5 Crop and Tree Root-system Dynamics

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Key questions

1. When do roots grow? Is internal resource allocation to roots predictable? How do interactions in more complex systems affect this?
2. Where will root expansion take place? How quickly can root systems adapt their distribution to changing soil conditions (water, nutrient patches)?
3. How long do (fine) roots live? Is root turnover a major source of C input to the below-ground food web and to C_{org} in the soil?
4. How can (or should) root system dynamics be represented in simulation models?

5.1 Introduction

Whereas the preceding chapter focused on the spatial aspects of tree roots, we will now consider the dynamics of root growth and decay in those crops, weeds, grasses, shrubs or trees that form a part of tropical agroecosystems, elaborating on van Noordwijk *et al.* (1996). Root turnover is important in the functioning of plants and agroecosystems for a number of reasons:

- Below-ground allocation of C (energy) may be around one-third of the C (energy) in the plant as a whole (Jackson *et al.*, 1997; Wu *et al.*, 2001).
- C (energy) provided by roots is a major source of C for the food web of soil biota.
- As roots are lost to 'rhizovory' (consumption), plants need to invest continuously in roots to maintain root length density.
- Through various channels, below-ground plant C allocation contributes to soil organic matter (C_{org}).
- Uptake by individual roots leads to 'depletion zones' being formed around them, and a situation whereby uptake is limited by the supply of nutrients via diffusion and mass flow (see Chapter 10, this volume); new roots can, therefore, start with a higher initial uptake rate.
- Through continuous root mortality and new root growth, a plant can adjust both the total size ('functional equilibrium') and the location ('local response') of its root system. This allows

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it to increase its access to the (currently) most limiting resource (van Noordwijk *et al.*, 1996), whilst maintaining its maintenance respiration cost at a level that can be sustained.

- As all plants have the ability to adjust their root systems (though the 'functional' and 'local' responses may differ in velocity and intensity), competitive interactions for below-ground resource capture should be seen as confrontations between organisms with different (long-term) strategies rather than just (short-term) tactics (which are determined by current root distribution, above-ground demand and supply of the below-ground resources).

The last decade has seen major progress in the quantification of root turnover at the plant and ecosystem levels (partially as a consequence of fears concerning the future impacts of elevated atmospheric CO_2, which have provided an impetus for the funding of such research). However, most, if not all, of the methods used to measure such dynamics are problematic (as we will discuss below); and we do not yet have comprehensive, well-tested models that relate all aspects of root turnover (as mentioned above) to the genotype and environment of plants. Of particular note is the fact that the rate at which root systems can adjust both their total size and spatial distribution (in order to meet the demands of the shoot and exploit supply in the soil) is still more a topic of speculation than of hard facts.

The standing biomass (or length) of the roots of any tree (perennial) or crop (annual) is the difference between cumulative root growth and cumulative root decay, from the time the plant begins to grow to the time of observation (Fig. 5.1). In annuals we can follow the process of root growth and decay from beginning to end because, almost by definition, all roots will die at the final harvest of the above-ground parts, which means that cumulative decay is equal to cumulative growth. In perennials, observation usually starts with an existing root system, and it may be found that their standing root biomass changes little, despite substantial growth and simultaneous decay.

The term *'root (biomass) turnover'* has been defined in various ways (Gill and Jackson, 2000; Schroth, 2003). However, different definitions usually all refer to 'cumulative root decay' (or 'root growth', assuming a steady-state size of the root system) divided by the average, maximum or minimum root

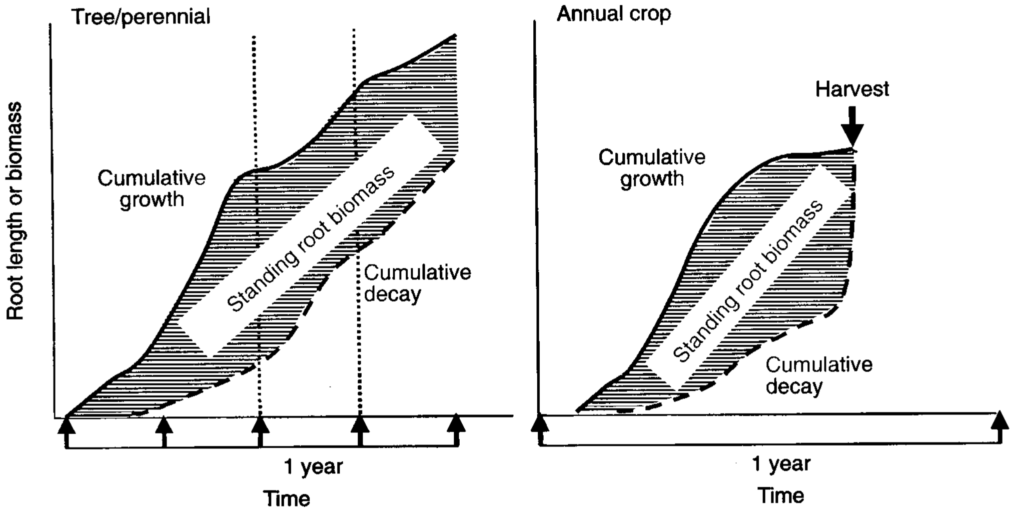

Fig. 5.1. Schematic representation of the dynamics of root growth and decay in trees (or other perennials) and in annual crops.

mass during the period. As Schroth (2003) discussed, use of the average will lead to more stable estimates. The same term ('turnover') is used to indicate different operational definitions in different publications, and care is needed when comparing the data obtained.

De Willigen and van Noordwijk (1987) defined *'root length turnover'* as the cumulative amount of roots that decayed during an observation period (1 year for perennials, one growing season, up to harvest, for annuals) divided by all roots that could potentially have decayed. The latter equals the standing root length at the start of the year *plus* the cumulative amount of roots that grew during the observation period. This definition results in a value for root turnover of 1 only where the standing root length becomes 0 at the end of the observation period. This definition can be used directly with measurement techniques that follow the fate of individual roots (such as minirhizotrons, see below), but not with methods based on sequential destructive sampling (see below).

Resource availability in the soil is dynamic in nature, with: (i) water entering from above as well as through subsurface lateral flows; (ii) nutrients either being released in the litter layer on top of the mineral soil or gradually weathering in the subsoil; and (iii) relative resource availability in the topsoil and subsoil changing with weather and seasons. The dynamic nature of soil resource availability therefore calls for a high degree of flexibility in root systems (higher than that normally found in the above-ground parts of plants). Such flexibility can be observed both when comparing plants of the same genotype growing on different sites, and when studying a single plant over its lifetime. Van Noordwijk *et al.* (1996) have already discussed the basic concepts of 'functional shoot/root equilibrium' and 'local response' in the context of agroforestry. In this chapter, we will explore how such concepts of the dynamics of tree–soil–crop interactions can be represented in simulation models.

Dead roots may be as important as live ones to the functioning of complex agroecosystems. Although the quantity of structural organic matter contributed to the soil by dead roots is generally less than the amount that arrives at the soil surface via litterfall, the specific location of decaying fine and coarse roots means that they contribute more to aggregate stabilization and the creation of soil structure (via biogenic macropores). The voids left by the partially decomposed remains of root systems can facilitate the growth of subsequent plant roots and their symbionts. An example of this is given in Fig. 5.2, which shows how the decaying roots of previous forest vegetation can provide a microenvironment that facilitates nodule development in subsequent tree plantations. In acid soils in the humid tropics, old tree root channels can play an important role in crop root penetration, water infiltration, the protection of

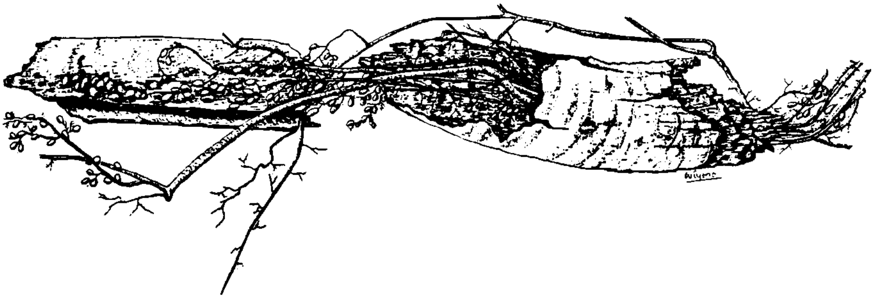

Fig. 5.2. *Acacia mangium* root growing inside a decaying tree root – a remnant of previous forest vegetation at a site in southern Sumatra (Indonesia). Inside this decayed tree root, the *A. mangium* roots had many root hairs and were profusely nodulated, whereas there was far less nodulation in mineral soil (drawing by Wiyono).

roots from Al toxicity and nitrogen management (van Noordwijk *et al.*, 1991a). Lucerne (alfalfa) has long been known to be a beneficial crop when planted in rotations with crops that have difficulties penetrating the subsoil. In a recent study, Rasse *et al.* (2000) found that lucerne root systems increased saturated hydraulic conductivity (K_{sat}) by 57%, total porosity by 1.7%, macroporosity by 1.8% (v/v) and the water recharge rate of the soil profile by as much as 5.4% per day. The enhanced soil structure resulted from the more severe drying/wetting cycles induced by lucerne, as well as from root turnover. The large increase in K_{sat} relative to the increase in porosity suggests that root decay specifically increases the connectivity of macropores rather than their volume as such (see also Chapter 10, this volume).

The rate of root decay is also important with regard to the timing of landslide risks following forest conversion on sloping land. In the temperate zone, structural tree roots (which help to anchor the upper soil layer and the root mat to the subsoil) may take 5–10 years to decay. According to Sidle (1992), landslide risks following forest conversion peak in this period. In the tropics, with higher soil temperatures and more rapid decomposition, structural tree root decay may occur twice as quickly (e.g. 2–5 years), but no solid data exist yet to confirm such timing.

The rest of this chapter will describe patterns of root growth and root decay, before discussing: (i) empirical methods that may be used to quantify root dynamics; and (ii) the representation of these dynamics in simulation models. We will also discuss differences between different land-use types in root production and turnover – as the changes in root production and turnover that potentially result from a change in land use can trigger further changes in the below-ground ecosystem. This chapter is therefore meant to form the basis for the following discussions in this volume: root function (Chapters 6 to 10), below-ground carbon (Chapter 11), biological N_2-fixation (Chapter 13), mycorrhizas (Chapter 14), nematodes (Chapter 15) and below-ground food webs (Chapter 16).

