

The Ways Trees Use Water

**Four Review Papers
Edited by Joe Landsberg**

Produced as part of the
Joint Venture Agroforestry Program
'Agroforestry to Balance Catchment Health
and Primary Production' project

**Water and Salinity Issues
in Agroforestry No. 5**

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Foreword

Salinity threatens the productivity of huge areas of agricultural land in Australia. It is caused by an imbalance between groundwater recharge and discharge, which in turn is blamed largely on the removal of the native vegetation from the landscape.

One possible way of reducing the impact of salinity is to re-establish trees on farms. Landcare groups, government agencies and the timber industry have been doing this enthusiastically for more than a decade, although their task is far from over.

But scientists are still asking some fundamental questions about the role of trees in restoring the hydrological balance. Some such questions centre on the way trees use water. Are certain species better water-users than others? Will more efficient users grow more quickly? Are different planting configurations better? Does the root architecture of certain species allow them greater access to groundwater?

The four papers that make up this volume address these and other questions. They were prepared as part of a larger project funded by the RIRDC/LWRRDC/FWPRDC Joint Venture Agroforestry Program, which will culminate in new guidelines for the use of trees to address issues in soil hydrology.

This is the fifth report in a series published by the RIRDC/LWRRDC/FWPRDC Joint Venture Agroforestry Program on water and salinity issues in agroforestry. We still have much to learn. But this series is bringing to light what we do know and highlighting where we need to go next with our research and development efforts.

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Peter Core

Managing Director

Rural Industries Research and Development Corporation

Contents

Foreword	iii
Executive Summary	vi
1. TREE WATER USE AND ITS IMPLICATIONS IN RELATION TO AGROFORESTRY SYSTEMS (by J Landsberg)	1
Summary.....	1
Introduction.....	2
Biological and physical background	3
The question of species	19
Conclusions and recommendations.....	20
Appendix 1: The Penman-Monteith equation: derivation; equilibrium and potential evaporation; some representative numbers for tree water use.....	21
Appendix 2: The control of transpiration by soil water: the HYDRUS-2D package	25
References.....	27
2. DOES LEAF WATER EFFICIENCY VARY AMONG EUCALYPTS IN WATER-LIMITED ENVIRONMENTS? (by T Hatton, P Reece, P Taylor, K McEwan)	32
Summary.....	32
Introduction.....	33
Methods	34
Sites and Sampling.....	35
Results	36
Discussion	39
Acknowledgments	40
References.....	41
3. RELATIONSHIPS BETWEEN WATER USE EFFICIENCY AND TREE PRODUCTION (by J Landsberg)	45
Summary.....	45
Introduction.....	46
Background	46
Analysis of West Australian data	47
Analysis of WUE using a model	48
Discussion and conclusions	52
Acknowledgments	53
References.....	54
4. ROOT DISTRIBUTIONS AND WATER UPTAKE PATTERNS IN EUCALYPTS AND OTHER SPECIES (by J Knight).....	55
Summary.....	55
Introduction.....	56
Morphology of root systems related to water uptake.....	57
Soil water status and its effects on transpiration	68
Soil water uptake patterns inferred from stable isotope composition	71
Soil water uptake patterns inferred from soil water depletion	72
Theoretical models of root water uptake	75
Conclusions	78
Acknowledgments	78
References.....	78

Executive Summary

These review papers are the product of a multidisciplinary project being conducted by CSIRO Land and Water and CSIRO Forestry and Forest Products. The project's primary aim is to develop design guidelines to help people locate trees in the landscape to optimise catchment health and primary production.

The first paper, 'Tree Water Use and its Implications in Relation to Agroforestry Systems' reviews the biological and physical background of tree water use to provide a basis for analysing the impact of trees in various arrangements in the landscape, in terms of their water use. Since water use is governed by environmental conditions acting on leaf area, variations in leaf area per tree, and methods for determining it, are discussed.

One of the objectives of this paper was to determine whether there are significant differences in the water use per unit leaf area, and water use efficiency, of different tree species. The conclusion about stomatal behaviour indicates that significant differences are unlikely and we cannot make definitive general statements about the relative water use rates of tree species. Differences in water use rates have to be assessed in terms of the processes that determine water use, reviewed in the paper. Discussion of the factors that influence water use by different species, and the observations that should be made to provide the information needed to make decisions in relation to particular areas, is presented in the section on *The question of species*.

The paper recommends that the Penman-Monteith (P-M) equation be adopted as the standard to calculate the water use rates of trees in stands, lines or scattered across the landscape. Sample calculations are provided and discussed. The P-M equation is derived in Appendix 1, and the values of the parameters given.

The second paper, 'Does leaf water efficiency vary among eucalypts in water-limited environments?' tests the null hypothesis that tree water use per unit leaf area (*leaf efficiency*) is independent of eucalypt species. This is implicitly equivalent to the hydrological equilibrium hypothesis of leaf area as a function of climate, at least in cases where transpiration and growth are limited by soil moisture. Failure to reject this null hypothesis leads to several simplifications: (a) selection of tree species for water balance management, (b) the generation of regional-scale expectations of leaf area index, and (c) simplified estimation (monitoring) of the effectiveness of plantations in controlling site water balance.

The hypothesis was tested with tree water use data collected in natural multi-species stands across Australia, including sites in the wet/dry season tropical woodlands of the Northern Territory, the Mediterranean climate forests of Western Australia, and a woodland system in southern New South Wales subject to an even distribution of rainfall throughout the year. To extend this analysis, researchers included a test of the hypothesis in a multi-species tree plantation growing on a saline gradient.

Although there are reports to the contrary, especially from investigations on eucalypt plantations, this paper concludes that there is little evidence for rejecting the hypothesis that the rate of water use per unit leaf area does not vary significantly among sympatric eucalypt species in rainfall-limited (soil water limited) systems. This conclusion allows useful generalities about the hydrological role of trees in the Australian landscape.

The third paper, 'Relationships between water use efficiency and tree production', looks at the Water Use Efficiency (WUE) of trees, with a view to assessing the value of this parameter as a criterion for species selection or a basis for the management of stands in an agroforestry context. WUE may be defined as the amount of dry matter produced by a plant per unit of water transpired. It can be considered at the leaf, plant or stand level, and over a range of intervals. The paper focuses on the stand level, over periods up to a season.

It concludes that, although WUE may provide useful insights into the responses of trees to varying environmental conditions, it is unlikely to be of primary value as an index of tree performance for use at the relatively applied level of the design and management of agroforestry systems.

The fourth and final paper, 'Root distributions and water uptake patterns in Eucalypts and other species', reviews what is known about the structure and function of tree root systems in relation to the uptake of water and competition with other species. It confirms the conventional wisdom that deeper root systems enable Eucalypts and other trees to access water not available to shallow rooted trees and crops. Deep rooted trees are usually able to maintain their relatively high transpiration rates over dry summer periods.

The paper also critically examines information on the size and shape of Eucalypt root systems. Young Eucalypts have a deep tap root and a lateral root system. Most naturally occurring Eucalypts in savanna woodlands or forests have dimorphic root systems with widely spread lateral roots near the surface and deep sinker roots which grow down from the laterals as the trees mature. The lateral roots may spread for large distances (up to 20 m) into adjacent crop or pasture, particularly if water or nutrient supplies are more readily available there. Pruning or trenching is recommended to control lateral roots in agroforestry.

The single root model for root water uptake is able to provide a basis for modelling relative water uptake by trees and crops in the same soil volume. It can be used to predict the reduction in transpiration rate as the soil dries. For this model, soil hydraulic properties must be measured or estimated, and root length densities of the two species must be measured or estimated using a distribution such as the negative exponential. The single root model usually overestimates soil water uptake, but has been successfully modified by various authors to take account of factors such as poor root-soil contact, clumping of roots, and anaerobic conditions near saturation.

PAPER NO. 1

TREE WATER USE AND ITS IMPLICATIONS IN RELATION TO AGROFORESTRY SYSTEMS

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Summary

This paper reviews the biological and physical background of tree water use to provide a basis for analysing the impact of trees in various arrangements in the landscape, in terms of their water use. Since water use is governed by environmental conditions acting on leaf area, variations in leaf area per tree, and methods for determining it, are discussed.

Water use per unit leaf area is controlled by stomata but there is no evidence of significant and consistent differences in stomatal behaviour between species. Extant general models of stomatal behaviour are almost certainly good enough for most purposes, although the question of responses to drying soils may be difficult to resolve. The effects of atmospheric humidity on stomata are well documented, but the effects of dry soil appear to operate through rates of supply to the root system, and hence the leaves, and will remain difficult to quantify.

Root systems are immensely important factors determining the capacity of trees to use water, and survive under adverse (water stress) conditions. The paper presents some sample analyses of root systems and their effects. Transpiration rates by trees, in any arrangement, are the result of the interactions between the exposed leaf area and the atmospheric environment, interacting with the soil moisture in the rooting zone. The drying patterns produced by scattered trees have important implications for paddock-scale hydrology.

One of the objectives of this paper was to determine whether there are significant differences in the water use per unit leaf area, and water use efficiency, of different tree species. The conclusion about stomatal behaviour indicates that significant differences are unlikely and we cannot make definitive general statements about the relative water use rates of tree species. Differences in water use rates have to be assessed in terms of the processes that determine water use, reviewed in the paper. Discussion of the factors that influence water use by different species, and the observations that should be made to provide the information needed to make decisions in relation to particular areas, is presented in the section on *The question of species*.

It is recommended that the Penman-Monteith (P-M) equation be adopted as the standard to calculate the water use rates of trees in stands, lines or scattered across the landscape. Sample calculations are provided and discussed. The P-M equation is derived in Appendix 1, and the values of the parameters given.

Introduction

The research project on agroforestry being funded by RIRDC (1996-1999) is concerned with the effectiveness of trees as a means of ameliorating the problems of rising water tables being experienced in many agricultural areas on Australia, particularly the Murray Darling Basin and extensive areas in Western Australia. In more general terms, the project is concerned with the hydrological impacts of trees in the landscape, including windbreaks, parallel lines of trees used in alley-cropping or isolated trees in pastures. Where blocks of trees are planted for salinity control or woodlots, these blocks will seldom be large enough to allow the effects of advection to be discounted, so their rates of water use may be different from that of forest stands with the same structural characteristics. Trees scattered across the landscape, in whatever arrangements, will have significant effects on the flow of water over and through the soil.

Everyone agrees, in principle, that the re-introduction of as many trees as possible into agricultural areas would be a good thing from the hydrological point of view, but there are no clear guidelines that indicate how many trees would be needed, in a particular situation, to achieve useful results. Indeed it is not always clear what might constitute 'useful results' in terms of control of water tables, added to which there is the problem of competition between trees and crops or pastures. Farmers will often be unwilling to commit themselves to the expense of tree planting and maintenance because the economic benefits are not clear, and there is a significant probability that there will be disbenefits in terms of loss of productivity by crops influenced by the trees. These matters can be (and have been) argued *ad nauseam*, but the arguments will not be resolved until we have clear guidelines that can be applied to particular situations, that will enable the gains and losses - both short and longer-term - to be objectively, and preferably quantitatively, evaluated and compared.

