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Chapter 8

Root Distribution of Trees and Crops: Competition and/or Complementarity

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Introduction

This chapter examines what has been described as the 'hidden half', the roots, which are invisible and much harder to work with than the above-ground components of plants. Interactions between trees and crops for below-ground resources are often at least as important as those for light and above-ground space (Anderson and Sinclair, 1993). As the basic efficiency of use of water and nutrients for photosynthesis probably does not differ greatly between trees and C_3 crops in most agroforestry systems, tree growth does not constitute a 'free lunch' in any agroforestry system. However, the below-ground resource base for tree growth, and thus the degree of potential competition or complementarity between trees and crops, is usually more difficult to assess than that for annual crops. Because of their perennial nature, the root systems of trees can explore larger soil volumes, both laterally and vertically, and exploit zones of rich, localized, supplies of water and/or nutrients. If these zones are largely out of reach of annual crops, the resources required by the trees are provided for and trees can increase the total production of the system, although they may not improve crop growth as such, having positive, neutral, or negative impacts, depending on tree/crop combinations and local environmental conditions (see Black *et al.,* Chapter 4, this volume). This is especially true for deep rooted trees, which can exploit deep soil water reserves, either stored in the water table or as part of subsurface flow pathways. Tree roots can assist the weathering of saprolite or bed-rock layers which are inaccessible to crops, and intercept water and nutrients leaching down the soil profile below the crop rooting zone. Thus there are opportunities for both spatial and temporal complementarity and competition (Ong *et al.,* 2014), especially since only 5-30% of rainfall is used by annual crops in many agricultural systems (Rockstrom *et al.,* 2007; Wallace, 2000). The general concept that all trees are deep rooted may be greatly overstated, however, particularly on shallow soils, as there are large differences between species and sites and the horizontal scavenging ability of tree roots is often underestimated. Root systems and their functions are important both at the low end of the soil fertility range where 'access' is the key limitation for efficiency of uptake, as well as at the high end where 'excess' is the starting point for off-site environmental problems, affecting the efficiency of the production system as a whole (van Noordwijk and Cadisch, 2002).

What should not be forgotten is that trees and crops do not simply exist as separate potentially competing entities, since their rhizospheres, which have been described as the 'hidden half of the hidden half' (Bowen and Rovira, 1991) have a wide range of both positive and negative impacts on plant growth. In particular, >90% of plant species form associations with mycorrhizal fungi which play a significant role in the mineral nutrition of plants (Kuyper *et al.,* 2004). Indeed it is often considered that it is the external hyphae of the mycorrhizal fungi which provide the direct physical link between plants and their soil resources e.g. Miller *et al.* (1995); Smith and Read (2008), rather than roots. Most short-lived crops form associations with arbuscular mycorrhizal fungi (AMF), or are non-mycorrhizal, while trees associate with AMF or with ectomycorrhizal fungi (EMF) depending on their species. While the fungi benefit from the association by drawing photosynthates, the external

fungal mycelium greatly increases the volume of soil which can be explored by a host root and hence they are especially important in the uptake of immobile ions, such as phosphorus and zinc from the soil, especially under nutrient deficient conditions. These mycorrhizal fungi may also interconnect plants of the same or different species through common mycorrhizal networks (van der Heijden and Sanders, 2003; Smith and Read, 2008).

A cautionary note for agroforestry researchers is that, while experiments with annual crops often use closely-spaced small plots, these are entirely unsuitable for agroforestry studies because the extensive roots of the tree component may exploit the soil in adjacent plots, including the 'no tree control' plots as well as their own. This is likely to reduce crop yield in the control plots and, in the long term, increase that in the agroforestry plots. Both effects lead to an overestimate of the positive yield effect of agroforestry. This situation has been found for the semi-perennial species, cassava, and may invalidate many experiments which concluded that cassava is not responsive to N fertilizer (van Noordwijk *et al.,* 1992). Such effects can be more pronounced for trees and many of the early experiments on alley cropping and other agroforestry systems are difficult to interpret, because root interactions in the so-called no-tree control plots were not properly excluded (Hauser, 1993; Coe, 1994). A basic understanding of the root distribution of the various components in specific systems is thus needed to conduct valid agroforestry field experiments. In on-farm studies, and in agroforestry systems where trees are planted on boundaries, trees may mine adjacent areas (including the neighbour's land) and farmers' perceptions of the advantages of trees may also be biased for this reason. Indeed, the design of experiments involving trees requires careful consideration and planning to ensure that the objectives are reached: an experiment involving annual crops can be easily repeated the following year, but an experiment with tree crops requires long term investment (Coe *et al.,* 2002).

Generalizations about deep-rooted or horizontal scavenger roots are common, but few researchers make the effort to observe roots under their particular field conditions, yet the characteristics of tree and crop root systems and their potential for competition and complementarity are crucial for the development of successful agroforestry systems and should be determined in field trials (Schroth, 1998; Akinnifesi *et al.,* 2004; Rao *et al.,* 2004). However, while field observations are very valuable, the multitude of potential perennial / annual species combinations under different climates, soils, time frames and types of management, makes it impossible to replicate all options in these trials. Systems modelling approaches are needed to explore and understand the significance of different factors, although ultimately farmers' adoption of particular systems may be influenced further by their local knowledge, their attitudes to risk, and gender and socioeconomic issues. Ghezehei *et al.* (Chapter 3, this volume) have already discussed and highlighted many aspects of agroforestry models, in terms of the above factors, enumerated several of the models developed and highlighted the development of a hedge intercropping model.

This chapter returns to the roots of agroforestry modelling and examines some of the fundamentals and hypotheses underlying development of below-ground model components, describes some methods for field assessment of below-ground activity and highlights a potential 'farmer friendly' assessment method.

Basic Root Ecological Concepts

Distribution of tree and crop roots

An understanding of the distribution and dynamics of tree and crop roots and their seasonal variation in relation to the availability of nutrients and water in the soil is required to interpret the factors important in competition and complementarity in tree and crop growth. Surface soil layers may be wet or dry, depending on rainfall input, surface evaporation and use of soil water by plants, and thus are highly variable in terms of soil moisture. Most roots of short-lived crops occupy this zone. Some of this water may gradually percolate further down the soil profile beyond the reach of crop roots, and eventually reach the water table, a few or many tens of metres below the soil surface. Water may also be redistributed in the soil by tree roots through 'hydraulic lift' or two-way 'hydraulic equilibration' resulting in the movement of water from wetter to drier soil layers (Bayala and Wallace, Chapter 6,

this volume; Bayala *et al.,* 2008). The distribution of nutrients in the soil is also spatially and seasonally variable, depending on their sources and mobility, and the extensive and more permanent nature of tree roots again provides wider access to nutrient sources, both in space and time.

Rooting depth of different species in plant mixtures is crucial to determining competition for water and nutrients. Annual crops are relatively shallow rooted, with most roots in the top 80–100 cm of soil. In their early stages of development, they are dependent on soil moisture in the most superficial layers of soil, so lack of rain after germination can severely affect crop establishment (Odhiambo *et al.,* 2001). Longer lived trees and shrubs also rely on surface water during the early stages of their development, but rapidly develop roots below the crop rooting zone and may eventually develop very deep root systems reaching the water table e.g. Stone and Kalisz (1991) and Akinnifesi *et al.,* (2004). Consequently trees are less vulnerable to conditions at the soil surface once they have become established. However, surface tree roots in the crop rooting zones are still retained and competitive with crops. Whether there is complementarity or competition between trees and crops for below-ground resources will ultimately depend not only on the distribution and density of roots, but also on the activity of the roots of different species within specific soil layers. However, the extent of interactions between tree and crop roots will be largely determined by the dominant and perennial trees, as crop roots have no alternative niches to occupy and exploit, whereas tree roots do. The influence of trees on the system is progressive as negative effects due to competition for water may become rapidly apparent close to trees, but increase in their spatial extent as trees mature year by year (e.g. Wilson and Ndufa, 2014), whereas positive effects through soil fertility improvement may take many years to develop (Rao *et al.,* 1997; Kho *et al.,* 2001).

Tree root systems comprise a framework of long-lived coarse roots, which provide the overall structure of the system. On these, fine roots (<2 mm in diameter) develop, which are more ephemeral and have rapid turnover. It is these fine roots, with their associated mycorrhiza, and root hairs, which are involved in nutrient and water uptake. Following their death, they contribute greatly to soil fertility: and although there is little evidence that N is retranslocated within tree root systems, approximately 30% of P and K may be retained (Gordon and Jackson, 2000).

Morphological and functional shoot:root balance

Serious root observations in agricultural systems began over a century ago (van Noordwijk and van de Geijn, 1996). Root characteristics across plant species apparently vary independently of their shoot characteristics (Kutschera and Lichtenegger, 1982), and trees show immense variation in their rooting depth and lateral extent (Stone and Kalisz, 1991). Natural selection has led to a large number of root and shoot combinations, apparently adapted to different environmental conditions. There is, thus, ample scope for selection, breeding and biotechnology to modify the genetic determinants of root development, if only we knew in what direction they should be changed.

Early agricultural researchers found that a better root development was often correlated with a higher yielding crop, and a 'basic law' of agriculture was formulated that any restriction to root growth by adverse soil conditions would lead to a reduced yield (Hellriegel (1883) quoted in van Noordwijk and de Willigen (1987). Evidence contradicting this 'basic law' gradually accumulated (ibid.), and it was eventually replaced by the hypothesis of a 'functional equilibrium' between root and shoot growth Brouwer (1963, 1983).

Insert Figure 8.1 near here

Figure 8.1 shows a generalized form of the response of above- and below-ground parts to increased water and/or nutrient supply Schuurman (1983). At the lower end of the range, both shoot and root biomass increase with improved resources, but the maximum root biomass is generally obtained at a lower level of resources than maximum shoot biomass. Hence the shoot:root ratio changes according to the supply of resources. This scheme can be used to explain the conflicting evidence in the literature about external factors 'increasing' or 'decreasing' root growth in experiments which cover only part of the range.

Although primarily developed for annual plants, the functional equilibrium concept appears to be equally valid for perennial species, when expressed as the ratio of leaves to fine roots. However, as the large quantities of storage and stability tissue, both above- and below-ground, complicate comparisons of total biomass, other measures, which are more closely related to functionality, such as leaf and fine root surface area/biomass may be more appropriate than biomass for woody perennials. Gower (1987), for example, reported that fine root biomass in tropical wet forests is inversely related to phosphorus and calcium availability. Vitousek and Sanford (1986) found that shoot:root ratios in tropical forest decrease with decreasing soil fertility. Leuschner *et al.*, (2007) found that the ratio of root biomass to above-ground biomass increased 10 fold with altitude in tropical forest at 1050 and 3060 m elevation, and Zhu *et al.* (2013) found that nitrogen addition to an N-rich old growth forest decreased fine root biomass by 31%. A review of above- and below-ground production in forest ecosystems found that the highest fine root biomasses were found at locations where soils were high in Al and Fe and nutrient limited (Vogt *et al.*, 1996). Mokany *et al.* (2006) reviewed literature for various terrestrial biomes.

Dhyani *et al. (*1990) found that root dry weight ranged from 27% (*Leucaena leucocephala)* to 72% (*Eucalyptus tereticornis*) of total tree biomass in a comparison of five tree species at two years of age. Toky and Bisht (1992) found for six year-old trees (of 12 species) that root dry weight ranged from 9% *(Acacia catechu)* to 27% (*Morus alba)* of total dry weight, with a median value of 20.3%. These figures probably do not reflect the relative importance of roots in current carbon allocation in trees, as roots may have a higher turnover rate than above-ground tissues. Sanford (1985) estimated fine root turnover in the top 10 cm of soils in Venezuelan forests was 25% per month. Berish (1982) observed a fine root biomass under successional vegetation of around 40% of that in adjacent natural forest. Fine root biomass reached the undisturbed level after only five years, at the same time as the leaf area index.

According to the 'functional equilibrium' concept (Brouwer, 1963), the allocation of growth resources in plants to root and shoot meristems is modified by the major current environmental conditions. If water or nutrients are in short supply within plants, the root system will receive a larger share of the carbohydrate supply within the plant and will increase in size relative to the shoot (as measured in shoot:root ratio) or even in an absolute sense (Fig. 8.1). Subsequent research (Lambers, 1983) showed that the underlying mechanism is more complex than the direct resource limitation of shoot and root meristem activities envisaged by Brouwer (1963) and that there is more variation between plants in how rapidly and to what extent they adjust to modified conditions. The functional equilibrium is, however, still a source of inspiration for hypotheses about actual plant responses, as it explains their overall functionality.

When light (or CO_2 supply) limits plant production, shoots will increase in size relative to the root system. The empirically observed response of shoot:root ratios in elevated CO_2 experiments appears to depend on whether water or nutrients are the growth-limiting resource. As the CO_2 concentration impacts on water use efficiency at stomatal control level, no increase in proportional allocation to roots is expected where water is the factor determining current root system size, while for nutrients a proportionally larger root allocation is expected and observed (van Noordwijk *et al.,* 1998).

