
sed	0.21	0.13	0.20	0.049	0.209	0.087	0.200	0.90
-mulch	2.6	1.5	1.6	0.29	0.54	0.37	0.69	7.6
+mulch	2.6	1.5	2.2	0.43	1.14	0.82	1.66	10.4
sed	0.13	0.13	0.11	0.028	0.087	0.044	0.140	0.41

Significant Interactions:

Hedge * P: 97LR

Mulch * Hedge: 96LR, 97LR

Mulch * P: 95LR, 96LR

Mulch * Hedge * P: 95LR, 96LR, 96SR, total

The most dramatic decrease in yield occurred in the treatments without applications of phosphorus and mulch (MH and M). These treatments showed minimal yields after the third season (about one tenth of yields in the first season).

Alley-cropping treatments with additions of either P or mulch (MH+P, MHm) declined almost as rapidly to about one fifth of the yield in the first year. Yields of the alley-cropping treatment with P and mulch (MHm+P) halved over the whole period of seven seasons.

When comparing the treatments within the seasons, P-application increased maize grain yield 1.5-3 times in all the seasons.

The fertility effect of mulch was apparent from the third season onwards, and increased maize yields 1.5-2.5 times for all seasons thereafter. The competition effect of the hedges was apparent from the third season onwards and was evident in the long-rainy seasons. It decreased the maize yields 1.5-3 times. Statistically significant interactions between mulch, hedge and P occurred in the long rains of 1995, 1996 and 1997 (Table 2). The effect of mulch on maize yield was not significant in alley-plots without P (MHm vs. MH), while it was significant in alley-plots with P (MHm+P vs. MH+P) and both sole maize +P (Mm+P vs. M+P) and sole maize -P (Mm vs. M). This held for the total sum of yields as well. Similarly, the effect of P-application was not significant in alley-plots without mulch (MH+P vs. MH), but was significant in alley-plots with mulch (MHm+P vs. MHm) and both sole maize + mulch (Mm+P vs. Mm) and sole maize -mulch (M+P vs. M).

Competition and Fertility effects on maize yield

Results of the calculations of competition (C) and fertility (F) effects and their balance (I) according to the equation $I = F - C$ are shown in Table 3. Because of the statistically significant interactions in the analysis of variance of Table 2, +P and -P are taken separately here. Cells in Table 3 are shaded when the difference between the variates was significant ($\alpha=0.05$).

Fertility (F)

Fertility effects, were calculated by MHm-MH ($F(2)$ = fertility effect in presence of competition) or by Mm-M ($F(1)$ = fertility effect in absence of competition). There is a clear difference between these two, especially in the -P treatments. This indicates that F differs between situations with and without hedge-competition.

We consider $F(2)$ as a more appropriate measure of F than $F(1)$, because in complete alley-cropping systems hedges are present in the field.

$F(2)$ was statistically significant from the third season onwards in systems +P but not in -P. In this last case, the fertility effect was only significantly positive in the short-rains of 1996. The frequently lower positive values in the short rainy seasons compared with the long rainy seasons were related to overall lower yields in the SR compared to LR.

Table 3 Hedge competition and fertility effects on the maize yield, with or without P-application according to the simplified Equation of Ong:

$I = F - C$, at Maseno, Western Kenya, 9n the period 1994-1997. I=total hedge effect on crop, F=fertility effect of hedge on crop (by mulch), C= competition effect by hedge on crop, MHm= Maize with Hedge with mulch, Mm= Sole maize with mulch, MH = + Hedge without mulch and M = Sole maize without mulch. Shading of cels means that differences are significant or that (I) is a result of significant differences in F and C.

	Fertility			Competition			Interaction				
Without P	F(1) Mm-M (t/ha)	F(2) MHm-MH (t/ha)	se F	C (1) Mm-MHm (t/ha)	C (2) M-MH (t/ha)	se C	I(1) = F(2)-C(1) (MHm-MH)-(Mm-MHm) (t/ha) % of M		I (2)= F(2)-C(2) (MHm-MH)-(M-MH) (t/ha) % of M		
	94LR	0.30	-0.30	.257	0.92	0.32	.354	-1.22	-54	-0.62	-28
	94SR	0.22	0.07	.260	0.28	0.13	.256	-0.20	-19	-0.05	-5
	95LR	0.62	0.21	.215	0.77	0.36	.326	-0.56	-43	-0.15	-12
	95SR	0.11	0.09	.055	0.05	0.02	.080	0.04	23	0.07	37
	96LR	0.72	-0.03	.174	0.96	0.21	.321	-0.99	-225	-0.24	-54
	96SR	0.46	0.40	.087	0.15	0.09	.137	0.25	82	0.31	101
	97LR	1.44	0.23	.280	1.34	0.13	.337	-1.11	-485	0.10	45
	total	3.88	0.68	.820	4.47	1.27	1.390	-3.79	-66	-0.59	-10
	With P	F(1) Mm-M (t/ha)	F(2) MHm-MH (t/ha)	se F	C (1) Mm-MHm (t/ha)	C (2) M-MH (t/ha)	se C	I(1) = F(2)-C(1) (MHm-MH)-(Mm-MHm) (t/ha) % of M		I (2)= F(2)-C(2) (MHm-MH)-(M-MH) (t/ha) % of M	
94LR		-0.42	0.36	.257	-0.15	0.64	.354	0.51	15	-0.27	-8
94SR		-0.18	0.11	.260	0.22	0.51	.256	-0.11	-5	-0.40	-18
95LR		0.60	1.02	.215	0.74	1.15	.326	0.28	10	-0.14	-5
95SR		0.17	0.20	.055	0.02	0.05	.080	0.17	39	0.15	34
96LR		0.84	0.86	.174	0.57	0.59	.321	0.29	28	0.27	26
96SR		0.32	0.59	.087	0.08	0.35	.137	0.51	77	0.24	36
97LR		1.22	0.96	.280	1.98	1.73	.337	-1.02	-49	-0.77	-37
total		2.54	4.10	.820	3.47	5.02	1.390	0.63	5	-0.92	-7

Although -P plots received more mulch than +P plots (Chapter 3), this is not reflected in fertility effect (F) between +P and -P treatments. Apparently, the mulch added in the -P treatments was less effective, per unit mulch, than the mulch added in the +P treatments. In absence of hedges, as calculated by F(1), the different amounts of mulch did not lead to any significant difference in fertility effect either.

Competition (C)

The competition effect (C) was not the same when calculated by M-MH (competition effect without mulch at low soil fertility level) or by Mm-MHm (competition effect with mulch at higher soil fertility level). We chose Mm-MHm (C(1)) as a more realistic measure of competition, because the alley-cropping trial was set up to use the mulch to improve soil fertility. If the hedge material had been exported (e.g. as fodder) M-MH (C(2)) would have been a more relevant competition-indicator.

Competition effects differed between +P and -P and between C(1) and C(2). In -P treatments, competition was statistically significant only in the long-rains in the +mulch treatments (C(1)=Mm-MHm). During the short-rains and in all -mulch treatments (C(2)=M-MH) there was no significant competition (yields did not differ significantly). In the +P treatments (lower half of table 3) competition was significant in the long-rains of '95 and '97 in both +mulch and -mulch and in the short-rains '96 for +P -mulch. Thus competition was more frequent and more serious in -mulch than in +mulch treatments, while in -P situation this was opposite.

These different trends in +P and -P, with mulch and without mulch contribute to the mulch*P*Hedge significant statistical-interactions in the analysis of variance of table 2.

Interaction (I)

Interaction (I) is a measure of the change in maize yields in alley-cropping (MHm or MHm +P) compared to the control treatment (either M or M+P) and is given in table 3 in yield weight and %. Results of interaction varied highly with the type of F and C effects chosen, with as extreme case the -P 97LR yield, showing a 45% increase in yield compared to the control if I is calculated by F(2)-C(2) and a 485 % decrease in yield compared to the control if I is calculated by F(2)-C(1).

This alley-cropping experiment was set up to investigate whether with hedges growing in the crop-field, the mulch effect would off-set the hedge competition effect and create a sustainable land-use-system. Thus, we chose to calculate interaction I(1) by fertility effect in the presence of the hedge minus competition effect in the presence of mulch F(2)-C(1).

However, the real difference between the alley-cropping treatment and the sole-maize is I calculated by $I(2) = F(2) - C(2) = (MHm-MH)-(M-MH)$. This interaction I(2) provides the direct difference between full alleycropping treatment and sole maize.

For the alley-cropping system -P, the interaction I(2) was negative, especially over the first few seasons and in the long-rains. Only in the 1996 short-rains was the interaction significantly positive. Over the total of all seasons the yield decrease compared with sole maize was 66%.

For the alley-cropping system +P, the interaction I(2) was significantly positive except for the first two and the final season. Over the total of all seasons, the yield increase compared with sole maize was significant at only 5%.

Performance of systems -P are nearly always similar if calculated by I(1) or I(2), but performance of systems +P becomes less positive, if calculated by I(2) compared to I(1) and interaction over all yields of all seasons together change from positive (5%) to negative (7%).

Discussion

Competition (C)

Competition effects (C) from the hedge on the crop were stronger in the long rainy seasons than in the short rainy seasons, in -P treatments +mulch and in +P treatments -mulch. These opposite pattern is understandable, if an initial increase in the availability of one resource (P, water, mulch-effect) caused the maize to grow more vigorously, in turn causing an increase in maize-demand for other resources, which were used by the hedge as well, leading to increased competition. Contrary, if resource availability from the start of the season is low (no P, no mulch, little water), the demand of the maize crop was so low that the hedge used resources which were not used by the crop (complementarity).

These opposite trends in (C) when comparing +P with -P treatments can also be explained by the equation of Kho. Competition can be seen as the sum of *negative* tree-effect x environmental-limitation terms in Kho's equation. In our experiment, the tree-effect on availability of phosphorus and bases (P) and possibly the tree-effect on water-availability (W) was negative. If mulch (nitrogen) or water is added in -P treatments with a negative tree-effect on availability of phosphorus and bases (P is negative), the environmental limitation of nitrogen (n) (or the environmental-limitation of water (w)) decreases accordingly. A decrease in (n) and/or (w) increases (p), which is the degree of limitation of phosphorus + bases, because $n + w + p = 1$ (Kho, 2000). Thus the *negative* term $p \times P$ becomes larger.

In +P treatments competition appears to be larger in -mulch plots than in +mulch plots. In +P treatments the environmental limitation of phosphorus (p) is lower than in -P treatments. A decrease in (p) increases (n) and/or (w), because $n + w + p = 1$. Without mulch the tree-effect on nitrogen availability (N) is negative. An increase in (n) would make the negative term $n \times N$ larger, increasing competition.

This analysis according to Kho's equation supports the explanation given above, that an initial increase in availability of one limiting resource increases competition between plants, because of their higher demand for other resources. Only if this demand for other resources can be satisfied as well, competition decreases again.

Thus competition between hedge and crop at the spacing used in this experiment, is low either at very low resource availability or at high availability of all resources. At very low resource availability, the growth of hedge and crop is restricted by overall environmental limitations. Their combined resource demand is low and their resource depletion zones overlap minimally. At high resource availability (with CO₂ as environmental limitation to growth) the supply of resources is able to satisfy the demand of hedges and maize at higher growth rates. Thus competition between plants seems to occur if the supply of all different resources in the environment is not in balance with the demand for all different resources of the species, at their growth rate as determined by the environment in general. Buck (1986, in Garrity et al, 1995) mentioned that in general, competition occurs when the available supply of a resource is below the joint requirement of two organisms and as a result the performance of one or both is impaired. Indeed, if one resource is below the requirement of the combined demand of two plants, plant-plant competition occurs. If a resource is even below the demand of one plant, the plant-growth is reduced due to limits set by the environment, and plant-plant competition becomes less again.

Fertility (F)

Fertility effects can be seen as the sum of *positive* tree-effect x environmental-limitation terms in Kho's equation. Calliandra mulch may increase available nitrogen, and may have some positive influence on soil-water-holding capacity and the availability of other nutrients. Thus N is clearly positive, W and P may be slightly positive.

The fertility effect (F) was lower in the short-rainy seasons than in the long rainy-seasons. This can be explained by the equation of Kho, when realising that the degree of limitation of water (w) increases when the supply of water is lower. If (w) increases, (n) decreases because $w + n + b = 1$. Thus the positive term $n \times N$ decreases, explaining the lower fertility effect F in short rainy seasons. In long rainy seasons the (w) and thus the $w \times W$ term is smaller and thus Kho's equation mainly consists of $I = n \times N + p \times P$. This explains the significance of F(2) in +P treatments and its absence in -P treatments. When phosphorus is added, (p) decreases and thus (n) increases, which means that when N is positive, the $n \times N$ term increases and causes the significant F.

When only looking at treatment differences within the seasons, alley-cropping does not perform better than sole maize in a situation where P is limiting production, like other authors (Woomer et al., 1995) have mentioned. The analysis according to Kho's equation leads to the same conclusion. In a situation with P, the alley cropping system investigated here in this environment performs often, but not always better than sole maize.

The late start of significant (F) effect from the third season onwards, indicates that the fertility effect is delayed.

Interaction (I)

Interaction can be assessed in four ways. Two of them were logic for this experiment.

The two ways gave different results for I. For the systems –P, the two I's were similar; I was slightly negative, over time shifting from clearly negative towards somewhat positive in some of the later seasons. However, for the systems +P the two I's were contradicting one another when using the different ways of calculating I. With I calculated by (MHm-MH)-(Mm-MHm) alley cropping would seem to give a slightly superior performance than sole maize, while the opposite occurred when I was calculated by $I = (MHm-MH)-(M-MH)$.

Cannell et al (1996) attempted to explain the resource base of Ong's equation. They split F in $F_{comp} + F_{noncomp}$, where F_{comp} represents the resources acquired by the trees in competition with the crop and $F_{noncomp}$ the resources acquired by the trees that the crop would otherwise not acquire. They split C in $C_{recycled} + C_{nonrecycled}$, where $C_{recycled}$ represents the resources that the crop is deprived of by the trees, but which will be recycled to the next crop, and $C_{nonrecycled}$ represents the resources that the crop is deprived of and which are used in tree growth and are not recycled.

Our choice of F(2) to calculate I is contrary to that of Cannell et al. (1996), who would use F(1) (=Mm-M), because they suggest I should be calculated by $I' = F_{noncomp} - C_{nonrecycled}$. Their argument holds if the part of F which is acquired in competition with the crop (F_{comp}) is equal to the part of C which is recycled back as fertility ($C_{recycled}$), like they assume. However, during the period that all resources taken up by the tree in competition with the crop are not yet recycled, $C_{recycled} > F_{comp}$. In our experiment this time-lag seems to be longer than one season. This causes that our choice of F and C comes closer to the difference between sole maize cropping and alley-cropping.

The methods of Ong and Kho are not able to evaluate the consequences of such a time-lag between different terms of the equation, because they miss a temporal dimension.

A temporal dimension is important for the assessment of the performance of the system over time. The evaluation of yield trends over time should certainly be treated if we consider that sustainable production was the initial aim of alley-cropping, and of agroforestry in general. Our yield data show that in situations with P application yield levels drop to about 40-50% of that in the first 2 seasons. In -P situations yield levels drop to 20-25% of that in the first two seasons (only long rainy seasons considered). This shows that, although alley-cropping performance may be slightly better than sole maize cropping, the system is certainly not sustainable, in the sense that it is able to keep production at a more or less constant level over time.

The split within F and C, made by Cannell et al (1996), indicates a similar interaction between hedge-effects and mulch effects as we found. Simple sums like used in both Ong's and Kho's equation are therefore not fully applicable in situations in which the different terms interact. We conclude that, the methods for the assessment of alleycropping-performance developed by Ong and Kho have both their advantages and disadvantages. The main advantage of Ong's method is its simplicity. It requires a simple experimental setup and measurements of yields, but the results are indeed only valid for the one system x environment for which it is used. Kho's method on the other hand allows for prediction of how a system would function in another environment (as long as resource capture determines the performance and not factors like pests and diseases). It also provides some insight in the tree characteristics and resource availabilities, that determine performance. However, using this method quantitatively requires a very complex experimental setup. Using the method of Ong as a basis and the logic of Kho's method to explain some of the peculiarities arising in the Ong-type analysis as is done above, can increase the understanding of the system.

However, the two methods do neither address long-term trends and time-lags nor interactions between equation-terms. In these cases research after the mechanisms of positive and negative interactions between tree and crop will be necessary.

Relating crop-performance to capture of resources in an alley-cropping system

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Abstract

Performance evaluation methods of alley-cropping systems described in literature address the systems' functioning at one location and/or one point in time, and assess final performance as a sum of positive and negative effects. Although these methods give useful performance assessments, the validity of these assessments is limited to environments where interactions between the positive and negative factors are of minor importance, and they do not cover performance over the longer term. This paper describes how relatively simple mechanistic research of key factors determining crop production (nutrients, water and roots) in field trials, complemented by statistical/mathematical calculations, can help to explain the assessments of performance analysis methods and add a time dimension.

The alley-cropping trial had the following treatments; maize alone, maize alone +mulch, alley-cropping without and with mulch, all treatments with and without P-application. We measured maize and calliandra root length densities, soil water contents, contents of N, P and K in soil, maize and calliandra. Nutrient balances were determined, using measured data supplemented with. Gaps in the statistically fitted terms and assessments according to functions found in the literature.

The results indicate that the long term decline in yield of the alley-cropping system, was related to negative nutrient balances. In the total-nitrogen-balance the hedge-input was smaller than the export by maize and branches. The inorganic-N balance was even more negative, due to slow mulch mineralization, which caused a delay in fertility effect.

Little competition occurred in alley-cropping -P because of the poor crop-growth; root growth was restricted and P-depletion zones around roots of crop and hedge did not overlap. In alley-cropping treatments +P competition for N and K was more severe, due to quickly overlapping of root-depletion zones for these nutrients.

Soil water contents were minimally affected by hedge and mulch.

Partitioning of assimilates within the maize-crop reinforced the differences in total biomass as caused by hedge, mulch and P-application.

This research added a long-term perspective and explanation of some underlying processes, which determined the alley-cropping system performance. Performance-analysis methods may help to direct mechanistic research towards the determinants of performance, and prevents that process research drowns into studies of single aspects with limited importance for the overall performance.

Introduction

Methods for alley-cropping performance-analysis can provide a useful image of alley-cropping performance compared with sole crop performance. Differences in systems' performance are either expressed in positive fertility effects and negative competition effects (Ong, 1995; Sanchez, 1995) or in positive and negative effects from trees on resource availability (Kho, 2000). However, these methods become less applicable in situations with interacting factors, because a simple sum does not cover such situations anymore. Another shortcoming of these methods is that they do not cover long-term trends and time lags between different effects, due to absence of time dimension (Chapter 2).

Single factors influencing the tree-crop interaction have been investigated in alley-cropping research that focuses on understanding the mechanisms underlying the performance of these systems. Within plots, roots (Schroth and Zech 1995a, 1995b; Lehmann and Zech, 1998; Akinnifesi et al, 1998; Peter and Lehmann, 2000), pests/diseases (Anoka et al 1991; Girma et al 2000; Banful et al 2000; Rosenmeyer et al, 2000), soil-water contents (Lehmann et al, 1998; Jose et al, 2000; Lefroy et al, 2001) and soil- and/or plant-nutrient contents (Van der Meersch et al, 1993; Samsuzzaman et al, 1999) have been examined. Studies on biological nitrogen fixation (Sanginga et al, 1995; Dakora and Keya, 1997), mulch-quality and decomposition (Palm and Sanchez, 1991; Palm, 1995; Lehmann et al, 1995; Mugendi et al, 2000) were conducted to feed into the nutrient balances of the whole system (overall plot scale). Computer models (van Noordwijk and Lusiana, 2000; Mobbs et al, 1998; Mayus et al, 1999) have been developed to be able to link and synthesize the different aspect and assess combined effects on crop and tree production, as well as to predict a systems' performance in other environments.

The advantage of the mechanistic approach is that it is based on resource availability and capture, which are the processes determining the performance of the system. Interactions between resources, time lags between uptake and recycling and long-term balances can be investigated. The main disadvantage is, that the number of processes playing a role in the overall alley-cropping performance is large. Therefore most research done so far treats a fragment without pulling all parts together to derive the actual performance of the system from all processes.

The mechanistic research described in this paper was conducted to complement the system performance analyses according to the methods of Ong and Kho as described in chapter 2. The overall aim of the research was to explain the performance of the maize-Calliandra alley-cropping system.

Our research differs from single-factor mechanistic research in alley-cropping systems because our aim is to understand overall system performance (not single aspects within the plot). The interest in overall system performance and its explanation lead to the use of relatively straightforward and simple measurement techniques and analysis of results on overall plot-scale. These were complemented by mathematical/ statistical calculations to derive nutrient balances and analyze interactions, in order to come to a more meaningful understanding of the system.

The three and a half years lasting maize-Calliandra alley-cropping system examined was situated on level land, with a deep Ferralsol/Oxisol in the subhumid highlands of Western Kenya. Phosphorus is usually the first limiting resource to crop production. After application of P, nitrogen and/or potassium become limiting. Alley-cropping performance is dependent on the P-status for its success

(Woomer et al, 1995). Therefore, the experiment consisted of all necessary treatments with and without P application.

Competition for light is minimized by regular pruning of the hedge, and the main crop-pests of this environment are striga and nematodes, which are not significantly increased by the hedge (Desaeger, pers. comm.). Thus possible tree-crop interactions in our experiment were limited to belowground resources; nutrients (NPK) and water.

Our main objectives were, to investigate the mechanisms by which the hedge influences crop-production in positive and negative ways, to examine the cause of the declining production over time and causes of delays between resource-uptake, competition and recycling of these resources. The hedge influences nutrient-uptake by the crop, through its effects on nutrient availability and its sink strength for nutrients relative to the sink-strength of the crop, as determined by demand and root-length, and its effect on nutrient mobility. Therefore, we examined root-length densities of hedge and crop, N, P and K levels of the soil as influenced by the presence of hedge and mulch. Reduced soil water contents may affect crop-growth by direct water-limitation and/or by its effect on nutrient transport to roots (especially important for P which has lowest mobility in soil), and therefore their relation with mulch and hedge was examined as well.

Long term trends in crop yield level are likely determined by nutrient-balances over the whole period. These balances were made for N and P. Reasons for time lags between resource-uptake, competition and recycling of these resources were revealed by nutrient-balances and nutrient-transport calculations.

Materials and methods

Site Description

The maize-Calliandra alley-cropping experiment was conducted between 1994 and 1997 at the Vet-farm in Maseno, (Equator, Longitude 34°35 East, Altitude 1560m), a sub-humid site with two cropping seasons. Rainfall totals of the long rainy seasons from 1994-1997 were 1050 mm, 910 mm, 1230 mm and 550 mm respectively. Rainfall totals of the short rainy seasons from 1994-1996 were 800 mm, 550 mm and 750 mm respectively. Further site characteristics are given in chapter 2.

Experimental Set-up and field layout

The field layout was a completely randomized block design, with land-use-system (sole maize and alley-cropping maize-Calliandra) and phosphate-level (with and without P-application) as main plots and a split for mulch-level (with and without mulch application). This resulted in the eight treatments shown in table 1. The experiment was continued for three and a half years (1994-1997), i.e. four long rainy seasons and three short rainy seasons.

Table 1. Treatments in experiment with set-up according to Ong's method, with and without P-application. M=maize, H=hedge, m=mulch and P= phosphorus.

MHm	Alley-cropping + mulch
MH	Alley-cropping without mulch
Mm	Maize alone + mulch
M (= control)	Maize alone without mulch
MHm + P	Alley-cropping + mulch + P
MH + P	Alley-cropping without mulch + P
Mm + P	Maize alone + mulch + P
M + P (= control+P)	Maize alone without mulch + P

Plant management and determinations

Calliandra seedlings were planted in April 1994 and cut back to a height of 0.3 m above ground level in November 1994, February, May and September 1995, April, September, November 1996, March and June 1997, coinciding with land preparation time and times when the hedge was judged to start competing with the crop for above ground resources. During periods without crops (January-February) the hedge was allowed to grow unchecked. Leaves and twigs were used as mulch while all woody branches were removed (Chapter 2).

Nitrogen (N) and phosphorus (P) contents of the hedge biomass were determined in the first 3 prunings. These were also used to estimate nutrient yields obtained during the subsequent prunings. The amount of biomass from the specific pruning determined which nutrient contents were taken, because small biomass yields of only young material had higher P and N contents than large biomass yields of older material, as reported also by Mathuva et al. (1998).

Maize harvesting and yields are described in chapter 2.

The partitioning of assimilates was calculated using measured maize stover, grain and root weight.

For the estimation of N and P balances, maize N and P contents of other experiments carried out in this region were used. Later work in this same experiment by Imo (pers.comm., 1999) showed that the N content of maize was not significantly ($\alpha=0.05$) influenced by the hedge, application of P or mulch. The P-content of maize was slightly affected by mulch-application, but this effect was less than the mulch effect on maize biomass. Therefore, total-N and total-P in biomass is mainly determined by differences in biomass and not by differences in N- and P-concentration. Thus one N and one P-concentration of maize was used for the calculations. Core biomass was not included in the balances, because few data were available and core weight and nutrient contents are both low compared to stover and grain. Maize stover was removed from the trial, to conform to local farmer's practice.

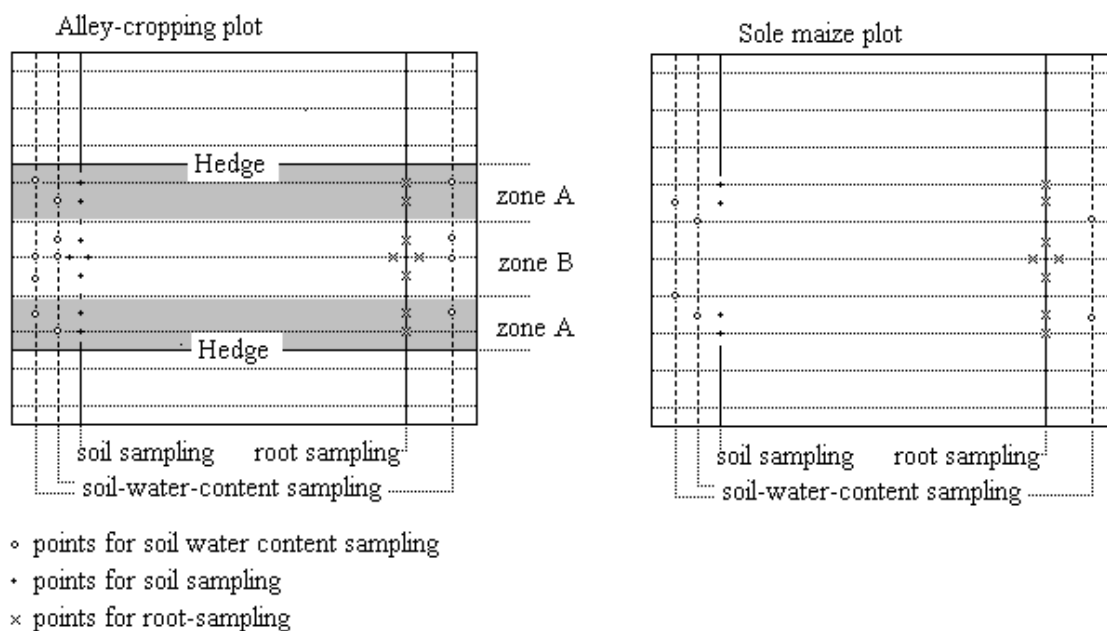


Figure 1. Plot layout and sampling points of alley-cropping trial at Maseno, Western Kenya

Soil and root sampling

During the long-rainy season of 1997 measurements were conducted to assess the underground mechanisms of competition and the overall functioning of the alley-cropping system with or without P addition.

In the long rains of 1997, the maize crop was sown on 12 April 1997 and harvested on 30 August 1997. The soil water content was determined on four occasions during the growing season; 19 May, 9 June, 3 July and 5 August. The last time coincided with soil sampling for nutrient content determination. Root-samples were taken immediately after maize tasselling.

The soil was sampled by an Edelman auger (for water and nutrient contents) and bucket auger (for roots). Sampling points within the plots are shown in figure 1. Close to the hedge and in the middle between the hedges four points (for soil nutrient and root sampling) or two points (for soil-water-content sampling) were sampled and mixed. Half of the points were taken within a maize row, half in the middle between two maize rows. The two zones in treatments with hedges should allow for differentiation: zone A close by the hedge, zone B about 2 m away from the hedges in the middle of the alley. In treatments without hedge, only one set of four (or two) points was sampled or (in case of root-sampling) the data from the two sets were averaged before any further analysis.

The sampling depths were: 0-15 cm, 15-30 cm, 30-50 cm and 50-150 cm.

Soil determinations

Gravimetric soil water content was determined by the weight difference between moist and dry soil (after oven-drying at 108°C during 24 h).

Inorganic-nitrogen was determined using moist soil samples, by extraction with 2 M KCl and subsequent colorimetric determination of ammonium. Nitrate plus nitrite was determined by cadmium reduction (Dorich and Nelson, 1984) with subsequent colorimetric determination of NO₂ (Hilsheimer and Harwig, 1976). For simplicity, no effort was made to separate NO₃ and NO₂ and the values were reported as NO₃, because NO₂ was likely small relative to NO₃. Inorganic nitrogen contents were expressed in kg ha⁻¹ using bulk density data.

Bulk density was determined by hammering 4 fixed volume rings of 100 cc in a horizontal plane at the desired depths, at three different sites over the experimental area. The rings were dried for 48 h. at 108°C, after which they were weighed, and the bulk density calculated.

Resin-P was determined by shaking air dry soil with HCO₃⁻-saturated resin (Dowex 1-X8(Cl⁻) for 16 hours, after which the P was recovered from the resin by shaking with 0.5 M HCl for 30 minutes, and colorimetric determination after color-development with ascorbic acid and molybdate reagent.

Exchangeable K was determined by modified Olsen extraction with 0.5 M NaHCO₃ + 0.01 M EDTA (pH 8.5).

Root determinations

Bucket auger samples were weighed in the field to check strong changes in bulk density, indicating large holes. When the target depth of 1.5 m was impossible to reach due to stones, the final depth of the hole was measured to calculate the volume sampled. The samples of the four points were mixed, soaked in water overnight and washed the next day through sieves of which the bottom one had a mesh size of 0.5 mm.

After washing, the roots were stored in a 1 % acetic acid solution and hand-sorted, differentiating between maize roots, Calliandra roots and debris (including weed-roots). The sorted roots were stained with methyl purple, manually spread on glass trays and scanned for length and diameter on a Delta-T Scanner by its image analyses software, using the intersection method. The roots were collected, dried in an oven at 60°C for 48 hours, and the dry weight recorded.

Root length densities were calculated using adjusted soil volumes and total root lengths.

Calculations

A P-balance of the soil at plot level (total-P inputs to soil minus total-P exports from soil) over the entire period of seven seasons was calculated by:

$$P_{\text{final}} - P_{\text{init}} = P_{\text{fertilizer}} - P_{\text{hedge_shoot}} + P_{\text{mulch}} - P_{\text{crop_shoot}} - P_{\text{leach}} \quad (\text{eq. 1})$$

Only the terms on the right hand side of the equation were measured. The balance is negative if the right hand total is negative and vice versa.

Similarly a N-balance of the soil at plot level (total-N inputs to soil minus total-N export from soil) over the entire period of seven seasons would be:

$$N_{\text{final}} - N_{\text{init}} = N_{\text{rain}} + N_{\text{fix}} + N_{\text{mulch}} - N_{\text{hedge_shoot}} - N_{\text{crop_shoot}} - N_{\text{leach}}, \quad (\text{eq. 2})$$

However, more interesting is the balance of available-N, the inorganic-N-balance of the soil at plot level (inorganic-N-inputs to soil minus inorganic-N-exports from soil) over the entire period of seven seasons. Assuming that all N-uptake by hedge and crop is inorganic-N from soil and biologically fixed-N returns to the soil only via mulch, this balance is calculated by:

$$iN_{\text{final}} - iN_{\text{init}} = iN_{\text{rain}} + iN_{\text{min}} - (iN_{\text{hedge_shoot}} - iN_{\text{fix}}) - iN_{\text{crop_shoot}} - iN_{\text{leach}}, \quad (\text{eq. 3})$$

$$\text{with: } iN_{\text{min}} = N_{\text{mulch}} * fN_{\text{min}} \quad (\text{eq. 4})$$

where: iN_{final} = Final inorganic N

iN_{init} = Initial inorganic soil-N including original soil organic matter N (all native SOM-N except mulch-N applied) mineralized over the considered period (3.5 year)

iN_{rain} = N supplied by rain

iN_{fix} = N supplied by biological nitrogen fixation (BNF) of the hedge

N_{mulch} = total mulch-N

fN_{min} = mulch mineralization factor ()

$iN_{\text{hedge_shoot}}$ = N in total above-ground biomass of hedge

$iN_{\text{crop_shoot}}$ = N in total above-ground biomass of crop

iN_{leach} = leached inorganic N, includes other N-losses (denitrification, volatilization)

All quantities iN are expressed in kg ha^{-1} .

Organic soil N was not included (except the labile fraction which became inorganic over the considered 3.5 year, which is part of N_{init}). The amount of inorganic N cycled back to the soil by mulch application was assumed to be total-mulch-N (iN_{mulch}) turned into inorganic-N by a mineralization factor (fN_{min}).

Some of the variables of the equation were measured quantities, while others were assessed as described below.

iN_{final} = Measured by soil sampling at the end of the 3.5 year, and analysis of ammonium and nitrate.

iN_{init} = unknown, supposed to be a constant, similar for all treatments, assuming minimal effects of fertilizers and other inputs on mineralization of native soil organic N.

iN_{rain} = calculated by : $N(\text{kg ha}^{-1}) = \sum_{3.5 \text{ yr}} 0.14 * \sqrt{(\text{annual rainfall}) [\text{mm yr}^{-1}]}$ (Smaling et. al. 1993)

iN_{fix} = unknown, supposed to be a fraction (fN_{fixupt}) of total hedge N-uptake

N_{mulch} = total N in hedge leaf, calculated as $\sum \text{leaf biomass} * \text{N-content}$ (sum of all pruning times).

fN_{min} = unknown, mineralization factor of mulch-N minus the fraction of mulch-N first mineralized than leached ()

$iN_{\text{hedge_shoot}}$ = Calculated by $\sum \text{leaf-biomass} * \text{N-content} + \text{twig-biomass} * \text{N-content}$ (sum of all pruning times)

$iN_{\text{crop_shoot}}$ = Calculated by $\sum \text{stover-biomass} * \text{N-content} + \text{grain-biomass} * \text{N-content}$ (sum of all yields)

iN_{leach} = unknown, calculated as:

$$iN_{\text{leach_max}} - (fN_{\text{leach_red_maize}} * iN_{\text{crop_shoot}}) - (fN_{\text{leach_red_hedge}} * iN_{\text{hedge_shoot}}) + (fN_{\text{leach_mulch}} * N_{\text{mulch}})$$

Where $iN_{\text{leach_max}}$ is the possible maximum of N-leached (unknown, supposed to be a constant similar for all treatments), $fN_{\text{leach_red_maize/hedge}}$ is the reduction in N-leaching caused by maize/hedge growth and assumed to be a fraction of maize/hedge-N-uptake, and $fN_{\text{leach_mulch}}$ is the increase in N-leaching caused by extra N-supply of mulch and supposed to be a fraction of mulch-N.

It was assumed that inorganic-N-uptake in root biomass equals inorganic-N liberated from root biomass. Some of the unknown variables mentioned above were compounded because they could not be separated:

$$iN_{\text{init}} - iN_{\text{leach_max}} = iN_{\text{init-leachmax}}$$

$$fN_{\text{fixupt}} + fN_{\text{leach_red_hedge}} = fN_{\text{hedge-effects}}$$

$$fN_{\text{min}} - fN_{\text{leach_mulch}} = fN_{\text{mulch}}$$

The variable $iN_{\text{init-leachmax}}$ was assumed to be similar for all treatments.

The remaining single unknown factor is:

$$fN_{\text{leach_red_maize}} = \text{leaching-reduction factor by maize}$$

All measured/calculated variables were combined to one single value iN_{quant} :

$$iN_{\text{quant}} = iN_{\text{final}} - iN_{\text{rain}} + iN_{\text{hedge_shoot}} + iN_{\text{crop_shoot}} \quad (\text{eq. 5})$$

Subsequently, equation (3) was rearranged to the regression equation:

$$iN_{\text{quant}} = iN_{\text{init-leachmax}} + (fN_{\text{mulch}} * N_{\text{mulch}}) + (fN_{\text{hedge-effects}} * iN_{\text{hedge_shoot}}) + (fN_{\text{leach_red_maize}} * iN_{\text{crop_shoot}}) \quad (\text{eq.6})$$

Regression analysis was done in GENSTAT (2000) to estimate $iN_{\text{init-leachmax}}$, fN_{mulch} , $fN_{\text{hedge-effects}}$ and $fN_{\text{leach_red_maize}}$, with the eight treatment averages.

Competition of Calliandra and Maize roots for different nutrients.

Inter-root-competition between Maize and Calliandra roots was assessed by comparing the diffusion distances (r_2) with the half-inter-root distances (r_1). If $r_2 > r_1$ there is overlap of depletion zones and thus direct competition between roots. If $r_2 < r_1$ there is no overlap of depletion zones and no direct competition between roots for the nutrient considered.

Using mean root-length densities of the treatments, for each depth and location half-inter-root-distances (r_1) [cm] were calculated by using the sum of the Calliandra and Maize root-length-densities (sumlr_v) [cm cm⁻³] in the equation:

$$r_1 = 1 / \sqrt{(\pi * \text{sumlr}_v)}$$

assuming that the roots were regularly distributed throughout the soil (De Willigen & Van Noordwijk, 1987).

Diffusion distances as a linear distance towards the roots, were calculated for N, P, and K, at high and low buffer capacities of the soil, by:

$$r_2 = \sqrt{(2 * t * D_e)}$$

$$\text{with } D_e = f_1 * \theta * D_1 * C_l / C_s \quad (\text{Barber, 1995})$$

with $f_1 = 0.97 * \theta - 0.17$ (derived for clay soils from (De Willigen & Van Noordwijk, 1987))

With r_2 as the diffusion distance (radius) [cm], t as the time [s], D_e [cm²s⁻¹] as effective diffusion coefficient, f_1 [] as the impedance factor, (θ) [] as soil water content (vol.%), D_1 [cm²s⁻¹] as diffusion coefficient of the specific nutrient in water, and C_l [mmol L⁻¹] as the concentration of the nutrient in

solution, while C_s [mmol/1000cc] is the amount of nutrient adsorbed, and thus C_l/C_s [] as measure of adsorption/buffering.

The buffer values (C_l/C_s) used for N were derived from Hartemink et. al. (1996). The buffer values for P were derived from Nziguheba et. al. (1998). Both of similar ferralsols in our area. The values for K were taken from Barber (1995).

Statistical analyses

The total Calliandra biomass removed was analysed by ANOVA, with a split plot design, with 2 main plots and 2 split plots per main plot. Maize assimilate-partitioning parameters were analysed by ANOVA, with a 2*2*2 factorial with split design.

Calliandra root densities were analyzed by ANOVA, with a split plot design, with 2 main plots and 2 split plots per main plot. Soil nutrient and water contents and maize root densities were analyzed by ANOVA, with a 2*2*2 factorial with split design. Differences between locations within hedge plots for soil water content and soil inorganic N, resin-P and exchangeable-K contents, were analyzed by ANOVA, with a split-plot design, with 2 main plots, a split for + or - mulch and a second split for location within the plot (A close by hedge, B in middle of alley).

All these analyses were carried out using GENSTAT (2000).

Results

Calliandra biomass yield and nutrient content

Mean data on biomass and N and P inputs and outputs are shown in Table 2.

Biomass of Calliandra in plots where maize received P fertilizer in the planting hole was often significantly lower (about 20%) than in the unfertilized plots, suggesting more competition of maize, with its higher growth-rate after P-application (Chapter 2).

Leafy Calliandra biomass contained on average 0.15-0.16% P and 2.8-3.5% N and these values were not influenced by the application of P-fertilizer.

Total amounts of P and N removed by pruning and added through mulch were higher in -P plots than in +P plots. In treatments without P, about 24 kg ha⁻¹ P and 476 kg ha⁻¹ N were removed, while in treatments with P, prunings contained about 21 kg ha⁻¹ P and 405 kg ha⁻¹ N. Amounts of N and P applied by mulch (only leaves, no branches) were 365 kg N ha⁻¹ and 18 kg P ha⁻¹ in -P plots and 315 kg N ha⁻¹ and 16 kg P ha⁻¹ in +P plots. The difference in amounts of nutrients removed and added as mulch, is due to the export of woody branches, hence 20% of all nitrogen and phosphorus in the prunings was exported.

