

9 Uptake, Partitioning and Redistribution of Water by Roots in Mixed-species Agroecosystems

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Key questions

1. How is the water budget of a cropping system modified by trees?
2. What controls uptake and partitioning of soil water in species mixtures?
3. What is bidirectional flow?
4. How are partitioning and the bidirectional flow of water measured and modelled?

9.1 Introduction

The fate of rainfall on any agroecosystem can be described in terms of a water budget. For a crop monoculture, transpiration (E_t) is balanced against precipitation (P) by evaporation directly from the soil (E_s), evaporation of rainfall intercepted by canopy surfaces (E_i), surface runoff (R), drainage out of the rooting zone (D) and the change in storage of soil water ($\Delta\theta$), which is written:

$$P = E_t + E_s + E_i + R + D + \Delta\theta \quad (9.1)$$

Modification of the water budget results when species are mixed together. In a simultaneous agroforestry system, transpiration is split into tree (E_t^t) and crop (E_t^c) components, as is interception (E_i^t , E_i^c) (Wallace, 1996). Changes to microclimate and below-ground interactions between the tree and

crop root systems cause modification of E_s , R , D and $\Delta\theta$. We can therefore write a water budget for the tree–crop mixture as

$$P = E_t^t + E_t^c + E_i^t + E_i^c + E_s^* + R^* + D^* + \Delta\theta^* \quad (9.2)$$

where the asterisks (*) denote spatial averages that integrate values for the tree and crop components. The term $E_t^t + E_t^c$ represents a productive use of rainfall, as transpiration enables the production of biomass by photosynthesis. All remaining terms to the right-hand side of the equation are not productive, as they do not add to biomass production. Runoff and drainage may supply water that can be used to provide valuable services elsewhere on the farm or in the wider community and ecosystem.

A common aim of mixed agroecosystems, at least in environments where availability

of water limits farm productivity, is higher efficiency of rainfall utilization – more biomass is produced per unit rainfall. Rainfed agriculture in dryland environments is, typically, strikingly ineffective at making productive use of rainfall. A model-based analysis of water use by millet (*Pennisetum glaucum*) grown on low-input farms in Niger, for example, concluded that a mere 4–9% of available water was used by the crop for transpiration (Röckstrom *et al.*, 1998). In the case of agroforestry, integration of trees into cropping systems can theoretically increase productive use of rainfall by reducing non-productive use of water. Trees may arrest runoff, reduce drainage and cut soil evaporation by the shading of bare soil, which saves water for use by plants if the reduction in E_s exceeds E_i^t .

Trees are thus able to increase rainfall utilization in cropping systems by trading the non-productive use of water for productive uptake by plants. A danger associated with using trees to modify the water balance in favour of plant uptake is that *competition* can occur and the trees deprive the crop of water. Competition affects the growth and survival of plants when one neighbour gains an advantage over another because it is able to acquire more of a resource that is required for growth and is in limited supply (Anderson and Sinclair, 1993). For agroforestry to succeed, therefore, competition between trees and crops should be avoided. Cannell *et al.* (1996) expressed this as the central biophysical hypothesis for agroforestry. They stated that, in the case of water: '... benefits of growing trees with crops will occur only when the trees are able to acquire resources of water ... that the crops would not otherwise acquire.'

The latter criterion can be satisfied if there is *complementarity* in water use by trees and crops. In those cases in which water uptake by the root systems of trees and crops occurs from spatially discrete sources or at discrete times, water use is complementary and productive use of water can be enhanced without there being any negative impacts of competition. 'Over-yielding' (where the productivity of agroforestry exceeds the additive yields of tree and crop

monocultures) can result from complementarity and increased resource-use efficiency.

Bidirectional flow of water in root systems adds complexity to below-ground interactions in species mixtures. There is now strong evidence that reversal of flow in roots causes redistribution of soil water where the root network spans soil horizons with contrasting water potentials. In agroforestry, bidirectional flow could facilitate the coexistence of trees and crops or increase the competitive advantage of trees, depending on whether water is transferred into or out of the crop rooting zone.

The key to determining how competition for water, complementarity and reverse flow phenomena affect the outcome of agroforestry or other species mixtures is understanding the partitioning of water between coexisting root systems. Partitioning is driven both by the processes that control uptake by each species and by bidirectional flow. Insight into these processes is available from theory and measurement. Ultimately, modelling of partitioning is required to enable the simulation of system performance. Our objective here is to relate evidence of competition, complementarity and bidirectional flow to the modelling of partitioning by reviewing the principles of water uptake by plants. These principles are examined on the basis of both relevant theory and measurements, drawn principally from agroforestry research.

9.2 Competition and Complementarity for Water Use in Mixed-species Systems

9.2.1 Impacts on productivity

In mixtures of trees and crops, production from component species is determined by their success at capturing and effectively utilizing essential resources that limit growth (Squire, 1990). In seasonally dry environments, where rainfall is variable and frequently deficient, a lack of available water commonly limits growth. Biomass production (B , g/m²) in an agroforestry system is then a function of cumulative transpiration by the trees and crop (ΣE_i^t and ΣE_i^c , mm)

and their water use efficiencies (e_w^t and e_w^c , g/mm) (Black and Ong, 2000):

$$B = e_w^t \Sigma E_t^t + e_w^c \Sigma E_t^c \quad (9.3)$$

Water-use efficiencies vary with atmospheric humidity deficit and between C_4 and C_3 species. However, a major benefit derived from combining trees and crops in water-limited environments is a reduction in non-productive losses from the water budget (i.e. an increase in $\Sigma E_t^t + \Sigma E_t^c$). This benefit is weakened or lost if, in violation of the hypothesis of Cannell *et al.* (1996), acquisition of water by trees reduces ΣE_t^c because of competition.