The concept of biomass allocation, as encapsulated in ratios of shoot:root, photosynthetic: non-photosynthetic tissues, or leaves:roots has merit, but also has a number of problems (Poorter and Sack, 2012). An alternative approach is to analyse allocation within an allometric framework, which scales the change in size of one plant organ against the changes in the size of others, enabling wider interdependencies between organs to be examined; see Poorter *et al.* (2012) for a meta-analysis of biomass allocation and allometric relationships of a wide range of plant groups.

Maximum plant productivity can be obtained with relatively small root systems, provided that the daily water and nutrient requirements are met by technical means (van Noordwijk and de Willigen, 1987). Better possibilities for uptake mean that a smaller root system can supply the needs of shoots. The answer to the question 'How many roots does a plant need?' thus depends on the environment in which plants grow and their intrinsic growth rate. With agricultural intensification, human control over the supply of water and nutrients has gradually increased; the endpoint of this

development has culminated in horticulture based on soil-less culture techniques. Reducing the size of the root system has a limit, however, when the physiological capacity for uptake is reached - this limit may be encountered first of all for water (de Willigen and van Noordwijk, 1987; van Noordwijk, 1990). Plants growing in free water still need a considerable root surface area, as can be approximated (for non-saline conditions) by:

$$A_{r,w} = \frac{E_p}{L_p \Delta H_p}$$
(Eqn 8.1)

where
$A_{r,w}$ = root surface area required for water uptake [m^2],
E_p = transpiration rate per plant [$cm^3\ s^{-1}$],
L_p = hydraulic conductance of roots for water entry [$cm^3\ m^{-2}\ MPa^{-1}s^{-1}$],
ΔH_p = maximum acceptable difference in plant water potential between root xylem and the adjacent soil environment [MPa].

Applying parameters for fully grown tomato (*Solanum lycopersicum* L.) or cucumber (*Cucumis sativus* L.) plants to Equation 8.1 predicts that the required root surface area is *c.* 1 or 2.4 m^2, respectively, or 50% of the leaf area in both species. The actual root surface area formed under non-restrictive conditions was 50-100% of the leaf surface area in a series of experiments (de Willigen and van Noordwijk, 1987). Shoot:root ratios expressed on a dry weight basis may reach 20-30 in this situation. The specific root area (root surface area per unit dry weight) can be ten times higher than the specific leaf area (being 0.2 and 0.02 $m^2\ g^{-1}$, respectively). For oak and aspen saplings grown in pots, (Wiersum and Harmanny, 1983) observed a root surface area of approximately twice the leaf surface area.

In the field, the required size of the root system is not determined by the maximum physiological ability of individual roots, but rather by the transport rates of water and nutrients in the soil and hence by the need to reduce transport distances and the required water potential and concentration gradients as determined by uptake requirements per unit root length in an extensively branched root system. Thus, the more restricted the water supply, the larger is the root system needed relative to the shoot; however, maintenance of the root system imposes costs to the plant in terms of assimilates and other organic substances. Hence, there is an interplay between root length density, root diameter, soil water content, the diffusion coefficients and distribution of nutrients, to which is added the complication that much of the tree root system has no role in nutrient acquisition, but provides support, transport and storage functions. White *et al.* (2013) and Lynch (2013) proposed a number of root ideotypes for crops for efficient acquisition of phosphorus, potassium and nitrogen.

Root densities and nutrient and water uptake

Model approaches

Although large root systems may not be needed for maximum growth rates, roots are of direct importance for the efficient use of available soil water and nutrient reserves, and hence in reducing negative side effects of agriculture. As a first approximation, it may still expected that 'the more extensive the root system is, the higher nutrient and water uptake may be' (van Noordwijk and de Willigen, 1991). The possibility of obtaining a higher resource uptake efficiency can only be realized if the total supply of nutrients and water is regulated in accordance with the crop demands and the resource use efficiency attainable. On a field scale, both resource supply and possible crop production show spatial variability and inadequate techniques for dealing with this variation may reduce the resource use efficiency much below what is demonstrated in the normally small experimental units considered for research (van Noordwijk and Wadman, 1992).

In modelling nutrient and water uptake a number of levels of complexity can be distinguished (van Noordwijk and van de Geijn, 1996):

1. 'Models without roots', based on measured or estimated 'uptake efficiencies' (ratio of uptake and quantity of available resources); roots remain implicit in such models
2. Models predicting uptake efficiency on the basis of measured root length density and distribution; these models must integrate the activities of single roots to the root system level
3. Models based on descriptive curves fitted to root growth in space and time under non-limiting soil conditions, e.g. negative exponential functions to describe root length density as a function of depth or deterministic root branching models driven by time or cumulative temperature (Diggle, 1988; Pagès *et al.*, 1989)
4. Models based on functional equilibrium concepts, relating overall root growth to the internal water, nutrient and carbohydrate status of the plant. The distribution of new roots at various soil depths may follow either of approaches 2 or 3 above
5. Models including root growth as in 4 above, but adding the differential response of root growth to zones with differing environmental conditions (e.g. nutrient, water, oxygen supply, mechanical impedance) to account for observed rooting patterns in soil. This leads to functional-structural plant models in which root and soil processes are mechanistically simulated as a part of whole-plant physiology, with explicit consideration of spatio-temporal complexity (e.g. SimRoot, see recent review by Dunbabin *et al.* (2013).

Such model concepts (1–5) have been developed for single cropping systems and further extended to the development of various models for multi-species agroforestry systems where combinations of rapidly growing annual and slower growing perennial species with differing access to above- and below-ground resources and differing root activity are integrated (see reviews by Matthews *et al.* (2004) and Malezieux *et al.* (2009)). Models involving trees and crops include HyPAR (Mobbs *et al.,* 1998), WaNulCas (van Noordwijk and Lusiana, 1999) and Yield-SAFE (van der Werf *et al.*, 2007). Recently developed models of type 5 focus increasingly on fine-scale complexity and interaction in crop plants (Dunbabin *et al.*, 2013), and can operate as 'virtual plants'. Combining field observations with model simulations can highlight the most significant factors influencing crop yield in a particular system and suggest the possibility of additional factors: using WaNuLCAS to investigate hypotheses concerning the factors influencing crop yield in a *Grevillea robusta/ Cassia spectabilis – Zea mays* system. Radersma *et al.* (2005) found that small reductions in soil water had a significant impact on P diffusion, leading to a P deficiency caused by soil drying, at the same time, data suggested rhizosphere modifications by *Cassia*.

Insert Figure 8.2 near here

As models at level 2 are a prerequisite for any of the subsequent levels, considerable efforts have been made to develop and test them (Nye and Tinker, 1977; Barber, 1984; de Willigen and van Noordwijk, 1987; Gillespie, 1989). Earlier models described the nutrient uptake rate of roots as being determined by the external concentration, based on Michaelis-Menten kinetics or similar relationships between concentration and uptake rate. However, when external supply exceeds the current crop demand, such models overestimate uptake as internal feedback mechanisms down-regulate uptake in most plant species under such circumstances. By contrast, when demand exceeds supply, the affinity of the uptake mechanisms for nutrients is so high that roots can deplete the concentration at the soil solution-root interface to virtually zero. The model description of de Willigen and van Noordwijk, (1987, 1994a, b) is therefore based on a notion of crop nutrient demand, similar to potential transpiration rates, regulating uptake per unit root length when supply is sufficient and a 'zero-sink' (actually an infinite sink strength leading to a concentration of zero) when supply is limiting. The quantity of available nutrients left in the soil at the transition between these two situations is termed N_{res}. Figure 8.2 shows a concentration profile in the soil surrounding a single root; if the roots are regularly distributed, the soil 'belonging' to each root is approximately a cylinder of constant radius. N_{res} is defined as the integral of the concentration in this cylinder at the moment when transport towards the root just falls

short of uptake demand. It determines the highest uptake efficiency that can be achieved without reducing crop growth:

$$\text{maximum efficiency} = \frac{\text{crop demand}}{\text{crop demand} + N_{\text{res}}} = 1 - \frac{N_{\text{res}}}{\text{crop demand} + N_{\text{res}}} \qquad \text{(Eqn 8.2)}$$

When nutrient supply is less than the sum of crop demand and N_{res}, the uptake efficiency may be (slightly) higher. When supply becomes limiting, nutrient uptake can gradually deplete the N_{res} nutrient stock, asymptotically approaching complete depletion.

Model for simple root-soil geometry

de Willigen and van Noordwijk (1987, 1991, 1994a,b) derived, under simplifying assumptions on root-soil geometry, an equation for N_{res} as function of root length density L_{rv} and root diameter, which can be used to predict uptake efficiency from a single homogeneous layer or which can be part of dynamic uptake models from layered soils.

$$N_{\text{res}} = \frac{A(K_a + \theta)D_{\text{m}}^2 G(\rho, v)}{4H(a_1\theta + a_0)\theta D_0} \qquad \text{(Eqn 8.3)}$$

where:
A = daily nutrient demand [kg ha^{-1}d^{-1}]
K_a = apparent adsorption constant [ml cm^{-3}]
θ = soil water content [ml cm^{-3}]
a_1 and a_0 = parameters describing the decrease of effective diffusion coefficient with decreasing θ,
H = depth of soil zone considered [cm]
D = diffusion coefficient of nutrient in free water [cm^2 d^{-1}]
D_{m} = root diameter used for model [cm]
where:

$$\rho = 2(\pi L_{rv}D_m^2)^{-0.5} \qquad \text{(Eqn 8.4)}$$

$$G(\rho, 0) = \frac{\rho^2}{8}\left[-3 + \frac{1}{\rho^2} + \frac{4\ln\rho}{\rho^2 - 1}\right] \qquad \text{(Eqn 8.5)}$$

A slightly more complex definition is used if mass flow is included and the dimensionless group based on transpiration rate, v, is not zero (de Willigen and van Noordwijk, 1987). As diffusion constants do not differ much between most solutes, the zero-sink concentration profile for all major nutrients NO_3^-, NH_4^+, K^+ and $H_2PO_4^-$ can be treated in a similar way. Only the demand parameter A and the adsorption parameter K_a (which relates the total available amount to the concentration in soil solution) will differ considerably between them; K_a for $H_2PO_4^-$ is 100-1000 ml cm^{-3}, while for NO_3^- adsorption may be negligible. Thus the factor $(K_a + \theta)$ is 300-5000 times larger for P than for N. N_{res}/A expresses the residual amount as the number of days with unconstrained uptake which would be possible for an infinitely dense root system ($N_{\text{res}} = 0$ for $L_{\text{rv}} = \infty$). For nitrate N_{res}/A may be only a few days, while for P it easily encompasses one or several growing seasons. So and Nye (1989) showed that for a tenfold decrease in effective diffusion constant $(a_0 + a_1\theta) D_0$ from its value at field capacity ($pF = 2.0$) a sandy loam has to dry out until the soil matric potential $pF = 3.3$ and a silty clay until $pF = 4.5$. Such a decrease in soil water content renders N_{res} for NO_3^- in a dry soil similar to that of K^+ at field capacity. The strongest inhibiting effect of dry soil conditions on nutrient uptake, however, may be on phosphorus, as its effective diffusion is already slow in wet soil (Radersma *et al.,* 2005).

A similar approach is possible for water uptake if the factor A is replaced by the potential transpiration rate and the concentration is replaced by the matrix flux potential (de Willigen and van Noordwijk, 1987, 1991); for a more refined treatment of water uptake, however, the hydraulic

conductance of roots, L_p, should also be considered. Under wet conditions L_p will dominate the total soil-plant resistance and water uptake may be proportional to root length density; in drier soil the soil resistance gradually becomes more important (de Willigen and van Noordwijk, 1991).

Figure 8.3 near here

Figure 8.3 shows N_{res} as a function of L_{rv}, A and θ for a standard parameter set for NO_3 uptake (de Willigen and van Noordwijk, 1987). N_{res} becomes less than 10 kg ha^{-1} for L_{rv} values in the range 0.2-2 cm cm^{-3} (lower values for wetter soil and lower daily NO_3 demands); increasing root length density above this value will allow only a small amount of additional N uptake. Some of the simplifying assumptions, especially on the uniformity of root diameters and on the effects of root distribution pattern can now be avoided (van Noordwijk and Brouwer, 1997).