Table 2. Mean data on Calliandra biomass and amounts of N and P removed by pruning and applied by mulch application at Maseno, Western Kenya over the entire period of 7 seasons. MHm: + Hedge + mulch, MH: + Hedge – mulch, +/- P: means of MH+P and MHm+P respectively MH and MHm, +/- mulch: means of MHm and MHm+P, resp. MH and MH+P

Treatment where biomass is removed		Total biomass removed (t/ha)	Total N removed in prunings (kg/ha)	Total P removed in prunings (kg/ha)	Total mulch (leaf) applied (t/ha)	Total N applied in mulch (kg/ha)	Total P applied in mulch (kg/ha)	Treatment where mulch is applied
MHm		20	463	23	12	355	18	MHm
MH		21	489	24	12	376	19	Mm
MHm+P		17	398	20	10	309	16	MHm+P
MH+P		18	412	21	11	321	17	Mm+P
sed		1.1						
sed same P		0.7						
-P	MHm, MH	21	476	24	12	365	18	MHm, Mm
+P	MHm+P, MH+P	17	405	21	10	315	16	MHm+P, Mm+P
sed		1.0						
-mulch	MH, MH+P	19	451	23	0	0	0	MH, M, MH+P, M+P
+mulch	MHm, MHm+P	18	430	22	11	340	17	MHm, Mm, MHm+P, Mm+
sed		0.5						

Lower amounts of biomass from the hedge did not affect the fertility effect on maize caused by mulch (Chapter 2), probably because the difference in amounts of mulch were too small to detect a difference in fertility effect. Alternatively, the combination of mulch with P-fertiliser had some positive interaction effect, that offset the effect of lower amounts of mulch.

Partitioning of Assimilates

Table 3 shows the partitioning of maize assimilates over grain, stover and roots, and the ratios between above ground biomass and root, and between grain and above-ground biomass (harvest index), in the 1997 long-rains.

Addition of P and mulch increased the maize root-biomass, but this was much less than the increase in above-ground biomass. As a result the shoot:root ratio was significantly higher in +P than –P, in +mulch than in -mulch, and in -hedge than in +hedge treatments. An increase in shoot : root ratio upon increasing fertility, especially P, is common (Marschner, 1991b). Larger amounts of roots relative to shoot, when hedges are present, may be a response to competition for below-ground resources. The equilibrium concept of Brouwer (1983) states that relatively more assimilates are spent in the root-system when below-ground resources are limiting, like in our -P and -mulch situations. Competition with another species also limits below-ground resources.

Harvest index followed the same trend as shoot:root ratio and total biomass. In +P, +mulch and -hedge treatments, relatively more assimilates ended up in grain compared to -P, -mulch and +hedge treatments. Though it has been suggested that nutrient deficiencies do not have consistent effects on harvest index (Squire, 1993), harvest index was higher in +P than in –P treatments. This may be related to the fact that P-application decreased the length of the vegetative growth phase. Maize

tasseling was earlier, possibly at a period of better water-supply, which is an important determinant for grain yield.

Summarizing, differences between treatments in maize grain yields were caused by differences in i) total biomass production, ii) partitioning of assimilates over shoot and root, and iii) partitioning of assimilates over stover and grain. All three factors reinforced each other.

Table 3. Effects of hedge, P-application and mulch-application on partitioning of assimilates in maize biomass, at Maseno, Western Kenya (long rainy season 1997). MHm: +Hedge+mulch, Mm: sole maize+mulch, MH:+hedge no mulch, M: sole maize no mulch, +/-P: means of all +P or -P treatments, +/-hedge: means of all +hedge or sole maize treatments, +/- mulch: means of all +mulch or -mulch treatments.

Treatment	Total biomass (t/ha)	Root biomass (t/ha)	Above ground biomass (t/ha)	Stover (t/ha)	Grain (t/ha)	Harvest index ()	Shoot : root ratio ()
MHm	1.5	0.4	1.1	0.8	0.3	0.3	4.0
MH	0.9	0.4	0.5	0.4	0.1	0.2	1.5
Mm	3.8	0.6	3.1	1.5	1.7	0.5	5.1
M	1.2	0.3	0.9	0.6	0.2	0.3	3.1
MHm+P	3.5	0.8	2.7	1.4	1.3	0.5	3.4
MH+P	1.6	0.4	1.1	0.8	0.4	0.3	2.8
Mm+P	6.1	0.8	5.3	2.0	3.3	0.6	7.2
M+P	4.4	0.9	3.5	1.4	2.1	0.6	4.6
sed	0.59	0.13	0.53	0.23	0.35	0.04	0.82
sed same M(H)*P	0.41	0.13	0.39	0.18	0.28	0.04	0.83
-P	1.8	0.4	1.4	0.8	0.6	0.3	3.4
+P	3.9	0.7	3.2	1.4	1.8	0.5	4.5
sed	0.36	0.07	0.32	0.14	0.20	0.02	0.41
-Hedge	3.9	0.7	3.2	1.4	1.8	0.5	5.0
+Hedge	1.9	0.5	1.4	0.8	0.5	0.3	2.9
sed	0.36	0.07	0.32	0.14	0.20	0.02	0.41
-mulch	2.0	0.5	1.5	0.8	0.7	0.3	3.0
+mulch	3.7	0.6	3.1	1.4	1.7	0.5	4.9
sed	0.21	0.07	0.19	0.09	0.14	0.02	0.41
sig. interactions	h*P*m	P*h*m	P*h ⁻¹		h*m	h*P*m	
.1 = 0.1 else 0.05	h*m ⁻¹		h*m		h*P		
	h*P ⁻¹		P*h*m ⁻¹				

Soil Inorganic Nitrogen

Soil inorganic nitrogen contents (NH_4^+ and $\text{NO}_3^- + \text{NO}_2^-$) are shown in Table 4.

Mulch applications increased soil N up to a depth of about 50 cm.

P-application decreased soil N significantly up to a depth of about 50 cm. This decrease was related to the higher uptake of N by the better growing maize.

The presence of hedges had significant effects on N content over depth.

In the top layer (0-15 cm) soil N-content was higher in plots with hedge than in those without hedge, although this was not significant. In the second layer (15-30 cm) there were no significant differences. In the third layer (30-50 cm) soil N was significantly lower in plots with hedge than without hedge. In the fourth layer (50-150 cm) soil N contents are much lower in plots with hedge than in plots without hedge.

Table 4. Effects of hedge, P-application and mulch-application on mean soil inorganic nitrogen contents (kg ha⁻¹), in July 1997 at Maseno, Western Kenya. MHm: +Hedge+mulch, Mm: sole maize+mulch, MH: +hedge no mulch, M: sole maize no mulch, +/-P: means of all +P or -P treatments, +/- hedge: means of all +hedge or sole maize treatments, +/- mulch: means of all +mulch or -mulch treatments.

	Depth (cm)	0-15	15-30	30-50	50-150
Treat					
MHm		33	37	55	165
MH		25	29	32	173
Mm		31	36	62	280
M		23	30	57	301
MHm+P		19	21	31	136
MH+P		18	16	26	144
Mm+P		11	16	52	305
M+P		13	11	38	236
sed		5.0	6.0	9.2	74.2
sed same M(H)*P		5.1	3.4	8.2	66.3
+ P		15	16	37	205
- P		28	33	51	230
sed		2.5	3.9	5.0	40.6
+ Hedge		24	26	36	155
-Hedge		20	23	52	280
sed		2.5	3.9	5.0	40.6
+ mulch		24	28	50	221
- mulch		20	22	38	213
sed		2.5	1.7	4.1	33.2

These changes over depth may be related to N-uptake by the hedges at depth and a decrease in N uptake by maize in the top-soil. Alternatively, increases in N-content in the top-soil of hedge plots may be related to N_2 fixation by the hedge. With increasing depth, likely the balance tended to be determined by the uptake of N by the hedges.

There was significantly more N in the top-soil (0-30 cm) of the alley-cropping treatment -P than in the top-soil (0-30 cm) of the continuous maize treatment -P. This was similar but insignificant for the +P treatments. In contrast, the sub-soil (30-50 cm) and especially (50-150 cm) of the alley-cropping treatments contained less N than the sub-soil of the sole maize treatments.

Thus, sole maize systems had higher N-contents in depth, while alley-cropping systems had higher N contents in the surface soil, supporting the theory that hedges of trees tap resources from the sub-soil and relocate them to the surface.

Nitrogen-Balance

The estimates of the variables of the N-balance (eq. 6) as derived from regression analysis, are shown in Table 5a and lead to the balances shown in Table 5b.

The total-N balance is the same as the inorganic-N balance, except that the mineralization-factor of mulch-N is *not* used. Thus we follow eq. 3 excluding fN_{min} .

In the alley-cropping -P (MHm) total-N-addition caused by the hedge, partly due to biological nitrogen fixation (BNF), partly due to reduction of leaching is $fN_{hedge-effect} * N_{hedge-shoot}$ and was 269 kg ha⁻¹. Total-N-export, due to maize biomass ($N_{crop-shoot}$) was 173 kg ha⁻¹ and export of hedge-branches ($N_{hedge-uptake}$ minus N_{mulch}) was 108 kg ha⁻¹, giving a negative balance of $269 - 173 - 108 = -12$ kg ha⁻¹. Thus even in the total-N balance, N-export from the system is slightly larger than N-addition by the hedge. Only the N-input by rain and reduced N-leaching due to maize-growth ($64 + 20 = 84$ kg ha⁻¹) prevent a negative total-N-balance.

Similarly, in the alley-cropping +P (MHm+P) total N-addition caused by the hedge was 231 kg ha⁻¹, while total N-export in maize biomass (304 kg ha⁻¹) and hedge-branches (398-309 kg ha⁻¹) was 393 kg ha⁻¹, giving a negative balance of $231 - 393 = -162$ kg ha⁻¹. Rain-N and reduced N-leaching due to maize-growth ($20 + 112 = 132$ kg ha⁻¹) do not even cover this, and the overall total-N balance is negative.

The inorganic-N-balance was even more negative, because the fraction of mulch-N mineralized and not leached thereafter (fN_{mulch} in table 5a) was estimated by the regression analysis at 0.2. From the early mulch applications a higher fraction might have become available, from the latest applications the fraction was likely less. The rest-fraction of 0.8 was partly mineralized and leached, and partly

Table 5. Estimates of factors in the N-balance equation 6, using regression analysis and the mean data of the 8 treatments (a) and inorganic-N balances (export from and input into soil, excluding root-cycling) at Maseno, western Kenya (b) whole profile: 0-150 cm, bold numbers are calculated/measured values, italic numbers are fitted in multiple regression.

(a)		$fN_{\text{hedge-effect}}$	$fN_{\text{leach-red-maize}}$			
Estimate	$N_{\text{init-leachmax}}$	fN_{mulch}	effect	maize	%var	
s.e.	505	0.20	0.58	0.37	94	
	56.3	0.074	0.065	0.196	n	8

(b)	$N_{\text{init-leachmax}}$	N_{rain}	N_{mulch}	fN_{mulch}	$N_{\text{hedge shoot}}$	$fN_{\text{hedge-effect}}$	$N_{\text{crop-shoot}}$	$fN_{\text{leach-red-maize}}$	N_{final}	N_{final}
				$*N_{\text{mulch}}$		$*N_{\text{hedge-shoot}}$		$*N_{\text{crop-shoot}}$	calculated	measured
	kg ha ⁻¹	kg ha ⁻¹	kg ha ⁻¹	kg ha ⁻¹	kg ha ⁻¹	kg ha ⁻¹	kg ha ⁻¹	kg ha ⁻¹	kg ha ⁻¹	kg ha ⁻¹
				* 0.2		* 0.58		* 0.37		
MHm	505	20	355	71	463	269	173	64	293	290
MH	505	20	0	0	489	284	148	55	226	259
Mm	505	20	376	75.2	0	0	274	101	428	409
M	505	20	0	0	0	0	186	69	408	411
MHm+P	505	20	309	61.8	398	231	304	112	228	208
MH+P	505	20	0	0	412	239	208	77	221	203
Mm+P	505	20	321	64.2	0	0	390	144	344	383
M+P	505	20	0	0	0	0	327	121	319	298

$N_{\text{init-leachmax}}$ = initial below-ground inorganic N stock (including SOM-N present at the start of the experiment) minus maximum N-leached over entire 3.5 yr period

N_{rain} = N supplied by rain over entire 3.5 yr period

N_{mulch} = total N in mulch supplied over entire 3.5 yr period

$fN_{\text{mulch}} * N_{\text{mulch}}$ = Mulch-N mineralized minus mulch-N leached

$N_{\text{hedge shoot}}$ = total above-ground N-uptake by hedge

$fN_{\text{hedge-effect}} * N_{\text{hedge-uptake}}$ = BNF-N plus hedge-reduction in N-leaching

$N_{\text{crop-shoot}}$ = total above ground N-uptake by maize crops

$fN_{\text{leach-red-maize}} * N_{\text{crop-uptake}}$ = crop-reduction in N-leaching

MHm = + Hedge + mulch

Mm = Sole maize + mulch

MH = + Hedge - mulch

M = Sole maize - mulch

not yet mineralized organic N, which was less available for plant-uptake. Palm [1995] reported that N-release from Calliandra leaves is around 20%, quoting research findings of 11-40%. Thus, our calculated mineralization factor seemed plausible.

The factor $fN_{\text{hedge-effect}}$ was estimated to be 0.58, combining BNF-N and reduction-in-leached-N. In general BNF contributes about 30-50% to total N-uptake (Cadisch, pers. comm., 1999), which would suggest that 0.3-0.5 times $N_{\text{hedge-shoot}}$ was caused by BNF, and 0.08-0.28 times total-hedge-uptake represented the reduction in leaching. Cadisch et al (1997) report a 5-10% reduction in leaching by *Peltophorum*, which has relatively much roots in depth. Thus we presume that our hedge-leaching reduction was probably near the lower limit (0.08) of its range and BNF towards the higher limit (0.5) of its range. Thus BNF-N should be about 245 kg ha^{-1} , and leaching-reduction caused by the hedge should be about 30 kg ha^{-1} , over the seven seasons studied.

The $fN_{\text{leach-red-maize}}$ factor estimate of 0.37, represented reduction of N-leaching caused by crop growth. The absolute amount of leaching-reduction was between $55\text{-}144 \text{ kg ha}^{-1}$. These amounts are higher than the leaching reduction by the hedge, probably due to the relatively low water and nitrogen use of the hedge compared with maize in the growing seasons, due to hedge-pruning. The constant $N_{\text{init-leachmax}}$ in table 5a and 5b of 505 kg ha^{-1} contains the initial inorganic-N; the N mineralized from soil-organic-matter, the N cycling in root systems and the maximum N-leaching and gas-N losses. It is assumed to be similar for all treatments.

The estimates for the not-measured components of the N-balance were reasonable and they led to a close match of calculated and measured N_{final} .

Soil phosphorus and P-balance

Soil analysis results for resin-P and exchangeable-K are shown in table 6.

We combined data of the three top layers because they showed similar levels and treatment differences. P-applications increased the resin-P content in all three layers of the top 50 cm of the soil. It is unlikely that inorganic P moved down the profile. Thus, the increase in resin-P values especially in the 30-50 cm layer could be due to soil sample contamination, or to maize root growth and turnover. Mulch-P content and mulch decomposition were too low to attribute the increase in resin-P beyond 30 cm depth to organic-P-leaching from mulch.

Mulch application increased resin-P significantly. The cause of this increase may be twofold; i) mineralization of mulch supplied P and ii) organic matter decomposition products like organic anions (Comerford & Skinner, 1989) and polyphenols (Pohlman & McColl, 1988) may have occupied adsorption sites, decreasing phosphate adsorption and increasing its availability.

Calliandra hedges did not affect resin-P significantly.

Table 6. Resin Extractable Phosphorus and Exchangeable Potassium in Soil, at Maseno, Western Kenya. MHm: +Hedge+mulch, Mm: sole maize+mulch, MH:+hedge no mulch, M: sole maize no mulch, +/-P: means of all +P or -P treatments, +/- hedge: means of all +hedge or sole maize treatments, +/- mulch: means of all +mulch or -mulch treatments.

Treat	Depth (cm)	Resin-P (mg kg ⁻¹)		Ex-K (cmol _c kg ⁻¹)	
		0-50	50-150	0-50	50-150
MHm		2.2	1.8	0.08	0.04
MH		1.8	1.8	0.07	0.05
Mm		2.8	1.9	0.06	0.06
M		2.2	2.0	0.06	0.06
MHm+P		5.4	1.8	0.06	0.04
MH+P		5.7	1.9	0.05	0.04
Mm+P		6.1	1.7	0.06	0.04
M+P		4.7	1.6	0.06	0.04
sed		1.03	0.29	0.008	0.009
sed same M(H)*P		0.44	0.29	0.008	0.007
+ P		5.5	1.7	0.06	0.04
- P		2.3	1.8	0.07	0.05
sed		0.70	0.14	0.004	0.055
+ Hedge		3.8	1.8	0.06	0.04
-Hedge		3.9	1.8	0.06	0.05
sed		0.70	0.14	0.004	0.006
+ mulch		4.1	1.8	0.06	0.05
- mulch		3.6	1.8	0.06	0.05
sed		0.22	0.14	0.004	0.003

Table 7. P-balances (equation 1) over entire period of 3.5 yrs. (export from and input into soil). MHm: +Hedge+mulch, Mm: sole maize+mulch, MH:+hedge no mulch, M: sole maize no mulch, Pfertilizer: P added by fertilizer, Phedge-shoot: P in total hedge above ground biomass, Pmulch: P returned to soil by mulch application, Pcrop-shoot: P in total crop above ground biomass.

Treatment	P _{fertilizer} kg ha ⁻¹	P _{hedge-shoot} kg ha ⁻¹	P _{mulch} kg ha ⁻¹	P _{crop-shoot} kg ha ⁻¹	P _{final} - P _{init} kg ha ⁻¹
MHm	0	23	18	13	-19
MH	0	24	0	11	-36
Mm	0	0	19	22	-3
M	0	0	0	14	-14
MHm+P	91	20	16	25	62
MH+P	91	21	0	17	53
Mm+P	91	0	17	32	76
M+P	91	0	0	26	65

P-balances are shown in table 7. Balances were negative in treatments without P addition from -3 kg ha⁻¹ (Mm) to -36 kg ha⁻¹ (MH)) as known from earlier work in alley cropping systems (Palm, 1995), while the treatments with P addition showed positive P-balances (50-75 kg ha⁻¹). The P-balance is more negative in alley-cropping (MHm) than in sole maize (M), mainly due to export of hedge branches. Export of P via harvested maize was similar in alley-cropping and sole-maize.

Soil potassium

Table 6 shows only small differences between treatments in exchangeable potassium contents. All exchangeable K values were below the level at which K becomes limiting to crop-growth (about 0.1 cmol kg⁻¹), and were lower than the initial K-values of 0.14 cmol_c kg⁻¹ in 1994 (chapter 2). Evidently, K-balances over the entire period were negative and alley-cropping did not alleviate K-deficiency. K-deficiency may limit crop-growth especially in treatments where P is applied and mulch covers (part of) the N-supply.

Neither P nor K analyses demonstrated significant difference among soil samples closer by or further away from the hedge in alley-treatments.

Water

Soil water contents are shown in table 8. Trends in soil water content were similar for the three top layers, and hence data for the three layers were combined.

Hedge and mulch-application influenced soil water contents. Hedges increased surface soil water contents but decreased soil water content in depth, relocating water in a similar way as nitrogen.

Table 8. Effects of hedge, P-application and mulch-application on plot averages of gravimetric soil water contents (%), at Maseno, Western Kenya. +/-P: means of all +P or -P treatments, +/- hedge: means of all +hedge or sole maize treatments, +/- mulch: means of all +mulch or -mulch treatments.

Depth (cm)	0-50				50-150			
	5/19/97	6/9/97	7/3/97	8/5/97	5/19/97	6/9/97	7/3/97	8/5/97
+ P	24.9	19.1	21.9	21.3	27.8	26.5	26.0	24.5
- P	24.7	20.9	22.8	22.0	28.2	26.7	27.2	26.1
sed	0.35	0.38	0.38	0.20	0.38	0.56	0.41	0.35
+ Hedge	24.7	20.3	22.8	21.9	27.8	26.4	26.8	25.8
-Hedge	25.1	19.1	21.1	21.0	28.4	27.1	26.1	23.7
sed	0.35	0.38	0.38	0.20	0.38	0.56	0.41	0.35
+ mulch	25.1	20.0	22.4	21.4	28.4	26.7	26.5	24.9
- mulch	24.5	20.0	22.3	21.9	27.6	26.6	26.7	25.7
sed	0.25	0.25	0.25	0.21	0.36	0.21	0.31	0.45
sign. interactions	h*P*m				P*m		h*P	
							h*P*m	

Mulch initially increased soil water contents, but decreased soil water contents later in the season. Decreases in soil water contents due to enhanced maize growth was the general trend in +P treatments.

However, differences in soil water contents were small, only 1-2%, and less than the overall variability during the season. The small and opposite effects of mulch and hedge suggest that it is unlikely, that alley-cropping effects on maize growth were caused by changes in soil water contents, even in this relatively dry long-rainy season.

Roots

Root densities of maize and Calliandra are shown in table 9. Data of the three top-layers showed similar differences and were therefore combined.

Table 9. Maize and Calliandra root length densities measured at tasseling in the long rainy season of 1997. MHm: +Hedge+mulch, Mm: sole maize+mulch, MH:+hedge no mulch, M: sole maize no mulch, +/-P: means of all +P or -P treatments, +/- hedge: means of all +hedge or sole maize treatments, +/- mulch: means of all +mulch or -mulch treatments.

	0-50 cm depth	0-50 cm depth	50-150 cm depth	50-150 cm depth	0-30 cm depth
	Maize r.l.d (cm cm ⁻³)	Calliandra r.l.d. (cm cm ⁻³)	Maize r.l.d (cm cm ⁻³)	Calliandra r.l.d. (cm cm ⁻³)	smallest 1/2 inter-root distance (cm)
MHm	0.47	0.090	0.068	0.045	0.64
MH	0.44	0.098	0.080	0.036	0.62
Mm	0.61	-	0.060	-	-
M	0.32	-	0.014	-	-
MHm+P	0.89	0.125	0.097	0.011	0.47
MH+P	0.50	0.118	0.045	0.039	0.58
Mm+P	0.73	-	0.091	-	-
M+P	0.81	-	0.087	-	-
sed	0.094	0.039	0.029	0.0194	
sed same M(H)*P	0.073	0.018	0.032	0.0118	
+ P	0.73	0.12	0.081	0.025	
- P	0.46	0.09	0.054	0.040	
sed	0.055	0.037	0.013	0.0175	
+ Hedge	0.58	-	0.081	-	
- Hedge	0.62	-	0.054	-	
sed	0.055		0.013		
+ mulch	0.68	0.11	0.072	0.028	
- mulch	0.52	0.11	0.063	0.038	
sed	0.036	0.013	0.016	0.0084	

sign. interactions

h*P*m

Up to 50 cm depth maize root densities were higher in +P treatments and + mulch treatments than in -P treatments and -mulch treatments.

Calliandra hedges did not significantly influence maize root densities up to 50 cm depth. Between 50 and 150 cm depth, maize root densities were significantly higher in the plots with hedges, probably in response to competition (Schroth and Zech, 1995b).

Root length densities of Calliandra were not affected by phosphorus or mulch application.

Competition of Calliandra and Maize roots for different nutrients.

The shortest half-inter-root distances derived from root densities in the top 30 cm of hedge plots, ranged from 0.47-0.64 (Table 9 last column). Calculated diffusion distances of N, P and K in a linear distance away from the root at high and low buffer capacities of the soil for these nutrients are shown in table 10.

Table 10. Diffusion distances of N, P, and K towards roots in 1 day and 120 days, at Maseno, western Kenya. Values used in calculations are: vol. soil water content $\theta = 0.32$ (measured, quite wet) and $DI(N) = 1.9 \cdot 10^{-5}$, $DI(P) = 8.9 \cdot 10^{-6}$ and $DI(K) = 1.98 \cdot 10^{-5}$ (Barber, 1995).

	High buffer capacity (Cl / Cs) of soil				Low buffer capacity (Cl / Cs) of soil			
	Cl / Cs ()	De ($\text{cm}^2 \text{s}^{-1}$)	diff. dist. 1day (cm)	diff. dist. 120 days (cm)	Cl / Cs ()	De ($\text{cm}^2 \text{s}^{-1}$)	diff. dist. 1day (cm)	diff. dist. 120 days (cm)
N	0.05	4.27E-08	0.086	10.3	1	8.54E-07	0.384	46.1
P	0.0002	8E-11	0.004	0.4	0.0035	1.4E-09	0.016	1.9
K	0.025	2.22E-08	0.062	7.4	0.05	4.45E-08	0.088	10.5

For P, diffusion is the main transport mechanism to the roots. It is clear, that over a growing period of 120 days, in situations with low soil P (no additions and high buffer capacity), the calculated maximal diffusion distance around a root was still smaller than the smallest half-inter-root distance in any of the treatments without P.

In situations with P addition (lower buffer capacity), individual roots of Calliandra and Maize could compete for P after uptake by a root for 30-40 days (30-40 times 0.016), because after such a period the diffusion distance became larger than the inter-root distances. Such short inter-root-distances occurred around maize flowering, when the root densities were highest. These long periods suggest that real competition for P and overlap of depletion zones, played a minor role during the vegetative development of the maize crop.

Thus, over the whole period of maize vegetative growth inter root competition for P only played a minor role in treatments where P was applied, and was negligible in treatments without P-

application. A decrease of soil-P status in the long run may however cause reduced P-availability in following seasons.

Inter-root-competition for K was much more probable, because even at high K-buffering, the diffusion distance reached half-inter-root-distances in 8-10 days. At lower root-densities at the start of the season the period before depletion zones overlap will be longer. However, it is likely that roots of maize and Calliandra competed for K during a considerable part of the vegetative growth phase of maize and thereafter. Moreover, mass-flow also plays a role in transport of K to the roots, and could have increased the overlap of depletion zones and competition.

Inter-root competition for N is even more pronounced than for K, because N is a more mobile nutrient. The soils of this experiment showed a relatively low N-sorption compared with other soils (Hartemink et. al., 1996). Hence, inter-root-competition for N at low buffer-capacity could have taken place in 1-2 days at the period of maximum root-density. Moreover, part of N was supplied to the roots by mass flow, again increasing overlap in depletion zones. Thus, inter-root-competition of maize and Calliandra roots for nitrogen was probably high during most of the maize vegetative growth phase. Little competition between hedge and crop for N may have occurred, if the supply of N was higher than the demand of hedge and crop. Relatively high N-supply occurred in +mulch treatments, and low N-demand occurred in -P treatments. Thus competition between hedge and crop was likely lowest in the alley-cropping +mulch -P (MHm).

In general, in more fertile situations (+P, +mulch) maize root length densities and plant-demand for other more mobile resources (N, K) are higher, hence competition is more an issue.

Discussion and conclusions

In the alley-cropping system examined here, nutrient balances were generally negative. N-balance was negative because export of N in harvested grain, maize stover and hedge branches was higher than N-gains by safety-net function of the hedge and biological nitrogen fixation. Inorganic-N-balance was even more negative due to slow mineralization of N from mulch. The stronger negative inorganic-N-balance compared with total-N-balance over 3.5 years, shows that there is a large time lag between hedge-N-uptake and available N-supply from mulch mineralization. Cannell et al (1996) split competition effect (C) in $C_{\text{recycled}} + C_{\text{nonrecycled}}$, where C_{recycled} represents the resources that the crop is deprived of by the trees, but which will be recycled to the next crop, and $C_{\text{nonrecycled}}$ represents the resources that the crop is deprived of and which are used in tree growth and are not recycled. They assumed that in the long run $F_{\text{comp}} = C_{\text{recycled}}$. This does not yet hold for this system over this time-period of three and a half year. Within this time-period $F_{\text{comp}} < C_{\text{recycled}}$ and therefore the choice to calculate F in presence of competition (Chapter 2) comes closer to reality

than the choice resulting from the theory of Cannell et al (1996) to calculate F in absence of competition as in $I = F_{\text{noncomp}} - C_{\text{nonrecycled}}$.

The P-balance was only positive if P-fertilizer was applied. Soil potassium levels declined over the entire period to below the sufficiency limit, indicating a negative K-balance as well. The negative nutrient balances indicate that this alley-cropping system is indeed not sustainable and is likely the cause of the decline in crop yields over time (Chapter 2). The decline in crop-yields in +P alley-cropping is likely due to negative N- and K- balances, but the more serious decline in –P alley-cropping is likely due to increasing P deficiency, which was already severely limiting crop-production. Differences in N and P balances between alley-cropping and sole maize (MHm vs. M and MHm+P vs. M+P) were not clearly reflected in yield levels (Chapter 2). Thus balances may explain the long-term trend but not all the treatment-effects.

Direct competition for P between roots of hedge and maize was calculated to be low in our soils especially in –P treatments, because depletion zones do not overlap. This may have caused the lower competition (C) values in –P compared to +P treatments as measured by Ong's equation in chapter 2). In alley-cropping +P, competition between roots of hedge and maize will likely be for N and K, because in topsoil depletion zones for K and N around roots quickly overlap, because of their higher mobility in soil. Higher root length densities and higher plant-demand for other below ground resources in situations where P and/or mulch were supplied caused larger competition effects, as described in chapter 2. This is in agreement with Kho (2000), who argues that when the degree of limitation of one resource decreases (like P here), the degree of limitation of other resources increases. But in case P is applied, competition is even larger than Kho's equation suggests, because direct competition for N and K is more likely than for P, due to their high mobility in soil. Thus competition will be direct if N and K are limiting growth, but occur with a delay in case P is limiting, via reduced overall soil-P level in the longer run instead of overlap in depletion zones. Alley-cropping effects on soil water content were small and no significant cause of positive or negative crop-growth responses, neither direct (water-limitation) nor indirect (limiting nutrient-transport).

Partitioning of assimilates towards grain reinforced the differences in biomass among the treatments.

This study shows that long-term performance of alley-cropping, which is not considered in the methods of Ong and Kho can be addressed by investigation of yields and nutrient balances. The measured yield decline over time was related to negative balances.

The nitrogen balance showed also a considerable delay in N-mineralization, clarifying (part of) the discrepancy between the way Cannell et al (1996) proposed to use Ong's equation, and the way we

used the equation (Chapter 2). Competition for P was another delayed process, and explained the lower competition (C) in -P than +P alley-cropping (Chapter 2).

This study shows that complementing system performance analysis methods of alley-cropping systems with nutrient balances and mechanistic research can increase the understanding of tree-crop interactions in the system, and reduce the risk of wrong performance prediction either over time or towards other environments.

Can trees mobilize phosphorus for crops? I. Organic anions, phosphatase activity and phosphorus fractions in the rhizosphere

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Abstract

In agroforestry systems on Ferralsols/Oxisols in the tropics, where crop yields are low due to phosphorus-deficiency, trees do not add P to overcome this deficiency for crops. However, if tree species adapted to P-fixing soils are able to use unavailable P-sources, and increase P-availability, the maize-crop with limited adaptations, may profit.

We measured the concentration of organic anions, acid phosphatase activity and P-fractions in the rhizosphere soil of the crop *Zea mays* L. as well as in the perennial species *Grevillea robusta* (Cunn.), *Cassia spectabilis* (syn. *Senna spectabilis*) (DC.), *Tithonia diversifolia* (Hemsl.) Gray, *Eucalyptus grandis* (Hill ex Maiden) and *Cedrella serrata* (Royle). Maize and trees were grown simultaneously at field sites and in a barrel experiment at field conditions. Citrate recovery and citrate effect on P-availability in moist field soil incubations was tested to reveal the relation between quantities added and recovered, and effect of citrate on measured P-fractions in absence of plant uptake

Rhizosphere soil of *Cassia* showed high levels of water extractable oxalate ($\sim 3 \mu\text{mol g}^{-1}_{\text{soil}}$), which was 15-30 times higher than citrate concentration in the rhizosphere of either *Tithonia* or *Grevillea*. Very low (1%) recovery of the citrate added to field moist soil indicated that the organic anion levels measured in rhizosphere soil of *Cassia* were derived from an exceptionally high soil loading rate of about $12 \mu\text{mol g}^{-1}_{\text{soil}} \text{d}^{-1}$ or an exudation rate of $73 \mu\text{mol m}^{-1}_{\text{root}} \text{d}^{-1}$.

There was no effect of organic anions on P fractions in rhizosphere soil. This may be partly due to minimal ligand exchange at high pH, and partly due to a balance of P-mobilization and P-uptake of the tree. This infers that little P will become available to a coexisting crop, unless its roots grow quickly along active tree-roots.

Acid phosphatase activity in rhizosphere soil compared to bulk soil was 5 times higher for *Grevillea*, 2.5 times higher for *Eucalyptus* and 1.5 times higher for *Cassia*, *Cedrella* and maize. Phosphatase activity was related to a shift from organic P to inorganic P in measured soil-P fractions, especially in *Grevillea* rhizosphere soil. Even in maize rhizosphere soil, at lower acid phosphatase activity organic-P fractions were depleted. This suggests that the crop is able to hydrolyze organic-P itself and tree-roots may not positively affect P-availability for the crop.

In conclusion, organic anion exudation of tree roots can only favor P-uptake for a crop if crop-roots are growing in the tree-root rhizosphere during its exuding period, and the exudation of organic anions does not occur at the same time of pH-increases. High phosphatase activity of tree-roots does not increase crop P-acquisition.

Introduction

Agroforestry systems combine trees or shrubs with cropping, with the aim of developing a productive and sustainable form of land-use. Van Noordwijk and Ong (1999) hypothesize that land-use systems that mimic patterns of resource use in natural systems are most likely to achieve long-term sustainability. However, in natural systems of low nutrient-availability (nitrogen, phosphorus), species generally adjust by slow growth rate, because this answers best to the aim of species survival in sub-optimal conditions (Chapin, 1980). This survival strategy is hard to combine with farmers' aim of high productivity. Nevertheless, some plants in low nutrient conditions exhibit specific

attributes that can increase nutrient availability. For example, some leguminous plants can add N to a soil-plant system by biological N-fixation, and agroforestry systems generally utilize N-fixers to ameliorate N-deficiencies. There are no similar ways in which trees can add P to the soil-plant system.

Phosphorus is the most limiting nutrient for crop production in large parts of the tropics. Phosphorus limitations to growth and productivity of crops are primarily a consequence of adsorption and precipitation reactions with sesquioxides in strongly weathered Ferralsols/Oxisols rather than low amounts of total P (Sanchez, 1976; Hue, 1991). In order to overcome P-deficiencies, P supply to crops must somehow be increased.

The challenge of agroforestry research is to identify species that are able to transform “unavailable-P” into forms that may be utilized by the crop, either by nutrient cycling or by direct root-effects. Increased P-uptake and cycling of P-rich litter to maize crops systems has been recently examined, particularly of the composite *Tithonia diversifolia* (Jama et al., 2000). Other perennial species, such as the trees *Grevillea robusta* and *Eucalyptus grandis*, are used for timber and pole production and are often planted as borderlines along crop fields. However, the litter quality of such trees is generally low (i.e. the C:P ratio is high) to add sufficient available-P to the soil to enhance crop growth (Palm, 1995).

If trees in a simultaneous agroforestry system exhibit P-mobilizing adaptations then these species may acquire P from sources in a way that is not in competition with the crop. Further, if the rhizospheres of tree and crop roots overlap, i.e. if the tree and crop roots do not exclude one another, there is a potential for the crop to benefit from the increased P-availability in tree-rhizosphere soil (van Noordwijk et al, 1999). The primary adjustments to low P-availability trees may exhibit, and which may profit the maize-crop, are related to mobilization and hydrolysis of P in the rhizosphere by i) organic anion exudation (Marschner et al. 1987; Dinkelaker et al. 1989; Hoffland, 1989; Grierson 1992), ii) increased phosphatase activity (Ridge and Rovira, 1971; Tarafdar and Chhonkar, 1978; Mc Lachlan, 1980), iii) iron-reduction (Gardner et al, 1983), iv) pH increase/decrease (Hendrix, 1967; Hoffland 1989, 1992; Bertrand et al. 1999; Hinsinger, 2001), and v) rhizosphere microbial effects (Bowen and Rovira, 1999).

High relative amounts of organic anions in the rhizosphere are a result of root-exudation and/or microbial metabolism (Marschner et al. 1987; Dinkelaker et al. 1989; Grierson 1992; Marschner, 1995). In Ferralsols / Oxisols with high contents of variable charge colloids, organic anions may desorb P (organic and inorganic) by ligand-exchange with phosphate sorbed on iron- and aluminum-(hydr)oxides (Nagarajah et al. 1970; Gerke, 1992; Tani et al. 1993; Gerke et al. 1994), or they may

form complexes with iron and aluminum in solution, causing dissolution of phosphate (Bolan et al. 1994; Fox and Comerford, 1990; Gerke et al. 1994; Gerke, 1995), or mobilization of phosphate-organic-metal complexes (Barber, 1971; Kepert et al. 1979; Gardner et al. 1983), which can be broken down at the root surface (Gardner et al. 1983). Generally, the effectiveness of organic anions in ligand exchange decreases in the following order: tricarboxylic > dicarboxylic > monocarboxylic and depends further on distance of reactive groups within the organic anion, $\log K_{Al}$ (if aluminum is an important complexing agent) and pK of the organic acid (Nagarajah et al. 1970; Parfitt, 1979; Hue, 1991; Kpombrekou and Tabatabai, 1994; Bolan et al. 1994). The relative abundance of the different iron and aluminum forms in bulk soil determine which complexation and adsorption/desorption reactions determine P availability. The main form of P in tropical Oxisols/Ferralsols are reductant-soluble iron phosphates (Sanchez, 1976).

Phosphatase enzymes catalyze the hydrolysis and subsequent mineralization of organic P (Tarafdar and Chhonkar, 1978; Dinkelaker and Marschner, 1992; Findenegg and Nelemans, 1993). Acid phosphatase activity (APA) in the rhizosphere may be increased by root exudation, mycorrhizal fungi and by other rhizosphere microorganisms (Ridge and Rovira, 1971; Boero and Thien, 1979; McLachlan, 1980; Tarafdar and Chhonkar, 1978). However, while organic-P is a large fraction of total-soil-P in tropical Oxisols/Ferralsols (Sanchez, 1976), much of the organic-P is sorbed to Al/Fe (hydr)oxides in a similar way to inorganic P (Anderson et al. 1974). Consequently, much of this organic P may not be available for hydrolysis despite adequate amounts of phosphatase enzyme in the soil (Boero and Thien, 1979; Findenegg and Nelemans, 1993).

So far, very few studies have attempted to explore the above mentioned mechanisms of P-mobilization in agroforestry systems under field conditions.

This study investigated the extent to which perennial species planted in agroforestry systems might affect P-uptake and yield of a maize crop, by mobilization of P in the rhizosphere. We measured organic anion contents and phosphatase activity of rhizosphere soil, and their relation with P fractions in rhizosphere soil. We tested the extent to which individual organic anions affected different P fractions by amending soils with either citrate or oxalate and then estimated anion-recovery from soil without plants and plant-uptake.

Our experiments were under field conditions, with trees and maize growing simultaneously in Western Kenya. In Western Kenya a large part of the agricultural fields consist of nutrient depleted Ferralsols / Oxisols, with primarily a P-limitation to crop-production. Smallholder farmers generally cannot afford buying sufficient fertilizers, and organic inputs do not compensate for P lost through crop harvests (Smaling, 1993). The amount of trees planted in the area has recently increased with increasing population density (Shepherd et al, 1992), with trees and tree-lines in, or bordering crop fields. Maize is the main staple crop.

Materials and methods

Field trials

Investigations were done in two field trials with tree-lines in the middle of maize (*Zea mays*) fields on deep, P-depleted Ferralsols/Oxisols at Nyabeda, Western Kenya (Latitude 0.08 °N, Longitude 34.24 °E, Altitude 1300m). The site was sub-humid with an annual rainfall of about 1500 mm, distributed over two main cropping seasons; the long rainy season from March to June/July (~900mm) and the short rainy season from September to December/January (~600mm). The experiment was established on level land, which was formerly cropped with maize or left fallow. Soils of both trials were similar. Initial topsoil characteristics of the trials are shown in table 1.

Trial 1 was a 4x2 factorial design with split-plots and four replicates. The treatments were four crop/agroforestry treatments; three maize plots with a tree line in the middle of *Grevillea robusta*, *Cassia spectabilis* (syn. *Senna spectabilis*) and *Calliandra calothyrsus* and a sole maize treatment without a tree line. The plots were split into one half with P-application (500 kg ha⁻¹ applied as TSP in 1997) and the other half without P-application.

Table 1. Bulk soil characteristics of the field trials' topsoils. Organic C was determined by wet oxidation with heated sulfuric-acid dichromate followed by colorimetric determination of Cr³⁺ (Anderson and Ingram, 1989). Exchangeable Ca, Mg, and acidity were determined by extraction with 1 M KCl. Extractable P and Exchangeable K were determined by extraction with 0.5 M NaHCO₃ + 0.01 M EDTA (pH 8.5). Sequentially extracted P-fractions, at gradually increasing pH (resin-P at bulk soil pH=5.5, bicarb. pH=8.5, hydroxide pH=13.5), were done according to the method of Tiessen and Moir (1993).