A major objective of the agroforestry research project is to produce the necessary guidelines. This review aims to present some of the basic empirical and theoretical information on which our understanding of tree water use is based and, on the basis that information, to indicate what we can and cannot calculate with reasonable confidence, what measurements should be made to test the calculations and what information we need to assess the likely benefits of agroforestry, particularly in relation to the question of tree water use. The body of the paper considers some of the biological factors relating to trees that must be taken into account when considering both their water use and competitive effects, and provides information about the rates of tree water use that can be expected. The last section provides suggestions about the experimental measurements needed to test the models underlying the calculations and provide parameter values that can be applied in practical situations. There are two Appendices: Appendix 1 provides the derivation of the Penman-Monteith (P-M) equation, which is recommended as the standard method of calculating tree water use for stands, scattered trees or trees in lines. It also provides parameter values and calculated water use rates for irrigated Eucalypts at various locations. Appendix 2 provides technical details of a model used to evaluate soil water use and extraction patterns by single trees.

One of the objectives of the agroforestry research project was the comparison of water use per unit leaf area, and water use efficiency (dry mass production per unit water used) between the 'significant plantation species' in Australia. This review leads to the conclusion that these are not useful objectives because there is no evidence for significant differences in water use per unit leaf area (see also Hatton et al. this volume), and because water use efficiency can be affected by so many factors that it is useless as a selection factor for trees (see the paper on Water Use Efficiency; this volume). The objectives, and measurements that should be made in relation to species comparisons, are discussed and clarified.

The paper is not a comprehensive review of empirical data relating to tree water use in Australia. Such data are not, in themselves, particularly useful as guides to what can be expected where conditions are different from those where measurements were made; their greatest value lies in testing the models that must be used to calculate the probable consequences of the presence or absence of trees in a landscape, and the number, size and arrangement of those trees. Farrington and Salama (1996) tabulated water use data from 13 separate studies, on various Eucalyptus species, which illustrate the point. The values presented cover a very wide range and are not readily comparable with one another. To obtain any information from them that would be useful in a general sense it would be necessary to examine the report of each study for the details of tree size and leaf area per tree, arrangement (if not forest stands), population, soil types, weather conditions and possible measurement errors, and convert all the data to a standard form - i.e. with the same time base and biological base.

Tree size and leaf area, arrangement, weather and soil conditions all affect the patterns of water use within landscape units, and water use rates by the landscape as a whole. These rates, in turn, interact with topographic

and geologic features and influence patterns of groundwater flow and the distribution of groundwater recharge and discharge sites. Information about tree water use provides the input to hydrogeological models that include information about landscape features and tree distribution. This paper does not include a review of hydrogeological effects and considerations, which would be a major exercise in its own right. For the same reason the paper does not deal with the effects of soil salinity.

Biological and physical background

The most elementary facts about trees, in relation to their water use, are that they consist of an upper leaf-carrying part, and roots, and that the transpiration rate of trees, i.e. the rate at which they can extract water from the soil, is driven by atmospheric conditions. Under particular atmospheric conditions the transpiration rate depends on the surface area of the leaves exposed to the atmosphere, the extent of the root system which absorbs water from the soil, and the amount of water in the soil. A (relatively) small tree in wet soil can transpire faster than a larger tree in drier soil under the same conditions of atmospheric demand. There is no such thing as a 'standard tree'; we cannot make statements about the effects of trees, in terms of water uptake and/or their effects on surrounding crops or pastures, unless we specify the size of the trees, how many there are in a given space, how they are arranged and their leaf area. Relating water use to stem diameter is not useful, except insofar as stem diameter reflects the leaf area of the tree (see below).

These obvious facts are sometimes overlooked in discussions about water use by trees in agricultural land. To provide a basis for calculating water use by trees, and assessing water uptake and drying patterns in the soil, we have to be able to describe tree canopies and root systems.

The leaf area of trees

Tree canopies may range from full cover - where the stem population (per unit area) is high enough to produce a continuous cover of leaves (full canopy) - to individual trees that do not affect, and are not affected by, their neighbours. (The question of mutual effects applies to both root systems and canopies.) The existence of a full canopy does not necessarily imply that the trees are large: a high population of small, young trees can produce a full canopy which, in wet soil, is likely to lose water as fast as a smaller population of much larger trees. In drying soil trees with limited root systems will be much more likely to suffer from water stress, because they will exhaust the reservoir of water available to them and will not be able to maintain the supply of water to the leaves. The structure of forest canopies, and the implications for leaf microclimate, are discussed in some detail by Landsberg (1986) and by Landsberg and Gower (1997), but they do not deal with scattered trees or trees in lines.

The exposure of leaves, to both radiant energy and the wind, may be very different in a full canopy and in a tree that is far enough from its neighbours for their influence to be small. There is a continuum of decreasing populations from fully stocked (in forestry terms) stands through woodland, to scattered trees and isolated trees (no influence of neighbours). Various alternative arrangements were outlined in the pamphlet produced from a RIRDC workshop in 1996 (Stirzaker et al. 1997; see Figure 1); one of the objectives of this project must be to determine the influence of tree spacing and arrangement on water use. This will, obviously, depend to a considerable extent on the size, conformation and leaf area of the trees. As tree population densities decrease we can expect the shape and conformation of individuals to reflect, increasingly, their genetic characteristics, unmodified by the effects of competition. In most species trees that are not significantly affected by neighbours will have more branches and be more spherical in shape, with a larger leaf area, than trees that are subject to competition from neighbours during their development.

The structure of tree crowns varies considerably, so information about their leaf area (L , m^2 ; we will assume all values of L refer to projected - not total - leaf area) may not, in itself, be enough to allow estimation of energy interception and water use rates. In the case of full canopies the parameter of most importance for calculating water use is leaf area index (L^* , $m^2 m^{-2}$) - the area of leaf surface per unit ground area. In scattered trees the important parameter is leaf area density (ρ_f , $m^2 m^{-3}$) - leaf area per unit canopy volume. Assuming that foliage is randomly distributed through the canopy volume, ρ_f is obtained directly from L and an estimate of canopy volume for modelling purposes, tree crowns can be described by a series of standard mathematical forms, e.g. spherical, ellipsoid, truncated ellipse or conical, and in terms of parameters such as height to the lowest foliage-bearing branches, height of the top of the canopy and crown diameter. Similarly rows of trees, such as windbreaks, can be described in terms of their cross-sectional shape and dimensions. It will be important to collect these basic descriptions for any systems and species under study in the agroforestry project

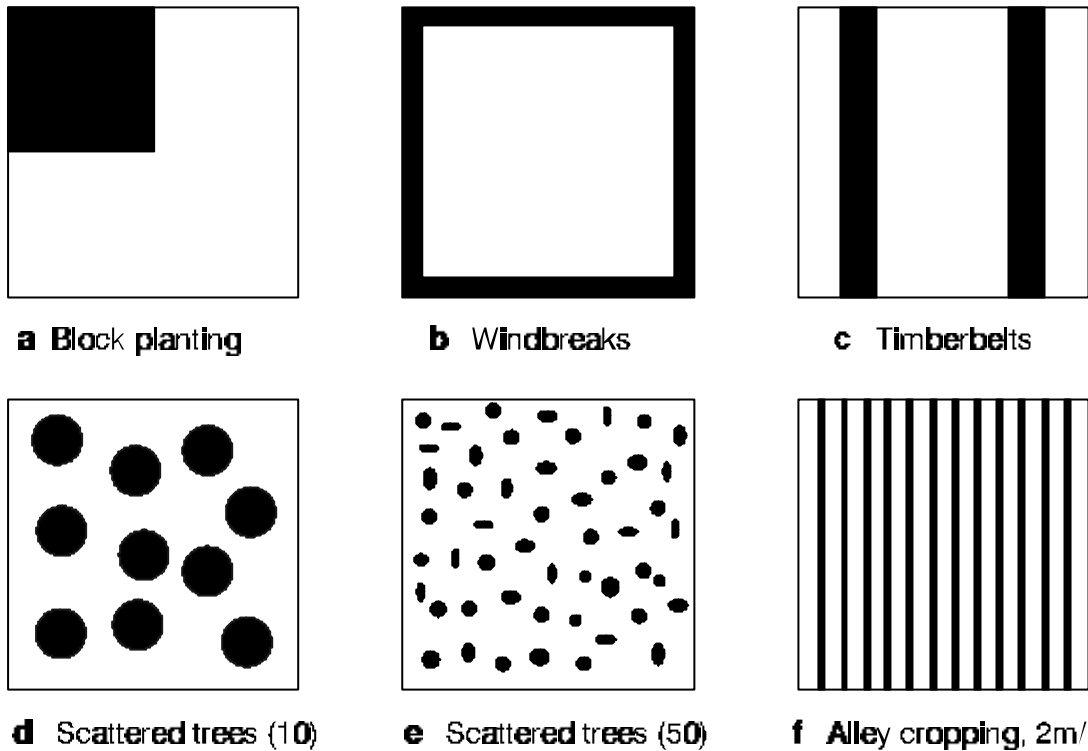


Figure 1. Different arrangements of trees in the landscape. The area of trees, as a fraction of total land area, is approximately the same ($\approx 30\%$) in each case.

We can estimate the leaf area of trees from the allometric equations that describe the relationship between stem diameter and leaf area per tree. The parameter values for these equations are usually determined from data obtained by destructive harvesting of trees. There are many publications in the forestry literature (e.g Gholz et al. 1979; Gholz, 1982; Pearson et al. 1984) that present these relationships, which can usually be described by equations of the form

$$w_f = c_f d_b^n \quad (1)$$

where w_f is foliage dry mass, c_f is a constant, d_b is stem diameter and n is a coefficient.

Grier and Waring (1974) established a linear relationship between foliage mass and sapwood cross-sectional area of conifers (see also Whitehead, 1978); this is generally of less practical value than equation (1) because of the need for information about sapwood cross-sectional area. Vertessy et al. (1995) fitted equation (1) to *Eucalyptus regnans*, with L (not w_f) as the dependent variable, and Teskey and Sheriff (1996) found a linear relationship between L and stem basal area. Landsberg (1980) showed that equation (1) holds for apple trees in full leaf. To convert w_f to L we need to know the Specific Leaf Area (σ_b $\text{m}^2 \text{kg}^{-1}$) - the area of leaf that will result from a given mass of foliage. Some typical values for the parameters of equation (1), and the leaf area values they indicate, are given in Table 1.

Table 1. Parameter values and the leaf area per tree predicted by equation (1), for various species. The equation is usually applied to leaf mass, which can be converted to Leaf Area by multiplying by Specific Leaf Area (σ_l), taken as $6 \text{ m}^2 \text{ kg}^{-1}$ for all the listed cases.

The *E. regnans* equations (Vertessey et al. 1997) were derived directly for Leaf Area; note the differences in c_f values*. All the values were obtained from trees in forests or plantations - not open grown trees. The hemlock and Douglas fir values are presented for comparison.

Species	Approx. age (yrs)	Stem diam. range (cm)	Constant (c_f)	Power (n_f)	Leaf Area range
<i>E.grandis</i> ¹	~ 10	5-15	0.05	2	7-67
<i>E.grandis</i> ²	3-24	10-40	0.1	1.44	16-121
<i>E.grandis</i> ²	2-10	11-20	0.065	1.67	18-58
<i>E.regnans</i> ³	11	10-40	0.003*	3	3-190
<i>E.regnans</i> ³	56	40-90	0.005*	2.5	56-439
<i>E.globulus</i> ⁴	4	1-12	0.04	2	0.2-34
<i>E.globulus</i> ⁴	9	3-16	0.01	2.4	0.8-46
Various pines ⁵	2-100	2-26	0.009	2.32	0.3-103
<i>P.radiata</i> ⁶	9-14	14-26	0.04	1.97	43-147
Hemlock ⁷	old	20-100	0.016	2.12	55- 1668
Douglas fir ⁷	old	5-100	0.06	1.7	18-756

¹ Deniliquin, NSW. Data from Dr Jim Morris ² South Africa. Data from Dr Peter Dye

³ from Vertessey et al. (1997). ⁴ from Tasmania. Data from Mr Charlie Turnbull.