Figure 8.4 near here

Mycorrhizal hyphae and heterogeneity in root diameter

If root systems containing roots of different diameter are compared at equal root length density (length x diameter^0), the larger the diameter, the smaller N_{res} and thus the more efficient uptake can be. If the comparison is made at equal surface area (length x diameter^0 x π), N_{res} decreases with decreasing root diameter (de Willigen and van Noordwijk, 1987). If the comparison is made at equal root volume (length x diameter^2 x $\pi/4$) or weight, the advantage of the smaller root diameters is even more pronounced. The most stable result was obtained for a comparison at equal length x diameter$^{0.5}$. Figure 8.4 shows the required P availability in the soil, as indicated by the water-extractable P_w index - when root systems of different diameter are compared on the basis of equal root length, root surface area, root volume or sum of root length x diameter$^{0.5}$. The more efficient the root system, the lower the required P level of the soil. Calculations were made with the P model of van Noordwijk *et al.* (1990), which is based on N_{res} and P adsorption isotherms, and parameters for the growth of the velvet bean (*Mucuna pruriens*) on an ultisol in Lampung, Indonesia (Hairiah *et al.,* 1995). With the length x diameter$^{0.5}$ index, calculated results are approximately independent of root diameter over at least one order of magnitude. We thus have a method to add hyphal length of mycorrhizal fungi (which are about 25 times smaller in diameter than the finest roots) to the crop root length, approximately 1/5 (or 25$^{0.5}$) of the hyphal length can be added to the root length density. If only 'infection percentage' data are available for the mycorrhiza, we have to assume a reasonable length of hyphae per unit infected root length (a value between 10 and 100 seems reasonable, say 50 as first estimate), and we thus obtain an increased root length density by a factor of 1+ (0.5 x %inf/5). For a normal infection percentage of 15%, this means that the effective root length density is 2.5 times that of the length of roots alone (van Noordwijk and Brouwer, 1997). The lack of adequate methods for quantifying hyphal length makes this a priority area for research, if mechanistic P uptake models are to be used for mycorrhizal plants, i.e. for nearly all species found in agroforestry (Miller *et al.,* 1995; Bainard *et al.*, 2012). A similar method can be used to obtain a weighted average root diameter for a branched root system, with a diversity of root diameters.

Non-regular root distribution

Root systems adapt to heterogeneity in the soil. Lateral roots develop preferentially on roots that are effective in the uptake of resources (water, N, P or K) that are currently limiting the plant as a whole. Root branching can also respond to the current root-soil contact situation (Bao *et al.,* 2014). Where single-root uptake models have usually assumed a cylindrical geometry and regular spacing, as well as a homogeneous resource, the real soil is heterogeneous in terms of supply as well as root distribution.

With the 'root position effectivity ratio' R_{per}, the uptake efficiency for any actually observed root distribution pattern can be related to that for a theoretical, regular pattern. The effects of

incomplete root-soil contact can be incorporated as well, in an approximate manner (van *Noordwijk et al.,* 1993a; 1993b). R_{per} is defined as a reduction factor on the measured root length density, to account for the lower uptake efficiency of real-world root distributions, when compared with the theoretical, regular pattern assumed by most existing uptake models (based on a cylindrical geometry of the root-soil system), including the model used to derive Equation 8.1. For random root distributions, R_{per} is approximately 0.5 (i.e. root length density *X/2* in a regular pattern has the same N_{res} as a random pattern at density *X*). For clustered root distribution, as may be expected in structured soils, where roots grow mainly along cracks, R_{per} values in the range 0.05-0.4 can be expected. R_{per} tends to decrease with higher absolute root length densities. The other side of the coin, however, is that non-regular root distributions can be expected to develop in response to heterogeneous soil, and the synlocation of roots and resources can enhance (perhaps double?) uptake efficiency. As these two errors (assumed regular root spacing and resource homogeneity) might balance out, the uncorrected model is probably acceptable as starting point.

Dynamics of root growth and decay

Estimates of L_{rv} normally have a fairly wide confidence interval, because of the considerable spatial variability of root length density. If root growth and decay are estimated from a time series of destructive sampling, the results tend to have an unacceptably large uncertainty. If sequential non-destructive observations can be made on the same roots, e.g. those located next to a mini-rhizotron, and the resulting images are analysed for changes relative to the root length present, a much smaller sampling error can be obtained. However, there is a potential bias in using this method, as the observation method may affect root behaviour (Gijsman *et al.,* 1991; Anderson and Ingram, 1993; van Noordwijk *et al.,* 1994a). From the few agroforestry mini-rhizotron data sets analysed for fine root longevity, a median lifespan of about two months emerges as typical value (van Noordwijk *et al.,* 2004), but measurement under a wider set of conditions is still desirable.

Effective root length density as function of time and depth

For minirhizotron observations, (van Noordwijk and Brouwer, 1997) derived an 'effective root length density' L^*_{rv} as a function of time and depth as:

$$L^*_{rv}(i,T) \ = \ R_{per}(i,T).\frac{\int_{t=0}^{T}\big(G(i,t) - D(i,t)\big)\,dt}{\int_{t=0}^{S}\big(G(i,t) - D(i,t)\big)\,dt} \cdot \frac{\sum_{j=0}^{n}L_{rv}(i,s,j)\sqrt{D_j}}{\sqrt{D_m}} \qquad \text{(Eqn 8.6)}$$

where:
$L^*_{rv}(i,T)$ = effective root length density (cm cm^{-3}) in layer *i* at time *T*
$L_{rv}(i,s,j)$ = measured root length density in layer *i* at time of sampling *s* for root diameter j,
$R_{per}(i,T)$ = root position effectivity ratio (procedure defined in (van Noordwijk *et al.,* 1993b)
$G(i,t)$ = observed root growth along minirhizotrons as a function of time in zone i
$D(i,t)$ = observed root decay along minirhizotrons as a function of time in zone i
D_m = root diameter used for model calculations,
D_j = root diameter for diameter class *j* and observed root length density $L_{rv}(j)$

If R_{per} is *c.* 0.4 and the mycorrhizal correction factor is 2.5, the two correction factors may, accidentally, cancel and the use of direct L_{rv} values can be correct in practice.

Critical densities for various functions

van Noordwijk (1983) gave an indication of the root length densities L_{rv} needed to meet the demands of an average crop for water and nutrients from a normal agricultural soil in northwest Europe: 0.1 - 1 cm cm^{-3} for NO_3^-, 1 - 10 cm cm^{-3} for $H_2PO_4^-$ and intermediate values for K^+ and water uptake. Root length densities beyond these ranges will have a relatively small effect on decreasing N_{res}, although for P uptake L_{rv} increases up to 30-50 cm cm^{-3} may still be meaningful. The carbon investments required for additional

root growth can be balanced against the carbon fixation that is made possible by additional water uptake. In climatic conditions where re-wetting of dried soil is rare or in situations where fine roots will not survive a drying-wetting cycle, root length densities L_{rv} above 3-5 cm cm^{-3} may not be economical for a plant in terms of its C economy. The values given here are no more than indications of the order of magnitude, as both soil (K_a, θ, H) and crop parameters (A, D_m) affect their values.

Allocation of uptake in multilayer systems

In stratified soils (by layer or any other division in internally relatively homogeneous zones), an algorithm is needed for allocating total demand (A) over the various strata in those situations where total supply exceeds demand. Although there are insufficient physiological data to choose between them, a number of algorithms is possible. For example, the demand can be allocated proportional to:
1. relative root length density
2. N_{res}, or
3. the external nutrient concentration in each stratum

   de Willigen and van Noordwijk (1989, 1991) used an algorithm that is based on allocation method 1 if total supply exceeds demand, but which will increase the demand allocation to zones where supply exceeds demand stepwise if certain zones cannot meet the originally allocated demand

Allocation of uptake in multispecies systems

The simplest description of competition for water and nutrients is based on zero-sink uptake by both or all species competing for the same resource. The relative competitive strength will then be proportional to the N_{res} value for each component, based on its effective root length density in the zone or layer where competition occurs. For more refined descriptions differences in phenology (leading to different A values over time) and root development (different $L_{rv}*(i,T)$) should be taken into account as well and a dynamic simulation model is needed. Below-ground competition is for resources that are stored in the soil and thus is affected by the recent history of uptake, in contrast to competition for light and CO_2.

   In developing agroforestry or intercropping models, there have been essentially two approaches:

1. Create an interface at the level of soil resources between a well-calibrated crop model and a well-calibrated tree model (as in HyPAR; Mobbs *et al*., 1998))
2. Start from a combined uptake model interacting with soil and have explicit algorithms for the way total uptake is shared over the component species (as in WaNuLCAS; van Noordwijk and Lusiana, 1999)

Although approach A is attractive where well-calibrated models exist, results proved to be sensitive to the order in which the crop and the tree uptake modules were implemented, leading to an alternating days schedule (on even days the crop first, on uneven days the tree first, for example). Extensions to more than two species may be complex. The algorithm used for case B can be readily extended to multiple species interacting with a single volume of soil. However, where individual plant have multiple layers of soil from which they can potentially meet their daily demand, , the interactions between actual uptake in respective layers are difficult to solve without an iterative loop.

Root growth and distribution patterns

Genotype × environment interactions

Although certain generalizations about deep/shallow or narrow/wide root distribution patterns can be made at a species or genotype level, the actual root pattern is based on genotype x environment interactions (Kerfoot, 1963). van Noordwijk (1991) contrasted the results of root ecological studies at the single root, whole plant and split-root levels (where different parts of a plant root system are

placed in different conditions of nutrient or water supply). For root response to factors such as P supply, Al^{3+} concentration, soil compaction and O_2 concentration these three levels of complexity may lead to contrasting results. Of special interest, is the 'split-root' level, which can be used to analyse the local response of root systems to heterogeneities in the environment. The response of a root tip to its local environment depends in many ways on the conditions elsewhere in the root system (around other roots) as well as in the shoot. For example, lateral root development is often stimulated in zones of relatively high P supply; this response is absent, however, when P supply in the plant as a whole is adequate. Thus. the generalization that 'phosphate stimulates root growth' is only partially true. The results can be explained by assuming that root meristems with direct access to P have priority in using it and may thus attract a larger share of the carbohydrates necessary for growth in plants in which internal P is a growth-limiting resource. Once the local needs of roots are met, P supply to the shoot increases, and by internal redistribution in the phloem, also P supply to other roots. This phenomenon has been extensively studied for crop plants (de Jager, 1985), but also applies to wild species (Caldwell *et al.*, 1992). Similarly, Hairiah *et al.* (1993) showed that fewer roots of *Mucuna pruriens* develop in a solution containing a relatively high Al^{3+} concentration if part of the root system is grown in a solution without Al^{3+}; yet, if this Al^{3+}-containing solution is used for the whole root system, it will stimulate root growth compared with a homogeneous control solution. The response of a root tip to Al^{3+} thus depends on the environment around other roots. However, no separate Al-signalling mechanism needs to be invoked to explain these results, as the Al-avoidance response disappears if P supply to the plant is improved, and may be based on Al-induced P shortage in exposed roots.

In the local response of root growth, a distinction should be made between the growth of main axes and lateral root development. Most of the responses appear to be based on stimulated lateral root development and can also be described as a reduced degree of apical dominance, the mechanism by which the apical meristem of shoots or roots reduces or delays the development of lateral axes. In perennial root systems, a large proportion of the finer lateral roots is relatively short-lived, but new lateral roots can develop annually from the surviving secondary thickened transport roots (van Noordwijk *et al.*, 2004). Wiersum (1982) noted a pronounced branching response of coconut roots to local fertilizer application and proposed a simple soil nutrient test. Roots of mature, field grown trees can be induced to grow in a mini-basin with nutrient solution of various compositions. The intensity of the local stimulation of lateral root development can be taken as an indicator of which nutrient is in short supply in the tree as a whole. A similar method, based on a modified in-growth core technique, was used by Hairiah *et al.* (1991). However, despite a wide range of approaches to assessing nutrient uptake by tree roots, considerable methodological problems remain (Lucash *et al.*, 2007).

Putz and Canham (1992) found no differences between trees and shrubs in below-ground architectural plasticity or in root extension along a nutrient gradient. Species from poor habitats, however, tended to have higher root plasticity (response to local nutrient supply) and root growth rates than species generally occurring in more nutrient rich habitats. This finding is contrary to a prediction by Grime (1979), but is consistent with a higher relative spatial heterogeneity of nutrient availability on poor soils.

Deep rooting is common in xerophytic species such as *Alhagi camelorum* (25 m recorded), *Glycyrrhiza glabra* (10-15 m), *Andina* sp. (18-19 m) (Daubenmire, 1959) and *Acacia senegal* (32 m) (Deans, 1984; *cf*, Chapters 4.6). Where there is no access to a ground water table, however, desert shrubs may have a very extensive horizontal root system to intercept rainfall from a large area. Roots of the small desert shrub *Tamarix* were found to extend up to 40 m (Ladover (1928),as quoted in Daubenmire (1959)). Moreno *et al.* (2005) observed that roots of *Quercus ilex* in Spain extended 33 m laterally, seven times the projected area of the canopy. Akinnifesi *et al.* (2004) concluded that trees were deeper rooting in seasonally dry environments, however many studies of agroforestry trees have only evaluated tree roots in the crop rooting zone and thus have provided no evidence of the overall distribution of tree roots, or the proportions of roots in surface and deep horizons.

Although Vandenbeldt (1991) found clear differences in rooting depth of young plants of *Faidherbia albida* genotypes from western and southern Africa, and Mulatya *et al.* (2002) noted that root architecture of *Melia volkensii* is influenced by site and climatic conditions, tree age and

provenance, there is generally insufficient knowledge about the variation in root architecture within agroforestry tree species, and whether this is due to genotypic or environmental effects. Tropical agroforestry trees are largely undomesticated, and there may be extensive undetected variation in their rooting characteristics. By contrast, many crop species are of known varieties and there is increasing understanding that their rooting characteristics are under strong genetic control e.g. Postma and Lynch (2012), York *et al.* (2013). Simple observation methods are thus needed to 'ground-truth' generalizations about root patterns in trees. However, even where tree species are perceived to have a generally favourable root architecture, this may be over-ridden by other factors, such as shallow soils, preventing tree roots from extending into deeper zones (Smith *et al.,* 1999).