	Trial 1	Trial 2
pH	5.5	5.6
Exch. acidity (mmol _c kg ⁻¹)	1.0	1.0
Exch. K (mmol _c kg ⁻¹)	2.0	1.5
Exch. Mg (mmol _c kg ⁻¹)	19	20
Exch. Ca (mmol _c kg ⁻¹)	59	45
Olson-P (mg kg ⁻¹)	1.0	1.2
Resin-P at pH-5.5 (mg kg ⁻¹)	2.35	3.56
Bicarb.Pi at pH 8.5 (mg kg ⁻¹)	4.92	4.34
Bicarb.Po at pH 8.5 (mg kg ⁻¹)	23.9	22.1
NaOH Pi at pH-13.5 (mg kg ⁻¹)	75.8	71.5
NaOH Po at pH-13.5 (mg kg ⁻¹)	213	178
C _{org} (g kg ⁻¹)	17	15
Clay (%)	50	58
Sand (%)	20	15.5
Silt (%)	30	26.5

The plot size was 20 m x 15 m with the tree-lines in the middle of the 15 m side over the whole 20 m length, and a spacing within the tree lines of 0.3 m for *Cassia* and *Calliandra* (which were pruned to just above the soil-surface at the start of each cropping season, forming a shrub-hedge) and 1 m for *Grevillea* (grown to produce poles). Trees were planted in 1993. The treatments discussed in this chapter are *Cassia spectabilis* –P and +P.

Trial 2 was a 5x2 factorial design with four replicates. The treatments were a complete factorial combination of two phosphorus levels; one with P (250 kg.ha⁻¹ at the start of the experiment in April 1997 and an extra dose of 50 kg.ha⁻¹ in April 2000) and one without P, and five crop/agroforestry treatments; four maize plots with a tree line in the middle of *Cedrella serrata*, *Grevillea robusta*, *Eucalyptus grandis* and *Markhamia lutea* and a sole maize treatment without a tree-line. The plot size was 13.5 m x 15 m with the tree lines in the middle of the 15 m side over the whole 13.5 m length. Trees were planted in 1997.

The treatments discussed in this chapter are sole maize –P and +P, *Grevillea robusta* –P and +P, *Cedrella serrata* –P and +P and *Eucalyptus grandis* –P and +P.

Rhizosphere soil of maize and tree line species was sampled in the middle of the wet season (first half of May 2000). Topsoil around the base of the trees was loosened using a hoe, roots were pulled out, and shaken gently to remove loosely adhering soil. Soil that adhered to the roots (rhizosphere soil) was removed by further shaking. Rhizosphere soil was collected in a plastic bag and stored in a cool-box with ice-bottles for transportation to the laboratory. Samples were then stored in a freezer at –18°C until extraction. Rhizosphere soil was collected in all four replicates of the specified treatments in the two trials, giving four samples for each species-P combination. Two replicates of bulk soil were also collected from both trials, by combining about 10 random samples from sole maize –P plots across the site.

All rhizosphere and bulk soil samples of the field trials were analyzed for acid phosphatase activity, organic anions and P-fractions.

Barrel-trial

Polythene barrels of about 50 L capacity were packed at a bulk density of about 1.15 kg L⁻¹ using top-soil (0-20 cm depth) taken from cover-crop area (no fertilizer applied, far from tree lines) of field trial 2. The barrels were placed in full sunlight outside the research station at Maseno (Equator, Longitude 34°35 East, Altitude 1550m), and were subject to normal weather conditions of the Western Kenyan highlands. All barrels had a black-polythene skirt to avoid growth of algae on the inner sides of the pots.

One seedling of each perennial was grown (from February 1998 to August 2000) together with three maize plants during crop-growing seasons, resulting in the following treatments; i) *Grevillea*

robusta + maize , ii) *Cassia spectabilis* + maize and iii) *Tithonia diversifolia* + maize. A fourth treatment consisted of four maize plants only. Each treatment was replicated four times. The species chosen are commonly used in agroforestry-technologies. Between the growing seasons of maize (March-June 1998, Dec. 1998 -Feb 1999, April-June 1999 and August-November 1999), the perennials grew alone in the pots, and the sole maize pots were kept bare. Trees were pruned at the start of the cropping seasons.

Holes in the side of the barrels allowed for monitoring soil water content using Time Domain Reflectometry (TDR). Soil water-contents were maintained at equal level in all treatments over time by regular watering. Weeds were removed regularly.

At the start of the last two maize-growing seasons, a solution containing 1.66 g K₂SO₄, 1.57 g MgSO₄·7H₂O, 1.65 g CaSO₄·2H₂O, 0.29 g EDTA-Fe-Na-salt, 3.5 g Urea (46% N) and 3.19 ml ETH (micronutrient solution) was added to all barrels. This was calculated to be the total amount of nutrients (except P) needed for a whole growing season of maize at the level of biomass measured at harvest of the plants (about halfway the vegetative growth).

Rhizosphere soil from the pot trial was collected in June 1999 in the manner described for the field trials. Rhizosphere soils were analyzed for organic anions only.

Oxalate and citrate in field soil; anion recovery over time and effect on extractable P

Soils were collected from Trial 2 (0-20 cm depth), outside experimental plots and without fertilizer addition, as described in Table 1. Soil was air-dried to approximately 16% soil moisture, sieved to < 2 mm, and mixed thoroughly.

Incubation experiment 1

The first experiment examined the effect of different loadings of citrate and oxalate on a series of sequentially extracted P-fractions. Citrate and oxalate were prepared at three concentrations (100 mM, 200 mM, 300 mM), adjusted to pH 5-5.5 using NaOH. Then, 10 mL of either citrate or oxalate solutions were well mixed with each 100 g air-dry soil, giving loadings of 10, 20 and 30 $\mu\text{mol.g}^{-1}$ air-dry-soil and soil water content of 31 g g⁻¹. Amended soils were packed in plastic pots, compacted to field-bulk density and covered by wet foam, which allowed air exchange but prevented the soil from drying out. Pots were placed in the dark at about 25°C for a week. After a week, soils were sub-sampled and stored frozen. Soils were analyzed for P fractions according to the method of Tiessen and Moir (1993) and for modified Olsen-P (ISFEIP, 1972), determined by stirring the soil for 10 mins with 0.5 M NaHCO₃ + 0.01 M EDTA (pH 8.5), color development of supernatant with ascorbic acid and molybdate reagent and subsequent colorimetric determination at 880 nm.

Incubation experiment 2

A second experiment examined the recovery over time of organic anions added to soil. Soils were amended with citrate and oxalate as described above, but only at a concentration of $30 \mu\text{M.g}^{-1}$ air-dry-soil, and incubated as previously described but for a total of four weeks. Soils were sub-sampled half an hour after addition of the organic anion (T0), after one week (T1), after two weeks (T2) and after four weeks (T3). For each sub-sample, all soil was taken out of a pot, mixed, a sub-sample taken and the remainder of the soil put back in the pot, pressed, covered with wet foam and put in the dark at 25°C . Soil sub-samples were frozen at -18°C before extraction for organic anions in water and NaOH as described below.

Analysis of low molecular weight organic anions

Organic anions were extracted from soil by shaking in either water or 0.1M NaOH (Whitehead et al. 1981; Baziramakenga et al. 1995). Frozen soil samples were thawed and 10 g of the moist samples shaken with 10 mL of deionised water for 1.5 h at 250 rec./min. Samples were then centrifuged at 10,000 g for 10 mins and the supernatant filtered through $0.45 \mu\text{m}$ filter. Samples extracted with 1M NaOH, were centrifuged at 15,000 g for 15 mins and the supernatant filtered through Whatman #42 filter papers. The filtrate was acidified to pH 2-3 with 1M H_2SO_4 , and left overnight to precipitate organic matter. Filtrate with precipitated organic matter was centrifuged at 15,000 g for 15 mins and the supernatant filtered through $0.45 \mu\text{m}$ filter. Both water and NaOH extracts were stored frozen.

Organic anions were separated by high performance liquid chromatograph (HPLC), using an acid-specific column (BIO-RAD, AMINEX Ion Exclusion HPX-87H, 300 mm x 7.8 mm I.D) at 45°C , using an isocratic elution of 0.005 M H_2SO_4 as carrier solution at a flow rate of 0.01 mL s^{-1} . Organic anions were detected at 210 nm using a Waters 486 Tunable Absorbance Detector. Standard acids were prepared as individual stock solutions, using Sigma free acids, and then combined to give a diluted working reference standard. Organic anions were identified by comparing retention times of unknowns to pure organic anions and by comparison with an internal standard (succinate). HPLC Analysis were done at the Botany Department of the University of Western Australia / Perth.

Acid phosphatase activity

Acid phosphatase activity (phosphomonoesterase, EC 3.1.3.2) (APA) was analyzed by the method of Tabatabai and Bremner (1969) as modified by Eivazi and Tabatabai (1977). Briefly, soil samples were incubated with *p*-nitrophenyl phosphate (*p*-NPP) as the substrate for enzyme activity for 1 hour. The reaction was terminated with 1M NaOH and absorbance determined spectrophotometrically at 400 nm. Controls without soil were processed in parallel to correct for background coloration. Enzyme activities were expressed as $\mu\text{mol p-NP g}_{\text{soil}}^{-1} \text{ h}^{-1}$.

P fractions in the rhizosphere

Soils were analysed for P fractions by the sequential extraction method of Tiessen and Moir (1993) excluding the last step (extraction by H_2SO_4). Soil-samples are subject to a series of extractions; i) resin-extractable P, ii) bicarbonate ($0.5M \text{ NaHCO}_3$) extractable inorganic-P and organic-P, iii) hydroxide ($0.1M \text{ NaOH}$) extractable inorganic-P and organic-P. After addition of ascorbic acid and molybdate reagent to the extracts, colour developed over one hour and P concentration was determined by spectrophotometer at 880 nm.

Statistical Analysis

The organic anion contents in rhizosphere soils of the barrels-trial were analyzed by ANOVA for an incomplete design without blocks and with three reps for *Cassia* and *Grevillea* and four reps for maize and *Tithonia*.

Phosphatase activity in the rhizosphere soil of the field trials were analysed by ANOVA, using a 5x2 (species x P-level) factorial block-design, with four replicates. Bulk soil phosphatase activity (only 2 replicates) was not included in the analysis.

P-fractions in rhizosphere soil of the field trials were analyzed by ANOVA, using only the 4 –P treatments of trial 2 in a block design with four replicates. Bulk soil was not included in the analysis. P-fractions of rhizosphere soil of *Cassia* are shown separately to be compared with bulk-soil P-fractions from trial 1.

P-fractions in soils incubated with organic anions were also analyzed by ANOVA, with the different levels of anions as different treatments and four replicates each. Because of a skewed distribution in Olsen-P measurements, $\ln(\text{Olsen-P})$ was used for statistical analysis.

Results

Organic anions in rhizosphere soil

The results of organic anion (OA) analysis in the water extracts of rhizosphere soil of the barrel-trial are shown in Table 2. The predominant OA's identified varied among species, as did the amounts extracted. Relatively high concentrations of oxalate ($\sim 3 \mu\text{mol g}^{-1}$ soil) were extracted with water from the rhizosphere of *Cassia*, but oxalate was barely detectable in the other species examined. Citrate concentrations did not differ significantly in rhizosphere soil of *Tithonia*, *Grevillea* and *Cassia* at a level of $0.1\text{-}0.2 \mu\text{mol g}^{-1}$ soil. The high concentration of water extractable citrate in maize rhizosphere soil ($\sim 1.2 \mu\text{mol g}^{-1}$ soil), was not confirmed by any other analysis and may be due to poor separation of the peaks of citrate and maleate in this HPLC analysis. Maleate has a much higher absorbance than citrate, thus high citrate levels may be maleate at much lower concentrations.

Fumarate was identified in all water extracts but was present in low concentrations, with the greatest amounts in the rhizosphere of *Tithonia* ($0.004 \mu\text{mol g}^{-1}$ soil). Lactate and formate were present in nearly all rhizosphere soils (data not shown), but could not be quantified, and the variation in peak size did not seem to be related to plant species. Occasionally peaks of *cis*- and *trans*-aconitate, tartarate, malate and glutarate were found (not shown), but amounts were relatively small and were not consistent among species. HPLC analysis of water and NaOH-extracts of field-trial rhizosphere soil and NaOH extracts of the barrel-trial showed a large peak just before the retention-time of oxalate. This high noise in HPLC analysis was probably caused by inorganic anions in field-soils like nitrate, sulphate and phosphate (Grierson, 1992), and prevented identification and quantification of peaks most extracts.

Species	n	Citrate	Oxalate	Fumarate
Cassia	3	0.12	2.96	<0.001
Grevillea	3	0.11	0.04	<0.001
Maize	4	1.17	0.00	<0.001
Tithonia	4	0.23	0.01	0.004
sed n3-n3		0.220	0.170	0.0013
sed n3-n4		0.206	0.159	0.0013
sed n4-n4		0.191	0.147	0.0012

Table 2 Organic anions in water-extracts of rhizosphere soil of barrel-trial ($\mu\text{mol g}_{\text{soil}}^{-1}$). Other organic anions detected irregularly at conc. < 0.001 (only tartarate and glutarate at concentrations up to 0.05), malate(1), tartarate (3), *cis*-aconitate (1), *trans*-aconitate (5), glutarate (3), lactate (13) and fumarate (11), within brackets are the number of samples in which the organic anion was measured, not consistently for one species, n: number of replicates.

Table 3 Organic anions peaks detected in HPLC-analysis of NaOH-extracts of rhizosphere soil from field-trials. n = total number of replicates, rel.ret.time = relative retention time to succinate spike, no. of peaks = the number of extracts in which the peak is found at the particular size no. of peaks = the number of extracts in which the peak is found at the particular size, sizes: 1=small, 2 intermediate, 3 large.

Species	P	n	Rel.ret.time	Organic anion	no.of peaks size 1	no.of peaks size 2	no.of peaks size 3	other
Cassia	-P	4	0.543-0.546	Oxalate	1	-	3	
Cassia	+P	4	0.542-0.547	Oxalate	1	-	3	
Grevillea	-P	4	0.884-0.898	Tr. Aconitate	3	1	-	
Grevillea	+P	4	0.886-0.895	Tr. Aconitate	2	2	-	*
Eucalyptus	-P	4	-	-	-	-	-	
Eucalyptus	+P	4	0.892	Tr. Aconitate	1	-	-	
Cedrella	-P	4	0.890-0.894	Tr. Aconitate	2	-	-	**
Cedrella	+P	4	0.885-0.895	Tr. Aconitate	2	-	-	
Maize	-P	4	0.887-0.896	Tr. Aconitate	4	-	-	
Maize	+P	4	0.883-0.894	Tr. Aconitate	4	-	-	
bulk soil	-P	2	-	-	-	-	-	
bulk soil	+P	2	-	-	-	-	-	

* in 1 extract 1 peak size 1 at rel.ret.time 0.601

** in 1 extract 1 peak size 1 at rel.ret.time 0.761

Only in the NaOH-extracts of field rhizosphere soil, some of the larger side-peaks could be distinguished and qualitatively separated in three size groups (table 3). *Cassia* extracts had a relatively large side-peak at the retention time of oxalate, thus confirming results of the barrel-trial rhizosphere-soil. The high citrate levels of maize were not confirmed. Analysis of rhizosphere soil of *Grevillea* and maize showed small side peaks at the relative retention time of trans-aconitate. The small size of these peaks and the high absorbance of trans-aconitate on HPLC, suggests that concentrations were likely >>10 times lower than the observed peaks of oxalate in *Cassia* rhizosphere soil. Trans-aconitate is a breakdown product of citrate, and may therefore be an indicator of citrate exudation.

Table 4. Acid phosphatase activity measurements in rhizosphere of trees and maize of the field-trials. phosphatase activity ($\mu\text{mol p-NPP g}^{-1} \text{ h}^{-1}$).

Species	mean of +P and -P	+P	-P
Cassia	475	506	443
Cedrella	464	455	472
Eucalyptus	645	577	713
Grevillea	1370	1398	1342
Maize	417	422	413
s.e.d.	50.0	70.7	
bulk soil (mean of 2 mixed samples)		288	

Phosphatase activity in rhizosphere soil

Phosphatase activity of rhizosphere and bulk soil of the field trials is shown in table 4.

All soils, including bulk soil showed acid phosphatase activity. Compared with bulk soil, phosphatase activity was about 1.5 times higher in rhizosphere soil of maize, *Cassia* and *Cedrella*, over 2 times higher in rhizosphere soil of *Eucalyptus* and even 5 times higher in rhizosphere soil of *Grevillea*. The differences between these three levels were highly significant. There were no significant differences in phosphatase activity of rhizosphere soil between +P and –P treatments within one species. This is contrary to the literature in which low-P treatments showed generally higher phosphatase activity (Mc Lachlan, 1980; Tadano and Sakai, 1991; Tadano et al. 1993; Gilbert et al. 1999). In our field situation the original fertilizer-P was probably adsorbed and immobilized quickly, thus decreasing soil solution-P and causing a root response of increased phosphatase activity even in the fertilized plots.

Sequential-P fractions in rhizosphere soil

The results of sequential-P analysis of rhizosphere soil in the –P treatments of the field trials are shown in table 5. In general, bicarbonate-P (organic and inorganic) was lower and hydroxide inorganic P was higher in bulk soil than in the rhizosphere soils. The resin-P and hydroxide-organic P were in the same range in bulk and rhizosphere soil. Resin-P values were lowest in rhizosphere soil of Maize and highest in rhizosphere soil of Eucalyptus. Differences between the treatments were not statistically significant except for the Maize-Eucalyptus difference.

Table 5. Sequential P measurements (mg kg⁻¹) in rhizosphere of trees and maize in the topsoil of the field trials, Pi: inorganic P, Po: organic P.

	Resin-P	NaHCO ₃ -Pi	NaHCO ₃ -Po	NaOH-Pi	NaOH-Po	tot.extr.P
trial 1						
Cassia	3.62	5.52	34.6	54.8	202	301
bulk soil	2.35	4.92	23.9	75.8	213	320
trial 2						
Cedrella	3.94	5.40	30.2	53.1	176	269
Eucalyptus	4.69	5.91	29.3	51.5	170	262
Grevillea	3.44	8.20	26.9	64.3	154	256
Maize	3.02	5.16	27.1	50.3	154	239
s.e.d.	0.835	0.468	1.55	3.85	6.2	9.5
bulk soil	3.56	4.34	22.1	71.5	178	280

Bicarbonate extractable inorganic P ($\text{NaHCO}_3\text{-Pi}$) was significantly higher in *Grevillea* rhizosphere soil compared to the other species' rhizosphere soil and bulk-soil. Maize rhizosphere $\text{NaHCO}_3\text{-Pi}$ was lower than in *Cassia*, *Cedrella* and *Eucalyptus* rhizosphere soil, although not significantly. Bicarbonate extractable organic P ($\text{NaHCO}_3\text{-Po}$) seemed to be lower in *Grevillea* and maize rhizosphere soil than in *Eucalyptus*, *Cedrella* and *Cassia* rhizosphere soil, but again the difference between these two groups was not significant.

Sodium-hydroxide extractable inorganic P (NaOH-Pi) was significantly higher in *Grevillea* rhizosphere soil than in rhizosphere soil of the other species and bulk soil. Sodium-hydroxide extractable organic P (NaOH-Po) was significantly lower in *Grevillea* and maize rhizosphere soil than in *Eucalyptus*, *Cedrella* and *Cassia* rhizosphere soil.

Total extractable P of these fractions seemed lower in maize rhizosphere soil than in the other species' rhizosphere soil, but only the difference with bulk-soil was significant.

Table 6. P-measurements (mg kg^{-1}) after 1 week incubation of 3 levels of citrate loading in field bulk-soil (incubation experiment 1)

	Olsen-P	ln(Olsen P)	resin-P	$\text{NaHCO}_3\text{-Pi}$	$\text{NaHCO}_3\text{-Po}$	NaOH-Pi	NaOH-Po	HCL-P
control	2.82	1.02	1.59	3.66	19.5	45.1	137	2.91
cit10	3.34	1.19	1.77	3.33	18.3	41.6	140	2.52
cit20	4.60	1.48	2.02	3.09	15.6	44.4	145	2.69
cit30	6.60	1.79	3.84	2.88	14.4	46.1	142	2.53
sed		0.211	0.475	0.367	1.42	1.63	5.4	0.629

Incubation experiments

In incubation experiment 1, citrate was added to soil at different concentrations, and incubated for a week. The soils were analyzed for available P, as shown in table 6. Olsen-P and resin-P increased with increasing citrate loading. The highest citrate loading ($30 \mu\text{mol g}^{-1}$ soil) yielded a P-Olsen and a resin-P value, which were both more than twice that of the control. Significant differences in Olsen-P values occurred when citrate loading of treatments differed $\geq 20 \mu\text{mol g}^{-1}$ soil. In resin-P, the only significant differences were between the control and the treatment with $30 \mu\text{mol g}^{-1}$ soil. The bicarbonate extracted fractions decreased with increased citrate loading, while citrate loading did not seem to affect NaOH extractable fractions significantly.

The incubation experiments of oxalate went wrong, likely due to precipitation of Na-oxalate.

In incubation experiment 2, citrate breakdown was examined, as shown in figure 1. The water-extractable citrate as measured by HPLC decreased exponentially over time (figure 1). Even half an hour after adding citrate at a concentration of $30 \mu\text{mol g}^{-1}$ air dry soil, only $0.3 \mu\text{mol g}^{-1}$ moist soil was recovered by the water-extraction and HPLC analysis.

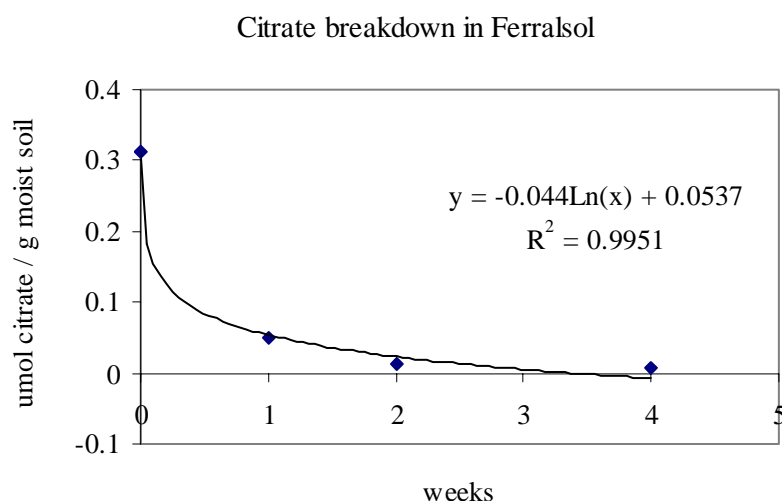


Figure 1. Recovered citrate concentration over time after $30 \mu\text{mol g}^{-1}$ soil addition at $t=0$ (incubation experiment 2)

Discussion

Organic anions in rhizosphere soil and their relation with sequential-P-fractions

Phosphorus mobilization as a result of organic anion exudation might be shown by a shift from P in the less mobile fractions towards the more mobile fractions. A shift from the carbonate extractable fractions towards the resin-P seemed to occur after one-week incubation of citrate in bulk soil (Table 6). A shift from NaOH to NaHCO_3 P-fractions seemed to occur in all rhizosphere soils as compared with bulk soil (Table 5). However, there was no clear relation between type and concentration of organic anions as measured in rhizosphere soil of *Cassia*, *Grevillea* and maize (Table 2 and 3) and any of the sequential-P fractions (Table 5), i.e. the high oxalate levels measured in rhizosphere soil of *Cassia* did not result in a significant increase in the P-fractions of *Cassia* rhizosphere soil.

The lack of differences in sequential P-fractions of different rhizosphere soils (species) may be due to two reasons. The first reason is, that the P-analysis methods do not reflect the effect of anions on P-availability. Addition of $30 \mu\text{mol citrate g}^{-1}$ soil, incubated for a week, more than doubled the available-P as measured by Olsen-extraction or resin-P. The effect of citrate loading on other sequential-P-indicators was negative (NaHCO_3 -P) or absent (NaOH-P). This suggests a shift from

bicarbonate fractions to resin-P. Increases in P as a result of organic anion ligand exchange is only visible in the resin-P fraction and not in the bicarbonate or hydroxide extractable P-fractions. This is very likely due to the high pH of the latter extractions (NaHCO_3 at pH 8.5 and NaOH at pH 13), because citrate, oxalate or polygalacturonate ligand exchange effects on P-availability cease at $\text{pH} > 7$ (Nagarajah et al. 1970; Violante et al. 1991; Geelhoed et al. 1998). Thus, out of the tested P-analysis methods, only Olsen-P⁷ and resin-P are likely able to detect any effect of organic-anions on P-availability in our soil. An implication of the negative interaction between high-pH and organic-anion effect (Nagarajah et al. 1970; Violante et al. 1991; Geelhoed et al. 1998) is that, if pH-increases and organic anion exudation happen along the same roots, high pH may minimize the ligand exchange effect of organic anions. This necessitates investigation of the spatial and temporal distribution of different rhizosphere effects in the root system.

The second reason for a lack of differences in the resin-P fraction of different rhizosphere soils (species), may be that P fractions in the rhizosphere soil reflect the net result of P-mobilization and P-uptake (Gerke et al. 1994). If high levels of organic anions in the rhizosphere mobilize phosphate, but this mobilized-P is taken-up by the plant itself, the rhizosphere P will not be different from bulk-soil levels. Only if in the rhizosphere more P is mobilized than taken up, rhizosphere soil may show higher levels of measured mobile-P (resin-P) fractions than bulk soil, and opposite, if P-uptake is higher than P-mobilization, measured resin-P in rhizosphere soil may be lower than in bulk soil. The absence of a difference in resin-P in the rhizosphere of the different species, and especially *Cassia* with its high oxalate concentration, suggests that P-mobilization caused by organic anions was more or less equal to P-uptake.

A balance between P-mobilization and P-uptake may be caused by a) adjusting P-mobilization to P-demand or b) adjusting plant growth and P-demand to P-supply including limited P-mobilization. Adjusting P-mobilization to demand is likely to occur in species, which are hardly affected by P-fertilization, in our case *Cassia* (M. Gunga, personal communication), *Grevillea* and *Cedrella* (Chapter 7). Adjusting plant-growth and P-demand to P-supply including limited P-mobilization has likely occurred in species which show significant growth-rate increases upon P-fertilization like maize and *Eucalyptus* (Chapter 7). Species generally reduce demand for nutrients by low metabolic demand (Grierson and Adams, 1999).

The recovery of citrate over time showed that only about $0.3 \mu\text{mol citrate g}^{-1}$ moist soil of citrate was recovered by water extraction and HPLC analysis in soil sampled half an hour after addition of

⁷ Modified Olsen-P uses also NaHCO_3 , but stirring with this extractant is only 10 minutes. This short time probably prevents that the soil-solution mix shows the same pH-effect on citrate-P exchange as the NaHCO_3 extraction in the sequential analysis, with an extraction period of a whole night.

30 $\mu\text{mol citrate g}^{-1}$ air dry soil. The other 99% of the citrate was likely sorbed on soil colloids broken down by microbes or not recovered and detected in the analysis for other reasons. Breakdown by microbes was likely a minor part, because Jones et al. (1996) found that breakdown of malate by microbes at 25°C was only about 10% after half an hour.

In the calculations below we assume that oxalate behaved similarly to citrate in our soil and that recovery of organic anions was primarily caused by adsorption and not by microbial break-down. We also assumed that oxalate was sorbed 10 times less⁸ at loadings $> 200 \mu\text{mol g}_{\text{soil}}^{-1}$. Using these assumptions, the measured levels of 3 $\mu\text{mol oxalate g}^{-1}$ soil in rhizosphere soil of *Cassia* are derived from oxalate exudations of about 12 $\mu\text{mol g}_{\text{soil}}^{-1} \text{ d}^{-1}$ or, translated to exudation per unit root length (for a 1.5 mm \varnothing root with 3 mm \varnothing rhizosphere and soil-bulk density of 1.15), an exudation of 73 $\mu\text{mol m}_{\text{root}}^{-1} \text{ d}^{-1}$. These estimates are very high compared with the 1.3 $\mu\text{mol citrate+malate m}_{\text{root}}^{-1} \text{ d}^{-1}$ exuded by P-starved rape (Hoffland et al. 1989), the 0.008 $\mu\text{mol oxalate g}_{\text{soil}}^{-1} \text{ d}^{-1}$ calculated for *Pinus radiata* by Fox and Comerford (1992), or the 0.11 $\mu\text{mol citrate+malate m}_{\text{root}}^{-1} \text{ d}^{-1}$ of maize (Jones and Darrah, 1995). The last data were per unit root-weight so we used a maize-root weight-length conversion factor of 66.8 m g^{-1} derived from our own maize root data average of 256 samples. Only the citrate concentration in the rhizosphere soil of Lupin proteoid root clusters seemed larger with 47.7 $\mu\text{mol g}^{-1}$ soil (Dinkelaker et al. 1989) but this is a total after unknown period of exudation and a whole root-cluster, containing many centimeters of root. Therefore, *Cassia* seemed to exude very high amounts of oxalate per unit root length compared with these studies.

Loading of 30 $\mu\text{mol citrate g}^{-1}$ soil more than doubled the resin-P (table 6). Because this loading is much lower than the above calculated oxalate loading around *Cassia* roots, the increase in resin-P in *Cassia* rhizosphere soil has likely been much higher, even if oxalate ligand exchange with phosphate is less effective, than citrate (because oxalate has two and citrate has three carboxyl-groups). Citrate is twice as effective as oxalate in desorption of P from goethite (Nagarajah et al. 1970; Parfitt, 1979) and gibbsite (Nagarajah et al., 1970), but 1.5 times less effective in desorption of P from kaolinite. This suggests that *Cassia* is an effective mobilizer of P from P-fixing soils.

Many authors have found high malate (Hoffland, 1989; Jones and Darrah, 1995) and citrate levels (Gardner et al. 1982; Dinkelaker et al. 1989; Hoffland et al. 1989; Grierson, 1992) in root-exudates. Exudation of oxalate would be much cheaper to the plant than exudation of citrate, if measured per carboxyl-group, because oxalate needs only two C atoms in a mol with two carboxyl groups, while

⁸ Using the oxalate adsorption isotherm on goethite of Parfitt et al (1977), assuming zone 1 not to occur in our soil because of the higher pH, and with a 10 x lower C_s/C_l in zone 3 (loadings $> 200 \mu\text{mol g}_{\text{soil}}^{-1}$) as compared to zone 2 (loadings from 0-200 $\mu\text{mol g}_{\text{soil}}^{-1}$).

citrate needs six C atoms in a mol with three carboxyl groups. Thus, if citrate is less than three times as efficient as oxalate in P-desorption, it would be cheaper, measured in C-cost for a plant to exude oxalate than citrate.

Phosphatase in the rhizosphere and its relation with sequential-P fractions

In rhizosphere soil of *Grevillea* the high phosphatase activity coincided with an increase in inorganic-P at the expense of organic-P (table 4 and 5), in both bicarbonate and hydroxide extractions. This may be explained by an increase in hydrolysis of organic-P into inorganic-P catalyzed by *Grevillea*'s high phosphatase activity. There seemed to be a similar but smaller and not significant shift from organic-P to inorganic-P in the bicarbonate extraction of *Eucalyptus* rhizosphere soil, probably caused by the slightly higher phosphatase activity in *Eucalyptus* rhizosphere, compared with the maize, *Cassia* and *Cedrella*.

However, even lower levels of phosphatase activity, like in maize rhizosphere soil, seemed sufficient to hydrolyze organic-P available in the rhizosphere, because organic-P contents of bicarbonate and hydroxide extractions of rhizosphere soil of maize are as low as in rhizosphere soil of *Grevillea*. Unlike in *Grevillea* rhizosphere soil, the lower level of bicarbonate and hydroxide organic P in rhizosphere soil of maize are not accompanied by an increase in bicarbonate and hydroxide inorganic P. This suggests, that all roots were able to hydrolyze organic-P, even at the relatively low phosphatase activity level of maize. *Grevillea* hydrolyzed significantly more organic-P than it needed, resulting in an increase in bicarbonate and hydroxide inorganic P. If indeed all plants, including maize were able to use organic-P forms, high phosphatase activity of tree-root rhizosphere is likely to have a minor effect on maize P-nutrition. Boero and Thien (1979) and Findenegg and Nelemans (1993) mentioned that organic-P mobility and thus substrate availability limits P-uptake more than phosphatase activity and P-hydrolysis. This seems to happen in our soils too.

We conclude that within the rhizosphere of the tree roots in our experiments, P-fractions were not significantly increased or decreased compared to bulk-soil, except that high phosphatase activity shifted some organic P to inorganic P. The absence of increases in P-fractions in rhizosphere soil indicates that P-mobilization mechanisms are likely to favor mainly the roots, which exert these activities, and have no residual P-effect for crops later on. Even so, this self-supply of unavailable P may minimize the use of directly available P and limit direct competition for available P between the trees and maize. Moreover, if crop-roots occupy rhizosphere of tree-roots at the time the trees are mobilizing P, the crop root may get a share of the mobilized P. However, conjunction of organic anion exudation and possibly phosphatase activity with pH changes likely affects the effect on P-mobilization.

**Can trees mobilize phosphorus for crops? II. Synlocation of roots and
conjunction of chemical changes in the rhizosphere**

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Submitted to: Plant and Soil

Can trees mobilize phosphorus for crops? II. Synlocation of roots and conjunction of chemical changes in the rhizosphere.

Simône Radersma and Pauline Grierson

Abstract

Phosphate-mobilization in the rhizosphere of trees adapted to low P-availability may increase P-acquisition by crops in a simultaneous agroforestry system on a Ferralsol. The total transfer depends on temporal and spatial distribution of tree rhizosphere effects and crop roots.

Our objectives were i) to examine spatial and temporal distribution of different P-mobilization mechanisms in the rhizosphere of a range of tree/shrub species and maize (*Zea mays* L.) and ii) to examine the growth of crop-roots into the tree-root rhizosphere (root “synlocation”) of tree and crop roots and therewith the possibility that the crop uses P mobilized by the tree roots.

We examined the spatial distribution of roots, pH-changes, acid phosphatase activity and mobilization of iron-phosphates over time using soil-root-wall images and imprints. Imprints were made using pH-indicator gels, gels with iron-phosphate precipitate and filter papers impregnated with α -naphthyl-phosphate and diazonium salt Fast Red TR.

Local increases in pH occurred over a period of 21-56 days along a fraction of fine roots (1.5-2.5mm Ø) of *Cassia spectabilis* (syn. *Senna spectabilis*). Similar pH increases occurred around cluster-roots of *Grevillea robusta* over 5-30 days.

Black imprints developed in the iron-phosphate precipitate gels preceded the pH increases. Acid phosphatase activity was observed on a much larger fraction (60-70%) of the total fine root-length at any point in time.

Maize-*Cassia* root synlocation was nearly twice that expected of root-overlaps at regular-root-distribution, because maize roots grow regularly along the same channels as the tree roots.

We conclude that, *Cassia* is more likely to favor maize-P-uptake than *Grevillea*, given the longer period of root-induced changes in the rhizosphere, the higher level of synlocation of roots and the relatively lower sink strength of tree roots compared to maize roots in the rhizosphere zone of *Cassia* as compared to *Grevillea*.

Introduction

In highly populated areas of Western Kenya, crop-yields are insufficient to cover the needs of the farm families and farmers seek to supplement income by planting trees to sell for firewood, building materials or fruits (Shepherd et al, 1992). However, trees often compete with crops (Ong, 1995).

Effects of trees on crops depend on how trees affect growth resources (nutrients, water) and especially the main limiting growth-resource of the environment (Kho, 2000). In large parts of western Kenya, crop growth is primarily limited by low phosphate availability of Ferralsols. This is due to adsorption and precipitation reactions with sesquioxides in Ferralsols (Sanchez, 1976; Hue, 1991), as well as depletion of inorganic P due to continuous farming. Application of sufficient fertilizers and manure is generally not feasible for the farmers.

As P is the main resource limiting crop growth, impacts of trees on growth of crops are most likely to occur via tree-effects on P-availability to crop-roots.

Strong competition takes place if the tree uses much water, which results in a soil-drying-induced P-deficiency on the crop. However, near a *Cassia* tree line, where soil drying did not take place, maize yields were increased by about 15%, without any organic matter applications (Chapter 8). We hypothesized that, in this situation without mulch/litter addition, trees have positive effects on crop growth via mechanisms that enhanced P-availability and acquisition.

Previously, we measured organic anions (low molecular weight carboxylic acids), acid phosphatase activity and P-fractions in rhizosphere soil of field grown tree species and maize (Chapter 4). We concluded that 1) high concentrations organic anions in soil did not increase P-fractions at high pH because ligand exchange of organic anions with phosphate occurred only when rhizosphere pH was not simultaneously increased 2) high concentrations of oxalate in the rhizosphere of *Cassia spectabilis* did not increase the most available P fraction (resin-P), possibly because any P mobilized was balanced by P-uptake, and 3) relatively low acid phosphatase activity in the rhizosphere of maize was sufficient to hydrolyze any organic P reaching the root surface, i.e. the availability of organic P at the root surface is probably more limiting than hydrolysis of organic P.

Biochemical modifications of the rhizosphere have been studied in pot- and solution-cultures. Such studies have provided a valuable basic understanding of the type of changes in the rhizosphere that occur, and how different factors such as increases/decreases in pH may affect P-availability. However, the use of artificial media and growth circumstances and the lack of emphasis on simultaneous processes (e.g. pH changes in conjunction with phosphatase activity) infer that results have only limited relevance to field-situations.

Increase or decrease of rhizosphere pH are a result of imbalances in anion/cation uptake by roots (Barber, 1971; Keptert et al, 1979; Nye, 1984; Marschner et al, 1986; Haynes, 1990; Hinsinger, 2001), active exudation of H^+ or HCO_3^- against charge imbalances (Haynes, 1990), and H^+ exudation accompanying organic anions. H^+ exudation acidifies the soil, or H^+ can be used as reductant to Mn^{4+} and Fe^{3+} , thus alkalinizing the soil (Parfitt 1979; Gardner et al, 1982a, 1983; Marschner et al, 1986, 1987; Dinkelaker et al, 1989; Jones and Darrah 1994). Respiration has little effect on pH in aerated soil because CO_2 diffuses quickly away from the roots (Marschner, 1995). Changes in pH in the rhizosphere can affect P-availability directly. In soils with a high content of iron/aluminum (hydr)oxides, such as Ferralsols, P-availability generally increases upon a rise in pH (Hingston et al, 1967, 1972; Anderson et al, 1974; Parfitt, 1980; Tiessen and Moir, 1993). A pH-increase up to above 7 will therefore usually cause P-desorption. However, at high aluminum content of the soil, increasing pH may increase P-sorption (Darrah, 1993; Gerke, 1995).

Changes in pH in the rhizosphere may interact with other factors such as exudation of organic acids or phosphatase enzymes. For example, addition of citrate (Geelhoed et al, 1998), oxalate (Violante et al, 1991) or polygalacturonate (Nagarajah et al, 1970) at pH < 7 desorbed phosphate from iron/aluminum (hydr)oxides considerably, but adding these organic anions at higher pH had no effect. Acid phosphatase activity is optimal in pH range 4-6 (Ridge and Rovira, 1971; Ozawa et al, 1995; Mc Lachlan, 1980; Dodd et al, 1987; Pant et al, 1994). On the other hand a positive interaction possibility of organic anion exudation (desorbing Po and increasing Po availability at the root surface) and acid phosphatase activity may occur.

Spatial and temporal differentiation or overlap of pH-changes, organic anion exudation and acid phosphatase activity in the rhizosphere, may theoretically cause synergy of positively interacting effects, fade-out of negatively interacting effects or temporal/spatial separation of effects. Moreover, localized exudation of e.g. organic anions causes highly concentrated effects on P-availability along specific parts of the root system. This concentration may be more effective for P-mobilization than if activity was distributed evenly among all root-surfaces, possibly because adsorption on soil colloids, breakdown of anions or microbial use of phosphate are minimized (Grierson and Attiwill, 1989; Marschner et al, 1986, 1991a; Darrah, 1991a; Jones and Darrah, 1994; Seeling and Jungk, 1996).

Changes in pH occur along most roots if caused by imbalance of cation/anion uptake caused by NO_3^- , but is more localized where H^+ accompanies anion exudation (Marschner et al, 1986; Hoffland et al, 1989; Jaillard et al, 1996). Organic anion exudation is greatest in apical root zones up to 5 cm from the root-tip and at sites of lateral branch formation (Jones et al, 1994; Jones and Darrah, 1995). Phosphatase activity is relatively higher in root-tips and lateral initials (Hall and Davie, 1971; Ridge and Rovira, 1971; Duff et al, 1994). Phosphatase activity, organic anion exudation and Fe-reducing capacity is high in cluster-roots (Gardner et al., 1982a, Neumann et al, 1999; Grierson, 1992; Grierson and Comerford, 2000), although this is probably not due to higher exudation per unit root length, but to high root density of the clusters (Grierson, 1992).

In this study our aim was to assess the possibility that rhizosphere effects of tree-roots increased P-acquisition of maize in a field situation. Our first objective was to assess the degree in which tree and crop roots occupy the same rhizosphere, to assess the possibility that maize can take up P mobilized in the rhizosphere of tree-roots, before the tree-roots have taken up all mobilized-P themselves. Because in a field situation positive and negative interactions between different rhizosphere modifications may occur, our second objective was to examine spatial and temporal distribution of pH-changes, organic-anion exudation and phosphatase activity in the rhizosphere and their overlap and separation.