⁵ from Gower et al. (1994). ⁶ from the Biology of Forest Growth project; see For. Ecol. and Manage. 52.

Snowdon and Benson (1992), pp 87-116. Dbh data corresponding to the biomass data in the Appendixi provided by Mr Martin Benson. ⁷ from Gholz (1982).

Equation (1) suggests stable relationships between stem size and leaf area, but they do, of course, vary. The parameter values in Table 1, although surprisingly consistent, must be regarded as statistical means; they cannot be expected to give the correct value for the leaf area of a particular tree in any situation. For evergreens, which includes all the Eucalyptus species, and the pines, we can expect variation through the year, and in response to water availability, fertility and spacing - although the *P.radiata* data from the Biology of Forest Growth project (see Snowdon and Benson, 1992) showed no differences between the relationships for trees grown under a very wide range of water and fertility conditions. Deciduous trees (of which there are few in Australia) shed all their leaves seasonally and produce a new 'crop' each year: clearly their capacity to use water, provide shelter and compete with agricultural crops or pastures will vary enormously in synchrony with changes in their leaf area.. The relative rates of leaf loss and production, integrated over any specified time period, determine L at time t. Rates of loss are strongly affected by water - a period of drought may result in significant leaf fall (see Linder et al. (1987) for an illustration of the effects on *P. radiata* and Pook (1986) for illustration of the effects on Eucalypts - and will undoubtedly be affected by soil salinity.

It follows that a single relationship between leaf mass or area, and some measure of stem size, established for a particular tree species at a particular time, cannot be definitive so it is important that the parameter values of equation (1) be established for as many as possible of the tree species used in agroforestry, and for as wide a range of conditions, as possible. It will generally be more useful if data are provided in primary form, i.e. in terms of leaf mass and specific leaf area (σ_f) rather than relating L directly to stem diameter. That provides no information about σ_f which can vary widely in the same species grown in different areas, particularly if there are large differences in aridity; σ_f in trees that grow in dry areas may be twice as large as in trees that grow in moist areas (see Specht and Specht, (1989) and Landsberg and Gower (1997), pp 55- 57, for discussion of the implications). Some of the problems arising from variability in relationships between d_b and w_f can be overcome by the use of non-destructive methods of determining the leaf area of trees, notably the LAI-2000 instrument (Li-Cor Inc.) and the Demon system with the Demsoft package (CSIRO, CEM) (see Lang et al. 1985; Lang and Yuegin, 1986; Lang, 1987; Welles, 1990). The best approach will, in most cases, probably be a combination of destructive sampling combined with non-destructive measurements, and the use of non-destructive measurements on a regular basis to follow changes in leaf area with time.

An interesting relationship, with respect to leaf area per tree, has been (apparently independently) identified by Specht (1972) and other authors. Specht applied a water balance analysis to a wide range of different areas in Australia, and came to the conclusion that ' the climax vegetation of a particular area fully exploits the soil

moisture available for plant growth'. In effect, he said, the structure and leaf area of climax vegetation must be such that transpiration is limited to the available water stored in the soil, plus rainfall (after correction for interception, run-off and drainage). This means that, in low rainfall areas, leaf area index will be low, and that high rainfall areas can support vegetation with high L^* . This seems, at first sight, like an obvious truism, but Specht must be given credit for demonstrating and supporting it with comprehensive data. Grier and Running (1977) demonstrated the relationship when they calculated the annual water balance for forest types ranging from the massive trees of the Oregon coastal range to the treeless plains east of the Cascade mountains, and plotted L^* against the water balance. They obtained a straight line with an r^2 value of 0.99. (Note that the actual values L^* used by Grier and Running were later found to be overestimates (Marshall and Waring, 1986). This does not affect the finding.) Woodward (1987) identified the same relationship, and used it in a model to simulate the global distribution of vegetation, as did Neilson (1995), who produced MAPSS, a model to simulate the distribution of vegetation across North America. The fundamental assumption under which MAPSS calculates water-limited vegetation types and density is that the leaf area of the vegetation in a region will tend towards a maximum that just utilizes available water. This is the assumption that vegetation will tend towards structural and functional equilibrium with its environment (see also Hatton and Wu, 1995).

Examples of experimental studies in Australia that support the conclusion that native vegetation, in water limited areas, will use all the water available to it, and develop a leaf area and structure adapted to do that, are those of Nulsen et al. (1986) and Dunin et al. (1985). Nulsen et al. carried out detailed hydrologic measurements, over an 11-year period, of the water balance of a West Australian catchment covered with undisturbed heath and mallee and found that rainfall was balanced by evapotranspiration. Dunin et al. found that, over five years, the water use by a Eucalypt forest (dominated by *E. maculata*) on the south coast of NSW, measured by a lysimeter, was approximately the same as rainfall. Dunin et al. (1995) subsequently wrote a note on the same data, in which they commented that the Eucalypts used water 'conservatively'. In fact, this is misleading: the trees used all the water available, and the results should not be taken to indicate innate 'conservativeness' in water use by Eucalypts. On some days when soil moisture content in the lysimeter was high, transpiration rates reached 6 mm day⁻¹, although the leaf area index of the community was about 3. All the indications are that where there is ample water available, Eucalypts will develop large leaf areas and transpire at high rates, when these are demanded by atmospheric conditions and water is relatively freely available in the soil. This assertion is supported by data of Myers et al. (1996): irrigated *E. grandis* in the Wagga Wagga area (the "Flushing Meadows" experiment) produced L^* of > 6 within three years and maximum transpiration rates reached almost 8 mm per day. Cromer et al. (1993) irrigated *E. grandis* in southern Queensland and produced trees with $L^* \approx 6$, while unirrigated trees had $L^* \approx 1.5$. The differences were undoubtedly caused by the effects of water stress on foliage growth, and by changes in carbon allocation, to favour roots over topgrowth when growing conditions were unfavourable (see later discussion under *The species question*; also Landsberg and Waring, 1997).

It seems unlikely that relationships between the leaf area of long-established vegetation communities in equilibrium with their environments, and available water, can be used as a guide to the leaf area that might be developed by isolated trees or relatively isolated groups of trees in the same area. Few land areas can now be regarded as undisturbed, so the conditions that lead to these equilibrium relationships may not exist, particularly if trees are deliberately planted, or their environment is radically altered by clearing round them. For example, if trees are in a run-on or (non-saline) discharge area, they may have access to considerably more water than is available from rainfall. Similarly, below-ground lateral flow, increased because of clearing, may provide, in effect, sub-surface irrigation. The presence of water tables, developed because of clearance of natural vegetation, or large volumes of stored water in deep soil, may allow the establishment and growth of species that would not thrive under the original environmental conditions. In the opposite direction, trees on shallow soil on hillsides or mounds, with poor infiltration, may receive much less benefit from a given amount of rain than trees on deeper soil on flat ground. The structure of the trees will also affect their hydrology. I noted earlier that isolated trees tend to have larger individual canopies than trees in closed-canopy communities. These will enhance the tendency to intercept and redistribute rainfall before it reaches the soil surface. Nulsen et al. (1985) noted that the mallee trees they studied, where the projected canopies covered about 21% of the land surface, redirected up to 30% of incident rain down the stems. This has a considerable effect on the distribution of water in the root zone, which in turn is likely to have a significant - possibly beneficial - effect on surrounding vegetation. (This can often be observed in pastures where, in summer, the grass under trees is often more green and dense than grass in the open; not only is it shaded, and so protected from high-intensity radiation, but it has access to more water round the base of the tree.) It is also likely that advection will cause the water use rates of trees in any of the arrangements depicted in Figure 1 to be significantly different, on a leaf area basis, from the rates that would be expected from large stands with continuous canopies (see *Transpiration and the water balance*).

Stomatal control

Water is lost from leaves through the stomata - minute pores on the surface of the leaves through which CO₂ moves to the wet mesophyll cells of the sub-stomatal cavities, from which water vapour evaporates. Stomata act as valves, opening and closing in response to changing conditions, and so controlling water loss from plants. The relative importance of stomatal conductance (g_s) and leaf area, in isolated or scattered trees, can be simply evaluated using the equation describing transpiration per unit leaf area in terms of the leaf-air vapour pressure gradient (ΔD , kPa) and a leaf conductance (g_l) - which includes stomatal conductance and the boundary layer conductance (g_a), assumed constant for this argument. (Appropriate values of the boundary layer conductance can be obtained from an empirical relationship with wind speed, derived by Landsberg and Powell (1973), which accounts for the mutual sheltering of clustered leaves.)

$$E = c \cdot g_l \Delta D \quad (2)$$

In equation (2) E is mass flux density ($\text{kg m}^{-2} \text{s}^{-1}$), c denotes a set of physical constants required for dimensional consistency and g_l has the units m s^{-1} . Since the equation is linear it indicates that any variation in either g_l or L will induce directly proportional differences in E for a given value of ΔD (assuming D is not high enough to induce stomatal closure). So if g_l is (statistically) the same for two similarly-exposed trees, over a period of time, then the total water loss in kilograms - obtained by multiplying E by and time (t) - will be proportional to L .

There has been a great deal of research aimed at finding out whether there are significant differences in the way the stomata of different tree species respond to environmental conditions - including water shortage - but there have been few demonstrations that the observed differences are significant. One of the problems is that it is difficult to make good measurements of stomatal conductance in the field: the variation tends to be enormous (see, for example Beadle et al. 1985a, b) and it is difficult to make enough measurements to establish whether differences are real or not. A study by Smith (1995), on windbreaks in an agroforestry project in the Sahel, provides the best data that I could find in support of the argument that differences in stomatal behaviour should be considered as major factors in evaluating possible differences in water use rates by trees. Smith made measurements on two Acacia species (*A. holoserica* and *A. nilotica*), which showed that stomatal conductance was consistently higher in *A. holoserica*. Over a 14-day period, water use per unit leaf area by *A. holoserica* was $1.13 \text{ kg m}^{-2} \text{ day}^{-1}$ compared to $0.88 \text{ kg m}^{-2} \text{ day}^{-1}$ from leaves of *A. nilotica*. (difference of 25% of the mean). However, on a projected crown (ground) area basis, over a cropping season, water use by *A. holoserica*, was about 347 mm, compared to 307 by *A. nilotica* (difference of 12 % of the mean).

In general, it seems likely that, in the case of isolated trees or sparse tree populations, differences in L will be far more important than differences in stomatal responses. Numerous papers, concerned with a wide range of tree species, have shown that differences in g_s are neither large nor consistent over time or position in the canopy [for some examples see Leverenz et al. (1982); Körner and Bannister (1985); Dye and Olbrich (1993); White et al. (1994)], while differences in leaf area between trees are often large. This conclusion is supported by the results in the paper by Hatton et al. (this publication).

