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

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Introduction

This chapter takes a look at the 'hidden half', because interactions between trees and crops for below-ground resources are often as important as those for light and above-ground space (Anderson and Sinclair, 1993). The basic efficiency of utilization of water and nutrients for photosynthesis is probably not very different between trees and C$_3$ crops, so 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 shorter-lived crops. Because of their longer lifetime, tree root systems have the chance to explore larger areas, both laterally and vertically, and exploit zones of rich localized supply of water and/or nutrients. If these zones are largely out of reach of annual crops, the lunch bill for the trees is provided for and trees can increase the total production of the system, although they may not improve crop growth as such. This is especially true for deep rooted trees, which can exploit deep soil water reserves, either stored or part of subsurface flow pathways, and weathering saprolite or bed-rock layers inaccessible to crops, or intercept leaching water and nutrients on the way down, below the crop root zone.

The general concept that all trees are deep rooted may be greatly over-stated, however, as there are large differences between species and sites and the horizontal scavenging ability of tree roots is often underestimated. Everyday examples are urban trees in front of a house, surrounded by pavements and stones, which thrive on roots passing under the house and exploiting the back garden, or the septic tank there.

Experiments with annual crops often involve closely-spaced small plots. If such experimental layouts are used for agroforestry experiments, the tree component may exploit the soil of the (fertilized) 'control' plots as well as their own; this is likely to reduce crop yield in the control plot and, in the long run, 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 cassava plant and may invalidate many experiments leading to the conclusion that cassava is not responsive to N fertilizer (van Noordwijk *et al.*, 1992). It can be more pronounced for trees and many of the previous 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 idea of root distribution of the various components in a system is thus needed to do valid agroforestry field experiments. On small farm plots, trees may mine neighbouring areas (the neighbour's plots?) and the farmers' perceptions of advantages of trees may be biased for this reason too.

Roots are often discussed and wild generalizations about deep-rooted or horizontal scavenger roots are common, but few people take the effort to observe roots under their particular conditions. Chapter 3 illustrated that agroforestry systems are only viable if the tree and crop components represent approximately equal direct value to the farmer relative to the area occupied, unless there is a strong complementarity in the use of above-and/or below-ground resources.

In this chapter some of the existing concepts for studying the below-ground functioning of both tree and crop component separately are reviewed, a number of hypotheses on below-ground interactions between trees and crops are developed which can be tested with currently available methods and the methods available for simple observations and detailed tests of hypotheses are briefly described.

Basic Root Ecological Concepts

Morphogenetic and functional shoot: root balance

Serious root observations in agricultural systems started more than a century ago. The relation between above- and below-ground growth has

fascinated researchers for a long time and almost every layman expects that there is a clear relation between the height of a plant (tree) and the depth of its root system, or between the lateral spread of the shoot or crown and the lateral spread of the root system. The 'root atlases' published by Kutschera and Lichtenegger (1982) show that no generalizations of this nature are valid, however. Root characteristics across plant species vary apparently independently of shoot characteristics. 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.

The relationship between above- and below-ground growth should first of all be investigated within a single genotype to be meaningful. Often researchers found that a better root development was 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 directly lead to a reduced yield (Hellriegel (1883) quoted in van Noordwijk and De Willigen, 1987). Although evidence contradicting this 'basic law' was gradually accumulating (ibid.), it took a long time before the law itself was refuted and replaced by the hypothesis of a 'functional equilibrium' between root and shoot growth (Brouwer, 1963, 1983).

Figure 9.1 shows a generalized form of the response of above- and below-ground parts to increased water and/or nutrient supply, based on Schuurman (1983). In a part of the range both shoot and root biomass increase with improved resource supply, but the maximum root biomass is generally obtained at a lower level of resource supply than maximum shoot biomass. The shoot:root ratio may increase gradually to the left of the maximum root biomass and sharply above that point. This scheme can be used to explain the conflicting evidence in literature about external factors 'increasing' or 'decreasing' root growth in experiments which cover only part of the range. Classical statements such as 'phosphorus stimulates root growth' are based on only part of the range; elsewhere one may find that 'lack of phosphorus stimulates root growth'.

Although primarily developed for annual plants, the functional equilibrium concept appears to be equally valid for perennial plants, when expressed as the ratio of leaves and fine roots. The large amounts of storage and stability tissue, both above and below ground, complicate comparisons of total biomass, however. 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 decrease with decreasing soil fertility. We here follow the convention of the older Dutch literature of expressing shoot:root, rather than root:shoot ratios, as common in the English literature; roots are a more elegant basis for this ratio as the roots of a seedling emerge before the shoot.
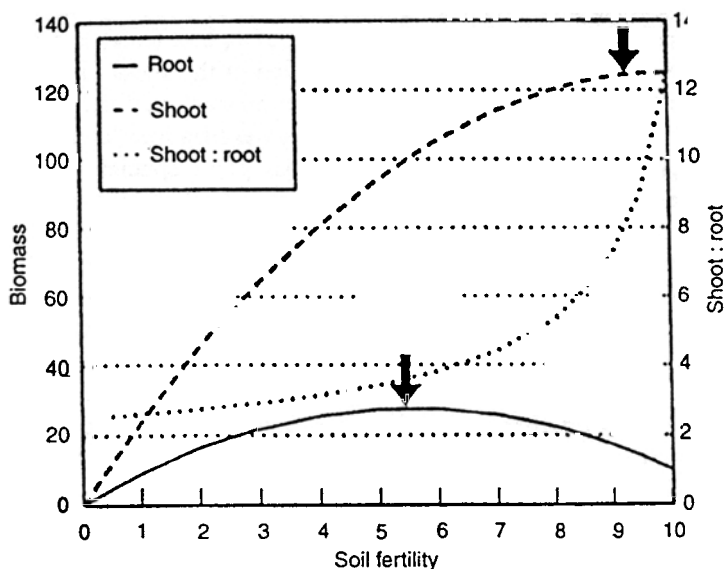
Fig. 9.1. Schematic relationship between shoot and root biomass production and soil fertility. The maximum root size is often obtained at intermediate shoot biomass and between the optimum conditions for root and those for shoot growth the uptake rate per unit root (reflected in the shoot:root ratio) increases rapidly (based on Schuurman, 1983).

Dhyani *et al.* (1990) found that root weight ranged from 27% (*Leucaena leucocephala*) to 72% (*Eucalyptus tereticornis*) of total tree biomass in a comparison of five tree species at 2 years age. Toky and Bisht (1992) found for 6-year-old trees (12 species) that root biomass ranged from 9% (*Acacia catechu*) to 27% (*Morus alba*) of total biomass, 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 Venezuela in the top 10 cm at 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 5 years, at the time that leaf area index reached the control level as well.

According to the 'functional equilibrium' concept (Brouwer, 1963) the allocation of growth resources in the plant to root and shoot meristems is modified by the major current environmental conditions. If water or nutrients are in short supply within the plant, the root system will get a larger share of the carbohydrate supply within the plant and will increase in size relative to the shoot (as measured in a shoot:root ratio) or even in an

absolute sense. When light (or CO_2 supply) is limiting plant production, the shoot will increase in size relative to the root system.

Subsequent research (Lambers, 1983) has shown 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 of hypotheses about actual plant responses, as it explains their overall functionality. In the actual coordination of activities of shoot and root meristems plant hormones play a role as signals, but the mechanisms are not yet clearly understood by which they receive and transmit the information about the current environmental situation or internal conditions in the plant as a result of this.

Maximum plant production 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 is sufficient to supply the needs of a shoot. The answer to the question 'How many roots does a plant need?' thus depends on the environment in which the plant grows and its intrinsic growth rate. During agricultural intensification human control over the supply of water and nutrients has gradually increased; the endpoint of this development may be reached in horticulture based on soilless culture techniques. Reducing the size of the root system has a limit, however, where 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). A plant growing in free water still needs a considerable root surface area, as can be approximated (for non-saline conditions) by:

$$A_{r,w} = \frac{E_p}{L_p \Delta H_p} \tag{9.1}$$

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 root environment $[MPa]$.

Equation 9.1 and parameters for full grown tomato or cucumber plants predict that the required root surface area is approximately 1 or 2.4 m^2, respectively, or 50% of the leaf area in both species. Shoot:root ratios expressed on a dry weight basis may reach 20–30 in this situation. 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). The specific root area (root surface area per unit dry weight) can be ten times higher than the specific leaf area (with 0.2 and $0.02 \text{ m}^2 \text{ g}^{-1}$ as order of magnitude, respectively). For oak and aspen trees 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 abilities of the 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 gradients as determined by required uptake per unit root length in an extensively branched root system. The more restricted the water supply, the larger is the root system needed relative to the shoot.