Our experiments were field-based or in barrels carried out under field conditions, with trees and maize growing simultaneously, so that we could investigate multiple effects of tree-root-exudation on a maize crop under realistic conditions.

Materials and Methods

Field trials

Investigations were done in two field trials with tree-lines in the middle of maize (*Zea mays*) fields on deep, P-depleted Ferralsols at Nyabeda, Western Kenya (Latitude 0.08 °N, Longitude 34.24 °E, Altitude 1300 m). The site was sub-humid with an annual rainfall of about 1500 mm, distributed over two main cropping seasons; the long rainy season from March to June/July (~900 mm) and the short rainy season from September to December/January (~600 mm). The experiment was established on level land, which was formerly cropped with maize or left fallow.

Initial topsoil characteristics of the trials are shown in table 1.

Table 1. Bulk soil characteristics of the field trials' topsoils. Organic C was determined by wet oxidation with heated sulfuric-acid dichromate followed by colorimetric determination of Cr^{3+} (Anderson and Ingram, 1989). Exchangeable Ca, Mg, and acidity were determined by extraction with 1 M KCl. Extractable P and Exchangeable K were determined by extraction with 0.5 M NaHCO_3 + 0.01 M EDTA (pH 8.5). Sequentially extracted P-fractions, at gradually increasing pH (resin-P at bulk soil pH=5.5, bicarb. pH=8.5, hydroxide pH=13.5), were done according to the method of Tiessen and Moir (1993).

	Trial 1	Trial 2
pH	5.5	5.6
Exch. acidity ($\text{mmol}_c \text{ kg}^{-1}$)	1.0	1.0
Exch. K ($\text{mmol}_c \text{ kg}^{-1}$)	2.0	1.5
Exch. Mg ($\text{mmol}_c \text{ kg}^{-1}$)	19	20
Exch. Ca ($\text{mmol}_c \text{ kg}^{-1}$)	59	45
Olson-P (mg kg^{-1})	1.0	1.2
Resin-P at pH-5.5 (mg kg^{-1})	2.35	3.56
Bicarb.Pi at pH 8.5 (mg kg^{-1})	4.92	4.34
Bicarb.Po at pH 8.5 (mg kg^{-1})	23.9	22.1
NaOH Pi at pH-13.5 (mg kg^{-1})	75.8	71.5
NaOH Po at pH-13.5 (mg kg^{-1})	213	178
C_{org} (g kg^{-1})	17	15
Clay (%)	50	58
Sand (%)	20	15.5
Silt (%)	30	26.5

Trial 1 was a 4x2 factorial design with split-plots and four replicates. The treatments were four crop/agroforestry treatments; three maize plots with a tree line in the middle of *Grevillea robusta*, *Cassia spectabilis* (syn. *Senna spectabilis*) and *Calliandra calothyrsus* and a sole maize treatment without a tree line. The plots were split into one half with P-application (500 kg ha^{-1} applied as TSP in 1997) and the other half without P-application. The plot size was 20 m x 15 m with the tree-lines in the middle of the 15 m side over the whole 20 m length, and a spacing within the tree lines of 0.3 m for *Cassia* and *Calliandra* (which were pruned to just above the soil-surface at the start of each cropping season, forming a shrub-hedge) and 1 m for *Grevillea* (grown to produce poles). Trees were planted in 1993. The treatment discussed in this paper is *Cassia spectabilis* –P. *C. spectabilis* is a non-N-fixing legume that showed high oxalate levels in its rhizosphere (Chapter 4).

Trial 2 was a 5x2 factorial design with four replicates. The treatments were a complete factorial combination of two phosphorus levels; one with P (250 kg ha^{-1} at the start of the experiment in April 1997 and an extra dose of 50 kg ha^{-1} in April 2000) and one without P, and five crop/agroforestry treatments; four maize plots with a tree line in the middle of *Cedrella serrata*, *Grevillea robusta*, *Eucalyptus grandis* and *Markhamia lutea* and a sole maize treatment without a tree-line. The plot size was 13.5 m x 15 m with the tree lines in the middle of the 15 m side over the whole 13.5 m length. Trees were planted in 1997. The treatments discussed in this paper are *Grevillea robusta* –P, *Cedrella serrata* –P and *Eucalyptus grandis* –P. *G. robusta* is a proteaceae with cluster-roots, showing moderate citrate levels in its rhizosphere. Significant levels of organic anions in rhizosphere of *C. serrata* and *E. grandis* were not found (Chapter 4).

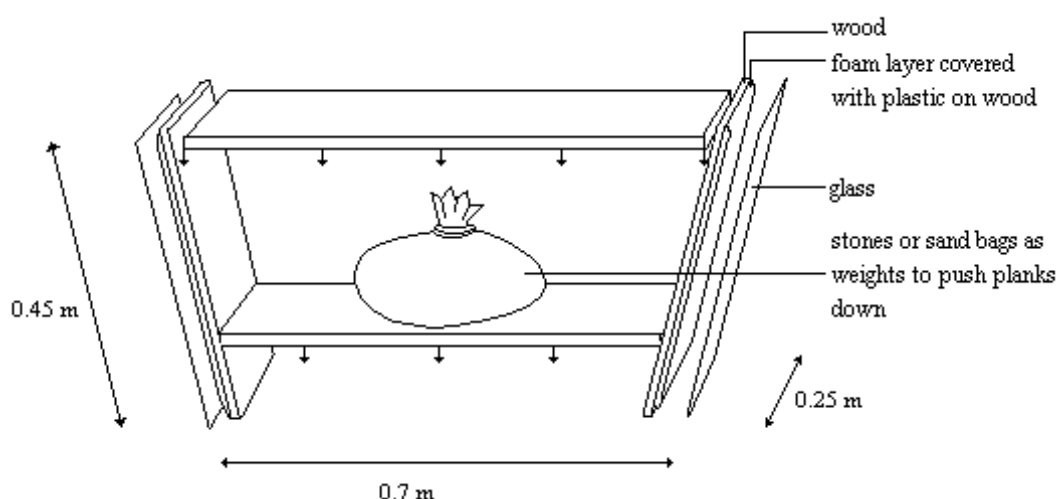


Figure 1. Construction of simple rhizotrons in field-pit with two soil-root walls for observations.

Rhizotrons (figure 1) were installed in soil-pits in the treatments; *Cassia spectabilis* –P (trial 1), *Grevillea robusta* –P, *Cedrella serrata* –P and *Eucalyptus grandis* –P (trial 2). Pits were dug at about 1 m distance from the tree lines, with two opposite steep-sloping flat soil-walls of the pit perpendicular to the tree line. Glass covered with thin polythene sheet (to prevent sticking to the wall) was pressed against the flat steep-sloping soil-walls, which were covered with a layer of water-saturated soil to create a good soil-window contact. Then, wood planks covered with foam and plastic were pressed against the glass. Finally, the horizontal planks were put in and pushed down, using bags filled with soil, pressing the layers of wood-foam and glass firmly against the soil-walls. Once the roots had grown along these soil-root walls, the planks and glass windows were regularly removed, to make gel- and filter-paper prints. The rhizotrons were installed in April 2000, and all prints taken in July-August 2000.

Barrel-trial

Polythene barrels of 50 L were packed with topsoil from field trial 2 (table 1) at bulk density of

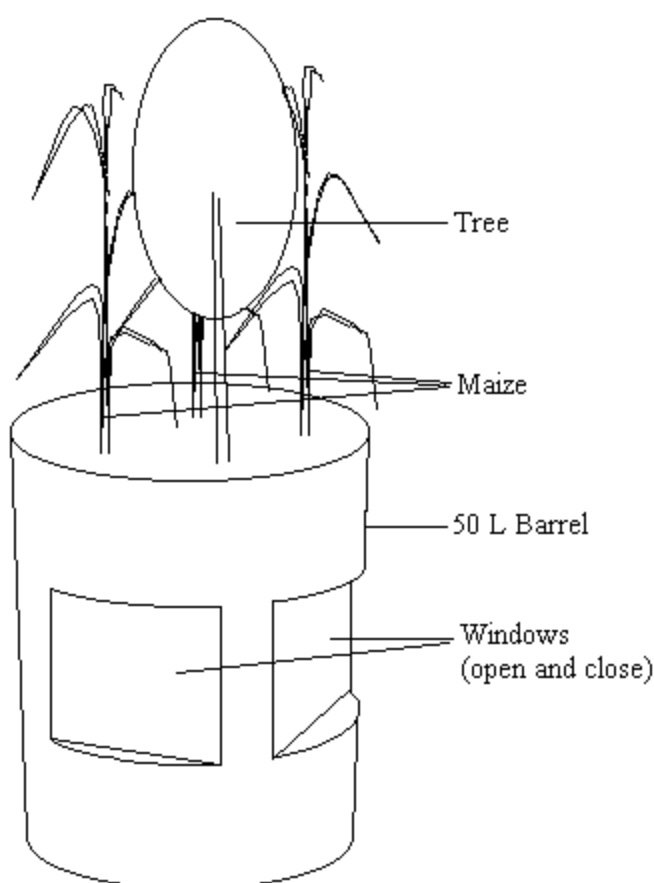


Figure 2. Barrels with windows for root-observations as used in the barrel-trial.

about 1.15 kg L^{-1} . The barrels were placed outside the research station at Maseno (Equator, Longitude $34^{\circ}35'$ East, Altitude 1550m), and were subject to normal weather conditions of the Western Kenyan highlands. All barrels had a black-polythene “skirt” to avoid growth of algae. Trees and maize were grown in the barrels (figure 2) according to the following treatments; i) *Grevillea robusta* (1) + Maize (3), ii) *Cassia spectabilis* (1) + Maize (3), iii) *Tithonia diversifolia* (1) + Maize (3), and sole Maize (4). The number in brackets indicates the number of plants per pot.

Each treatment had four replicates. The species chosen are commonly used in agroforestry-technologies. Between and after the growing seasons (March-June 1998, Dec. 1998 -Feb 1999, April-June 1999 and August-November 1999) the maize was removed from the barrels with trees and the sole maize pots were bare. Trees were pruned at the start of the cropping seasons. Holes in the side of the barrels allowed for monitoring soil water content using Time Domain Reflectometry (TDR). Soil water-contents were maintained at equal level in all treatments over time by regular watering. Weeds were removed regularly. At the start of the last two maize-growing seasons, a solution containing 1.66 g K_2SO_4 , 1.57 g $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$, 1.65 g $\text{CaSO}_4 \cdot 2\text{H}_2\text{O}$, 0.29 g EDTA-Fe-Na-salt, 3.5 g Urea (46% N) and 3.19 ml ETH (micronutrient solution) was added to all barrels. This was calculated to be the total amount of nutrients (except P) needed for a whole growing season of maize at the level of biomass measured at harvest of the plants.

Two windows in the sides of each barrel (figure 2) could be opened by sliding the outer glass window sideways through a rail, and folding the inner plexi-glass window outwards. Between the plexi-glass window and the soil-wall was a thin sheet of black polythene material.

pH prints

Agar gels (10 g kg^{-1}) at soil pH (5-5.5) were prepared as described by Dinkelaker et al. (1993), using bromocresol-green and bromocresol-purple as pH-indicators. For the soil-root walls of the barrels, gels were prepared in petri-dishes (9 cm \varnothing). A circle was cut out of thin plastic sheet, fitting on the bottom of the petri-dish, but with some lips folded upwards to lift the plastic circle with gel out of the dish. For the soil-root walls of the field trials, gels were prepared similarly on plastic trays of approximately 25x35 cm.

After removing the barrel-windows or shutters of the field soil-root-walls, plastic sheets with gels were gently pushed against the soil-root surface for about 0.5 h.

In the barrel-trial, prints with pH-gels were made between June 1999 and January 2000. After initial testing to determine which plant species showed pH changes on what type/age of roots, the duration of pH-changes were investigated by regularly repeating the imprinting on the same roots (*Cassia* once every 7 days, *Grevillea* every 2 days).

In the field trial pH-gel-prints were only used to test which species showed pH changes in the rhizosphere.

The percentage of the root system that showed a pH increase was assessed by measuring (potentially) active root length and total root length on the root wall images of soil root walls of both barrel-trial and field-trial. Root length measurements were made using a map-distance-reader on an enlarged slide projection of the root-wall images.

The width of root and zone of pH-increase around the root was also measured on the enlarged slide projections. Blurred edges of the area of color change corresponding to pH were attributed to diffusion within the gel during the print-period of half an hour and were not included in the estimates of width.

Iron-phosphate precipitate gels

A solution was prepared of 27.0 g. $\text{FeCl}_3\text{H}_2\text{O}$ and 13.6 g. KH_2PO_4 , dissolved separately, mixed and made to 1 L to form a 0.1 M $\text{FeCl}_3\cdot 6\text{H}_2\text{O}$, 0.1 M KH_2PO_4 solution following Blanchar and Frazier (1991). The solution was prepared in a conical flask closed with a stopper to prevent aeration. A precipitate of iron phosphate was formed, by adjusting the solution pH to 5, using 2 M KOH. After continued stirring over night, the pH had decreased to 3.5 and was increased to pH 5 by further additions of KOH. The precipitate was centrifuged, oven dried, and ground into a fine powder. Phosphorus-content of the dried precipitate was 12.8 %, significantly less than the 32 % in pure FePO_4 .

Iron phosphate gels were prepared in petri dishes (9 cm Ø) or on trays, like the pH-gels.

Briefly, 10 g kg^{-1} agar-gel was prepared by boiling until the agar solution was clear and poured as a bottom layer in the petri dish. An upper layer of agar-gel with 10 g kg^{-1} iron-phosphate precipitate was poured on the bottom layer, prepared by stirring the iron- phosphate precipitate after cooling down the agar solution to 50°C. Plastic overhead-sheets within the petri dish or trays were used to be able to take the gel from the dish and bring it on the soil walls, like described for the pH-gels. The iron-phosphate gels were gently pressed against a soil-root wall for 10 days. The soil was kept wet by watering the field, to prevent drying and cracking of the gel. Iron-phosphate prints were made between May and August 2000.

Soil-root wall phosphatase prints

Filter papers for visualizing acid phosphatase activity at the root surface were prepared as described by Dinkelaker and Marschner (1992), but reagents contained a 4 fold higher concentration of all chemicals, necessary in the clayey, sesquioxide-rich soil of our experiments. Filter papers were treated with a mixture of α -naphthyl phosphate as substrate and diazonium salt Fast Red TR as an

indicator. After enzymatic hydrolysis by root exudates, α -naphthol forms a red complex with Fast Red TR. Thus, active roots appear as red prints on the filter papers. Filter papers were gently pressed against the soil-root walls for 1.5 h. Phosphatase prints were made on the soil-root-walls of the field trial in July/August 2000. The percentage of roots that showed phosphatase activity was estimated by measuring active root length and total root length on the root wall images and imprints, as described for pH-gels.

Monitoring root-growth

In the barrel trial, slides were taken of all soil-root-walls every 2-3 weeks between December 1998 and January 2000. Root life-time (including the period that the dead root was still visible but not decomposed) and degree of overlap of maize roots with the rhizosphere of tree roots were only assessed for maize in conjunction with Cassia roots and with Grevillea cluster-roots, being the two tree species showing pH-effect and/or high organic anion exudation.

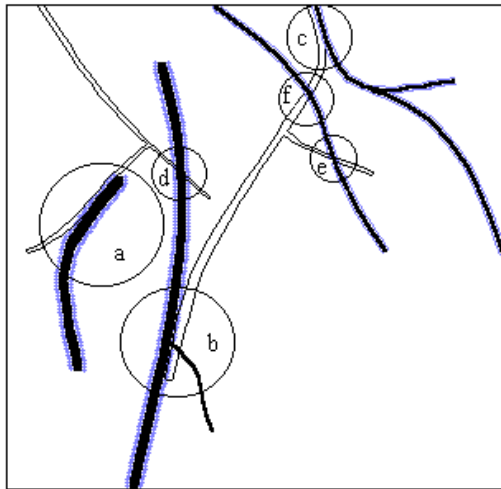
A similar approach to that described for the imprints using enlarged slide projections of soil-root-walls was used to assess the degree of overlap of maize roots with rhizosphere of Cassia (synlocation). The ratio between overlap in reality and overlap at regular root distribution gave the synlocation of each image. One image of all 8 root-soil walls (4 barrels with each 2 windows) of the Cassia was used for this assessment.

Overlap *at regular root distribution* was calculated by measuring total root-surface of maize and total rhizosphere-surface of *Cassia* (root-surface x rhizosphere extension as measured on pH-gels), divided by the total surface of the soil-root-wall, giving the fractions of the surface occupied by maize roots and Cassia rhizosphere. The fraction Cassia rhizosphere x fraction maize root is the expected overlap *at regular root distribution*. This is shown in figure 3.

Overlap of maize roots with Cassia rhizosphere *in reality* was measured by adding up all overlapping surfaces as shown in the circled parts of figure 3.

Measuring the root- and rhizosphere-surfaces was done, by subdividing both root systems (maize and tree) in two root-size classes (fatter and thinner fine roots), with an average diameter. Of each combination of species x diameter class, the total root-length was measured by map-distance-reader and the root surface of maize was calculated as length x width (= diameter if 3-dimensional) and the *rhizosphere*-surface of cassia as length x width x rhizosphere width. With rhizosphere width 1.0 (x root diameter), as measured in the pH-gels. Cassia *root* surface was extracted/excluded from all surface measurements, because maize-roots crossing over or under or laying behind *Cassia* roots belong to the dimension perpendicular to the wall surface and not to the wall-surface itself.

Figure 3. Measurement of root-rhizosphere overlap on root-soil walls to determine synlocation



A. The fraction of the total surface which would be the expected overlap of maize-root surface and cassia rhizosphere surface at regular root distribution is measured and calculated as follows:

- black lines are cassia-roots, divided in thin and thick fine roots. Root surface is calculated as total length x width of each root-class
 - white roots are maize, divided in thin and thick fine roots. Root surface (A_m) is calculated as total length x width of each root-class
 - grey-shading around black roots is cassia-rhizosphere. Rhizosphere surface (A_c) is calculated as $1.0 \times$ cassia-root surface
 - total surface of the window is its length x width minus the surface of cassia roots (A_t)
 - fractions of surface occupied by maize-roots (f_m) and cassia rhizosphere (f_c) are (A_m / A_t) and (A_c / A_t) respectively
- at regular root distribution, the expected overlap would be $f_m \times f_c$

B. The fraction of the total surface which is real overlap of maize-root surface and cassia-rhizosphere-surface is measured by summing up all measured overlaps and dividing them by the total surface as follows:

- a - thin maize root along thick cassia-root, overlap calculated as measured length x width
 - b - thick maize root along fat cassia-root, overlap calculated as measured length x width
 - c - thin maize root along thin cassia-root, overlap calculated as measured length x width
- in a, b and c the width is the smallest of the two factors 1) maize-root diameter or
2) one sided cassia rhizosphere width (= 0.5 cassia root width of that class)

d - crossing of thin maize root and thick cassia root, overlap is measured length of cross x 2-sided rhizosphere width

e - crossing of thin maize root and thin cassia root

f - crossing of thick maize root and thin cassia root

the amount of crossings e + f are counted, overlap is calculated as:

(weighed average width of maize root) x (width of 2-sided thin cassia rhizosphere) x number of crossings

Synlocation = B / A (measured overlap / expected overlap of maize roots and Cassia rhizosphere)

Results

pH changes and iron-phosphate reactions in the rhizosphere.

The first series of pH-gel tests on root-soil-walls of the barrel-trial and the field trial, revealed that all species (*C. spectabilis*, *G. robusta*, *T. diversifolia*, *E. grandis*, *C. serrata* and *Z. mays*) exhibit sometimes small increases in rhizosphere-pH. Regular and large pH-increases were only observed around cluster-roots of *Grevillea* and along the 1.5-2.5 mm Ø fraction of the fine roots of *Cassia* (figure 4). No decreases in rhizosphere pH, were observed for any species in either the barrel or field experiments.

Table 2. Periods of observed pH increases around *Cassia* roots and *Grevillea* cluster-roots (from barrel-trial)

days pH-increase	days between appearance to pH-increase
<i>Grevillea robusta</i>	
23	?
19	?
17	?
12	5
27	?
5	4
6	3
<i>Cassia spectabilis</i>	
56	7-10
21	7-10
14	7-10
14	7-10
56	7-10

The duration of pH increases around *Cassia* roots (table 2) was 2-8 weeks, with large variation among roots and trees (=replicates). Increases in pH began about 7-10 days after appearance of the roots, when the color of the roots changes from yellow to black. *Cassia* roots did not disappear from the windows within the 13 months of regular observations, but some roots observed in April 1997 had disappeared in December 1999, indicating that fine root life plus decomposition is longer than 13 months but shorter than 1³/₄ year.

The duration of pH increases around *Grevillea* cluster-roots (table 2) was 5-27 days, beginning about one week after cluster-root-initiation and lasting after roots had begun to senesce, and their appearance was grey and withered. Cluster roots were white with hairy rootlets for about 10-20 days in both barrel and field experiments. Restriction of rhizosphere effects to certain stages in cluster-root development, has been previously noted by Neumann et al (1999). Not all roots showed this clearly visible pH effect. For instance, pH-increases were mainly observed in cluster-roots of *Grevillea*, with hardly any changes in pH associated with fine laterals (figure 5). For *Cassia*, the long lasting and strong pH effects were mainly observed around fine roots of 1.5-2.5 mm diameter, and only seldom around fine roots with a diameter < 1.5 mm.

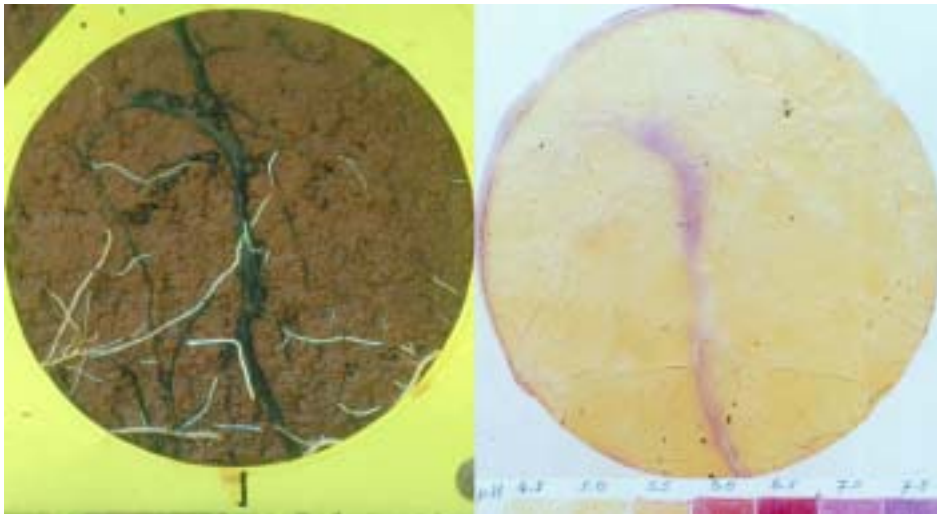


Figure 4. Characteristic pH-gel print from Cassia soil-root-wall of the barrel trial.



Figure 5. pH-gel on Grevillea roots on a soil-root-wall in the field trial.

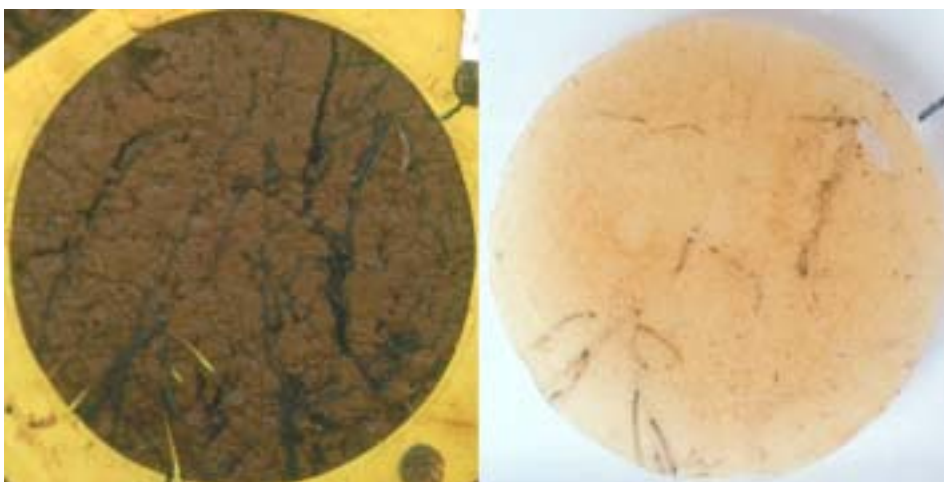


Figure 6. Print in an iron-phosphate precipitate gel on a Cassia soil-root-wall of the barrel-trial



Figure 7. Print of phosphatase activity on *Grevillea* soil-root-wall in the field trial.



Figure 8. Print of phosphatase activity on *Eucalyptus* soil-root-wall in the field trial.

Table 3 Measurements of maize-Cassia root-synlocation and fraction 1.5-2.5 mm Ø Cassia-roots on soil root walls of field and barrel-trial. With synlocation - $fx / (fm*fc)$, in which fx = total maize-root surface within cassia rhizosphere / total window surface minus cassia-root surface, with fm = total maize root surface / total window surface minus cassia-root surface, with fc = total cassia rhizosphere surface / total window surface minus cassia-root surface, n - number of windows.

measurement	mean	se	n	window surface (m ²)
fraction of Cassia roots 1.5-2.5 mm Ø (barrel-trial)	0.25	0.020	8	0.032
fraction of Cassia roots 1.5-2.5 mm Ø (field-trial)	0.18	0.145	4	0.135
Cassia-Maize root-synlocation (barrel)	1.87	0.283	8	0.032

The fraction of total fine root length of *Cassia*, showing a strong pH-increase is shown in Table 3. Assessing root-life at 15 months (450 days), duration of pH-increase at 21-56 days and pH-increasing roots (of 1.5-2.5 mm Ø) at 18.0-24.6 %, the percentage of fine roots active at any point in time is about 1-3 %. The high standard error of the fraction 1.5-2.5 mm Ø roots in the field trial (table 3) was due to limited colonization of the soil-root-walls.

The width of the pH-increase around the root, after being in contact with the soil-root-wall for half an hour is about twice the root diameter (including root-width itself).

When *Cassia* roots were left in contact with iron-phosphate precipitate gels, they often developed a black imprint (figure 6). The black print was most intense for newly developed roots, but faded over the following 2-3 weeks. The black imprints on the iron phosphates formed along the same root sections that showed a pH-increase.

If comparing the period of the black prints with the period of the pH-increase, the strongest black prints occurred before the period of pH-increase, although there may be an overlap with pH-increase of 1-2 weeks. *Grevillea* cluster-roots also showed evidence of a black imprint, but the imprints were

not clear. The long time required before a print became clear (10 days) suggests that if roots are active for only a few days, the print may not become visible.

Acid phosphatase activity

Phosphatase activity imprints were most intense around roots of *Grevillea*, *Eucalyptus* (figures 7 and 8) and *Cedrella*, and least intense around roots of *Cassia*. We observed little phosphatase activity away from the root-surface. A large fraction (60-70%) of total root length showed phosphatase activity (Table 4). Kroehler and Linkins (1988) found an even distribution of phosphatase activity along roots, but Grierson and Comerford (2000) found a high concentration of phosphatase activity in cluster-roots and phosphatase activity along 10-30 % of the normal root-surface.

Print colors could not be quantified, but were deepest red around *Eucalyptus* and *Grevillea* roots, slightly less red around *Cedrella* roots and pink around *Cassia* roots. The relation of this qualitative color intensity with measured phosphatase activity as described in chapter 4 is not clear. The acid phosphatase activity for *Cedrella* and *Cassia* were of the same level, but filter-paper prints of *Cassia* roots are much less clear than those of *Cedrella* roots. Similarly, *Grevillea* and *Eucalyptus* filter paper prints had similar color intensity, but acid phosphatase activity of rhizosphere soil of *Grevillea* was twice as high than in of *Eucalyptus* rhizosphere soil. The color-print gave sharp lines of the paper-root contact suggesting that phosphatase activity is mainly root-wall bound, as also noted by Dodd et al (1987). This is of importance, because the hydrolyzed P can be taken up by the root rather than being re-adsorbed on the soil. Moreover, enzymes in soil loose part of their activity upon adsorption on soil colloids (Tarafdar and Jungk, 1987).

Synlocation of tree and crop roots

Synlocation of *Cassia* and maize roots was around 1.87, which was significantly higher than 1 (Table 3). A synlocation value > 1 means that more roots of maize occupy *Cassia* rhizosphere than can be expected from regular crossing on this two dimensional surface.

Species	mean	se	n	total surface of n windows (m ²)
Grevillea	0.73	0.011	2	0.086
Eucalyptus	0.61	0.007	3	0.075
Cedrella	0.62	0.090	3	0.055

Table 4. Fraction of root-length showing acid phosphatase activity. With n: number of different windows).

This relatively high “synlocation” of roots is mainly due to sections of maize roots growing closely alongside *Cassia* roots, and concentration of root-growth of both species in the same areas of the total surface of the soil-root wall. It is not clear whether this degree of synlocation is a “strategy” of maize to profit from enhanced P-mobilization and other rhizosphere effects around *Cassia* roots, or whether maize roots are simply utilizing existing root channels, or reflect a localized availability of resources that is not attributable to the *Cassias*.

Discussion

Increases in pH have major implications for P-availability (Hingston et al, 1967, 1972; Anderson et al, 1974; Parfitt, 1980; Tiessen and Moir, 1993). Moreover, pH increases (above pH 5.5 of the soil in our experiments) may decrease the effectiveness of ligand exchange of organic anions with phosphate (Nagarajah et al, 1970, Violante et al, 1991, Geelhoed et al, 1998) and may decrease acid phosphatase activity (Ridge and Rovira, 1971, Dodd et al, 1987; Pant et al, 1994).

Significant increases of pH within the cluster-roots of *Grevillea* and around the larger fine roots of *Cassia* occurred structurally, although much more roots, including the finer *Cassia* roots, normal *Grevillea* roots and maize or *Tithonia* roots showed sometimes vague purple prints. This second type of slight pH increase, which is largely confined to the root surface, is probably due to nitrate-uptake and charge balancing (Barber, 1971; Maschner, 1986; Haynes 1990). The intense and localized pH increases extending away from the root surface and observed along *Cassia* and *Grevillea* roots is less likely a result from nitrate-N nutrition and imbalance of cation-anion uptake, because nitrate uptake and resulting pH-increases are usually dispersed along the entire length of the roots (Hoffland et al, 1989; Marschner, 1995). There are many possible causes for the local pH increases we observed, including active HCO_3^- or OH^- exudation (Haynes, 1990), iron-reduction (Parfitt, 1979; Gardner et al, 1982a) and or equilibration of exuded anions with the soil solution (Jones and Darrah, 1994).

The black prints in the iron-phosphate precipitate gels may be related to organic anion exudation (Ai et al, 1994). Moreover, rhizosphere soil of *Grevillea* and especially *Cassia* showed high contents of citrate and oxalate respectively (Chapter 4). The observation that pH-increases occurred on the same root-stretches but after the black prints on iron-phosphate gels, suggests that the pH-increase may at least partially result from degradation of organic anions. However, this shifts the question to why there are no pH-decreases at the time of the black prints in iron-phosphate gels, if the black prints are caused by organic anion exudation. The absence of pH decrease in that earlier stage suggests that organic anions are exuded without co-transport of H^+ , either against charge balance, or with co-

transport of other cations, or balanced by uptake of other anions (nitrate, phosphate). If the black print in the iron-phosphate precipitate gel is caused by organic anion exudation, major exudation along *Cassia* roots seemed to occur before the period of pH increase. Thus temporal separation of organic anion-exudation and pH-increase occurs, avoiding a negative interaction. Alternatively, black prints of lighter intensity during the period of overlap with pH-increases, may indicate that organic anions react less with the iron-phosphate precipitate in the gel at higher pH (Nagarajah et al., 1970; Violante et al., 1991; Geelhoed et al., 1998), and negative interaction of pH-increases with ligand-exchange may be the cause of the lower intensity of the black prints.

Sequentially extracted P-fractions from field soils (table 1) showed that increasing the pH (bicarbonate and hydroxide extraction) made considerably more P available ($\sim 5 \text{ mg kg}^{-1} \text{ P}_i$ and $\sim 25 \text{ mg kg}^{-1} \text{ P}_o$ at pH 8.5 and $\sim 75 \text{ mg kg}^{-1} \text{ P}_i$ and $180\text{-}210 \text{ mg kg}^{-1} \text{ P}_o$ at pH 13). This suggests that the observed pH rises in the rhizosphere of *Cassia* and *Grevillea* roots will have mobilized part of the bicarbonate inorganic and organic P. According to Tiessen and Moir (1993) the bicarbonate and hydroxide extractable fractions represent a continuum of Fe and Al associated P, which is more extractable with increasing pH in highly weathered acid soils like ours.

The inorganic P is likely directly available to plant-uptake, but organic P would need to be hydrolyzed, or mineralized. Acid phosphatase activity at the root-wall or in the rhizosphere seemed to be sufficient to hydrolyze mobile organic P reaching the root-wall (Chapter 4), but at increasing pH acid phosphatase activity decreases (Ridge and Rovira, 1971; Mc Lachlan, 1980; Dodd et al., 1987; Ozawa et al, 1994; Pant et al, 1994), while the supply of organic P increases. This may lead to a situation in which the organic P supply at the root surface is large and suggests that phosphatase activity needs to be higher in rhizospheres that are subject to increases in pH, as measured in e.g. *Grevillea* cluster roots. High acid phosphatase activity may also be of increasing importance when organic-P availability at the root surface increases owing to ligand-exchange of organic-anions for sorbed organic-P, thus showing a positive interaction between organic-anion exudation and high phosphatase activity.

A possible negative interaction of decreased acid phosphatase activity at increasing pH may have caused that, although *measured* acid phosphatase activity in rhizosphere of *Cassia* and *Cedrella* (Chapter 4) were similar, phosphatase imprints of *Cassia* were of a much lighter intensity than the imprints of *Cedrella*. Similarly, although rhizosphere soil of *Grevillea* showed much higher acid phosphatase activity than rhizosphere soil of *Eucalyptus* (Chapter 4), the phosphatase imprints of *Grevillea* roots had no stronger intensity than the imprints of *Eucalyptus* roots.

The question whether the maize crop can profit from rhizosphere effects on P (table 3) availability around tree roots depends on the ability of maize roots to grow into tree-rhizosphere soil before the rhizosphere effect is past time. This means that the longer the effect around a tree-root lasts, the more likely maize can profit. On the other hand, the ability of the maize roots to compete with tree roots, the relative “sink-strength”, in this altered rhizosphere zone plays a role. Assuming a zero-sink situation for P of both tree and crop roots, the species with most root-surface in the altered rhizosphere soil will profit most. Both, duration of e.g. pH-increase in the rhizosphere and relative sink-strength, indicate that *Cassia* is more likely to favor the simultaneously growing maize than *Grevillea*, because *Cassia*’s rhizosphere-effects last longer than *Grevillea*’s and *Cassia* has much less root-surface in its altered rhizosphere soil than *Grevillea* in its root cluster-zone. Moreover, *Cassia* roots crossed freely with maize roots and grew partly together along the same course, causing a nearly two times higher synlocation than expected.

This study demonstrates that, in order to understand performance of plants in the field, and how plants can influence P-availability, all major rhizosphere effects on P-availability and their interactions need to be considered. The spatial and temporal distributions need to be investigated to know the extent of overlap of interacting rhizosphere effects, and to derive real concentrated local effects from overall rhizosphere-soil measurements. In order to assess if and how much one plant species can affect P-uptake of another species, as in our simultaneous agroforestry system described here, it is also necessary to examine the extent to which the roots of a species with less impact on rhizosphere chemistry occupy the rhizosphere of a more active species. The relative sink strength of the roots of the two species in the altered rhizosphere and the duration of rhizosphere modifications need to be known as well.

This study provided evidence that *Cassia* trees may have increased maize P-acquisition and yields by belowground interactions in the rhizosphere. *Cassia* altered its rhizosphere chemistry by mobilizing P, which could be taken up by maize.

**Determinants of water-use of tree-lines in sub-humid Western Kenya;
importance of leaf area versus micrometeorology**

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Determinants of water-use of tree-lines in sub-humid Western Kenya; importance of leaf area versus micrometeorology

Simône Radersma, Chin K. Ong and Richard Coe

Abstract

Views on what are the main determinants of water-use in forest stands differ. One side stresses the importance of leaf-area, the other stresses the importance of microclimate once the leaf area index is above 3.5. In tree lines the importance of both factors seem to increase. Because of advection, tree lines are more closely coupled to the atmosphere, which suggests that microclimatic factors are more important. Alternatively, increases in leaf-area in tree-lines gain importance, because they exert a dual effect by decreasing canopy resistance and increasing the radiation-intercepting surface.

We examined the relative importance of leaf-area versus microclimatic factors in tree lines. We measured tree water-use by heat-balance technique, leaf-area, bulk-air vapor pressure deficit, daily radiation, and soil water content, in an experiment with tree-lines within crop-fields. The tree species were *Eucalyptus grandis*, *Grevillea robusta* and *Cedrella serrata*, grown to produce poles on a phosphorus-fixing Oxisol/Ferralsol with or without P-application, in sub-humid Western Kenya.

Doubling the leaf area of *Cedrella* and *Grevillea* doubled water-use in a leaf area (LA) range of 1-11 m². The response of *Eucalyptus* water use (W) to increases in leaf area was slightly less marked as shown by the power relation $W=LA^a$, with $a<1$. Leaf-efficiency (e_l) was the other important determinant of water use, being affected by both tree-species and P-fertilization. A doubling of vapor pressure deficit (VPD), seemed to half the water-use of all trees except for *Cedrella*+P, which water-use increased. Soil water content effect on water use was only found in *Grevillea*-P, with a small increase (60%) as available water increased from 1.4 % to 8.9 % above wilting point (32%). This low response to soil water content is probably due to the extensive tree-root systems and the deep clayey soils supplying sufficient water to meet the evaporative demand.

Our results showed that water-use of tree lines is more determined by leaf-area and leaf-efficiency than by micro-meteorological factors. This is due to the large range of linear response of water-use to leaf area in a tree line, a specific characteristic of tree-line configurations, which distinguishes them from forest stands. In the tree-lines light interception and canopy conductance increase much more than a similar leaf-area increase would cause in a closed canopy.

Introduction

Tree- lines bordering crop fields may compete with crops for water, especially in drier environments. In more humid tropical environments with P-fixing soils, decreases in soil-water content, due to tree-water-use, may limit crop growth, due to soil-drying induced P-deficiency (Chapter 8). Therefore, an understanding of the main determinants of water-use by tree lines is crucial.

Water-use of plants is determined by 1) available energy (radiation R) and the fraction of total R which is used for evaporation of water (latent heat λE), 2) vapor pressure deficit (VPD) and

aerodynamic resistance (r_a), which depends on relative humidity, temperature, wind-speed and height and structure of the plant-surface, 3) leaf-area (index) (LAI) and 4) plant species characteristics which determine the hydraulic conductance of water through the soil-plant-atmosphere continuum. The latter two factors determine the canopy resistance (r_c).

The most straightforward and still the most comprehensive energy budget equation was developed by Penman and modified by Monteith. This equation is useful in predicting water-use of canopies (Jensen and Rosbjerg, 1991; Mc Naughton and Jarvis, 1983). Other more complex energy balance models have been used to predict water use from canopies (Cienciala et al., 1994; Whitehead et al., 1994), tree lines (Smith et al., 1997) and single trees (Landsberg and Mc Murtrie, 1984; Vrecenak and Herrington, 1984). When all factors mentioned above were measured and energy balance equations were used for the calculations, these predictions were highly accurate. However, for more practical purposes, simpler approaches to assessing water-use and its main determinants are desirable.

Mc Naughton and Jarvis (1983) developed a simplified approach to energy budgets for closed canopies, to understand and predict the effects of changing watershed vegetation from forest into grass. They introduced an Ω -factor ranging from 0-1 which indicated whether canopies were more (closer to 0) or less (closer to 1) coupled to the surrounding atmosphere, with its effect on canopy water-use. Canopy water-use was in general higher and more sensitive to changes in wind-speed and VPD if Ω approached 0 (e.g. forest), and was generally lower and sensitive to changes in R if Ω approached 1 (e.g. grass).

Views about the main factors that determine tree water use in forest stands are contradictory. Kelliher et al. (1995) showed that meteorological variables are more important than leaf area for LAI > 3.5. In contrast, Hatton et al. (1998) and Calder (1992) found a strong dependence of water-use on leaf area (or basal cross-sectional area) in Eucalyptus stands at lower LAI.

However, tree lines or single trees differ in several ways from forest canopies. The relatively simple Penman-Monteith equation or the use of the Ω -factor are not appropriate because in single trees and tree lines advection is high, and thus trees or tree-lines are likely to be closely coupled to the atmosphere. This suggests a high importance of air humidity, wind, tree-height and tree-structure as determinants of tree water-use.

On the other hand, leaf-area may be an important determinant of water-use in tree-lines because an increase in leaf-area increases canopy conductance to water-flow and enhances the amount of

radiation intercepted by the tree, more than in closed canopies. An increase in vertical leaf-density reduces R-losses, as in closed canopies. However in tree lines an increase in leaf area will also usually lead to increased canopy width and hence further R interception.