The above argument does not imply that g_s is not important - it is essential to have good estimates of its value(s) and the way it varies with time and environmental conditions. This information can be obtained from an appropriate stomatal response model. Numerous such models have been developed: one of the more widely used is that by Jarvis (1976); a simpler model, easier to parameterise, was developed by Thorpe et al. (1980), while the most rigorous mechanistic approach currently available has been provided by Leuning (1995). The problem with these stomatal conductance models lies in their treatment of the effects of soil moisture. The Jarvis model treats stomatal responses to leaf water potential empirically. Leuning and Thorpe do not deal with it¹. Running and Coughlan (1988), who produced a forest productivity model called FOREST-BGC, used a simple ratio of soil water content in the root zone to estimate minimum leaf water potential ($\psi_{\min}$), from which they calculated g_s as a linear function of vapour pressure deficit (D) and $\psi_{\min}$. The routine relies on threshold values of $\psi_{\min}$, maximum values of g_s and assumes the slopes of the g_s/D relationship for various values of $\psi_{\min}$. McMurtrie et al. (1990) used a similar procedure in the BIOMASS model. Williams et al. (1996) developed a more complex, iterative procedure in which hydraulic resistances per unit leaf area were specified for each layer of a forest canopy. These resistances, with the transpiration rate for the layer calculated from a detailed micrometeorological model, lead to leaf water potential (ψ_l) values for each layer. A threshold ψ_l -value for stomatal closure is specified. The Williams et al. model works over hourly time steps, and also iterates in relation

¹ Leuning has subsequently introduced a term to account for the effects of soil water content on stomata (Dr Ray Leuning, personal communication).

to internal CO₂ concentrations, so their approach is much more detailed than can be justified for most agro-forestry work.

In fact all the approaches outlined in the previous paragraph, with the exception of the Jarvis model, are consistent with the view that the generally-observed stomatal response to vapour pressure deficit (D ; see, for example, Leuning, 1995; and for the responses of Eucalypts, Dye and Olbrich, 1993; Pereira et al., 1986; Pereira et al., 1987) can be regarded as a reflection of the fact that at high D the soil-plant conducting system cannot sustain the rate of loss driven by D , so g_s must fall. This may occur almost regardless of the soil water content in the root zone (see Landsberg and Gower, 1997). Landsberg and Waring (1997) used this argument to model stomatal conductance—normalised to a maximum value of g_s —as dependent **either** on D **or** a (non-linear) function of soil water in the root zone, depending on which was the most limiting. Essentially, the response to D is short-term (hours) while significant reductions in soil moisture are likely to take days. It would probably be difficult, in field situations, to detect by measurement the difference between the Landsberg-Waring approach and that of FOREST-BGC or BIOMASS. The problem lies in determining the point at which the transpiration rate of a tree or group of trees falls below the atmospherically-driven ('potential') rate because the rate at which water can be moved from soil to roots to leaves is lower than the rate determined by atmospheric conditions: in effect, we have to determine the soil water constraint function (see Figure 3, and discussion relating to it). This exercise will be greatly aided by the increasing use of sap-flow measurements, which give a measure of water use rates by single trees. These, for trees of various sizes, in a range of soil types, analysed in relation to measurements of soil water in root zones and g_s values derived from the P-M equation (see Granier et al. 1996) solved for g_s , will contribute to the accumulation of a data base that will establish a firm empirical basis for the models. Detailed models, such as the HYDRUS-2D package discussed and used later in this paper, can also be used to develop or test simpler, empirical relationships between water uptake from the soil and the transpiration rates of trees.

Root systems

Any discussion of tree water use and water use efficiency must include consideration of root systems. The length of root permeating unit volume of soil (root length density, L_V , m m^{-3}) determines the distance water has to move before being absorbed by a root, therefore the distribution of roots beneath trees, in terms of the total volume of soil exploited, is a major factor determining the amount of stored water potentially available to trees. The water available to a tree is determined by the rooting volume and the water holding characteristics of the soil. The volume of soil exploited by the roots of a tree will depend on the species, the size and age of the tree and the soil type - roots grow more easily through low density soils, and they grow preferentially where conditions are good. The distribution of tree roots in soil will, obviously, depend on the tree population, as well as the factors mentioned above, and one of the tasks in this project will be to describe the rooting patterns and distribution of isolated trees, groups of trees and lines of trees. (See also the suggestion, later, about determination of effective rooting volumes.)

There are many detailed treatments of water uptake by root systems, and movement through soils; this area of study will be important in this project. General treatments, at a relatively simple level, are provided by Landsberg (1986) and Landsberg and Gower (1996). Fowkes and Landsberg (1981) provided a theoretical analysis that should be useful in assessing the role of deep roots in maintaining water uptake and transpiration when the surface soil layers are dry. We can assume that, for a given transpiration rate by a tree, the rate of water uptake from any particular unit volume of wet soil is proportional to L_V . The relationship is almost certainly non-linear; research in agricultural crops indicates an asymptotic relationship, of the type sketched in Figure 1, but there is considerable uncertainty when roots are widely separated, which is almost certainly generally the case when tree roots penetrate deep into the soil (although see data presented by Carbon et al. (1980), which indicated that L_V for *E.marginata* was relatively high ($10 - 20 \times 10^3 \text{ m m}^{-3}$) at depths of 15 - 20 m). However, in view of the sparsity of information about the distribution of tree root systems, and the enormous spatial variation that will be encountered in the field, the assumption will serve as a working hypothesis.

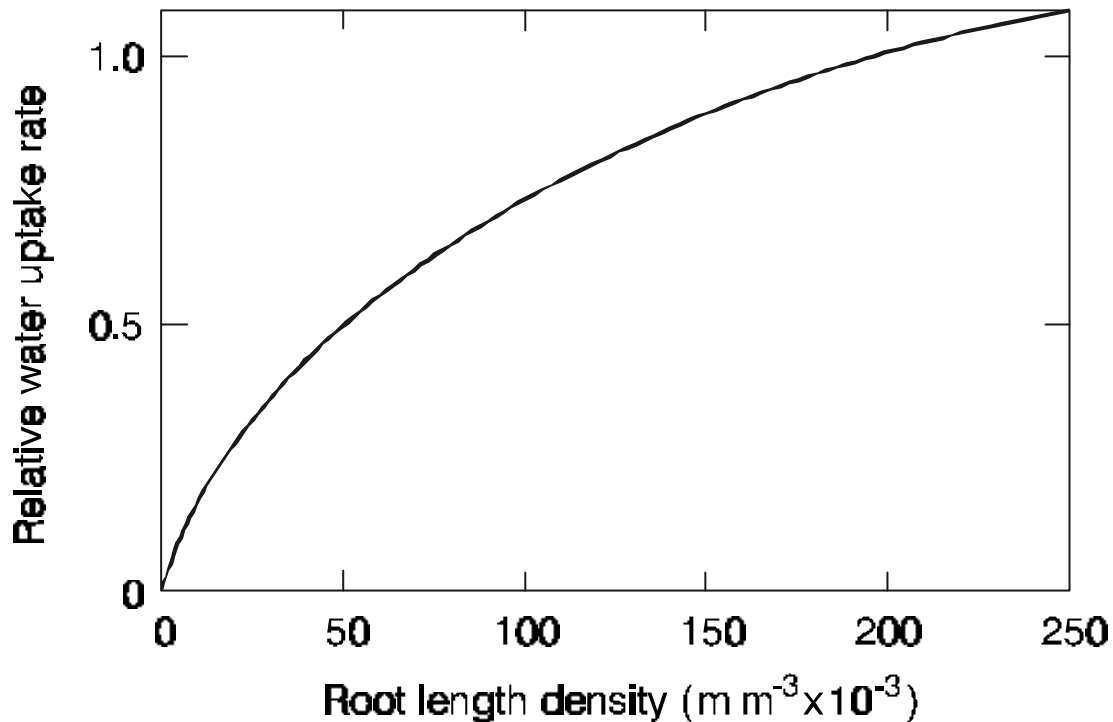


Figure 2. The general shape of the relationship between root length density (L_V) and water uptake. The exact shape of the curve and the point where additional roots make no further difference to water uptake will vary with soil type.

Tree roots vary enormously in size, from large structural roots to fine roots. The categories used to distinguish these root types are, of course, arbitrary, but are necessary. Roots of different sizes have different functions. Very large (diameters > 20 mm), large (10 - 20 mm) and medium roots (5 - 10 mm) are essentially structural support and framework roots, on which the fine (2 - 5 mm) and very fine (diameter < 2 mm) roots, that provide by far the greatest length and water and nutrient absorbing area, are carried. The root mass at any time is dominated by the larger categories, but fine/very fine (subsequently referred to as fine) roots provide the water and nutrient absorbing surfaces and are the largest sink for carbon (see Vogt et al. 1986). Their turnover rates are high; they tend to die off when the soil dries (see Deans, 1979) and regenerate when conditions become favourable. Detailed discussion of root mass and turnover in forests can be found in Landsberg, (1986, pp 103 - 109) and Landsberg and Gower (1997, pp 148-151).

There is an increasing amount of information about root systems in the forestry literature, relating to forest stands (including plantations and therefore blocks of trees in the landscape); the review by Vogt (1991), provides a mass of data on root biomass in forests. Haynes and Gower (1995) give equations, of the same form as equation (1), describing root mass of red pine in terms of d_b . Knight (this publication) provides an excellent review of information available, particularly about Eucalyptus roots.

A useful paper by Jackson and Chittenden (1981) gives regression equations describing the root mass of individual *P. radiata* trees. These have been used to calculate root mass and length for a (small) tree, with $d_b = 10$ cm, to provide the basis for calculations of root distribution and water uptake, the results of which are presented in Figure 3, in the next section. The estimate of total root (dry) mass for the tree is 5.2 kg, which would consist of about 8.5 m large/very large roots, 37 m of medium roots, 222 m small roots and 2.2×10^3 m fine roots, i.e. a total root length (L_{tot}) of about 2.4×10^3 m.

In most plants L_V tends to decline exponentially with depth (z). Gerwitz and Page (1974) collated data relating L_V to depth under crops and found the relationship to be general, i.e.

$$L_V = L_V(0) \exp(-k_L z) \quad (3)$$

Gale and Grigal (1987) found that root distribution of American tree species could be described by an equation consistent with equation (3). The coefficient k_L determines the rate of change of L_V with depth z . For forest stands - or uniform blocks of trees in the landscape - L_V is assumed horizontally homogeneous, but for isolated trees, or lines of trees such as windbreaks, it is reasonable to assume that the lateral change in L_V with distance

from the tree(s) will generally be described by equation (3). Experimentally, information on root length distribution can be obtained directly by excavation (total, or trenches) of the root systems of isolated trees or of windbreaks, or indirectly from water extraction patterns during drying cycles.

Landsberg and McMurtrie (1984) applied equation (3) to the radial change of L_V with distance from an isolated tree, and I have used it here to calculate the distribution of roots under the ‘sample’ tree considered above (other assumptions could be made) as a basis for calculations of water uptake patterns through the rooting volume, and their changes in time, presented in Figure 3, i.e.

$$L_V(z,r) = L_0 \exp(-k_1 z) \exp(-k_2 r_0) \quad (4)$$

Rooting volume is $V_R = \pi r_0^2 / 2 k_1$, where r_0 is the maximum radius of the root system and k_1 and k_2 are obtained by specifying that $L_V = 0.05 L_V(0)$ at the ‘limit’ depth and at r_0 . L_0 is then obtained as $L_0 = L_{tot} k_1 k_2^2 / 2$. Average L_V is L_{tot} / V_R ; in this example it is about $50 \times 10^3 \text{ m m}^{-3}$.