The mechanistic basis of competition for water in agroforestry was demonstrated by Govindarajan *et al.* (1996) and McIntyre *et al.* (1997). Their experiments in a semiarid region of Kenya showed that, where seasonal rainfall was insufficient to recharge soil below the crop rooting zone, the grain yields of maize grown in alley cropping systems with *Senna spectabilis* or *Leucaena leucocephala* were reduced by between 39% and 95%. Without available water below the crop rooting zone, uptake by the hedges deprived the maize of much of the water required for growth. In such cases, higher water use by trees causes increased suppression of crop yields (Fig. 9.1).

Combinations of trees and crops are most successful where competition is avoided and resource use is complementary. A classic example of temporal complementarity in water use in agroforestry occurs in the parkland system, which combines dispersed *Faidherbia albida* trees with crop production in West Africa. *F. albida* exhibits 'reverse phenology' and is leafless during much of the cropping season. The trees and crop therefore have discrete periods of demand for water, ensuring minimal competition for water with understorey crops (Sanchez, 1995; Rouspard *et al.*, 1999). Spatial complementarity for water uptake was demonstrated by Smith *et al.* (1997b), who showed that when the roots of windbreak trees had access to ground water, competition with adjacent crops for water from the crop rooting zone was minimal, a phenomenon associated with improved crop yields.

9.2.2 Importance and implications of bidirectional flow

Flow of water through root systems from one soil layer to another has been called 'hydraulic redistribution' (Burgess *et al.*, 1998). Transfer of water upwards, because of uptake from wetter soil at depth, reverse

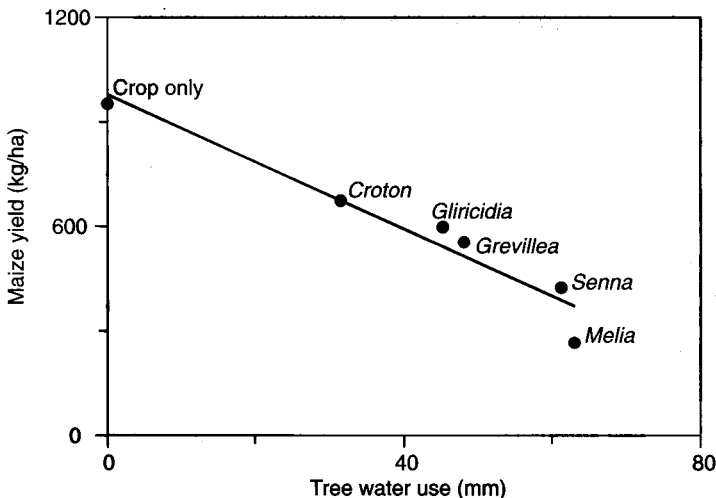


Fig. 9.1. Correlation of maize yields with water use among different tree species in adjacent linear plantings in Machakos, Kenya, during a growing season with low rainfall (250 mm). Redrawn from Ong *et al.* (1999).

flow in lateral roots and subsequent efflux in drier soil near the surface, is termed 'hydraulic lift' (Caldwell *et al.*, 1998). The reverse process, in which water is transferred from wetter soil near the surface into drier soil beneath, was termed 'downward siphoning' by Smith *et al.* (1999b).

There are uncertainties over both the quantities of water transferred by hydraulic redistribution and its impact on the soil water balance. Where gradients in water potential between soil layers are steep, there is some evidence suggesting that the proportion of uptake diverted by flow reversal in roots can be as high as 20% (Emerman and Dawson, 1996; Smith *et al.*, 1999b), though such high rates probably occur for only short periods. Burgess *et al.* (2001a) determined that 28 mm of water was transferred downward by roots over a period of 28 days when there was 96 mm of rainfall. Simulations suggest that the contribution to transpiration of reabsorption of water following hydraulic distribution is very small over seasonal timescales, but can be in the order of 20% on some days (Ryel *et al.*, 2002).

Both hydraulic lift and downward siphoning have implications for below-ground interactions, especially in agroforestry where component species commonly have contrasting maximum rooting depths. For shallow-rooted crops growing in drying soils adjacent to trees, hydraulic lift by the tree roots could provide a source of water and hence facilitate crop growth. This would require that the root system of the crop is established to an extent that would allow it to out-compete the trees for the water being made available. Alternatively, efflux from the tree roots would have to exceed uptake, which might occur, for example, if water potentials in the tree were consistently elevated because of the tree's access to ground water.

Downward siphoning of water by trees would tend to exaggerate their competitive advantage over crops. The water content of subsoil has been found to increase measurably because of hydraulic redistribution through the taproots of trees (Burgess *et al.*, 2001a), suggesting that water storage in the topsoil is concomitantly reduced.

Impairment of crop productivity because of reduced availability of water may result. Under waterlogged conditions, however, downward siphoning could have the benefit of moving excess water out of the topsoil and rewetting very dry subsoil (Burgess *et al.*, 2001a). Additionally, downward siphoning by trees may facilitate the growth of tree roots through dry soil layers, enabling access to ground water.

9.3 Partitioning of Water by Plant Root Systems: Theory

9.3.1 Principles of plant water uptake

Uptake of water by plants is driven by gradients in water potential along a pathway that links soil, roots, foliage and atmosphere (Fig. 9.2). Water potential declines continually from soil to atmosphere along the flow path. Evaporation within the substomatal cavities of leaves creates tension in a continuous column of water that connects leaves to root tips. Water moves into roots when water potentials are lower in roots than they are in the soil.