Horizontal and vertical distribution

Simplified curves fitted to actual root distributions can be used for models at level 3 (see above) as root length densities of most crops decrease with depth. Graphs of the logarithm of the root length density against depth normally show a linear trend, except for soils with specific layers restricting or stimulating root development. A two-parameter descriptive model based on an exponential decay can thus be used to describe $L_{rv}(h)$, the root length density as a function of depth h:

$$L_{rv}(h) = bL_{ra}e^{-bh} \qquad \text{(Eqn 8.7)}$$

where L_{ra} = root length per unit of cropped area (cm cm^{-2}) and b is the slope of the regression line of $\log(L_{rv})$ on h. Exceptions from this exponential pattern can be found in relatively deep-rooted trees such as *Dactyladenia (Acioa)* on acid soils (Ruhigwa *et al.,* 1992) or *Eucalyptus camaldulensis* (Jonsson *et al.,* 1988).

Root density normally also decreases with increasing horizontal distance from plants. The combined effect in a two-dimensional plane radial to a soil cylinder with the plant in its centre can be described by elliptical models of the general form:

$$L_{rv} = ae^{-b\sqrt{h^2+cr^2}} \qquad \text{(Eqn. 8.8)}$$

where r is radial distance to the plant and a, b and c are parameters. The parameter c indicates whether root length density decreases faster with radial than vertical distance ($c>1$) or vice versa ($c<1$). de Willigen *et al.* (2002) described two-dimensional models that describe fine root distribution by analogy to a diffusion process.

Branching models

A number of parameters are used as indicators of different root functions (van Noordwijk and de Willigen, 1991):
  1. length of the longest (deepest) root, roughly indicating the *exploration* of soil zones
  2. total length or surface area of live roots, governing the *exploitation* of most nutrients and water from the soil zones explored
  3. number of root tips and associated young unsuberized root sections, which govern cytokinin production and Ca uptake
  4. root dry weight, indicating the amount of carbon in the root system and giving an initial estimate of the C costs of producing and maintaining roots

Relationships between these parameters, such as specific root length or length per unit dry weight (van Noordwijk and Brouwer, 1991), indicate the constraints that plants face in combining these functions. The relationships can be studied in the actual shape of root systems, but can also be derived once the underlying morphogenetic branching rules are known. A combination of an easily observable indicator of root system size and knowledge of the morphogenetic rules will be of value for practical root studies.

Fitter (1986) Fitter *et al.* (1988) and Fitter and Stickland (1991) described the topological and fractal aspects of branched root systems. Fitter (1991) specified five types of information which are needed to reconstruct a three-dimensional model of roots: (i) the number of *internal* and *external* links (without and with apical meristem, respectively); (ii) the lengths of the links; (iii) the distribution of branches within the root, i.e. the *topology*; (iv) the branching angles; and (v) the diameter per link. If one is interested in total size, rather than three-dimensional distribution, the branching angles are not relevant. For the total length, rather than volume or weight, the diameters can be omitted and only the first three types of information are needed.

Leonardo da Vinci (Mandelbrot, 1983) claimed that the cross-sectional area of the main stem of a tree is equal to the sum of the cross sectional areas of its branches. The same rule might apply to rivers (at least in a landscape with constant slope), and may be based on the approximately constant volume of water passing through the river system from the sum of all sources to the final sink. A constant sum of squared diameters in trees might indicate a constant resistance to longitudinal water flow, if individual xylem vessels or tracheids have a constant diameter, the maximum for which is determined by the risk of cavitation in large cells (Milburn, 1979), and functional xylem forms a constant proportion of total stem diameter. For tree stems, stability and strength requirements may be as relevant as water transport capacities in determining stem diameters, but the 'constant squared diameter rule' or 'pipe-stem model' (Shinozaki *et al.,* 1964) at least provides a valuable point of reference in studying trees. Empirically a close relationship between cross sectional area of sapwood and total leaf area has been established (Waring and Schlesinger, 1985). A similar rule might apply to tree root systems and this assumption forms the basis of fractal branching models (Spek and van Noordwijk, 1994; van Noordwijk *et al.,* 1994b; van Noordwijk and Mulia, 2002). According to these models, a relationship can be expected between the diameter of roots at the stem base (proximal roots) and the total length of that root, given a few parameters of the branching pattern which can be obtained from small samples at some distance from the tree (Fig. 8.5). Tests of the assumptions underlying these models should be made under field conditions.

Figure 8.5 near here

Measuring the proximal diameter of roots, i.e. the diameter of the root segment connected to the stem base, is relatively simple (Fig. 8.5b i, Box 8.1a), and can be done after careful excavation, e.g. of a half sphere of 0.3 m radius, without damaging the tree (van Noordwijk *et al.,* 1991a). Relationships between proximal root diameters and the total length of all root links depend on the root branching pattern (Fig. 8.5a, Box 8.1b iii and iv), which can be determined from a relatively small sample of root.

Box 8.1 A. Protocol for quantifying proximal tree root diameters and the index of tree root shallowness and the competitivity index. B. Protocol for testing the fractal characteristics of root branching and measurement of parameters for predicting total root system size from proximal root diameters

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    A. *Proximal roots (also see Fig. 8.5b i and ii)*

1. Carefully excavate the first part of the proximal roots at the stem base (Fig. 8.5b). For a small tree, a 0.3 m half sphere is sufficient, for larger trees a 0.5-1.0 m half sphere is required. While excavating, all major roots should be left intact, but destruction of most of the fine roots is unavoidable. Check for 'sinker roots' (vertically orientated roots starting from horizontal roots, often close to the tree stem; trees may need to be supported during this process

2. Measure the diameter of all proximal roots (i.e. all roots originating from the stem base or as laterals from the top part of the tap root) and classify them by orientation (angle with a horizontal plane). The diameter measurements should be made outside the range of obvious thickening close to the branching point or buttress roots, which normally taper off rapidly.

3. Measure stem diameter either as 'root collar' diameter, or as stem diameter at breast height, depending on the size of the tree

4. These data can then be used to calculate the index of tree root shallowness and competivity index (see Eqn. 8.9 and 8.10)

B. *Test of fractal branching assumptions* (*also see Fig. 8.5b iii and iv*)
1. Expose parts of the root system by tracing roots from the stem base. For each branching point where the previous and subsequent 'links' have been exposed, measure the diameter of each link (either at the midpoint of the link or 5 cm from the previous branching point, avoiding the thickened zone which often accompanies branching). Also measure link length.
2. Analyse data by sorting the roots belonging to a common previous link and calculate the α parameter as $= D^2_{before}/\sum D^2_{after}$. Then analyse the regressions of α and link length on root diameter. If neither of these regressions has a significant slope, the basic assumptions of fractal branching models are met. The mean values of α and link length can be used in the equations for total length, surface area and volume given by van Noordwijk *et al*. (1994b); if either of these regressions has a significant slope, modified equations must be developed (e.g. on the basis of the numeric model given by Spek and van Noordwijk (1994)

Santantonio *et al.* (1977) reported a highly significant correlation of root diameter and the fresh weight of subtended roots in Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco), which could be used to estimate the biomass of roots broken off in windthrows, but also indicates that the proximal root diameter may be a good indicator of root system size. Some attempts have also been made to relate root biomass to total stem diameter at breast height (Santantonio *et al.,* 1977; Kuiper *et al.,* 1990). A close relationship between the logarithm of total root biomass and the logarithm of tree diameter at breast height was confirmed for tropical trees (Freezaillah and Sandrasegaran, 1969; Sanford; 1989), but not for fine root biomass (Egunjobi, 1975).

Analysing the architectural rules underlying root development (Atger, 1991; Francon, 1991) opens up perspectives for visualizing and predicting three-dimensional structures as they develop in time, but there are still considerable difficulties in incorporating the large plasticity in response to local soil conditions into the analytical framework. Recent studies of crop roots in mixed annual systems point the way forward for this work (Postma and Lynch, 2012). Still, to a considerable extent, secondary thickening of transport roots occurs in response to, and in coordination with fine branch root development, so the branching pattern present at any time is likely to contain more regularity and predictability than one would expect from the way it is formed. Mulia *et al.* (2010) showed that a dynamic fine root response to local uptake conditions can be reconciled in model algorithms with an emerging fractal branching architecture for woody roots.

Empirical relation between root pattern and tree growth rate

Coster (1932a) studied a large number of species as potential understorey trees for teak (*Tectona grandis*) plantations. Considerable variation was found in root patterns of different species growing on the same (deep, neutral) soil in Java. No simple relations between above- and below-ground dimensions existed, contrary to widespread beliefs that crown diameter and root spread are related. Hairiah and van Noordwijk (1986) re-analysed the data and classified the trees in three groups: those with a deep tap root and few superficial, horizontally oriented roots generally showed a slow initial growth of the shoot and had a shoot:root ratio on a dry weight basis of 0.4 to 2.5; those with a deep tap root and extensive horizontal root development in the topsoil showed a faster shoot growth and had shoot:root ratios of 2 to 6; and a group of shallow rooting trees and shrubs which had shoot:root ratios ranging between 2 and 30 (Hairiah and van Noordwijk, 1986).

Fig 8.6 near here

Figure 8.6 shows that shoot dry weight at six months of age was correlated with tap root length in trees without strong lateral root development. In trees with more than two long lateral roots, however, there was no relation between tap root length and shoot dry weight if the point in the upper right corner of the graph (*Sesbania sesban)* is regarded as an outlier. Average shoot weight was much higher for trees with at least two horizontal lateral roots of at least 1 m length than for trees without such exploration of the topsoil. The often heard requirement for 'fast growing trees with deep root development, causing little competition with shallow rooted crops' squares in the upper right corner of the graph but seems to ask for the impossible, at least based on initial growth. However, previous data (Coster, 1932a,1932b) showed that *Leucaena leucocephala* and *Acacia villosa* were the best options to complement the relatively shallow root system of *Tectona grandis*: after a moderately rapid establishment phase with some horizontal roots in the topsoil as well as a deep tap root, subsequent root development was largely confined to the subsoil.

Effects of tree management on root distribution and activity

The over-riding purpose of agroforestry systems in which deep-rooted trees are mixed with annual crops, is to increase productivity, and tree management is required to reduce competition. Few trees in agroforestry systems are allowed to grow undisturbed as branches are lopped, crowns raised, trees are pollarded or pruned to obtain fodder, fuelwood or green manure and/or reduce shading of crops. All leaves of apple trees in East Java (Indonesia) are regularly stripped off to induce flowering in a tree which does not receive the needed environmental trigger from its original area of distribution in temperate regions. In Embu, Kenya, farmers heavily prune and pollard *Grevillea robusta* trees to manage them for timber production and control competition with adjacent crops (Bamwerinde *et al.,* 1999). In the south of France, ploughing and intercropping between rows of poplar and hybrid walnut was found to cause a more vertical profile of fine tree roots and provided trees with access to deep reserves of water, which in turn contributed to higher tree-growth rates in the agroforestry system compared to the forestry controls (Mulia and Dupraz, 2006). A similar pattern of increased coarse root distribution at depth was observed in the UK, when poplar trees were planted in rows between cultivated alleys, compared with uncultivated controls (Upson and Burgess, 2013).

While most tree management practices focus on above-ground plant parts, on the basis of the functional shoot-root equilibrium concept we may expect them also to produce below-ground effects. Reducing the leaf canopy decreases transpirational losses and thus the 'need' for new root growth, but also reduces carbohydrate supplies to the root system required for root growth and maintenance. Under more severe pruning regimes, recovery of trees depends on the remobilization of stored energy reserves in parts of the stem or storage roots not affected by pruning. Reduced carbohydrate supply to the roots after removing part of the tree foliage may be expected to cause dieback of fine roots and nodules, but few hard data exist on such effects (Fownes and Anderson, 1991; Smucker *et al.,* 1995). As root death and subsequent decay increase nutrient mineralization in the soil, crops can benefit from pruning the tree component, not only by reducing shading but also by improving nutrition from both above- and below-ground sources. The latter may be especially relevant for well-nodulated trees where direct transfer of N to crop roots is possible after dieback of the tree roots. Rapid transfer of P from dying roots to living ones has been found in mycorrhizal roots, perhaps through direct hyphal links (Ritz and Newman, 1985). The decomposition rate of roots is likely to be slower than that for leaves and appears to be primarily determined by root chemistry, whereas leaf decomposition rates are primarily determined by climate (Silver and Miya, 2001). Decomposition rates for roots were found to decrease with decreasing root diameter (Fahey *et al.,* 1988; Fan and Guo, 2010).

The effects of partial pruning or lopping off branches are not fully understood, but will partly depend on stem anatomy. In trees with well-integrated transport tissue i.e. diffuse-porous trees, the loss of a few lower branches will only moderately reduce total carbohydrate supply and no effects on the root system may be noticeable. In trees with a direct connection between individual branches and roots (i.e. ring-porous trees with large diameter xylem vessels), removal of branches will directly affect the associated roots, and *vice versa* (Perry, 1989). Studies of the growth of intercrops in conjunction with *Alnus acuminata, Casuarina equisetifolia, Grevillea robusta, Maesopsis eminii* and *Markhamia lutea* indicate that partial pruning of some surface roots may increase the activity of the

remaining surface roots, thus providing no overall improvement in crop yield, but have little effect on tree growth (Wajja-Musukwe *et al.,* 2008).