Root length density will, clearly, vary with soil type, and the exponential distribution used here is unlikely to be a good description in specific cases. It is important that we gather more information about L_V , particularly in situations where scattered trees or trees in rows are being studied: there are strong indications that the root systems of trees in these arrangements may spread laterally much further than would be expected from studies on trees in communities (Chin Ong; personal communication. See also Knight, this publication). If this is the case it has very important implications for local hydrology, since root distribution is of primary importance in determining water uptake patterns, the length of time trees will continue to transpire rapidly and the extent to which trees will compete with surrounding crops and pastures. It will not be possible to obtain precise information in any particular situation, nor is this a useful objective: the aim must be to gather indicative information about the roots of various species and their distribution in a range of soil types and in different arrangements. A suggestion about simplifying the interpretation of these data is offered in the discussion following Figure 3.

Transpiration and soil water balance

The physics of transpiration and water use by vegetation are well established and thoroughly documented. Landsberg (1986) summarised the theory and gave parameter values for the equations for continuous forest canopies; Landsberg and Gower (1996) updated that treatment. We can, with a high degree of confidence, calculate the water use rates of full-canopy stands, particularly when they are not short of water (see, for example, McMurtrie et al. 1990; Hatton et al., 1993; Hingston et al., 1995). Essentially, for continuous canopies with $L^* < 3$, we need an estimate of the radiant energy absorbed by the canopy (net radiation), the air saturation deficit (vapour pressure deficit) and values for the canopy conductances. When $L^* \geq 3$ there are general relationships from which conductances can be estimated (see Kelliher et al. 1995). The point that I would add to the treatment presented by Kelliher et al. is the need to correct canopy conductance for (the almost universal) stomatal response to humidity.

A range of methods is used to measure or estimate tree water use rates, but the problem of interpreting the results, with a view to making generalisations, or extrapolating from them, is often compounded by the fact that data may not be reported in a standard way. The point was made at the beginning of this review, and bears repetition: under particular atmospheric conditions the rate at which trees transpire depends on the surface area of the leaves exposed to the atmosphere, the extent of the root system which absorbs water from the soil, and the amount of water in the soil. Therefore, it is important that information about leaf area be provided and that, if results are reported in terms of stem diameter or basal area, or crown size, values for the parameters of equation (1) are supplied so that leaf area can be calculated. Similarly, it is not helpful to provide estimates of tree age, or even stand density, unless there is sufficient additional information to allow calculation of L^* or leaf area per tree.

It is also important to provide as much information as possible about the weather conditions pertaining when tree water use measurements are made. Clearly measurements made across hourly and daily intervals will show variation in transpiration rates from zero to (possibly) high midday values, if the weather is hot and dry and there is adequate soil moisture available. When measurements are made over weeks or months (eg water balance data) the peaks will be masked and the average result will depend on the range of weather conditions - particularly rainfall, in the case of unirrigated systems - experienced over the study period.

Maximum transpiration rates will occur when the soil is wet, the air is dry (high values of D) and radiant energy income is high. Some representative values are given in Table 2. Minimum rates may, of course, fall to zero,

although all the studies represented in Table 2 indicate normal minimum transpiration rates of about 1-2 mm day⁻¹.

Table 2. Maximum measured transpiration rates from full-canopied Australian forests.

Species and situation	Transpiration rate (mm day ⁻¹)	Data source
<i>P.radiata</i> (ACT), irrigated	8	Myers and Talsma (1992)
<i>P.radiata</i> (Sth Aus.), unirrigated	6-7	Teskey and Sheriff (1996)
<i>E.maculata</i> , unirrigated	6-7	Dunin et al. (1985)
<i>E.nitens</i> , <i>E.delagatensis</i> (Tas.) unirrigated	> 4	Honeysett et al. (1992)
<i>E. grandis</i> (Qld), unirrigated	5.7	Eastham et al. (1988)
<i>P.radiata</i> , <i>E.grandis</i> (NSW), irrigated	6-7	Myers et al. (1996)

For trees in rows, and single trees, the papers by Butler (1976), Thorpe (1978) and Green (1993) provide detailed treatments of leaf energy balance (see also Leuning and Foster, 1990) and the use of combination (energy balance- mass transfer) equations to calculate transpiration rates per unit leaf area. They show that, given an estimate of leaf net radiation, the appropriate weather data and estimates of g_s , the P-M combination equation can be used to calculate rates of tree water use with considerable accuracy. Green compared calculated rates with sap flow measurements and obtained correspondence within $\pm 10\%$. The tree water use rates used to develop Figure 3 were based on Green's data; during the period of his experiment transpiration per unit leaf area varied from about 0.5 to 1.5 kg m⁻² day⁻¹ (cf. the data from Smith (1995) cited earlier) ; multiplying these by $L = 13 \text{ m}^2$ indicates that water use rates of 6, 12 and 18 litres per day cover the normal range for a tree of this size. It is interesting to note that, on a leaf area basis, Teskey and Sheriff's (1996) measurements on *P.radiata* showed maximum transpiration rates of about 1 kg m⁻² day⁻¹ - the failure of these trees to reach higher rates is almost certainly caused by the lower leaf net radiation in the canopy, and differences in g_s : Green (1993) showed 2-fold differences in g_s in sunlit and shaded leaves.

When the soil is wet the central problem, in relation to calculations of water use by scattered or isolated trees, is the characterisation of the degree of interference between neighbours, in terms of radiant energy and air flow. The radiant energy problem can be solved by the use of detailed models of energy interception, which require the tree crown to be divided into segments. The leaf energy balance is solved for the foliage of each segment on hourly time-steps. The use of such models is limited by knowledge about crown dimensions and diurnal radiation regimes, although they may be used to develop and improve simplified operational relationships between short-wave incoming solar radiation (ϕ_s), net radiation on a land area basis (ϕ_n) and leaf net radiation - the energy available for transpiration at the leaf surface - for trees of different sizes, shapes and leaf area density. However, in most cases simple empirical relationships will suffice. The uncertainties associated with using them are likely to be much smaller than the uncertainties arising from inadequate knowledge about, or variation in, tree crown characteristics, the volumes of soil exploited by roots and soil water holding properties. Examples of calculations of water use by spaced trees are given in Table 3 in the section on 'Implications of tree arrangement'.

If the soil is dry the rate at which water can move through the soil to the roots, in response to the water potential gradients created by transpiration and extraction, will be lower than the rate required to meet the demand, and transpiration rates will fall (see discussion in Landsberg and Gower, 1997; pp 108 - 110). This question of whether tree root systems can obtain water from the soil fast enough to meet transpiration demand is central to the calculation of tree water use rates over extended periods of time, which may include long periods when the soil in much of the root zone is relatively dry (see Figure 3 and associated discussion). Three papers on Eucalypts demonstrate the differences that can occur, depending on the depth of soil exploited by the roots. Dye (1996) measured water uptake by two stands of *E. grandis* in South Africa, both of which had rainfall excluded from the soil surface for many months. At both sites trees extracted water from depths to 8 m from the beginning of the experimental period, which suggests that L_v at that depth remained high enough to produce short pathlengths between roots and hence low soil-root resistance to flow. The uptake patterns changed surprisingly little over the period of the study, and the trees did not show much sign of stress. However, transpiration rates increased markedly when the covers were removed from the surface of one plot, after seven months, and soil water was replenished. In contrast, a study by Eastham et al. (1988) in Queensland, also with *E. grandis*, showed that the trees extracted all the available water to a maximum depth of 5.6 m in 1985, reaching a maximum transpiration rate of 5.6 mm day⁻¹. Rainfall in 1986 was lower, stored water in the soil was not replenished and consumption by the trees was significantly lower in that year. The measurements made by Honeysett et al. (1992) showed that, between November 1986 and April 1988, apart from three 14-day intervals in the first year when net recharge of

soil profiles occurred following high rainfall, there was cumulative loss of soil water and decrease in transpiration rate of both *E. nitens* and *E. delegatensis*; when available soil water in the root zone - measured by neutron probe - was almost depleted transpiration rates had fallen to 27% of the maxima. Measurements were made to 1.2 m in this study and 'encompassed the total root zone and in most instances the total soil profile' (Honeysett et al., 1992). An interesting example of the influence of root systems on tree growth occurred in Western Australia, where two plantations of *E. globulus* completely exploited the water to a depth of about 1.5m, which resulted in drought stress and death of some of the trees (Hingston et al., 1995). In other plantations, where there was a greater depth of soil, or the trees had access to water tables, there was no tree death, and it does not usually occur in the native trees in the area. Nulsen et al. (1985) found that deep-rooted - albeit relatively small - native trees such as mallee (*Eucalyptus* species) may continue to transpire through long rainless periods.

Figure 3 provides a clear and interesting illustration of the influence of soil moisture on transpiration rates. It was produced using a software package (HYDRUS-2D) which calculates water uptake from soil exploited by plant roots - essentially the analysis described by Landsberg and McMurtrie (1984). The object of the exercise was to determine whether a detailed model of water uptake by root systems can provide information on the limitations imposed on transpiration rates by declining soil water content in the root zone. We assumed a soil with the moisture characteristics of a sandy clay, and a tree root system with lengths given by the Jackson and Chittenden (1981) equations, extending for a radius (r_0) of 1.5 m from the trunk, and to depth 2m. Root length density (L_V) decreased exponentially away from the stem base in both lateral and vertical directions. The leaf area of the 'sample' tree was estimated using equation (1) with general values for c_f and n (see Landsberg and Waring, 1997) and $\sigma_f = 6 \text{ m}^2 \text{ kg}^{-1}$, giving $L = 13 \text{ m}^2$. 'Potential' transpiration rates of 12 and 18 litres day^{-1} were used (see discussion about transpiration from single trees). The technical details are provided by Dr John Knight as Appendix 2 to this paper: essentially water uptake is proportional to root length density - which determines the pathlength across which water must move from soil to root surface - and bulk soil water potential (ψ_s) in any part of the soil-root volume. When the soil in any region is wet, uptake is proportional to L_V , but the rate decreases linearly after a critical value of ψ_s , reaching zero at a specified value of ψ_s .

