10 Catching and Competing for Mobile Nutrients in Soils

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Key questions

- 1. How many roots does a plant need for the adequate uptake of water and nutrients?
- 2. Do soil macropores enhance or decrease leaching of nutrients?
- 3. Can below-ground competition between plants be predicted from the root length density of each plant?

10.1 Introduction

The mobility of nutrients in soil is of prime importance with respect to plant nutrition and nutrient losses from a system. Nutrient movement in soils is closely linked to water dynamics and nutrient depletion in the rhizosphere (i.e. plant demand) as well as to the properties of the soil and the nutrient itself. The plant components of ecosystems significantly influence water movement, and hence nutrient utilization and losses, by altering infiltration, runoff, water usage drainage. Particular emphasis has been given, in the past, to the effect of agroecosystems and their management on the occurrence of macropores and their potential effect in terms of reducing/increasing leaching of nutrients (van Noordwijk et al., 1991a; Dierolf et al., 1997). Deep-rooted trees, crops and pastures have the potential to reduce leaching by acting as a 'safety net' and intercepting nutrients moving through the soil profile (Rowe et al., 1999). Soil properties, such as cation and anion exchange capacity, further act as an inherent nutrient safety net (Mekonnen et al., 1997; Suprayogo et al., 2002). Introducing more diverse cropping systems and mixed-species systems may enhance nutrient capture and recycling efficiency. This is particularly true where species in mixed systems have complementary, rather than competitive, nutrient resource acquisition strategies. Multispecies systems may better exploit underutilized resources or may exploit new resource niches (Cadisch et al., 2002a). Evidence of root plasticity in competition is response to emerging (Gathumbi et al., 2002a; Chapters 4 and 5, this volume), which may lead to a better exploitation of the available resources in mixed-species systems (Schroth,

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There is still great uncertainty as to how many roots per unit soil volume (i.e. fine root length density) are needed to exploit or intercept leaching nutrients (van Noordwijk and Brouwer, 1991; Cadisch et al., 1997). Chapter 9 discusses, in detail, soil-plant interactions with regard to water, and simplified ways to describe soil hydraulic properties (pedotransfer functions), which determine, to a great extent, the mobility of nutrients in the soil solution. Here, we describe factors determining nutrient transport in, and losses from, soils, and investigate ways to describe how plants compete for nutrients or act as safety nets, with examples from recent research.

10.2 Nutrient Mobility in Soil Solutions

10.2.1 Mobility of nutrients in uniform soil conditions

The basic transport equation for a substance in a porous medium reads:

$$\frac{\partial S}{\partial T} = -\nabla . F + U \tag{10.1}$$

where S is the bulk density of the substance (mg/cm^3) , T is time (days), F is the flux $(mg/cm^2/day)$, ∇ is the gradient operator (cm^{-1}) and U is the production or consumption (mg/cm³/day). This equation states mathematically that the rate of increase or decrease of a substance in a small volume of soil is due to the difference of in- and outgoing flows over its surface plus possible production or consumption in the volume. If, for instance, the substance in question is nitrate, it can be produced by mineralization and subsequent nitrification or consumed by denitrification. The flux of nutrients can, at least within the scope of this book, be assumed to consist of two components - a convective component (F_c) and a diffusive component (F_n) :

$$F = F_C + F_D \tag{10.2}$$

The convective flux (F_C) is brought about by transport of water, and the resulting flux is proportional to the concentration of the nutrient in that water:

$$F_C = VC \tag{10.3}$$

where V is the volume flux of the water (cm/day) and C is the concentration of the nutrient in water (mg/cm³). The diffusive flux (F_D) is assumed here to be given by Fick's first law (i.e. flux is proportional to the gradient of the concentration):

$$F_D = D\nabla C \tag{10.4}$$

where D is the diffusion coefficient (cm²/day). The convective flux, or mass flow, is the dominant mechanism in leaching, whereas the diffusive flux is often the most important process when transport in the vicinity of the root is being considered. Substitution of Equations 10.2, 10.3 and 10.4 into 10.1 results in:

$$\frac{\partial S}{\partial T} = \nabla \cdot VC + \nabla \cdot D\nabla C + U \tag{10.5}$$

This then is the general equation that is used to describe transport in the soil to the root.

10.2.2 The inherent 'safety net' of soils

The total amount of a nutrient in the inorganic form consists of the amount in solution, which is mobile, and the amount in the solid phase, which is considered immobile. Here, the immobile form will be assumed to consist of two pools: a pool, Q (mg/cm³), which exchanges at a fast rate with the pool in solution, and another pool from which transfer to the solution is so slow that it can be ignored for our purposes. Thus:

$$S = Q + \theta C \tag{10.6}$$

where θ is the volumetric water content of the soil (cm³/cm³). It will be assumed here that at any time there exists a unique functional relationship – the adsorption isotherm – between Q and C, symbolized by:

$$Q = f(C) \tag{10.7}$$

Substitution of Equations 10.6 and 10.7 into Equation 10.5 yields an equation with only *C* as the dependent variable:

$$\left[f'(C) + \theta\right] \frac{\partial C}{\partial T} = \nabla \cdot D \, \nabla C - \nabla \cdot VC + U \qquad (10.8)$$

In the following equations, we will neglect the production/consumption term U, which reflects mineralization and plant uptake, as it is dealt with below (Equation 10.16). In Equation 10.8, the role of the soil's chemical properties is given by the derivative of the adsorption isotherm with respect to concentration, as shown on the left-hand side of Equation 10.8. The soil's physical properties and conditions manifest themselves via their influence on the transport parameters V and D. Water is both the carrier of solutes (reflected in the role of the flux V) and the medium through which diffusion takes place. The diffusion coefficient in soil is very much dependent on water content and can be calculated as (Nye and Tinker, 1977):

$$D = D_0 f_l \theta \tag{10.9}$$

where D_0 is the diffusion coefficient in water and f_l the impedance factor, a function of water content. Equation 10.8 assumes special forms, of which some examples follow, depending on subsequent assumptions. If we consider first the case of leaching without root uptake (consumption), then one usually assumes transport in a vertical direction only:

$$\left[f'(C) + \theta\right] \frac{\partial C}{\partial T} = \frac{\partial}{\partial z} D \frac{\partial C}{\partial z} - \frac{\partial VC}{\partial z}$$
(10.10)

In ecosystems, plant roots play an important role in nutrient transport, in terms of plant consumption and depletion of nutrient stocks, and hence leaching. An obvious and widely used assumption, when transport to a root is considered, is that of the cylindrical form of the root, which leads to the choice of expressing Equation 10.8 in cylindrical coordinates rather than in rectangular coordinates as was done in Equation 10.10. When tangential and vertical gradients are assumed to be negligible, Equation 10.5 (not considering leaching) assumes the form:

$$\left[f'(C) + \theta\right] \frac{\partial C}{\partial T} = \frac{1}{R} \frac{\partial}{R} DR \frac{\partial C}{\partial R} - \frac{1}{R} \frac{\partial RV_R C}{\partial R}$$
(10.11)

where R is root radius (cm) and V_R is volume flux to the root (cm/day). When transport is dominated by diffusion, and the mass flow component can be neglected, Equation 10.11 simplifies to:

$$[f'(C) + \theta] \frac{\partial C}{\partial T} = \frac{1}{R} \frac{\partial}{R} DR \frac{\partial C}{\partial R}$$
 (10.12)

provided that D is independent of C and the adsorption isotherm is linear, i.e.

$$f(C) = K_a C \tag{10.13}$$

(where K_a is the adsorption coefficient (cm^3/cm^3)); then Equations 10.10, 10.11 and 10.12 are linear equations, which can be solved analytically by classical mathematical techniques. If, however, the adsorption isotherm is non-linear (e.g. in the case of phosphate), the equations have generally to be solved by numerical methods. When the diffusive flux can be neglected with respect to the mass flow (e.g. in the case of leaching) and adsorption is linear, substitution of Equation 10.13 into Equation 10.10, and some rearranging, leads to:

$$\frac{\partial C}{\partial T} = -\frac{1}{K_a + \theta} \frac{\partial VC}{\partial z}$$
 (10.14)

This shows that the flux of a dissolved nutrient is retarded by the retardation factor N:

$$N = \frac{1}{K_a + \theta} \tag{10.15}$$

For nutrients with a non-linear adsorption isotherm (e.g. phosphate) the situation is more complicated. The retardation here depends on the concentration itself and the shape of the adsorption isotherm (see also Chapter 7, this volume).