5.2 Root Growth, Functional Shoot–Root Equilibrium and Local Response

5.2.1 Shoot : root ratios

Brouwer (1963, 1983) formulated the hypothesis that plants maintain a 'functional equilibrium' between shoot and root growth. He connected patterns in shoot : root ratios expressed by plants of the same genotype growing in different environments to a simple, hypothetical physiological mechanism. The growth of both shoot and root meristems requires resources acquired both above ground (carbohydrate) and below ground (water and nutrients), but the priority of access to these above- and below-ground resources differs between root and shoot meristems. When water and nutrients are in short supply, root growth can thus be favoured; where products of photosynthesis are in short supply, leaf growth can thus be favoured. Brouwer's hypothesis of shifts in the relative allocation of growth resources to root and shoot growth emphasized the ecophysiological functionality of these shifts, hence the name 'functional equilibrium'. Although the physiological mechanisms used by plants are certainly more complex than Brouwer formulated, this hypothesis is in line with broad patterns in relative root allocation across ecological zones (Chapin, 1980; Sanford and Cuevas, 1996). Shoot : root ratios in tropical forests range from 0.7 (on poor spodosols) to 2 (in tropical deciduous forests where seasonal water shortages occur), 4 (in montane forests) and 8 (in lowland humid forests). In wet ecosystems, the extremes are shoot : root ratios of 1 (for mangroves with well-adapted below-ground systems) and 100 (in riparian forests without a substantial below-ground compartment).

Broadly speaking, the main 'choice' for below-ground resource capture by plants is between exploring large areas of surface soil with lateral roots, and focusing on the capture of deep resources through a predominantly vertical orientation of roots. Mixed strategies are also possible, of course. Knapp (1973), Schulze (1983) and Breman and Kessler (1995) reviewed data on life histories and shoot–root allocation across ecological zones. Along a gradient from arid to humid climates, a number of shifts occur. The most arid environments are dominated by opportunistic, short-lived herbs with high shoot : root ratios that avoid drought conditions by setting seed early. Perennial strategies in extreme desert conditions are possible only for plants that hardly protrude above the ground (e.g. 'living stones'). Extreme differences in shoot–root allocation strategies can thus occur close together geographically, depending on the intervals between rainfall events (which are critical to perennials) and intensity of rainfall (which are especially relevant to the annuals that need to complete their life cycle on the water provided by a single rainfall event).

With slightly higher rainfall, dominance of the opportunistic herbs can be replaced by dominance of persistent perennial species that have drought-tolerance mechanisms and generally low shoot : root ratios. In many (semi)arid environments, the perennial strategy is only successful when deep roots can access below-ground water stores harvested from a substantial area or derived from long-distance subsurface flows. In such cases, plant establishment may depend on relatively wet episodes in the climatic cycle, which allow some of the roots to reach these deep resources. With increasing rainfall, the relevance of the 'lateral' strategy increases in the 'parklands' of the savannah zone. In this zone, a low tree density above ground is supported by a near-complete exploration of the topsoil by tree roots, which may extend to a distance of 50 m around a tree's stem. With a further increase in rainfall, an overall increase in shoot : root ratio is possible, and this is reflected both in an obvious increase in tree density and in increases in tree size, which occur to cope with the increased competition for light.

Shoot : root ratios are successively higher in savannah systems, tropical deciduous forests and lowland rainforests, increasing in each as the associated water supply increases. However, exceptionally deep-rooted trees in the humid tropics do occur and may be able to benefit from the light intensities of the 'dry' or 'bright' season for new leaf expansion (van Schaik *et al.*, 1993; Nepstad *et al.*, 1994; Wright, 1996). Where humidity is sufficiently high and the forest vegetation sufficiently dense, the herb layer is essentially replaced by an epiphyte layer inside the tree canopy (Holbrook and Putz, 1996). As these epiphytes have no access to the soil (which could be used as a buffer against temporary droughts), they may either 'avoid droughts' by physiologically shutting down between rainfall events, or by investing in large root systems, thus replicating the 'choice' in strategies obvious in the desert margin. In the rainforest zone, water availability may allow roots to focus on the surface layers, where most nutrients are available. In fact, on nutrient-poor soils (where plants resorb most nutrients from their leaves before litterfall, and thus where 'litter quality' is low and decomposition slow) a substantial part of the root system may be found in the 'root mats' within the surface layer, on top of the mineral soil. Buttress and stilt roots emerge above the soil surface to provide stability to the tall trees, as opportunities for the growth of taproots, and thus for below-ground anchorage, are limited. Under such circumstances, nutrient cycling can occur without the involvement of the mineral soil with its strong chemical (Al and Fe) sinks for P (Tiessen *et al.*, 1993). Where litterfall is the major nutrient resource, above-ground deposits of litter in stem forks become an asset (Nadkarni, 1981). De Foresta and Kahn (1984) and Sanford (1987) described tree roots creeping up the trunks of their neighbours to benefit from above-ground litter deposits in Amazonian forests.

A recurrent theme in this tour of the world's biomes is the importance of seasonality, in the relative advantage of perennial versus short-lived strategies (with ample opportunity for coexistence in transition zones) and also in the shifts between lateral and vertical emphasis in root exploration. Within the life cycle of plants, a 'choice' must be made between the opportunistic strategies of fine roots (diebacks in unfavourable periods followed by regrowth when growth-limiting resources reappear) and root maintenance during periods of low activity.

In the past, agriculture was guided by the principle 'the more roots the better the crop growth'. However, evidence provided by simple agricultural systems points towards this being an overstatement (van Noordwijk and de Willigen, 1987; van Noordwijk *et al.*, 1996), indicating that the highest level of crop production may be obtained in systems with relatively small root systems, which (even in terms of absolute size) are smaller than the root systems produced with a suboptimal water and nutrient supply. Selection pressure for high yields under monoculture may thus result in lower allocation to roots, although there is little evidence to date that such an effect is associated with high yielding cultivars of any of the major food crops. In intercropping situations, however, having a more extensive root system is valuable to the component species, as such extensive root systems increase competitive strength, even if they have limited benefits for system-level productivity. Models such as HyPAR (Mobbs *et al.*, 2001) and WaNuLCAS (van Noordwijk and Lusiana, 1999) can evaluate both total water and nitrogen capture by combined root systems and the way these resources will be shared between the different plants (see Chapters 9 and 10). The 'functionality' of increased allocation of energy (or carbohydrate) resources to roots can thus be evaluated more quantitatively. It may well be that the 'functional equilibrium' response of plants has stronger 'functionality' for a plant when it grows in a multispecies situation, rather than in a monoculture.

When applying the 'functional equilibrium' concept in models (see below) it becomes evident that, in most situations (except in the case of small plants), increasing root length will be too slow a response to allow a meaningful immediate reduction of current stress conditions. This implies one of two things: (i) either the plant must rely on 'early-warning' indicators, rather than on the onset of stress, to signal that allocation should be modified (with all the usual uncertainty of what 'early-warning' signals actually mean in a fluctuating environment); or (ii) that the plant's response is only 'adaptive' when multiple stress/recovery cycles are involved.

Experiments with trees beyond the seedling stage have provided mixed (neutral or positive) results for the 'functional equilibrium' hypothesis. Joslin *et al.* (2000) compared 'normal' plots in a mixed deciduous forest at ambient rainfall with treatments where throughfall was diverted, so creating treatments with zero and two times the ambient throughfall. They found little change in net fine root production or standing root biomass, but there was some indication that both production and decay of fine roots in the wet treatment were higher than in the other treatments.

Seasonal drought in tropical moist forest may be the cue for fine root death and turnover. It may also trigger root growth in deeper layers, to access subsurface water and/or nutrients. Yavitt and Wright (2001) examined these possibilities by measuring fine root (<2 mm diameter) biomass and the timing of root growth and decay in an old-growth tropical moist forest on Barro Colorado Island (Republic of Panama) in the fifth year of a dry-season-irrigation experiment. Mean fine root biomass (at a soil depth of between 0 cm and 30 cm) was 3.7 Mg/ha within the control plot, versus 2.9 Mg/ha within irrigated plots. The direction of this change is in line with the functional equilibrium theory, but may be related to a faster rate of decay rather than to decreased allocation to new root growth. Average root longevity was estimated to be 1.14 years in the control and 0.82 years under irrigation.

The functional equilibrium hypothesis implies that (relative and potentially absolute) allocation to roots under non-stressed conditions is less than maximum. This implies that the energy/carbohydrate costs of root growth and maintenance constitute a substantial part of the overall carbon economy of the plant.

5.2.2 The carbon economy of the plant

The carbohydrate costs of developing and maintaining root systems are certainly not negligible (Buwalda, 1993). Therefore, an adequate representation of the amounts of photosynthate used in the growth, maintenance and uptake activity of roots is an essential part of accounting for the difference between 'gross' and 'net' photosynthesis, the former representing CO_2 entering stomata, the second the increase in above-ground biomass. The way below-ground respiration (CO_2 release) is partitioned over growth, maintenance, uptake and rhizosphere respiration is still subject of debate. It is difficult to draw a distinct line between roots and their co-habitants in the soil (Fig. 5.3), because sloughed-off root cap cells maintain metabolic activity while detached from the plant, mycorrhizas provide a continuum from plant to fungal tissue, and cell walls leak soluble carbohydrates. Therefore, no simple operational definition of the root–rhizosphere boundary exists that allows unequivocal measurements of the respective respirational activities.

New methods for separating the root from the rhizosphere component of total respiration make use of 'reporter genes', which indicate the specific activity of rhizosphere bacteria. So, further progress can be expected in this research area (Killham and Yeomans, 2001).