The upper diagram of Figure 3 shows the time course of transpiration for the two potential transpiration rates: as the soil dries, and the water uptake rate from the soil falls below the potential transpiration rate, so the actual transpiration rate falls. This is the situation on which comment was made earlier (in relation to the effects of D on g_s) - the soil-plant conducting system cannot sustain the rate of loss driven by atmospheric demand, so g_s must fall. To illustrate this point I have used the P-M equation to calculate the potential transpiration rates, then solved for g_s at a number of points on the actual transpiration rate curves. The resulting $g_s/g_{s,\text{max}}$ values are given on the curves in the top

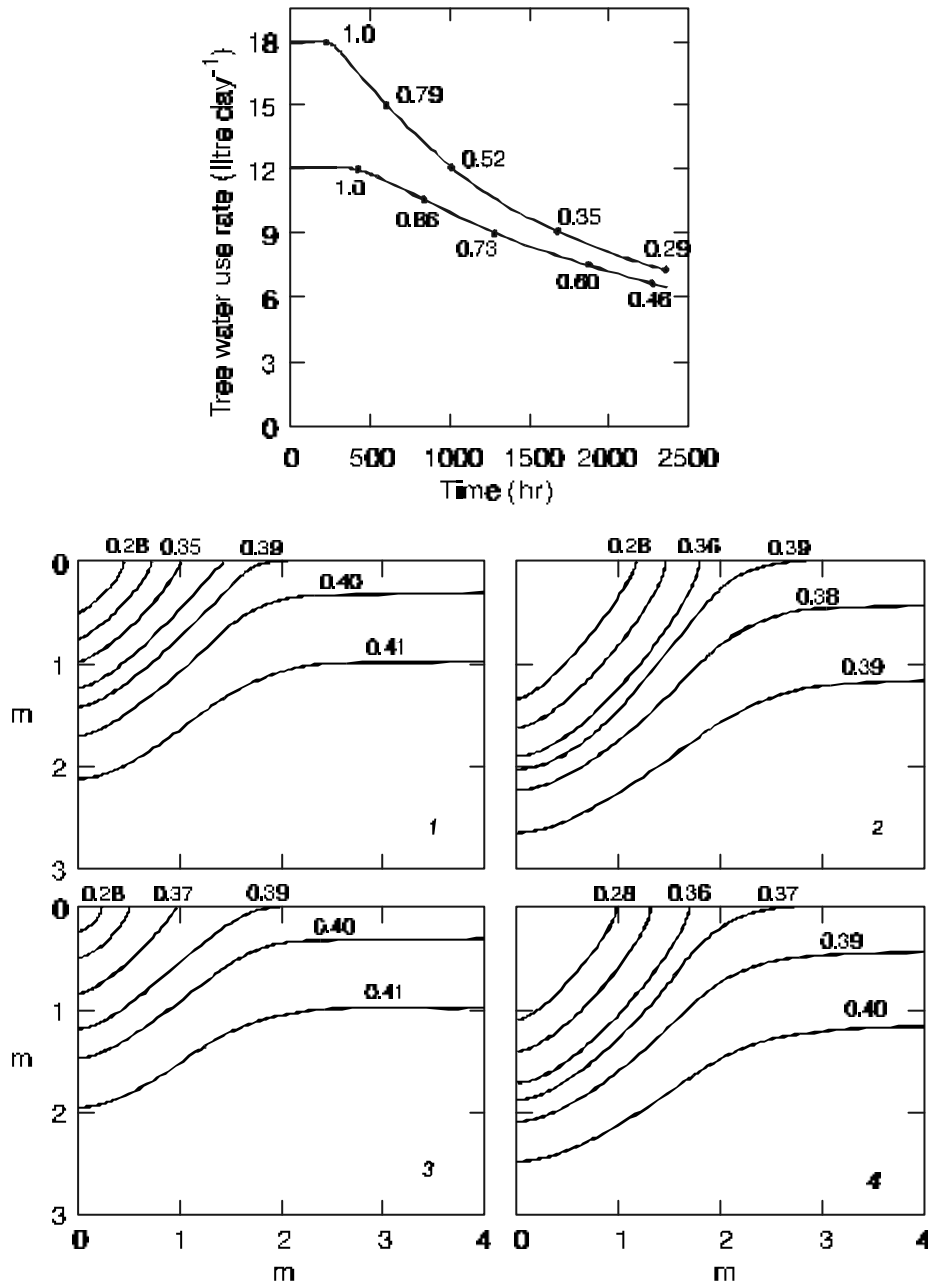


Figure 3. Results from HDRUS-2D. The upper graph shows the time course of transpiration rate by a tree with $L = 13 \text{ m}^2$. The potential transpiration rate (E_{pot}) was $18 \text{ litre day}^{-1}$ (top curve) and $12 \text{ litre day}^{-1}$ (lower curve). The soil was initially wet. The curves reflect the rate at which water can be extracted from the soil by the root system, and so indicate actual transpiration rates. The numbers on the curves are the ratios ($g_s/g_{s\text{max}}$) of the values of stomatal conductance consistent with the actual transpiration rates (g_s), relative to the values when the trees were transpiring at the potential rate ($g_{s\text{max}}$). The shape of the curves is consistent with the model of the effect of soil water content on stomatal conductance used by Landsberg and Waring (1997)

The lower graphs show the distribution of soil water content with distance from the tree stem at about the time $g_s/g_{s\text{max}}$ first fell below unity (1,3), and after 2400 hrs (2,4). Numbers on the curves are volumetric water contents (θ). The upper pair relate to $E_{\text{pot}} = 18 \text{ litre day}^{-1}$ and the lower pair to $E_{\text{pot}} = 12 \text{ litre day}^{-1}$

part of Figure 3. (Note: the two sets of g_s values are not exactly comparable with one another because slightly different values of ϕ_{nf} were used to make the two sets of calculations. However, the g_s values are realistic). These calculations demonstrate quantitatively the interactions between stomatal conductance and soil water content at a given leaf area. If soil water stress is prolonged to the point where leaf fall results, and then restored (by rainfall), transpiration rate per tree, under specified conditions, will be determined by the new leaf area, i.e. it will be reduced until new leaves are produced. Hatton and Wu (1995) have presented an equation for transpiration rate per tree in terms of leaf area, with a term which is dependent on soil water and reflects the probability that leaves will shed in response to periods of water stress. Their analysis is based on the assumption, noted earlier, that

trees tend to hydrological equilibrium with their environment. This is not contentious, but trees do not adjust their leaf areas constantly and rapidly: on a day-to-day basis the balance with the environment is maintained by stomatal adjustment.

The transpiration rates in Figure 3 do not reach zero - in fact the rate of reduction slows as soil water content decreases and, at both potential rates, the actual transpiration rate remains steady at about one-third of the potential after 2500 hours. This is, apparently, because the model allows movement of water from the wet soil outside the root zone, into the root zone. This slow movement will continue for a long time. Its significance in 'real world' situations is doubtful. For present purposes I have assumed that the soil moisture content at which water uptake stabilises at a low rate indicates the limit of available water. The bottom four diagrams in the figure show the drying patterns that can be expected as trees dry the soil volume. The way these are re-wetted by rainfall, and the accompanying stem-flow, is likely to be of considerable hydrological significance.

The HYDRUS-2D package is a research tool. Analyses such as those leading to the results in Figure 3 are not likely to yield exact predictions of what will happen in any practical situation because we are never likely to have the necessary information about root length density and distribution, nor are the (implicit) assumptions about soil homogeneity in the root zone likely to be satisfied in the field. However, such analyses provide insights into the way systems function, and can be used to explore the consequences of, and sensitivity to, various assumptions. Furthermore, analyses taking account of a great deal of system detail, such as those that can be done with the HYDRUS-2D package, allow the development of simpler relationships that are likely to be of much greater value for practical decision-making or assessment of the results of particular actions or decisions, such as the effects of tree planting. The suggestion in the next paragraph illustrates the possibilities.

An idea that emerges from Figure 3 is that it should be possible to estimate an 'effective rooting volume' for trees, based on the changing patterns of transpiration as the soil dries. (The argument applies to trees in stands as well as to isolated trees or trees in lines.) If we measure the transpiration rate of a tree when the soil is wet, and monitor the changes over a suitable drying cycle, we can calculate the amount of water used by the time transpiration falls to some value such as (say), 10% of the potential rate. The potential rate would be defined in terms of the tree leaf area and the value of g_s when the soil was wet. The only other information required would be volumetric soil water content near saturation (θ_{sat}). For example, in the case of the soil considered in Figure 3, for which $\theta_{sat} \approx 0.43$, the amount of water transpired in 2500 hours was about 1.2 m^3 so the 'effective rooting volume' would be $1.2/0.43 \approx 2.8 \text{ m}^3$. The criterion for defining the lower limit of available water in practice might be the ratio of actual to potential transpiration rate under standard conditions, some variable such as pre-dawn water potential or, in the rather extreme case, the commencement of leaf fall in response to water stress. The lower limit of available water will **not** be defined by a measure of soil moisture content, although such measurements would be useful adjuncts to this type of investigation. Estimates of the effective rooting volume, and root distribution, would provide useful insights into the extent to which the same tree species was able to exploit different sites, and valuable comparative data illustrating differences between trees of different sizes (see Figure 4).

The other factor influencing isolated trees or trees in small blocks will be advection: if trees in pasture, or adjacent to crops, have access to water at depths that the pasture or crop cannot reach, the trees will continue to transpire while the smaller plants have closed stomata. The radiant energy incident on the pasture/crop will be largely dissipated as sensible heat, raising air temperatures and vapour pressure deficit. The warm, dry air advected onto the trees will raise transpiration rates per unit leaf area above those that would be expected from the same trees contained in a large stand. This has been demonstrated analytically by Raupach (1993) for landscapes broken up into 'microscale' patches of forest and crop. The enhancement in evaporation rate, for tree cover that constitutes 30% of the area, would be about 16% under Raupach's assumptions. It seems likely that, for isolated trees, or very small patches, the effect could be larger. If the surrounding pasture/crop is transpiring freely, the advection effect would be negligible.

Transpiration is an important component of the hydrology of a system, but all the terms of the hydrologic equation have to be accounted for to calculate the soil water balance and content at any time. The principles of water balance calculations are straightforward, and encapsulated in the hydrologic equation:

$$P - I - q_R - q_D \pm q_{lat} - \Delta\theta - E = 0 \quad (5)$$

where P is precipitation, I is intercepted water which will be evaporated from the canopy, q_R is surface run-off, q_D is drainage out of the root zone, q_{lat} is the lateral (below-ground) flux, $\Delta\theta$ is the change (Δ) in volumetric soil moisture content (θ) and E is evaporation and/or transpiration. Equation (5) may be applied to any volume of

soil, from a catchment to the volume exploited by a plant. In any given situation where the influence of trees on the local (or regional) soil water balance is to be assessed, it is necessary to measure or calculate all the terms in the equation to solve it for $\Delta\theta$ over the time interval of interest. For the example considered in Figure 3 we, in effect, reduced the equation to $\theta(t) = \theta(t-1) - \Delta\theta$, where $\Delta\theta$ (per day) = E . However, in any study of tree water use, regardless of the way the trees are arranged, it is important that we have estimates of I and q_R for rain events of varying intensity and size. Aston (1979) provided useful data on the amount of water that could be held on the foliage of individual trees and q_R will vary with slope, soil wetness, and surface condition - including the presence of grass or crops. Given this information, the estimation of $\theta(t)$ becomes a matter of 'accounting'; q_D is added to the water table. Vertessy et al. (1993) have described a complex model (TOPOG-Yield) that deals with saturated and unsaturated water flow in the soil, in both vertical and horizontal planes. TOPOG-Yield requires a contour map of the catchment being analysed, as well as data characterising the soil hydraulic properties. The model calculates the water balance of catchment elements, which can be assigned different vegetative characteristics. When water tables, or saturated regions, develop in the soil lateral sub-surface flow (q_{lat}) is allowed. TOPOG-Yield will be the tool needed to explore, at catchment level, the implications of variations in tree water use discussed here (see also Vertessy et al., 1995). Other examples of Australian studies on soil water dynamics and the water balance, are those of Sharma et al. (1987), in Western Australia and Honeysett et al. (1992) in Tasmania. A simplified model-based treatment of evapotranspiration by trees, and its impact on water stored in the soil, was provided by Leuning et al. (1991).

Implications of tree arrangement

Tree arrangement may have considerable implications for hydrology. We may examine this by reference to Figure 1, arrangements *a* (block planting) and *e* (scattered trees), and some sample calculations.