Relationships between flow and the drop in water potential (ψ) along the uptake pathway can be represented as an Ohm's law analogue. The hydraulic properties of each segment of the flow path are modelled as a transport coefficient termed the hydraulic conductance, k (which is the inverse of the resistance to flow). In the simple linear model depicted in Fig. 9.2, flow in all parts of the pathway is equal to the rate of evaporation from the leaves (E), and is related to gradients in potential between the soil (ψ_s), root surface (ψ_{rs}), base of the stem (ψ_b) and leaf (ψ_l), as described by Newman (1969):

$$E = (\psi_s - \psi_{rs})k_s = (\psi_{rs} - \psi_b)k_r = (\psi_b - \psi_l)k_{sh} \quad (9.4)$$

where k_s , k_r and k_{sh} are hydraulic conductances for the soil, root system and shoot, respectively. Shrinkage of roots in very dry soil can create an interfacial resistance to uptake, causing a sharp decline in k_s .

When expressed per unit root length, k_r becomes root hydraulic conductivity (κ_r). As

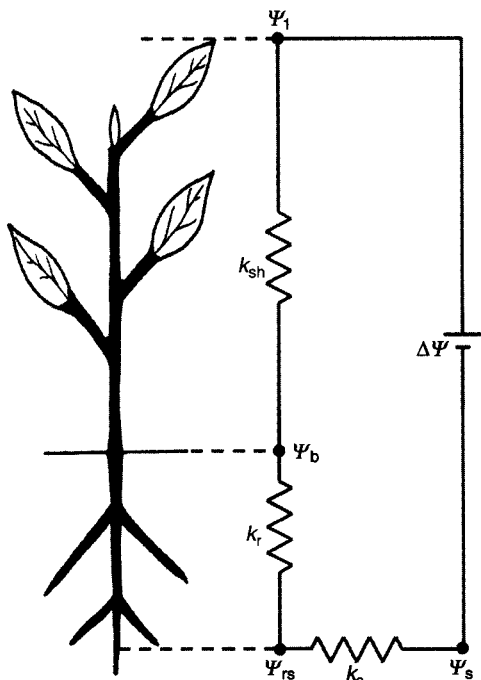


Fig. 9.2. The Ohm's Law analogy for water uptake by plants. Water flow is driven by differences in water potential between the soil (ψ_s) and foliage (ψ_l). In this simple linear model (Equation 9.4), hydraulic conductances for the soil (k_s), root (k_r) and shoot (k_{sh}) connect in series to intermediate water potentials at the root surface (ψ_{rs}) and base of the stem (ψ_b).

defined here, κ_r combines the components of conductivity for radial transport across the root, from the root surface to xylem, and axial transport to the base of the stem. Soil hydraulic conductivity (κ_s) can also be expressed per unit root length (Rowse *et al.*, 1983). The rate of uptake of water (S) by a root system of root length density L_v and occupying soil volume V is then

$$S = \frac{(\psi_s - \psi_b)}{(1/\kappa_s + 1/\kappa_r)} \cdot L_v V \quad (9.5)$$

Unless roots are very sparse, S is most limited by κ_r at soil water contents above the wilting point. Uptake from soil with water potential ψ_s is therefore dependent on the water potential within the plant, the hydraulic conductivity of the root system and the density of the root network.

9.3.2 Partitioning in species mixtures

Equation 9.5 can be written for uptake by each species within a mixed stand of vegetation. In agroforestry or intercropping systems, partitioning of soil water is thus determined by the integrated effects of differences between species in root distributions, root hydraulic properties and plant water potential. From Equation 9.4, the latter is dependent on the hydraulic architecture of the plant and the evaporative flux at the leaves, which is determined by above-ground microclimate and stomatal behaviour.

Three hypothetical scenarios can be constructed to illustrate how the principles of water uptake by plants control partitioning between coexisting root systems, at least over short timescales. Partitioning also depends on relative rates of root growth (and dieback) over longer periods. The following statements are true for a soil layer with uniform ψ_s containing both tree and crop roots:

- With equal root densities and equal root water potential (say ψ_b , Equation 9.5), partitioning of water is determined by the relative values of κ_r for the trees and crop.
- Where the trees shade the crop, partitioning is determined by the relative values of ψ_b , and therefore by canopy-level microclimate and stomatal opening, if root densities and κ_r are equal.
- With equal ψ_b and κ_r , but with one root system being more sparse than the other, water is partitioned in proportion to relative values of L_v .

Competition could result from each of these scenarios if partitioning favoured one species and placed a neighbouring species at a disadvantage because of insufficient availability of water. Complementary use of water could result if the root distributions of the two species were vertically stratified, or if periods of demand for water by each species were discrete.

9.3.3 Mechanisms for bidirectional water flow in roots

Efflux of water from roots into soil is possible where water potential is higher in roots

than in the surrounding soil. This results in the reversal of flow in the root. Rather than flowing towards the stem, efflux results in flow towards the root tips. Water efflux is driven by gradients in either osmotic or hydrostatic potential. Osmotic gradients can cause efflux of generally small amounts of water. Under hydrostatic gradients, efflux can occur in dry soil if water potential remains higher in the root than it is in the soil, because of hydraulic connections to other parts of the root system present in wetter soil at a higher potential. As water potentials in the plant are highest when the evaporative flux from leaves is close to zero, efflux is most common at night. Efflux from roots occurs principally from young, relatively unuberized roots (Caldwell *et al.*, 1998).