Retardation factors (Table 10.1) can significantly reduce leaching of nutrients. The effectiveness of this inherent 'safety-net' function of soils in reducing mineral N leaching in tropical cropping systems was investigated by Suprayogo et al. (2002), using the WaNuLCAS model (Box 10.1; van Noordwijk and Lusiana, 1999). Simulation of different cropping systems in humid tropical conditions in Sumatra, Indonesia (Box 10.2; Suprayogo et al., 2002) suggested that the ammonium retardation mechanism reduced leaching of mineral N by between 5% and 19% (Table 10.2). Effective retardation increased when crops and trees were present, due to their direct uptake of mineral N, and as an indirect result of their uptake of soil water, which decreased net drainage through the rooting zone. When the retardation factors in the model were activated, the simulated leaching

	Diffusion coefficient (cm²/day)			
Cad	Water (25°C)ª	Soil ^a (range)	Adsorption coefficient (K_a) $(cm^3/g)^f$	
Nitrate	1.6	10 ⁻¹ -10 ⁻²	0.03-0.17 ^{b,d} (Ultisol) 0.07-0.28 ^c (Acrisol)	
Ammonium	n/a ^e	n/a	1.5–1.8 ^b (Ultisol)	
Phosphorus	8.0	10 ⁻³ -10 ⁻⁶	n/a ´	
Potassium	1.7	$10^{-2} - 10^{-3}$	n/a	

Table 10.1. Diffusion and adsorption coefficients of nutrient ions.

Source: aJungk (1991); bSuprayogo et al. (2002); cWong et al. (1987).

Box 10.1. WANULCAS (Water Nutrient Light Capture in Agroforestry Systems).

WANULCAS (van Noordwijk and Lusiana, 2000; Fig. B10.1) offers a good compromise between spatial and process-orientated complexity. The model is particularly suited to the evaluation of spatial interactions (such as above-ground shading and competition for water and nutrients), which may occur over a range of distances in mixed-species systems. The resource-capture framework for modelling plant growth used here is based on shoot and root biomass, allocation to leaf and root area index (LAI and RAI, respectively) and its spatial distribution (based on 'architecture'), and capture of light, water and nutrients.

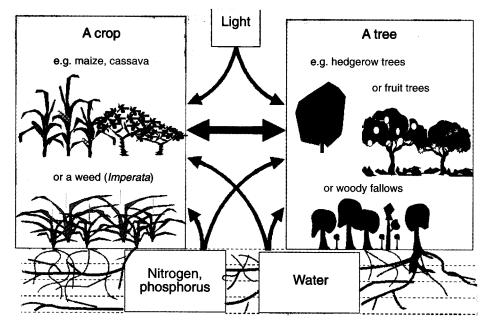


Fig. B10.1. Scope of the WANULCAS model.

Continued

^dpH dependent; $^{\rm e}$ n/a = not available; fby taking into account soil bulk density $K_{\rm a}$ can be expressed per volume as in Equation 10.13.

Box 10.1. Continued.

Water balance: Upon infiltration, a 'tipping bucket' model is followed for wetting subsequent layers of soil, filling a cascade of soil layers up to their effective 'field capacity'. Field capacity is estimated from the water retention curve using pedotransfer functions (see Chapter 9). Soil evaporation depends on ground cover (based on the LAI of trees and crops) and soil water content of the topsoil; soil evaporation then stops when the topsoil layer reaches a water potential of -16,000 cm.

In WANULCAS 2.0, a simple representation of by-pass flow is added and there is an option for a dynamic simulation of macropore structure. The user can define an initial saturated hydraulic conductivity value that differs from the default value predicted by the pedotransfer value. During the simulation, the value will tend to return to this default value (at a rate determined by the *S_KStructDecay* parameter). Water uptake by the plants is driven by their transpirational demand, within the possibilities determined by root length densities and soil water content in the various cells to which a plant has access.

Leaching of N (and P) is driven by percolation of water through the soil and by the average nutrient concentration in soil solution. The latter is derived from the inorganic nutrient stock, the soil water content and the apparent adsorption constant (K_a) . Macropore flow bypasses the soil solution contained in the soil matrix. A multiplier N_B as M_B is used in the leaching equation, to describe preferential macropore flow.

Nutrient uptake: A target N content is contrasted with the current nutrient content, to derive the 'Nutrient deficit'. The N deficit can be met either by atmospheric N_2 -fixation or by triggering an increased nutrient demand for uptake from the soil. Potential nutrient uptake (Uijk) from each cell (ij) by each component (k) is calculated from a general equation for zero-sink uptake (de Willigen and van Noordwijk, 1994) on the basis of the total root length in that cell, and is allocated to each component in proportion to its effective root length:

$$U_{ijk} = \frac{L_{rv,ijk}}{\sum_{k} L_{rv,ijk}} \frac{\pi D_0 (a_1 \Theta_{ij} + a_0) \Theta_{ij} H_{ij} N_{stock,ij}}{(K_a + \Theta_{ij}) [-\frac{3}{8} + \frac{1}{2} \ln \frac{1}{R_0 \sqrt{\pi \sum_{k} L_{rv,ijk}}}]}$$
(B10.1)

where L_{rv} is root length density (cm/cm³), D_0 is the diffusion constant for the nutrient in water, Θ_{ij} is the volumetric soil water content, a_1 and a_0 are parameters relating effective diffusion constant to $\Theta_{ij'}$ H is the depth of the soil layer, N_{stock} is the current amount of mineral N per volume of soil, K_a is the apparent adsorption constant and R_0 is the root radius. Real uptake S_{ijk} is derived after summing all potential uptake rates for component k for all cells ij in which it has roots. Total uptake will not exceed plant demand. The definition of 'demand_k' is based on the current biomass and a target nutrient concentration appropriate for that biomass (van Noordwijk and van de Geijn, 1996), minus a fraction derived from atmospheric N_2 -fixation.

events in the crop-only and in the tree-based systems agreed reasonably well with the actual, measured, leaching values of 6.5 and 2.0 g N/m², respectively (Suprayogo, 2000).

Whereas adsorption of ammonium in this plinthic Acrisol significantly decreased the simulated N leaching, the much smaller nitrate adsorption coefficient (Table 10.1) had only a minor effect in reducing leaching. This was exacerbated by the shallowness (0.8 m)

of the effective rooting depth of the investigated and simulated soil due to the plinthic subsoil. Thus, anion (and cation) adsorption may more effectively reduce leaching in deep soils with less intensive rainfall. Nitrate adsorption coefficients increase with increasing soil depth. This is associated with: (i) the decrease in soil pH with depth, because of the soil's pH-dependent variable charge (which is more positive at depth); and (ii) the often

Table 10.2. Effect of including the adsorption coefficients for NH_4^+ and NO_3^- (Table 10.1) in the simulation of leaching of mineral N below 0.8 m over 1 year, in different tropical cropping systems, with fertilizer additions of 30 kg N + 60 kg N/ha, on a Plinthic Acrisol in the humid tropics. (Adapted from Suprayogo *et al.*, 2002.)