Let us assume two one-hectare paddocks, one with 200 trees in arrangement *a*, the other with 200 almost identical trees in arrangement *e*. The remaining area, in each case, is grass-covered. We also assume that the soil in the tree root zones is wet enough for transpiration to proceed at rates determined by atmospheric conditions. The leaf area of the trees is $20 \text{ m}^2 \text{ tree}^{-1}$. The trees in the block are spaced at $2 \text{ m} \times 3 \text{ m}$, so they occupy 1200 m^2 with L^* slightly greater than three. In arrangement *e* average ground area per tree is about 50 m^2 . We consider a day when, at midday, incoming solar radiation is, say, 800 W m^{-2} (giving net radiation ϕ_n of about 450 W m^{-2} from standard empirical relationships for a closed canopy - see Landsberg, 1986). For the scattered trees we take the same environmental conditions, but assume - following Thorpe (1978) and Green (1993) - that the energy available at the leaf surfaces (leaf net radiation, $\phi_{n,l}$) is $0.5\phi_n$. Vapour pressure deficit and the appropriate conductance values are given in Table 3. Midday transpiration rates are calculated from the P-M equation. Assuming a 14 hr day, with sinusoidal variation in transpiration rates, integration gives the daily water use (last row, Table 3).

Note the comment made earlier, that it will be of considerable value if canopy conductance values for scattered trees are derived from stem flow measurements, when the P-M equation can be solved for g_c (see Granier et al., 1996)

Several points arise from the results presented in Table 3. First, it would obviously not be informative, and may be misleading, to use the transpiration rate of the 1200 m^2 block to derive an average transpiration rate for the whole (1 ha) area. Second, it is interesting that

Table 3. Comparative rates of water loss from a block of 200 trees (arrangement *a*, Figure 1. LAI in the block ≈ 3), and the same trees scattered uniformly across one hectare (arrangement *e*, with 50 m^2 ground area tree^{-1}). Leaf area $\text{tree}^{-1} = 20 \text{ m}^2$.

Variables	Block	Scattered
Net radiation (W m^{-2})	450 (unit ground area)	225 (unit leaf area)
Vapour pressure deficit	$1.5 \text{ kPa} = 9 \times 10^{-3} (\text{kg kg}^{-1})$	
Boundary layer conductance (m s^{-1})	$0.2 (g_a, \text{canopy})$	$0.02 (g_a, \text{leaf})$
Canopy/stomatal conductance (m s^{-1})	$0.015 (g_c)$	$0.005 (g_s)$
Midday. transpiration rate	$0.72 (\text{mm hr}^{-1}; \text{unit ground area})$	$0.245 (\text{kg m}^{-2} \text{ s}^{-1}; \text{unit leaf area})$
Daily water use	$7.7 \times 10^3 (\text{litres ha}^{-1} \text{ day}^{-1})$	$43.7 (\text{kg tree}^{-1}) = 8.7 \times 10^3 (\text{litres ha}^{-1} \text{ day}^{-1})$

The effects of falling soil moisture contents in the root zone would be reflected in changing values of canopy/stomatal conductance. To illustrate, we may correct g_s by $g_s/g_{s,max}$ ratios similar to those shown on the upper part of Figure3, and calculate the resulting transpiration rates for the scattered trees. For

$g_s/g_{s,max}$	=	0.95	0.75	0.55	0.35	0.15
these are		0.24	0.21	0.16	0.12	0.05
equivalent to		42.8	37.4	28.5	21.4	8.9
		litres tree ⁻¹ day ⁻¹				

the calculation for scattered trees gave a slightly higher water use rate than that for the block planting, although we cannot attach too much significance to this; the results obtained depend on the assumptions made. We could argue that the difference should have been significantly greater, since scattered trees would almost certainly have a larger leaf area per tree than trees in competition with one another in a block. Furthermore, the calculation takes no account of advection - if the pasture between the scattered trees was dry they would be subject to significantly enhanced energy loads because of radiation reflected from the ground, and possibly higher values of D because of sensible heat from the ground, warming the air. Guided by Raupach's (1993) analysis, we would be justified in increasing the water loss from the scattered trees by 15-20%, which would indicate rates of water loss up to 30% higher, for the pasture as a whole, than from the trees in arrangement *a*. These calculations and assumptions need to be tested by appropriate measurements, but they indicate that, if the grass and upper soil layers are dry, transpiration per hectare can be expected to be higher from trees scattered across paddocks (arrangement *e*), than from the same number of trees in a block on part of the paddock (arrangement *a*). We would not expect this if the pasture was transpiring relatively freely.

The different tree arrangements clearly have within-paddock hydrological implications in terms of processes such as rainfall interception, wetting patterns and groundwater movement, as well as tree water use. The lateral spread of the root systems will influence the drying patterns, and consequently the soil re-wetting and groundwater re-charge patterns. At paddock scale we cannot pretend that soil water content is uniform, and calculate probable recharge on the basis of average depth of water extracted per unit land area. It may be necessary to deal with rainfall interception and soil water recharge in terms of the proportion of an area covered by trees, and that covered by grass. These various possibilities are apparent from Figure 4, but are not explored further here.

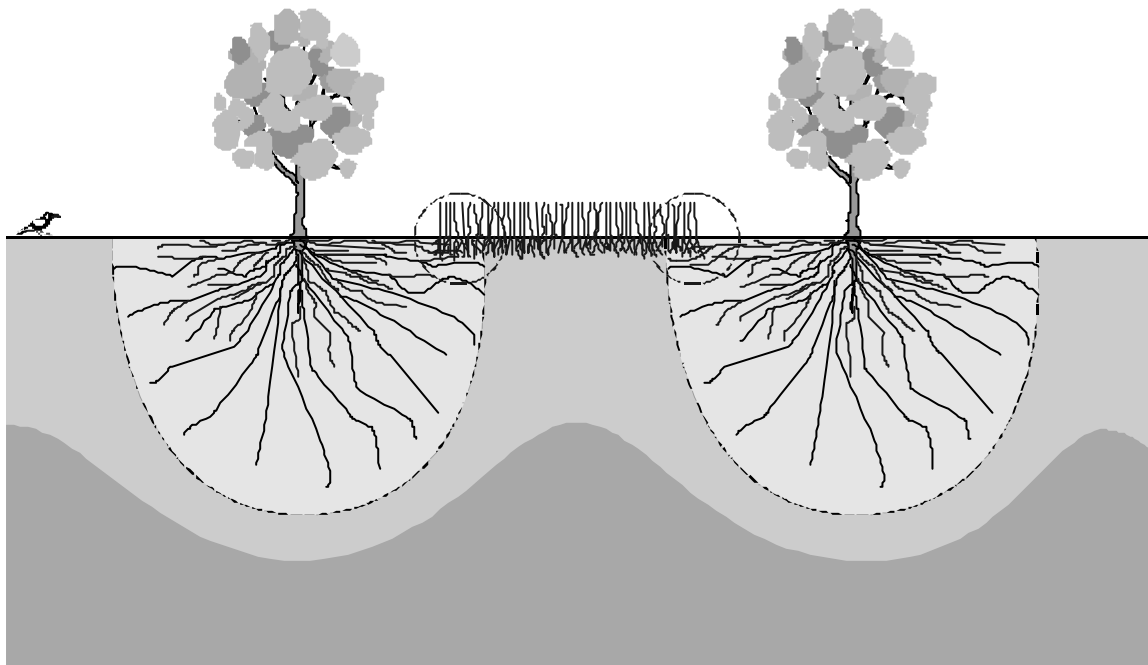


Figure 4. Diagrammatic representation of the root systems of scattered trees, or trees in lines, and the way they will interact with crop/pasture root systems. We would expect water extraction patterns to produce the sort of wet soil profiles sketched. The major 'interaction zones' are circled. The soil is likely to dry out most rapidly in those areas, after which the trees will tend to draw most of their water from deeper in the soil. Clearly the very different water content of the various zones will cause different wetting patterns when rain events are not large

enough to completely wet the depleted volumes below the trees. Heavy rain will cause water table recharge preferentially beneath the crop/pasture.

The question of species

The question of what species to plant in a particular place is always one of the first asked in any discussion about agroforestry. The answer, of course, depends on the objectives of the tree planting, but if a primary objective is water use and the amelioration of water balance problems it must depend on 'old fashioned' knowledge about what will establish and grow well. Essentially, the trees that grow best and biggest in a particular place will use the most water. Species selection cannot be based on consideration of tree water use per unit leaf area and I have found no evidence of systematic and consistent variation in the water use rates of different tree species. This is not to say that such differences do not exist, but they are not identifiable. A brief re-statement of the factors considered in this review shows why.

The water use rates of trees (different species) may be different if, under the same growing conditions, they produce (approximately) the same leaf area, in the same crown structure, but have significantly different stomatal conductance. There is no evidence that this happens. If it did (and assuming the hypothesis outlined here with regard to g_s in relation to soil water and root water uptake is correct), physiological differences in stomatal functioning will only be significant under conditions of non-limiting soil water. When soil water becomes limiting the relationship between the soil volume exploited by the roots, and the leaf area of the trees, becomes the factor controlling water use. Furthermore, the trees with higher initial values of g_s will deplete the soil water more rapidly, so the amount of water used over a drying cycle may not be greater than that used by trees with a more conservative strategy.

It follows, from these arguments, that we are unlikely to learn anything definitive about the relative performance of species, in terms of water use efficiency, by studying them at leaf level; i.e. by measurements of stomatal conductance and photosynthetic performance. Measurements of g_s should be made, and will provide useful data, but the growth patterns of trees in particular sites will be the major factor determining tree water use. Information is needed about growth rates in terms of the production and maintenance of the tree crowns and leaf area. But, for sustained high water use, the trees must also produce large, deep root systems, not because these enable them to remove water from above deep water tables but because such root systems will enable them to survive long periods of drought. In this respect the equilibrium hypothesis provides a useful framework for considering the best species for an area: trees that grow rapidly on water stored in soil profiles, but die when that water is exhausted - as happened in Western Australia - are not, in the long term, useful. The survivors that use all the water are those like *E.marginata* (Carbon et al., 1980) or the mallee species (Nulsen et al., 1986) that produce large, deep root systems.

There is a cost associated with large root systems. The production of roots diverts carbon from the production of stems, branches and foliage. Trees tend to allocate more carbon to their root systems when growing conditions become unfavourable (see Landsberg and Waring, 1997, for review and discussion). This can be illustrated by some elementary algebra:

if the dry mass increment (net primary production) over a given interval is ΔW , this must be allocated to stem and foliage growth ($w_{s,f}$) and roots (w_r);

if the allocation coefficients are $\eta_{s,f}$ and η_r , where $\Sigma \eta_i = 1$, we have

$$\Delta w_r = \Delta W \eta_r \text{ and } \Delta w_{s,f} = \Delta W(1 - \eta_r).$$

If poor growing conditions cause η_r to increase from, say, 0.25 (about the minimum allowable for root system maintenance) to 0.5 - a reasonable expectation - stem and foliage growth decreases from 0.75 to 0.50, a 30% reduction in topgrowth. This simple calculation, which appears to be well-founded in biological reality, indicates why the trees that survive in dry areas tend to be small (*vide* the mallee) and slow growing (e.g. jarah). There is, in a famous phrase, 'no free lunch': one of the most important factors influencing the ability of species to grow - and use water - in dry areas is the considerable variation in the capacity of species to allocate carbon to their roots.