9.4 Measurement of Water Uptake and Bidirectional Flow

Quantification of water uptake and partitioning is important for studies of competition and complementarity in mixed-species agroecosystems. In monoculture stands, it can be sufficient to estimate uptake by difference after measurement of the water budget terms in Equation 9.1. The method is limited by challenges in measuring drainage; a further limitation in plant mixtures is that it is not possible to distinguish uptake by individual species from the water budget. More direct measurements of water use are therefore needed in studies of partitioning in intercropping or agroforestry.

9.4.1 Measurement of sap flow in trees and crops

The most direct method available for the quantification of uptake of water by individual plants is measurement of the rate of sap flow in stems (Smith and Allen, 1996). Several methods are available (Table 9.1) that use heat as a tracer for sap movement. All are suitable for use on woody stems, though each is most suited to a specific range of stem sizes. However, only stem heat balance gauges are non-invasive and can be used on herbaceous stems. Uptake of water can be partitioned in plant mixtures by simultaneous measurement of sap flow in each species (Fig. 9.3). Sap flow thus provides a powerful means for the direct quantification of partitioning of water in agroforestry or intercropping. Because of limitations on the number of instruments that can be operated at one time, attention must be given to spatial scaling of sap flow rates from plant to stand, in order to give rates of uptake for unit land area. Scaling must account for heterogeneity in rates of uptake and the spatial distribution of plants (Smith and Allen, 1996).

9.4.2 Measurement of sap flow in roots

Sap flow can be measured in, and compared among, individual roots in order to provide insight into uptake from different zones in the soil. For example, the contribution made by deep roots to the uptake of water has been evaluated by the comparison of sap

Table 9.1. Methods of sap flow measurement used on trees and crops. For use on tree roots, the ability to measure flow in both directions is required because of the possibility of bidirectional flow. A general review of methods is given by Smith and Allen (1996).

Operating principle	Method	Crops	Trees	Diameter range (mm)	Tree roots	Reference
Heat balance	Constant power	√	√	2–125	√	Sakuratani (1981)
	Constant temperature	√	√	2–125		Weibel and Boersma (1995)
	Trunk sector		√	> 120		Cermak <i>et al.</i> (1984)
Heat pulse	Compensation		√	> 30		Green and Clothier (1988)
	Heat ratio		√	> 30	√	Burgess <i>et al.</i> (2001b)
Empirical	Thermal dissipation		√	> 40		Granier (1987)

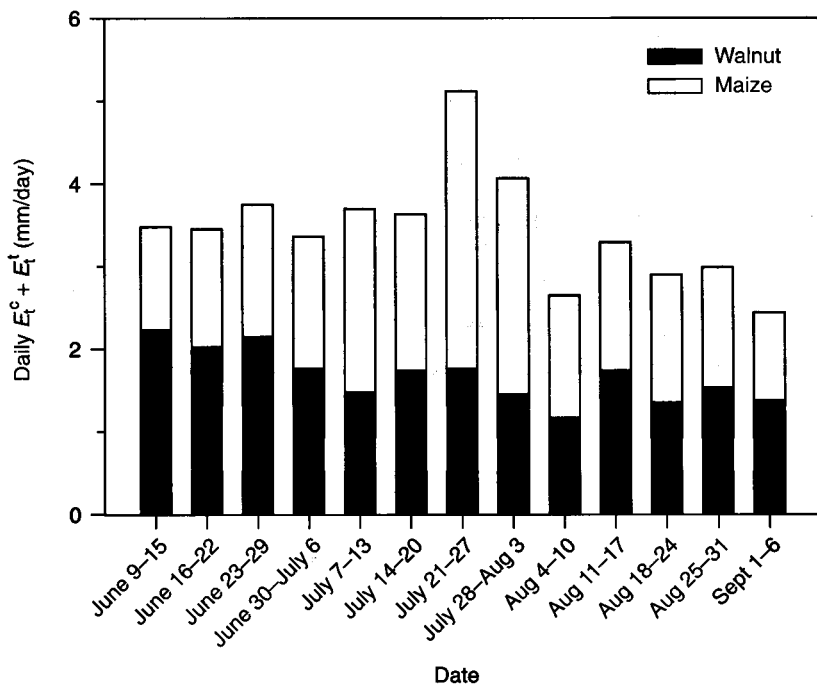


Fig. 9.3. Partitioning of transpiration between trees (E_t^t) and crop (E_t^c) in an alley cropping system combining maize and walnut (*Juglans nigra*) in mid-western USA, measured using sap flow techniques. Redrawn from Jose *et al.* (2000) after scaling to the area occupied by the tree-crop combination.

flow in lateral roots and vertical sinker or tap roots. The installation of sap flow sensors on herbaceous roots is generally not possible, because they are, typically, too fine and fragile. However, installation on woody roots is easily accomplished using the same procedures used for stems. Care must be taken in selecting the method used, as bi-directional flow can only be detected using the heat ratio and constant-power heat balance methods (Table 9.1). Other methods are used on roots, but there is then a risk that reversal of flow is masked by limitations in instrumentation. An example of flow reversal in roots is shown in Fig. 9.4.

9.4.3 Assessment of sources of water used by trees and crops

Variation in the natural abundance of the stable isotopes of water (^2H and ^{18}O) in soil profiles, and in rainfall and groundwater, can provide a means of tracing the sources

of water used by plants. Changes in the isotopic composition of water do not occur when it enters roots or during its flow through roots or suberized stems. Thus, the isotopic composition of water in xylem reflects the source of uptake. If multiple sources of water are exploited, the isotopic composition of sap is a blend of the sources used. In practice, the isotopic ratios $^{18}\text{O}/^{16}\text{O}$ or $^2\text{H}/\text{H}$ are compared for water from the soil, water table and samples of stems or branches (Dawson, 1993). Isotopic ratios of water in samples are measured using a mass spectrometer after the recovery of water from tissue and soil by distillation or by using an equilibration method (see Smith *et al.*, 1997b).