Moreover, there may be interaction effects between meteorological factors and leaf-conductance, which complicate the understanding of water-use by tree lines. In tree lines and single trees, with their low aerodynamic resistance between atmosphere and leaf-surface, responses to reduce stomatal conductance and transpiration may control tree-water use. Trees are likely to be specialized in control-responses because they are more closely coupled to the atmosphere than low crops (Mc Naughton and Jarvis, 1983). This response may be even more noticeable in tree lines than closed canopies. The main control-mechanism is via canopy resistance, as a function of stomatal resistance and leaf-area. Stomatal resistance may increase at increasing vapor pressure deficits (Dye and Olbrich, 1993; Cienciala et al., 1994; Meinzer et al., 1997), or at decreasing soil water availability (Jing and Ma, 1990; Mc Murtrie and Landsberg, 1992). Other plant responses to high atmospheric water demand or low soil water supply are leaf rolling (Dingkuhn et al., 1989; Sobrado, 1990) or leaf-shedding (Hatton and Wu, 1995), which reduce the leaf area.

The objectives of the research described here were, 1) to examine the relative importance of vapor pressure deficit, radiation, soil water content, leaf-area and leaf-efficiency (water-use per unit leaf area) in determining the water use of tree-lines 2) to understand why some factors are more important than the others and to which extent this is specific for tree-lines. The investigations were carried out in sub-humid Western Kenya using lines of *Eucalyptus grandis*, *Cedrella serrata* and *Grevillea robusta* grown in maize fields.

Materials and methods

Site Description

An experiment was conducted on a farmer's field at Nyabeda/ Western Kenya, (Latitude 0.08 °N, Longitude 34.24 °E, Altitude 1300 m). The site is sub-humid with an annual rainfall of about 1500 mm, distributed over two main cropping seasons; the long rainy season from March to June/July (900 mm) and the short rainy season from September to December/January (600 mm). The experiment was established in March 1997 on level land, which was formerly alternately cropped with maize or left fallow and was of generally low fertility status. Meteorological parameters were monitored in a station 500 m away from the experiment.

Average short-wave radiation during the day (12-13h) was usually between 0.35 - 0.55 kJ m⁻² s⁻¹, with occasional days of 0.2 - 0.3 kJ m⁻² s⁻¹ in the long rainy season. Daily minima of relative humidity varied only slightly from around 50% in drier periods (January-March, sometimes July/August) up to 60-70 % in wetter periods. Wind-speed at 2 m height was around 1 m s⁻¹ during most of the year, but in January, February (dry season) and May (probably accompanying thunderstorms) wind speeds of 2 - 4 m s⁻¹ were more common.

Experimental Set-up and field layout

The experiment was a 4x2 factorial design, with four replicates. The treatments were a complete factorial combination of two phosphorus levels (with and without P fertilizer) and four tree-crop systems (a maize plot with a tree line of either *Cedrella serrata*, *Grevillea robusta*, or *Eucalyptus grandis*, and a sole maize treatment without a tree-line).

Phosphorus was applied in the +P treatments at a dose of 250 kg ha⁻¹ at the start of the experiment in April 1997 and an extra dose of 50 kg ha⁻¹ in April 2000. Nitrogen (70 kg ha⁻¹ yr⁻¹) and potassium (15 kg ha⁻¹ yr⁻¹) were applied regularly to all treatments.

The plot size was 13.5 m x 15 m with the tree-lines in the middle of the 15 m side over the entire 13.5 m length, with a spacing of 0.5 m in the first year thinned to 1 m thereafter. Maize hybrid 511 or 512 was used in the long rainy seasons and sorghum seredo in the short rainy seasons. Maize spacing was 0.75 m x 0.25 m and sorghum spacing was 0.60 m x 0.15 m in all treatments. The distance between the tree line and the first crop row was 75 cm for maize and 60 cm for sorghum.

Plant and plot management

Seeds of *Grevillea robusta* (prov. Loitoktok from ICRAF MPT GRU) and *Eucalyptus grandis* (prov. Kaimosi Kakamega from KEFRI/Muguga) were sown on 23 October 1996, and seeds from *Cedrella serrata* (prov. Arboretum de Ruhande from Rwanda) were sown on 10 December 1996, in a nursery. Seedlings were transplanted to the field in April 1997. Pruning was done according to farmers' rules to produce poles and reduce shading of crops. All branches up to ¾ of the tree height were cut. Pruning dates were 22 December 1997, 14 May and 30 September 1998 and 20 April and 27 October 1999.

The plots were weeded manually by hoe, twice during each cropping season.

Root interference between plots was avoided by trenching. In February 1999 this was done 1 m deep over a stretch of 6 meter, 3 m to each side where two tree lines met. In the long dry season of 2000 a trench of 1.5 m deep was dug over a stretch of 10 m, 5 m to each side where two tree-lines met, and the rest (2.5 m) of the width of the plot was trenched up to 1 m deep. This last time also the lengths of the plots (parallel to the tree line at 7.5 m distance) were trenched up to 0.60 m depth.

Figure 1 shows a summary of the measurements done and relations derived necessary to relate leaf-area to tree water use. Specific leaf area (SLA) of the tree species was derived from destructive sampling of the trees (figure 1 measurement 2). From each treatment and each of the 4 replicates two leaf samples of 10-100 g fresh weight were taken. One of these was oven-dried and weighed again to derive dry-weight : fresh-weight ratio. The leaves of the other sample (6 smaller samples for Cedrella, 5 samples of different size for Grevillea and 4 large samples for Eucalyptus) were glued on paper and scanned by Delta-T scanner, using Delta-T image analysis software to measure the surface area.

Relations between stem-diameter below canopy (\varnothing_c) and canopy height (h_c) with leaf-area (LA) were derived from destructive sampling at the end of the long rainy seasons in 1998, 1999 and 2000 (figure 1 measurement 1). Canopy height and stem diameter just below the canopy were measured, the tree was cut and all leaves stripped and weighed. A sub-sample of the leaves was taken, weighed, dried and weighed again to get the dry-weight : fresh-weight ratio.

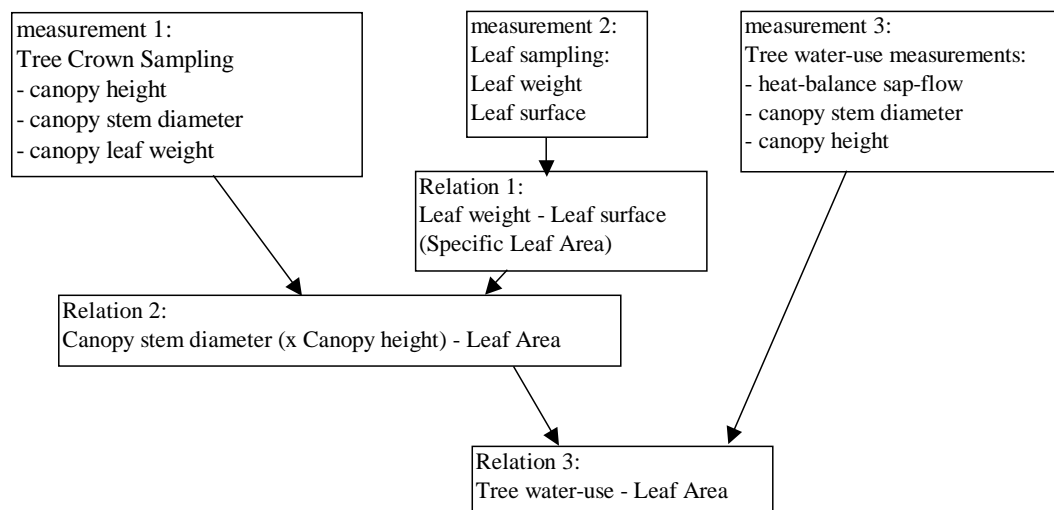


Figure 1. Summary of the measurements done and relations derived to calculate tree water use per unit leaf-area.

Water-use of the trees (W) was measured by the heat balance technique (Baker and van Bavel, 1987) (figure 1 measurement 3). Heater coil and thermo-couples were covered by styrofoam and aluminum-foil to prevent heat-losses or heat-additions from incoming radiation (Khan and Ong, 1995). Hourly data were collected using a Campbell C21X data logger. From July 1998 to July 1999 heat-balance measurements were done every two months on 3 trees of 4 treatments. An extra dry-period measurement on 3 trees of all 6 treatments was done in February/March 2000. In May-June 2000 (wet season) in all treatments, sap-flow of 3 trees was measured for two weeks. After the first week, the canopies of two of these trees were severely pruned up to 1/2 or 1/3 of their original height, to cross-check the importance of leaf-area as determinant of tree water-use. Daily water-use was calculated by adding the sap-flow measurements of all 24 hours, and extracting 24 times a base-line value (= average of night hours). Sap-flow and \varnothing_c and h_c (to estimate LA) were measured, at the same time on the same trees.

To determine the importance of radiation (R), vapor pressure deficit (VPD) and soil water content (θ) on tree water-use, hourly data (short-wave radiation, temperature, relative-humidity, wind speed) were collected from a meteorological station 0.5 km away during the periods of sap-flow measurements. These data were used to calculate total daily R, daily average wind-speed and average daily VPD. VPD was calculated as $(e_{a(Tmin)} + e_{a(Tmax)}) / 2 - e_d$ with e_a and e_d calculated from $Tmin$, $RHmax$, $Tmax$ and $RHmin$ (FAO,1992).

Soil water contents were measured every month from August 1998 (Chapter 7), and interpolated to derive the values at the times of sap-flow measurement.

Statistical Analysis and Calculations

Specific leaf areas (SLA), the ratio leaf area : leaf-weight, both dry and fresh were analyzed by analysis of variance

Regression analysis was used to develop relationships for prediction of leaf area (LA) from stem diameter just below the canopy (\varnothing_c) alone, or multiplied with canopy-height (h_c), or from conical volume ($1/3 \times (1/2 \times \varnothing_c)^2 \times \pi \times h_c$). LA was derived from leaf weight, using the fresh-leaf SLA relation or the dry-leaf SLA relation. The two best fits were both used to calculate LA from \varnothing_c alone, or multiplied by h_c . The average of these two calculations was used as assessment of LA and related to water-use (W) measurements.

First, the relations between LA and W were analyzed for all 6 treatments (tree-species x P-level) together to examine whether there were significant differences between the treatments in leaf-efficiency (e_l). Only data from a leaf-area range of 0 to 12 m² were used for all treatments. However,

maximum leaf-area of Cedrella +P was only 4.3 m², Cedrella-P and Grevillea +P and -P reached 8-11 m².

Secondly, after the analysis showed that the e_i -relations differed between treatments, the best fitting relations were determined for each treatment. For these analyses, period averages of daily sap-flow measurements (averages of the different daily values within one sap-flow measurement period) were used.

Multiple regression with W as response and leaf area (LA) soil water content (θ), radiation (R) and vapor pressure deficit (VPD) as explanatory variables was used to examine the extend to which variables other than LA contribute to understanding variation in W. The number of observations used for this analysis was slightly less than in the LA-W ($=e_i$) regressions, because some of the met-station data were faulty and could not be used. The regression was done separately for each treatment. Soil water contents (θ) were expressed in vol % above wilting-point (~32 vol %). Statistical analyses were done using Genstat (2000).

Results

Specific leaf area (SLA)

Specific leaf areas for Eucalyptus, Grevillea and Cedrella are shown in Table 1.

The Grevillea had a significantly lower SLA, thus thicker leaves, than Cedrella and Eucalyptus.

Table 1. Specific leaf area (SLA), using fresh and dry leaves of Cedrella, Eucalyptus and Grevillea, at Nyabeda, Western Kenya.

	n	SLA-fresh cm ² g ⁻¹	SLA-dry cm ² g ⁻¹
Cedrella	3	55	133
Eucalyptus	3	45	134
Grevillea	4	32	90
	sed 3-3	2.4	6.6
	sed 3-4	2.2	6.1

Table 2. Best fitting relations between canopy height and/or stem-diameter-below-canopy, and leaf area (derived from leaf weight and fresh or dry SLA).

Species / LA-range (m ²)	can.diameter - leafarea		can.diam.*height - leafarea		SLA used
	equation	r ²	equation	r ²	
Cedrella [0.27;8.95]			y=81.5x ^{1.05}	0.86	dry
			y=86.9x ^{1.04}	0.83	fresh
Eucalyptus [1.20;62.6]	y=5637x ^{2.38}	0.97			dry
	y=6134x ^{2.20}	0.97			fresh
Grevillea [0.20;11.4]			y=106.2x+336	0.89	dry
			y=75.8x+2413	0.88	fresh
	x=canopy diam. (cm)		x=canopy diam.*height (cm ²)		
	y=leaf area		y=leaf area		

Climatic conditions (drought, temperature) affect SLA, as Dye and Olbrich (1993) found a fresh-leaf SLA of 32 cm²g⁻¹ for *Eucalyptus grandis*, which is lower than the 45 cm²g⁻¹ we found here, and Lott et al. (2000) found a dry-SLA for *Grevillea* of 31 and 69 cm²g⁻¹ in two different sites in semi-arid Central Kenya.

Relation of canopy-stem-diameter (\varnothing_c) and canopy height (h_c) with leaf area (LA)

The best relations to derive LA from h_c and/or \varnothing_c are shown in Table 2.

All relations have the form $y=cx^n$ (Landsberg and Mc Murtrie, 1984). For *Eucalyptus* x is \varnothing_c alone and $n=2$, while for *Cedrella* and *Grevillea* x is best represented by the product $\varnothing_c \cdot h_c$ with $n=1$. All relationships are therefore dimensionally equivalent (m²).

Relation leaf area (LA) with water-use (W)

The relation between W and LA giving the leaf-efficiency relation (e_l) is plotted in Figure 2.

Accumulated analysis of variance, explaining W by LA, treatment and LA x treatment, showed significantly different leaf-efficiency (e_l) relations for the different treatments. Because of these significant differences, best e_l relations were assessed by regression per treatment, using the whole range of leaf-areas for each *Cedrella* and *Grevillea* treatment, and up to 28 m² for *Eucalyptus* (=leaf area at maximum pole size of the other species). These e_l relations are given in Table 3. For *Cedrella* –P a linear relation using untransformed leaf-area values fitted best. For *Cedrella*+P and the two *Eucalyptus* treatments a power relation using untransformed leaf-area values fitted best, and for *Grevillea* the best fitting relation was linear using square-root (leaf-area).

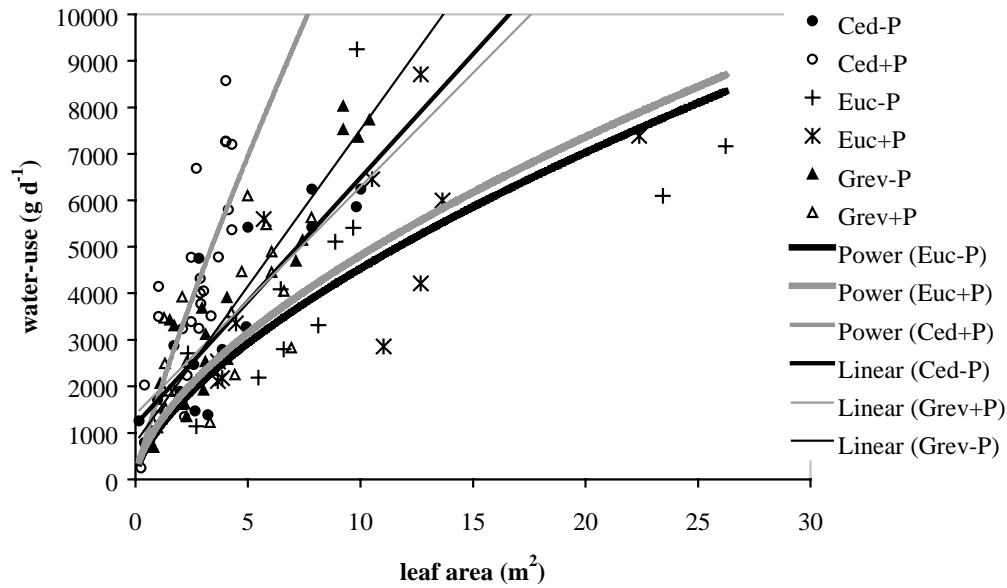


Figure 2 Relation between leaf-area and daily water-use

The steeper the slope (in Figure 2), the lower the leaf-efficiency (e_l) and the higher the water-use per unit leaf area. Thus Cedrella+P had the lowest e_l and both Eucalyptus treatments the highest e_l . Both Grevillea treatments and Cedrella-P showed intermediate levels of e_l . Application of P affected e_l of Cedrella. Cedrella +P had a much lower e_l , than Cedrella -P. In contrast, Grevillea +P seemed to have a slightly higher e_l , than Grevillea -P. According to Sheriff et al. (1986), fertilization increases the N and P contents of leaves and increase water-use efficiency. This was probably true for Grevillea, but opposite to what we observed in Cedrella.

Table 3 Regression relations between leaf-area (LA) and daily water-use (W). With $rtLA=LA^{1/2}$.

Species	P	Water-use ($g\ d^{-1}$) - Leaf-area (m^2) equation	R^2
Cedrella	-P	$W=LA*531+1177$	0.75
	+P	$W=1766*LA^{0.85}$	0.73
Eucalyptus	-P	$W=1058*LA^{0.63}$	0.62
	+P	$W=1173*LA^{0.61}$	0.60
Grevillea	-P	$W=rtLA*2856-1862$	0.84
	+P	$W=rtLA*1793-68$	0.51

Table 4 Multiple regression of tree-water-use with leaf area, soil-water content and evaporative demand: ranges of explanatory factors and related predicted range of tree-water-use. With LA: untransformed leaf-area, rtLA: $LA^{1/2}$ and rt3LA: $LA^{1/3}$, VPD - average daily vapor pressure deficit, R - daily shortwave radiation, $\theta > wp$ - soil water content above wilting point, W - daily water use, n=16 - number of period averages used for the regression, xx % - percent variance explained by the multiple regression.

	explanatory factor		range of explanatory factor	range of predicted water-us	
				kg d ⁻¹	s.e
Cedrella-P n=16 75.3 %	LA	(m ²)	[0.2;10]	[1.6;6.1]	0.45,0.59
	R	(MJ m ⁻² d ⁻¹)	[17;22]	[3.6;3.2]	0.43,0.62
	VPD	(kPa)	[0.54;0.89]	[4.2;2.9]	0.63,0.49
	$\theta > wp$	(vol%)	[4.4;9.1]	[4.0;3.1]	0.63,0.42
Cedrella+P n=18 78.2 %	LA	(m ²)	[0.25;4.3]	[0.6;5.6]	0.44,0.39
	R	(MJ m ⁻² d ⁻¹)	[16;23]	[4.6;2.4]	0.82,0.56
	VPD	(kPa)	[0.38;0.80]	[2.3;3.7]	1.2,0.54
	$\theta > wp$	(vol%)	[1.4;9.1]	[4.1;2.8]	0.99,0.64
Eucalyptus-P n=8 53.2 %	rtLA	(m)	[1.7;3.1]	[1.9;5.1]	2.6,1.8
	R	(MJ m ⁻² d ⁻¹)	[17;19]	[6.8;0.05]	2.7,3.5
	VPD	(kPa)	[0.62;0.77]	[3.1;6.0]	1.1,2.8
	$\theta > wp$	(vol%)	[5.9;10]	[-2.0;10.0]	3.5,3.7
Eucalyptus+P n=16 68.2 %	rt3LA	(m ^{2/3})	[1.5;4.2]	[3.5;9.9]	0.72,1.07
	R	(MJ m ⁻² d ⁻¹)	[16;22]	[5.0;6.9]	1.0,1.1
	VPD	(kPa)	[0.39;1.1]	[6.8;4.5]	1.2,1.9
	$\theta > wp$	(vol%)	[1.4;10]	[6.4;5.6]	1.4,0.98
Grevillea-P n=19 95.3 %	rtLA	(m)	[0.90;3.2]	[0.9;7.1]	0.23,0.27
	R	(MJ m ⁻² d ⁻¹)	[16;24]	[3.2;4.7]	0.19,0.32
	VPD	(kPa)	[0.54;0.87]	[4.6;2.7]	0.26,0.30
	$\theta > wp$	(vol%)	[1.4;8.9]	[2.7;4.3]	0.28,0.19
Grevillea+P n=18 65.4 %	rtLA	(m)	[0.89;2.8]	[1.4;5.5]	0.43,0.52
	R	(MJ m ⁻² d ⁻¹)	[17;24]	[3.4;3.0]	0.49,0.43
	VPD	(kPa)	[0.56;0.98]	[3.8;2.7]	0.50,0.49
	$\theta > wp$	(vol%)	[1.4;8.6]	[3.4;3.1]	0.44,0.33

Results of multiple regression and the ranges of leaf-area, θ (% above wilting point at ~32 vol%), R and VPD and predicted W ranges with standard errors are shown in Table 4.

In Grevillea –P environmental variables explained 12.5% more of the variance in water-use than leaf area alone. In all other treatments the extra variance explained was only 4-6 %. An increase in VPD from around 0.5 kPa to around 1 kPa seemed to result in a lower water use in Grevillea, which is significant in Grevillea –P (42 % lower water-use), less clear in Grevillea+P, Eucalyptus +P and

Cedrella -P (31-34 % lower water-use). Cedrella +P seemed to use more water upon an increase in VPD, but this is not significant. The VPD range of Eucalyptus -P was too small to be conclusive, and the low replication (n=8) made the results of this analysis questionable.

Changes in R over the ranges in our environment showed again no significant and contradictory effects, except in Grevillea -P again. In Grevillea -P an increase in R of slightly more than 50 % resulted in a predicted increase of water-use just under 50 %. Eucalyptus +P showed a similar relation but this is not significant.

Table 4 showed that θ has no or contradictory effects on tree-water-use, once the extreme cases were excluded from analysis. Only in the data series of Grevillea-P (which showed in all analysis least unexplained variance) there seemed to be a significant and understandable increase in water-use with an increase in θ from 1.4 to 8.9 (% above wilting point). Soil water content (θ) close by wilting point explained some extremely low W data at high stem-diameter in Eucalyptus.

Discussion

Multiple regression of water-use explained by leaf-area, meteorological parameters and soil-water-content gave an indication of the importance of the determinants of water-use in our tree-line situation, where the Penman-Monteith equation was not applicable and the energy balance equations with a higher level of sophistication, requiring measurement of all energy fluxes and resistances (Smith et al., 1997) was not feasible.

Comparing the variance accounted for by leaf-area alone with the variance accounted for by leaf-area, VPD, radiation and soil-water-content, showed that the last three factors together explained at most 12.5 % more of the variance of the water-use, compared with the variance already explained by leaf-area alone (51 % to 84 %). In the Grevillea-P treatments, which showed the least unexplained variance, all variables LA, VPD, R and θ had a significant effect.

Multiple regression of water-use explained by leaf-area, meteorological parameters and soil-water-content is risky, because some of these variables do not affect transpiration in one direction or in a linear way, and need careful interpretation.

An increase in VPD increases the evaporative demand, thus increasing transpiration. On the other hand, transpiration can be decreased if trees respond to increases in VPD by closing their stomata or shedding leaves, especially if accompanied by drying soil. We found that an increase in VPD was accompanied by a decreased water-use, and thus the effect of VPD on stomatal conductance and/or

leaf-shedding, decreasing transpiration, was generally stronger than its transpiration-enhancing effect through an increase in evaporative demand. Only in *Cedrella* +P the transpiration enhancing effect through an increase in evaporative demand seemed to be stronger than the tree-response effects. This P-effect on *Cedrella*, reducing its water-use limiting responses, probably caused the low e_1 we found of *Cedrella* +P.

Plants often show a non-linear response of water-use (W) to soil drying, with a threshold above which soil drying has little effect on tree-water-use and below which its effects on tree water-use are serious (Raison and Myers, 1992; Jing and Ma, 1990).

Soil-water-contents (θ) did not have much effect on the water-use, except that severe water-stress severely reduced *Eucalyptus* water-use. This may be due to the switch-point effect of soil water content below a certain threshold as mentioned above. This threshold may be the soil water content at which soil-resistance starts to determine plant-water-uptake, instead of plant-resistances (Hillel et al., 1976).

The large effect of LA and e_1 , and the small effects of θ , VPD and R on water-use of the tree lines in this experiment, were probably due to the two reasons.

The first reason is related to the characteristics of tree lines and the way they differ from a forest canopy. In the tree-lines, an increase in leaf area not only decreases the canopy resistance, but also increases the surface-area of the canopy and thus the amount of radiation intercepted and the amount of energy available for water-evaporation at the leaf surfaces. This increase in interception was much larger than what a similar leaf-area increase in a closed canopy would add to light-interception. Leaf-area increases within a canopy would also decrease canopy resistance, but this would have little effect on water-use due to a higher aerodynamic resistance within the canopy, determining total conductance from leaf to atmosphere.

The second reason for the high importance of leaf area is related to the first one and has to do with the largely different breadths of ranges of the determining variables. Leaf area ranges of the growing tree lines were large with more than ten-fold increases, from 0.2-10 m² for *Cedrella*, from 1-10 m² for *Grevillea* and from 3-28 m² for *Eucalyptus*. In contrast, ranges in VPD and R only resulted from a doubling of values.

Large radiation ranges were mainly found when daily fluctuations were measured. The day course of water use closely follows radiation (e.g. Dye and Olbrich, 1993; Vertessy et al., 1997; Smith et al., 1997), also observed in our sap-flow measurements. However, day-sums had a narrower range. In our situation, using average daily radiation for the sap-flow-period for (means of 5-7 days) the

range was small [16.5;24.0] MJ m⁻² d⁻¹. This is a climatic feature, with a predominantly clear sky even in the wet season.

The small range in vapor pressure deficit [0.5;1.0] kPa, was probably due to the proximity of Lake Victoria. Doubling of VPD caused a 30-40 % decrease in predicted water-use in most treatments. Only in Cedrella +P it caused a 60 % increase in predicted water-use. Other studies (Cienciala et al., 1994; Smith et al., 1997) considered VPD effect as an important determinant of water use, but these studies worked with a larger VPD range and a smaller leaf-area range.

The range of soil water content was quite wide, but did not affect water-use strongly. Soil water content is more likely to affect plant-water-use in water-limiting environments and coarse soils, or on shallow soils and if root systems are superficial (Dye, 1996; Vrecenak and Herrington, 1984). On our deep clayey soils, the extensive root system was able to extract sufficient water to meet the demand, except at extreme soil drying of the whole rooted soil-volume.

If we compare the response of water-use to equal changes in different explaining variables; e.g. doubling the VPD halved water-use, and doubling the LA doubled water-use, changes in LA and VPD are similarly important. However, unlike VPD differences, leaf area differences were much larger than this factor 2. The range of leaf-area in our experiment was from close by zero to greater than 10 m², and especially in this range the leaf-area – water-use relation was close to linear.

For comparison with canopies we need to translate our leaf-area per tree into LAI. If we assess the spread of the canopies of our tree lines to about 1 m on each side, together with a tree spacing of 1 m, each tree covers 2 m². At a leaf-area of 12 m², the tree lines have a LAI of 6. Up to LAI 6, water-use responds more or less linearly to leaf area increases (Figure 2). This upper limit of the linear response of water-use to leaf area index is much larger than for canopies. Kelliher et al. (1995) showed that linear response of canopy conductance to LAI occurs only up to LAI ~2; the response decreases strongly between LAI 2-6 and ceases altogether at LAI>6. One reason for the fast decrease of water-use-responses to increases in leaf-area in canopies is self-shading. Another reason is the higher aerodynamic resistance within canopies. Self-shading and aerodynamic resistance are lower in tree lines.

Therefore, the wide range over which water-use shows a (nearly) linear response to increases in leaf area is a specific characteristic of tree-lines, as compared with canopies, and explains the high importance of leaf-area as a determinant of water-use.

Because of the importance of leaf-area, leaf-efficiency as a measure for water-use per unit leaf-area is another important determinant of tree-water-use in tree lines.

Clear differences in leaf-efficiency of different species were also found by Myers et al. (1996), who mentioned *Eucalyptus grandis* having a three times higher leaf area than *Pinus radiata*, transpired only 22% more water, which indicated clearly different e_l in these two species. On the other hand, Hatton et al. (1998) and Meinzer et al. (1997) did not find large species differences in leaf-efficiency. But Hatton et al. (1998) compared only different Eucalyptus species and Meinzer et al. (1997) compared four species in a tropical rain-forest, where boundary layer conductance was low and stomatal conductance was high, and thus boundary layer conductance determined tree water use to a large extent and stomatal responses were of lower importance. This suggests that differences in leaf-efficiency show the ability of a tree-species (or treatment) to respond to close coupling to the atmosphere.

In conclusion, we showed that leaf-area and leaf-efficiency were main determinants of daily water use in tree lines in western Kenya. Leaf-efficiency was an important determinant of water use of tree lines, probably because of close coupling of tree lines to the atmosphere due to low boundary resistance. It differed among the different species and was also affected by phosphorus application. The importance of leaf-area in tree lines is more pronounced because of the relative large range in leaf-area showing linear response of water-use to leaf-area, and the relatively small ranges of other water-use determinants. If tree-lines occurred in circumstances with larger VPD and radiation ranges on coarser or shallower soils, then these factors would probably assume more importance in determining tree-water-use. However, even then the linear response of water-use to leaf-area over a wide leaf-area-range would make the leaf-area an important determinant of water-use.

**Spatial distribution of root length density and soil water of linear
agroforestry systems insub-humid Kenya; implications for agroforestry
models**

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Spatial distribution of root length density and soil water of linear agroforestry systems in sub-humid Kenya: implications for agroforestry models

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Abstract

In simultaneous agroforestry systems trees can compete with crops for water, especially in semi-arid areas. However, in the (sub)humid tropics, on P-fixing Oxisols/Ferralsols small decreases in soil water content cause a decrease in P-transport to roots and therewith a soil-drying induced P-deficiency.

The aim of this study was to assess the spatial distribution of soil water contents near tree lines and its relation with root-length-densities, using four tree species bordering maize fields in sub-humid Western Kenya on a degraded Oxisol/Ferralsol. Tree transpiration, soil water content and tree-root length densities were measured over a period of two years.

Soil water contents were significantly reduced (2-7%) near two of the three fast-growing tree species, *Eucalyptus grandis* and *Grevillea robusta*, but not near *Cedrella serrata* and the slower growing *Markhamia lutea* (Benth.) Schum. These differences were related to differences in water-use, but not to root length density distribution. Root length density distribution differed among species and changed over time. Eucalyptus and Grevillea had a slightly more superficial root system than Cedrella at the first sampling, but root density at depth of Eucalyptus and Grevillea increased in the second year. Grevillea root density hardly changed with distance from the tree row whereas eucalyptus and Cedrella root length densities decreased with distance from the tree. After twelve months the root systems became more widespread and deeper.

The relationship between root length density and water extraction is not inversely proportional, unlike the assumption in most water-uptake models, including those of agroforestry models. The absence of a clear relation between root length density and water-extraction can be explained by a decrease in water potential gradient in roots with distance from the tree trunk. If the change in root length density is much larger than the change in water potential, then root-length density profile is the main determinant of the soil water profile, this happens usually over the vertical dimension. However, if the change in root length density is similar or smaller than the change in water potential gradient, the decrease in water potential gradient is of similar or larger importance for determining soil water profile, this occurs horizontally with distance from the tree. This stronger decrease in potential gradient than in root length density occurred over distance from the Grevillea, and caused the absence of a relation between root length density and water-extraction. Thus, the horizontal water-extraction cannot be assumed to be directly related to root-length density as used in agroforestry models.

Introduction

Water deficiency can be an important limitation to crop-growth, not only in semi-arid environments, but also in environments where phosphorus is the main limitation to crop-growth, because transport of P in soil is highly dependent on soil water content. On a P-fixing Oxisol/Ferralsol in western Kenya we found that a soil water content reduction of 2-3% by associated trees may cause a

decrease in maize-production of 30-40% (Chapter 8). In such situations, trees are likely to affect crop-growth by soil-drying induced P-deficiency.

Trees can affect soil water contents in different ways. They can increase soil water content by decreasing soil-evaporation (Wallace et al 1999; Jackson & Wallace, 1999), by hydraulic lift (Caldwell & Richards, 1989; Dawson, 1993) and by hampering growth of other plants with a higher water-use per surface area. They decrease soil water contents by their own water-use, or prevent rain from reaching the soil by interception (Broadhead, 2000; Wallace et al, 2002.). In tropical climates with an annual rainfall of 1000-1500 mm interception losses (i.e. decreasing soil water inputs under the trees) are only slightly larger than evaporation reductions (i.e. decreasing soil water outputs under the trees), leading to only a few percent lower total water input under the tree canopies (Wallace et al, 1999) compared to water inputs outside the area shaded by tree-canopies. Therefore, tree water-uptake is the main determinant of soil water content distribution in the soil volume near tree lines. In Chapter 6 we examined the determinants of total water-use of the tree, and hence the total water-extraction from the soil. Leaf area and water-use per unit leaf area (both showing wide ranges) of the different tree-species determined water-use of tree-lines more than meteorological factors (with small ranges).

Root density distribution of trees and crops is usually seen as a main indicator of competition between trees and crops (Schroth, 1995; Smith et al, 1999), assuming that at equal supply, the resource uptake is related to the amount of root length per soil volume. Therefore, most crop and forest water-uptake models assume that water-extraction rate is closely related to root length density (Rowse et al 1978; Belmans et al., 1979; Lascano and van Bavel 1984; Barataud et al, 1995). This relationship between water extraction and root length is also used in agroforestry models like WaNuLCAS (van Noordwijk and Lusiana, 2000), HyPar (Mobbs et al, 1998) and WIMISA (Mayus et al, 1999). However, rather than one vertical dimension considered in crop-growth-models and forest models in simultaneous agroforestry systems there are two (or three) spatial dimensions. Therefore we want to investigate whether tree-water-extraction with a vertical and horizontal dimension in the soil volume is indeed closely related to root-length density.

In the research described in this paper we examined the profiles of water-extraction with distance from tree rows and its relation with tree-root distribution in a field experiment on a deep P-fixing Ferralsol/Oxisol in sub-humid Western Kenya. Four trees species selected for pole-production were grown along maize fields. For two years, soil water contents were monitored on a monthly basis and roots were sampled twice, both over depth and with distance to the tree-line, in order to determine i) the effect of the tree-lines on soil water contents over depth and with distance from the tree line, ii) differences in tree root distribution between the species and over time, iii) the relation between root

density distribution and soil water extraction, and iv) whether the root-distribution – water-extraction relation is similar to those used in agroforestry models.

Material and methods

Site description

An experiment was conducted on a degraded farmers field at Nyabeda, Western Kenya, (Latitude 0.08 °N, Longitude 34.24 °E, Altitude 1300 m). The site was sub-humid with an annual rainfall of about 1500 mm, distributed over two main cropping seasons; the long rainy season from March to June/July (~900 mm) and the short rainy season from September to December/January (~600 mm). The experiment was established on level land, which was formerly cropped with maize or left fallow.

The soil was an Oxisol/Ferralsol, which is a major soil type in the area (Shepherd et al, 1992). Soil texture was 58% clay, 16 % sand and 26 % silt in the top 0-15 cm. Clay contents increased to 73% towards depth (3m). Bulk density remained $< 1.3 \text{ kg dm}^{-3}$ over the first 1.6 m depth, due to high sesquioxide content and a good soil structure. Soil pH (1 : 2.5 soil/water suspension) was 5.6 over the entire depth, and Olsen-P was 1.2 mg kg^{-1} in the top 15 cm decreasing with depth to 0.3 mg kg^{-1} . Soil organic carbon decreased from 1.7 % in the topsoil to 0.3 % at 2-3 m depth.

Experimental set-up and management

The experiment was a 5x2 factorial design, with four replicates. The treatments were a complete factorial combination of five crop/agroforestry treatments; four maize plots with a tree line in the middle of *Cedrella serrata*, *Grevillea robusta*, *Eucalyptus grandis* and *Markhamia lutea* and a sole maize treatment without a tree-line and two phosphorus (P) levels; one with P and one without P. The plot size was 13.5 m x 15 m with the tree-lines in the middle of the 15 m side over the whole 13.5 m length, with a spacing of 0.5 m in the first year thinned to 1 m thereafter. Trees were transplanted to the field experiment in April 1997 at an age of 4-6 months.

Pruning was done according to farmers' practice to produce poles (cutting all branches up to about $\frac{3}{4}$ of the tree height), and to decrease shading of crops. Pruning dates were 22 Dec. 1997, 14 May and 30 September 1998 and 20 April and 27 October 1999.

Only in +P treatments phosphorus fertilizer was applied at a basal dose of 250 kg.ha^{-1} at the start of the experiment in April 1997 and an extra dose of 50 kg.ha^{-1} in April 2000. Nitrogen ($\sim 70 \text{ kg ha}^{-1} \text{ yr}^{-1}$)

¹) and potassium ($\sim 15 \text{ kg ha}^{-1} \text{ yr}^{-1}$) were applied regularly in all plots, to prevent these elements to become limiting crop and tree growth.

The plots were weeded manually by hoe, twice during a cropping season.

Plot interference was largely avoided by trenching. In the February 1999 this was done

1 m deep over a stretch of 6 meter, 3 m to each side where two tree lines met. In the long dry season of 2000 a trench of 1.5 m deep was dug over a stretch of 10 m, 5 m to each side where two tree-lines met, and the rest (2.5 m) of the width of the plot was trenched up to 1 m deep. In addition, the lengths of the plots (parallel to the tree line at 7.5 m distance) were trenched up to 0.6 m depth.

Further details about the experiment are given in chapter 6.

Measurements

Soil water contents were measured by neutron probe (Didcot Instruments, Wallingford, UK), every month between July 1998 and August 2000 in all treatments. Access-tubes for these measurements were installed at three distances from the tree line, 0.94 m, 2.44 m and 6.94 m. Measurements were done in all four agroforestry treatments and all four replicates over eight depths at 20 cm intervals to 160 cm depth. Neutron-probe measurements were calibrated in the same field. First ten neutron-probe measurements were taken in a tube in a water-barrel (as usually), then each depth in a soil-installed tube was measured seven times, and finally again ten water-barrel measurements were taken. This resulted together in the usual soil-count : water-count ratios. On the same day, a horizontal plane was dug out at 17.5 cm (20 cm minus half of the length of the fixed volume ring) around the pipe, and four fixed volume rings were inserted, dug-out, leveled to contain exactly 100 cc, weighed moist, oven-dried for four days at 108°C , and weighed dry. This was done for each measurement depth. Seven access-tubes all around the experiment were used for calibration, three tubes in the driest periods, two tubes in the wettest periods and two tubes in periods with intermediate soil water contents.

Root densities were measured at 15 and 27 months after transplanting the tree-seedlings to the field in all treatments except the *Markhamia* plots for three replicates. Measurement dates coincided with maize tasseling in the long rainy season of 1998 and 1999. A bucket-auger of 10 cm \varnothing was used to sample pairs of points (one within a maize-row and one in between two maize rows) at an average distance to the tree-line of 0 m, 0.94 m, 2.44 m and 4.69 m in 1998, or 0.94 m, 2.44 m, 4.69 m and 6.94 m in 1999. Each point was sampled up to 200 cm depth, separating the layers 10-30 cm, 30-50 cm, 50-100 cm, 100-150 cm and 150-200 cm (in 1998 the 100-200cm was sampled as one layer). The layer 0-10 cm was not sampled, because weeding twice during the cropping season cut most roots. If an auger-hole could not reach the specified depth due to occasional stones, final depth of

the hole was taken and sample volume adjusted accordingly before calculating root length densities. Both sides of the tree lines were sampled in this way. In 1998 the samples of the two sides were analyzed separately, after which an average of the root-length-densities of both sides was used. In 1999, samples from both sides were mixed in the field and analyzed together. The whole volume of soil+roots was taken for further root length measurement, except for samples of depth 100-200 cm, which were too large volumes (>20L). Hence, the soil was mixed thoroughly and a sub-sample of half or quarter of the total weight was taken.

Buckets with soil+root samples were soaked overnight. The next day the mixture was washed through a double sieve with mesh size 0.5 mm for the bottom-sieve. Further analysis for root length densities were by hand-sorting, staining, spreading and scanning following the method described by Smith et al (1999).

Statistical analysis and calculations

Soil-water-content data of the four most contrasting layers; 20 cm, 60 cm, 120 cm and 160 cm depth, were analyzed separately. Data of measurement times within the wet seasons and within the dry seasons showed similar trends as far as differences in soil water-contents with distance to the tree-lines were concerned. Therefore the average of all measurement times in the last three wet seasons and the average of all measurements times in the last two dry seasons were used for analysis of soil-water-content differences with distance from the tree line (Δd). These Δd values were analyzed by ANOVA as 5x2 factorial design with 4 replicates.