Cropping system ^a		Adsorption coefficients included in simulation				
	-KaNH4-KaNO3	−K _{aNH4} +K _{aNO3}	+K _{aNH4} -K _{aNO3}	+KaNH4+KaNO3		
	Mine	Mineral N leaching in g/m² (% change in parentheses)				
-C-H	11.8 (0)	11.8 (0.1↓)	11.3 (4.7↓°)	11.3 (5.0↓)		
+C-H	10.7 (0)	10.6 (0.8↓)	8.7 (Ì8.9↓)	8.6 (Ì9.9√)		
+C+H	8.3 (0)	8.2 (0.6 ¹)	6.9 (16.8 ↓)	6.8 (17.4 √)		

 $^{^{}a}-$, without; +, with; C, maize–groundnut rotation; H, *Peltophorum dasyrrachis* hedge; $^{b}K_{aNH_{4}}$ and $K_{aNO_{3}}$, adsorption coefficients for NH $_{4}^{+}$ and NO $_{3}^{-}$; $^{c}\downarrow$ = % decrease.

increased clay content at depth in highly weathered soils. An important factor is also the decrease in organic matter content (SOM) that occurs with soil depth. This is because, with decreasing SOM, the number of negative charges (CEC) decreases and the number of anion exchange sites (AEC) increases (see also Chapter 6, this volume). Mekonnen et al. (1997) found large accumulations of nitrate under maize monoculture systems in a Lixisol in Western Kenya (see also Chapter 6, this volume). This may be explained by the great subsoil depth in that Lixisol (>4 m), which, when compared with the Acrisol investigated in Sumatra (<1 m rooting depth), may have greatly increased the 'safety-net' opportunities.

Nitrogen can be leached not only in mineral form but also in a dissolved organic form (DON). The presence, in soil solutions, of DON in concentrations greater than either NH ⁺₄ or NO ⁻₃ has increased scientific interest in the form and function of this pool of N. Studies by Bhogal et al. (2000) and Murphy et al. (1999a) concluded that leached DON could be an important route of N loss (e.g. under arable and grassland systems DON was found to comprise 10% and 20% of total N leached, respectively). Even larger amounts of DON were found to exist in the soil profile and were not lost into drains or watercourses (Murphy et al., 1999b), probably due to effective adsorption mechanisms. However, in South American forests, DON losses into the rivers accounted for >70% of the N budget (van Breemen, 2002).

10.2.3 Mobility of nutrients in heterogeneous soil conditions

Understanding nutrient movement under field conditions necessitates a better knowledge of the flow of water in aggregated soils. Water flow depends on pore distribution and pore size and hence on soil structure and texture. Well-structured soils often exhibit macropore water flow, allowing percolating water to pass rapidly through the soil without displacing the resident soil water contained in micropores (Beven and Germann, 1982); there is thus little nutrient movement out of the soil matrix. Within macropores (Fig. 10.1), dissolved nutrients move downwards rapidly with low rates of adsorption. The result may be increased soil water drainage with increased or reduced leaching of nutrients. The latter will depend on the ratio of nutrients present in macropores to nutrients present in the soil matrix (i.e. whether the nutrients derive from surfaceapplied fertilizer and are contained in the macropore solution, or whether they derive from mineralization in aggregates and so are contained in the micropore solution).

Macrofauna (such as earthworms and termites), through their burrowing, directly increase the occurrence of macropores (Lavelle et al., 1992). There is also evidence that tree roots change the pore-size distribution in soils. Van Noordwijk et al. (1991a) found evidence of substantial macropore flow in channels developed from decaying tree roots on a previously forested site.



Fig 10.1. Decaying roots (indicated by organic-rich (black) material in pore) provide macropore channels for root growth, water and nutrient flows.

Equally, living root systems can contribute to improved soil structure and hence can enhance soil hydraulic properties. Recent evidence suggests that roots are more impor-

tant in the formation of water-stable aggregates than incorporated foliage litter is (Chapter 11, this volume; Cadisch et al., 2002a). On a plinthic Acrisol, field hydraulic conductivity decreased more rapidly with decreasing soil water content under maize monoculture than it did under hedgerow intercropping systems (Fig. 10.2; Box 10.2), implying that the presence of trees resulted in a greater proportion of larger pores. These results, relating to internal drainage, thus suggest that hedgerow intercropping systems can cause greater 'bypass flow' through macropores than monoculture cropping systems can. Indeed, at a distance of 0.4 m from the hedgerow trees, the average macropore flow after 5 min saturation comprised 12% (± 4%) of the total flow under hedgerow intercropping systems, and 8% (± 3%) of the total flow under monoculture (Suprayogo, 2000). The challenge in dealing with macroporosity is the often large heterogeneity found in fields.

Several models simulate salt movements in aggregated soils by using a 'two-region' approach, e.g. convection and dispersion transport through pores or cracks and diffusion movement inside the micropores (van Genuchten and Dalton, 1986). A simplified approach was incorporated in the WANULCAS Version 2.0 agroforestry model (Box 10.1) in order to describe the flow of water through macropores that bypasses the soil solution contained in the soil matrix.

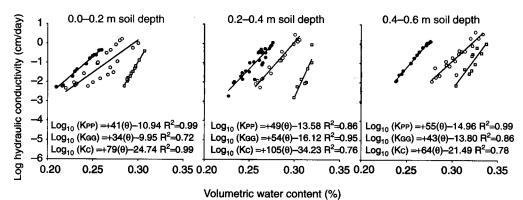


Fig. 10.2. Relationship between field soil hydraulic conductivity and soil water content of a plinthic Acrisol under different cropping systems: (●) *Peltophorum dasyrrachis* and (○) *Gliricidia sepium* hedgerow intercropping systems and (□) maize monoculture. Adapted from Suprayogo (2000).

Box 10.2. Mixed tree-crop cropping systems in Lampung, Indonesia.

Safety-net functions of trees, and competition between trees and crops, were evaluated and simulated in an experiment that was carried out at the Biological Management of Soil Fertility (BMSF) project site of Universitas Brawijaya (Malang, Indonesia)/ICRAF/Wye College (UK)/PT Bunga Mayang (North Lampung, Sumatra) (4°31′S, 104°55′E), on a field with a gentle slope (4%). Annual rainfall is about 2500 mm distributed between December and June and the soil is a coarse loam Acrisol (Ultisol) with a clayey plinthic, Al-rich layer beyond 60–80 cm (van der Heide *et al.*, 1992).

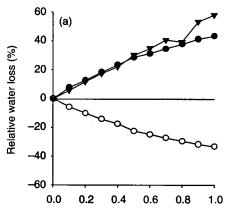
Six cropping systems were established in 1985–1986. Those relevant to this chapter were a system with no hedgerows ('monocrop'), hedgerow intercropping systems using *Peltophorum dasyrrhachis* (P-P) and *Gliricidia sepium* (G-G), and a system in which hedgerows of the latter two species alternated (G-P). Hedgerows were 4 m apart and trees were 50 cm apart within the row. Hedgerows were pruned two to four times per year depending on light competition. Average yields of prunings were (1993–1999) 8.4 t/ha for G-G and 7.2 t/ha for P-P with production of *G. sepium* occurring mainly during the rainy (crop) season while *P. dasyrrachis* grew better during the fallow (dry) period.

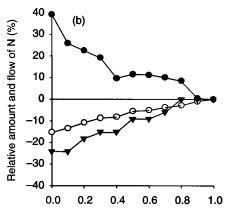
Two crops were generally grown per year, maize (December–February) followed by groundnut (March–June). KCl (60 kg K/ha) and triple super-phosphate (60 kg P/ha) were applied to each crop. Mean maize/groundnut yields (t/ha) over four cropping seasons (between 1993 and 1997) were 2.3/0.3 (monocrop with 90 kg N/ha), 1.2/0.2 (G-G, 0 N), 1.8/0.5 (P-P, 0 N) and 1.7/0.4 (G-P, 0 N). For comparison, in the 1998/99 cropping season, equal N fertilizer treatments (90 kg N/ha) yielded 2.1 (monocrop), 1.3 (G-G), 2.6 (P-P) and 1.9 kg/ha (G-P) of maize grain on average.