Pruning of branches may affect subsequent root distribution (Rao *et al.,* 1993). van Noordwijk *et al.* (1991a) reported that reducing the height of pruning *Peltophorum dasyrachis* trees, resulted in more numerous proximal roots, of smaller diameter. The hypothesis was formulated that reduced stem height after pruning decreased the survival and apical dominance of the apical meristems of main root axes. Regrowth of the root system during and after recovery of the shoot thus increasingly depends on new roots being produced at the stem base. Hairiah *et al,*(1992) confirmed this hypothesis for several tree species (*Calliandra calothyrsus*, *Senna siamea, Gliricidia sepium, Paraserianthes falcataria* and *Peltophorum dasyrachis*), although *Gliricidia* forms thick fleshy storage roots at reduced stem pruning heights. The larger number of proximal roots formed at reduced pruning height is, however, associated with a more superficial root distribution. Thus, while a lower tree pruning height may be desirable to reduce above-ground competition and/or to induce death of fine rootlets to increase nutrient transfer to crops, and also tends to increase competition between trees and crops in the topsoil.

Tree root distribution and root activity

While the distribution of tree roots is determined by various factors, including species, management and soil conditions, it is their activity in the cropping zone which determines the extent to which trees compete with crops below ground. Subsoil root activity can make an important contribution to water and nutrient uptake by trees (Lehmann, 2003), although evidence from sapflow studies highlights the ability of tree root systems to switch their activity from one part of the root system to another, according to the availability of soil moisture in different parts of the soil profile (Smith *et al.,* 1998; Ong *et al.,* 2002). Thus, although tree roots have better access to subsoil than crop roots, providing opportunities for complementarity in resource use, their activity during the cropping season, with incoming rain, may still be focussed in the crop rooting zone. However, the ability to access deeper soil water and nutrients than crops contributes to improved nutrient cycling and increases the overall potential productivity of the system relative to monocropping with short-lived, shallow rooted crops. Stable isotope studies of *Acacia senegal* suggest plasticity in water use efficiency strategies, such that young shallow-rooted seedlings have high water use efficiency, but that this control is relaxed in older plants as their tap roots reach ground water (Gray *et al.,* 2013).

Roots and their symbionts

Any account of root ecology, however brief, must mention the major root symbionts, mycorrhizal fungi and the nitrogen-fixing bacteria, *Rhizobia* and *Frankia.*

Mycorrhiza (fungus + root) formation rather than root development *per se* is the norm in most tree and crop species, although there are notable exceptions in several plant families. There have been considerable efforts to understand the function of these structures and the way mycorrhizas might be managed in tropical systems (Sieverding, 1991; Haselwandter and Bowen, 1996; Kuyper *et al.,* 2004; Cardoso and Kuyper, 2006; Ba *et al.,* 2010). The predominant mycorrhizal type of both trees and crops in tropical systems is the arbuscular mycorrhiza, although some tropical trees, notably pines, some eucalypts, Dipterocarps, Caesalpinioid legumes, and Casuarina species, are often ectomycorrhizal. Some genera have the capacity to form both types of mycorrhiza. These mycorrhizal types differ in their structure and functioning: ectomycorrhiza are particularly important in accessing organic P and N pools and water, whereas arbuscular mycorrhizal fungi access inorganic P and other elements. Both types of mycorrhiza require carbohydrates from their host plant (Read, 2002). The literature still tends to emphasize 'infection percentages' rather than 'live hyphal length' as the main parameter, partly due to methodological problems in quantifying the latter. Thus, the uptake possibilities of mycorrhizal systems are currently more difficult to quantify than systems consisting of roots only. Where trees and their intercrops share mycorrhizal fungi (Ingleby *et al.,* 2007; Shukla *et al.,* 2012), there are also possibilities for transfer of nutrients between plants of the same and different species, and trees may act as reservoirs of inoculum for annual crops. The ability of mycorrhiza to

increase nutrient uptake either due to their extensive foraging mycelium, or to their ability to access otherwise unavailable nutrients further extends the complexity of tree–crop interactions, especially as particular mycorrhizal associations can change the balance of plant species within mixed communities (van der Heijden and Wagg, 2013) and mycorrhiza are also implicated in water uptake (e.g. Allen, 2011; Lehto and Zwiazek, 2011).

Turnover rates for the hyphae of mycorrhizal fungi are much shorter than for fine roots. Godbold *et al.* (2006) calculated this to be around nine days. Estimates seem to be lacking on the balance between fine root and fungal turnover in agroforestry systems, but a recent EU COST action study estimated that turnover may contribute 0.9 t ha^{-1} yr^{-1} of carbon flow into the soil compared with 0.4 t ha^{-1} yr^{-1} from the turnover of fungal mycelia associated with roots (Brunner *et al.*, 2013).

Rhizobia and *Frankia* associations are more restricted to particular plant genera than mycorrhiza. They occur in addition to mycorrhizal associations and thus further complicate understanding of nutrient uptake in agroforestry systems. *Rhizobia* are responsible for N$_2$ fixation in some, but not all, genera of the *Leguminosae,* and *Frankia* occur with a number of tropical species including *Casuarina.* Giller and Wilson (1991). Vanlauwe and Giller (2006) reviewed nitrogen fixation and other nutrient issues in tropical cropping systems and included references on tree crops and multipurpose trees.

Proteoid roots, which occur in *Grevillea* and other agroforestry tree species, are also important in locally enhancing nutrient uptake (Skene *et al.,* 1996) through secretion of organic acids which release insoluble phosphate within the soil matrix.

The importance of these associations and functions should not be underestimated, Verboom and Pate (2006) argued that large woody plants in semi-arid environments, with their associated microorganisms, have the capacity to radically alter their soil habitat and create niches for optimising capture and utilisation of resources.

Concepts for tree-crop interactions

Sequential versus simultaneous agroforestry systems

The relevant root parameters for predicting uptake efficiency depend not only on the resource involved, but also on the complexity of the agricultural system. In intensive horticulture with almost complete technical control over nutrient and water supply, fairly small root systems may allow very high crop production in a situation where resource use efficiency ranges from very low to very high, depending on the technical perfection of the often soil-less production system (van Noordwijk, 1990). In field crops grown as monocultures, the technical possibilities for ensuring supplies of water and nutrients where and when needed are far less and the soil has to act as a buffer, temporarily storing these resources. Adjustment of supply and demand in both time and space (synchrony and synlocation) become critical factors. In mixed cropping systems including grasslands, the below-ground interactions between the various plant species add a level of complexity to the system; on one hand it opens possibilities of complementarity in using the space and thus the stored resources, hence improving overall resource use efficiency, but it also means that root length densities which would be sufficient for efficient resource use in a monoculture may be insufficient in a competitive situation. Agroforestry systems are yet another more complex step, as the perennial and annual components have separate time frames in which to interact and the perennial component, if not managed, becomes increasingly dominant as it increases in size.

The supply of nutrients such as nitrogen from organic sources will never be completely synchronous with nutrient demand by crops. In so far as supply precedes demand, temporary storage of mineral nitrogen is required in the crop root zone. In climatic zones without a rainfall surplus during the cropping season, such storage is possible and there is no compelling need to improve synchrony in order to achieve a high uptake efficiency. In climates such as the humid tropics, however, where rainfall exceeds evapotranspiration during the growing season, products of early mineralization leach into deeper layers of the soil (Fig. 8.7). If crop rooting is shallow, as is common on the acid soils typical of this climatic zone, nutrients will be leached beneath the crop rooting zone.

Deep rooted components of mixed cropping systems can then act as a 'safety net' (Suprayogo *et al.,* 2002) intercepting N on its way to deeper layers (van Noordwijk and de Willigen, 1991; Fig. 8.8.

Insert Figs. 8.7 and 8.8 near here

Within agroforestry systems, a distinction should be made between those where trees and crops use the same land simultaneously, and sequential systems such as improved fallows (*cf.* Chapter 4). Trees with abundant superficial roots may not be suitable for simultaneous agroroforestry systems, but may be desirable for sequential systems. In the latter case, soil conditions at the time of transition between the tree and crop phase are the most important criterion as the trees may have left a considerable litter layer on the soil surface and a network of decaying roots in the soil. Effects on the subsequent crop may be based on the total soil organic matter and nutrient mineralization potential of the soil, but also on more specific facilitation of crop root development by using channels produced by decomposition of old tree roots. The latter is especially relevant on soils where soil compaction or Al^{3+} toxicity restrict crop root development. Old tree root channels provide easy pathways into a compact soil and a coating of organic matter which may help to detoxify Al^{3+} (van Noordwijk *et al.,* 1991b). In simultaneous agroforestry systems, below-ground interactions are likely to be dominated by competition for water and nutrients. Complementarity in resource use is possible, however, especially under conditions where leaching rates are high.

Soil water balance, as affected by climate, irrigation and drainage, has a major influence on root functions. In the temperate climatic zone of the northern hemisphere, the main crop growing season normally has a rainfall deficit: drying soil conditions hamper diffusive transport and hence increase the root length density required for uptake, but it also means that leaching is mainly confined to the autumn and winter period, after the growing season. A lack of synchrony between N mineralization and N demand which would lead to a build-up of mineral N in the topsoil is not a real problem under these conditions. In fact, the main problem is that mineralization is too slow in spring. In the humid tropics, however, with a net rainfall surplus during most of the growing season, mineral N produced by mineralization will be leached rapidly from the topsoil to deeper soil layers. Under such conditions synchrony of N mineralization and N demand is essential for obtaining high N use efficiencies

Nutrient pumps and safety nets

A letter to the *Tropical Agriculturalist* (Colombo, Ceylon) in 1887 stated that: *'Grevillea is valuable in the field, as its light shade if planted at, say, 30 to 36 feet apart, is rather beneficial to tea. But the great good it does is the bringing up of plant food from the subsoil, and distributing the same in the form of fallen leaves,... which, too, are useful in preventing surface wash while decomposing on the ground'* (Harwood and Getahun, 1990).

The concept that trees act as 'nutrient pumps' was therefore established more than a century ago. Few hard data have accumulated, however, as it is not easy to identify which part of the net nutrient uptake of a tree comes from deep or superficial soil layers (*cf.* Chapter 4). A large amount of circumstantial evidence is available, however. The nutrient pump hypothesis could be valid for both sequential and simultaneous agroforestry systems, although a number of conditions need to be met, *viz.*;

1. the tree should have a considerable numbers of fine roots and/or mycorrhiza in deep soil layers;
2. deep soil layers should contain considerable nutrient stocks in directly available form or as weatherable minerals or in a saprolite layer in the soil;
3. soil water content at depth should be sufficient to allow diffusive transport of nutrients to the roots.

These conditions indicate that the possible role of deep-rooted trees as nutrient pumps is likely to be small in climates with a limited annual depth of wetting. In situations where there are

limited weatherable minerals in the subsoil (e.g. most oxisols and ultisols), nutrient pumping may still occur if the tree roots have been acting as a safety net for leaching. Uptake activity from deeper layers may be expected especially where nutrient stock and root development in deeper layers is larger than that in more superficial layers of the soil and total demand cannot be met from the topsoil.

If trees or shrubs develop a root system under the main crop root zone and with sufficient horizontal spread, this may act as a safety-net, intercepting mineral nutrients leaching from the crop root zone (Fig. 8.8). Through litterfall or pruning. such nutrients may be returned to the topsoil and be absorbed by crops. In contrast to the 'nutrient pump' hypothesis, the 'safety-net' hypothesis is not restricted to specific soil types, but depends on a rather specific root distribution pattern of the tree and crop component of an agroforestry component and on a water balance leading to leaching of nutrients beyond the crop root zone. While complete pruning of tree crowns may result in the loss of 'safety net' functions, leaving a single live branch may enable the retention of such functions (Chesney, 2008).

The safety-net role seems particularly valid for simultaneous agroforestry systems, but under certain conditions may also apply to sequential systems. van Noordwijk (1989) used a simple leaching model related to time-depth curves to analyse under what leaching rates (and consequently for which combinations of net precipitation surplus and apparent nutrient adsorption constants, K_a) a deep rooted component can intercept nutrients leached beyond the reach of a previous, shallow rooted component (Fig. 9.9). A limited window of opportunity exists for such interception, but only when the rooting depth of the fallow vegetation substantially exceeds that of the crop (Table 8.1). The chances for recovery of leached nutrients increase when K_a increases with depth, as may occur in soils with substantial nitrate adsorption capacity in deeper layers.

Insert Fig. 8.9 near here

Table 8.1. Range of values for the annual excess of rainfall over evapotranspiration $L_w(l)$, approximate annual rainfall zone and apparent adsorption constant K_a which allow a deep rooted fallow (crop rooting depth 0.3 m, fallow rooting depth 0.75, 1.5 and 2.5 m in year 1, 2 and 3, respectively) (van Noordwijk, 1989).