Isotopic tracing of water sources has been used in a number of settings to provide qualitative information about the partitioning of water in plant mixtures. At semiarid sites in Niger, isotopic tracing showed that water acquisition by *Azadirachta indica* trees in windbreaks and adjacent millet was verti-

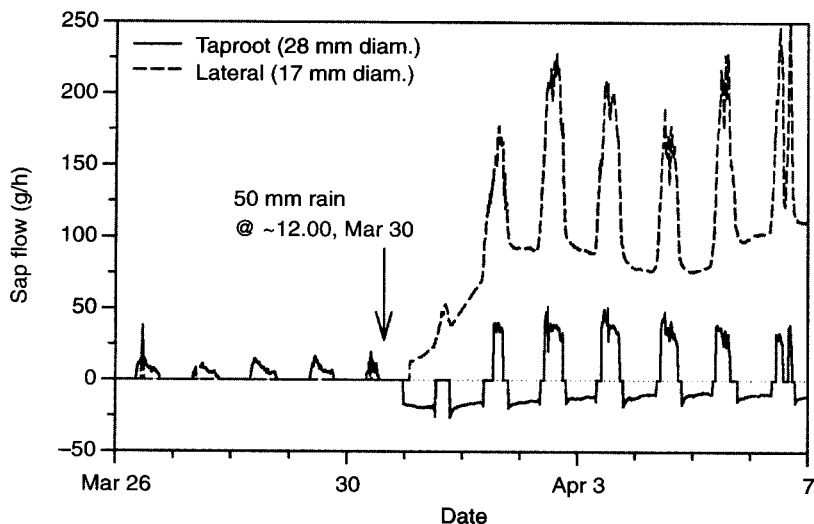


Fig. 9.4. Sap flow in a lateral root and vertical root of a *Grevillea robusta* tree before and after the first rainfall after the dry season, measured using constant-power heat balance gauges. Positive flow was towards the trunk and negative flow was towards the root tips. Rainfall on dry soil created a gradient in water potential between the topsoil and subsoil, causing reverse flow in the taproot during the night (Smith *et al.*, 1999b).

cally stratified only where ground water was accessible to the trees' roots (Smith *et al.*, 1997b) (Fig. 9.5). Similarly, Roupsard *et al.* (1999) found vertical stratification of water uptake at a site where *Faidherbia albida* trees accessed ground water. A discrete source of water available only to trees is thus a precondition for spatial complementarity with regard to water, at least when trees are combined with annual crops.

An awareness of the following is of critical importance: an essential requirement for tracing water sources using this approach is that differences in the abundance of stable isotopes must exist between water sources or within the soil profile (Burgess *et al.*, 2000). When the distribution of isotopes in the profile results in non-unique isotopic ratios among depths and sources, so-called pulse-chase experiments may prove helpful. In this approach, a small amount of water with a distinct isotopic ratio is applied to the soil. Percolation of this labelled water occurs after subsequent rainfall events. Sequential sampling of the isotopic profile in the soil and sap allows an assessment to be made of the depth of water uptake by plant roots.

9.5 Control of Water Partitioning

It was concluded from Equation 9.5 that partitioning of soil water between coexisting species is determined by the combined effects of differences between them in terms of root distributions, root hydraulic properties and the relationship between plant water potential and evaporative flux from the canopy. Consequently, investigation of the mechanisms controlling partitioning requires the evaluation of the role played by all three attributes in determining uptake by each species.

9.5.1 Root distributions

Methods available for the measurement of root length densities are described in detail by Smit *et al.* (2000b). Results from studies of root distributions in mixed agroecosystems are reviewed in Chapter 4 of this volume.

9.5.2 Plant water potentials, microclimate and leaf conductances

Differences in the driving force for uptake of water between species growing in combi-