Jackson *et al.* (1997) estimated that as much as 33% of the global annual net primary production (NPP) is used for fine root production. Changes in the production and turnover of roots in forests and grasslands, in response to rising CO_2 concentrations, elevated temperatures, or altered precipitation or nitrogen deposition, could be key links between plant responses and longer-term changes in soil organic matter and ecosystem carbon balance (Norby and Jackson, 2000). The potential relevance this has for the global change debate has triggered substantial new research efforts to quantify root turnover (Vogt *et al.*, 1998; Gill and Jackson, 2000). The results of experiments in which the CO_2 and/or the temperature around the shoot were increased have not been easy to interpret, as the short-term physiological response of plants tends to be overtaken by longer-term plant coordination effects and limitations of resource supply. A clear difference can be expected (van Noordwijk *et al.*, 1998b) between situations in which water is the limiting below-ground resource and situations in which nutrients are the limiting factor. Increased CO_2 concentrations allow for a change in the physiological water use efficiency (amount of water lost in transpiration

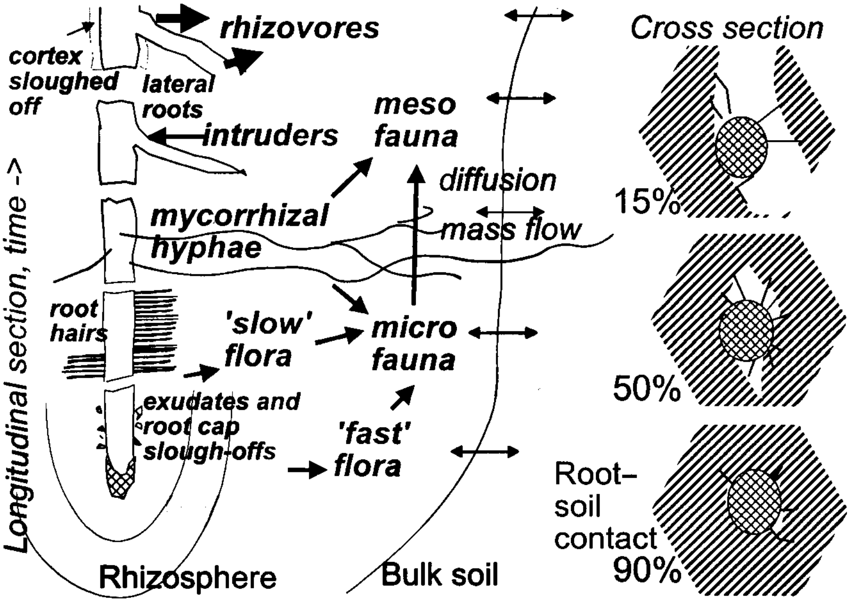

Fig. 5.3. Schematic view of events during the life of a single root axis (based on Clarholm, 1985, and Dhillion and Zak, 1993) (left-hand side of the figure), and a cross section (right-hand side) highlighting the range of root–soil contact situations that is likely to exist in structured soils (van Noordwijk *et al.*, 1993).

per unit CO_2 absorbed), and thus allow higher plant growth rates to occur without a change in shoot/root allocation in instances where water is the limiting resource. Where nutrient supply is limiting, higher growth rates under elevated CO_2 will lead to (or increase) nutrient stress, and we can expect the allocation of carbohydrates to roots to increase (Pritchard and Rogers, 2000; Woodward and Osborne, 2000). In many tropical soils, P supply will probably remain the dominant limitation, in which case increased root allocation may be expected.

5.2.3 Optimum root longevity?

Costs and benefits of root turnover can be viewed from the perspective of a plant's carbon or energy balance, i.e. how much energy is needed to maintain roots in periods of low root activity (e.g. when the soil layer around the roots has dried out), compared with the energy costs entailed in making new fine roots as soon as conditions favour uptake again (Pritchard and Rogers, 2000)? Van Noordwijk *et al.* (1998b) calculated that for a growth respiration rate of 2 g CH_2O/g root tissue and a maintenance respiration rate of 0.03 g CH_2O/g root tissue per day, the break-even point (where maintaining roots in dry soil is as costly as letting them die and replacing them with new ones when conditions become favourable) would be about 60 days. Maintaining and rapidly revitalizing existing roots may give a competitive edge over plants that have to re-establish their fine root systems from main axes; so, we may assume that this 60-day estimate is low. Eissenstat *et al.* (2000) reviewed data on maintenance respiration in tree roots and found a value of 0.03 g CH_2O/g root tissue per day at 23.5°C for sugar-maple roots with a root N concentration of 1.5%. Roots with a 0.6% N concentration were found to respire at only 20% of this rate, whereas roots with up to 4% N were found to respire at four times the rate of roots with a 1.5% N concentration (probably due to a higher protein content). If the growth respiration rate were to be the same for these different types of roots, it would suggest that the break-even points occur at 300 days for roots containing low N concentrations (0.6%) and 15 days for roots containing 4% N. Maintenance respiration data given in the literature on this subject are, however, variable. Recently, Rasse *et al.* (2001) quoted values for fine and coarse tree roots of only 0.0006 and 0.0002 g CH_2O/g root tissue per day for, respectively, beech (*Fagus sylvatica*) and Scots pine (*Pinus sylvestris*) trees. These values would suggest much longer root lifespans at the break-even point than the examples discussed earlier.

5.2.4 Local response

Van Noordwijk *et al.* (1996) discussed the way plant roots respond to nutrient-enriched zones in the soil by enhancing local branch root development. This 'local response' is intricately linked with the nutrient and carbohydrate supply in the plant as a whole, and disappears if the plant as a whole is already well stocked with the nutrient locally available. Such branch root development is thus not just a response to local conditions, and can be understood in terms of competition between root meristems for carbohydrates and nutrients (either from external or internal sources).

The local response thus reflects coordination at the level of the root systems as a whole, rather than simply a mechanistic response to local conditions. Direct influences of local soil conditions on root growth do occur, however, as too much moisture may cause aeration problems, whereas too little may cause increased mechanical impedance and thus difficulties in terms of roots penetrating soil layers. Plants may differ in the degree to which these 'local responses' are expressed, even if we could make a comparison at equal internal nutrient supply and plant water status. In a study involving both grass and trees, nutrient enrichment of cores with NPK increased grass fine root production but, surprisingly, decreased oak root densities (Cheng and Bledsoe, 2002). A full mechanistic understanding of this differential response is lacking thus far, and simulation models have to rely on (over)simplified representations of these responses.

5.3 Problems and Opportunities for Measuring Root Dynamics

Summary of this section: new perspectives on methods for studying root system dynamics

1. Sequential destructive sampling methods: a lot of research time is still wasted on insufficiently replicated sampling methods that give inconclusive results.
2. Minirhizotron methods: use of improved schemes for analysing the data lead to higher turnover estimates than a previously used method, which used cumulative growth and decay data.
3. Experimental manipulations: root exclosures and modified soil patches (ingrowth cores) can be used to test hypotheses on root–root interactions.

Despite all the efforts made, commonly used methods for estimating root turnover can lead to biased results (systematic errors), uncertainty and wide confidence intervals. This is true both for those methods based on sequential sampling and for those based on repeated observations of individual roots using minirhizotrons (Vogt *et al.*, 1998). Good introductions to the various root research methods discussed here can be found in Bengough *et al.* (2000), for sampling strategies; Oliveira *et al.* (2000), for auger sampling and ingrowth core methods; Smit *et al.* (2000a), for root observations at transparent interfaces with soil; and Hooker *et al.* (2000) for the measurement and analysis of fine root longevity. Schroth (2003) summarized how these methods can be applied in agroforestry research.

5.3.1 Sequential sampling

The idea underlying sequential sampling is a simple one: if one repeatedly samples root density in the same field or (agro)ecosystem, an increase in the value between two sampling dates indicates root growth whereas a decrease indicates root decay. As it is certainly possible that both an increase and a decrease occur in a given interval, one may expect such a method to give a conservative (under)estimate of root turnover. The method can, however, also overestimate root turnover, as the measurement of root density at any point in time contains 'measurement error' or uncertainty, due to the spatial variability of the roots in soil. In response to this uncertainty (for point estimates), the method has been modified to include a statistical test (normally a *t*-test), which can be used to assess whether a later data set differs 'significantly' from the one before. If the null hypothesis that two samples in a chronological sequence come from the same population is rejected, one records an increase as indicating net growth and a decrease as indicating root decay. However, a study by Singh *et al.* (1984 showed that serious (positive or negative) bias can occur in this method depending on the pattern of root growth and decay, the sampling interval and the number of replicates used. The method is, however, still commonly used without the potential for bias being properly acknowledged.

A simple way to understand the problem associated with this method is to realize that all estimates of root density (except the first and last of the series) are used twice in the estimation of differences and, thus, that the subsequent *t*-tests are not independent of each other. A root density estimate that, by chance, is rather high (i.e. one based on samples taken in areas of high root density) is likely to lead to the possibly erroneous conclusion that root growth occurred in the preceding interval, and root decay occurred in the subsequent interval. Although a restriction of the estimates to the 'statistically significant' differences takes out many of the relatively small differences from the summary of root turnover, it will include most of the large ones, even in the absence of any real change, simply due to the sampling errors. Figure 5.4 gives an example of the problem, which is derived from a spreadsheet calculation (available from the authors on request). The calculation includes sampling errors based on the 'coef-

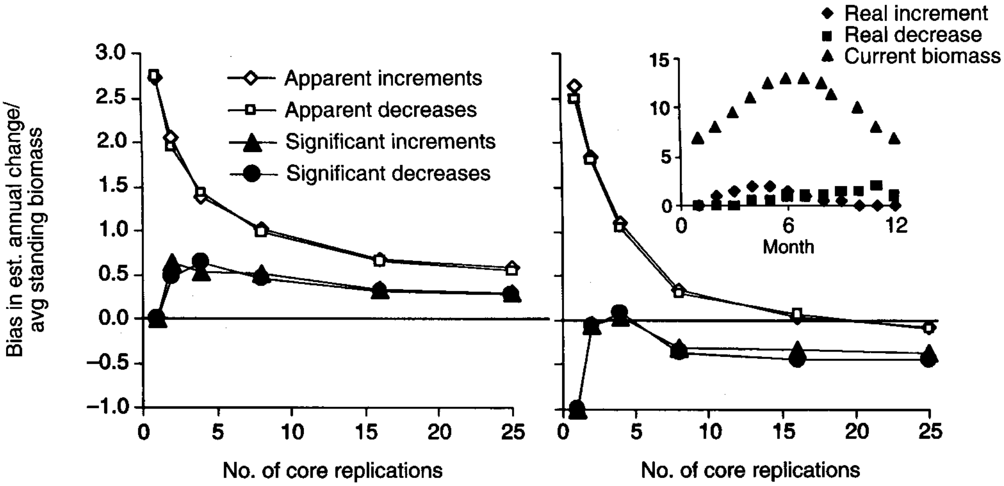

Fig. 5.4. Bias in estimates of annual root turnover based on a simulation of sequential core sampling, as a function of the number of replicate samples at each time interval. Different variants of the method were simulated, including either all apparent increments and decreases, or only those that indicate 'statistically significant' changes (with a *t*-test and 95% confidence limits). Results are shown relative to the average standing biomass, as averages for 25 years of observation using a monthly sampling scheme, and a conservative estimate of the coefficient of variation for individual cores (0.4) was used. On the left-hand side no change in roots was supposed to occur; on the right-hand side an annual turnover of 1 was assumed, along with one period where root growth dominated and one period where decay dominated (see insert for assumption about the root dynamics).

ficients of variation' that normally apply to root-core samples, even in 'homogeneous' vegetation (0.4–1.0; Bengough *et al.*, 2000). For any number of replicates we can, therefore, estimate the sampling error of the mean, and simulate the data collection process using random numbers (assuming a *normal* distribution of the results per sample). Without restricting the increments to those that are 'statistically significant', the bias will be large in studies with a small number of samples, but still substantial in studies where 25 replicates would be used. Restriction to the 'statistically significant' changes still leads to a considerable positive bias (around 40% of average standing biomass) in the absence of change, and a negative bias of similar size in a simulation including a seasonal growth and decay pattern, even when 25 replicates are used. We can conclude that the bias obtained will be substantial when using this method, and that its sign (positive or negative) depends on the actual pattern of growth and decay being estimated. This means that we cannot easily apply a bias correction. Despite all the hard work that would go into such a sampling exercise, the results are likely to be disappointing or, worse, misleading.