Because the trees were not all of the same size, root density data of each plot were adjusted to average basal stem cross-sectional surface per treatment (average of three replicates), by multiplying root densities by a ratio $S_{\text{measured}} : S_{\text{average}}$, in which S_{measured} is the sum of the surface of the 3 tree-stem cross-sections closest to the sampling transect in one plot, and S_{average} is the average of the three replicates of S_{measured} . These average root-length density profiles with distance from the tree line were analyzed by non-linear fitting to derive the variables of the elliptical function as described by (van Noordwijk and Lusiana, 2000):

$$\text{rld}(i,j) = X0 * DD * \exp. \left(\frac{-DD * (\text{Depth}_j^2 + (DS * \text{Dist}_i)^2)^{1/2}}{X0} \right) \quad (\text{Eq.1})$$

In which:

$rld(i,j)$ = root length density (cm cm^{-3}) at distance (i) and depth (j).

$X0$ = total root length per unit area (cm cm^{-2}) at a distance of 0 m from the tree stem.

DD = parameter (cm^{-1}) governing the decrease with depth of root length density (for $X = 0$, at a depth of $0.699/DD$ the root length density has half of its value at the soil surface)

DS = dimensionless parameter governing the shape of the tree root system; (when rld at 5 m distance is the same as at 1 m depth then $DS = 0.2$)

Results

Tree growth

There were only slight differences in growth-rates in response to P-application for Cedrella and Grevillea. Grevillea trees were slightly taller than Cedrella trees, but the last had a larger diameter. Figure 1 shows the growth in height and diameter of the trees over time in the different treatments. Growth rates of Eucalyptus +P were clearly highest, followed by Eucalyptus -P, Cedrella and Grevillea.

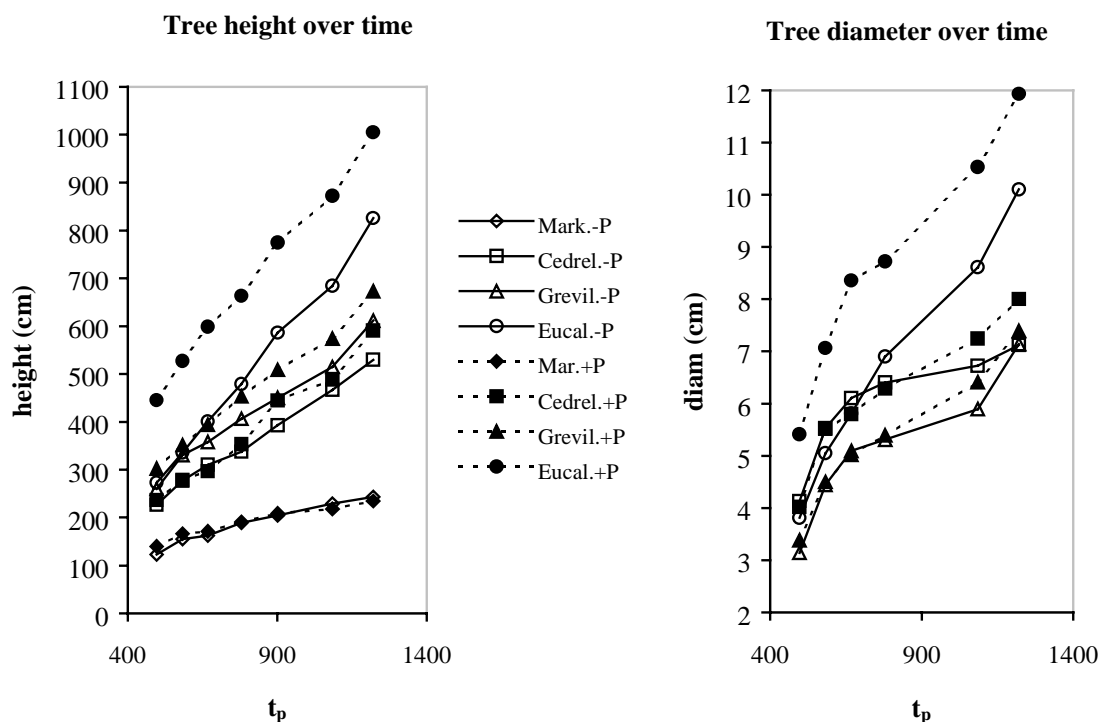


Figure 1. Tree height and tree-stem diameter over time in tree-line field experiment at Nyabeda, Western Kenya. The dip in diameter measurements is due to a severe pruning event, which reduced growth rate, and change in height of diameter measurements to 30cm above soil surface (first 5cm). With t_p - time after transplanting.

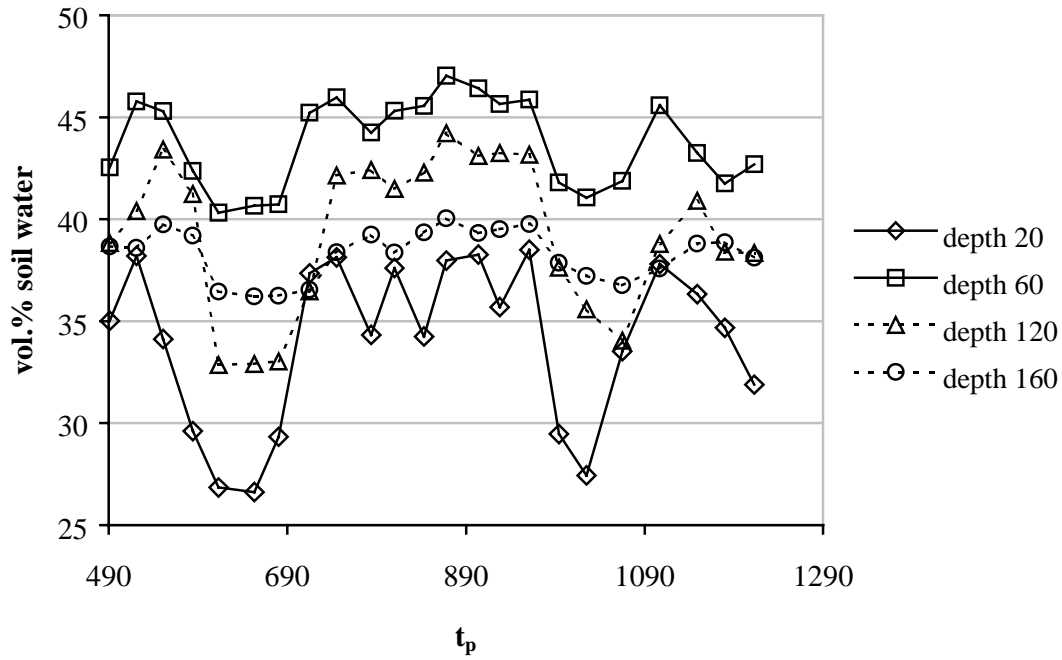


Figure 2 Mean soil water content in sole maize fields over time in tree-line field experiment at Nyabeda, Western Kenya.

Markhamia hardly grew in height. The slow-down in diameter-growth between the last two measurements before 900 t_p , is due to a severe pruning event. The first measurement after 900 t_p marks another change; the height of diameter measurements changed from 5 cm to 30 cm above soil surface.

Soil water contents

Average soil water contents over two years in sole maize fields are shown in figure 2. The small time-lag in drying and wetting cycles of the different soil-layers, shows that hydraulic conductivity of the soil is quite high, in both wet and dry circumstances, as may be expected from an Oxisol/Ferralsol (El-Swaify, 1980).

The amplitude and average level of soil moisture contents in dry and wet season, differs for the different layers. The amplitude in volumetric soil water content (θ) was largest for the upper soil layer (around 11%), with θ at a mean value of 32%. At 60 and 160 cm depth amplitudes were lower, 6 vol% and 3.5 vol% respectively, with θ at higher mean values of 43% and 38% respectively. In between these layers, at 120 cm depth, the amplitude is larger again (10 vol%) with θ at a mean value of 38%.

Because water-contents at 244 cm and 694 cm distance away from the tree lines did not yet differ significantly, they were averaged to reduce variability. This average minus the measurements at 94 cm distance from the tree lines, was used to calculate the Δd values. These are shown in Table 1a

and 1b. Table 1a shows the Δd values for the means of the last three wet seasons (which showed similar trends and were therefore averaged). Positive Δd values, indicating lower soil-water contents near the tree line

compared to far from the tree line were clearest (2.5-6.9%) in Eucalyptus +P, and significant in all layers except the first. Positive Δd values (1.2-2.5%) seemed to occur in all layers of eucalyptus-P as well, but these were not significant. Positive Δd values (1.2-3.2%) occur in the three lower layers of Grevillea +P, but are only significant at 120 cm depth. In Grevillea-P positive Δd values occurred in the two deepest layers, but this was only significant at 160 cm depth.

By extracting the significant positive Δd values from the water content during the wet periods (figure 2), the soil moisture regimes near the different tree lines can be compared with the normal annual

Table 1a. Changes in soil water contents in maize-fields approaching the tree line, in tree-line field-experiment at Nyabeda Western Kenya. Average over last 3 **wet** seasons. With Δd : difference in soil water content with distance from the tree. Significant positive values mean a lower soil water content near the tree line.

Species	P	depth 20cm	depth 60cm	depth 120cm	depth 160cm
		Δd (vol.%)	Δd (vol.%)	Δd (vol.%)	Δd (vol.%)
Cedrella	+P	-0.13	-0.34	1.39	0.58
Cedrella	-P	0	1.28	-0.43	-0.92
Eucalyptus	+P	2.51	2.72	6.92	3.86
Eucalyptus	-P	1.68	1.22	2.45	1.07
Grevillea	+P	0.57	1.22	3.17	1.28
Grevillea	-P	-0.23	0.5	2.07	2.4
Markhamia	+P	0.72	0.51	0.61	0.71
Markhamia	-P	0.57	0.93	-0.22	0.56
sole Maize	+P	0.6	-0.34	0.56	0.9
sole Maize	-P	-0.94	0.48	0.91	0.17
sed		1.423	1.108	1.309	1.207
Cedrella		-0.07	0.47	0.48	-0.17
Eucalyptus		2.09	1.97	4.69	2.46
Grevillea		0.17	0.86	2.62	1.84
Markhamia		0.64	0.72	0.19	0.63
sole Maize		-0.17	0.07	0.74	0.54
sed		1.006	0.784	0.925	0.853
	+P	0.85	0.75	2.53	1.46
	-P	0.22	0.88	0.96	0.66
sed		0.636	0.496	0.585	0.54

fluctuation of soil water-content. This shows that the soil near Eucalyptus +P dries out to 25-100% of

its normal annual soil water content range; depth 20 cm 2.51% : 11% = 23%, depth 60 cm 2.71% : 6% = 45%, depth 120 cm 6.92% : 10% = 70% and depth 160 cm 3.86% : 3.5% > 100%. Near the other tree lines drying is less severe, but compared with seasonal fluctuations it is still considerable.

The significance of Δd values is partly explained by tree-growth (Eucalyptus +P is largest and shows largest Δd , Markhamia is very small and does not show any significant Δd) and partly to daily water-use of a species at a particular size (Cedrella and Grevillea of about the same size, show different daily water-use (see Chapter 6)). Decreased water-use by maize near the tree lines, especially near Eucalyptus, will have counteracted the development of large Δd values, especially in the top layers.

Table 1b. Changes in soil water contents in maize-fields approaching the tree line, in tree-line field-experiment at Nyabeda Western Kenya. Average over last 2 **dry** seasons. With Δd : difference in soil water content with distance from the tree. Significant positive values mean a lower soil water content near the tree line.

Species	P	depth 20cm	depth 60cm	depth 120cm	depth 160cm
		Δd (vol.%)	Δd (vol.%)	Δd (vol.%)	Δd (vol.%)
Cedrella	+P	-0.58	-0.14	1.12	0.60
Cedrella	-P	0.09	0.91	-0.11	-1.13
Eucalyptus	+P	0.24	0.88	3.51	3.11
Eucalyptus	-P	-1.31	-0.61	0.66	0.99
Grevillea	+P	-0.97	0.34	2.16	1.01
Grevillea	-P	-1.54	0.58	2.44	2.74
Markhamia	+P	1.80	-0.34	-1.22	0.94
Markhamia	-P	-0.35	0.53	0.18	0.38
sole Maize	+P	1.17	-0.57	0.27	0.22
sole Maize	-P	-0.56	0.73	1.95	0.28
sed		1.535	1.255	1.677	1.316
Cedrella		-0.24	0.39	0.50	-0.27
Eucalyptus		-0.54	0.13	2.08	2.05
Grevillea		-1.25	0.46	2.30	1.87
Markhamia		0.72	0.10	-0.52	0.66
sole Maize		0.31	0.08	1.11	0.25
sed		1.085	0.888	1.186	0.931
	+P	0.33	0.03	1.17	1.18
	-P	-0.74	0.43	1.03	0.65
sed		0.686	0.561	0.750	0.589

A reason for the strong tree-caused drying of deeper layers compared to seasonal drying at depth may be that the roots cause close or 'shortcut' contact between the deep layers and the atmosphere. This shortcut is absent without roots (e.g. maize field in dry season), causing that the low soil conductivity determines the drying rate.

The Δd values in the dry season are shown in Table 1b. The Δd values for the first two layers (20 cm depth and 60 cm depth) were generally not significantly different from zero, and thus soil water contents did not change significantly with distance from the tree-lines. The Δd values in the lower layers (120cm and 160 cm depth) were still persistent in the dry season. The smaller Δd values in the dry season suggests that soil water contents near the tree line reached their minimum early in this season, and the main tree-water-uptake shifted to regions further away from the tree with higher moisture contents, lower suction of the soil and therefore higher potential gradients between root and soil.

Tree-roots

The elliptical-function parameters differed per species but were not affected by P treatment. Therefore, the root length density (rld) data for +P and -P were adjusted to same stem size for all three reps used (as done before for all reps of one treatment) and averaged before plotting in figure 3 and table 2.

The parameter, X_0 , is the total root-length per unit surface at distance 0 from the tree line. Thus high maximum and average rld values, especially near the tree line are reflected in higher X_0 values of the elliptical function. The X_0 values were partly dependent on tree-size, and because Eucalyptus and Cedrella were much larger than Grevillea, their X_0 value is larger as well. However, when the two sampling times (1998 vs 1999) are compared, there is no relation between bss and X_0 . In 1999 the trees and the bss were larger, but the X_0 is lower than in 1998. Figure 3 also shows that absolute root densities are lower in 1999 compared to 1998. The decrease in absolute root length densities and in X_0 -values of the elliptical function and in the ratio of X_0 : bss (basal stem surface) ratio, is likely due to tree-management and root-system growth dynamics as also found by Smith et al. (1999) and Odhiambo et al. (1999). Before the long rains of 1999, tree canopies were severely pruned, which may cause root-mortality, thus reducing the X_0 : bss ratio.

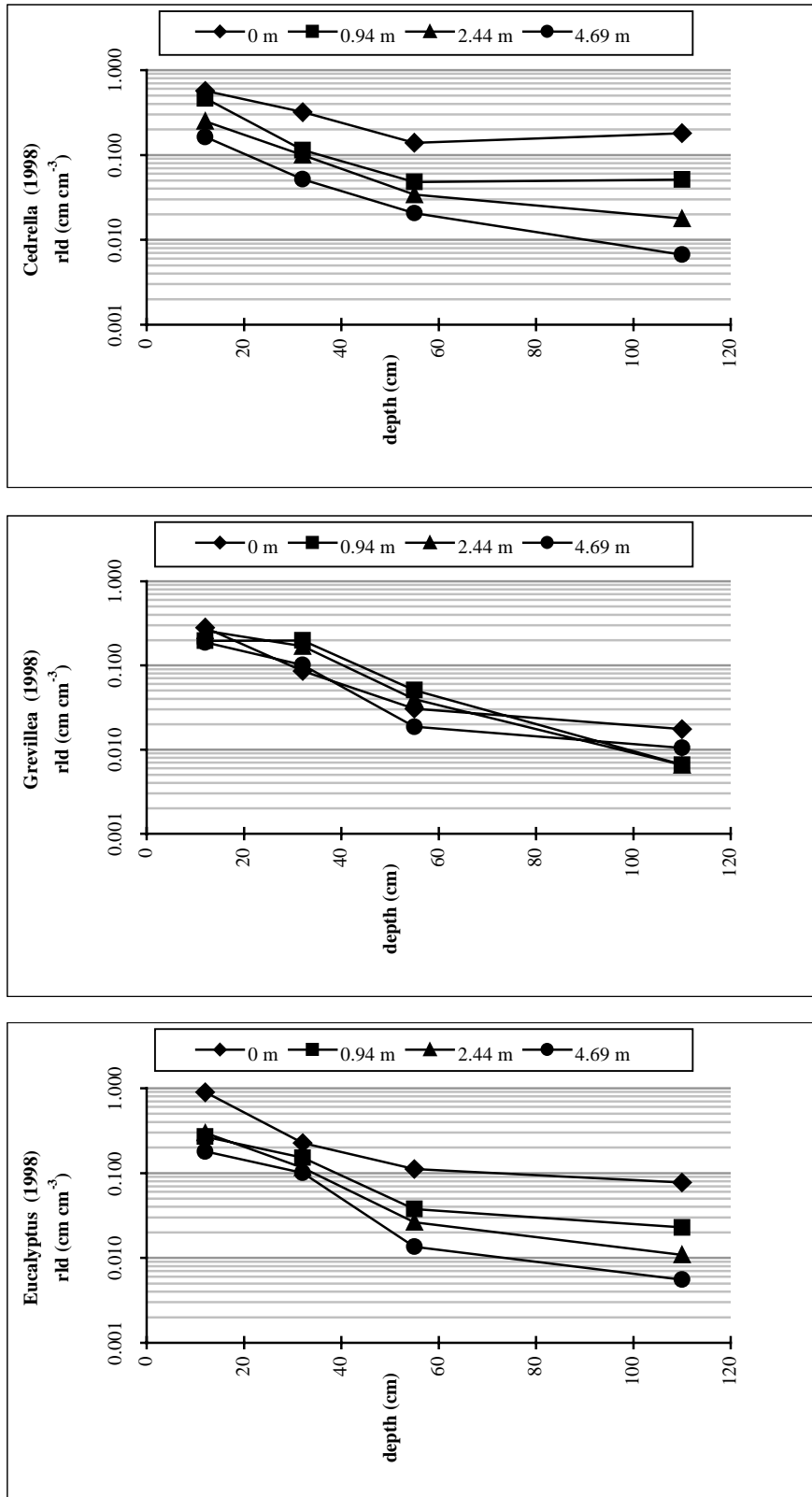


Figure 3a Tree root length density distribution in 1998, in tree-line field experiment at Nyabeda, Western Kenya. Because of exponential decrease in rld over depth, mean rld of layer 10-30 cm is plotted at 12 cm depth, layer 30-50 at 32 cm depth, layer 50-100 at 55 cm depth and 100-200 at 110 cm depth.

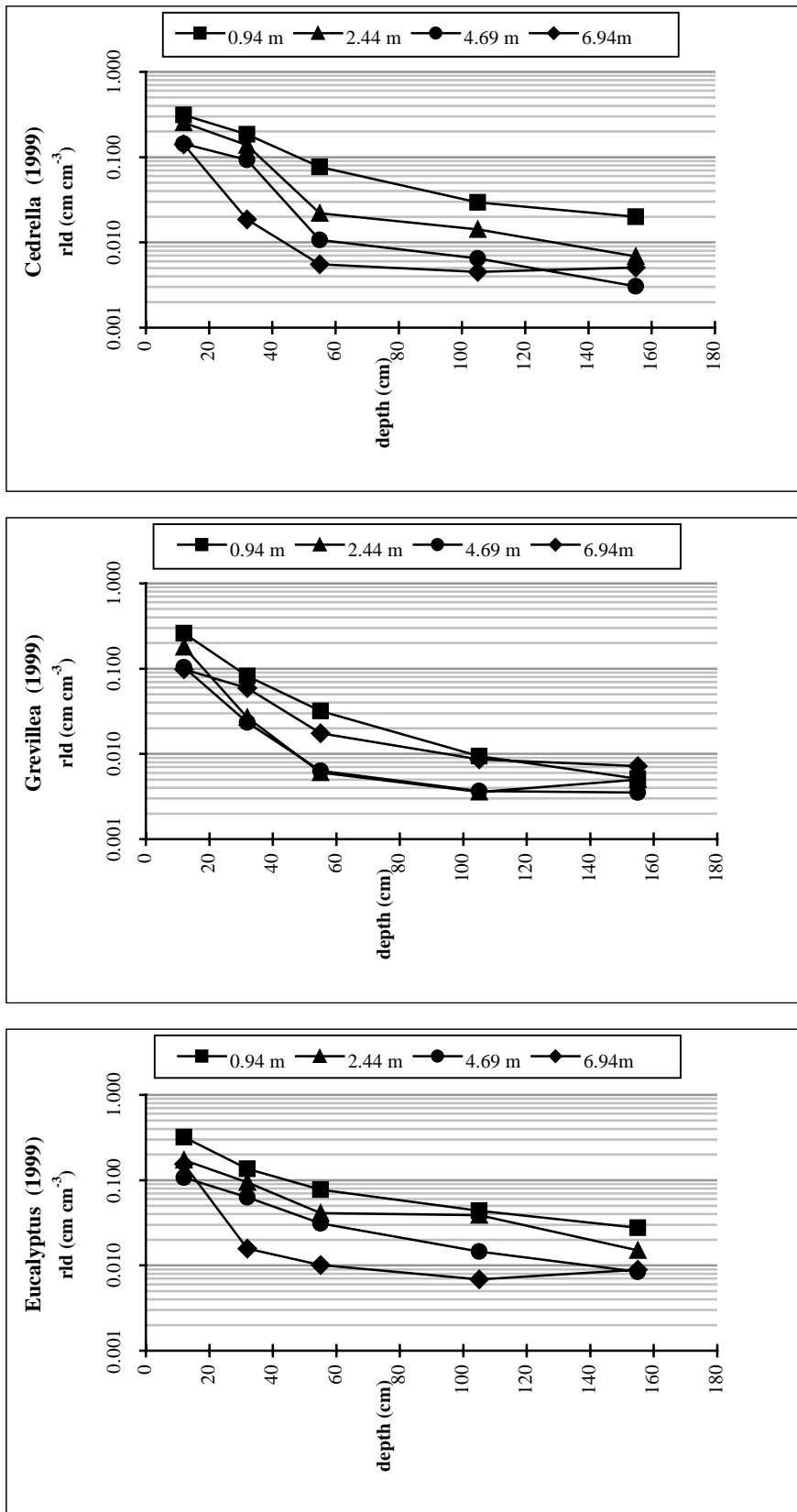


Figure 3b. Tree root length density distribution in 1999, in tree-line field experiment at Nyabeda, Western Kenya. Because of exponential decrease in rld over depth, mean rld of layer 10-30 cm is plotted at 12 cm depth, layer 30-50 at 32 cm depth, layer 50-100 at 55 cm depth and 100-200 at 110 cm depth.

Table 2 Ellips-function parameters of fine tree-root distribution (eq. 1) measured in the soil below tree-lines of *Cedrella serrata*, *Eucalyptus grandis* and *Grevillea robusta* in June 1998 and June 1999, all calculated with depth and distance in (cm). With bss: mean basal stem surface of trees next to root-sampling transect, X0: total root length per unit area (cm.cm^{-2}) at a distance of 0 cm from the tree stem, DD: parameter (cm^{-1}) governing the decrease with depth of root length density (for $X=0$ at a depth of $0.699/DD$ the root length density has half of its value at the soil surface) and DS - parameter governing the shape of the tree root system (when rld at 5 m distance is the same as at 1 m depth, than $DS = 0.2$).

	1998			1999			1998		1999			1998		1999	
	bss	X0	se	bss	X0	se	DD	se	DD	se	DD	DS	se	DS	se
	(cm^2)	(cm cm^{-2})		(cm^2)	(cm cm^{-2})		(cm^{-1})		(cm^{-1})		(cm^{-1})	(\circ)		(\circ)	
Cedrella	13,5	23,0	6,76	49,8	15,3	5,51	0,025	0,0059	0,027	0,0040	0,21	0,055	0,14	0,031	
Eucalyptus	11,7	19,0	5,92	55,9	16,1	3,93	0,033	0,0057	0,020	0,0030	0,14	0,039	0,17	0,032	
Grevillea	5,2	10,1	1,78	30,4	4,1	0,85	0,034	0,0034	0,022	0,0036	0,04	0,033	1E-11	*	

The DD variable describes the shape of the vertical root profile. A low slope is equivalent to a high DD value. The DD values are not significantly different for the tree species. However, the DD value of 1999 root-data is significantly smaller than that of 1998 for eucalyptus and for Grevillea but did not change for Cedrella. This infers that for eucalyptus and Grevillea relatively more roots have grown at depth than in the surface layers. Relatively high levels of rld at depth for Grevillea are also mentioned by Smith et al. (1999). However, the exponential decrease in rld of Grevillea over depth is much less than what we found, likely due to the dryer environment of their experiment.

The DS variable of the elliptical function describes the shape of horizontal root distribution in relation to the vertical distribution. In our situation, with all trees showing similar vertical distribution (DD), if DS is 0, root densities do not decrease over distance, and the lines in figure 3 should overlap. If DS is large, the root densities decrease rapidly with increasing distance from the tree line and lines in figure 3 are far apart. Thus, the very low DS of Grevillea, which is not significantly different from 0, and the overlap of the lines in figure 3, shows that Grevillea root length density did hardly decrease with increasing distance to the tree. DS values of Eucalyptus and Cedrella are significantly higher than 0, hence in the figure the rld lines at increasing distance to the trees become closer to the Y-axes, and root length density decreases with increasing distance to the trees. DS values change not significantly between 1998 and 1999.

Comparing root profiles with water-extraction profiles, we see that Grevillea root densities hardly changed with distance to the tree line, but soil water contents were significantly lower close by the tree line. On the other hand, Cedrella root densities decreased with distance to the tree- line but soil water contents were not significantly different when measured close by or far from the tree line. Hence, there is no direct relation between root-density distribution and changes in soil water contents as determined by tree water-extraction.

Discussion

Our results show that fast-growing trees such as Eucalyptus and Grevillea decreased soil water content during the wet season even in the sub-humid conditions of western Kenya. We consider this depletion of soil water during the wet season to be mainly determined by tree and crop water uptake rather than by rainfall interception. For example, a water balance study of *Grevillea robusta* –maize agroforestry systems in semi-arid Kenya (750 mm of annual rainfall) showed that the small reduction in rainfall input due to canopy interception was partly off-set by a reduced soil evaporation (Wallace et al 1999). Therefore it is unlikely that interception explains the large

reduction in soil water content observed in our present study. We ascribe tree-water use as the main cause of decreased soil water contents near the tree lines.

We did not find a relationship between root-density distribution and soil water extraction in the wet season, which is in contrast with the relationships used in most computer models (Rowse et al 1978; Belmans et al., 1979; Lascano and van Bavel 1984; Barataud et al, 1995), the general descriptions of how water-extraction is modeled (Campbell, 1991; Simmonds and Kuruppuarachchi, 1995), and with the way it is employed in agroforestry models such as WaNuLCAS (van Noordwijk and Lusiana, 2000) Hypar (Mobbs et al, 1998) and WIMISA (Mayus et al, 1999). In all these models water-uptake is closely related to relative root length density.

The discrepancy between the general assumption (and models), that water-uptake is closely related with root length density, and our observations in this study that root length density distribution and water-uptake are not closely related, can be explained by figure 4a. This figure can either represent a main root with branches, in which each branch is connected to a similar root-length density at their ends, or it can represent a tiny piece of root in which the branching resistance are channels for radial water inflow into the root. This small section shows already the increase in resistance, the decrease in potential and the resulting drop in influx with increasing distance from the original water-potential at the stem-base. If these small sections were multiplied to form a whole root, the decline in potential and water-uptake with distance from the base would occur according to a function e^{-xy} , as shown in figure 4b with x being the distance and y being a function of radial resistance, root-branching and axial resistance.

The principles used here are the physical principles of water-extraction by plants analogous to Ohm's electrical circuit, with a potential gradient as driving force and resistances limiting the flow rate: $q = \Delta\psi / r$ (Hillel et al., 1976; Scott Russell, 1977), with q as flux/flow, $\Delta\psi$ as potential gradient and r as resistance. Canopy and aerodynamic resistance to evaporative demand determine the suction (or potential ψ_c) at the "crown" (stem base of plant). A gradient between this plant-potential and the soil-potential (sum of matrix, gravitational and osmotic potentials) determines the direction of the flow (flux q) and the strength of suction giving $\Delta\psi_c$. Resistances in soil (1/hydraulic conductivity) and root system (as a function of root length, radial resistance and axial resistance) limit the water flow (flux q), in such a way that the highest resistance or lowest conductance is the main determinant of resistance to flow (Hillel et al., 1976; Belmans et al., 1979). Over moist and wet soil-water-content-ranges (like in our wet

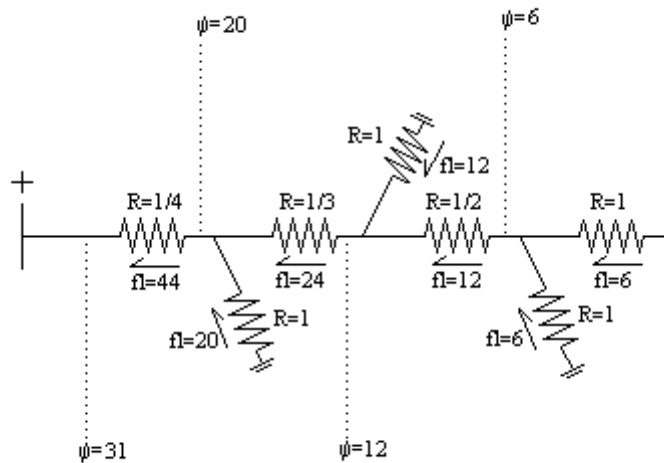


Figure 4a Section of root as electric circuit ($fl = \Delta\psi/R$). Root-branches with similar uptake-resistance (e.g. similar root-length-density or similar radial-resistance) are chosen $R=1$. The axial resistances in the main root are represented by $R=1/2, 1/3, 1/4$, all chosen smaller than the uptake resistance. At the earth-sign end of uptake-branches the potential $\psi = 0$. Flux/flow (fl) and potential (ψ) at different sites along the branched circuit/root are calculated by $fl = \Delta\psi/R$. The flux/flow into the first uptake-resistance near the + (stem-crown) is clearly higher (20) than the flux/flow into the latter uptake resistances (12, 6 resp.) and also the ψ in the circuit / main root decreases with increasing distance from the + (stem-crown).

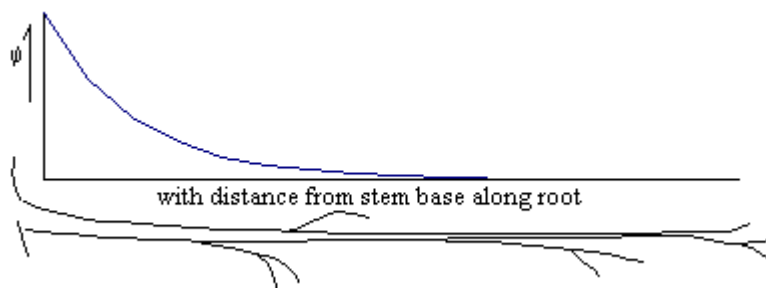


Figure 4b Course of decrease in hydraulic potential along root.

season), root-resistance usually exceeds soil-resistance (Belmans et al., 1979; Reid & Hutchinson, 1986). The situation in which soil resistance exceeds root resistance occurs only in dry soil or at high transpiration rates in coarse soils (Hillel et al. 1976; Weatherley, 1979; Hainsworth and Aylmore, 1989), and caused probably the decrease in Δd values in our dry seasons. Close to the tree lines, dry soil with higher suction and high hydraulic resistance limits water uptake, and root uptake shifts to areas with a lower suction and a higher potential gradient between root and soil.

It is generally agreed that radial root resistance is much larger than axial resistance (Burch, 1979; Reid and Hutchinson, 1986; Peterson and Steudle, 1993), and is therefore the main determinant of root resistance. Using the analogue with Ohm's electrical circuit, a doubling of root length density, doubles the amount of parallel radial resistances and thus halves the total radial resistance, so that root resistance in general is strongly related to root length density.

The origin of the assumption that water-uptake is closely related to root length density can be found in earlier soil-water-extraction models, which were made for crop fields or forest stands with a one-dimensional profile, in which root density and water extraction only varied vertically with depth. Generally, root length densities decrease exponentially over depth; hence root-resistance increases exponentially over depth, and is the main determinant of soil water extraction. As a result, in models with only a vertical dimension, water-extraction was modeled as proportional to (relative) root length density. However, if the root length density does not decrease horizontally away from the *Grevillea* tree base, and thus the total radial resistance hardly changes, differences in other flux determining factors gain importance. This is the axial resistance along a root with distance to the tree, and the water-potential of the root with distance to the tree as shown in figure 4a.

Decreasing water-uptake per unit root length as a consequence of increasing axial resistance has also been mentioned by Hainsworth and Aylmore (1989). Doussan et al (1999) show that indeed there is already a severe drop in water potential-difference over half a meter along roots away from the base of a peach tree, and that therefore, main water-uptake occurs close by the tree-base, in an equally wet soil. Taylor et al (1992) show a generally lower potential in a deeper point on a cotton taproot than on a higher point. From water profile figures of Green & Clothier (1999) it is clear that highest water extraction occurred around the tree-bases, although root densities did not show horizontal variation with distance to the tree-base in their orchard of trees.

Changes in axial resistance and root water-potential occur in the vertical direction as well, but cause smaller changes than the exponential decrease in root length density (and exponential increase in radial resistance), and could therefore be neglected, although Belmans et al (1979) mention that the fit of modeled and experimental data would probably be better if axial resistance was included.

Summarizing, if the root length density decreases far more than the decrease in water-potential gradient, water extraction can be modeled as inversely proportional to (relative) root length densities. In the soil volume this occurs in the vertical direction. But if root length-density does not change far more than root-water-potential, the decrease in root-water-potential and/or axial resistance needs to be included to avoid large errors in water-uptake distribution. This may occur in the horizontal direction.

Root distribution profiles with distance from a tree line were different for the different tree species, and changed over time, which may pose another problem to agroforestry models. Over a period of one year the root systems generally extended horizontally and reduced vertical exploitation. It may be that if a tree grows fast over a short period of time in a wet period, its root-growth is mainly by increasing root length density. On the other hand, in a dry season and after a severe pruning event, fine roots may have died, and carbohydrates for new root-growth may be preferably allocated to

extend the root system. A strategy to cover a larger soil volume, instead of producing high root densities in a small volume agrees with Fitter et al (1991). They mention that a rooting architecture with long links and branching predominantly on the main axis, although expensive in use of carbohydrates, will mainly occur in nutrient poor soils. This indicates that our observations may not only be caused by management, but also by a root-system distribution strategy adapted to depleted soils. Whether caused by management or by resource-availability, not only total root length and extent changes over time, but also tree-root-distribution, and thus elliptical parameters derived from measurements at one point in time may not be valid during the whole growth of the tree, and use of these parameters in agroforestry models (i.e. WaNuLCAS) may lead to errors.

However, as far as water-uptake is concerned, the changes in gradients of water-potential between root and soil with distance to the stem base are much larger than root-distribution changes over time. Thus it is more vital to incorporate water-potential gradients in models with a horizontal dimension, than changes in root distribution over time, as far as water-uptake is concerned.

Simulation of soil-drying-induced phosphorus deficiency and rhizosphere effects as determinants of maize growth near tree-lines

Simône Radersma, Betha Lusiana and Meine van Noordwijk

Simulation of soil-drying-induced P-deficiency and rhizosphere effects as determinants of maize growth near tree lines on a P-fixing Ferralsol.

Simone Radersma, Betha Lusiana and Meine van Noordwijk

Abstract

The effect trees have on the growth of crops, is not always explained satisfactorily by the current tree-crop interaction equations and may require understanding of interaction processes. For instance, on a P-fixing Oxisol/Ferralsol in sub-humid Western Kenya maize growth near the low nutrient demanding *Grevillea robusta*, was strongly reduced close by the tree-lines, while maize growth was slightly increased near the high nutrient demanding *Cassia spectabilis* (syn. *Senna spectabilis*).

After application of phosphorus these differences in maize growth disappeared.

These observations could not be explained by methods analyzing agroforestry system performance.

Therefore we examined tree-effects on processes determining crop-P-uptake, by using the mechanistic tree-crop-interaction model WaNuLCAS. Soil-P parameters were as measured in Kenyan and Indonesian P-fixing Ferralsols. Parameters for the rhizosphere-P-mobilization part of the model were derived from sequential-P analysis of rhizosphere and bulk soil, measurements of organic anion levels in the rhizosphere soil, incubation of organic anions in the bulk soil of field and pot-trials and root-window observations on pH-increases around *Cassia* roots.

The model simulations confirmed our hypothesis, that the 30-40% decrease in maize growth near the *Grevillea* tree line was due to 2.5 vol.% lower soil water contents (at mean levels of 38 vol%), causing decreased P-diffusion to roots and a cumulative decrease in crop and root-growth over time.

The model simulations also confirmed our second hypothesis, that high oxalate exudation and pH-increases in *Cassia* rhizosphere, are responsible for the increase in maize growth near the tree line.

Without any rhizosphere effect of *Cassia* roots on P-availability, maize growth near the *Cassia* line would have been seriously decreased, due to *Cassia*'s high demand for P.

Simulation of positive *Cassia* rhizosphere effects together with negative *Grevillea* soil drying effects, revealed that the negative water-induced-P-deficiency easily offsets any positive rhizosphere effect on maize growth.

Thus, management options, including choice of tree species, that lead to low tree water use can decrease negative effects of trees on crop yield on P-limiting tropical soils, even if water is not limiting crop growth per se. Once soil drying is prevented, high P-mobilization of the tree becomes important to prevent direct competition for available P between tree and maize crop and to increase the performance of the neighboring maize crop.

Introduction

Trees are a common feature in the agricultural landscape of Western Kenya and many other tropical areas with small-scale subsistence farming. Attractiveness of agroforestry systems depends on the combined value of the components, including market and socio/cultural considerations. The biophysical performance of such a system may be taken as a starting point in assessing its feasibility (Cannell et al, 1996). Biophysical performance of simultaneous agroforestry systems is determined by tree and crop yields, modified by tree crop interactions.

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 in

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, combined with an environmentally specific degree of limitation. These methods have the advantage that they are relatively simple to use and give useful assessment of performance in many cases. Although they are usually applied on plot scale they can also be used for zones with increasing distance to trees. The disadvantage of these methods is, that they have no time dimension and therefore i) do not allow for evaluation of system performance over multiple crop cycles and long-term sustainability, and ii) do not deal with delayed processes (e.g. nutrient mineralization). Moreover, the simple sums used in these equations cannot cope with situations where two determinants of performance interact. Mechanistic research is more appropriate in situations where the above-mentioned disadvantages are important.

In an experiment in Western Kenya, we observed that maize growth was decreased near *Grevillea* tree lines, while there was a small but significant increase in maize growth near *Cassia* tree lines. Ong's method would point out that, because F is absent (no organic material from the tree applied), only 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 at this site 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*. Evidently, the methods of Ong and Kho could not explain the observed tree effects on maize yields and led to the following questions:

- 1) what causes *Grevillea* to compete with maize in this primarily P-limiting environment, while its demand for nutrients is relatively low,
- 2) how is *Cassia* able to improve maize yield when all organic matter is continuously removed and its nutrient-demand is relatively high, and
- 3) to which extent do the mechanisms responsible for above mentioned effects (negative and positive effects on maize growth) outweigh one another, if they were effects from the same tree.

Because P is the main limitation to maize growth in Western Kenya, we assumed that trees affect crop-growth by their effects on crop-P-uptake.

Factors important for P-uptake are: the available fraction of total soil P, root-length densities (+mycorrhiza) and soil water content. The last two factors are especially important for P uptake at low levels of available P, because P-mobility in soils is low.

Trees decrease available-P because they use P themselves and they may increase available-P by root exudate effects. Root exudates can increase P-desorption and dissolution and may turn organic-P into inorganic-P, as examined for e.g. Cassia, Grevillea and maize (Chapter 4).

Trees may also affect root length densities of crops by allelopathy (Ridenour and Callaway, 2001) or through increases in root:shoot ratio in case of competition (Marschner, 1995). However, lower amounts of assimilates allocated to shoot result in lower biomass production rates and to smaller amounts of assimilates allocated to root in the following time step. This causes that aboveground crop growth is both positively and negatively affected by increasing root:shoot ratio, likely minimizing the total effect.

Tree-roots with their mycorrhizal associations may also increase the rate of mycorrhization 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 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 various possible tree-effects on crop growth

WaNuLCAS (van Noordwijk et al, 1999; van Noordwijk and Lusiana, 2000), a mechanistic model of tree-crop interactions, 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.

Materials and Methods

The trial

The field trial, tree lines bordering maize fields, was established on depleted farmers' land in sub-humid Western Kenya in 1993.

The soil was a deep (>3 m), depleted Oxisol/Ferralsol, with a pH of 5-5.5 and clay contents ranging from 50% in the topsoil to 80% in the subsoil.

The experimental design was a randomized complete block with four treatments and four replicates: sole maize, maize with a line of *Grevillea robusta*, maize with a line of *Cassia spectabilis* and maize with a line of *Calliandra calothyrsus*. Plot sizes were 16 * 20 m with the tree lines in the middle of the 16 m side, over the whole 20 m length of the plots. Spacing of the trees in the line was 0.5 m for Cassia and Calliandra and 1 m for Grevillea. Maize rows were 0.75 m apart, parallel to the tree line

(first maize row 0.37 m next to tree line) with inter-plant spaces of 0.25 m. Plots were weeded once or twice per season.