K_a, (ml cm^{-3})	$L_w(l)$ (m)	Annual rainfall (m)
0	0.1 - 0.25	1.1 - 1.6
1	0.2 - 0.5	1.2 - 1.8
3	0.4 - 1.0	1.4 - 2.3
5	0.6 - 1.5	1.6 - 2.8
10	1.1 - 2.75	2.1 - 4.0
20	2.1 - 5.25	3.1 - 6.5

Hydraulic lift and heterogeneous water infiltration

As previously highlighted in Chapter 6, hydraulic lift by tree roots is an important process for the redistribution of water in the soil profile, potentially enhancing survival of lateral roots in the dry season, influencing nutrient availability and alleviating water stress of shallower rooted neighbouring plants, although the latter will depend upon the extent of reabsorption of this water by surface tree roots, rather than crop roots (McCulley *et al.,* 2004; Prieto *et al.,* 2012). The total quantity of water leaking from root systems during hydraulic lift is generally small compared with daily transpirational

demand, but can facilitate nutrient uptake from topsoil layers. In semi-arid climates, trees may also have a pronounced effect on the pattern of water infiltration (*cf.* Chapter 6). Their canopies intercept rainfall and, especially isolated trees with a 'funnel' shaped canopy, can have a high rate of stemflow, causing deep water infiltration under their stem (Knapp, 1973). Trees with umbrella-shaped canopies tend to have a high rate of water infiltration at the perimeter of the canopy.

Complementarity and competition

Without competition between plants, environmental resources would probably not be used efficiently. Maximum light interception depends on a closed crop canopy, where each plant experiences considerable competition, and reaches a much smaller size than in a more open stand. Competition between component plant species is only a problem if its effects are more pronounced than those of intraspecific competition, and especially when this affects the plant component which is most highly valued (*cf.* Chapter 4). For light, plant canopy height is a simple index for the competitive strength of any plant, but below-ground resources cannot be treated in a similar one-dimensional way. As water and nutrients are stored in the soil, time of use must be considered, as well as at least two dimensions for describing horizontal and vertical stratification.

As a first approach to a process-based description of 'below-ground competitive strength', it may be assumed that the term of Equation 8.3 indicates the amount left in the soil. If the combined demand A of all plants cannot be met, their relative 'competitive strength' may be based on their N_{res} value, and thus be related to local root length density.

The general wisdom is that complementarity in root distribution is the primary key to the success of simultaneous agroforestry systems. Evidence for this hypothesis is widespread. *Paulownia* species are widely grown in China, intercropped with wheat, maize, groundnut and other crops. The trees have high value and most of their fine roots are in the 40-100 cm layer, beneath the main part of the crop rooting zone. When intercropped with winter wheat, for which benefits in crop yield have been reported, the *Paulownia* trees are dormant during the germination and tillering stages, and only compete with wheat during the last month of grain filling (Wang and Shogren, 1992). The apparent success of this intercropping system, similar to the *Grevillea* system in Kenya, coincides with a complementarity in fine root distribution, accompanied by a favourable above-ground tree morphology and phenology (Huxley *et al.,* 1994).

Table 8.2 summarizes the types of below-ground interactions which can occur in simultaneous and sequential agroforestry systems, and indicates techniques for measuring the various possible effects and which tree characteristics are desirable to optimize tree-crop species combinations.

Species selection is one option to obtain desirable tree characteristics, but tree management can be a useful practice. Above-ground tree management, including pruning, has immediate effects on root function (demand for water and nutrients) and longer term effects on root distribution, while root pruning and other methods of root management (Korwar and Radder, 1994; Rao *et al.,* 2004) have direct effects on the spatial distribution of roots and their activity. The use of pruning has the potential to improve complementarity between tree species and their intercrops, enabling farmers to plant tree species chosen for their value more than for their inherent non-competitiveness.

Table 8.2. Types of below-ground tree-crop interactions and desirable characteristics for trees in sequential and simultaneous agroforestry systems

Interaction process	Measure of effect	Desirable characteristics of trees	
		Sequential	Simultaneous
Competition for water	Positive crop response on tree root pruning, especially in dry periods; measurement of	-	Deep rooted trees

	water flow in horizontally oriented proximal roots		
Modified water infiltration	Water infiltration rates with and without trees and/or tree mulch	-	Slowly decomposing tree mulch for erosion prevention
Hydraulic lift (water transfer to topsoil)	Day/night cycles in soil water tension close to tree roots; water tracer movement	-	Deep rooted trees
Competition for N, P, K etc.	Positive crop response to tree root pruning, especially during dry periods;	-	Relatively deep rooted trees
Vertical nutrient transfer to topsoil under trees	Nutrient contents of prunings	Deep rooted trees	Relatively deep rooted trees
Horizontal nutrient transfer to topsoil under trees	Nutrient content of prunings	Efficiently scavenging trees	Rapid lateral spread; low root density, but large soil volume exploited
Arresting sediment flows ('erosion control')	Biological terrace formation by contour plantings	Creating effective terraces as high fertility zones	Non-competitive 'fertility traps'
Transfer of N *etc.* from root and nodule turnover	Quantification of tree root nodule turnover		Rapid root decay especially after pruning
Soil organic matter maintenance by root turnover, litterfall *etc.*	Quantification of tree root turnover and litterfall; measurement of decomposition rate of dead tree roots	Abundant roots in topsoil, rapid root turnover, high content of lignin and polyphenolics	Rapid root turnover, high content of lignin and polyphenolics
Facilitation of crop root growth in old tree root channels (overcoming of soil profile constraints of density or Al or toxicity)	Visual check of crop root positions in the soil	Deep rooted trees, slow decomposition of the exodermis	
Stimulation of root symbionts	Symbiont infection of crop roots with or without trees	Common symbiotic partners	Common symbiotic partners
Stimulation of root pathogens and pests	Crop root damage with or without trees	Lack of common pathogens and pests	Lack of common pathogens and pests
Stimulation of soil fauna (e.g. earthworms)	Faunal activity in crop root zone with or without trees	Year round food supply, by high lignin/ polyphenolic content	

Methods for Root Studies in Agroforestry

Separating below- and above-ground interactions

A first question is how to separate above- from below-ground interactions experimentally. A common approach is to prevent encroachment by tree roots into adjacent crop plots, either by inserting a barrier, or by trenching between trees and crops. This approach has relatively short-term effects, as tree roots may grow beneath barriers and open trenches, and will regrow across refilled trenches. Thus, field experiments using these approaches need to be carefully monitored to check that tree roots have not reinvaded (Coe *et al.*, 2002). Above-ground shading effects are usually less extensive than root effects. Putz and Canham (1992) tried to separate above- and below-ground competition effects

between *Pinus* seedlings and coppiced hardwoods and vines by a combination of root-trenching and tying back overtopping trees, and found that below-ground competition was more important than shading effects. While *separation* of effects is difficult to achieve experimentally, shade cloth can be used to *simulate* the shading effects of the tree canopy.

Some caution is needed in interpreting the results in the context of the tree-crop interaction equation (Ong and Kho, Chapter 1, this volume; equation 1.4), because root pruning may reduce shoot growth and thus above-ground interactions. Positive crop responses to tree root pruning should, ideally, be compared with responses to equivalent above-ground tree biomass obtained by other means (e.g. shoot pruning, although this can also have positive below-ground effects).

The direct effects of root trenching when applied to existing stands of trees can give evidence of direct below-ground competition effects, but not of the possible long term soil modification by trees which may compensate for or exacerbate the competitive effects. To estimate such long term trends, trees must be completely removed in some treatments and crop growth compared with that in control plots outside the reach of trees.

Separation between above- and below-ground interactions requires a judicious and labour-intensive approach. An appropriate experimental design to elucidate these interactions can be achieved by a soil-transfer experiment, although there are many difficulties in undertaking this satisfactorily. At the onset of the growing (rainy) season, undisturbed soil columns, preferably PVC or stainless steel cylinders, are taken from beneath the tree canopy (Fig. 8.10, zone A) and outside the tree canopy but within the zone exploited by tree roots (Fig. 8.10, zone B). These columns can then be interchanged (positions 3 and 6). Next to the positions 3 and 6, cylinders are driven into the soil (positions 2 and 5), thus cutting the tree roots. Underneath and outside the trees, a dense, homogeneous annual crop or grass is sown. This results in seven different crop production situations or treatments:

- on 'native' soil underneath the tree in the presence of tree roots
- on 'native' soil underneath the tree without active tree roots
- underneath the tree on soil from outside the canopy without active tree roots
- on 'native' soil outside the canopy in the presence of tree roots
  on 'native' soil outside the canopy without tree roots
- on soil from underneath the tree placed outside the canopy without the presence of tree roots
- on 'native' soil outside the influence of tree roots (zone C).

Comparison of crop production and nutrient uptake for the different production situations enables the effects of microclimate and soil fertility and effects induced by the presence of tree roots to be distinguished. Relevant differences in microclimate underneath and outside the canopy (air and soil temperature, radiation level, soil humidity) need to be measured. Although theoretically simple, practical and statistical aspects may complicate such experiments. The small surface of the cylinders and the small differences in crop growth between treatments necessitate many replicates, but these will be limited by the space available under each tree.

Different trees cannot always be considered as repetitions as canopy characteristics and function may differ among trees, so that allowance must be made for orientation under the tree. To enable satisfactory data interpretation, the root distribution of the studied tree species needs to be known.

Quantifying root distribution and activity

Basic methods for observing and quantifying tree and crop root biomass and length (Anderson and Ingram, 1993; Smit *et al.*, 2000) and involve trenching and profile wall studies (van Noordwijk *et al.*, 2000), coring and fakir beds (do Rosario *et al.*, 2000), combined with root washing and sieving. Studies in agroforestry systems require the ability to distinguish between the roots of different species. Root excavation can be used to characterise the structural root systems of trees (Mulatya *et al.*, 2002). Minirhizotrons are an alternative, non-destructive approach (Gijsman *et al.*, 1991; Johnson *et al.*,

2001; Jose *et al.,* 2001) for determination of fine root dynamics: however, in semi-arid Kenya, Odhiambo *et al*. (2001) studied spatial and temporal variation in root distribution of trees and crops using minirhizotron and soil coring approaches. Athough the minirhizotrons were in place for three years, they found poor colonisation of minirihizotron windows by roots and concluded that this approach was not suitable under circumstances where root densities are low. Although new methods are being developed for shallow root systems (*cf.* Chapter 9, examination of deep roots still relies on extremely labour intensive methods such as coring and trenching, which may be carried out to depths of 4 – 5m (Maeght *et al*., 2013); root architectural analysis linked to proximal root diameters still the best way to combine intensive case studies with replicated field assessments.

Stable isotope techniques (Dawson *et al.,* 2002) provide a valuable non-invasive technique for determination of zones of nutrient and water uptake. Rowe *et al*. (2001) quantified simultaneous uptake of ^{15}N placed at various depths by maize and hedgerow trees; Rowe *et al*. (2006) found in similar experiments that tree management affects this uptake pattern.

Smith *et al*. (1997) found that water use by windbreaks of *Azadirachta indica* grown with millet in the Sahel depended on proximity to ground water: where ground water was available at 6-8 m depth, trees mostly extracted this water, while millet extracted water from close to the top of the soil profile, but where the water table was at 35 m depth, the trees and millet were in direct competition and extracted water from the top 2–3 m of the profile. Recently, Isaac *et al*. (2014) used a combination of ground-penetrating radar and plant-soil δ^{18}O ratios to estimate soil water acquisition zones at 0–50 cm soil depths in cocoa agroforestry systems: they found that water acquisition zones varied according to the presence or absence of shade trees and soil type.

Sap flow approaches enable evaluation of coarse to fine scale temporal variation in water uptake and can be applied at the level of whole trees, or individual roots. Studies in a *Grevillea* – maize agroforestry system (Lott *et al*., 2003) supported the hypothesis that *Grevillea* trees make extensive use of soil water outside the maize cropping season. Burgess and Bleby (2006) demonstrated multi-directional water transfer by roots, and the transfer of water *via* stem tissue between lateral roots of the same tree.

Need for simple, farmer-level criteria and observation methods

Successful design of agroforestry systems must draw together material from a wide range of sources and disciplines, requiring a variety of decision support tools (Ellis *et al*., 2004); models have been developed and databases constructed, but at the same time, farmers need simple methods which they can apply themselves to their own systems. Current root research methods for trees are laborious and cannot be directly related to a farmer's criteria for selecting and judging the performance of trees. If root research stays in the domain of 'experts' it will not contribute to the development of agroforestry systems in the real world. The validity of generalizations about deep- or shallow-rooted trees, competitive and beneficial ones, is likely to be vastly overestimated, unless we develop simple, non-destructive observation methods to check this.