Better results can usually be obtained (Schroth, 2003) with a compartment-flow model (Sanantonio and Grace, 1987), which applies estimates of the decay rate of dead roots in order to estimate outflow from the 'dead root' pool, derives the root decay from the difference between expected and measured pool size of dead roots, and then derives root growth from the difference between expected and measured live root pools. The method is obviously sensitive to the way the distinction between 'live' and 'dead' roots is drawn in data collection, the accuracy with which this distinction is made and the appropriateness of the assumption that the root decay rate is constant. Uncertainty in estimates of standing biomass and necromass pools, due to spatial variability and inadequate replication, still influence the turnover estimates derived in this way. Despite this generally acknowledged weakness in the methodology, sequential destructive sampling remains in use and is referred to by many published results. In a recent study in coffee gardens in Costa Rica, Chesney and Nygren (2002) encountered difficulties when applying the compartment-flow model devised by Sanantonio and Grace (1987) to fine root data, because necromass measurements did not match predictions made on the basis of a litterbag root decay constant of 0.00826/day. The main problems affecting their data are, probably, the erratic root biomass values they obtained, which do not fit any model and suggest undersampling of the spatial variation.

5.3.2 Minirhizotrons

Methods based on the repeated observation of individual roots growing in places where they can be observed (using rhizotrons, root observation boxes and minirhizotrons in the field) have become the main point of reference in studies of root dynamics (Hooker *et al.*, 2000; Smit *et al.*, 2000a). Observation techniques vary from tracings to photographic or video imagery. In subsequent analyses of change (using a number of visual criteria for root 'decay') a number of methods have been used, although all are related to the daily probability of survival (Box 5.1). Hooker *et al.* (2000) described methods

Box 5.1. Relationships between root longevity, turnover and daily root survival.

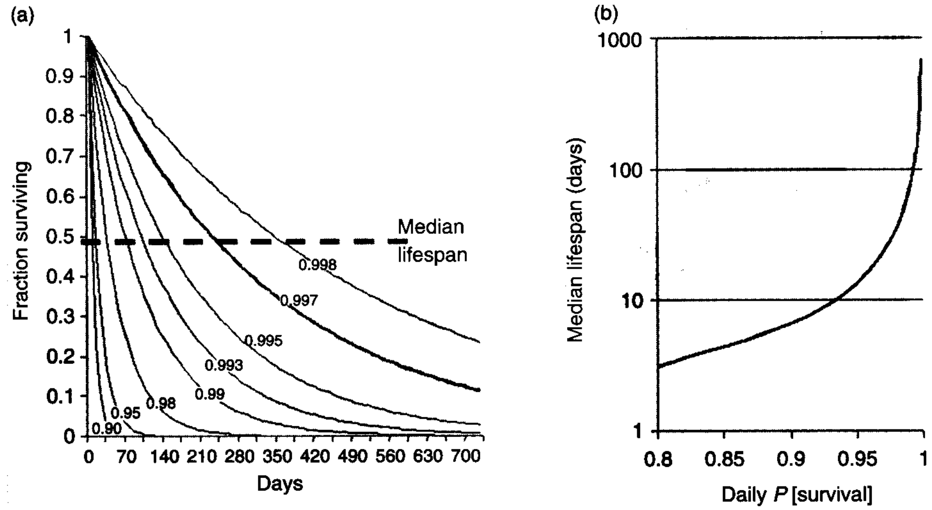

Fig. B5.1. (a) Expected survivorship curves for cohorts of roots with different values for daily probability of survival (*P*[survival]). (b) Relationship between daily probability of root survival and expected median root lifespan.

If p = daily probability of survival for a unit root,
dG/dt = daily growth rate,
G = cumulative amount of newly formed roots,
dD/dt = daily death (decay) rate,
D = cumulative amount of decayed roots,
L = median life span roots (number of days that 50% of the roots survive to) and
S = standing biomass,
then we can derive the following relations for a steady-state population of roots, where dG/dt, dD/dt and p can be approximated as constants.

Continued

Box 5.1. *Continued.*

The relation between half-life time and daily survival probability is:

$$p^L = 0.5, \text{ or } L = \log(0.5)/\log(p) \qquad (1)$$

On any day the following relations must hold for a steady-state system:

$$dG/dt = dD/dt = (1 - p)\, S, \text{ or } S = (dG/dt)/(1 - p) = (dD/dt)/(1 - p) \qquad (2)$$

With these definitions, we can derive the basic turnover rate r as:

$$r = (dD/dt)/S = 1 - p \text{ [per day]} \qquad (3)$$

Where turnover is expressed on a different time scale (e.g. per year), the p value has to be adjusted (e.g. p[survival for 1 year] = p[survival for 1 day]^{365} if p can be assumed to be time-independent).

The root length turnover (RLT) of de Willigen and van Noordwijk (1987) after N days of observation, and for a steady-state population, can be calculated as:

$$\text{RLT} = D_{\text{fin}}/(S_{\text{start}} + G_{\text{fin}}) = N\,p/(S + N\,p) = 1/(1 + S/(N\,p))$$

and thus increases with the length of the observation period N.

The 'root length replacement ratio' (RLRR) of de Willigen and van Noordwijk (1987) is:

$$\text{RLRR} = G_{\text{fin}}/S_{\text{fin}} = G_{\text{fin}}/(S_{\text{start}} + G_{\text{fin}} - D_{\text{fin}}) = 1/(1 + (S_{\text{start}} - D_{\text{fin}})/G_{\text{fin}}) = N\,p/S$$

and also increases with the length of the observation period. So a value of 1 is obtained if all roots present at the start have decayed at the end of the observation period, while all of the new growth remains present.

The daily probability of survival, p, may indeed be the most efficient indicator, as it relates directly to other measures.

based on following the development and fate of individual roots or cohorts of roots first seen at the same observation time. In the practical applications of this method there tends to be a problem, in so far as most cohorts are small. This is especially problematic if one wishes to analyse individual replicate samples to test the significance of certain experimental factors.

Van Noordwijk *et al.* (1993) used a simpler approach based on cumulative root growth and decay patterns, with logistical distributions fitted through both. The time between the date by which 50% of seasonal root growth had occurred (by interpolation) and the date by which 50% of seasonal roots had decayed is used as an indication of 'median root longevity'. Though simpler in its resulting data structure, the latter method may, however, lead to bias and uncertainty in the resulting estimates of root longevity, as shown in a recent analysis (M. van Noordwijk *et al.*, unpublished) and summarized in Fig. 5.5. For the study considered in Fig. 5.5, a number of possible growth curves for roots were used, together with stochastic predictions (p) of root decay, which were based either on a homogeneous probability of decay for any root during a standard interval or on a decay rate that depends on root age.

In the absence of random variation or age effects on root survival, root decay following a single pulse of root growth is correctly described by the method tested. Median lifespan and probability of survival are returned by the procedure without appreciable bias (Fig. 5.5). For exponentially increasing root growth patterns the bias is also very small, but for linear or logistical root growth the median longevity is overestimated by up to 3 weeks, whereas the saturation pattern (initial rapid root growth, at a declining rate) is overestimated by up to 8 weeks. The lower the weekly survival probability, the larger the bias in estimates of p. Whilst the method handled a single-pulse situation adequately, a double-pulse situation is particularly prone to bias, depending on the interval between the two pulses.

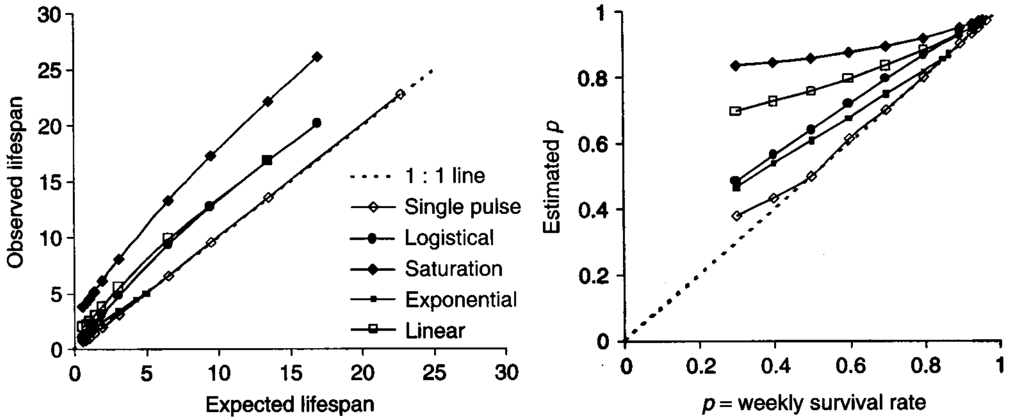

Fig. 5.5. Bias (difference between input parameters used for constructing data sets and output estimates derived from those data sets) in estimates of median lifespan and weekly survival when the data processing method of van Noordwijk *et al.* (1993) is simulated for a range of time patterns of root growth.