Where the trees bordered the plot, 2 m deep metal sheets were installed in trenches in the soil over about 3 m distance on each side of the tree line, to avoid tree-root penetration in neighboring plots. In this paper only the treatments of *Cassia* and *Grevillea* are discussed.

Measurements in the trial

Soil water measurements used were taken during half a year on 3 to 4 week intervals using a neutron probe (Didcot Instruments, Wallingford, UK). Water measurements were done at five distances from the tree line (0.37 m, 1.12 m, 2.62 m, 4.87 m 7.87 m), which coincide with maize rows, at six depths (0.35 m, 0.70 m 1.05 m, 1.40 m, 1.75 m, 2.10 m) on both sides of the plot. Calibration of the neutron-probe was done with 8 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-barrel-counts. Then, 7 volume rings (100cc) 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 20 cm radius around the measurement point. Rings were weighed wet, oven-dried for 48 hours (108 °C) and weighed dry, to derive the vol. % water. Bulk density was derived from the same procedure.

Maize was harvested per row (row 1-5 away from the tree-line) or two rows (6-11 away from the tree-line), combining both sides of the tree line, because no differences in side were visible. Fresh weight 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.

Brief description of WaNuLCAS, with special attention to phosphorus.

The tree-crop-interaction-model WaNuLCAS uses daily time steps. It divides the area bordering a tree line in 4 parallel zones, one tree-zone and three crop-zones with increasing distance to the tree-line, with each 4 soil-layers (Figure 1a). Zone width and layer depth are input values.

Uptake of mobile-P

Phosphorus uptake is modeled as shown in figure 1b. Phosphorus uptake on each day starts with calculating the target P-content for the current biomass of trees (split up in 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.

Next, potential nutrient-uptake from each cell (zone x layer) of each component (crop or tree) is calculated from equation 1, assuming zero-sink uptake:

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

Where U_{ijk} is the potential nutrient uptake from each cell ij by each plant-component k , Lrv is root length density (cm.cm^{-3}), D_0 is the diffusion constant for the P in water, θ is the volumetric soil water content, a_1 and a_2 are parameters relating effective diffusion constant to θ , H is the depth of the soil layer, P stock 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/ potential P-uptake) smaller than potential uptake. If P-demand exceeds potential P-uptake, actual P-uptake equals potential-P uptake. Finally, actual uptake has a feedback on plant growth (Figure 1b).

Tree and crop root densities and distribution can be modeled as fixed measured Lrv values, or as responding to above ground plant-growth. Mycorrhiza are modeled as an extension of root length density using three 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-Olson values and its availability depends on a chosen adsorption isotherm (range of isotherms as input available). The second pool is the immobile-P pool, which only feeds into the mobile P-pool by a weathering parameter or by rhizosphere-P-mobilization.

Further details on the overall structure of the model can be found in van Noordwijk and Lusiana (2000) and van Noordwijk et al. (1999).

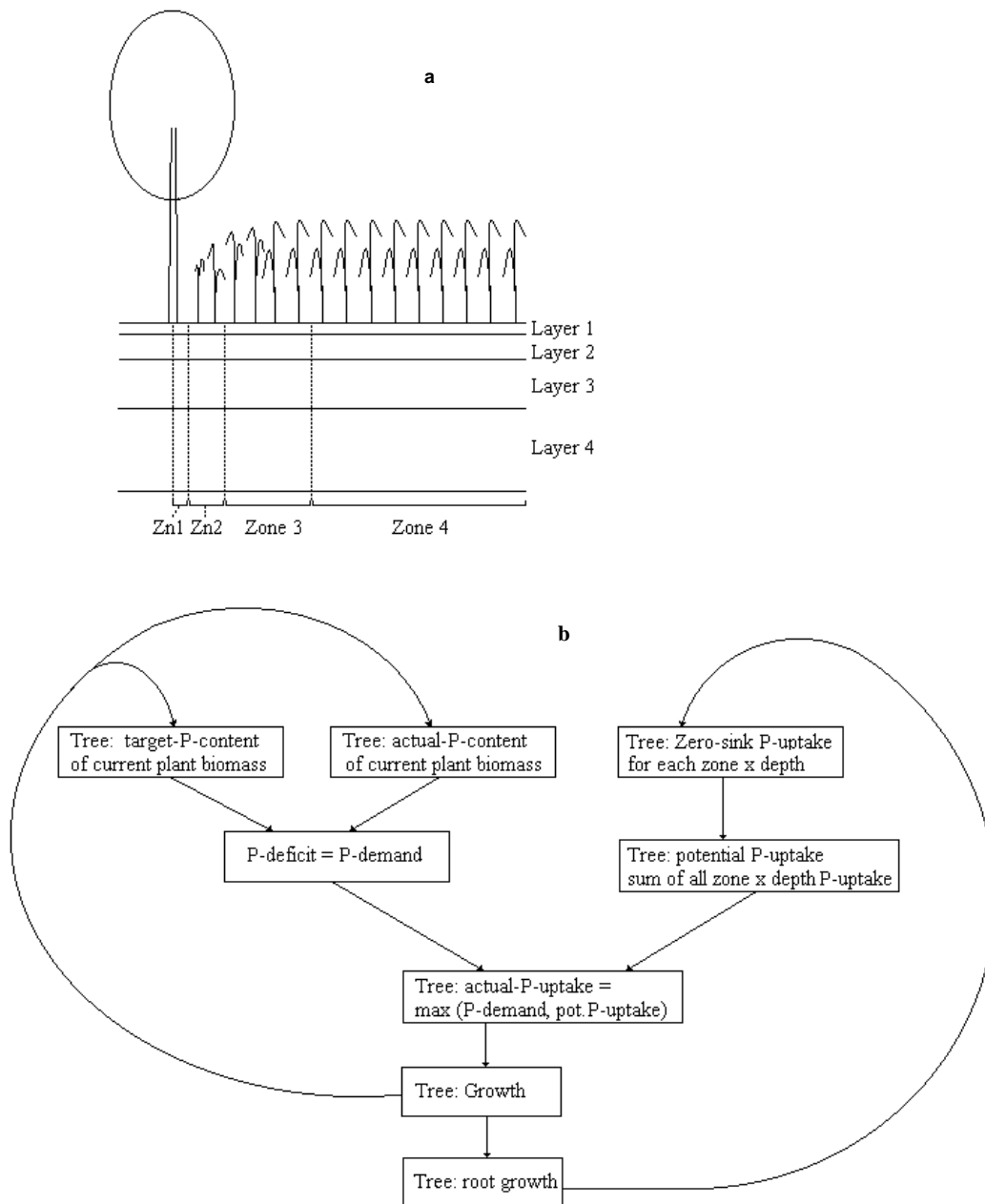


Figure 1. Spatial structure of WaNuLCAS as used in the simulations (a) and structure of nutrient and water model (b)

Rhizosphere effects on P-availability

Rhizosphere effects on P-availability were modeled as a) use of immobile-P (if P-uptake of one tree/crop component is equal to P-mobilization of the same component) or b) transfer from immobile to mobile P (if P-uptake is by other component as P-mobilization).

Ad a) If easily available P-fractions (i.e. resin-P) in 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* (Chapter 4)), 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. This use of immobile-P by trees needed an adjustment in the model, which was achieved by setting tree P-demand at zero⁹. 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 (Chapter 4)), we assumed that P-uptake and plant-growth adjust to low available P, and the model can be used as it is, with P-uptake from the mobile-P pool only.

Ad b) The extent to which a maize-crop can profit from having parts of its root-system in tree-rhizosphere soil at the time P-mobilisation takes place, was modelled as a transfer of P from the immobile to the mobile P-stock, by a tree-P-mobilisation parameter (T-Pmob). The T-Pmob calculated how much more immobile P becomes available in the rhizosphere due to 1) organic anions and 2) pH increases.

This T-Pmob of the tree rhizosphere was then multiplied by three factors i) the fraction of the total soil volume which was tree-rhizosphere for each cell (rhizosphere soil volume within cell / total volume of cell), 2) the fraction of total soil volume which was maize-root for each cell (maize root volume within cell / total volume of cell) 3) a synlocation parameter, which indicated whether the overlap of tree-rhizosphere and maize roots was above the expected overlap (synloc.>1) or below (synloc.<1) (Chapter 5).

Soil water content

The water-use and soil-water distribution part of the model was switched off. Instead, measured soil water contents were used in the simulations.

⁹ In the model, P-uptake is from the available-P pool. If the tree uses immobile-P via P-mobilization, the tree does not take P from the available-P pool. This zero use of available-P is achieved by setting P-demand at zero (all plant-part P-content are set at zero). This works fine for the short term in which tree-P-uptake is a minimal part of the immobile-P-pool.

Deriving the input parameters for WaNuLCAS

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

Choice of P-parameters

A list of soils with known double-Langmuir¹⁰ P-adsorption isotherm is provided. We chose a strongly P-sorbing Indonesian soil (Sitiung1¹¹) for the three lower layers, and a somewhat less sorbing Indonesian soil (Lampung BMSF¹²) for the top-layer. Alternatively, a more sorbing scenario was used with a higher sorbing Indonesian soil (RbujungU¹³) for the three deeper layers and Sitiung1 as top-layer.

Measured P-Olsen values of the trials described above, for the different layers were input values for initial mobile-P. The 3-4 year old tree lines did not have an effect large enough to cause different P-Olsen values in the different zones yet.

Because only the use of P-Bray was specified in the model, and original field P-contents in our trial were measured as P-Olsen, the values of P-Olsen were transformed in values of P-Bray, using the relationship $P\text{-Bray} = 1.60 * P\text{-Olsen}$ ($R^2=0.936$), derived from measurements in about 100 Kenyan soils (P. Smithson, unpublished data).

Total-P in the soil is about 500 mg kg⁻¹ (P. Smithson, personal communication) and this value was used to calculate initial immobile-P in each cell.

To allow available-P levels to change minimally over time and over distance to the tree line (like P-Olsen values in reality), 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.

Tree and Crop parameters

Tree input parameters were derived from measurements (table 1).

Root parameters were derived from measurements in the field trial for Grevillea and maize from chapter 7 and for Cassia from Livesley (unpublished data). For tree root densities over distance and depth, root type 1 was chosen. Root type 1 describes the root distribution as an elliptical function, derived from measured root length densities of the trees by a non-linear fitting procedure (Chapter 7).

¹⁰ Double-Langmuir isotherm: $P\text{-sorbed} = \text{SorbMax1} * \text{SorbAff1} * \text{Conc} / (1 + \text{SorbAff1} * \text{Conc}) + \text{SorbMax2} * \text{SorbAff2} * \text{Conc} / (1 + \text{SorbAff2} * \text{Conc})$

¹¹ Sitiung 1: $\text{SorbMax1} = 4.71 \text{ mg P cm}^{-3}$, $\text{SorbMax2} = 1.95 \text{ mg P cm}^{-3}$, $\text{SorbAff1} = 523 \text{ ml mg}^{-1}$, $\text{SorbAff2} = 666 \text{ ml mg}^{-1}$

¹² Lampung BMSF: $\text{SorbMax1} = 4.51 \text{ mg P cm}^{-3}$, $\text{SorbMax2} = 0.05 \text{ mg P cm}^{-3}$, $\text{SorbAff1} = 565 \text{ ml mg}^{-1}$, $\text{SorbAff2} = 725 \text{ ml mg}^{-1}$

¹³ RbujungU: $\text{SorbMax1} = 9.9 \text{ mg P cm}^{-3}$, $\text{SorbMax2} = 0.02 \text{ mg P cm}^{-3}$, $\text{SorbAff1} = 700 \text{ ml mg}^{-1}$, $\text{SorbAff2} = 1884 \text{ ml mg}^{-1}$

For maize root length densities over depth root type 1, an elliptical function with fixed lrv (root length densities) and root type 2, like type 1 but with lrv as function of above ground biomass growth, were used to compare their results in the simulations.

Rhizosphere effect parameters

We found that *Grevillea* and *Cassia* are mobilizing sufficient P to supply their own demand (Chapter 4). Therefore, the P-uptake from the mobile-P pool of both trees was set zero in the simulations, because if P-uptake equals P-mobilizations these trees tap from the immobile P-pool.

Transfer of immobile-P to mobile-P by the tree to the advantage of maize, was simulated only for *Cassia*, because only *Cassia* was likely to affect maize-P-uptake significantly, due to the relatively high synlocation of cassia and maize roots, the relatively long period of Cassia's rhizosphere modifications and the similar sink strength for P of maize and Cassia roots in the shared Cassia rhizosphere (Chapter 5).

The tree P-mobilization parameter (T-Pmob) was the sum of two factors, 1) the P-mobilization by pH increase and 2) the P-mobilization by organic anion ligand exchange.

Each of these two factors was calculated by:

$$P_{ex} / P_{tot} * t_{rhiz} / t_{rt} * fr_{rhiz} \quad (Eq. 2)$$

With P_{ex} as the extra P available at the specific level of that rhizosphere effect, P_{tot} as total P, t_{rhiz} as the period the effect lasted, t_{rt} as total root life length and fr_{rhiz} as the fraction of the root system, which showed this effect.

P_{ex} was calculated by:

$$(P_{rhiz} - P_0) / P_0 * P_{0mod} \quad (Eq. 3)$$

With P_{rhiz} as the measured available-P at the particular level of rhizosphere-effect, P_0 as the measured available-P without the rhizosphere effect and P_{0mod} as the available-P (initial Olsen-P) used in the model. In rhizosphere soil of Cassia, pH increases took place but the exact level was not measured. Therefore we tested two scenarios, pH 7 and pH 8.5. Similarly, organic anion loading over the whole period was not exactly known, but measurements of organic anions in the rhizosphere: citrate break-down curves and period-length of gel-prints (Chapter 4 and 5) led to a calculated loading range in rhizosphere soil of 120-600 mg_{oxalate} kg_{soil}⁻¹. The effects of this loading on transfer of immobile to mobile-P were derived from linear extrapolations from the increase in resin-P of a citrate loading of 30 mg kg⁻¹. The measurements for Cassia (Chapter 4 and 5), to derive the model-parameters are shown in table 2.

Table 1 Key parameters used in the WaNuLCAS simulations.

Soil-P parameters	layer 1	layer 2	layer 3	layer 4	Comments
P-adsorption isotherm	Lampung BMSF	Sitiung 1	Sitiung 1	Sitiung 1	sorbing scenario
	Sitiung 1	Rbujung U	Rbujung U	Rbujung U	strongly sorbing scenario
Initial immobile-P (mg kg ⁻¹)	500	500	500	500	
Initial Olson-P (mg kg ⁻¹)	1,3	0,5	0,55	0,7	
Pmob (d ⁻¹)	1.6*10 ⁻⁵	8*10 ⁻⁶	4*10 ⁻⁶	2*10 ⁻⁷	transfer of P from immobile to mobile P
Tree and Crop parameters					
	Cassia	Grevillea		Maize	Comments
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		-	
Potential growth rate (kg.m ⁻²)	0,02	0,015		0,028	
roots					
Type	1	1		1 / 2	type 1 - elliptical function with fixed lrv
X0 (cm cm ⁻²)	15,0	10,1		50,0	type 2 - type 1 but lrv dependent on shoot-growth
DD (m ⁻¹)	1	3,41		4,98	
DS ()	0,045	0,04		-	X0 and DD similar in all zones
T-Pmob at pH-7 (m ² d ⁻¹)	3.04*10 ⁻⁵	-		-	
T-Pmob at pH-8.5 (m ² d ⁻¹)	6.07*10 ⁻⁵	-		-	
T-Pmob at oa load 120 (m ² d ⁻¹)	1.01*10 ⁻⁴	-		-	
T-Pmob at oa load 600 (m ² d ⁻¹)	5.07*10 ⁻⁴	-		-	
T-M-root synlocation ()	1,85	-		-	
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	

Table 2. Measurement derived parameters to calculate the tree-P-mobilization (T-Pmob)

	pH - 7	pH - 8.5	oa - 120	oa - 600
$(P_{rhiz}-P_0)/P_0$ ()	0.65	1.3	8.36	41.8
t_{rhiz} (d)	38.5	38.5	10	10
t_{rt} (d)	450	450	450	450
fr_{rhiz} ()	0.21	0.21	0.21	0.21

The degree to which maize roots share Cassia rhizosphere (T-M-root-synlocation) is taken from chapter 5. It was determined from root-wall images, by multiplying the total fractions of maize-root surface with the total fraction of cassia-rhizosphere surfaces, giving the expected overlap, and comparing this expected overlap with the real measured overlap in the images.

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 a zone close by the tree to a zone far of the tree (as used in the simulations).

Soil water-contents over depth and with distance to the tree lines as measured in the trial were used in the simulations.

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

Model simulations

The first series of simulations examine the effect of small decreases in soil water contents on maize biomass-yield. These simulations are 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.

The third series of simulations investigates the effects of a Cassia tree line on the maize yield in the zones with distance to the tree. We tested the effects of slightly different soil water contents and rhizosphere effects on P-availability.

In the last series of simulations we combined the second and third series, including the hypothetical situations of Cassia rhizosphere effects with Grevillea water-effects on P-availability, transport, uptake and concomitant maize yields.

Results

Maize yield and soil water contents in the field trial

Maize biomass yields with distance to the tree line of Cassia and Grevillea are shown in figure 2. Yields were slightly but significantly higher near the Cassia tree line, except for the first row, which may suffered mainly above ground competition with the Cassia hedge. In contrast, maize yields decreased strongly and significantly with decreasing distance to the Grevillea tree line. Soil water contents are given in figure 3, and show a similar pattern as maize yields. Soil water contents close to the Cassia tree line seemed to be slightly higher than further away, and soil water contents near Grevillea decreased significantly to values of about 2.5 vol % less soil-water next to the tree line, suggesting that decreases in soil water content affected maize yield near the Grevillea tree-line. However, if P was applied, there were only small decreases in maize growth near the Grevillea tree-line (data not shown), suggesting that water deficiency per se was not a problem.

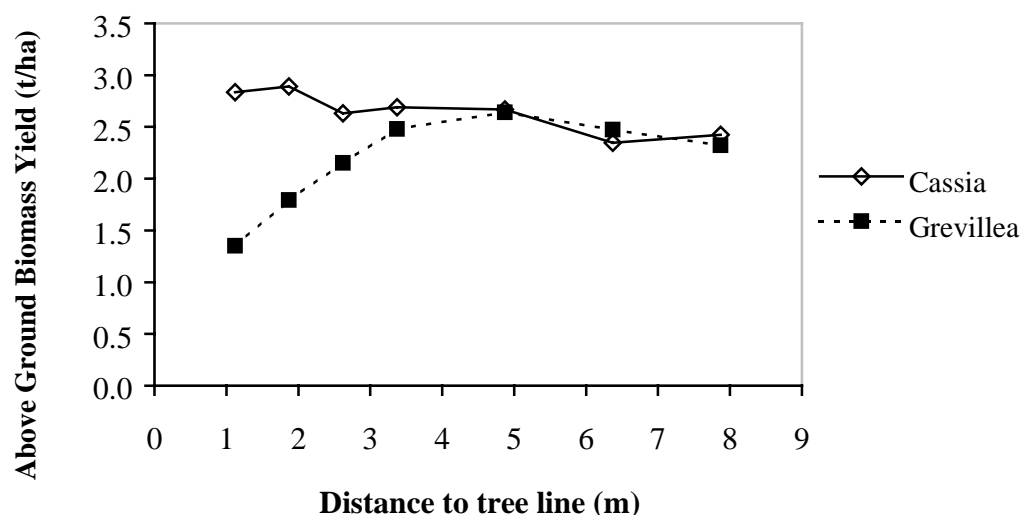


Figure 2. Maize biomass yield measured with distance to tree lines of Cassia and Grevillea in the field experiment.

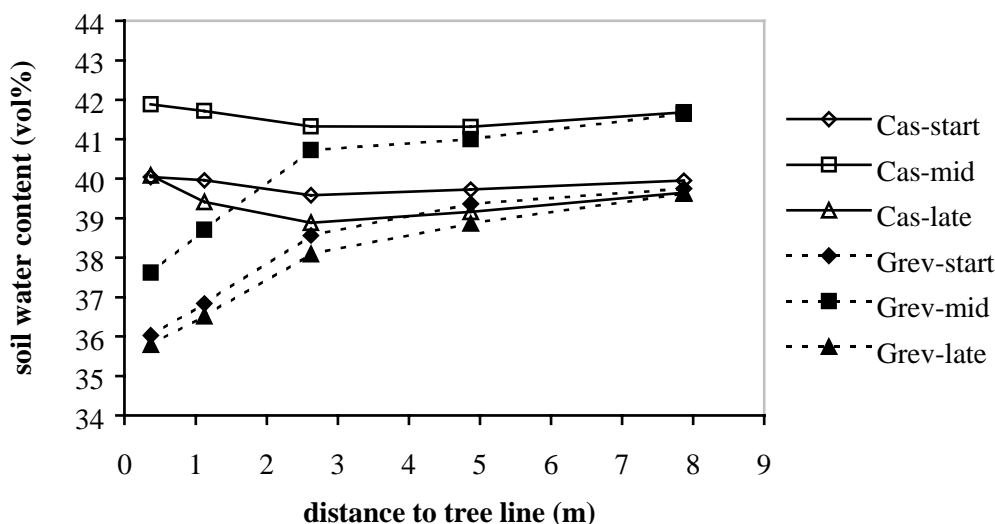


Figure 3. Soil water contents with distance to Cassia and Grevillea tree lines as measured in the field experiment.

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 maize biomass yields of zones at different distances from the tree lines (not shown), although absolute yield levels changed. Because in all simulations we used relative biomass yields (yield of zone (x) : yield of zone (4)) in comparison with measured yields, the choice of sorbing scenario did not affect the outcomes as described below.

First series: Effects of soil water contents as measured near Grevillea on maize

The first series of model simulations, investigating different aspects of soil-water content effects on P-transport, uptake and crop-growth are shown in figure 4.

In the first simulation of the first series (Figure 4a) lower soil water contents in zone 2 decreased P-diffusion to roots, and caused that biomass yield in zone 2 (the first crop-zone near the tree line) was 87 % and in zone 3 (the second crop zone away from the tree-line) 89 % of the yield in zone 4 (the crop zone furthest away from the tree-line). Root length densities of maize are the same in all zones, independent of aboveground biomass growth (Irv in figure 4a). In figure 5a the relative yield levels of this run for zones 2, 3 and 4 are plotted as squares called Mod.P.wat. Clearly the relative yield levels reached by only simulating the differences in P-diffusion does not yet come close to the measured yield levels.

The second simulation of the first series (Figure 4b), shows the difference in crop above ground biomass yields in the zones as affected by P-diffusion and with root-growth dependent on above-ground biomass growth. This infers that an iterative / cumulative effect occurs: At day 1 in the

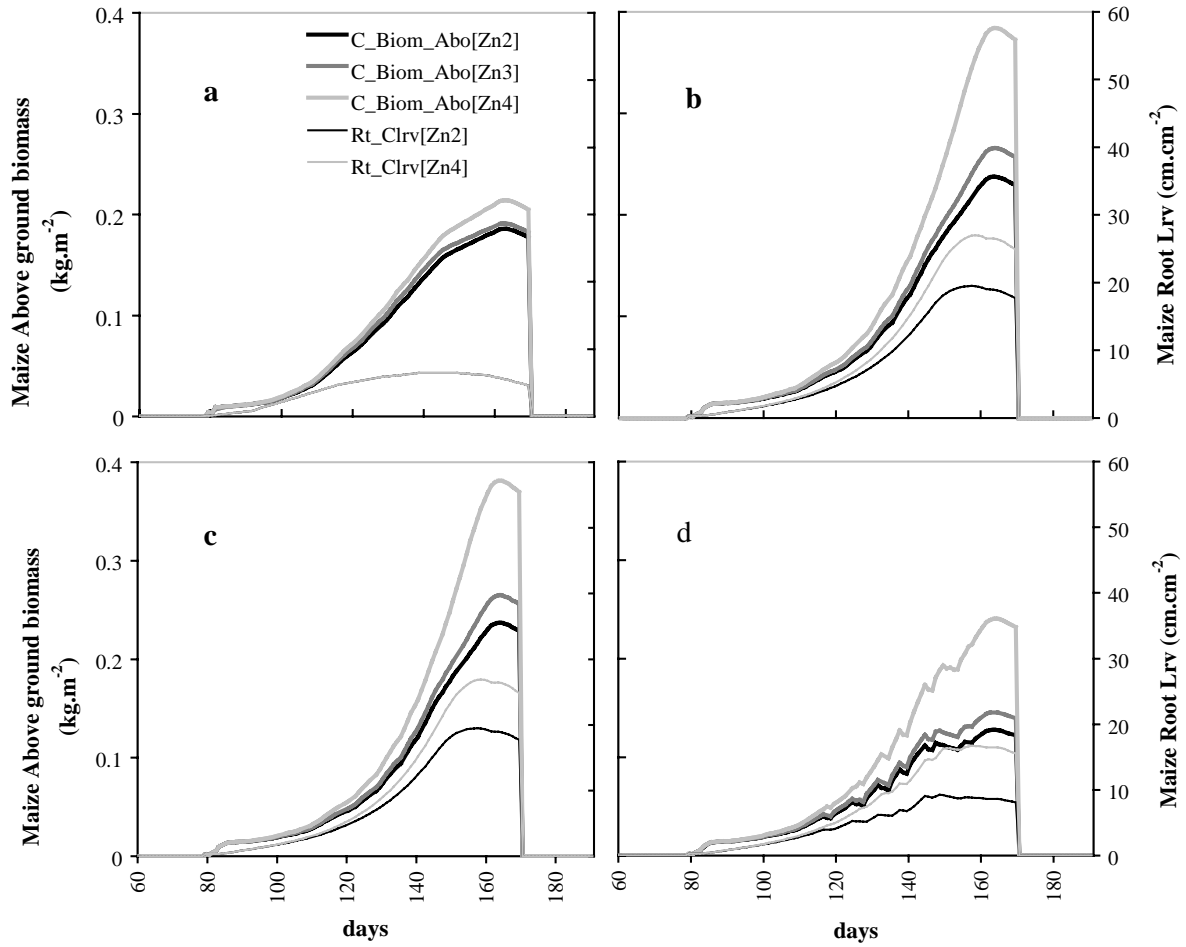
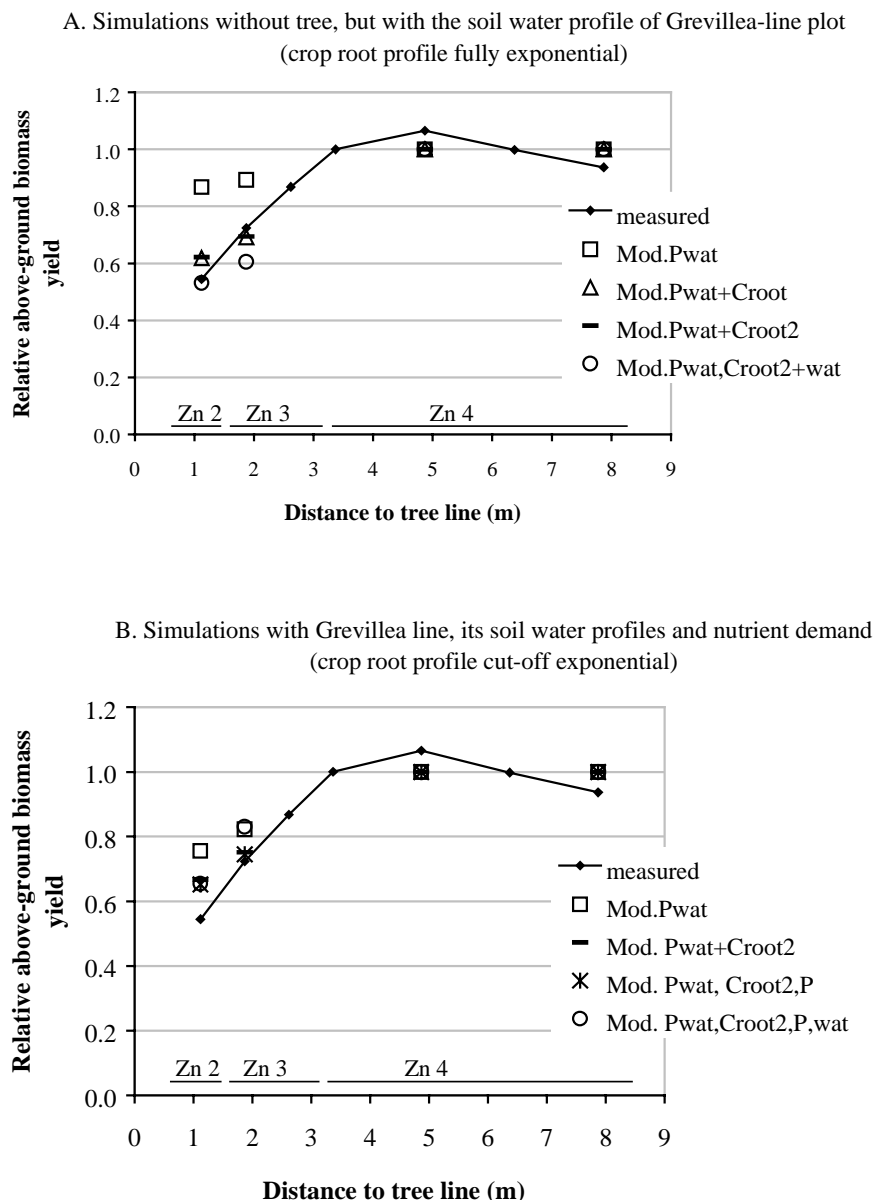


Figure 4 Simulated maize aboveground biomass production (C_Biom_Abo) and root length densities (Rt_CLrv) at different soil water contents as measured with distance to Grevillea tree line (zone 2 lowest, zone 3 intermediate and zone 4 highest), but all in a high pF range. Image a. with fixed crop-root profile (same in all zones, two Rt_CLrv lines follow same course), b. with maize root growth dependent on above ground biomass growth, c. with flexible root : shoot ratio, responding to local resource availability and d. including water-deficiency per se.

simulation, lower soil water contents cause less P-uptake (through hampered diffusion) and cause decreased biomass growth, which again decreases root growth. In day 2 in the simulation both P-diffusion and root-length are lower in the zone with lower-soil-water-content, which in turn causes a seriously lower P-uptake. This continues during all days of the vegetative growth period of this simulation and results in relative yield levels compared to zone 4 which are 62 % in zone 2 and 69 % in zone 3, which is much closer to the measured yield levels, as shown by the triangles in figure 5a (called Mod.Pwat+Croot).

Figure 5. Measured and simulated relative maize biomass yields. Figure a. without tree-line but with soil water contents as measured near Grevillea, and figure b. with Grevillea-line, its soil water profile and P-



demand, but with modified crop root system (not fully exponential as in a. but with a maximum at the lrv-level of 10 cm depth).

The third simulation of this series (Figure 4c) adds to the second simulation that root : shoot ratios are allowed to vary as reaction of the crop to local stress. In zones 2 and 3 where water contents are lower and thus P-stress is more severe, a slightly higher fraction of assimilates is allocated to roots (model output data not shown). The response allows for more optimal allocation of assimilates, but the relative biomass yields plotted as dashes called Mod.Pwat+Croot2 in figure 5a hardly differ from those in the second simulation (62 % in zone 2 and 69 % in zone 3).

The fourth simulation of the first series (Figure 4d) adds direct water stress effect to the former described effects on crop growth. This increases the difference between final crop biomass in the different zones slightly. The relative maize biomass yields compared to zone 4 are 53 % in zone 2 and 61 % in zone 3, plotted as circles called Mod.Pwat+Croot+wat in figure 5a. The relative yield levels reached by simulating indirect plus direct water stress effects comes even closer to measured relative yield level for zone 2, but is below measured relative yield level for zone 3.

The 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 is included, and some inputs were changed. The exponential root-profile of crops was changed into a cut-off exponential profile for crop-roots, with a maximum lrv at 10 cm depth and above instead of an increase of lrv to infinite values in the topmost centimeters of the soil. This prevents an unrealistically high competition between tree and crop for topsoil resources. This adjustment changed the results of the simulations of the second series (Figure 5b, squares, dashes and circles) somewhat as compared with the results of the simulations of the first series (Figure 5a, squares, dashes and circles). The direct P-diffusion effect on maize biomass yield became larger, and the iterative effect via root-growth became smaller. The direct water-limitation effect became smaller, likely because the lower fraction of roots allocated to the topsoil made the crop growth less sensitive to direct water stress due to drying topsoil.

The minimal difference between the simulation without and including P-demand of the Grevillea tree line (dashes called Mod.Pwat+Croot2 and stars called Mod.Pwat+Croot2, P in Figure 5b), shows that direct competition for P between the Grevillea and maize is minimal.

The third series: Effects of Cassia's soil water profile and rhizosphere effects on maize

The third series of simulations investigates the effects of a Cassia tree line (soil-water, P-demand and rhizosphere effects) on the maize yield in the zones with distance to the tree.

The first simulation of this series, at soil water contents as measured near Cassia tree lines in the field and assuming that Cassia takes up P from the mobile P-pool (no rhizosphere effects), is shown by the squares in figure 6. Clearly, at P-uptake by the tree from the mobile P-pool (without any root-

exudate effect) competition for P between tree and crop would cause that the relative maize yields would be considerably lower close by the tree line than far from it, which is not in agreement with the measured maize biomass yields.

The second simulation of this series, at the same soil water contents, but assuming that Cassia takes up P from the immobile P-pool (i.e. Cassia mobilizes as much P from the immobile P-pool as it takes up from the mobile P-pool), is shown by the triangles in figure 6. Because direct competition for mobile-P is absent, only water-contents determine P-uptake differences in the different zones and closely related to the soil-water-contents (Figure 3). The relative maize biomass yields in this second simulation are still below the measured yield levels of zone 2 and 3.

In the remaining 4 simulations of the third series (fine lines in figure 6), additionally to the settings of the second simulation, maize is able to take up P mobilized in the rhizosphere of Cassia. The range between minimum P-mobilization (oa120+pH7) and maximum P-mobilization (oa600+pH8.5) in the simulation, resulted in an increase in relative maize yields near the Cassia line, ranging from 109 % to 135 % in zone 2 and from 101 % to 113 % in zone 3. The measured relative yield levels

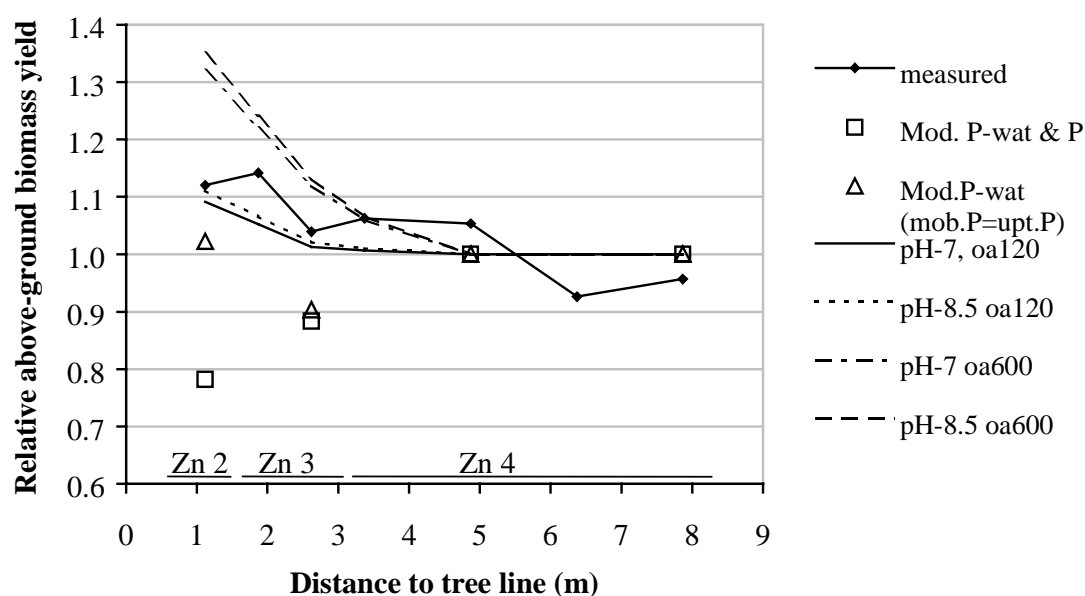


Figure 6. Simulated and measured relative maize biomass yields with distance to Cassia tree line. Squares called Mod.P-wat & P represent the simulated maize growth near cassia in which Cassia does not show any rhizosphere effect and its P-uptake is all from the small available P-pool, The triangles called Mod.P-wat represents the simulated maize growth near Cassia when Cassia taps from the immobile P-pool (assuming P-uptake = P-mobilization). The lines with pH..oa.. codes represent the simulated maize growth near Cassia when Cassia taps immobile-P and mobilized P in its rhizosphere is available to maize roots growing in Cassia's rhizosphere, at different combination of pH (7 or 8.5) and total organic anion loading of the soil (120 or 600 $\mu\text{mol g}_{\text{soil}}^{-1}$).

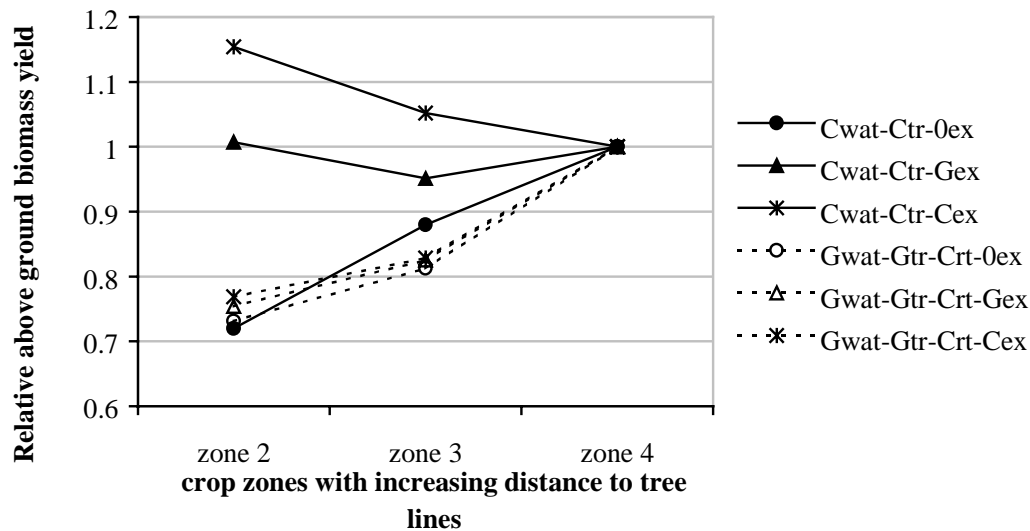


Figure 7. Simulated relative maize biomass yields as determined by soil water content, tree-P demand and root exudate effects on P-mobility. With Cwat: soil water profile as measured in Cassia tree-line plots, Gwat: soil water profile as measured in Grevillea tree-line plots, Ctr: Cassia tree characteristics (esp. nutrient demand and root-distribution), Gtr: Grevillea tree characteristics (esp. nutrient demand), but not its root distribution, Crt: Cassia's root distribution, 0ex: at no root exudate effect of the tree (tree competes directly with crop for mobile-P), Gex: at first root exudate effect of the tree (tree taps from immobile P-pool, its P-mobilization = P-uptake), Cex: at first and second root exudate effect, with the second exudate effect (maize taps from mobilized P in tree-rhizosphere) as fitted for Cassia.

are increases near Cassia of 112 % in zone 2 and 104 % in zone 3 are within the simulated range. If fitting a relative yield-line of a model simulation close to the measured relative maize yield line in the Cassia plots, the $\Sigma T\text{-Pmob}$ ($T\text{-Pmob}(\text{oa} + \text{pH})$) is 2.6×10^{-4} . This T-Pmob was used in the next simulations.

The fourth series: Combining effects of series 1 and 2 with those of series 3.

In the last series of simulations we combine second and third series (figure 7) six combinations were simulated.

The Cassia with its own soil-water-profile and its own rhizosphere effects (stars in continuous line called Cwat-Ctr-Cex in fig. 7) has the most favorable effect on maize biomass production, as we saw in figure 6 as well. Simulating maize growth near Cassia without any root exudate effect (black circles in continuous lines called Cwat-Ctr-0ex) shows that if Cassia did not modify its rhizosphere and tapped its

entire P-demand from the mobile P-pool, direct competition for P between Cassia and maize would be high and would decrease maize levels close by the tree-line to a similar extent as the soil-drying induced P-deficiency did near Grevillea, as shown by all dotted lines in figure 7.

In all simulations of maize at soil water profiles as measured near the Grevillea tree line, the decreases in maize-growth approaching the tree-line are prominent. This infers that the negative soil-drying-induced P-deficiency effect on maize growth is much stronger than even the best

exudate effect (Cex). Moreover, the differences in 0ex, Gex and Cex, which were large for Cassia, are minimized for Grevillea, partly because Grevillea's P-demand is relatively low, and therefore its direct competition for P with maize is less (explaining the small difference between Gwat-Gtr-Crt-0ex and Gwat-Gtr-Crt-Gex), and partly because a slight increase in available soil-P is of little use if its transport is hampered by decreased soil water contents.