As already discussed, uptake of water and nutrients is often directly related to above-ground demand, i.e. the size of the leaf canopy and the above-ground sink strength for nutrients. The 'pipestem' model and similar approaches suggest that the stem diameter of trees can give a first indication of this, at least within a species. The fractal branching models suggest that the total number of fine roots is related to proximal root diameters. Thus, the ratio of superficial roots to stem diameter can be used as a simple indicator of the degree to which the tree depends on topsoil resources, and thus for its competitive strength, when combined with shallow rooted crops. These attributes are encapsulated in the 'index of tree root shallowness' (van Noordwijk and Purnomosidhi, 1995) (or 'competivity index (CI)' (Ong *et al*., 1998) (*cf.* Fig. 8.5b; Box 8.1).
where

$$\text{Index of shallow rootedness} = \frac{\sum D^2_{horizontal\,roots}}{D^2_{stem}} \qquad \text{(Eqn 8.9)}$$

and $\quad \sum D^2_{horizontal\,roots}$ is the sum of the proximal diameter squared of all roots which descend into soil at angles of $<45°$ and

D^2_{stem} is the square of the stem diameter at breast height

Ong *et al.*(1998) found that the equation

$$\text{competivity index} = \sum D^2_{horizontal} \times D^2_{stem} \qquad \text{(Eqn 8.10)}$$

was a better predictor of the relative competition of different tree species and used it successfully in both linear agroforestry systems and farmers' fields (see also Mulatya *et al.* (2002)). Thus, simple observations of the number and dimensions of surface roots and stem size can provide a useful indicator of the competitiveness of different tree species, although it should be noted that these may change with age, propagation method and provenance. This still requires further testing, but it appears to provide farmer-level criteria which are soundly based on the allometrics of root branching patterns and the functioning of roots in resource uptake, which is one of the crucial aspects of tree-crop interactions in agroforestry systems.

Open questions and challenges

Root research in mixed tree-crop systems remains challenging as direct observation at the relevant spatial and temporal scales, in the context of real-world heterogeneity of soil conditions, requires a major effort (see also Chapter 4). A good understanding of plants as self-regulating organisms, and not as mechanistic implementers of a fixed genetic code, helps to appreciate the complex results. Models based on 'first principles' are to be preferred over purely empirical models, unless the latter can be calibrated over the full range of conditions that our potential research questions include. There has been progress in a 2-dimensional representation of a typical slice of a tree-crop system, but 3-dimensional representations at a meaningful spatial resolution remain a challenge.

From a practical agroforestry perspective, the opportunities for managing tree root distribution remain a key challenge. Root pruning by soil tillage at some distance from the tree may only help for a limited period of time, as deeper tree roots can resurface if superficial roots have been cut. Where manual labour is used, root pruning appears a major challenge; Wajja-Musukwe (2003) determined the time taken for workers to hand prune the roots of five year old *Grevillea robusta* trees in a linear planting in Uganda at a distance of 30 cm from the tree row, and to a depth of 30 cm. The average time taken for the first pruning was 10 min m^{-1}, but a repeat pruning of roots which had regrown six months later only took 2 min m^{-1}.

The glimpse that we so far have of opportunities to use a process such as hydraulic redistribution to the advantage of crop growth in critical, water-limited crop stages implies that the negative aspects of competition can potentially be balanced or exceeded by the positive aspects of complementarity. We have the basic concepts and models, we have a good set of tools, but the efforts needed for a comprehensive case study are beyond what a single PhD project can achieve, and funding priorities seem to have shifted elsewhere. The biotic connections of root dynamics in a changing climate are still an opportunity for major progress (van Noordwijk *et al.,* 1998).

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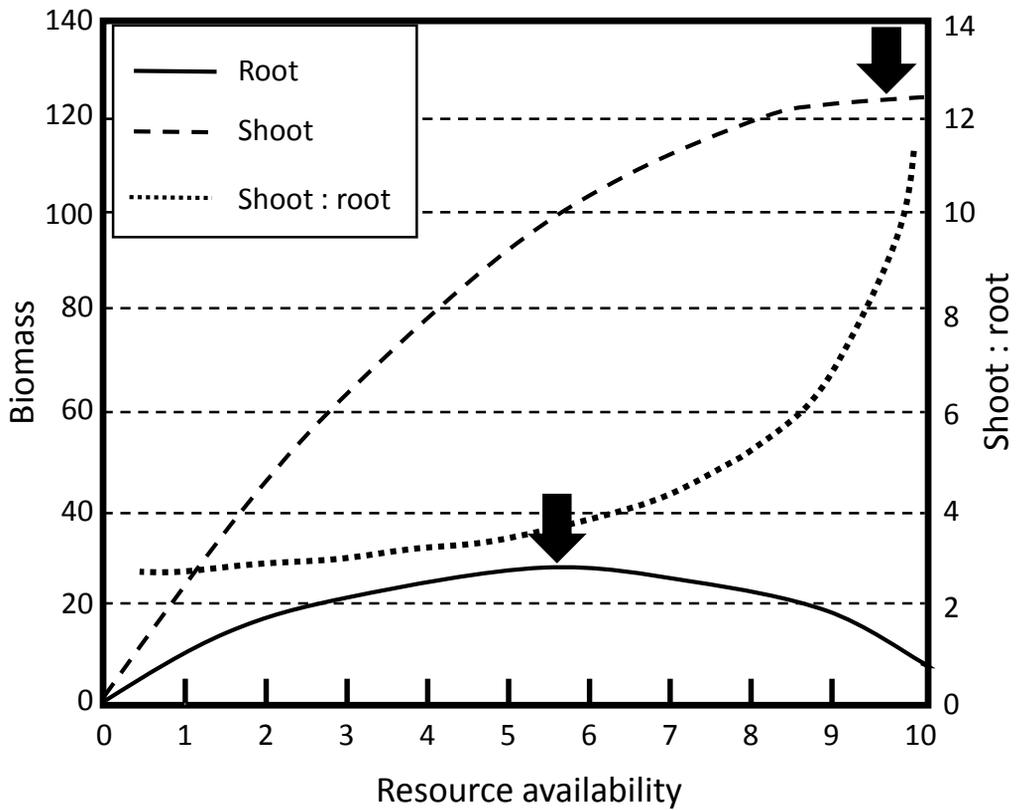
Fig. 8.1 Schematic relationship between shoot and root biomass production and below-ground resources of nutrients and water. The maximum root size is often obtained at intermediate shoot biomass. Between the optimum conditions for root and those for shoot growth the uptake rate per unit root (reflected in the shoot:root ratio) increases rapidly (based on Schuurman, 1983).
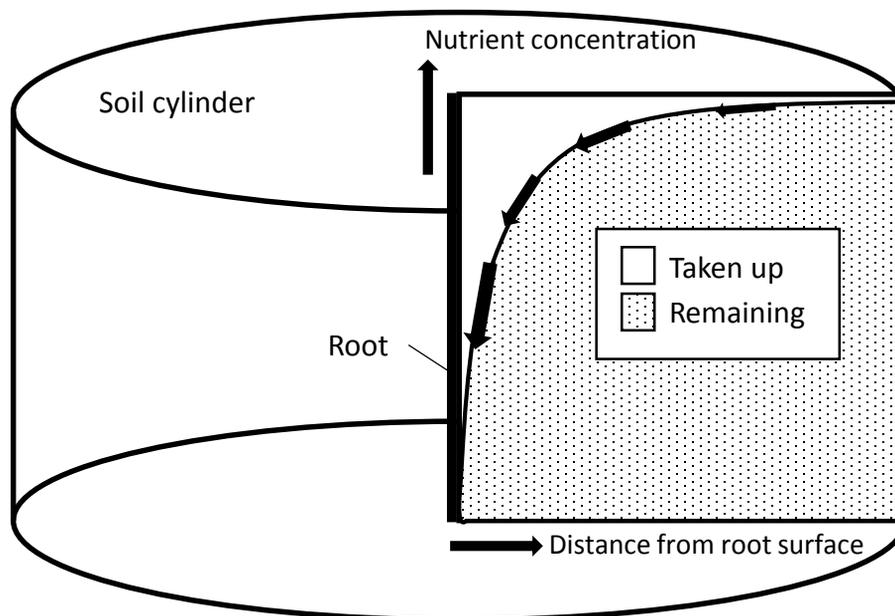
Fig. 8.2 Nutrient concentration profile in the soil surrounding a single root; if the roots are regularly distributed, the soil 'belonging' to each root is approximately a cylinder of constant radius.
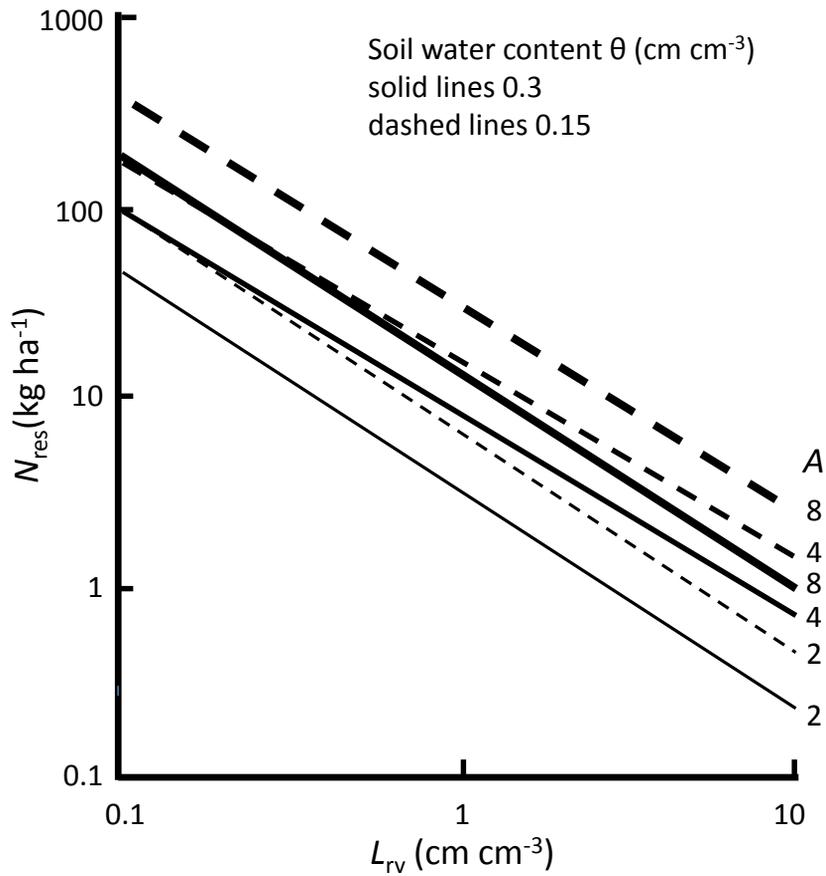
Fig. 8.3. The amount of mineral N, N_{res} in the soil (at two water contents θ), required to maintain crop demand A (kg ha^{-1} d^{-1}) (with three values representing high (8) – normal demands (2) for N), as a function of root length density L_{rv} (De Willigen and van Noordwijk, 1987).
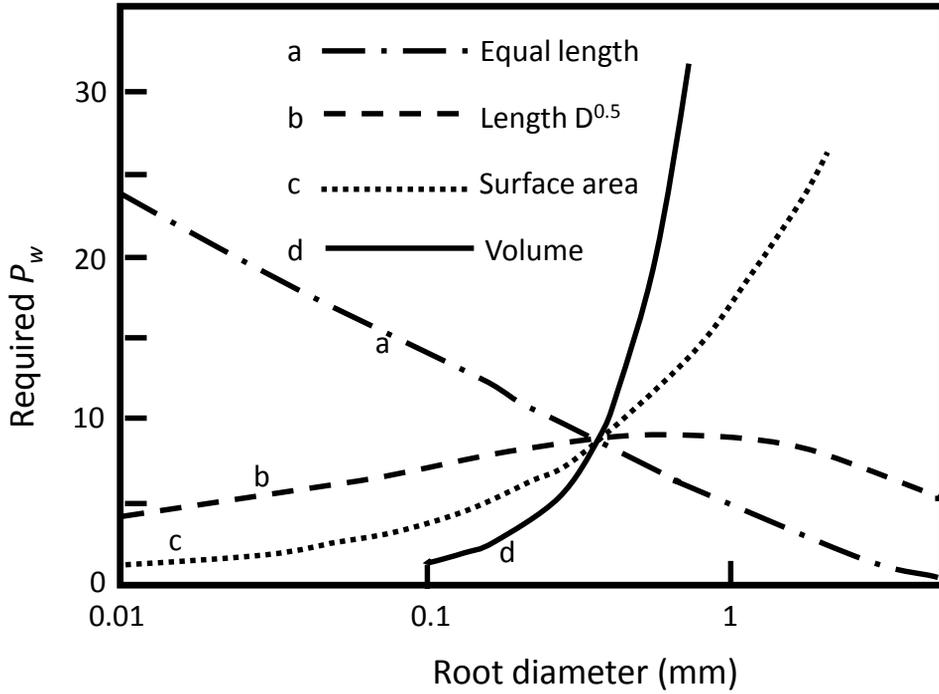
Fig. 8.4 Required P availability in the soil - indicated by the (water extractable) P_w index -when root systems of different diameter are compared on the basis of equal root length, root surface area, root volume or sum of root length x diameter$^{0.5}$.

a.