Root densities and uptake efficiency

Model approaches
Although a large root system may not be needed for maximum growth rates, roots are of direct importance for the efficient use of available water and nutrient reserves in the soil, and hence in reducing negative side effects of agriculture. As a first estimate, we may still expect that 'the more extensive the root system is, the higher nutrient and water uptake efficiency may be' (van Noordwijk and De Willigen, 1991). The possibility of obtaining a higher resource uptake efficiency can only be realized if 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 possible 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:

1. 'Models without roots', based on measured or estimated 'uptake efficiencies' (ratio of uptake and amount of available resources); roots remain implicit in such models.
2. Models predicting uptake efficiency on the basis of measured root density and distribution; these models have to 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, 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 in the plant.
5. Models that include differential response of root growth to zones with different environmental conditions (nutrient, water, oxygen supply, mechanical impedance).

Models at level 2 are a prerequisite for any of the levels following, and 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 determined by the external concentration, based on Michaelis–Menten kinetics or similar relationships between concentration and uptake rate. At times that the external supply exceeds the current crop demand, however, such models overestimate uptake, as internal feedback mechanisms down-regulate uptake in most plants under such circumstances. When demand exceeds supply, on the other hand, 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, 1994) therefore is based on a notion of crop nutrient demand, similar to potential transpiration rates, regulating uptake per unit root when supply is sufficient and a 'zero-sink' (actually an infinite sink strength leading to a concentration of zero) when supply is limiting. The amount of available nutrients left in the soil at the transition between these two situations is termed N_{res}. Figure 9.2 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:

$$\text{max. efficiency} = \frac{\text{crop demand}}{\text{crop demand} + N_{res}} = 1 - \frac{N_{res}}{\text{crop demand} + N_{res}}$$

(9.2)

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, 1994) 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
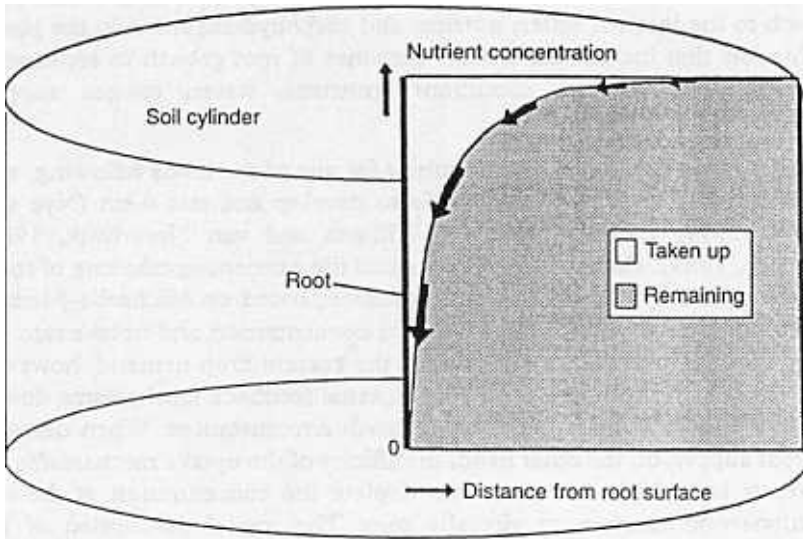
Fig. 9.2. Concentration profile in the soil surrounding a single root; if the roots are regularly distributed, the soil 'belonging' to each root is approximately a cylinder of constant radius.

dynamic uptake models from layered soils.

$$N_{res} = \frac{A(K_a + \Theta)D_m^2 G(\rho, v)}{4H(a_1\Theta + a_0)\Theta D_0}$$

where:

$A =$ daily nutrient demand [kg ha^{-1} day^{-1}],
$K_a =$ apparent adsorption constant [ml cm^{-3}],
$\Theta =$ soil water content [ml cm^{-3}],
a_1 and $a_0 =$ parameters describing decrease of effective diffusion coefficient with decreasing Θ,
$H =$ depth of soil zone considered [cm],
$D_0 =$ diffusion coefficient of nutrient in free water [cm^2 day^{-1}],
$D_m =$ root diameter used for model [cm].

with:

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

and

$$G(\rho, 0) = \frac{\rho^2}{8}\left[-3 + \frac{1}{\rho^2} + \frac{4\ln\rho}{\rho^2 - 1}\right] \tag{9.5}$$

and a slightly more complex definition if 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 a number of days with unconstrained uptake which would be possible for an infinitely dense root system ($N_{res} = 0$ for $L_{rv} = \infty$. 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 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.

For water uptake a similar approach is possible 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 be considered as well. 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 9.3 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 N 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, 1995).

Mycorrhizal hyphae and heterogeneity in root diameter
If root systems of different diameter are compared at equal root length density (length × diameter^0), the larger the diameter is, the smaller N_{res} and thus the more efficient the uptake can be. If the comparison is made at equal surface area (length × diameter^0 × π), N_{res} decreases with decreasing root diameter (De Willigen and van Noordwijk, 1987). If the comparison is made at equal root volume (length × diameter^2 × $\pi/4$) or weight, the advantage of the smaller root diameters is even more pronounced. The most stable result is obtained for a comparison at equal length × diameter$^{0.5}$. Figure 9.4 shows the required P availability in the soil – indicated by the
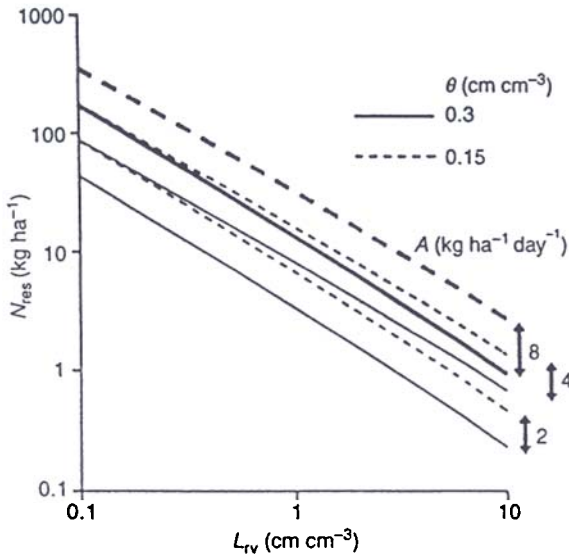
Fig. 9.3. The amount of mineral N, N_{res}, in the soil (at two water contents), required to maintain crop demand A (three values, representing high–normal demands for N), as a function of root length density L_{rv} (De Willigen and van Noordwijk, 1987).

(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 × 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* growth on an ultisol in Lampung, Indonesia (Hairiah *et al.*, 1995). With the length × diameter$^{0.5}$ index, calculation 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 a factor 25 smaller in diameter than the finest roots) to the crop root length: roughly 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 $1 + (0.5) \times$ %inf/5. For a normal infection percentage of 15%, this means that the effective root length density is 2.5 times the length of roots alone (van Noordwijk and Brouwer, 1995). The lack of adequate methods for quantifying hyphal length makes this a priority area for research, if mech-
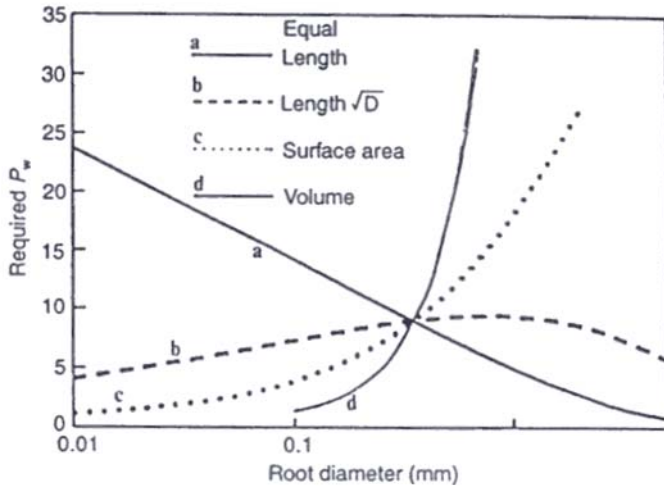
Fig. 9.4. Required P availability in the soil – indicated by the (water extractable) P_W index – when root systems of different diameter are compared on the basis of equal root length, root surface area, root volume or sum of root length × diameter$^{0.5}$ (van Noordwijk and Brouwer, 1995).

anistic P uptake models are to be used for mycorrhizal plants, i.e. for nearly all species found in agroforestry.

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

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, b). 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 cylinder geometry of the root–soil system), including the model used for deriving Equation 9.1. For ran-dom root distributions, R_{per} is approximately 0.5 (that means root length density $X/2$ in a regular pattern has the same N_{res} as a random pattern at density X); the figures shown by van Noordwijk *et al.* (1993a) are based on a different and incorrect definition of R_{per}, which was later corrected (van Noordwijk *et al.*, 1993b). 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.