A new method (M. van Noordwijk *et al.*, unpublished) was designed for estimating a daily survival rate *p* that is valid regardless of the root growth pattern. In the analysis involved in this new method, the observed cumulative root growth pattern was used as an input. The shape of the cumulative root decay curve was predicted for a range of values of *p*. The method (Fig. 5.6) then includes the selection of the *p* value with the least 'lack of fit', and a test for indications of the time-dependence of *p* (a spreadsheet with the whole procedure preprogrammed is available from the authors). The method yields an estimate of *p* that can be converted to give the time by which 50% of any cohort of roots can be expected to have died, indicated here as 'median longevity' of roots. Of course these estimates primarily refer to the longevity of roots at the observation surface: their relevance for roots growing in undisturbed soil remains a subject of debate.

Tierney and Fahey (2001) compared minirhizotron estimates of fine root longevity and production in the forest floor of a temperate broadleaf forest with observations made using surface windows (without any access tubes or modification of the root environment). Their conclusion, that the two methods gave the same survival rate for fine roots (< 0.1 cm in diameter), is comforting for all minirhizotron studies. Annual fine root production in the northern hardwood forest studied was approximately equal to standing biomass (for a median root longevity of 314 days), and had previously been underestimated using root ingrowth cores.

5.3.3 Other methods and comparisons between methods

5.3.3.1 Ingrowth cores

Qualitative data on the relative patterns of root growth during a year can be obtained by repeatedly inserting fresh 'ingrowth cores' into the soil and measuring the amount of roots that colonize each core. However, the absolute growth rates obtained cannot be directly compared, as it is impossible to avoid disturbance: existing roots will be cut when the core is inserted, and the repacked soil in the ingrowth core will differ in structure from the surrounding soil. Furthermore, ensuring contact between the surrounding soil and an ingrowth core is problematic, however much care one takes.

However, the ingrowth core technique may be most suitable for comparisons between cores that have been deliberately modified. Hairiah *et al.* (1993) exchanged subsoil and topsoil in a study of aluminium tolerance and avoidance by the velvet bean (*Mucuna pruriens*), with and without the

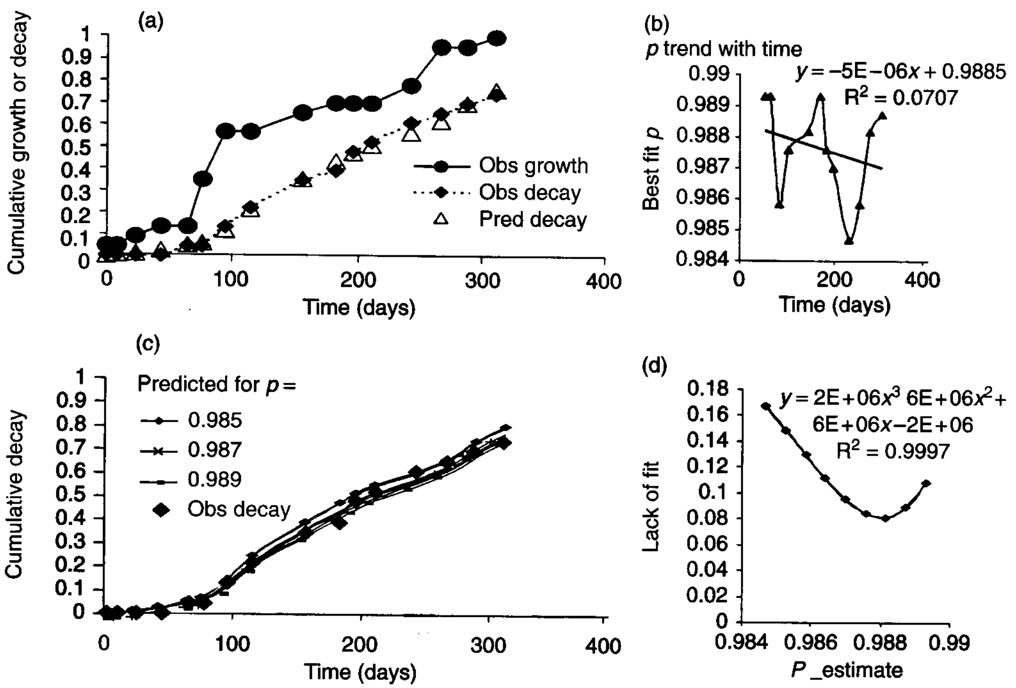

Fig. 5.6. Estimation of the best fitting daily probability of root survival, *p*, on the basis of reconstructed decay curves, given the observed root growth pattern at individual minirhizotrons (a); the procedure includes a check for trends of *p* with time (b), and calculations of the expected decay curve for a range of *p* values, to minimize the lack of fit (c, d).

addition of P to the soil. Williams (2000) compared a number of nutrient additions to ingrowth cores in young rubber plantations in the expectation that the relative 'local response' obtained would help to identify nutrient stress in the tree in a sensitive way. However, due to an exceptionally long dry season, little actual root growth occurred and the results did not confirm that this method can be used.

5.3.3.2 Pulse labelling

Root allocation of carbohydrates can be traced by the use of 'pulse-labelling' techniques, utilizing either the radioactive isotope ^{14}C or the stable isotope ^{13}C (or both). For example, on a highly productive temperate pasture in New Zealand, Saggar and Hedley (2001) used a ^{14}C pulse-labelling technique to measure seasonal changes in the assimilation and partitioning of photoassimilated C in plant, root and soil components of the agroecosystem. Of the net primary production rate of 32.8 Mg of C/ha/year of C, at the end of the year 18.2 Mg were found to have been respired, whereas 6.5 Mg remained in shoot biomass, 6.8 Mg in root biomass and 1.3 Mg in the soil. The half-life of C in the below-ground system (no distinction could be made between C in live roots, the rhizosphere and dead roots) differed between seasons, and was found to be 111 days for autumn roots, 64 days for spring roots and intermediate for the other seasons.

From a pulse-labelling experiment conducted on basket willow (*Salix viminalis*), de Neergaard *et al.* (2002) concluded that 41% of the ^{14}C recovered had been allocated to below-ground pools. Roughly 20% had been allocated to root biomass after 5 months (although this had peaked at 25% after 3 months). A further 9% was accounted for by root + soil respiration (mostly in the first month), 2% by microbial biomass and 10% (gradually increasing) by soil organic matter pools. Up to 13% of the carbon in the microbial biomass pool had apparently been assimilated by the willows in the preceding 4 weeks.

5.3.3.3 *Root litterbag incubation studies to look at root decay*

Root decay can be measured using the general approach of the 'litterbag' method for studying the decay of above-ground litter (van Noordwijk, 1993). However, the method is not as straightforward for root decay as it is for above-ground litter, as:

- roots decay when in close contact with the soil. So, separating them from soil to obtain their initial weight and then repacking them in pre-sieved (rootless) soil may lead to biased results, even if care is taken to let the soil's temperature and soil water content fluctuate in line with the surrounding soil;
- unlike above-ground litter, decaying roots cannot be intercepted at the time of 'litterfall', so the initial stages of decay are more difficult to capture. If one begins with samples from the pool of dead roots in the soil, results may be biased towards the more recalcitrant fractions.

The practical aspects of this technique and the results obtained have been discussed by Henrot *et al.* (1996). Van Noordwijk *et al.* (1998a) compared the decay of above- and below-ground inputs for four hedgerow species and found root decay to be slower than that of above-ground litter in all species. However, the relative ranking of these species in terms of root decay did not match that found for above-ground litter decay.

5.3.3.4 *Comparisons of methods*

Hertel and Leuschner (2002) compared four methods for estimating fine root production in a *Fagus–Quercus* mixed forest. They found differences of more than an order of magnitude between the four methods. Fine root production estimates derived by sequential coring in conjunction with compartmental-flow calculations were larger than those derived from sequential coring with maximum–minimum calculation of root production. Estimates obtained using either method were larger than those derived using the ingrowth core method and a recently developed root-chamber method for individual fine roots. A C-budget model for the site implied that 27% of net carbon gain was allocated below-ground, with a fine root production that was closest to (though 20% lower than) results for the sequential coring technique with the maximum–minimum method of calculation.

5.4 Empirical Data on Root Growth and Decay

Gill and Jackson (2000) compiled and analysed a global data set of 190 studies on root turnover estimates across climatic gradients and vegetation types, based on sequential root biomass estimates. The data refer to various methods and conditions, and a substantial scatter is thus to be expected. Root turnover was, for this overview, defined as annual root production divided by the maximum standing root biomass and thus was expressed on a per-year basis. Root turnover estimates increased exponentially with mean annual temperature, in the cases of: (i) fine roots in grasslands and forests; and (ii) total root biomass in shrublands – though for each vegetation type a large share of the variation observed remains unexplained. The Q_{10} value (the increase in process rate for a 10°C increase in temperature) for root turnover was 1.4 for fine roots (< 5 mm diameter) in forests, 1.6 for fine roots in grasslands and 1.9 for shrublands. After adjusting for the temperatures of the sites, there was no statistically significant relationship between turnover and precipitation. The slowest average turnover rates in the Gill and Jackson (2000) data set were found to occur in the whole tree root systems (0.10/year), followed by shrubland total root systems (0.34/year), and fine root systems in grasslands, wetlands or forest (all within the narrow range of 0.53–0.56/year). For tropical versions of these vegetation types, fine root turnover was typically 0.6–0.9/year. Data for forests show a strong relationship between root diameter and turnover, with average turnover being 1.2/year in roots of diameter 0–1 mm, 0.52/year in roots of diameter 0–5 mm, and turnover decreasing to 0.1/year for roots in the 0–10 mm diameter class (note that all of these classes may be indicated as 'fine tree roots' in various studies).

Root longevity can be positively correlated with mycorrhizal colonization and tissue density, and negatively related to nitrogen concentration, root maintenance respiration and specific root length (Eissenstat *et al.*, 2000). Hooker *et al.* (1995), however, reported that mycorrhizal roots live less long than non-mycorrhizal roots. Branched root axes, even if they have a small diameter, tend to live longer than unbranched axes of the same diameter (literature reviewed in Eissenstat *et al.*, 2000). Pritchard and Rogers (2000) reviewed published data on root longevity observed using the minirhizotron technique. For annual crops in the temperate zone, the values published range from 130 days (or virtually the whole lifespan of the crop) for leeks, winter wheat and sugar beet, to 24 days for groundnut and grain sorghum. For herbaceous perennials (i.e. lucerne and sugarcane), published values of mean root lifespan range from 14 to 131 days. Among fruit trees, apple roots (which have a relatively small diameter, a low tissue density and exhibit little lignification of the exodermis) have much shorter lifespans (50% of new fine roots may die within 2 weeks of being formed) than the roots of citrus (50% survive for about 300 days), the latter exhibiting completely opposite physical traits (Eissenstat *et al.*, 2000).