Sensitivity analysis of the impact of macroporosity on a hedgerow intercropping system (Box 10.2) indicated that the amount of vertical and lateral drainage increased by around 44% and 58%, respectively, when all flow occurred in macropores, as compared with a situation where no macropores were present (Fig. 10.3). Additionally, runoff was significantly decreased, which led to potentially important reductions in soil erosion and associated nutrient and organic matter surface losses. The model simulations demonstrated that the presence of macropores could proportionally reduce N leaching (by up to 30%) per unit of water drainage. However, in high intensity rainfall conditions, increasing the proportion of macropore flow increased total vertical and lateral leaching of mineral N by almost 15% and 24%, respectively, which was associated with increased drainage due to reduced runoff losses. Thus, the effects that macropores have on nutrient flows have to be viewed in the context of the whole system and offset against reduced erosion losses.

The movement of ¹⁵N-labelled fertilizer and organic residues added to this system (measured by Rowe, 1999) suggested that, proportionally, there was greater lateral

movement of mineral fertilizer N than there was of N derived from the mineralization of organic residues. This led to the hypothesis that fertilizer N applied in high-rainfall areas becomes mainly distributed in macropores, whereas N derived from residues is associated more with the matrix soil, i.e. in micropores and at exchange sites, as was also proposed by Haynes (1986). This is particularly likely in those cases where residues have been incorporated into the soil. N released from surface-applied residues, however, is more likely to behave like fertilizer N. In comparison with mineral fertilizer N, a lower level of leaching of organicderived mineral N is sometimes observed to occur, and this has also been associated with the temporary immobilization of N in the microbial biomass (Schroth, 2001). However, less-controllable N-release patterns from organic residues may lead to larger N losses in other systems. Currently, there are no data available on the distribution (between macropores and the soil matrix) of N derived from different sources that could be used to test the hypothesis that leaching losses of mineral fertilizer N are greater than those of N derived from organic residues.





Relative impact of macropores (1 = 100% flow via macropores)

Fig. 10.3. WANULCAS sensitivity analysis of the importance of bypass flow (0-1) = proportion of total flow as macropore flow) on (a) vertical drainage (\P), runoff (O) and lateral drainage (\P) relative to result of soil with no macropores; (b) mineral N stock at 0–0.8 m soil depth (\P), vertical N leaching (O) and lateral N movement (\P) relative to result with all flow via macropores in a 1-year cycle of a *Peltophorum dasyrrachis* hedgerow system intercropped with a maize–groundnut rotation at the Lampung site. Adapted from Suprayogo, 2000; Box 10.2).

10.3 Catching Nutrients in Singlespecies Stands

Plants mainly take up nutrients in mineral form, via either passive or active pathways. Recent studies suggest that some plants can also exploit dissolved organic N (DON) directly or via ericoid- or ecto-mycorrhizal associations. Raab et al. (1996) showed that the alpine sedge Kobresia myosuroides was able to take up glycine from nutrient solutions at higher rates than it could take up NH 4 or NO 3. This may be an adaptation that allows the plant to survive when inorganic N is severely limited (such as in cold upland situations) or a strategy to avoid competition for scarce resources. Turnbull showed evidence of organic-N (1995)uptake by Eucalyptus. However, the general direct availability of low- or high-molecularweight compounds to plants remains largely unknown. Thus, most of the currently available plant-soil models only consider nutrient uptake via the inorganic route.

10.3.1 Regulation of nutrient uptake processes

De Willigen and van Noordwijk (1987) derived an equation that described the fractional depletion (f) of a mineral nutrient as

a function of demand, root length density, root length, water content, its diffusion coefficient and water uptake (Equation 10.16). Fractional depletion is defined as the fraction of the available amount that can be taken up by the root system at a rate corresponding to the demand. The equation was derived under the assumptions that the roots being considered were parallel, regularly distributed, and all of the same length and activity:

$$f = 1 - \frac{A}{LD} \frac{R_0^2}{C_i} G(\rho, \nu)$$
 (10.16)

where A is the demand of the plant $(mg/cm^2/day)$, L the root length (cm), R_0 the root radius (cm), D the diffusion coefficient (cm/day) and C_i the initial concentration (mg/cm^3) . $G(\rho, v)$ is a function of the root length density and of transpiration:

$$G(\rho, \nu) = \frac{\rho^2}{4(\nu+1)} \left\{ \frac{\rho^{2\nu} - 1}{\nu} - \frac{\nu+3}{\nu+2} \right\}$$
 (10.17)

In Equation 10.17, ρ is a dimensionless parameter given by:

$$\rho = \frac{1}{R_0 \sqrt{\pi L_{rv}}} \tag{10.18}$$

where L_{rv} is the root length density (cm/cm³), and v is the dimensionless transpiration:

$$v = -\frac{E_T}{4\pi LDL_{rv}} \tag{10.19}$$

where E_T is the transpiration (mg/cm²). The diffusion coefficient is calculated as in Equation 10.9 where the impedance is a linear function of water content calculated, following Barraclough and Tinker (1981), as:

$$f_1 = a_1 \theta + a_2 \tag{10.20}$$

where a_1 and a_2 are parameters relating effective diffusion constant to θ .

From Equation 10.16 it can be seen that the fractional depletion is complete (i.e. f =1) when the diffusion coefficient is infinite. that is, when transport through soil is not limiting. For a given root length density, transpiration rate and diffusion coefficient, the fractional depletion increases with decreasing demand, decreasing adsorption and decreasing root radius. For certain nutrients, like phosphorus, it is further necessary to consider the symbiotic mycorrhizal hyphal network as an extension of the plant's root length, which can increase L_{rv} to several times that of a non-mycorrhizal plant. The above discussion pertains to a root system in soil where no other gains or losses of nutrients occur. The next section considers competition between root uptake and leaching.

10.3.2 Critical root length density for intercepting leaching nutrients: root safety net

The root length density required to remove mineral N from the soil is small in relation to that required for less mobile ions, such as phosphate. However, in the dynamic soil environment, if nitrate is not taken up quickly by a plant it may be lost through leaching or may be taken up by other plants; therefore, large root length densities may be needed to acquire N rapidly (Cadisch et al., 1997). We used WaNuLCAS (Box 10.1) to determine how efficiently tree roots intercept leaching nitrogen in a case study in Lampung (Box 10.2). The model runs simulated the December to March high-rainfall period. without N fertilizer application. The trees were pruned on the same day as the crop was planted, with prunings being added to the

soil. The safety-net zone (i.e. the zone below the crop root zone, which is explored by tree roots) was, in the simulation, defined as the 60–100 cm soil layer, in order to reflect restricted root subsoil exploration in this soil due to an aluminium-rich plinthic subsoil.

Simulations made using the WANULCAS model suggested that only around 20% of leaching N would be intercepted by tree roots in the 60-100 cm soil layer at a density of 0.5 cm/cm³ (Fig. 10.4). Measured tree root length densities at this depth were in the range 0.005-0.015 cm/cm3, sufficient to intercept less than 5% of leaching N according to this simulation. The safety-net zone beneath crop roots may, however, be considerably thicker than this, especially at early stages of crop growth or in soils that allow rooting. WaNuLCAS sensitivity analyses were used to examine the effects of root length density, safety-net layer thickness, rainfall and proportion of N derived from N₂-fixation on safety-net efficiency (SNE). This was defined as follows:

$$SNE = 100 \times \frac{TN_{\text{upt}}}{Leach_{\text{out}} + TN_{\text{upt}}}$$
 (10.21)

where SNE is safety-net efficiency (%), $TN_{\rm upt}$ is tree N uptake from the safety-net layer (mg/cm²) and $Leach_{\rm out}$ is N leached beneath safety-net layer (mg/cm²).