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. The cost of this, however, is a potential bias, as the observation method may affect root behaviour (Gijsman *et al.*, 1991; Anderson and Ingram, 1993). Details are given by van Noordwijk *et al.* (1994a), who presented results of an analysis of sugarbeet and winter wheat root turnover.

Effective root length density as function of time and depth

Combining these elements (Table 9.1), we can derive an 'effective root length density' L_{rv}^* as a function of time and depth from (van Noordwijk and Brouwer, 1995):

$$L_{rv}^*(i,T) = R_{per}(i,T) \frac{\int_{t=0}^{T} (G(i,t) - D(i,t))\,dt}{\int_{t=0}^{s} (G(i,t) - D(i,t))\,dt} \cdot \frac{\sum_{j=0}^{n} L_{rv}(i,s,j)\sqrt{D_j}}{\sqrt{D_m}} \qquad (9.6)$$

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 about 0.4 and the mycorrhizal correction factor 2.5, the two correction factors may, accidentally, cancel and the use of direct L_{rv} values can be correct in practice.

Table 9.1 Steps in describing root–soil geometry for uptake models (van Noordwijk and Brouwer, 1995).

1. Choose relevant sampling zones, based on depth, distance to crop rows, expected synlocation (spatial correlation) of roots and resources; measure the root length density, $L_{rv}(i,s)$, for each stratum i at sample time s close to the expected maximum root development).

2. Effective root length density for a root system with a known frequency distribution of root diameters (including hyphae):

$$L_{rv'} = \frac{\sum_{j=1}^{n} L_{rv,j}\sqrt{D_j}}{\sqrt{D_m}} \tag{9.9}$$

where D_m = diameter used for model calculations, D_j and $L_{rv,j}$ are root diameter and root length density of n diameter classes.

3. Extrapolation from sampling time s to any time t is based on:

$$L_{rv}(i, t) = L_{rv}(i, s)\frac{R_p(i, t)}{R_p(i, s)} \tag{9.10}$$

where $R_p(i,t)$ = relative root presence at zone i at time t on minirhizotron images.

$$R_p(i, t) = R_g(i, t) - R_d(i, t) \tag{9.11}$$

$R_g(i,t)$ = root growth in zone i till time t relative to year production,
$R_d(i,t)$ = root decay in zone i till time t relative to year production.

4. Measure effectiveness of the root distribution via the R_{per} method (van Noordwijk *et al.* 1993a, b) and derive the effective root length L_{rv}^* for time t at zone i:

$$L_{rv}^*(i, t) = R_{per}(i, t)L_{rv}(i, t) \tag{9.12}$$

where R_{per} = root position effectivity ratio, accounting for non-regular root distribution and incomplete root–soil contact; the sum of the G-functions (compare Equation 9.3) for the observed root pattern is the same as that for a regularly spaced pattern, where L_{rv} is reduced by the factor R_{per}.

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$_2$PO$_4^-$ 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 a stratified soil (by layer or any other division in internally relatively homogeneous zones), we need an algorithm 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 are 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.

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 × environment interactions (Kerfoot, 1963). Van Noordwijk (1992) contrasted the results of root ecological studies at the single root, the whole plant and split-root level. For the 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 here 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, branch 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 often made 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 a first choice in using it and may thus attract a larger share of the carbohydrates necessary for growth in a plant where P within the plant is a growth-limiting resource. Once the local roots' needs are met, P supply to the shoot will increase, 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 *Mucuna* roots develop in a solution containing a relatively high Al^{3+} concentration if part of the root systems grows 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. No separate Al-signalling mechanism has to be invoked to explain these results, however, as the Al-avoidance response disappears at improved P supply to the plant 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 branch root development. Most of the responses appear to be based on stimulated branch root development and can also be described as a reduced degree of apical dominance, the mechanism by which the top meristem of shoots or roots reduces or delays the development of branch axes. In perennial root systems, a large proportion of the finer branch roots is relatively short-lived (Chapter 7) but new branch roots can develop annually from the surviving secondary thickened transport roots. 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 a nutrient solution of various composition. The intensity of the local stimulation of branch 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).

Putz and Canham (1992 and personal communication) and Putz *et al.* (1994) found no differences between trees and shrubs in below-ground architectural plasticity or in root extension along a nutrient gradient. Species from a poor habitat, however, tended to have higher root plasticity (response to local nutrient supply) and root growth rates than species generally occurring in nutrient richer habitats. This finding was contrary to a prediction by Grime (1979), but is consistent with a higher relative spatial heterogeneity of nutrient availability on poor sites.

Deep rooting is common in xerophytic species like *Alhagi camelorum* (25 m recorded), *Glycyrrhiza glabra* (10–15 m), *Andina* sp. (18–19 m) (Daubenmire, 1959) and *Acacia senegal* (32 m) (Deans, 1984). 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) quoted in Daubenmire (1959)).

The considerable genotype × environment interactions mean that statements about the 'typical' root development of tree and crop species lose their validity when transferred to a substantially different soil type, soil fertility status or climatic zone. Simple observation methods are thus needed to 'ground-truth' generalizations about root patterns. Evidence of genotypic differences in tree root distribution is scarce, but this is probably due to a lack of suitable observation methods rather than to a true lack of genotypic variation in root characteristics. Vandenbeldt (1991) found clear differences in rooting depth of young plants of *Faidherbia albida* genotypes from western and southern Africa.

Considerable genotypic differences exist in tolerance to stress factors such as poor aeration, high soil bulk density and/or high Al^{3+} content. Coster (1932b) compared the waterlogging resistance of a large number of tropical trees and found considerable differences: some trees wilt and die back within one or a few days of waterlogging, other non-wetland trees can endure it for a half year or more. Waterlogging resistance is normally based on effective internal aeration structures (van Noordwijk and Brouwer, 1993), which are very well developed in mangrove trees, in addition to pneumatophores for 'breathing' above the soil or water surface. Many tree species, however, are able to develop at least some roots below the water table. The need for internal aeration structures above the water table (for short distance O_2 transport) depends on soil architecture and root–soil contact (Kooistra and van Noordwijk, 1995).

Horizontal and vertical distribution
Simplified curves fitted to actual root distributions can be used for models at level 3 (see above). 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:

$$L_{rv}(h) = bL_{ra}e^{-bh} \qquad (9.7)$$

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 *Dactyl-*

adenia (*Acioa*) on acid soils (Ruhigwa *et al.* 1992) or *Eucalyptus camaldulensis* (Jonsson *et al.*, 1988).

Root density normally also decreases with increasing distance to the plant in the horizontal direction. 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:

$$L_{rv} = ae^{-b\sqrt{h^2+cr^2}}$$

(9.8)

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).

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, governing cytokinin production and Ca uptake; and
4. root dry weight, indicating the amount of carbon in the root system and giving an initial estimate of the C costs of making 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 shapes of the 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 and co-workers (Fitter, 1986; Fitter *et al.*, 1988; Fitter and Stickland, 1991) have described 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 a root: (i) the number of *internal* and *external* links (without and with top 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 left out and only the first three types of information are needed.

Leonardo da Vinci (Mandelbrot, 1983) claimed that the cross sectional area (csa) of the main stem is equal to the sum of the cross sectional areas of tree 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 cells have a constant diameter (the maximum of which is determined by the risk for 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' (Shindzaki et al., 1965) at least forms 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). 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. 9.5). Tests of the assumptions underlying these models should be made under field conditions.

Measuring the 'proximal' diameter of roots, i.e. the diameter of the root segment connected to the stem base, is relatively simple (Fig. 9.5b), 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 obviously depend on the root branching pattern (Fig. 9.5a), but we may hope to identify this 'branching pattern' from a few relatively small samples, if we can find a suitable system for quantification.

Santantonio et al. (1977) reported a highly significant correlation of root end diameter and total root fresh weight in Douglas fir, which could be used to estimate the biomass of roots broken off in windthrows, but which also indicates that the proximal root diameter may be a good indicator of root size. Some attempts have been made to relate root biomass to total stem diameter at breast height as well (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 by Freezaillah and Sandrasegaran (1969) and Sanford (1989), but not for fine root biomass (Egunjobi, 1975).

Analysing the architectural rules underlying root development (Atger, 1991; Francon, 1991) opens perspectives for visualizing and predicting three-dimensional structures as they develop in time, but a major difficulty

(a)

Dichotomy Herringbone

(b)

A.

B.

Stem diameter at breast height D_s

Proximal root diameters

$D_{0.1} \cdots D_{0.2}$

Index of tree root competitiveness:

$$\frac{\sum D_{0.1}^2 \text{ horizontally oriented}}{D_s^2}$$

C.

$$\alpha = \frac{D_i^2}{D_{i+1,1}^2 + D_{i+1,1}^2}$$

$D_{i+1,2}$

D D_{i+}

D.