Dichotomous

Herringbone
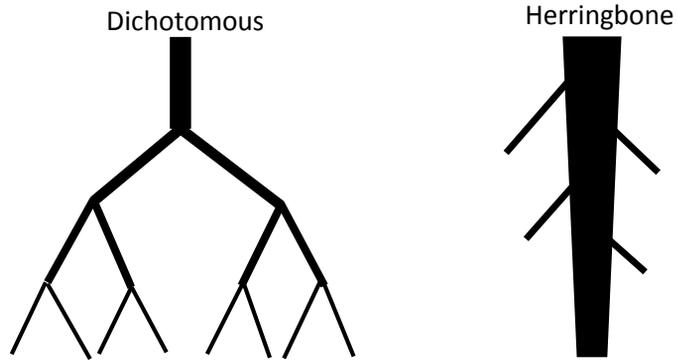
b. i.

Determine diameters of
lateral roots descending
at less than 45°
($D_{0.1\,....0.2}$horizontal)

$--------$ Stem diameter at breast height (D_{stem})

Excavate half-sphere 0.3m radius

ii.

Index of shallow rootedness $= \dfrac{\sum D^2_{horizontal\ roots}}{D^2_{stem}}$

iii.

$\alpha = D_1^2/(D_{1+1,1}^2 + D_{1+1,2}^2)$

$D_{1+1,2}$

D_1

$D_{1+1,1}$
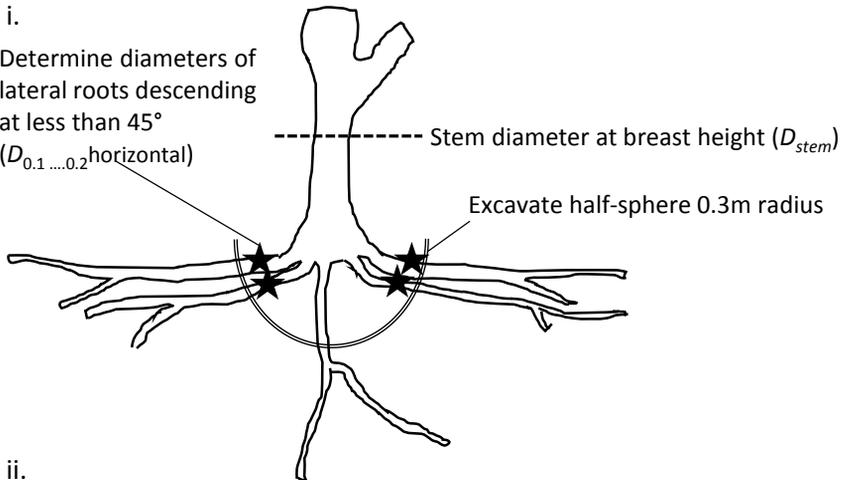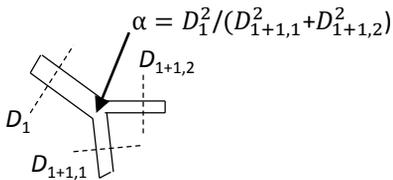
iv. The fractal model assumes that α is independent of D

α

D
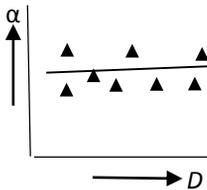
Fig. 8.5 (a) Two extreme types of root branching pattern: dichotomous and herringbone. Under the pipestem model the ratio between initial diameter and the number of links is the same for both patterns (and all intermediate ones) (van Noordwijk et al., 1994b) (b) measurement of proximal rooting diameters for determination of the index of shallow rootedness, and testing the assumptions of the fractal branching model
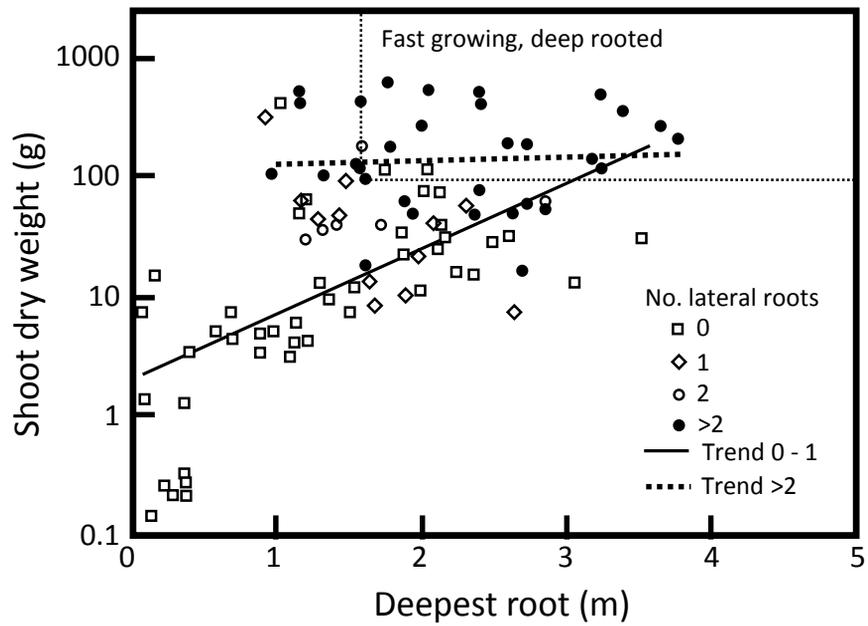
Fig. 8.6 Relationship between depth of the main root and shoot dry weight at 6 months, for a large number of trees and shrubs, classified according to the number of horizontal lateral roots of more than 1 m in length (data from Coster 1932a)
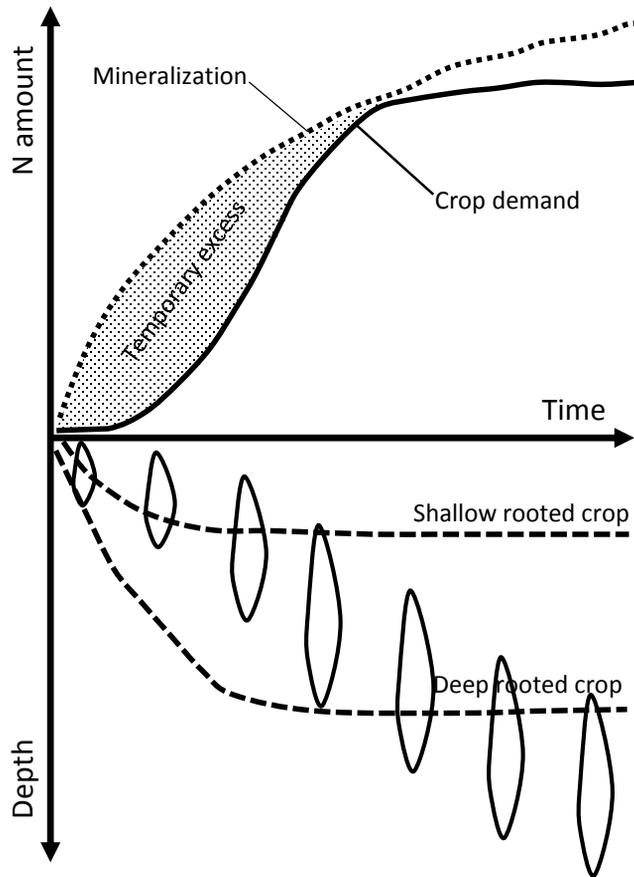
Fig. 8.7 Synchrony hypothesis: the time pattern of mineralization and crop demand (both shown in cumulative form) generally do not match; a temporary stock of mineral N in the soil will leach to deeper layers, depending on rainfall, and can be out of reach of shallow rooted crops by the time they need it.

A. Shallow rooted crop
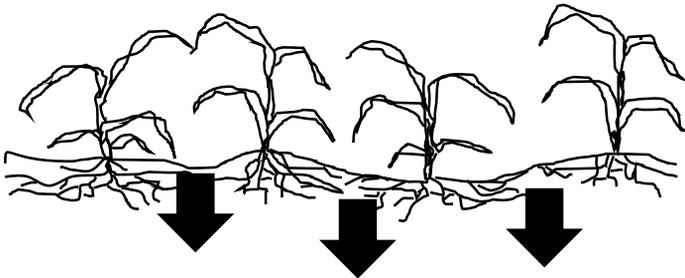
B. Crops + 'safety net' tree roots
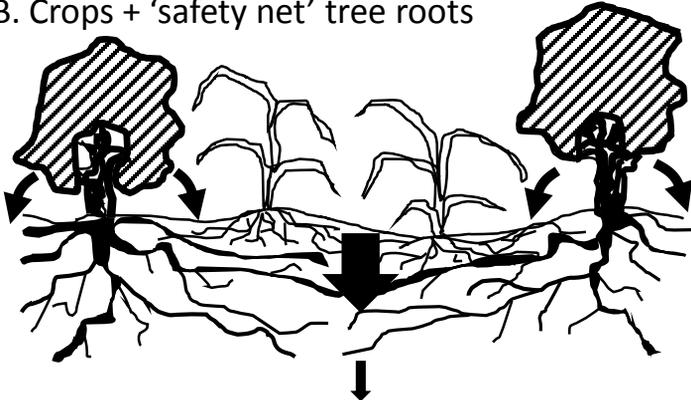
Fig. 8.8 Safety net hypothesis of tree roots intercepting nutrients leaching from a shallow crop rooting zone
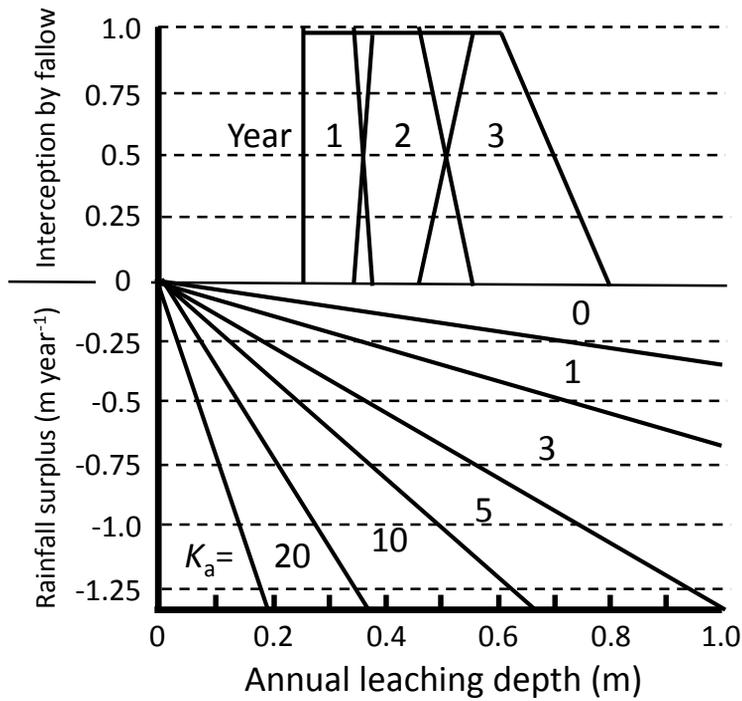
Fig. 8.9 Possibilities for deep rooted fallows to intercept nutrients leached from a shallow rooted crop. The lower part of the diagram gives a nomogram of nutrient leaching depth as a function of rainfall surplus (rainfall – runoff – evapotranspiration) and apparent adsorption constant K_a ml cm^{-3}. The upper part of the graph shows the chances of recovery by a deep rooted fallow vegetation of nutrients lost from a shallow crop root zone, given this annual nutrient leaching depth (van Noordwijk, 1999).
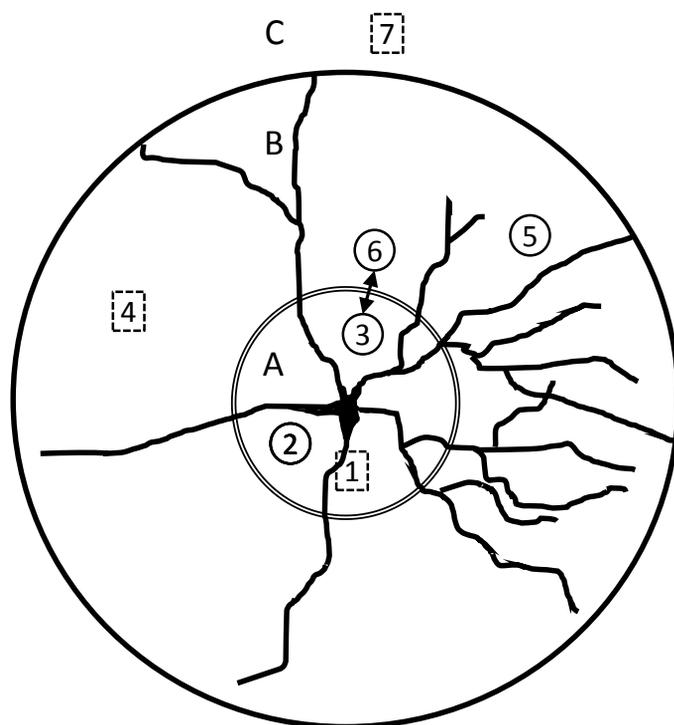
Fig. 8.10 Different cropping positions in 'soil-transfer' experiment, in zone A beneath the tree canopy, zone B outside the tree canopy but within the tree rooting zone and zone C outside the tree rooting zone. Circles represent soil cores in impermeable cylinders, squares represent locations of undisturbed soil in the different tree zones