Increasing root length density within the safety-net layer from 0 to 2 cm/cm3 led to an approximately linear increase in the efficiency of safety-net interception. However, further increases, above 2 cm/cm3, did not result in a larger proportion of leaching N being intercepted. This probably represents the situation in a field, where even a dense mat of roots would not intercept N leaching during periods of low tree demand, or during heavy rainfall events when residence time is short. Smaller amounts of rainfall achieved greater interception efficiencies, and a plateau level of efficiency was reached at a smaller L_{rv} than was the case in simulations with more rain. Simulations demonstrated the importance of safety-net layer thickness, and hence the maximum rooting depth of trees. With a safety-net layer 4 m thick, the interception efficiency achieved with a root length density of 0.02 cm/cm3 (15%) approached that

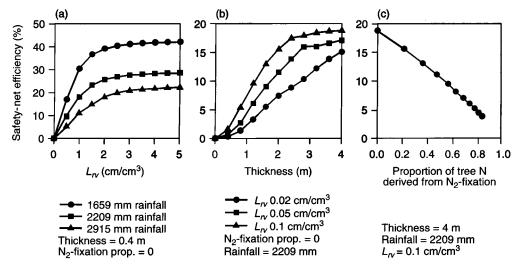


Fig. 10.4. Effects on safety-net efficiency within a *Peltophorum dasyrrachis* hedgerow intercropping system (Box 10.2), as simulated by WANULCAS (Box 10.1), of (a) tree root length density (L_n) in the safety-net layer and rainfall, (b) thickness of this layer and L_n , and (c) proportion of N derived from N_2 -fixation. The safety-net layer was assumed to begin at 60 cm depth. Adapted from Rowe (1999).

achieved with a root length density of 0.1 cm/cm³ (18%). The maximum depth of tree roots will be limited if soil conditions become more adverse with depth, but tree rooting depths of >20 m have been reported for tropical forests (Chapters 4 and 6, this volume), and safety-net layers of this thickness are certainly possible. However, even a thick layer with a high root length density does not intercept all of the leaching N. Saturation of the plant safety net occurs because of asynchrony between leaching and tree N demand. A reduction in tree N demand reduces safetynet efficiency; for example, satisfying a proportion of demand by N2-fixation results in an approximately linear reduction in safetynet efficiency. Using 15N injections at depth and the 15N natural abundance technique to estimate N2-fixation, Rowe et al. (1999) conthat the non-fixing Peltophorum dasyrrachis took up more N (42 kg N/ha) from beneath the main crop rooting zone than the N₂-fixing legume Gliricidia sepium (21 kg N/ha) (see also Chapter 6, this volume). In summary, safety-net efficiency is limited by the residence time of nutrients in the safety-net layer (e.g. rainfall intensity, layer thickness, retardation factors and water consumption by the trees), the tree root length density within this layer, and the N demand of the tree. Given that the latter factor has a large impact on safety-net efficiency, ensuring that plant demand is not restricted by deficiencies of other nutrients (e.g. phosphorus) or by environmental conditions is a matter of paramount importance (Giller et al., 2002).

10.4 Competing for Nutrients in Soil Solution

10.4.1 What strategies do plants have for dealing with competition?

The evaluation of the balance of positive and negative interactions in mixed-species systems remains a major challenge. Van Noordwijk $et\ al.$ (1998a) showed both that negative interactions dominate in many simultaneous hedgerow intercropping systems, and that fast-growing N₂-fixing species may not necessarily be the best trees to use in hedgerow intercropping systems. Competition for nutrients (and light) is a dominant factor in evaluating the efficiency of systems for resource utilization. Zhang $et\ al.$

(2001) estimated that a third of the positive effects of intercropping in wheat-maize and wheat-soybean could be attributed to better soil exploration. Root distribution of the component species has often been interpreted as a direct indication of competition and complementarity in mixed cropping systems, including agroforestry (van Noordwijk et al., 1996; Huxley, 1999; Wahid, 2001). Cadisch et al. (2001) have shown that the fallow species Sesbania sesban and Crotalaria grahamiana react directly to competition by altering their rooting pattern (root plasticity), in order to improve their exploitation of the available nutrient resources. However, such dynamic responses on the part of plants are not considered in most simulation models. Further examples of plant strategies for responding to competition are discussed in Chapters 4, 5, 6 and 17 of this volume.

10.4.2 How can we model plant competition for nutrients?

Although low root length densities may be sufficient for the uptake of mobile nutrients such as nitrate in a situation without competition (or one with intraspecific competition in a monoculture of identical plants), the relative competitive strength of plants in a situation with shared access to a soil layer is thought to be proportional to both their respective root length densities and plant nutrient demand. Nutrient acquisition is affected by the presence of competition, that is: (i) nutrient depletion by the other plants reduces nutrient availability; (ii) potential nutrient uptake per unit root length is reduced by the presence of other roots since the size of the soil cylinder depleted per average root decreases with increasing total root length density; and (iii) reduced soil water content reduces nutrient mobility. The severity of these effects can be off-set by plants that increase the availability of nutrients in

their rhizosphere and/or increase soil water content in nutrient-rich soil layers through the process of 'hydraulic lift' (see Chapter 9, this volume). Plants can indirectly increase their competitiveness by forming associations with mycorrhizas, which act as extended roots and hence increase apparent root length density, although this involves some carbon costs (Chapter 14, this volume).

In WaNuLCAS (Box 10.1), competition for water and nutrients is based on sharing the potential uptake rate for both - based on the combined root length densities $(L_{ry \text{ tot}})$ on the basis of relative root length multiplied by relative demand (A): (see bottom of page) where PotUpt gives the potential uptake rate (mg/cm²/day) for a given root length density (L_{rv}) . This description ensures that uptake by species k is: (i) proportional to its relative root length density if demand for all components is equal; (ii) never more than the potential uptake by a species in a monoculture with the same L_{r} ; and (iii) not reduced if companion plants with a high root length density have zero demand (e.g. a tree just after pruning). At this stage, this procedure is applied to four species (e.g. three trees plus a crop or weed in each zone), but the routine can be expanded to include a larger number of interacting plants.

The outcome of modelled competition depends not only on the description of L_{rv} and demand (A) but also on the sequence in which they are applied in different soil layers or nutrient patches. For example, in the multispecies agroforestry model HyPAR 4 (Mobbs et al., 2001), partitioning of resources starts at the soil surface layer (Box 10.3). Any unfulfilled demand in the upper soil layer is added to the demand from the next soil layer. This enables deep roots to extract more water and nutrients if necessary. The extracted nutrient is then partitioned to trees and crop in proportion to their demand. In future versions of HyPAR, the uptake routines will be modified in such a way that

$$PotUpt(k) = \min \left[\frac{L_{rv}(k) \times A(k) \times PotUpt(L_{rvtot})}{\sum_{k=1}^{n} (L_{rv}(k) \times A(k))}, PotUpt(L_{rv}(k)) \right]$$
(10.22)

Box 10.3. Below-ground competition in HyPAR v4.

HYPAR (Mobbs *et al.*, 2001) models the growth of trees and crops in agroforestry systems. The tree growth components within HYPAR are based on those in the HYBRID model (v3.0) whereas the crop components are based on the tropical crop model PARCH. The version of the model described here (HYPAR v4) runs continuously from year to year, allowing several annual crop seasons to be studied, with one or two crops per year.