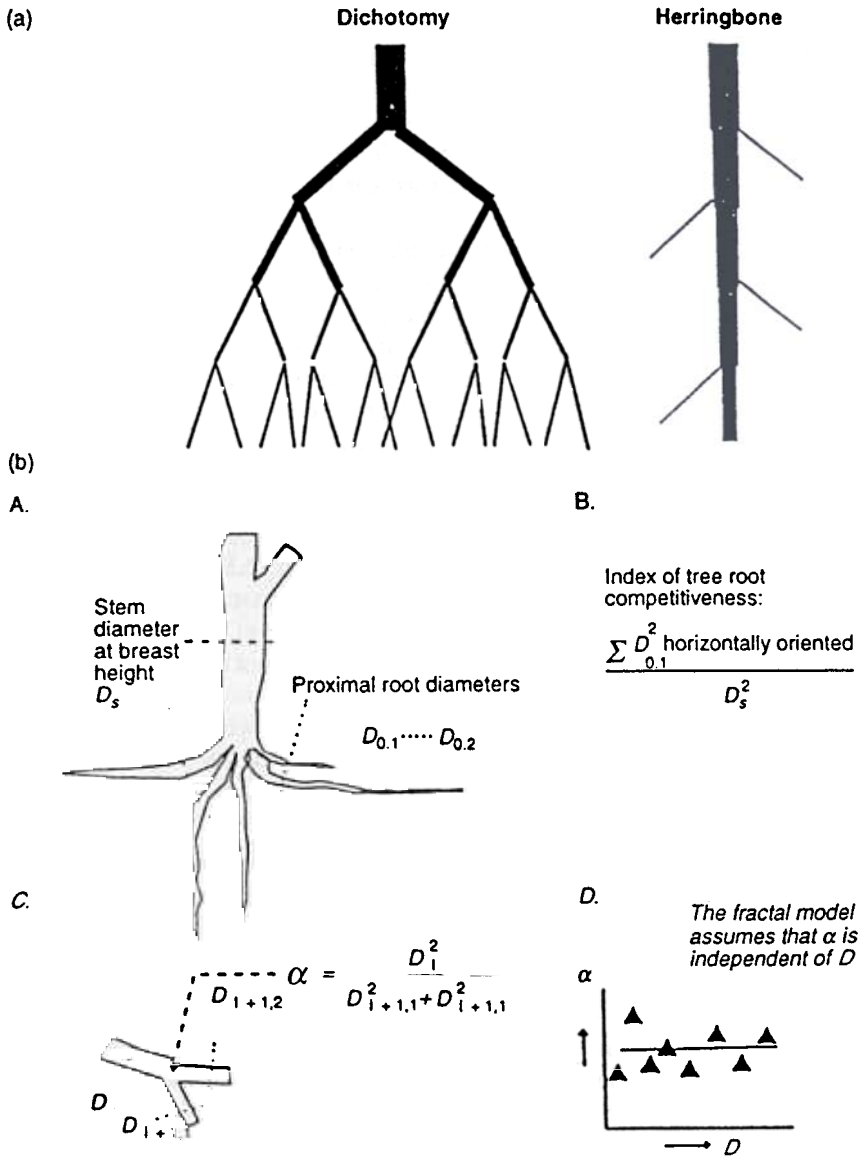The fractal model assumes that α is independent of D

α

D

Fig. 9.5. (a) Two extreme types of root branching: dichotomous and herringbone. Under the pipestem model the ratio between initial diameter and number of links is the same for both patterns (and all intermediary ones) (van Noordwijk et al., 1994b). (b) Measurement of proximal tree root diameters.

still is formed by difficulties of incorporating the large plasticity in response to local soil conditions into the analytical framework. 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.

Empirical relation between root pattern and tree growth rate

Coster (1932a) studied a large number of tree species as potential under-storey 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 (Fig. 9.6).

Trees 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. Trees with a deep tap root as well as extensive horizontal root development in the topsoil showed a faster shoot growth and had shoot:root ratios of 2 to 6. A group of trees and shrubs with only shallow rooting had shoot:root ratios of 2 to 30 (Hairiah and van Noordwijk, 1986). Figure 9.7 shows that shoot dry weight at 6 months is related to tap root length in trees without strong lateral root development. In trees with more than two long lateral roots, however, there is no relation between tap root length and shoot dry weight (if we consider the point in the upper right corner of the graph (*Sesbania sesban*) as an outlier). Average shoot weight is much higher for trees with at least two horizontal branch roots of at least 1 m length than for trees without such exploration of the topsoil. The often heard requirement of 'fast growing trees with deep root development, causing little competition with shallow rooted crops', i.e. squares in the upper right corner of the graph, seems thus to ask for the impossible, at least based on the initial growth.

The data from Coster (1932a, b) showed that *Leucaena leucocephala* and *Acacia villosa* gave the best chances to complement the relatively shallow *Tectona grandis* root system: after a moderately rapid establishment phase with some horizontal roots in the topsoil as well as a deep tap root, later root development was largely confined to the subsoil.

Unfortunately, the statement of Howard (1924) has not lost any of its actuality: 'it is remarkable ... that no detailed information on the distribu-tion of root activity during the year is available. Nevertheless it is clearly essential in the ecological studies of the future.' Yet many efforts and some real progress have been made. Srivastava *et al.* (1986) found maximum root growth of teak in each of the rainy seasons in a bi-modal pattern with the greatest seasonality in the finest roots.
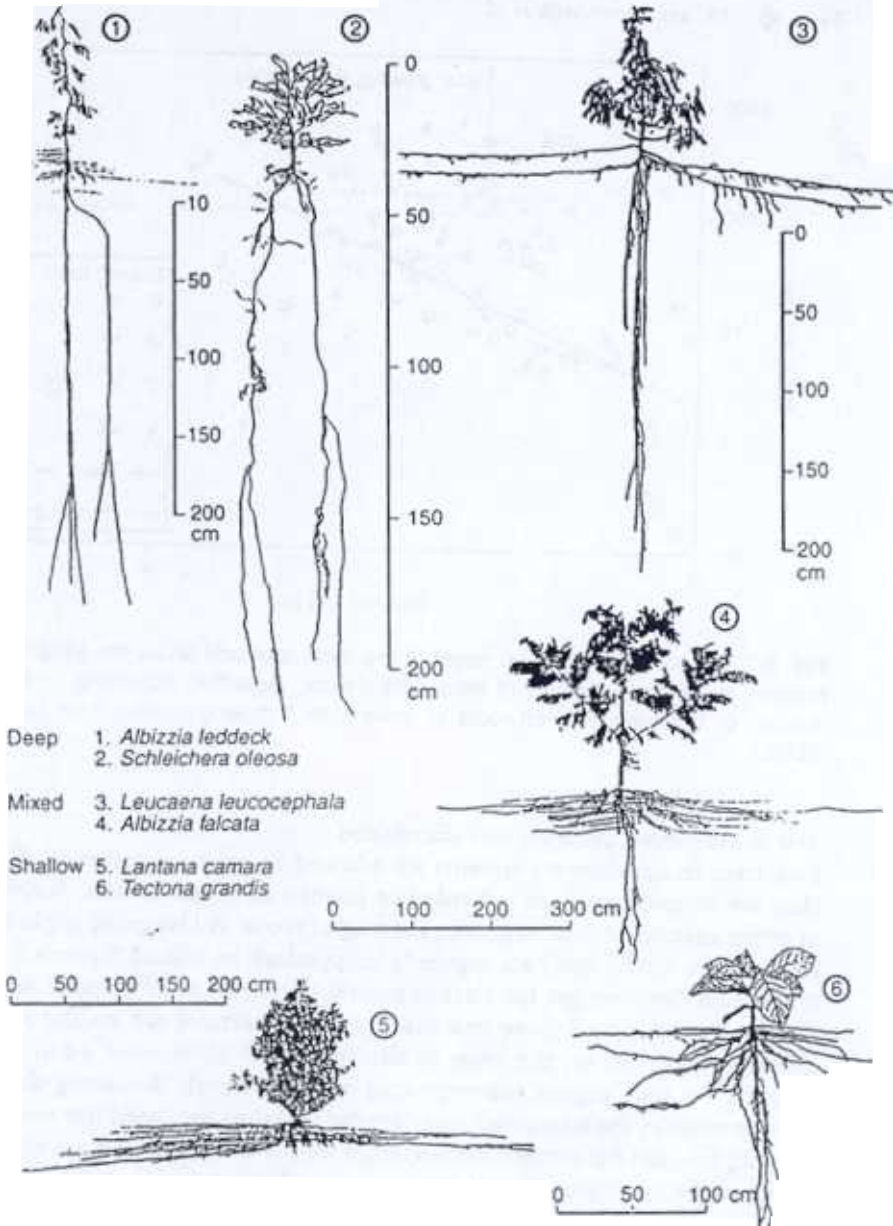
Deep   1. *Albizzia leddeck*
        2. *Schleichera oleosa*