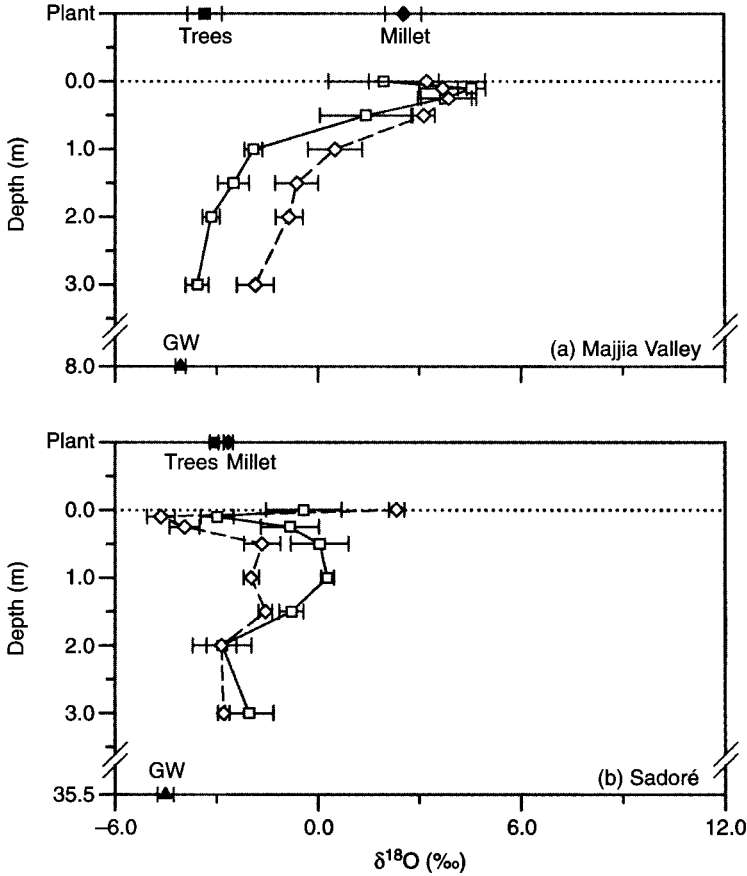


Fig. 9.5. Isotopic ratios for ^{18}O ($\delta^{18}\text{O}$) for the sap of *Azadirachta indica* trees in windbreaks (■), adjacent millet (◆), ground water (GW) (▲) and soil water beneath the trees (□—□) and millet (◇—◇) during a dry spell in the rainy season at (a) the Majjia Valley and (b) Sadoré, in Niger. Trees used water from below the crop rooting zone only at the Majjia Valley site, where groundwater was accessible to tree roots (Smith *et al.*, 1997b).

nation can be determined by comparison of their water potentials. The water potentials of leaves or small shoots are most readily measured after excision using a pressure chamber (Pearcy *et al.*, 1991). The same technique can be used to determine the water potential of stems if measurements are made on non-transpiring leaves attached to the stem. Leaves can be wrapped in plastic or aluminium foil for this purpose. If suckers are present near the base of a tree, this approach can be used to measure water potential in the trunk or root collar. Stem psychrometers provide an alternative method of measuring stem water potentials, but they have limited utility

under field conditions. Routine measurement of water potentials in roots or at the surfaces of roots is not possible using currently available techniques.

Water potentials decline (become more negative) as rates of transpiration increase; partitioning of water between species in mixtures is thus dependent in part on above-ground control of transpiration. Evaporation from leaves is driven by solar radiation, with energy use for evaporation determined by humidity deficits in the atmosphere, the efficiency of aerodynamic exchange and stomatal opening. The integrated effects of these variables on evaporation from single leaves or canopies are

commonly modelled using the Penman–Monteith equation (Monteith and Unsworth, 1990). Combining species in intercropping or agroforestry typically changes the microclimate, causing shading or a reduction in wind speed for example, which results in altered water use by each species. Instruments and methods used in monitoring microclimatic variables in agroforestry were reviewed by Brenner (1996).

In addition to a dependence on microclimate, partitioning of water among species is also dependent on plant responses to microclimate. Plants use a complex control system to reduce evaporation from foliage when the root system is unable to acquire water at the required rate. Loss of water from leaves is controlled by variation in the aperture of stomatal pores, modelled as a stomatal conductance. Many plants also shed leaves to control water use if dry conditions are prolonged. Control of water use by trees in agroforestry can similarly be achieved by shoot pruning, although feedback between stomatal opening and water potential means that reduction in water use may not be proportional to the leaf area removed. Such relationships and stomatal responses to microclimate can be measured in the field using porometers or by the measurement of leaf gas exchange using portable infra-red gas analysers, with leaf areas being measured directly, by destructive sampling, or using indirect methods (Hall *et al.*, 1993).

9.5.3 Root hydraulic properties

The hydraulic properties of roots have received less attention from researchers than above-ground controls of transpiration, root distributions or water movement through the soil itself, despite the importance of κ_r in Equation 9.5. As a result, uptake of water from soil has commonly been modelled using empirical functions of root length density and above-ground demand for water. When applied to species mixtures, there is an implicit assumption in this approach that the root systems of different species have equivalent hydraulic properties. There is evidence to the contrary, however, as root hydraulic

conductivities reported by Steudle and Heydt (1997) were an order of magnitude lower for a range of temperate tree species than they were for herbaceous species, at least when expressed per unit surface area of root. There is, therefore, a suggestion that, in general, water uptake is more rapid for herbaceous roots than for tree roots under equivalent potential gradients.

Most techniques used to measure root hydraulic conductances are suited only to use in the laboratory with pot-grown or solution-grown plants. Two methods are available for use in the field, however. Assuming steady-state flow, conductances can be calculated using Equation 9.4 from measurements of transpiration rates, soil water potential and water potential at the base of the stem. Provided the soil is moist, the error associated with assuming that $\psi_{rs} = \psi_s$ will be small. An alternative method uses a high pressure flow meter (HPFM) developed by Tyree *et al.* (1995). This device forces water into severed roots under hydrostatic pressure at known rates of flow. Water moves in the opposite direction to that which it would normally (i.e. towards the root tips). Water pressure is increased rapidly over a period of 1–2 min and recorded with flow rate. The hydraulic conductance of the root is given by the slope of the linear portion of the plot of flow rate against pressure. Close agreement has been found between results obtained using these two field methods for both trees and crops. Care must be taken when interpreting measurements of hydraulic conductance in roots, because the pathway for uptake, and hence conductance, is different for flow that occurs under osmotic and hydrostatic gradients in water potential (Steudle and Heydt, 1997).

A HPFM was used to compare the conductivity for roots of maize and of the tree *Grevillea robusta* grown in the field in semi-arid Kenya (Smith and Roberts, 2003). On the basis of unit root length, mean κ_r was 1.88×10^{-7} kg/s/MPa/m for *G. robusta* and 1.25×10^{-7} kg/s/MPa/m for maize. This difference was not significant, suggesting that the assumption of hydraulic equivalence between root systems may hold for some combinations of species. The contradiction

that exists between this result and the data from Steudle and Heydt (1997) demonstrates, however, that more measurements of this type are needed for a wide variety of species, especially tropical trees.