Below-ground interaction

Every simulation day, the tree and crop components of the model independently calculate the optimum uptake (or demand) of water and N by the plants. The actual uptake is the minimum of the demand, the available resource and a maximum uptake rate in each soil cell. The maximum uptake rate for water (mm (water)/mm soil/day) is

$$X_{i,pot} = \left(\frac{aw_i}{aw_{fc}}\right)^2 \sqrt{\frac{\rho_i}{\rho_{max}}} U_{max}$$
 (B10.2)

where aw_i is the available water in layer i, aw_{ic} is the available water when the soil is at field capacity, ρ_i is the total (tree and crop) root length density in the layer i, ρ_{max} is the maximum root length density and U_{max} is the maximum uptake rate of water per unit depth of soil. The maximum uptake rate for N by the trees and crop roots together is

$$U_{i,N} = 0.07 \left((1 - \exp(-0.09[N_i]) \right) \sqrt{\frac{\rho_i}{0.25 \rho_{\text{max}}}} \frac{a w_i}{0.5 \sqrt{a w_{fc}^2}}$$
(B10.3)

where $[N_i]$ is the nitrate concentration in the layer i.

If there is sufficient of a resource to meet the demand of all the trees and the crop, then the full amount is removed from the soil and there is no direct competition. If the sum of the demands in any soil cell is greater than that available, or if the combined extraction exceeds a maximum rate, then competition for resources takes place in that cell.

Competition

Water: Starting at the soil surface layer (in each plot independently), the available uptake is compared with the total demand. If the supply is limited, then all of the available water is removed from the soil and any unfulfilled demand is added to the demand for the next soil layer. This enables deep roots to extract more water if necessary. The extracted water is partitioned to trees and crop in proportion to their demand. When competition for water occurs, the crop suffers stress. The tree responds the following day through the effect of a change in soil water potential on stomatal conductance.

Nitrogen: Starting at the soil surface layer (in each plot independently), the available N uptake is compared with the demand. If there is sufficient, then the full amount is removed from the soil and added to the tree and crop internal storage pools prior to reallocation. If the supply is limited, then all of the available N is removed from the soil and apportioned to each tree and the crop in proportion to their demand. Unfulfilled demand in any one layer is passed down to the layer below, allowing extraction from depth where possible.

extraction of water will take place preferentially in wetter layers, rather than from the soil surface downwards (G. Lawson, Edinburgh, 2002, personal communication).

In a way similar to WaNuLCAS, HyPAR (Mobbs *et al.*, 2001) represents competition for water and nitrogen in a grid of soil columns with layers of variable depths (Box 10.3). We used HyPAR to predict the reduction in crop yield through time and space as trees grow and rooting density, and hence competition, increases (Fig. 10.5).

HyPAR also portrays the course of nitrate uptake by the tree and crop components at different depths through the growing season (Fig. 10.6). Close to the tree (Fig. 10.6a), crop growth is very poor (0.07 t/ha) and has little effect on tree N-uptake in an established system. Further from the tree (Fig. 10.6b), the moderately successful crop (2.8 t/ha) has roots that penetrate to layer 8 and which completely out-compete tree roots for nitrate in the latter half of the growing season. Beyond the tree rooting

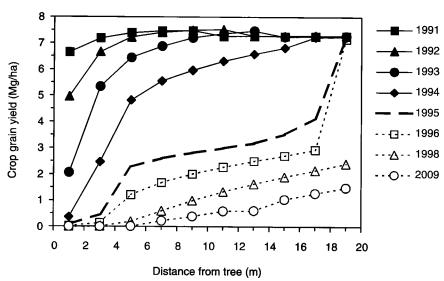


Fig. 10.5. Simulated yield of sorghum (using HYPAR, Box 10.3) for a site in Ghana with annual rainfall assumed to repeat an identical seasonal pattern for 20 years (1502 mm), in a sandy soil (80% sand, 3 m depth), with soil water and nitrogen conditions stabilized for a 10-year 'spin-up' period of bare soil prior to 'planting' a generic *Eucalyptus* tree of 4.8 cm dbh and 8 m height. At the end of 20 years this tree had grown to 23 m height and 45 cm diameter. Radius of the rooting zone had grown from 8 m to 16.5 m. Initial nitrogen is assumed to be equally distributed through the top 40 cm depth and to decline exponentially below this.

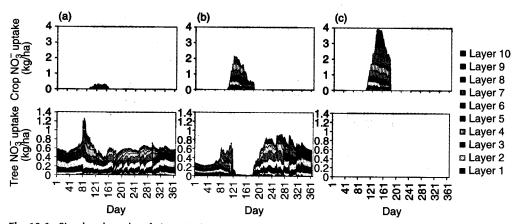


Fig. 10.6. Simulated uptake of nitrate (using HYPAR, Box 10.3) by the tree and crop during 1995, adjacent to the tree (a), 9 m from the tree (b) and 19 m from the tree (c). Layer 1 is the surface layer, and deeper layers are thicker (2, 4, 10, 14, 16, 19, 21, 34, 80 and 100 cm respectively – a total of 3 m). The spatial pattern of crop yield for this year is shown in Fig. 10.5.

zone (Fig. 10.6c), a much higher crop yield is predicted (7.2 t/ha), with nitrate supplies down to layer 9 being accessed by the crop roots in the latter half of the growing season. The nature of this competition for nitrogen is greatly affected by the parame-

ters assumed for the exponential decline in tree and crop root density with depth and with distance from the tree. The importance of making field measurements to obtain realistic crop and root density profiles is clearly illustrated.

Using WaNuLCAS, a sensitivity analysis for a tropical hedgerow intercropping system (Box 10.2) showed that total root length per unit soil area and relative distribution of tree root length density with depth may have complex effects on crop performance (Fig. 10.7). In situations where trees have the majority of their roots in the topsoil, negative effects via competition for water and nutrients reduce crop performance (van Noordwijk and Cadisch, 2002). The magnitude of these competitive effects depends on the total tree root length density. A higher total root length (i.e. higher absolute root lengths in both topsoil and subsoil) can have a moderate, positive effect on maize yield even with a large proportion of roots in the topsoil. Tree root systems with 20% or more of their roots in the subsoil had consistently positive effects on the crop: the higher the total root length, the more positive the impact on maize (Fig. 10.7). The resulting safety-net action of the trees increased the amount of N being recycled in the system and hence improved maize growth in systems where the N supply was limiting. The positive effects the trees had, via improved N recycling, would be expected to increase with time (current results show effects averaged over the first 2 years).

The model's output also suggested that there is a delicate balance between the positive and negative effects of trees. For example, at high total root length, the tree root systems with 60% of their roots below the topsoil led to slightly higher maize yields than those trees with more roots (up to of their roots) in the subsoil. Although this effect is too small to be recognized in the field, the differences in N uptake in crops associated with trees that have 0% of their roots in the topsoil and crops associated with trees that have 40% of their roots in the topsoil arise during dry spells in the cropping season. During these dry spells, the sparse crop roots in the deeper soil layers have slightly more N available in situations where the trees forage partly in the topsoil. Sensitivity analysis of the model thus shows that tree root

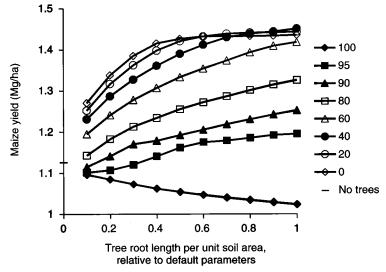


Fig. 10.7. Competition vs. complementarity: WANULCAS simulations of effects on maize yield in a hedgerow intercropping system (Box 10.2), when relative distribution of tree roots with depth, as well as total amount of tree roots, are varied independently. Whereas the 'default' tree root system had 21.5% of its roots in the top layer, a series of data was made that had 0–100% of its roots in the top layer and the remainder allocated to the deeper layers in proportion to the root length densities of the default case. For each of these root distributions, the total amount of roots was varied from 0.1 to 1 times the default, while maintaining the relative values. Adapted from van Noordwijk and Cadisch (2002).

length density below the main crop root zone may have complex and partially unexpected effects on crop performance in situations where negative effects via competition for water and positive effects via improved N supply vary in intensity during the growing season.