Mixed   3. *Leucaena leucocephala*
        4. *Albizzia falcata*

Shallow 5. *Lantana camara*
        6. *Tectona grandis*

Fig. 9.6. Three root distribution types of young trees tested as accompanying species for teak (*Tectona grandis*) plantations (Coster, 1932a).
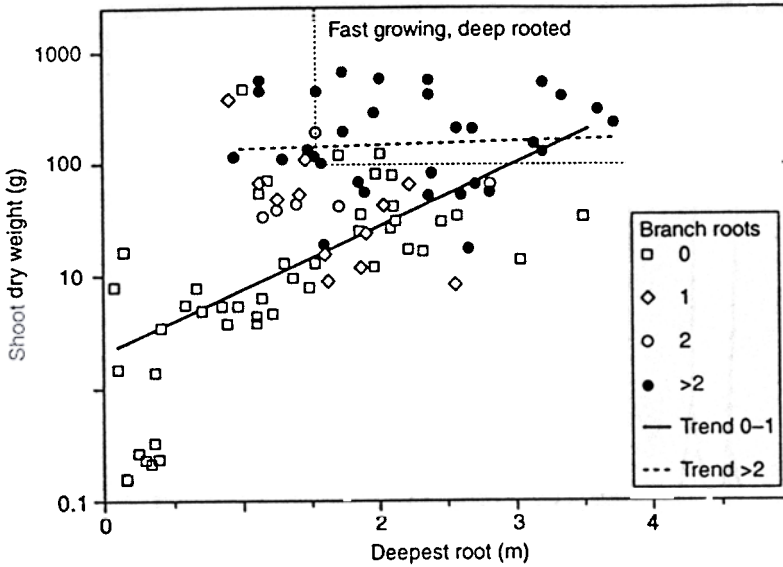
Fig. 9.7. Relationship between depth of the main root and shoot dry weight at 6 months, for a large number of trees and shrubs, classified according to the number of horizontal branch roots of more than 1 m length (data from Coster, 1932a).

Tree management effects on root distribution

Few trees in agroforestry systems are allowed to grow undisturbed. Branches are lopped, trees are pollarded or pruned to obtain fodder, fuelwood or green manure and/or to 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 get the environmental trigger from its original area of distribution. Most of these tree management practices are on the above-ground parts, but on the basis of the functional shoot–root equilibrium concept we may expect below-ground effects as well. Reducing the leaf canopy reduces the transpirational demand and thus the 'need' for new root growth, but also the current carbohydrate supply to the root system which is required for root growth and maintenance. Under more severe pruning regimes, recovery of the tree 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 a dieback of fine roots and nodules, but few hard data exist on such effects (Fownes and Anderson, 1991; Smucker *et al.*, 1994). Root death and subsequent decay will increase nutrient mineralization in the soil, so crops can benefit from pruning the tree by reduced shading as well as improved 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, due to higher fibre and lignin content, lack of easy access via stomata and perhaps because of higher concentrations of toxic metals such as Al (Bloomfield *et al.*, 1993). Decomposition rates for roots were found to decrease with root diameter (Fahey *et al.*, 1988; compare Chapter 7).

The effect of partial pruning or lopping off branches is inadequately known and will partly depend on the stem anatomy. In trees with well-integrated transport tissue, the loss of a few 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, cutting branches will directly affect the associated roots.

Pruning the trees may affect subsequent root distribution as well (Rao *et al.*, 1993). Van Noordwijk *et al.* (1991a) reported that the lower the height of pruning *Peltophorum dasyrachis* trees the greater the number and the smaller the diameter of proximal roots. The hypothesis was formulated that a reduced stem height after pruning reduces the chances of survival of, and maintenance of apical dominance by, meristems of main root axes. Regrowth of the root system during and after recovery of the shoot thus increasingly depends on new roots starting at the stem base. A further experiment (Hairiah *et al.*, 1992) confirmed the hypothesis for a number of tree species (*Calliandra calothyrsus*, *Senna siamea*, *Gliricidia sepium*, *Paraserianthes falcataria*, *Peltophorum dasyrrachis*), although *Gliricidia* forms thick fleshy storage roots at reduced stem pruning height. 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, it thus also tends to increase subsequent competition between trees and crops in the topsoil.

Roots and their symbionts
Any account of root ecology, however brief, has to mention the major root symbionts. Mycorrhiza (fungus + root) formation rather than root devel-opment is the norm in most trees as well as crops, although there are notable exceptions in a number of plant families. Janse (1896) was among the first to describe the morphological structures that give evidence of this symbiosis, based on plants growing in the botanical garden in Bogor. In the century after that, enormous progress was made in understanding the func-tion of these structures and the way mycorrhizas can be managed (Bowen, 1984; Sieverding, 1991). 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 uptake possibilities of mycorrhizal systems are more difficult to quantify as yet than it is for systems consisting of roots only.

The symbionts responsible for N_2 fixation in *Leguminosae* and a number of other plant families have also received due attention. Giller and Wilson (1991) reviewed nitrogen fixation in tropical cropping systems, and include references on tree crops and multipurpose trees.

Concepts for tree–crop interactions

Sequential versus simultaneous agroforestry systems
The relevant root parameters for predicting uptake efficiency depend not only on the resource studied, but also on the complexity of the agricultural system. In intensive horticulture with nearly complete technical control over nutrient and water supply, fairly small root systems may allow very high crop productions in a situation where resource use efficiency ranges from very low to very high, depending on the technical perfection of the often soilless production system (van Noordwijk, 1990). In field crops grown as a monoculture, the technical possibilities for ensuring a supply to the crop of water and nutrients where and when needed are far less; 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 im-proving overall resource use efficiency, on the other hand, it means that root length densities which would be sufficient for efficient resource use in a monoculture may not be sufficient 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.

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 rainfall surplus during the cropping season, such storage will be possible and there will be no compelling need for improving 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 will be washed into deeper layers of the soil (Fig. 9.8). If crop rooting is shallow, as is common on the acid soils typical of this climatic zone, nutrients will be leached beyond the crop roots. Deep rooted components of mixed cropping systems can then act as a 'safety net',
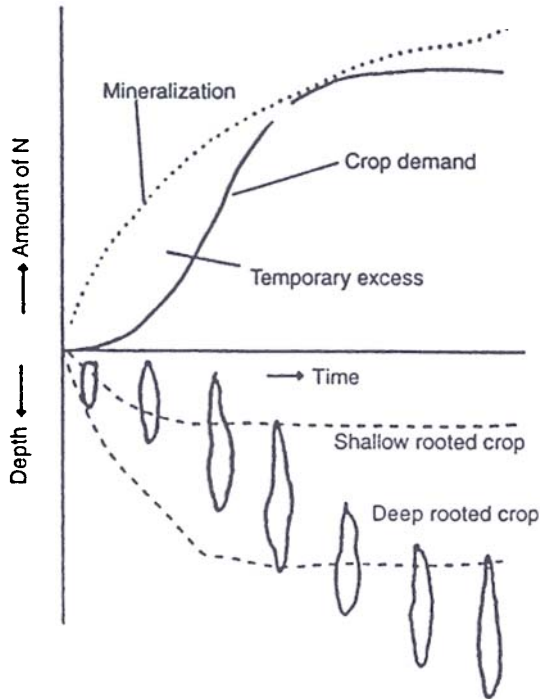
Fig. 9.8. Synchrony hypothesis: the time pattern of mineralization and crop demand (both shown in cumulative form) generally do not match; a temporary stock of mineral N in the soil will leach to deeper layers, depending on rainfall, and can be out of reach of shallow rooted crops by the time they need it.

intercepting N on its way to deeper layers (van Noordwijk and De Willigen, 1991; see below).

A distinction should be made between agroforestry systems where trees and crops use the same land simultaneously, and sequential systems such as improved fallows (E. Torquebiau, 1993, unpublished). Trees with abundant superficial roots may not be suitable for the first, but may be desirable for the second type of system. In sequential systems soil conditions at the time of transition of the tree to crop phase are the most important criterion. The tree may have left a considerable litter layer on the soil surface and a network of decaying tree 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 the old tree root channels. 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 of high leaching rates.

The 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, any accumulation of mineral N will be leached rapidly from the topsoil to deeper 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 idea that trees act as a 'nutrient pump' has thus been around for at least a century. Few hard data have accumulated, however, as it is no easy task to identify which part of the net nutrient uptake of a tree comes from deep or superficial soil layers (see 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. A number of conditions need to be met, however, for trees to act as nutrient pumps:

1. the tree should have a considerable amount 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 in the soil or in a saprolite layer;
3. soil water content at depth should be sufficient to allow diffusive transport to the roots.