A comparative study has also been made of pine (*Pinus resinosa*) and poplar (*Populus tristis* × *P. balsamifera*). The median longevity of fine pine roots (with a specific root length of 16 m/g, and a standing fine root biomass of 0.62 Mg/ha) was found to be 291 days, as compared with 149 days for poplar roots (with a specific root length of 57 m/g, and a standing fine root biomass of 0.36 Mg/ha; Coleman *et al.*, 2000). Where pine had half the average total root length per unit area, it maintained more root biomass; associated net CO_2 efflux into the soil was also slightly higher. Munoz and Beer (2001) measured fine root biomass (less than or equal to 2 mm) and productivity over 1 year in 16-year-old plantations of cacao (*Theobroma cacao*), shaded by 15-year-old *Erythrina poeppigiana* or *Cordia alliodora* and planted on a deep alluvial soil in Turrialba, Costa Rica. A fine root biomass of approximately 1.0 Mg/ha varied little during the year, giving (at the beginning of the rainy season) maximum values of 1.85 Mg/ha in the cacao–*C. alliodora* system and 1.20 Mg/ha in the cacao–*E. poeppigiana* system. Annual fine root turnover was close to 1.0 in both systems. Fine root production by both *C. alliodora* and *E. poeppigiana* (maximum of 205 and 120 kg/ha per 4-week period, respectively) was greatest at the end of the rainy season, whereas that of cacao was greatest at the beginning of the rainy season (34–68 kg/ha per 4-week period).

Some results obtained from minirhizotron studies in agroforestry experiments in Indonesia are summarized in Tables 5.1–5.3. The first data set was obtained in three long-term cropping system trials in Lampung (Hairiah *et al.*, 2000c; Table 5.1). The shortest fine root lifespans and highest daily turnover rates (1 – daily survival probability) were found to occur in the leguminous cover crop *M. pruriens*, followed by groundnut and maize. The median longevities of all three species were between 18 and 25 days, whilst all three had a turnover rate of about 5%/day. The various trees studied had median fine root longevities of about 100 days and turnover rates of about 1%/day. The longevity and turnover rate of the perennial grass *Imperata cylindrica* fell between those of the annual crops and trees in these experiments.

Using the same methodology, two experiments (in Jambi province, Sumatra) on the early phases of rubber agroforestry systems were also compared (Tables 5.2 and 5.3). The first experiment yielded a daily turnover of around 0.5% and a median lifespan of 290 days. Neither weeding intensity nor position with respect to the tree had any statistically significant influence on these esti-

Table 5.1. Root dynamics as observed using minirhizotrons at the Biological Management of Soil Fertility (BMSF) site in North Lampung, Sumatra, Indonesia, in cropping system trials during the period 1996–1999. Data from six minirhizotrons per species, with daily survival rate and median lifespan (age expected to be reached by 50% of each cohort of roots) evaluated for individual replicates.

Plant species	Remarks	Daily survival probability†	Median lifespan (days)	Daily turnover (%)
Gliricidia sepium	Regularly pruned in alley cropping	0.9904^{a}	116.8^{a}	0.96
Peltophorum dasyrrachis	Regularly pruned in alley cropping	0.9877^{a}	121.1^{a}	1.23
Flemingia congesta	Regularly pruned in alley cropping	0.9916^{a}	$96.1^{a,b}$	0.84
Zea mays (maize)*	In alleys or as monocrop	0.9435^{c}	25.2^{c}	5.65
Arachis hypogaea (groundnut)	In alleys or as monocrop	$0.9547^{b,c}$	20.4^{c}	4.53
Mucuna pruriens var. *utilis*	As cover crop in rotational system	$0.9534^{b,c}$	17.7^{c}	4.66
Oryza sativa (upland rice)	In alleys or as monocrop	$0.9614^{b,c}$	33.8^{c}	3.86
Imperata cylindrica	As weed on fallow land	$0.9844^{a,b}$	$55.2^{b,c}$	1.56
Grand mean		0.9679	59.8	
Probability		$P = 0.005$	$P < 0.001$	
Standard error of difference between means		0.0188	30.1	

†Means in one column labelled with the same letter are not significantly different at the 5% level.

*A separate test confirmed that maize root dynamics were not significantly different when maize was alley cropped (between three different species of hedgerow trees), intercropped with cassava or planted as a monocrop.

Table 5.2. Root dynamics as observed using minirhizotrons in a rubber (*Hevea brasiliensis*) agroforestry experiment in Rantaupandan, Jambi, Indonesia (Williams, 2000), during 1997 and 1998, with weeding intensity as the main experimental factor and the distance from the tree as the sampling position. Data from four minirhizotrons per sampling position and weeding intensity combination, with daily survival rate and median lifespan evaluated for individual replicates.

Experimental factor/sampling position	Daily survival probability	Median lifespan (days)	Daily turnover (%)
'High' weeding intensity	0.9960	241	0.40
'Low' weeding intensity	0.9955	344	0.45
Within tree row (0.25 m from tree)	0.9953	328	0.47
Between tree rows (1.5 m from tree)	0.9962	257	0.38
Grand mean	0.9958	293	
Probability	NS	NS	
Standard error of difference between means	0.00248	95.2	

NS, not significant.

Table 5.3. Root dynamics as observed using minirhizotron in a rubber (*Hevea brasiliensis*) agroforestry experiment in Sepunggur, Jambi, Indonesia, during 1997 and 1998, with two types of planting material (grafted clones of PB260 and GT1-derived seedlings) and fertilizer level (none, and recommended levels of N + P) as the main experimental factors and the distance from the tree as the sampling position. Data from two minirhizotrons per sampling position, planting material and fertilizer level combination, with daily survival rate and median lifespan evaluated for individual replicates.

Experimental factor/sampling position	Daily survival probability	Median lifespan (days)	Daily turnover (%)
PB260	0.9889	106	1.11
GT1	0.9861	71	1.39
Within tree row (0.25 m from tree)	0.9884	110	1.16
Between tree rows (1.5 m from tree)	0.9866	68	1.34
Grand mean	0.9875	89	
Probability	NS	NS	
Standard error of difference between means	0.00335	21.3	

NS, not significant.

mates. However, with regard to the median longevity, the standard error of the difference between means was about one-third of the mean, so the discriminatory power of the experiment was not very high with regard to such treatment effects.

In a second rubber experiment undertaken in the same province during the same time period, however, daily turnover was substantially higher at 1.2%, while the median lifespan was only 90 days. Again, no effects could be identified as having been caused by experimental factors (planting material or sample position). The difference between the two experiments, however, is remarkable. No solid explanation for this difference has yet been identified.

Overall, the relatively high variability between replicate minirhizotrons and the resultant low discriminating power of tests on treatment effects may provide a lesson for future research. That is, only large differences (such as those occurring between annual crops and trees) can be identified. For most situations, an 'order of magnitude' estimate, rather than a site- and management-specific value, is all that can be made using the methods currently available. So far, the simple model discussed above, containing a constant daily probability of survival for roots, appears to be consistent with the data, at least in the humid tropical environment in which the data for Tables 5.1–5.3 were collected.

5.4.1 Root turnover and consequences for uptake

In theory, rapid root turnover is beneficial because new roots produced in unexploited soil replace roots previously surrounded by depletion zones. By investigating the influence of P supply on total root production and root mortality during the barley growing season, Steingrobe *et al.* (2001) assessed the benefits of a more rapid root turnover on P acquisition. They found that shoot development and grain yield were reduced in a '−P' treatment. However, the standing root system in that treatment was nearly the same size as that in a '+P' treatment, and root production and turnover were greater. Through model calculations, the authors have shown that root renewal by continuous growth and mortality can contribute to P uptake efficiency. The physiological mechanism behind the higher root turnover is not yet clear, however. For a discussion of the long-term benefits of root foraging in heterogeneous environments, where patch depletion and root turnover may limit the long-term rewards of root foraging to perennial plants, see Fransen and de Kroon (2001).

5.5 Model Representations of Root Dynamics

Simulation models can treat below-ground resource capture at different levels of sophistication (Fig. 5.7; van Noordwijk and de Willigen, 1987):

0. Models that use empirical resource capture efficiency coefficients to represent the relationship between water and nutrient supply in the soil and the dynamics of plant growth (sometimes known as models *'without roots'*).

1. Models that differentiate between soil layers and use empirical data on relative root distribution to predict resource capture potential in each zone. Root distribution can be schematized via an exponential decrease with depth (Jackson *et al.*, 1996) or its two-dimensional elliptical variant (van Noordwijk *et al.*, 1995). Root length density can also be given as an 'independent' parameter for each layer or zone, and change of root length densities with time can be imposed on the basis of crop age.

2. Models that consider plants as organisms that have the capacity to adjust both the total amount of their roots (to complement the internal balance between above- and below-ground resource capture), and the location of new root growth (to ensure the growth of those parts of their root system with the best opportunities to take up the resource most limiting overall plant growth).

Models at level 0 have been successfully applied to many crop monocultures, and are the basis of Kho's approach to tree–crop interactions (Chapter 1, this volume). However, such models cannot give an account of below-ground interactions between plants at the process level. In the same way that *'pedotransfer'* functions (Chapter 9, this volume) allow estimates of quantitative soil parameters to be made on the basis of simple indicators (such as soil texture), we may need *'rhizotransfer'* functions that allow reasonable estimates to be made of the main root parameters without too much new data collection. The global data sets on root distribution (Jackson *et al.*, 1996; Chapter 4) and root turnover (see

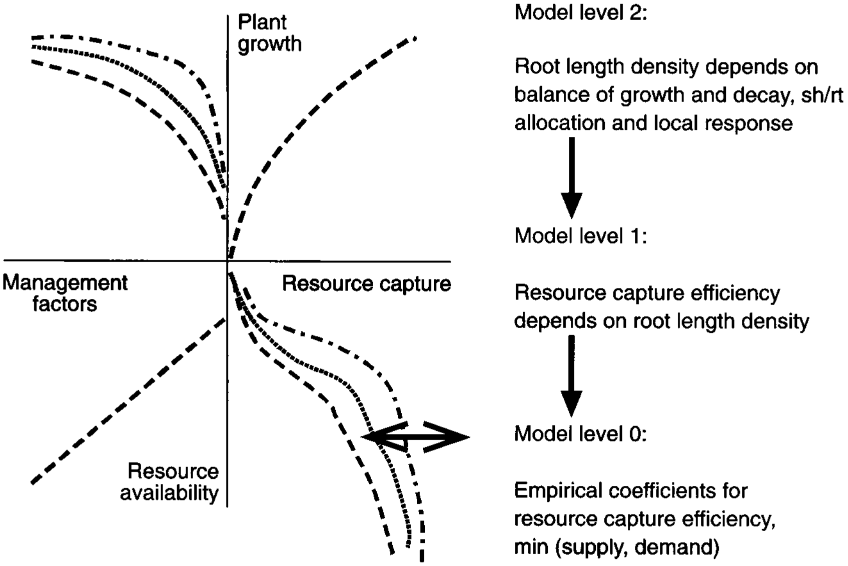

Fig. 5.7. Schematic representation of the relations between management factors, resource availability, resource capture (showing three different situations with different lines) and plant growth; three 'levels' for modelling resource capture are indicated; sh/rt = shoot/root (after van Noordwijk and de Willigen, 1987).

quotes above) form a starting point for this, but further work is needed.