Discussion

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 2-2.5 vol.% water close to the tree line decreased aboveground biomass production of the maize crop by 30-40%. Model simulations revealed that water limitation per se played a minor role in this effect, and that the main causes are two water-P-plant interaction mechanisms, 1) the decrease in soil water content decreases P-diffusion, and thus P-transport to the roots and P-uptake, and 2) root-growth (and thus uptake of resources) is reduced because of lower above ground biomass production caused by lower P-uptake through decreased P-diffusion. Decreased soil water contents were measured near a Grevillea tree line. Including the Grevillea tree line in the model simulation, thus adding nutrient-demand of the tree, showed that direct competition for P by the Grevillea (with low P-demand) on the crop was minimal compared with the soil-drying-induced P-deficiency effect.

In contrast, if soil drying was minimal, and the tree had a relatively high demand for P, like in our Cassia-maize system, direct (although delayed) competition for P reduced the maize yields near the tree line to a similar extent as the soil drying induced P-deficiency near Grevillea. Hence, high P-demand of a tree without P-mobilizing capacity can be as detrimental to crop-growth as soil-drying induced P-deficiency.

However, including P-mobilization in the rhizosphere of the tree, thus allowing the tree to tap from immobile P-sources, which the accompanying maize crop is not able to access, minimizes direct competition for P, but soil drying induced P-deficiency remains.

Therefore, if the tree-rhizosphere shows P-mobilizing capacity while the maize-rhizosphere does not, low water demand of the tree is much more important than low-P-demand to prevent competition by the tree on the maize crop in P-limiting situations.

The increase in maize growth near Cassia tree lines could be explained by including rhizosphere effects. The modifications in the rhizosphere of Cassia and their effect on P and maize yields were modeled in two steps. The first step shifted the P-uptake by Cassia from the mobile P-pool to the immobile P-pool. This was based on experimental evidence that in the rhizosphere of Cassia P-

mobilization equals P-uptake (Chapter 4). The second step calculated the increase in P-availability in Cassia's rhizosphere and the fraction of maize roots which are able to tap from this mobilized P. This was based on experimental evidence of organic anions and pH increases in the rhizosphere and their effect on mobile-P in our soil, combined with experimental results on period length of these effects and maize roots growing in Cassia's rhizosphere (Chapter 5).

Although the exact combination of pH and oxalate levels plus their exact effects on all different P-pools (organic and inorganic) in reality were not known, this simulation gave a rough but practical indication of the possible range of Cassia rhizosphere effects on maize growth.

Over longer periods of more than two seasons, the balance between negative water effects and positive rhizosphere effects depends on the residual effect of the rhizosphere effects. The negative water effect is more or less constant and does not accumulate, because water is continuously used by trees and regularly replenished by rain. However, positive rhizosphere effects might accumulate over time, changing the balance of negative and positive effects in the long term. However, rhizosphere effects do not seem to have a long residual period, because most factors causing the effects in the rhizosphere are short lived: phosphatases and organic anions denaturalize or break down (Dodd et al, 1987; Jones and Darrah, 1994) and pH effects are subject to diffusion and buffering by soil (Hinsinger, 2001), and because we did not measure increases in more mobile P-fractions in rhizosphere soil (Chapter 4).

Several authors (Bhat et. al.;1976; Hedley et al in: Dodd et. al.,1987; Marschner, 1991a; 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 all problems related to measuring P-pools and their availability in P-fixing soils (Gijssman et al., 1996), and the complexity of including adaptations of plants to low P-availability, like symbiosis with mycorrhizal fungi and root-exudation modifying the rhizosphere chemistry and P-availability. Each of these issues is complex. In this study we have tried to answer the practical question on how trees affect maize growth on an Oxisol/Ferralsol, that limits maize production by low available-P. To answer this question, we used the mechanistic agroforestry model WaNuLCAS.

Because WaNuLCAS simulates crop-growth in different zones with increasing distance to the tree-line, we circumvented some problems by looking at relative maize yield levels (maize yield ratio zone2 : zone4 and zone3 : zone4). This had the advantage, that model parameters, which were the same in all zones (initial soil parameters i.e. P-pools, mycorrhization of maize), needed a reasonable estimate, but no precise measurement. Rhizosphere effects on P-pools could be assessed by multiplying initial mobile-P with a factor derived from field measurements (e.g. resin-P in bulk soil after organic anion addition divided by resin-P before organic anion addition). This allowed a rough

but useful simulation of effects of rhizosphere modifications on P-availability and uptake by tree and crop and their subsequent growth, which agreed reasonably with measured relative maize yields.

The disadvantage of using relative yield levels is, that they show the same pitfall as the eye of a farmer: There is no absolute control-treatment. This led probably to underestimation of the rhizosphere effect. Because tree-roots were still present in the zone 4 (furthest from the tree-lines), positive rhizosphere effects likely increased maize yield in this zone as well. If the yield in zone 4 increased, the relative yield levels of zone 2 and 3 (zone2 : zone4 and zone3 : zone4) became smaller than they would be without yield increases in zone 4. Underestimation of direct competition for P between tree and crop would be a similar risk of using relative maize biomass yields. On the other hand, the negative tree-effect of soil-drying-induced P-deficiency would not suffer from underestimation, because real measured water-contents were used, and tree-water extraction in the wet season is concentrated to close by the stem base and was likely negligible in zone 4, even at considerable root-densities in zone 4 (Chapter 7). If, as a result of using relative yield levels, the positive rhizosphere effect was underestimated, while the negative soil-drying induced P-deficiency was estimated reasonably well, the balance looked more negative than it really was.

A mechanistic model like 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 (Barber, 1995; De Willigen and Van Noordwijk, 1987). 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 before. This soil-drying induced P-deficiency on P-fixing soils can, in a wider context, explain other 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 vol.% over small distances, and may cause large differences in biomass production in situations with low levels of available nutrients, where diffusion becomes the most important transport mechanism.

9

Conclusions

Conclusions

In the P-limiting environment of western Kenya, with soils low in available-P but with a considerable reserve in total-P, performance of crop-growth near tree-lines could not be explained by simple performance analysis methods as developed by Ong (1995) and Kho (2000), as discussed in chapter 2. Ong's fertility effect does not include root-exudate effects and Kho's method does not allow for interactions between different resources like the water-P interaction. Therefore a perspective looking at the main processes by which trees influenced crops was more appropriate, as discussed in chapter 3. However, Kho's attention for environmental limitations and his conclusion that the main environmental limitation influences the outcome of tree effects on crops to a large extent, is in agreement with the general argument followed in this research (Chapters 4-8). This argument was that in a P-limiting situation, trees are most likely to affect crop-growth by the trees' effects on crop-P-uptake. In such a way, Kho's method can qualitatively assist in hypothesizing what are the main tree-effects on crop growth in a specific environment, based on the main limitation of that environment. This may prevent that mechanistic research gets lost in a multitude of processes of which most determine part of the final performance, but only a few determine 80-90 % of the performance. In my research, only a few tree-effects on crop-P-uptake explained indeed most of the differences in crop-performance with distance to the tree lines.

Negative effects of trees on crops were either due to soil-drying-induced P-deficiency, or to high tree-P-demand in absence of tree-P-mobilization in the rhizosphere (Chapter 8). On the other hand, trees affected crops positively by high levels of rhizosphere-P-mobilization (Chapter 4, 5 and 8). The negative effect of high tree-P-demand was quickly offset by the tree's own P-mobilization. However, the positive tree-rhizosphere effects were quickly offset by the negative effect of soil-drying induced P-deficiency (Chapter 8).

Therefore, if the aim is to minimize competition from trees on crops, it is primarily necessary to choose tree species and to manage these trees in such a way that their daily water extraction from the soil is balanced by rain-inputs, thus avoiding soil-drying (Chapter 6). Minimizing daily water use of the trees can be done by choosing species with a low water-use per unit leaf-area and/or minimizing leaf-area. Minimizing leaf area can be done by pruning or by choosing species with a low leaf-area. Water-extraction from the soil will occur first in zones close to the trees, even if tree-root-length-densities do not decrease with distance from the tree. This is due to the decrease in water-potential gradient between root and soil with distance to the stem base (Chapter 7). This infers that soil drying in the cropping-season and therefore soil-drying-induced P-deficiency is mainly occurring in the zone close by the tree (lines). If tree-water-extraction in this zone cannot be totally replenished by

rain-inputs, these dryer zones should preferably be used for crops, which are less sensitive to P-deficiency (and not too sensitive to soil-water-content reductions).

Minimizing competition of trees on crops can further be achieved by choosing trees, which can mobilize soil P for uptake by trees and crops. Mobilization of soil P by trees will profit the tree itself first, because the tree has more roots in its own modified rhizosphere than any other plant. However, by taking care of its own P-supply from less available P-sources, the tree's direct competition for P with the crop is minimized (Chapter 4). My results indicate that, because of its P-mobilization even a tree with high P-demand (like Cassia) did not compete directly for P with the crop.

Moreover, Cassia's P-mobilization affected crop growth positively by a transfer of P from tree-rhizosphere to maize roots.

Maize roots crossing the modified rhizosphere of tree-roots, tapped from the P mobilized there. The extent to which this P-transfer occurred, increased with the length of P-mobilization period, the fraction of P-mobilizing tree-roots, the relative sink-strength of the maize-roots in the tree-rhizosphere and the synlocation of maize and tree-roots (chapter 5 and 8).

Thus, in order to minimize competition of the tree with the crop in P-fixing soils, species should be chosen which (on top of using little water) show P-mobilizing capacity. This capacity can probably be diagnosed by a small test, growing trees with and without P-fertilizer on a P-limiting soil. A tree, which does not respond to P-fertilizer, is likely able to tap from the less available P-sources by mobilizing less available soil P in its rhizosphere. These trees do not respond to P-fertilizer application, and likely will not compete with the crop for P directly, although they may compete with the crop due to soil-drying-induced P-deficiency. However, this test may not be totally watertight: If a tree-species has other adjustments to low-P availability (mycorrhiza, high density of fine roots) it may not respond to P-fertilizer and still compete directly with the crop for the same easily available P source.

Taking a step back, Kho's performance analysis method clarifies that the results of this research are only applicable to a P-limiting environment. For example, we found that Cassia competes little with the crop, but the same Cassia competes very much with a neighboring crop if the main / first limitation of the environment is nitrogen deficiency (K. Giller, pers. comm.). Then, the effect of trees on crops via the resource phosphorus (P) would be somewhat positive, say 0.5, but the effect of trees on crops via the resource nitrogen (N) would be more strongly negative, say -1, according to Kho's equation. In our P-limiting situation with the degree of environmental limitation of phosphorus (p) assessed at 0.9 and the degree of environmental limitation of nitrogen (n) assessed at 0.1, the equation would give: $p \cdot P + n \cdot N = 0.9 \cdot 0.5 + 0.1 \cdot -1 = 0.35$, which is a total positive effect. In an N-limiting situation with $n = 0.9$ and $p = 0.1$, the result would be -0.85, which is a total negative effect.

The performance analysis method of Kho appears especially useful to set research priorities, for the processes that have to be looked at first. Also, Kho's method helps to realize that the results of this research are valid in environments with this particular set of resource-limitations, but not in other environments with other resource limitations.

P-mining

The use of species which are able to tap from less available P-sources in the soil, demands for inquiry of P-mining. P-mining is defined here as depletion of soil P through uptake by crops without any replenishment of P. Calculations indicate that at a P-content of 1 mg per kg of maize and a harvested biomass of 3000 kg per ha per season, with two growing seasons per year, each year 6 kg P per ha is exported. The amounts total-P and available-P in the top meter soil are 6000 and 30 kg per ha, respectively, when assuming a bulk density of 1.2 kg per liter soil, 500 mg per kg total-P and 2.5 mg per kg available-P. Evidently, the export of 6 kg P per ha per year is much when compared with the available-P stock. However, if compared with the total-P stock of 6000 kg per ha, 6 kg per ha per year export is not disturbing. Therefore, increased use of plants with P-mobilizing capacity, which can tap from less-available-P sources, is not likely to deplete the less available P-source quickly.

I hope that these conclusions are sufficiently clear and practical to help resource-poor farmers in environments with P-fixing soils, and a main P-limitation to crop production, to optimize their tree-crop combinations, and push their minimal possibilities towards the possible maximum. And finally, I hope that this research of optimizing a marginal situation becomes superfluous.

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Summary

Trees are a common feature along and inside crop fields in sub-humid East Africa. Farmers plant trees to gain cash from tree-products, to cover costs of especially school fees and hospital bills. However, trees often compete with neighboring crops. Maize is the main staple-crop, and losses of maize production due to tree-competition increase the food-deficiency of farm families. This affects especially the farm families with small land-holdings, which form a large part of the population in western Kenya.

In this study I examined in which ways trees affect the maize crop on the prevailing phosphorus-fixing soils in western Kenya, where maize production is primarily limited by phosphorus availability.

I used various methods to investigate tree-crop interactions, 1) system performance analysis methods, applied to field experiments, 2) analytical methods that examine the mechanisms of tree-crop interaction in field and pot trials, and 3) simulation modeling. Although system-performance analysis methods are useful to get an overall impression of tree effects on crops, they proved to be less applicable in situations where the mechanisms determining tree-crop interactions affect each other (i.e. water-P interaction) or give a delayed response (i.e. nutrient mineralization). The system performance analysis methods applied in chapter 2 could not explain the observed maize-yield increases and decreases near tree lines on the phosphorus-fixing soil. Therefore I continued using mechanistic research methods, including field experimentation at different scales combined with computer-model simulations.

Because phosphorus was the main limitation to maize growth, I hypothesized that tree-effects on maize growth were most likely caused by tree-effects on phosphorus uptake by the crop. Phosphorus uptake by maize depends on 1) P-availability of the soil, 2) soil water content (important for P-diffusion to roots) and 3) maize root density.

In field-based trials I examined the rhizosphere of trees and maize, the total tree-water-use and tree-water-extraction from soil, and their determinants. The implications of the results of rhizosphere and water effects on maize P-uptake and maize growth were then investigated using the mechanistic tree-crop interaction model WaNuLICAS.

Rhizosphere modifications were largest for *Cassia spectabilis* (syn. *Senna spectabilis*), with high oxalate and intermediate citrate exudation and long lasting pH-increases. *Grevillea robusta* showed high levels of acid phosphatase activity and intermediate citrate exudation and pH-increases in its rhizosphere, which lasted less long than that for *Cassia*. Maize (*Zea mays*) and the other tree species

tested, *Eucalyptus grandis*, *Cedrella serrata*, *Tithonia diversifolia*, showed less rhizosphere modifications.

The high acid phosphatase activity in the rhizosphere soil of *Grevillea*, caused a shift from organic to inorganic P-fractions in the soil. However, although maize showed a much lower acid phosphatase activity in its rhizosphere, the depletion of organic P-fractions in the rhizosphere soil of maize was at a similar level as that in the rhizosphere of *Grevillea*. This indicates that the organic-P availability at the root surface, rather than the level of acid phosphatase activity is the limiting factor for uptake of P from organic-P pools in soil.

Additions of citrate to bulk soil increased available-P (resin-P) significantly. This increase was not measured in the rhizosphere soil of *Cassia* or *Grevillea*, and can be ascribed to a balance in simultaneous P-uptake and P-mobilization. For *Cassia* and *Grevillea*, showing no response to P-fertilizer, this balance in the rhizosphere is likely caused by adjusting P-mobilization to P-demand. Indirectly, *Cassia* and *Grevillea* tap from less available P-sources, which decreases the direct competition for P with the crop. For maize, showing a strong increase in growth upon P-fertilization, this balance in the rhizosphere is likely caused by adjusting growth and P-demand to the low available-P supply.

The balance of P-mobilization and P-uptake in the rhizosphere of *Cassia* and *Grevillea*, suggests that organic anion exudation is not likely to have a residual effect on P-availability in soil.

We examined how maize may profit from P-mobilization in the *Cassia* rhizosphere, by using the WaNuLCAS model, after some adjustments. Input parameters were derived from field and incubation trials, i.e. 1) fine root densities of maize and trees with distance from the tree lines, 2) the extent to which maize roots occupy *Cassia*-rhizosphere (root synlocation), 3) duration of pH-increases and period of organic anion exudation and root-longevity, and 4) effects of observed/measured pH increases and organic anion exudation on P-availability.

Measured yield increases near *Cassia* fell within the range of simulated maize yields at the possible range of rhizosphere modifications. This confirmed the hypothesis that the maize yield increases near *Cassia* are due to the effects of *Cassia*'s rhizosphere on P-availability.

Total water use of trees in tree lines grown over seven growing seasons, was mainly determined by leaf-area and leaf-conductance. Micrometeorological variables and soil water content had minimal effects on water use of trees in tree-lines, despite their close coupling to the atmosphere. This is unlike in tree-canopies, where micrometeorological variables affect total water-use much more, especially at higher leaf-areas. The small effect of micro-meteorological variables on water-use of trees in tree lines was partly due to the small ranges of these variables, vapor pressure deficit and

radiation. In contrast, the linear response of water use to leaf area extends over a much larger leaf-area range in tree lines than in tree-canopies, and this is a main difference in the water-use by tree-lines compared with tree-canopies.

Although total water use by trees of the tree lines determines total water extraction from the soil, and the potential level of soil-water extraction and soil drying, the distribution of soil water extraction is dependent on other factors.

The distribution of water extraction with distance to the tree lines (horizontal dimension) was not closely related to root length density of the tree. This became especially clear from soil water content and root density measurements with distance to *Grevillea* tree lines. Root-length densities of 2.5 yr. old *Grevillea* hardly decreased over the first 7.5 m away from the tree line, while soil water contents were significantly reduced near the trees compared with further away from the tree. The dryer soil near the tree lines could not be ascribed to interception of rain, but was ascribed to high water-extraction. High water extraction near the trees compared to far from the trees at equal root length density were due to a decrease in potential gradient of water between root and soil with increasing distance to the tree-lines. This potential gradient decreases similarly over depth. However, in the vertical dimension, root length densities (uptake-conductance) usually decrease more than the potential gradient. Therefore over the vertical dimension root density is the strongest determinant of water-uptake.

Agroforestry models, including WaNuLCAS, simulate water extraction as linearly related to relative root length density in both vertical and horizontal dimension. Therefore, in our model investigations of the effect of soil water content on P-uptake by maize and maize growth, we did not use the water-use and extraction part of the WaNuLCAS model, but imposed water contents measured in the field with distance to the tree lines.

Simulations of maize growth in different zones with distance to the tree lines showed that decreases in soil water contents of only 2.5 vol % (at high pF) as measured near *Grevillea* tree lines, decreased maize production by 30-40%. Part of this effect (13-26 %) was due to the decrease in P-diffusion to maize roots per se. The other part was due to the cumulative effect of decreased maize growth and decreased root growth. Final maize production as simulated with this soil-drying induced P-deficiency effect was very close to measured maize yields in the field at the same soil water contents. Water deficiency per se explained very little of the yield reductions at this relatively high soil water content.

In the model simulations, different levels of rhizosphere effects were combined with different levels of soil drying near the tree line. The simulation of maize production near a hypothetical tree with

soil water contents as measured near *Grevillea* and rhizosphere effects as measured of *Cassia* showed that rhizosphere effects were minimal if the soil-drying induced P-deficiency effect occurred. I argued that the effects from decreased P-diffusion (through the decreased soil water contents) masked the increases in available-P (through the rhizosphere effects). The simulation of maize production near a tree-line like *Cassia*, with a high P-demand, but without any rhizosphere modifications, showed that if *Cassia* had not mobilized P at all, decreases in maize production near the tree-line would have been as severe as those caused by water induced P-deficiency near the *Grevillea* line.

In Conclusion, negative effects of trees on crops in this P-fixing soil in western Kenya were either due to soil-drying-induced P-deficiency, or to high tree-P-demand in absence of tree-P-mobilization in the rhizosphere. Positive effects of trees on crops were due to mobilization of poorly available soil P in the rhizosphere.

The negative effect of high tree-P-demand was quickly offset by the tree's own P-mobilization. However, the negative effect of soil-drying induced P-deficiency has quickly offset positive tree-rhizosphere effects.

To minimize competition from trees on crops, it is primarily necessary to choose tree varieties and to manage these trees in such a way that the water extraction from the soil is more or less balanced by rain-inputs, thus avoiding soil drying. Minimizing daily water use of the trees can be done by choosing species with a low water-use per unit leaf-area and minimizing leaf-area. Minimizing leaf area can be done by pruning or by choosing species with a low leaf-area.

Water-extraction from the soil will occur firstly in zones close to the trees, even if tree-root-length-densities do not decrease with distance from the tree. This infers that soil drying in the cropping-season and therefore soil-drying-induced P-deficiency will occur mainly in the zone close to the tree lines. If tree-water-extraction in this zone cannot be totally replenished by rain-inputs, these dryer zones should be used for crops, which are less sensitive to P-deficiency (and not too sensitive to soil-water-content reductions).

Once the soil drying induced P-deficiency is prevented, use of species that exert P-mobilization effects would be best, to minimize competition and to improve maize yield. This capacity can probably be diagnosed by a small test of growing trees with and without P-fertilizer. A tree which does not respond to P-fertilizer, is likely able to tap from less-available P-sources by P-mobilization in the rhizosphere. These trees without response to P-fertilizer may not compete with the crop for soil P directly. However, this test may not be totally watertight, because if a tree-species has other

adjustments to low-P availability (mycorrhiza, high density of fine roots) it may not respond to P-fertilizer and still compete directly with the crop for the same easily available P source.

In this research I have tried to increase the understanding of how trees affect neighboring crops on P-fixing soils without fertilizer application. The results may be useful to extension services and farmers without demanding major financial inputs. Therefore, I hope that, although this will not bring about a green revolution, and even increase mining of the soil for P, it may help the farm families to live today, which I think is a premise to look at tomorrow.

Samenvatting

In grote delen van de humide tropen wordt de voedselproductie beperkt door gebrek aan fosfaat. In west Kenia leidt dit tot maïsopbrengsten die minder dan 25 % van het potentieel zijn. De voedselproductie van boeren families is vaak lager dan de consumptie. Kunstmest is voor de meeste boeren onbetaalbaar, aangezien zelfs kleine bedrijven van 0.2 ha ieder seizoen (2x per jaar) een hoeveelheid kunstmestfosfaat nodig zou hebben die zeven daglonen kost volgens het officiële dagloon-tarief (in praktijk vaak lager). Bovendien hebben de meeste boeren hun weinige geld nodig voor het betalen van schoolgeld voor hun kinderen of voor medische hulp.

Om zoveel mogelijk uit de vaak kleine bedrijfjes te halen, planten boeren bomen. Bomen zijn of voor eigen gebruik of een bron van cash, en worden veelal geplant langs gewasvelden. Dit levert het probleem op dat bomen en gewas concurreren om licht, water en planten-voedingsstoffen.

In dit onderzoek heb ik uitgezocht hoe bomen het voedselgewas beïnvloeden. Dit onderzoek kan bijdragen tot management waarbij negatieve effecten van bomen op het gewas geminimaliseerd en positieve effecten optimaal benut kunnen worden. De uitkomsten van dit onderzoek gelden voor gebieden waar fosfaat de grootste beperking vormt voor gewasgroei doordat het sterk aan de grond gebonden en daardoor weinig beschikbaar is.

De hoofdstukken 2 en 3 vormen een globale analyse voor het meer gedetailleerde onderzoek in de hoofdstukken 4 tot 8. In de hoofdstukken 2 en 3 onderzocht ik de geschiktheid van de verschillende methoden om boom-gewas interacties te analyseren. In hoofdstuk 2 blijkt dat de methoden die effecten van bomen op het gewas behandelen als een simpele som van apart geteste positieve en negatieve effecten op gewasgroei een ruw begrip van de uiteindelijke gewasgroei kunnen opleveren. Deze methoden geven echter minder reële resultaten in het geval dat verschillende groeifactoren elkaar beïnvloeden, of wanneer positieve dan wel negatieve effecten met een vertraging optreden. Bovendien wordt in deze methoden geen rekening gehouden met veranderingen op lange termijn. In hoofdstuk 3 onderzocht ik de achterliggende mechanismen van de boom-gewas interacties. Metingen van bodemvochtgehalte, plantenvoedingsstoffen en beworteling door bomen en gewas leidde tot meer inzicht in het waarom van de boom-gewas interacties. De afname van beschikbaarheid van alle planten-voedingsstoffen gedurende de 3½ jaar van het experiment, verklaarde de algemene tendens van verminderende opbrengsten.

Omdat de methoden van hoofdstuk 2 bepaalde waargenomen gewasgroeipatronen nabij bomen niet verklaarden, besloot ik om in mijn hoofdonderzoek (hfst. 4-8) de mechanismen te onderzoeken waarmee bomen de gewasgroei beïnvloeden.

Aangezien fosfaat de meest beperkende factor voor gewasproductie is, nam ik aan dat bomen de gewasgroei beïnvloeden door effecten op fosfaatopname. Opname van fosfaat door het gewas hangt

voornamelijk af van 1) de mate waarin fosfaat door de bodem geleverd wordt, de fosfaatbeschikbaarheid, 2) het transport van fosfaat naar de wortels, dat in geval van fosfaat sterk bepaald wordt door vochtgehalte van de bodem, en 3) de hoeveelheid wortels van de plant.

Bomen beïnvloeden de eerste factor, fosfaat-beschikbaarheid, doordat ze zelf fosfaat opnemen. Het is echter ook mogelijk dat sommige van de bomen door chemische veranderingen rond hun wortels de fosfaatbeschikbaarheid vergroten. Dit is een natuurlijk aanpassing van sommige planten voor gronden met een lage fosfaatbeschikbaarheid. Maïs en veel andere voedsel gewassen hebben die aanpassing niet. Bomen beïnvloeden ook het transport van fosfaat naar wortels doordat ze het bodemvochtgehalte verminderen, door eigen watergebruik.

Bomen beïnvloeden ook de hoeveelheid wortels die het gewas produceert maar dit heeft twee tegenstrijdige gevolgen voor de gewas-groei, die elkaar grotendeels opheffen.

In de hoofdstukken 4 en 5 beschrijf ik het onderzoek naar de mogelijke positieve effecten van bomen op fosfaatbeschikbaarheid door middel van chemische veranderingen rond hun wortels. In hoofdstuk 6 beschrijf ik het onderzoek naar het totale watergebruik van verschillende boomsoorten en de bepalende factoren voor dat totale watergebruik. In hoofdstuk 7 onderzocht ik de distributie van de wateropname uit de bodem met toenemende afstand tot de boomlijnen en de bepalende factoren daarvoor. In hoofdstuk 8 gebruik ik een computermodel om te berekenen hoe gemeten effecten van bomen op fosfaatbeschikbaarheid en bodemvochtgehalte de gewasgroei beïnvloeden, en dit te vergelijken met gemeten gewas opbrengsten.

In de hoofdstukken 4 en 5 heb ik gekeken naar 3 soorten chemische veranderingen rond wortels en naar hun relatie met het beschikbare fosfaatgehalte in de grond. De eerste chemische verandering is het gehalte aan organische anionen. Organische anionen kunnen zijn uitgescheiden door de wortels, en kunnen uitwisselen met door de bodem vastgehouden fosfaat, waardoor dat fosfaat beschikbaar wordt voor plant opname.

De tweede chemische verandering is een verhoogde fosfatase activiteit. Fosfatase is een enzym dat fosfaat vrijmaakt van organische stof (b.v. plantenresten) en op die manier de fosfaatbeschikbaarheid vergroot.

De derde chemische verandering is een stijging of daling van de zuurgraad (pH). In de meeste rode tropische gronden zoals die in mijn onderzoeksgebied (Ferralsols) zorgt een stijging van pH voor een grotere beschikbaarheid van fosfaat.

Metingen wezen uit dat vooral de boomsoort *Cassia spectabilis* (syn. *Senna spectabilis*) een hoog gehalte van voornamelijk twee types organische anionen rond de wortels had. Bovendien vertoonde *Cassia* ook de meest langdurige pH-stijgingen rond de wortels. Deze verschijnselen waren in mindere mate aanwezig rondom wortels van de boomsoort *Grevillea robusta* en waren niet meetbaar rondom wortels van de boomsoorten *Eucalyptus grandis*, *Cedrella serrata* en het maïs-gewas.

Een test waarin deze organische anionen aan onze grond werden toegevoegd, wees uit dat in dit geval de fosfaatbeschikbaarheid flink omhoog zou gaan. Deze hogere fosfaat beschikbaarheid was echter niet meetbaar in de grond rondom Cassia wortels. Hieruit concludeerde ik dat de boom kennelijk ongeveer evenveel fosfaat beschikbaar maakt als zelf weer opneemt. De pH-stijging verhoogt ook de fosfaat beschikbaarheid van onze grond. Verder onderzoek naar de groei van maïswortels langs Cassia-wortels wees uit dat, doordat maïswortels betrekkelijk vaak samenop groeien met Cassia wortels (ongeveer twee keer zoveel als per toevallige kruisingen zou gebeuren), en Cassia relatief langdurige chemische effecten rond de wortels vertoont, maïs toch kan profiteren van de hogere fosfaat beschikbaarheid rondom Cassia wortels.

Berekeningen met het computermodel (hfst 8) wezen inderdaad uit dat de 12% hogere maïsofbrengsten nabij Cassia boomlijnen inderdaad het gevolg kunnen zijn van deze chemische veranderingen rondom maïs wortels. Zonder enige chemische verandering rondom Cassiawortels zou de maïsofbrengst hoogstwaarschijnlijk sterk verminderd zijn door concurrentie van de boom met het gewas om fosfaat.

Alle bomen en maïs vertoonden hogere phosphatase-activiteit rond hun wortels dan gemeten in de bulk van de grond. Grevillea vertoonde de hoogste phosphatase-activiteit rond zijn wortels (10x hoger dan in de bulk-grond en 5x hoger dan in grond om maïs, Cedrella en Cassia wortels). Dit veroorzaakte hoogstwaarschijnlijk de gemeten verschuiving van een deel van het organisch gebonden fosfaat naar vrij fosfaat in de grond rondom Grevillea wortels. Overigens was het gehalte aan organisch fosfaat rondom maïswortels net zo laag als rondom Grevillea-wortels, wat erop wijst dat zelfs de lagere phosphatase-activiteit rondom maïswortels evenveel fosfaat van organische stof kon vrijmaken voor plantopname als de hoge phosphatase-activiteit rondom Grevillea wortels. Waarschijnlijk is de beschikbaarheid van organisch gebonden fosfaat, dat als geheel zelf ook door de grond vastgehouden wordt, de beperkende factor voor het benutten van deze fosfaatbron. Dat betekent dat een boom de fosfaat beschikbaarheid voor het gewas niet noemenswaardig kan verhogen door middel van hoge phosphatase activiteit.

In hoofdstuk 6 analyseerde ik het watergebruik van de bomen in boomlijnen, en de relatie van het waterverbruik met bladoppervlakte, watergebruik per eenheid bladoppervlakte, bodemvochtgehalte en meteorologische variabelen met name zonnestraling en luchtvochtigheid.

Het water verbruik van bomen in boomlijnen bleek zeer sterk afhankelijk te zijn van de bladoppervlakte en in mindere mate van het watergebruik per eenheid bladoppervlakte. De andere variabelen samen bepaalden minder dan 12 % van de variatie in watergebruik. Dit verschilt met wat er bekend is van bos. Het watergebruik van bomen in een bos is minder sterk afhankelijk van bladoppervlakte en sterker van bijvoorbeeld luchtvochtigheid. De oorzaak van dit verschil tussen boomlijnen en bos is dat meer bladoppervlakte aan een boom in een boomlijn zowel meer water geleid, alsook meer oppervlakte levert voor het opvangen van zonnestraling (zonnestraling levert de

energie voor verdamping). In een bos daarentegen, wordt bij een vergrootte bladoppervlakte alleen meer doervallend licht opgevangen, en neemt de geleiding van het bladoppervlak voor waterdamp wel toe, maar is de geleiding van de lucht naar de atmosfeer in de boomkruinen veel lager dan in de boomkruinen van een enkele rij bomen.

Omdat watergebruik van bomen in lijnen is in sterke mate afhankelijk van de bladoppervlakte kan het beperkt worden door snoeien.

In hoofdstuk 7 heb ik onderzocht waar de boom zijn water onttrekt in het aan de boom grenzende bodemvolume. Daarvoor mat ik zowel bodemvochtgehaltes als wortellengtes over diepte en met afstand tot de boomlijn. De verwachte goede relatie tussen wortellengte en bodemuitdroging was maar beperkt aanwezig.

In het bodemvolume grenzend aan *Cedrella* boomlijnen werd een concentratie van wortels dichtbij de boomlijn gemeten. Bodemvochtgehaltes verschilden echter niet duidelijk met afstand tot de boomlijnen. Dit is hoogstwaarschijnlijk veroorzaakt door het relatief lage water gebruik van *Cedrella* (kleine boomkruinen, laag bladoppervlak) dat in evenwicht gehouden wordt door neerslag. Daarentegen waren de wortels van *Grevillea robusta* boomlijnen in grote mate gelijk verdeeld over de eerste 7.5 m afstand van de boomlijnen, maar waren de bodemvochtgehaltes nabij de boomlijnen duidelijk lager dan verderop. Dit kan worden verklaard door een afnemende zuiging voor water in de wortels met toenemende afstand tot de stam (= bron van zuiging) doordat eerdere vertakkingen en wateropname over delen van het hele wortel kanaal al delen van het nodige water leveren.

Als de hoeveelheid wortels met afstand (of over diepte) veel sterker afneemt dan de zuiging, bepaald de relatieve hoeveelheid wortels de wateronttrekking uit dat volume (hoe meer wortels hoe meer opname). Dit gebeurt meestal over de verticale dimensie (diepte), maar dus niet altijd met toenemende afstand (horizontale dimensie), wanneer hoeveelheden wortels niet sterk afnemen.

In het droge seizoen, als de zones dicht bij de boomlijnen al flink uitgedroogd zijn, kan de grond dicht bij de boom zelf zo hard aan het water zuigen dat alleen boomwortels in de verder weg gelegen nattere zones nog water kunnen opnemen. Daarmee wordt het verschil dat in het natte seizoen is ontstaan tussen drogere zones nabij de boomlijnen en nattere zones verder weg, weer (gedeeltelijk) opgeheven.

Computersimulaties beschreven in hoofdstuk 8 wijzen uit dat een afname in bodemvochtgehalte van gemiddeld 2½ %, zoals gemeten nabij *Grevillea* boomlijnen, kan leiden tot een afname in maïs productie van 30-40 %. Deze afname wordt niet veroorzaakt door direct gebrek aan water, maar door verlaging van het fosfaattransport naar de wortels. Gedurende de hele maïs-groei-cyclus is het fosfaat transport naar de maïswortel iets minder bij deze iets lagere bodemvochtgehaltes. In de eerste tijdstap (uur, dag) nadat de zaadreserves zijn opgebruikt groeit de plant iets minder en produceert iets minder wortels. In de volgende tijdstap hebben minder wortels samen met een

verlaging van het fosfaattransport een dubbel negatief effect op de fosfaatopname. Zo cumuleert het aanvankelijk kleine negatieve effect van een iets lager bodemvochtgehalte gedurende de groei tot een groot verschil in uiteindelijke opbrengst. Het zo met het computer-model gesimuleerde opbrengstverlies is bijna gelijk aan het in werkelijkheid gemeten opbrengstverlies nabij Grevillea boomlijnen. De opname van fosfaat door Grevillea zelf is relatief laag, en veroorzaakt nauwelijks meer maïsopbrengstverlies.

Hypothetische simulaties laten zien, dat als een boom evenveel fosfaat nodig zou hebben als Cassia, zonder dat het zelf fosfaat beschikbaar maakt door chemische veranderingen rond de wortels, deze boom hoogstwaarschijnlijk wel direct met maïs zou concurreren om fosfaat. Dit zou ook een opbrengstvermindering van 30-40% tot gevolg hebben. Zodra die boom echter de fosfaat beschikbaarheid vergroot door chemische effecten rond zijn wortels, is dit negatieve effect opgeheven. De indirecte concurrentie, via verminderde bodemvochtgehalten, kan dan nog wel voorkomen.

Het positieve effect van chemische veranderingen rond boom wortels op maïsgroei is minimaal als dezelfde boom ook het bodemvochtgehalte vermindert.

De effecten van bomen op een gewas zoals maïs op bodems met een lage fosfaatbeschikbaarheid kunnen geoptimaliseerd worden door in eerste instantie bodemuitdroging tegen te gaan.

Bodemuitdroging door de boom kan worden tegengegaan door het bladoppervlak te verkleinen en/of door juiste keuze van bomen met een klein bladoppervlak en een laag gebruik van water per eenheid bladoppervlak, zodat het watergebruik van de boom in evenwicht is met regenwater aanvoer. In het geval dat dit niet mogelijk is kunnen de drogere zones nabij de boomlijnen beter beplant worden met een gewas dat minder gevoelig is voor lage fosfaatbeschikbaarheid (en drogere grond).

In tweede instantie kan de competitie van bomen met het gewas worden tegengegaan door bomen te kiezen die een lage vraag naar fosfaat hebben en/of zelf de fosfaatbeschikbaarheid verhogen door chemische veranderingen rond hun wortels. Een simpele test om uit te vinden of bomen de fosfaatbeschikbaarheid verhogen, zou zijn om boomsoorten op deze grond met en zonder fosfaatbemesting te laten groeien. Is er geen verschil in groei, dan is de boom waarschijnlijk in staat zelf de fosfaatbeschikbaarheid te vergroten. Deze test is niet geheel waterdicht, aangezien ook andere aanpassingen, bijvoorbeeld een dicht wortelstelsel, dit effect kunnen hebben.

In dit onderzoek heb ik geprobeerd uit te zoeken hoe een marginale landbouw situatie geoptimaliseerd kan worden. Ik hoop dat de uitkomsten van mijn onderzoek praktisch en begrijpelijk genoeg zijn om echt gebruikt te worden, hoewel het natuurlijk het allermooist zou zijn als het optimaliseren van zo'n marginale situatie onnodig werd. Maar dit gebeurt waarschijnlijk pas als het verantwoordelijkheidsgevoel van mensen iets verder bij eigen huis en portemonnee vandaan komt te liggen.

Om de vraag naar effecten van bomen op mais op een fosfaat-beperkende bodem te beantwoorden zijn methoden en kennis, die meestal worden ingezet bij het bestuderen van deelaspecten op kleinere schaal, toegepast op veldschaal. Hoewel de nauwkeurigheid van de metingen op veldschaal lager was dan die bij bestudering van deelaspecten op kleinere schaal (reductionistische onderzoeksbenadering), gaf de integratie van deelaspecten meer inzicht in hun relatieve belang voor gewasgroei op veldschaal (systeem-nivo, holistische benadering). Ogenscheinlijk kleine verschillen in deelaspecten kunnen een groot effect hebben wanneer geïntegreerd in het totale systeem. Een voorbeeld hiervoor was de kleine verandering in bodemvochtgehalte die via het effect op fosfaattransport en -opname en cumulatieve plantgroei, een groot negatief effect op de uiteindelijke maïsproductie had. Omgekeerd kunnen grote verschillen in deelaspecten een minimaal effect hebben wanneer geïntegreerd in het totale systeem. Een voorbeeld hiervan was dat de grote phosphatase activiteit rond *Grevillea* wortels niet leidde tot positieve effecten op maïsproductie.

Mijn proefschrift geeft aan dat onderzoek aan deelaspecten in combinatie met onderzoek aan het hele systeem vruchtbaar is om te komen tot toepassing van de resultaten in de praktijk. Zo bleek dat op fosfaat-fixerende bodems zonder bemesting in eerste instantie bodemuitdroging moet worden tegengegaan, evenals het gebruik van bomen met een hoge vraag naar fosfaat in afwezigheid van een voldoende fosfaatbeschikbaarheid verhogende activiteit. Pas als directe concurrentie voor fosfaat en indirecte concurrentie via bodemuitdroging voorkomen wordt, kunnen bomen die de fosfaatbeschikbaarheid verhogen een (klein) positief effect op de maïsopbrengst hebben.

Curriculum Vitae

Simône Radersma was born in Winsum (G.n.) in summer 1965 under two large chestnut trees. In 1983, after her secondary school (“VWO” at Chr. Scholengemeenschap / Leek) she went a year to the “Vrije Hogeschool” (Free Highschool) in Driebergen and next to the art-academy “Minerva” in Groningen. After finishing the art-academy with a degree in painting / graphics (teacher-education), she started her studies “Tropical Land-Use” at the Agricultural University / Wageningen (WAU) in 1989. She graduated in June 1994 (with distinction) with two theses. The first thesis was a study after saline acid-sulphate-soils used for small-scale rice-farming along the Casamance river / Southern Senegal. The second thesis was a study after tree-effects on soil and herbaceous layer in the Sahel (Niono / Mali). After her studies, she was employed for a short period at the Agronomy department of Wageningen Agricultural University (WAU), to do a literature research after the differences in water-use by trees and crops in West-Africa. In June 1995 she started to work as an associate-expert for ICRAF in Maseno / Kenya, where the research described in this thesis was her main job from 1997 to 2000. Writing of the thesis was done as guest-fellow at the Soil-Quality section of WAU.