These conditions indicate that the possible role of deep-rooted trees as nutrient pumps is likely to be small on soils with limited weatherable minerals in the subsoil (most oxisols and ultisols fall in this category) or in climates with a limited annual depth of wetting. 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, these roots may act as a 'safety-net', intercepting mineral nutrients leaching from the crop root zone (Fig. 9.9). Through litterfall or pruning such nutrients may return to the topsoil later on and have a new chance of uptake by crops. In contrast to the 'nutrient pump' hypothesis, the 'safety-net' hypothesis is not restricted to specific soil types, but it 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.

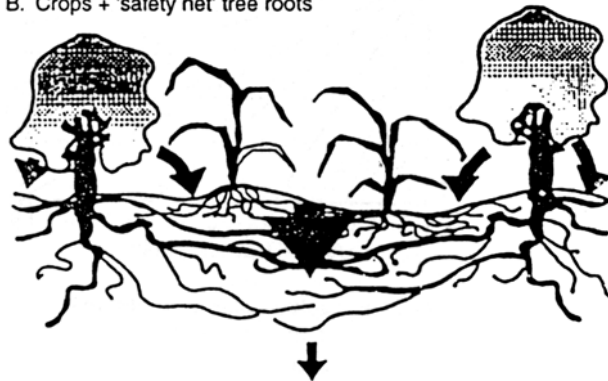A. Shallow rooted crop

B. Crops + 'safety net' tree roots

Fig. 9.9. Safety net hypothesis of tree roots intercepting nutrients leaching from a shallow crop root zone.

The safety-net role seems particularly valid for simultaneous agroforestry systems, but under certain conditions may apply to sequential systems as well. 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. 9.10). 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 9.2). 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.

Hydraulic lift and heterogeneous water infiltration

Roots have a physiologically determined resistance to entry of water, but they can also leak water to their environment, if the water potential in the surrounding soil is more negative than in the plant. This condition can be expected when the topsoil dries out while roots in deeper layers are still able to take up water; it is most likely at night when plant water potential can
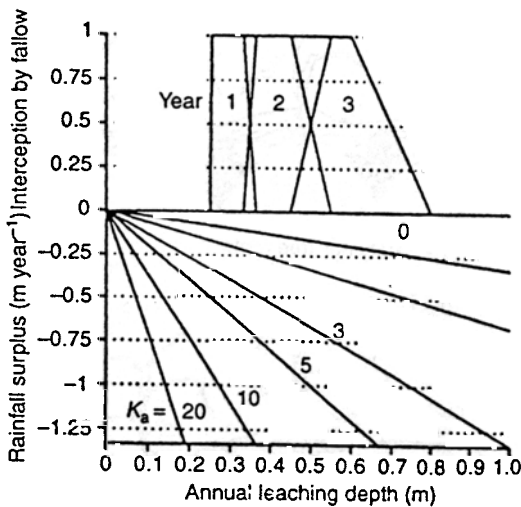

Fig. 9.10. Possibilities for deep rooted fallows to intercept nutrients leached from a shallow rooted crop. The lower part of the diagram gives a nomogram of nutrient leaching depth as a function of rainfall surplus (rainfall − runoff − evapotranspiration) and apparent adsorption constant K_a (ml cm^{-3}). 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, 1989).

Table 9.2. 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 years 1, 2 and 3, respectively) to intercept nutrients (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

recover from the daytime stress. The total amounts of water leaking out of root systems by this 'hydraulic lift' phenomenon are generally small compared with the daily transpirational demand, but they can facilitate nutrient uptake from topsoil layers. The water leaking out of the roots of a deep rooted plant can be utilized by other plants as well. Caldwell and Richards (1989) used tritium (^{3}H) labelled water to show that such transfer occurred between a deep rooted shrub and a more shallow rooted grass. The phenomenon has been demonstrated in 'split-root' experiments as well (Baker and Van Bavel, 1988; Xu and Bland, 1993).

In semi-arid climates, trees may have a pronounced effect on the pattern of water infiltration (see 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 all individual plants experience considerable competition, and reach a much smaller size than they would do in a more open stand. Competition between 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 (see Chapter 4). For light, plant canopy height is a simple index for the competitive strength of any plant. Below-ground resources cannot be treated in a similar one-dimensional way, however. Water and nutrients are

stored in the soil, so time of use should be considered, as well as at least two dimensions for describing horizontal and vertical stratification.

The general wisdom is that complementarity in root distribution is a 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 etc. *Paulownia* has the majority of its fine roots in the layer 40–100 cm deep, below the crop root zone (Table 9.3). 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).

Nelliat *et al.* (1974) suggested that horizontally separated root systems could be the basis for complementarity in coconut–cocoa–pineapple multistorey agroforestry systems. On the basis of the older literature on coconut in Indonesia (reviewed by Wiersum, 1982), a shallow, but extensive, root system can be expected and the topsoil of any mixed stand would probably be nearly completely exploited by the coconut.

As a first approach to a process-based description of 'competitive strength', we may assume that the N_{res} term of Equation 9.3 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.

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. Also, the 'pipestem' model and similar approaches suggest that tree stem diameter can give a first indication of this, at least within a species. The fractal branching models suggest that the total amount of fine roots is related to proximal root diameters. Thus the ratio of superficial roots and stem diameter can be used as a simple indicator of the degree to which the tree can depend on topsoil resources, and thus for its competitive strength, when combined with shallow rooted crops (see below).

A number of hypotheses have been put forward for positive tree–crop root interactions. Stimulated nodulation of trees in the neighbourhood of N-depleting crops was postulated by van Noordwijk and Dommergues (1990), but the available evidence is not conclusive as yet. Complementar-

Table 9.3. Root distribution of 10-year-old *Paulownia elongata* stands (average for three sites) in China, according to Zhu Zsao-Hua *et al.* (1986).

Depth (cm)	0–20	20–40	40–60	60–80	80–100	100–150	150–200
% of fine root weight	1.9	12.9	38.9	18.1	19.1	6.7	2.3

ity in P use could be based on very efficient P uptake by (ecto)mycorrhizal trees and recycling through organic P forms. Hard evidence on this type of facilitation is missing, but it is worth checking.

Table 9.4 summarizes the types of below-ground interactions which can occur in simultaneous as well as sequential agroforestry systems. The table indicates how to measure the various effects and which tree characteristics are desirable to optimize tree–crop species combinations.

Species selection is the major option to meet these desiderata, but tree management can have secondary effects. Above-ground tree management, including pruning, will have immediate effects on root function (demand for water and nutrients) and longer term effects on root distribution.

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. Figure 9.11 shows results of an experiment by Coster (1932b) on the interactions between mature *Tectona grandis* stands and neighbouring plots where trees and/or food crops were planted in a taungya system. The generally poor growth of tree seedlings and maize was dramatically improved when a trench was made around the old growth stand, excluding root competition. The shade effects only extended over a few metres from the old stand, while apparent root competition extended over approximately 20 m. The root trenches were refilled with soil and within 1 year *T. grandis* roots had re-invaded the neighbouring plots. Coster's approach to measure the below-ground competition effects by the positive yield effect of root separation is still used as a first approximation (see Chapter 4). A number of reports on root pruning effects have been published recently for hedgerow intercropping (Fernandes *et al.*, 1993; Nair *et al.*, 1994).

Some caution is needed in interpreting the results in the context of the tree–crop interaction equation (Chapter 1), because root pruning may reduce shoot growth and thus above-ground interaction as well. 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 have positive below-ground effects as such).

Putz (1992) tried to separate above- and below-ground competition effects between *Pinus* seedling growth and coppiced hardwoods and vines by a combination of root-trenching and guy-wiring back overtopping trees. In his situation below-ground competition was found more important than shading effects. In a similar analysis of the effects of the shrubs *Cornus*

Table 9.4. Types of below-ground tree–crop interactions and tree desiderata.

Interaction process	Measure of effect	Tree desiderata for agroforestry systems	
		Sequential	Simultaneous
Competition for water	Positive crop response on tree root pruning, especially in dry periods; measurement of water flow in horizontally oriented proximal roots		Deep rooted trees
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 on tree root pruning, esp. in dry periods		(Relatively) deep rooted trees
Vertical nutrient transfer to topsoil under the tree	Nutrient contents of prunings	Deep rooted trees	(Relatively) deep rooted trees
Horizontal nutrient transfer to topsoil under the tree	Nutrient contents 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 (nodule) turnover	Quantification of tree root nodule turnover		Rapid root decay (esp. after pruning)
Soil organic matter maintenance by root turnover, litterfall, etc.	Quantification of tree root turnover and litterfall; measurement of dead tree root decomposition rate	Abundant roots in topsoil, rapid root turnover, high content of lignin/polyphenolics	Rapid root turnover, high content of lignin/polyphenolics
Facilitation of crop root growth in old tree root channels (overcoming constraints of soil density or Al toxicity)	Visual check of crop root positions in the soil profile	Deep rooted trees, slow decomposing tree exodermis	

Table 9.4 (continued)

Interaction process	Measure of effect	Tree desiderata for agroforestry systems	
		Sequential	Simultaneous
Stimulation of root symbionts such as VAM fungi	Crop root VAM infection percentages with or without trees	Common VAM fungal partners	Common VAM fungal 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	

racemosa and *Rhus glabra* on the growth of tree seedlings (*Acer rubrum* and *Fraxinus americana*) below-ground competition dominated on a dry and nutrient poor soil, but above-ground interactions in a wet field with alluvial soil, and both were equally important on a more mesic field (Putz *et al.*, 1994).