The impacts of competition on competing plants differ between the initial phase of near-exponential growth (where a setback in current growth affects future growth as well) and the crop's closed-canopy stage of linear growth (when only current growth rates are affected). This means that negative early effects of competition cannot normally be compensated for by positive effects later on in the growth period. Interactions of positive and negative effects, acting at different spatial and temporal scales, require the use of simulation models that can keep track of such cumulative effects. As mentioned above, plants may respond to competition by exhibiting a differential response to the exploitation of underutilized resource patches in the field (e.g. root proliferation within nutrient-rich zones). However, most do not include such effects. Additionally, leguminous plants will satisfy an unsatisfied N demand by switching their source of N - from soil N resources to atmospheric N, via their ability to fix N2 in association with rhizobia (see Chapter 13, this volume).

10.4.3 Can competition be managed by managing demand?

Managing the distribution of tree nutrient uptake by designing systems where tree and crop roots are in separate regions of the soil is not the only way to reduce tree-crop competition. Tree nutrient uptake can be manipulated by pruning (see also Chapter 17, this volume). Removing shoot material instantly reduces transpiration demand and thus the rate of nutrient uptake through mass flow. Active nutrient uptake is also likely to be reduced since available root and stem carbon can be used for constructing new shoots. There may thus be potential for the use of pruning to

reduce nutrient uptake by intercrop trees during critical periods for crop growth, such as at establishment or pollination. On the other hand, shoot pruning reduces water consumption by the trees and hence may increase leaching; so, the net benefit for the crop is smaller than that which would be expected from reduced nutrient uptake by the tree.

The effect of pruning on soil nutrient demand is exacerbated due to remobilization of internal resources. This is illustrated by the delay, relative to stem regrowth, in uptake of soil N following a pruning event (Rowe, 1999; Fig. 10.8). In this study, hedgerow intercropping trees (Box 10.2) showed no significant soil N uptake during the period 5-14 days after pruning, even though some shoot regrowth occurred during this time. Shoot activity and root activity may not always coincide: tree roots may contain substantial reserves of nutrients and carbohydrates. allowing regrowth to take place with little nutrient uptake from the soil. Conversely, tree roots may take up nutrients during periods of shoot inactivity, an effect noted in temperate ecosystems where fruit tree roots took up N during the late autumn and winter when shoots were inactive (Tromp, 1983). The degree to which plants can uncouple root and shoot phenology depends on their carbohydrate and nutrient storage capacity. In WANULCAS, such delays in nutrient uptake can be simulated by changing the tree pruning time relative to the crop sowing date (Fig. 10.9). The optimal time for pruning to minimize nitrogen leaching whilst maximizing crop yield was, thereby, predicted to be at, or just before, the time of sowing.

Reducing tree competition depends on timing management operations to prevent strong competition occurring before the crop has become established. Having strongly growing trees adjacent to crops inevitably leads to competition, and management should aim at keeping regrowth small during the cropping period. The beneficial effects of trees will be maximized by allowing strong and rapid tree growth to occur during other stages of the crop cycle (i.e. in

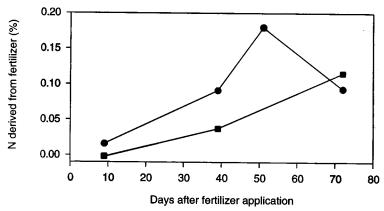


Fig. 10.8. Nitrogen uptake by *Gliricidia sepium* trees pruned either 4 (■) or 25 (●) days before fertilizer application in a hedgerow intercropping system in Lampung (Box 10.2), measured using ¹⁵N. Trees pruned 25 days before application (only) were given an additional pruning 51 days after application. Adapted from Rowe (1999).

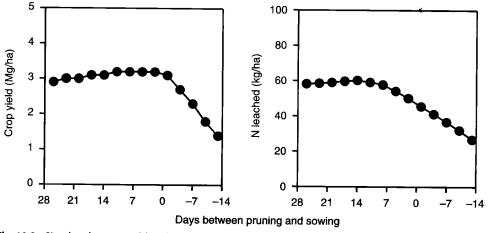


Fig. 10.9. Simulated maize yield and nitrogen leached during the growth of the maize crop in a *Gliricidia sepium* hedgerow intercropping system in Lampung (Box 10.2), as affected by the interval between pruning and sowing. Day 0 is pruning day and negative numbers are days after pruning. From Rowe (1999).

the later stages of crop growth and during any fallow periods). However, tree pruning management is labour intensive, and is particularly unwelcome when it coincides with labour demands for other activities. Labour demands make hedgerow intercropping barely economically viable (Whitmore et al., 2000) and are also one reason why farmers in central American coffee plantations exchange traditional legume shade trees for timber trees with less pruning requirements (Tavares et al., 1999).

10.4.4 Environmental modifiers

In a series of Wanulcas simulations that excluded P limitations on crop or tree growth, a gradual shift from water- to N-limited growth conditions was obtained (Fig. 10.10) by applying multipliers to the daily rainfall records for Lampung for a hedgerow intercropping system involving maize and groundnut (grown in rotation) and Peltophorum dasyrrachis or Gliricidia sepium hedgerows to which N fertilizer (90)

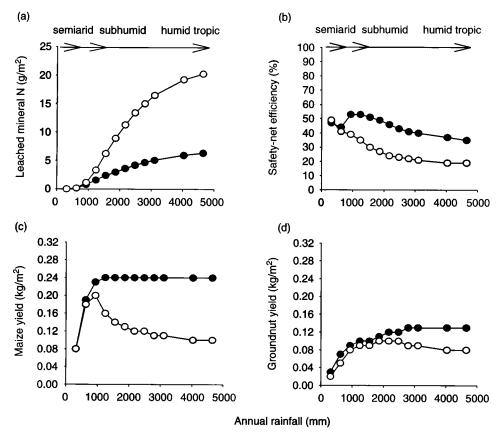


Fig. 10.10. WANULCAS simulations of the effect of different amounts of rainfall in (●) *Peltophorum dasyrrachis* and (o) *Gliricidia sepium* hedgerow intercropping systems on (a) amount of mineral-N leached (g/m²), (b) safety-net efficiency (%), (c) maize yield (kg/m²) and (d) groundnut yield (kg/m²). From Suprayogo (2000).

kg/ha) was applied (Box 10.2). The simulated rainfall represented semiarid 1000 mm annual rainfall), subhumid (1000-2000 mm) and humid (> 2000 mm) No leaching of mineral-N observed when rainfall was below 620 mm. as there was no net water drainage (Fig. 10.10a). Leaching of mineral-N was greatly increased when rainfall was above 900 mm, particularly in the system that contained the N₂-fixing tree Gliricidia. This was due to additional N inputs arising from biological N₂-fixation, as well as to the faster rate of mineralization that occurred with the highquality Gliricidia prunings, as compared with the polyphenol-rich Peltophorum prunings (Handayanto et al., 1994, 1997). Thus N₂-fixing systems appear to be more 'leaky'

than low-input systems without legumes. The N safety-net efficiency decreased with increasing rainfall above 900 mm (Fig. 10.10b). The maximum maize yield in the Peltophorum system was obtained above 1200 mm of rainfall, but in the Gliricidia system, the maximum yield was obtained at 930 mm of rainfall (Fig. 10.10c). The observed decrease in maize yield in the Gliricidia hedgerow system above 1000 mm of rainfall was due to the fast growth of Gliricidia trees and hence to a reduction in the amount of light available to the maize. However, this was not the case in the Peltophorum system due to the different canopy shape of Peltophorum trees and lower tree biomass production at the time of maize growth.