9.6 Modelling of Water Uptake in Mixed Agroecosystems

9.6.1 Uptake partitioning

The principles of water uptake by plants provide the basis for mechanistic models of the partitioning of soil water between species in mixtures. Such models thus incorporate control of uptake by above-ground evaporative demand, plant water potential, root distributions and root hydraulic properties. Unless root lengths can be considered constant, models must also account for the effects of root growth. Sillon *et al.* (2000) developed a model of partitioning in agroforestry with mechanistic features. In this model, the daily soil water balance is modelled for a two-dimensional soil profile containing tree and grass roots. Extraction of water by roots is determined by a 'sink term' for each species based on Equation 9.5, with a single conductivity term combining κ_s and κ_r . Potential evaporation is partitioned between species in proportion to fractional light interception, with actual evaporation being dependent on a stress function related to leaf water potential. Equations in the model are solved iteratively, to ensure convergence of the calculated uptake and transpiration.

Simpler approaches to modelling the partitioning of soil water are often required, however, because of limitations such as the lack of available data for model parameterization and the sheer complexity of dynamic models of growth and resource use in mixed vegetation. In common with other models of intercropping and agroforestry, the HyPAR model (Mobbs *et al.*, 1998) partitions available soil water in proportion to transpirational demand and root length densities for trees and crops in each soil layer. This approach successfully enables simulation of interspecific competition for water, but would result in reduced accuracy if coexisting root systems have markedly different hydraulic properties. In such cases, differences among species may be implicitly reflected in the empirical coefficients that are applied to uptake functions.

An intermediate approach is used in the WAnuLCAS model (van Noordwijk and Lusiana, 2000). As in Sillon *et al.* (2000), the soil water balance is modelled in two dimensions and partitioning is controlled by the combined effects of transpirational demand, root distributions and root hydraulic conductivities. Parameterization of the transport equations for soil water is achieved using pedotransfer functions (Box 9.1). Calculations of water uptake by roots are simplified by using an empirical function to relate actual and potential transpiration, thus eliminating the requirement for an iterative solution of the uptake equations. Examples of the output from WAnuLCAS are shown in Box 9.2.

Box 9.1. Pedotransfer functions.

Lack of data on soil hydraulic properties is commonly a limitation on the use of models of the soil water balance and water uptake, particularly for practical, non-experimental applications. The relations between volumetric soil water content (θ), pressure head (h) and soil hydraulic conductivity (K) can be measured in the laboratory or field, but only with specialized equipment and expertise. Consequently, simplified methods of estimating θ - h - K relationships greatly broaden the applicability of soil water models. An important innovation in methods for quantifying soil physical properties has been the development of pedotransfer functions (PTFs). These are sets of equations that enable the prediction of θ - h - K relationships from much more readily measured soil data, such as percentages of clay and silt, organic matter content and bulk density. A review of the determination and applicability of PTFs is given by Wösten *et al.* (2001).

Box 9.2. Simulation of water uptake in a hedgerow intercropping system using WANULCAS.

The WANULCAS model was used to simulate water uptake by trees and crop in a *Peltophorum dasyrrachis*–maize hedgerow intercropping system in Lampung, Sumatra. Mean annual rainfall for Lampung is 3100 mm. Simulations were made of a second cropping season (March–May) commencing after the end of a poor rainy season in which only 20% of normal rainfall was received. The effects that variation in tree and crop root length densities have on the uptake and partitioning of water were simulated. The system was assumed to have no nutrient limitations.

Results from the simulations are shown in Fig. B9.1. Reduction of tree root lengths had little effect on seasonal uptake in the monoculture tree stand but, in the tree–crop mixture, caused a small shift in partitioning in favour of the crop (Fig. B9.1a). The small influence that changes in root length had on water uptake by the trees suggests that the decline in ψ_b required to maintain S (Equation 9.5) for truncated root systems was not sufficient to limit uptake severely. This suggests water uptake may be more sensitive to tree root length in systems where the trees are not pruned, as higher potential transpiration would require lower ψ_b . The simulations also showed that reductions in crop water uptake in both the monoculture and hedgerow system were more substantial under similar relative changes in maize root densities (Fig. B9.1b). Uptake by the trees only partially compensated for reduced uptake by the crop, resulting in a decline in productive water use by the system (Equation 9.3).

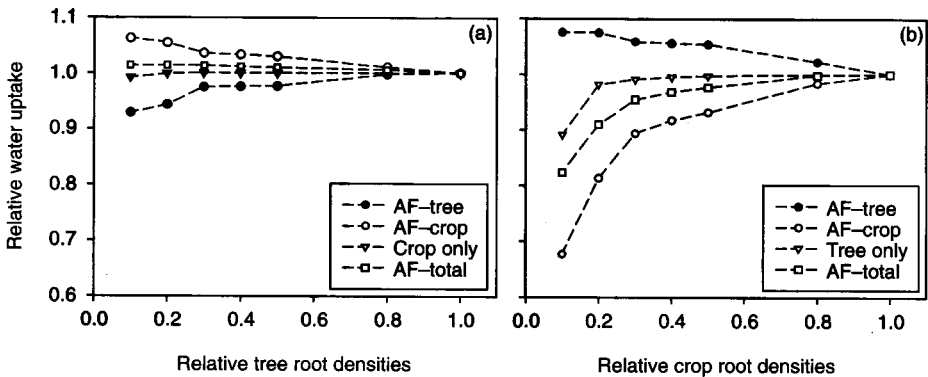


Fig. B9.1. Effects of root length densities on water uptake by the trees and crop in a *Peltophorum*–maize hedgerow system, as simulated using WANULCAS. Water use is expressed relative to its value at maximum root length density.