The direct effects of root trenching when applied to existing stands can give evidence of direct competition effects, but not of the possible long term soil improvement by the trees which may compensate eventually for part of the competitive effect. To estimate such long term trends, trees have to be completely removed in some treatments and crop growth here should be compared with that on controls outside the reach of trees.

Below-ground interactions between trees and crops are fairly well understood for intensively managed hedgerow intercropping systems in humid areas. However, interactions are less pronounced in semi-arid parklands and natural rangelands. Circumstantial evidence exists on the added value of tree in these systems (Breman and Kessler, 1995) and the positive role of tree roots (Groot and Soumaré, 1995), but data to separate and to quantify above- and below-ground interactions are lacking. Nutrient accumulation by the tree can be easily quantified, but whether it is based on horizontal or vertical accumulation is less obvious (Kellman, 1979), and whether or not it is effectively recycled to other components is questionable.

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
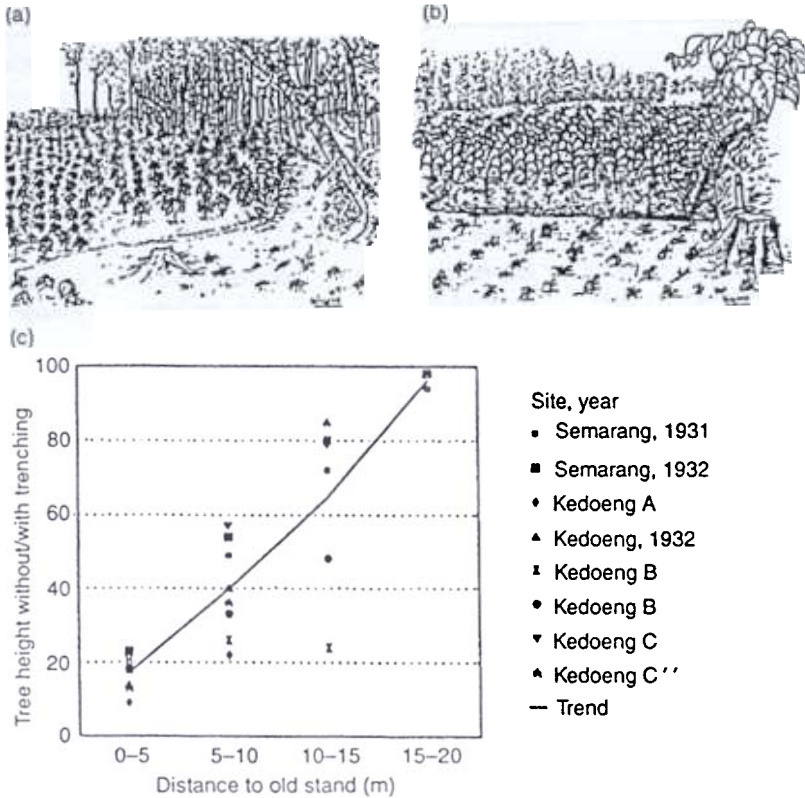
Fig. 9.11. Effects of root trenching (background = tree roots excluded, foreground = tree roots present) to prevent the roots of old *Tectona grandis* stands competing for water and nutrients with new *T. grandis* seedlings (a) and maize (b); (c) Growth of young *T. grandis* trees with and without root trenching as a function of distance to old *T. grandis* stands (Coster, 1933; (a) and (b) artist's impression (Mr Wihyono), based on old photographs).

beneath the tree canopy (Fig. 9.12, zone a) and outside the tree canopy but within the zone exploited by tree roots (Fig. 9.12, 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 tree, a dense, homogeneous annual crop or grass is sown.

This results in seven different crop production situations or treatments:

1. on 'native' soil underneath the tree in the presence of tree roots,
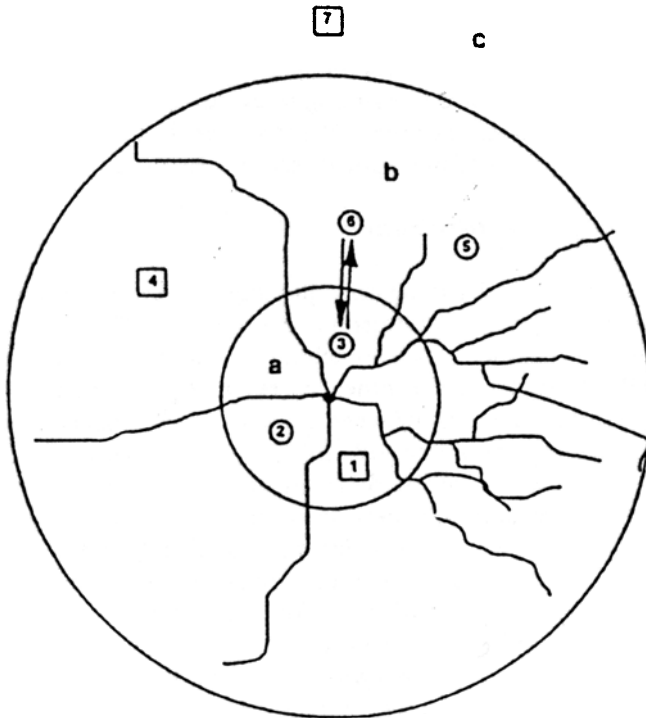2. on 'native' soil underneath the tree without active tree roots,

Fig. 9.12. Different cropping positions in so-called soil-transfer experiment.

3. underneath the tree on soil from outside the canopy without active tree roots,
4. on 'native' soil outside the canopy in the presence of tree roots,
5. on 'native' soil outside the canopy without tree roots,
6. on soil from underneath the tree placed outside the canopy without the presence of tree roots,
7. 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 the experiment. 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 etc. 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

Basic methods for observing and quantifying tree and crop root biomass and length are given by Anderson and Ingram (1993). New developments are based on the fractal root branching models and the allometry between proximal root diameter and other, more functional root characteristics.

To study interactions between trees and the herbaceous layer in semi-arid tropical savanna rangelands in Mali, West Africa, observations were made on root systems of two Sahelian tree species, growing on deep sandy or sandy loam soils, and the herbaceous layer surrounding them (Groot and Soumaré, 1995). To characterize the structural root system, for each species the root systems of five trees were excavated, by digging a pit around each trunk with a radius of 2 m. Soil was removed using shovels, small picks, hoes and knives; soil around roots was removed using paint brushes and toilet brushes. Only roots with diameter > 2 mm were considered. For each tree, four primary roots were excavated and total root length was determined. Cross-sections of representative structural root systems of two species are given in Fig. 9.13a, b.

Acacia seyal (Mimosaceae) was characterized by a thin deep tap root, reaching depths down to 6 m. Lateral roots were mainly concentrated in the upper 40 cm of soil (Fig. 9.13a) and their diameter decreased gradually with length. Several secondary roots branched vertically downwards, sometimes reaching depths of over 5 m. Lateral roots reached lengths up to 25.7 m, being seven times the crown radius; on average, the land exploited was 25 times the area covered by the tree crown. *Sclerocarya birrea (Anacardiaceae)* (Fig. 9.13b) has a thick, relatively short tap root, reaching depths of 2.4 m. Lateral roots branched at the upper 100 cm of the tap root and gradually curved towards the soil surface with increasing distance from the trunk. Lateral roots were thick at the trunk base but their diameter decreased sharply with length within the first 100 cm. Sinker roots were absent. Maximum lateral root length was 50 m (10.2 times the crown radius) and exploited land area 34 times the tree crown area.

A relationship between diameter of main roots as measured near the trunk base and their length was established, allowing estimation of the surface occupied by tree roots (Fig. 9.14). Root diameter measured at different distances from the trunk as a function of this distance was best described by a negative exponential regression curve ($D_L = D_0e^{-k \cdot L}$, where D_0 is base diameter and L represents the distance from the trunk).