Temporal development of the distribution of roots in the soil is important for the functioning of a root system, especially in models that use root length density distribution, rather than presence/absence of roots, as the basis for the predictions they make (de Willigen *et al.*, 2000). One way to describe root proliferation is to consider it as a process of diffusion with a first-order sink term (equivalent to a time-independent, daily probability of root survival) accounting for decay. De Willigen *et al.* (2002) derived analytical solutions for the two-dimensional diffusion of roots in both a rectangular area and a cylindrical volume. Root dry matter enters the soil domain at the plant base at a particular location on the soil's surface. The distribution patterns obtained strongly depend on the ratio of the diffusion coefficients in both horizontal and vertical directions. When dry matter permeates evenly across the complete surface (an approximation of what occurs in a relatively closely spaced crop), a steady state eventually results in which root length density decreases exponentially with depth, as is often found in experiments and natural vegetation (Jackson *et al.*, 1997).

The TRAP model (Rasse *et al.*, 2001) for 'Tree Root Allocation of Photosynthates' was developed to predict the partitioning of photosynthates between the fine and coarse root systems of trees in a series of soil layers. TRAP simulates root system responses to soil stress factors affecting root growth, such as temperature, soil penetrability, aeration and soil acidity. Validation data have been obtained from two Belgian experimental forests, one mostly composed of beech (*Fagus sylvatica*) and the other of Scots pine (*Pinus sylvestris*). TRAP accurately predicted ($R = 0.88$) night-time CO_2 fluxes from the beech forest for a 3-year period. It also predicted total fine root biomass to within 6% of the measured values. Fine root turnover was predicted to be 2.1 Mg C/ha/year, with an annual root turnover of 1.0 for fine roots and 0.02 for coarse roots. The TRAP model focuses on the C balance of the tree, however, and does not include the effects of root growth and decay on the uptake of water and nutrients.

Both the HyPAR model (Mobbs *et al.*, 2001) and WaNuLCAS (van Noordwijk and Lusiana, 1999) can predict competition for water and nutrients between trees and crops (or other plants) at level 1 (see above). WaNuLCAS can also be used at level 2, although, when so doing, spatial root distribution is restricted to the exponential-decrease-with-depth or elliptical distributions (the parameters of which are treated as dynamic).

If nutrient (N or P) or water stress occurs, the relative allocation of growth reserves to roots can increase quickly, from say 10% to 90% of the daily used reserves. Allocation of growth reserves to roots can increase under mild stress, but usually the 'functional response' comes too late and is too slow to 'head off' the stress. Under nutrient or water stress, the acquisition of new reserves by the plant will be limited. So, under such stresses, absolute allocation to roots may only temporarily be higher than it is under a no-stress scenario. For a plant, the key strategy is to use 'early warning' signals (such as 'drought-signal hormones') and respond before the stress becomes serious. Quantitative indicators of stress that are not yet affecting current plant production take the place of these hormones in the models.

'Local response' is simulated in WaNuLCAS by a gradual change in the parameters of the elliptical root distribution, and is constrained by the total length of new roots that can be produced with the carbohydrates allocated. The intensity of change depends on both a 'responsiveness' parameter and the degree to which effective uptake per unit root length of the currently limiting resource differs between soil layers and zones. If roots in deeper layers are more effective (e.g. in the case of water stress), root distribution can shift to a configuration that involves a more gradual decrease of root length density with depth, or perhaps even to a configuration where root length density increases with depth.

If roots in the topsoil are more effective (e.g. when P uptake is the factor most limiting to plant growth and the topsoil has a sufficiently high water content to keep the P mobile), roots will expand (mainly) in the topsoil. The example given in Box 5.2 shows that rainfall distribution (when the cumulative rainfall is constant) can lead to substantial shifts in predicted root distribution, depending on the predicted re-wetting pattern of the soil. Under frequent but small amounts of rainfall, the model predicts that roots will accumulate in the topsoil, whereas less frequent, heavier rainfall events (which wet the entire soil profile) are predicted to induce deeper rooting. It also shows that, though the 'functional response' of increased root allocation may be limited in a monoculture (where it does not increase total resource capture), it can reduce the negative effects of competition and as such be 'functional' in a competitive situation. Most 'functional equilibrium' studies have, thus far,

Box 5.2. WaNuLCAS exploration of tree functional and local response.

A series of simulations was made for a moderately deep soil (1 m) with an annual rainfall of 1000 mm. Rainfall patterns ranged from '1 = every day 3 mm of rain' and '2 = every second day 6 mm', to '6 = every 32 days 96 mm'. As the potential evapotranspiration was assumed to be 4 mm/day, this environment would not provide enough water to avoid water stress, even if all rainfall were to be fully used. The rainfall patterns lead to situations of permanent moderate stress (rainfall pattern 1), alternations of sufficient water and severe water shortage (rainfall patterns 5 and 6) or intermediate patterns. In the overall water balance, with a decrease in the number of rainy days (through patterns 1 to 6), a decrease in the values for the interception and soil evaporation terms can be noted, while the contribution to ground water (deep infiltration) and runoff increases but remains small in absolute value. Cumulative tree water use tends to increase through rainfall patterns 1 to 6. If a grass sward is added to the simulations, canopy interception increases and thus the amount of soil water available to either tree or grass is reduced. The grass water use is predicted to benefit more from rainfall patterns 5 and 6 than the tree, causing a bell-shaped response curve for the tree.

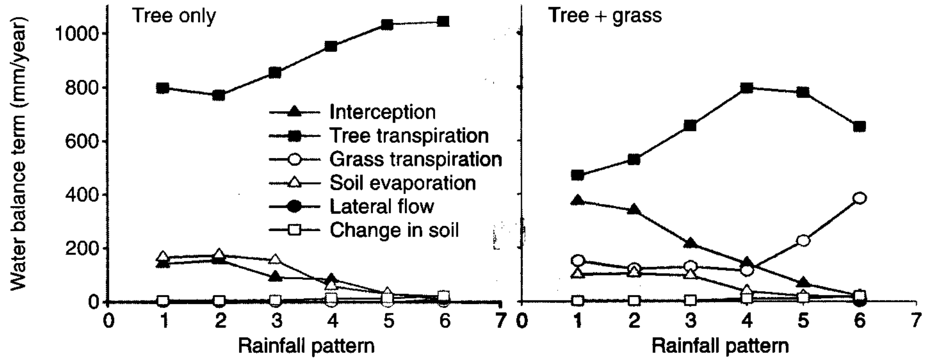

Fig. B5.2. Water balance for a range of WaNuLCAS simulations, in the absence of functional or local response of the tree, with and without a grass sward.

A sensitivity analysis was carried out on the two key parameters for the functional shoot/root balance and root distribution: 'Root_Allocation_Responsiveness' and 'local response'. Higher values of 'Root_Allocation_Responsiveness' lead to a more rapid shift of current growth resources to roots, at the expense of shoot growth, when the total uptake of water and/or nutrients falls short of current 'demand'. With increasing 'local response', root distribution shifts towards the soil layer and spatial zone in which roots are most successful (per unit root length) in taking up the most limiting resource. For both parameters, values of zero indicate no response, and values above 1 indicate a response that is more than proportional to the strength of the 'signal' (relative degree of below-ground stress for the Root_Allocation_Reponsiveness, and difference in actual uptake per unit root length for the 'local response', respectively).

Continued

Box 5.2. *Continued.*

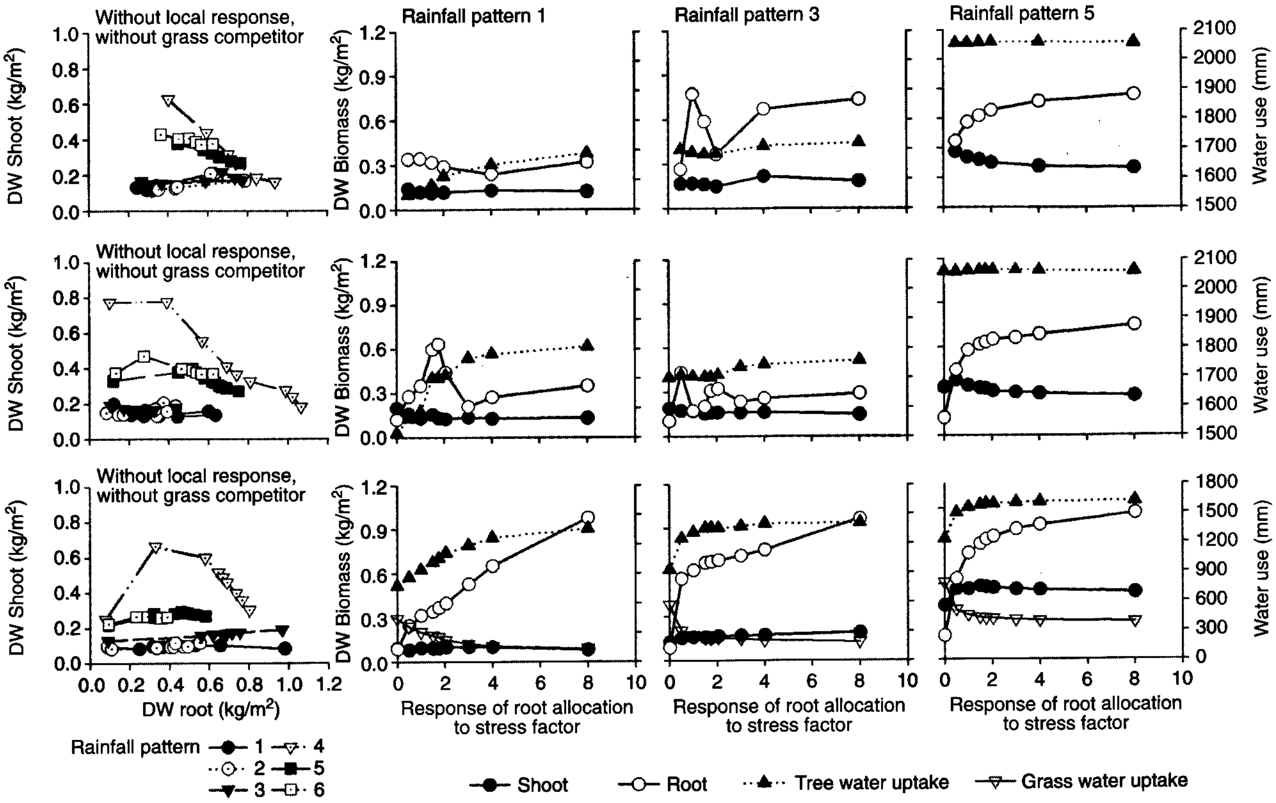

Fig. B5.3. Simulation results for shoot and root dry-weight (DW) biomass and tree (and grass) water use, for three rainfall patterns and a range of parameter values for the 'Root_Allocation_Responsiveness' parameter (see explanations Box 5.2). Simulations include situations with and without 'local response' (see text), and with and without competition from a grass sward.