There is emerging evidence that use of a simple parameterization for root hydraulic conductivity may result in the effects of root architecture on patterns of water uptake being overlooked. Doussan *et al.* (1999) used an intricate model of root conductance and architecture to contrast uptake by herbaceous and woody root systems. The higher transport capacity of large woody roots near the base of the tree resulted in preferential

uptake from soil close to the tree. Uptake by the herbaceous root system was more uniform. On the basis of theory, therefore, partitioning of water in tree–crop mixtures may depend to some extent on root system architecture, in addition to hydraulic conductances. Representation of this phenomenon may become a feature of future developments in the modelling of soil water partitioning in agroforestry.

9.6.2 Bidirectional flow and soil water redistribution

Physically based models of root function offer an advantage over more empirical approaches when the simulation of bidirectional flow in root systems is of interest. Flow of water from one soil layer to another through roots can be simulated if root systems are represented mathematically as a network of conductances that connect regions of a plant or of soil with differing water potentials. Reverse flow, from root to soil, is simulated when root water potential in any layer is higher than soil water potential, with the rate of flow being determined by the potential gradient and by the conductances of the flow path. WANULCAS (van Noordwijk and Lusiana, 2000) provides a capability for modelling of bidirectional flow using these principles, with the assumption that conductances for flow in either direction are equivalent. However, as reversal of flow entails movement of water from one root to another, flow paths for conventional and reverse flow are not exactly equivalent, suggesting that this assumption requires testing.

9.7 Summary and Conclusions

Combining species in agroecosystems can reduce non-productive loss of water and enhance total uptake by plants, resulting in increased biomass production. One danger associated with the mixing of species is competition for water. Unacceptable loss of crop yield can occur if trees deprive a crop of water. To succeed in water-limited environments, therefore, water use by trees and crops should be complementary: uptake by trees and crops should be from spatially discrete sources or should occur at discrete times.

Partitioning of water between coexisting root systems can be conceptualized using the fundamental principles of water uptake by plants. Partitioning of water therefore depends on the combined effects of differences between species in terms of the distributions, hydraulic properties and water

potentials of roots. Inequalities in root distributions, transpirational demand and root hydraulic conductivities may each result in partitioning favouring one species over a neighbouring species. Further complexity in below-ground interactions arises from bidirectional flow in roots, which is observed when root systems span soil layers with different water potentials. Flow reversal in roots causes redistribution of soil water, with hydraulic lift potentially facilitating the coexistence of trees and crops, but with downward siphoning enhancing the competitive advantage of trees.

Sap flow methods provide a powerful tool for the direct measurement of tree and crop water use and therefore for the measurement of partitioning. Some of these methods have been used on tree roots to contrast uptake by deep and shallow roots. Qualitative insights into the vertical stratification of uptake by tree and crop roots can also be obtained from an analysis of variation in the natural abundance of deuterium or ^{18}O among water sources. Sap flow methods have, additionally, enabled direct quantification of bidirectional flow for the first time; this has resulted in the consideration of this interesting phenomenon as an ecological process with potentially important impacts, rather than as a theoretical oddity. A full understanding of its effects awaits further research.

The mechanistic basis for partitioning can be investigated by the study of root distributions, physiological and microclimatic control of transpiration, and root hydraulic conductivities. Knowledge of the processes controlling partitioning in agroforestry has advanced in the last decade, and has enabled the modelling of water use in mixtures to move beyond simplistic dependencies on root length distributions. However, there remains a need for new data that would enable parameterization of these models, especially in relation to root hydraulic properties.

Modelling has a key role to play in ensuring that recent progress on research into below-ground interactions and water results in real improvements in the management of complex agroecosystems. In water-

limited environments, strategies for controlling competition and promoting complementarity in water use are imperative in agroforestry. However, the system-wide impacts of modifications made to management strategies can be hard to predict without reliable models. Advances in our ability to model uptake and the partitioning of water by competing root systems should,

therefore, make the task of developing and promoting more sustainable systems of land use easier. Ultimately, however, future models must enable analysis of economic trade-offs caused by the modification of water budgets at the catchment scale, in order to relate improvements in agroecosystem management to better livelihoods for rural communities.

Conclusions

1. Trees can modify the water budgets of cropping systems to increase rainfall utilization, trading non-productive use of water for productive uptake by plants.
2. Partitioning of soil water in species mixtures is determined by the integrated effects of differences in root distributions, root hydraulic properties and canopy-level control of transpiration; approaches to modelling uptake and partitioning are based on representations of these effects, with varying levels of simplification.
3. Bidirectional flow occurs when root networks span gradients in soil water potential, causing reversal of flow in roots and transfer of water from wetter to drier soil.
4. Sap flow methods provide a powerful tool for direct quantification of partitioning and bidirectional flow; qualitative assessment of vertical stratification in uptake in species mixtures is possible where differences occur in the isotopic composition of water from different sources.
5. Competition for water in agroforestry is severe where rainfall is too low to recharge soil below the crop rooting zone, unless a water table is accessible to tree roots.
6. Spatial complementarity in water use requires both deep sources of water and differential tree and crop root distributions; deep-rooted trees alone are not sufficient.
7. Pruning, the use of species with 'reverse phenology', and sequential planting in agroforestry systems permit temporal partitioning of uptake; however, there is a need to ensure that high water use in one phase of the production cycle does not reduce water availability in subsequent phases.

Future research needs

1. To further investigate bidirectional flow: what quantities of water are involved, what are its impacts in real systems and what are the physiological controls on flow reversal in roots?
2. To collect data on root hydraulic properties for field-grown tropical trees and crops, and to elucidate relationships between root hydraulic conductances and root system architecture.
3. To quantify economic trade-offs from changes in the water budget and to develop methods for the scaling-up of these trade-offs from plot to catchment and community.