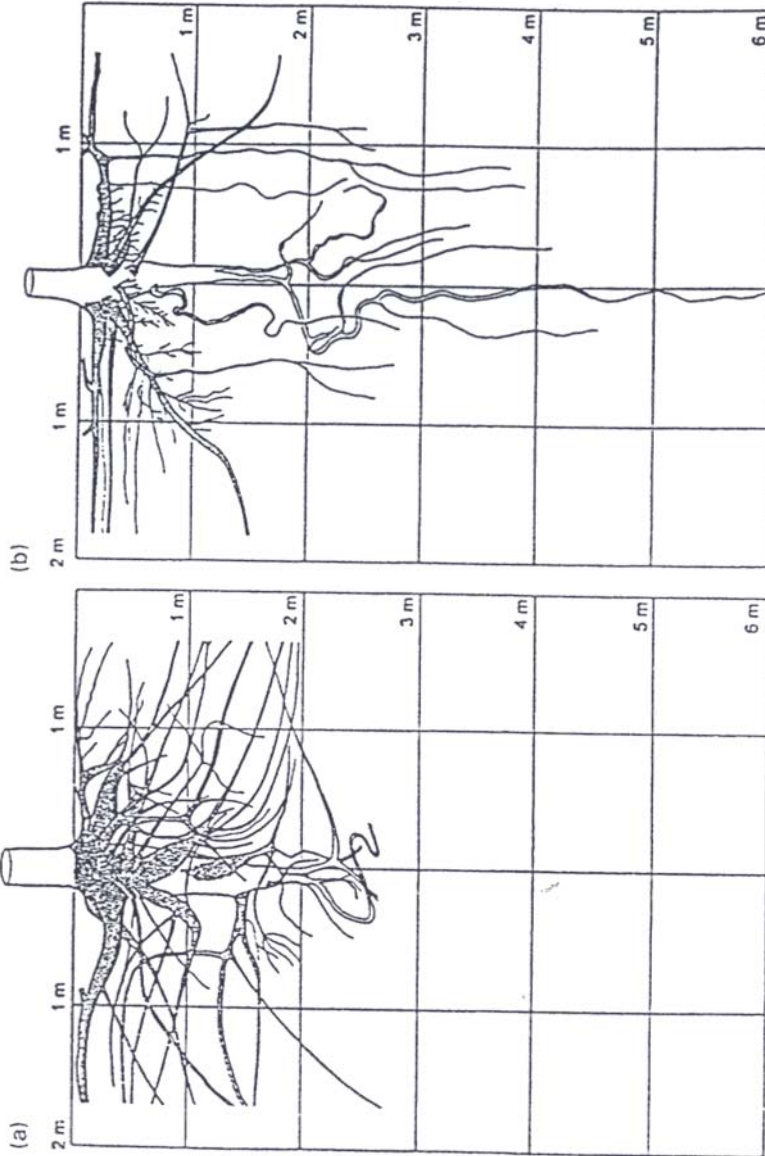To investigate fine-root distribution of both trees and herbs, so-called

Fig. 9.13. Distribution of the structural root system of *S. birrea* (a) and *A. Seyal* (b) within 2 m of the tree trunk.
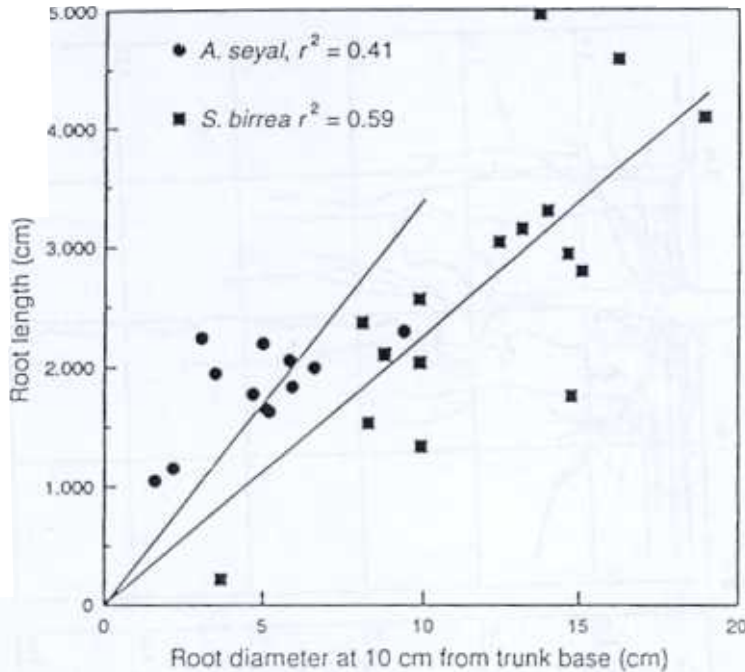
Fig. 9.14. Relationship between proximal root diameter (at 10 cm from the stem) and root length for *Sclerocaryea birrea* and *Acacia seyal* in Mali.

fakir-bed or pinboard monolith soil samples were taken perpendicular to the tree radius on two trees of comparable size for each species, at the crown limit (*r*), at 2*r* and at 3*r*. After washing the monolith, roots were cut in 10-cm compartments corresponding to soil layers and were separated into tree roots and herbaceous roots, and oven-dried. Only roots with a diameter < 2 mm were considered. The obtained root weights were averaged for the two trees. Results are presented in Fig. 9.15. For both species, biomass of fine roots under trees was considerably higher as compared with the open field, which explains partly the higher levels of organic matter and soil fertility often observed under and near trees. The majority of fine tree roots were located below those of herbaceous roots, showing that trees might recycle nutrients which, in the absence of trees, are lost from the system by leaching.

Need for simple, farmer-level criteria and observation methods

Current root research methods on 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
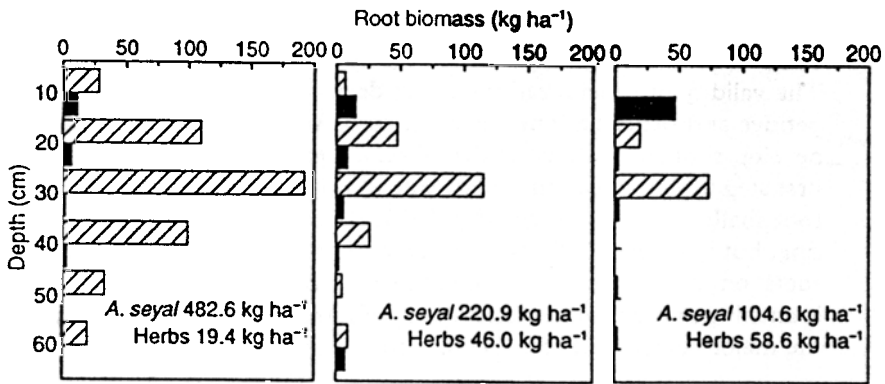
Root biomass (kg ha⁻¹)

Fig. 9.15. Weights of fine roots (< 2 mm) of *A. seyal* and the herbaceous layer (from left to right) at the crown limit (*r*), and at two zones away from the crown (2*r* and 3*r*). ■, Herbs; ▨, *A. seyal*.

Table 9.5. A. Protocol for quantifying proximal tree root diameters and the index of tree root competitiveness. B. Protocol for test of fractal characteristic of root branching and measurement of parameters for predicting total root system size from proximal root diameters.

A. Proximal roots

1. Carefully excavate the first part of the proximal roots at the stem base (Fig. 9.5b). For a small tree a 0.3 m half sphere may be sufficient, for larger trees a 0.5–1 m half sphere will be needed. While excavating all major roots should be left intact; destruction of most of the fine roots cannot be avoided. Check for 'sinker' roots (vertically oriented roots starting from horizontal roots, often close to the tree stem).

2. Measure the root diameter of all proximal roots (i.e. 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). Root diameter measurements should be made outside the range of obvious thickening close to the branching point or buttress roots (they 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. Calculate the sum of root diameter squares for roots with a horizontal (angle with horizontal plane less than 45°), ΣD_{hor}^2, and vertical orientation, ΣD_{vert}^2.

5. A tentative *index of root shallowness* is then calculated as $\Sigma D_{hor}^2 / D_s^2$.

B. Test of fractal branching assumptions

1. Expose parts of the root system, by tracing roots from the stem base. For each branching point where both the previous and subsequent 'links' have been exposed, measure the diameter of each link (halfway from the link or at 5 cm from the previous branching point, outside the thickening often accompanying branching).

2. Analyse data by sorting the roots belonging to a common previous link and calculate the α parameter as $D_{before}^2 / \Sigma D_{after}^2$. Then analyse the regression 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 average value of α and link length can now be used in the equations for total length, surface area and volume given by van Noordwijk *et al.* (1994b); if either of the regressions has a significant slope, modified equations will have to be developed (e.g. on the basis of the numeric model given by Spek and van Noordwijk (1994)).

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 a first step in that direction, the proximal root method and the 'index of tree root shallowness' is presented in Table 9.5. It definitely needs further testing, but it appears to bridge farmer level criteria ('trees where you can see roots on the surface are competitive') through the allometrics of root branching patterns to the functioning of roots in uptake, and thus to one of the major components of tree–soil–crop interactions.

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