Box 5.2. *Continued.*

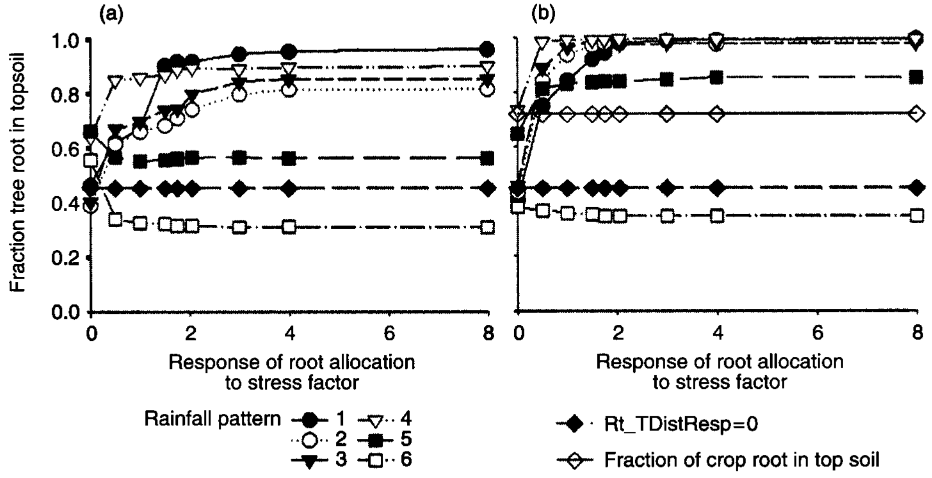

Fig. B5.4. Relative tree root biomass in the upper 25 cm of the soil profile for a range of values of the factor that governs the response to stress of the biomass allocation to roots, with (b) and without (a) a competing grass; the grass is assumed not to show a functional or local response, so it has a constant fraction of its roots in the topsoil; the line Rt_TdistResp = 0 indicates a situation without 'local response', so the 'response to stress' can modify total root biomass, but not root distribution for this setting.

been performed in monocultures, and they may thus have missed important aspects.

Dunbabin *et al.* (2002a,b) developed a 3-D model (WaNuLCAS is essentially 2-D), which includes plastic response to external nutrient supply, and which they parameterized for lupin and a variable nitrate supply. Uptake per unit root can double with a decreasing fraction of the root system inside a nutrient-rich patch (indicating considerable 'down regulation' of uptake in the normal situation), with preferential root development in enriched patches being responsible for further compensation and maintenance of the plant's total uptake capacity.

5.6 Management Implications

5.6.1 Changes in root production after land-use change

As standing root biomass and root turnover are substantial components of the below-ground ecosystem, changes in roots as a result of land-use change can be important. Idol *et al.* (2000) studied changes in the seasonal and spatial dynamics of root growth, mortality and decomposition that occur following the removal of standing forest vegetation. Four upland, temperate, deciduous forest stands in southern Indiana, USA, were compared (during the forest recovery phase) 4, 10, and 29 years after the forest overstorey trees were cut down. A mature stand (80–100 years since last harvest) was chosen to represent the preharvest conditions. A combination of soil cores and ingrowth cores were used to assess stand-level rates of root growth, mortality and decomposition. Root growth increased significantly after harvesting, but declined as the stand matured (if we may indeed interpret these data as a 'chronosequence'). In all stands, fine root mortality and decomposition were nearly equal to, or greater than, fine root growth.

Castellanos *et al.* (2001) examined the effects of slash-and-burn land-clearing of tropical dry forest and the establishment of pasture on fine root biomass and productivity in a site in Mexico. In the pastures (composed of *Cenchrus ciliaris, Panicum maximum* and *Andropogon gayanus*), both the productivity and mortality of fine roots (1 mm in diameter) were 30% lower than in the tropical dry forest in the top 5 cm of soil. However, this difference was partially compensated for by the pasture having more roots below that depth. In forest and pasture, fine root productivity in the top 5 cm of soil accounted for 86% and 76%, respectively, of the total fine root productivity throughout the sampled soil profile.

Rao *et al.* (2001) studied root turnover and nutrient cycling in native and introduced pastures in tropical savannah in the eastern plains (Llanos) of Colombia. Measurements of root production and turnover were made on two introduced (9-year-old) pastures (grass only, *Brachiaria dictyoneura* CIAT 6133; and a grass + legume mixture, *B. dictyoneura* + *Arachis pintoi* CIAT 17434), and compared with measurements made in a native pasture. Annual root production (biomass and length) was significantly greater in the introduced pastures than in the native pasture. Although root biomass turnover (2.2/year) and root length turnover rates (1.8–2.4/year) were similar among native and introduced pastures, the greater total annual root production (6 Mg/ha/year versus 2.4 Mg/ha/year) in the introduced pastures contributed to their strongly superior root turnover (and N and P cycling).

5.6.2 Management implications for multispecies agroecosystems

Knowledge of root distribution and dynamics can be used to increase the probability that applied nutrients (fertilizer) are preferentially used by the most economically important component(s) of the agroecosystem. Fertilizer should be placed closer to the tree trunk, rather than at the canopy edge (as is the current recommendation) in order to maximize P uptake by clove roots (Purbopospito and van Rees, 2002). Seasonal differentiation exists, in terms of root activity, between trees and grass (Cheng and Bledsoe, 2002) and between trees and crops (Odhiambo *et al.*, 2001). Munoz and Beer (2001) discussed the opportunities that exist for reducing nutrient competition between shade trees and cacao based on the different times at which their root growth flushes occur. In their view, competition could be minimized by early fertilization at the beginning of the rains, immediately after the shade trees were pruned. Schroth and Zech (1995b) showed that maximum tree root growth can even be pushed into the dry season through pruning.

Changes in above-ground phenology, including tree pruning, can have substantial impacts on root survival and on subsequent root patterns (van Noordwijk *et al.*, 1996). The 'lung branch' technique, which involved retaining a single branch on pruned *Erythrina poeppigiana* trees, was observed to allow better fine root and nodule survival in a study by Chesney and Nygren (2002).

A major opportunity for 'managing' root turnover and thus for affecting the way turnover contributes to the overall functioning of an agroecosystem is the choice of species (and genotypes within that species) that will be planted. Literature on the genetics of root exudation (quality and quantity) has been assessed by Rengel (2002), who concluded that the best-studied phenomenon, thus far, may be the genetically controlled variation in citrate production in roots, which is linked to partial alleviation of Al-toxicity stress. P solubilization through organic chelating agents (such as citrate) and pH changes is relatively well understood, and there is good agreement between models and measurements of such (Kirk, 2002a,b; Chapter 7, this volume).

5.7 Research Issues and Priorities

Although the methods currently available still have major limitations and weaknesses, they can be used for further comparative studies. Actual data collection in tropical agroecosystems has been limited, and most of what we think we know is derived from temperate zones. Although the processes may be essentially the same, the quantities involved cannot be directly transferred to other conditions. Further studies on how root dynamics are affected by shoot growth (seasonality and phenology) and management (e.g. tillage) in monocultures and intercropping systems remain an important need. Thus far, we have little understanding of how heterogeneous root turnover rates are *within* a root system (e.g. is this affected by the position of the fine roots within the system or by the distribution of rhizovores?). Observed differences in root turnover between crop and tree roots may be related to differences in maintenance costs (linked to protein content).

Model representations can certainly be refined if further data become available that can be used to test predictions made concerning the 'plastic' response to stress factors and opportunities for local root activity.

Conclusions

1. When do roots grow? Generally 'ahead of' the above-ground parts of the plants; tree root growth can be asynchronous with crop root growth in seasonal environments. The functional shoot/root equilibrium needs time to adjust to new situations.
2. Where do roots grow? Definitely not just anywhere. Constraints are placed on this by the root system's branching pattern, and the need for connectedness between fine and coarse transport roots. Competition for resources within the plant can explain local response in (temporarily) favourable locations.
3. How long do fine roots live? From 2 weeks up to 1 year.
4. What can simulation models do? They can incorporate all these ideas into the prediction of below-ground interactions between plants; but parameterization for any specific situation is no simple task in the absence of effective 'rhizotransfer' functions.
5. Roots respond to nutrient-enriched zones in the soil, and such responses can be species-specific. This could be exploited by localized applications of fertilizer.
6. Root and shoot pruning have definite effects on root turnover and root distribution. This could be exploited by management operations.
7. The fine roots of trees live longer than those of crops (3–8 months vs. 2–4 weeks). So crop roots may respond more quickly to management interventions (although available data are very limited!).

Future research needs

1. How are root dynamics affected by shoot growth (seasonality and phenology) and management (e.g. tillage)?
2. How heterogeneous are root turnover rates *within* a root system (e.g. is this affected by the position of the fine roots within the system or by the distribution of rhizovores)?
3. How do environmental conditions and/or the ecological life history of a species or crop determine the plasticity of its root system, and how can we improve our methods to measure this in a more reliable way?