The maximum yield of groundnut, grown as a second sequential crop, was obtained above 2000 mm of rainfall in both Peltophorum and Gliricidia systems, mainly as a result of the fact that growth was restricted by water deficiency towards the end of the rainy season at lower rainfall levels (Fig. 10.10d). Thus, in the presence of hedgerow trees, water can be the growth-limiting factor on 5-10% of the days in the cropping season, even with an annual rainfall of 2000 mm. Cannell et al. (1998) suggested that below 800 mm of rainfall the trees in an agroforestry system have a low productivity, which is not sufficient to compensate for the loss in the yield of associated grain crops that results from competition for light and water. Their results also suggested that between 800 and 1000 mm of rainfall, total productivity of trees may compensate for the loss in crop grain yield, with only a small increase in total site productivity. Moreover, results confirmed that above 1000 mm of rainfall, total productivity can be increased by the presence of trees. The simulated results do not take into account the effects of trees that result in improved microclimate conditions for crops, or the case of trees with inverse phenology (such as Faidherbia albida), which may alter the range of rainfall conditions in which simultaneous agroforestry systems can be considered useful.

10.4.5 Risk management

Because of the complexity of interactions in mixed-species systems, many farmers have resorted to monocrop systems. Moreover, mixed-species systems may not yield more than the best monocrop species unless cropping density can be increased with the introduction of a new species (Gathumbi et al., 2002b); that is, the additional species must acquire resources that the crop would not otherwise acquire (Cannell et al., 1996). Apart from improved resource utilization, risk management is another important factor to consider in designing new systems (Yachi and Loreau, 1999; Loreau, 2000).

Diseases, pests and adverse weather conditions (e.g. drought or flooding) commonly affect plant production in tropical regions. In fact, management of risk or stress(es) may in many cases be of greater importance than resource utilization. Resource capture may thus become limited by risk factors via a reduced resource demand. Equation 10.23 describes the effect of reduced demand on the potential nutrient uptake of each species. Thus, the impact of stress events on resource capture of the system will depend on which species is most affected and what its proportional demand for resources is. On the other hand, there may be some compensatory growth (ε) on the part of the more stress-tolerant species due to underutilization of resources and space e.g.

$$PotUpt = \varepsilon \times \sum_{k=1}^{n} PotUpt(k)stress$$
 (10.23)

where:

$$\varepsilon = (1 - s) \times \sigma \tag{10.24}$$

where s is an integrated stress factor (0-1)denoting the reduced nutrient demand and σ is a factor (0-1) depicting the compensatory growth potential of the more tolerant species. Thus, mixed-species systems are most likely to have an advantage over highly productive monocrops under conditions of increased environmental stress and when the species mixture constitutes a betbuffered system (Fig. 10.11). Van Noordwijk and Ong (1999) used a slightly different approach to assess risk reduction in diverse systems based on average expected yield (mean) and its variance due to environmental stress. They suggested that risk reduction through increased diversity is least effective against 'disasters' and most effective (leading to the lowest system variance) when a small number of strong competitors are present, which vary primarily in relation to tolerance to specific biotic stress factors.

10.5 Conclusions

The process of catching mobile nutrients in soils cannot be described simply by mapping root distributions in soils, as it depends to a

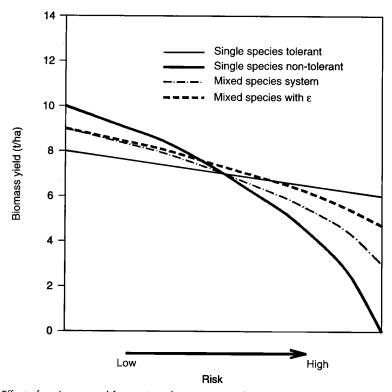


Fig. 10.11. Effect of environmental factors (weather, pests) on advantages of a mixed-species stand vs. monocrops of different susceptibility to stress, without and with compensatory growth (ε) capabilities.

large extent on plant nutrient and water demand and residence time of the nutrient in the rooting zone. Soils have inherent safety nets, in the form of cation and anion retardation mechanisms. However, the impact of retardation factors for nitrate appears to be small in relation to the overall effects of the cropping system on water dynamics and soil structure. More diverse systems, with intense root activity as well as increased soil cover and recyclable organic material, favour the formation of macropores, which have the potential to reduce leaching of nutrients due to a fast bypass flow and limited exchange with nutrients in micropores. However, in high-intensity rainfall areas, macropore flow results in increased drainage, which may or may not result in greater leaching depending on the (mostly unknown) distribution of nutrients in macropores/micropores. consequent reduction in runoff may decrease losses of soil, organic matter and nutrients via

erosion, and thus there should be an overall net benefit to the system.

With increased environmental concerns, more emphasis is given nowadays to the nutrient use efficiency of systems and, in particular, to their safety-net or filter function. Safety nets are strongly dependent on the presence of sufficient L_{p} , at lower depths and hence species selection is crucial. Given that demand has a large impact on safetynet efficiency, ensuring that plant demand is not restricted by other nutrient (e.g. phosphorus) deficiencies or by ill-adapted is of paramount importance. Recycling of the nutrient resources captured in the safety net has the potential to increase crop productivity in nutrient-limited systems, but we have to ask why a species should preferentially explore less fertile lower soil depths when nutrient-rich patches exist mainly in the topsoil. This points to the need to search for less-com-

petitive, deep-rooted species for use in simultaneous mixed species systems, rather than fast-growing N2-fixing species (which are commonly perceived to be the best for such systems). However, root distribution is governed by genotype × environment interactions, and competition, with the resulting root plasticity, may be necessary for creating the complementarity in soil exploration that is necessary for efficient resource use, as noted by Schroth (1998). Simulations and existing data also suggest that N2-fixing systems appear to be more 'leaky' than nonfixing ones. Future challenges include the evaluation of how the safety-net functions of systems at the landscape scale can help to reduce nutrient losses (pollution) into

stream waters, whilst benefiting those systems at a lower position in the watershed.

Mixed-species systems remain a challenge, due to their complex interactions. Thus benefits must be sought beyond resource capture advantages (e.g. risk management, etc.) for them to become viable alternatives to farmers. The development of mechanistic agroforestry models has greatly advanced our understanding and prioritization of complex interactions in multispecies systems. However, for site-specific recommendations to be developed, a major effort towards the calibration of such models is needed, in order to initialize soil conditions and plant performance, because these are not determined only by the parameters described in the model.

Conclusions

- 1. There is no universal critical root length density (L_n) for efficient nutrient interception, since this is determined mainly by the mobility of the nutrient in question, and by plant demand and net drainage.
- 2. Systems that promote the formation of macropores may reduce leaching of mineral N, but the associated reduction in erosion appears to be equally important.
- 3. Soil anion retardation factors have a smaller impact on nutrient retention than does the type of cropping system.
- 4. Low-input legume-based systems appear to be more N 'leaky' than similar systems without N₂-fixing legumes.
- 5. Potential options for managing nutrient interception by perennial components include pruning (timing and severity), species selection (slow/fast growth), and arrangement in relation to lateral flows of nutrients.
- 6. The balance between competition and safety-net efficiency in mixed-species systems appears to be better achieved by slow-growing, deep-rooted and well-adapted species than by fast-growing N_2 -fixing legumes.

Future research needs

- 1. Investigation of the partitioning of nutrients and roots between matrix soil and macropores.
- 2. Studies on the effect of management options in mixed-species systems on temporal changes in demand.
- 3. Studies to determine whether changes in L_{rv} distribution due to competitive plasticity will have a major effect on plant performance or filter/safety-net efficiency.

Acknowledgements

This publication is an output from projects funded by the UK Department for

International Development (DFID, NRSP and FRP) for the benefit of developing countries. The views expressed are not necessarily those of DFID.