The possible permutations of the processes affecting water use, and water use efficiency are endless. We have to be clear about why we want the trees (to solve a groundwater problem, as windbreaks, for alley-cropping...) and, in each case studied, we have to make the measurements and observations that will provide the information needed to determine what is happening at a particular place, and why some species appear to do better than others under specified conditions.

Conclusions and recommendations

A number of conclusions emerge from this review of water use by trees in relation to agroforestry and trees in the 'agricultural landscape'. They are:

- given an adequate physical description of a canopy, we can make accurate calculations of transpiration rates by tree canopies (from full canopy to isolated trees), particularly if soil water is not limiting, i.e. if the trees can obtain water from the soil fast enough to meet the demands imposed by current atmospheric conditions. "Accurate" means that errors in the calculations of transpiration per unit leaf area, for real situations, are likely to be smaller than uncertainties attributable to factors such as the amount of leaf present or the effects of soil water content in the root zone on water uptake rates
- there are extant stomatal response models that are good enough to provide the estimates of stomatal conductance (g_s) needed to calculate transpiration rates when soil water is not limiting. Models that include the effects of soil water appear to provide satisfactory results (in terms of correspondence between observed and simulated soil water balances under forests), but these require evaluation, and probably improvement, in relation to scattered trees or trees in lines. We need to 'calibrate' canopy leaf conductance values against transpiration rates measured by methods such as stem flow under a range of soil moisture conditions. The accumulation of a body of empirical data, founded on a sound theoretical base, will allow increasingly confident prediction of 'real world' system behaviour
- we can calculate the patterns of water uptake from root systems with specified distribution of root length density. The limitations, in terms of correspondence with reality, are likely to be imposed by inadequate knowledge of root mass, length and distribution. Such calculations could be used heuristically by evaluating a range of soil types with 'best guess' estimates of root distributions. Combined with realistic corresponding values of leaf area and transpiration rates, they will lead to improved information about stomatal responses to soil water and effective root volumes and root distributions

A number of requirements for experiments and measurements emerge from this review. To provide the data needed to test and refine the models we already have we must:

- describe the systems we are working with in agreed, physically-meaningful terms. In the case of tree size, shape and distribution, the descriptions should be in terms of height, crown size and shape, leaf area and the coordinates of trees in the landscape. The coordinate system used is probably best based on a reference point at each site
- gather data that allow the calculation of parameter values for the allometric equation (equation 1) so that the variation in those values with tree species, size, age and arrangement can be assessed and general relationships formulated. Use non-destructive methods to monitor changes with time
- carry out studies on root mass and distribution wherever possible to determine the limits of root biomass, the general structure of the root systems of various species and the influence of soil type and condition on root growth
- measure soil moisture content, and the way it changes with depth, distance from the trees and time, in relation to isolated trees and trees in various arrangements. The hydraulic properties of the soils should be adequately described. These measurements will be crucial in providing test data for calculations made with transpiration/soil water balance and distribution models
- measure stem flow rates on trees in various situations. These measurements will provide test data for transpiration calculations and, crucially, allow evaluation of the effects of drying soil on water uptake rates
- at all experimental sites ensure good quality, continuous weather measurements, including measurements of short-wave incoming radiation. Rainfall should, preferably, be measured by automatic gauges that give the intensity and duration of storms, as well as total precipitation over 24-hour periods
- stem flow and canopy drip measurements would be very useful, particularly where detailed measurements of soil moisture are being made.

We need to be clear about the difference between modelled scenarios and testing models against real situations. The knowledge and models we now have are probably good enough to give useful indications of what is likely to happen in particular (scenario) situations. The experimental work of the agroforestry project will test and refine those models. The final guidelines will be based on scenarios and the models will be available to evaluate particular, properly described, situations.

Appendix 1: The Penman-Monteith equation: derivation; equilibrium and potential evaporation; some representative numbers for tree water use

The Penman-Monteith (P-M) equation was originally derived by H.L. Penman (1948). He obtained an expression for evaporation from open water, bare soil and (well-watered) short, green grass that combined the energy and mass transfer processes in a single equation. Monteith (1965) reduced the empiricism of the equation, particularly in the mass transfer term, where he introduced a boundary layer resistance derived from the aerodynamic roughness properties of the surface and a canopy resistance, linked to stomatal resistance, to account for the influence of the plants.

The P-M equation is soundly based in physics and the interface with plant physiology has stood the test of a great deal of careful (and sometimes rigorous) examination. There has been an enormous amount of research, leading to a very large number of papers, concerned with testing the equation, establishing parameter values for various surfaces and situations, using it as an analytical tool and evaluating its implications. We have now reached the point where, it is probably true to say, it can also be used with confidence as a predictive tool. It ought to be used—and tested—in that way in this project, since it provides the means for calculating water use by trees, in any specified situation, without having to rely on empirical measurements, with all the uncertainties associated with extrapolating from them. There will, of course, always be uncertainties in the calculations, arising from inadequate knowledge of leaf area and leaf net radiation, stomatal responses and the microclimate in and around tree canopies, but these will not, in my view, outweigh the advantages of using a soundly based, well established and universally applicable equation to provide the information we need about tree water use.

It is not true to say that there are various versions of the P-M equation. There are indeed various algebraic formulations and, unfortunately, a plethora of different symbols for the same things—which can cause confusion. There are also various simplifications and assumptions that can be made, for different situations, to derive values for the resistance/conductance terms; these may depend on the time scale to be used, on the emphasis being placed on the particular analysis, or on the information available for the situation under study. In addition, there are also refinements such as corrections for differences in the diffusivity of heat and water vapour in air, and the introduction of isothermal radiation. However, the basic, underlying principles remain the same. They are outlined here, where I have presented the essential steps in the derivation of the P-M equation, in the most common and well-known algebraic form, with the most commonly-used symbols.

Two formulations arising from the P-M equation—the (so-called) equilibrium and potential evaporation—sometimes cause confusion. They are presented here, with brief explanations of their physical basis and implications. Both are important and may play a role in the agroforestry project.

Derivation

The P-M equation is often called the ‘big leaf’ equation because it treats canopies as a single, large leaf, ignoring the complications and problems that arise from the fact that canopies are three-dimensional and the sources and sinks for water vapour and heat may be at different levels (see Raupach and Finnigan, 1988). We therefore derive the equation from the energy balance of leaves:

$$j_n = IE + H \quad (A1.1)$$

where ϕ_n (W m^{-2}) is the radiant energy absorbed by the leaves (the available energy), which is partitioned into latent heat and H is sensible heat. ϕ_n depends on the balance between short-wave incoming radiation and the long-wave fluxes to and from a surface.

Writing separate equations for latent and sensible heat we get

$$IE = \frac{rc_p}{g} (e_s(T_l) - e_a) g_v \quad (A1.2)$$

and

$$H = rc_p (T_l - T_a) g_a \quad (A1.3)$$

where λ is the latent heat of vapourisation of water ($2.47 \times 10^6 \text{ J kg}^{-1}$), E is the flux density of water vapour ($\text{kg m}^{-2} \text{ s}^{-1}$) and the conductances for the transfer of water vapour (g_v) and heat (g_h) are the reciprocals of the resistances (the equations can be derived and written in terms of either; conductances tend to be more widely

used). I am not going to distinguish, here, between the aerodynamic conductances for heat and water vapour, but will use a 'generic' boundary layer conductance, g_a :

$$g_v = 1 / (r_a + r_s), \quad g_a = 1 / r_a \quad (\text{A1.4})$$

When the equation is being applied to canopies g_v is canopy resistance, denoted g_c (see the papers by Kelliher, 1993; 1995). The other symbols in these equations denote air density (ρ), the specific heat of air at constant pressure (c_p), the psychrometric constant (γ , kPa °C⁻¹), saturated vapour pressure at leaf temperature T_l ($e_s(T_l)$, Pa), actual vapour pressure (e_a) and air temperature (T_a , °C) (see *Parameter values*).

The difficulty with equations (A1.2) and (A1.3) is that they require knowledge of surface temperature, which is almost never available. Penman solved this problem with an approximation based on the fact that the vapour pressure difference between the evaporating surface and the air, $(e_s(T_l) - e_a)$, can be expressed as

$$e_s(T_l) - e_a = [e_s(T_l) - e_s(T_a)] + [e_s(T_a) - e_a] \quad (\text{A1.5})$$

which is, approximately

$$\approx (T_l - T_a)s_* + D \quad (\text{A1.6})$$

where s_* is the slope of the curve relating saturated vapour pressure to temperature, which can be assumed linear over the range $T_l - T_a$, and D is the vapour pressure deficit of the ambient air. Substituting (A1.6) in (A1.2), using the result with (A1.3) to eliminate $T_l - T_a$ and substituting for H in (A1.1) gives

$$LE = \frac{rc_p}{g} \left[\frac{(j_n - LE)s_*}{rc_p g_a} + D \right] g_v \quad (\text{A1.7})$$

This leads to

$$LE = \frac{g_v}{(s_* g_v + g_a)} (s_* j_n + rc_p D g_a)$$

which is usually written

$$LE = \frac{s_* j_n + g_a rc_p D}{s_* + g(g_a / g_v)} \quad (\text{A1.8})$$

There are other algebraic versions, but this is probably the most common.

There are two special cases of equation (A1.8) that should be noted. The first is the so-called *equilibrium* transpiration rate (see McNaughton and Jarvis, 1983), which is the rate that would occur when E is in equilibrium with the existing atmospheric vapour pressure deficit, so evaporation is driven by energy input only and equation (A1.8) reduces to

$$LE = \frac{s_* j_n}{s_* + g} \quad (\text{A1.9})$$

There are suggestions (Dunin et al., unpublished) that, over periods of about a year, the rate of water use of (non-irrigated) Eucalyptus forests is essentially the same as equilibrium evaporation, but it seems unlikely that this formulation will be accurate in relation to isolated trees or blocks of trees.

The second case arises from equation (A1.8) when we set g_c equal to g_a , i.e the situation that would arise with a wet canopy, when we assume all evaporation is from the free water surfaces. This gives the *potential* evaporation rate (E_p). There are other definitions of potential evaporation rate: one commonly used is the rate of evaporation from open water, usually estimated from measurements of (Class A) pan evaporation (E_{pan}). This is not a good reference/baseline because it varies with the exposure of the pan - results from a pan on the edge of an airfield will be different from those obtained, under the same weather conditions, from a pan near irrigated land or a forest - as well as its cleanliness and general maintenance. It may be justifiable to use E_{pan} when appropriate meteorological data are not available; it is not recommended for this project. The other definition of potential evaporation is essentially historical, stemming from Penman's (1948) original definition of E_p as the rate of water loss from short, green grass freely supplied with water; this was the reference surface for the original calibration of the Penman equation. It is not particularly helpful in the present context; equation (A1.8), with $g_c = g_a$ reflects the properties of the surface of interest, and is recommended as the reference form.

Parameters, variables and some results

Values of the physical parameters (ρ , c_p) and procedures for calculating s^* and D are given in the last section (*Parameter values*). The procedure for calculating ϕ_h is not discussed: when dealing with complete canopies net radiation should, where possible, be measured, but if it is not there are well-established empirical relationships based on short-wave incoming radiation (ϕ_s) that will give good estimates over periods of several days. If ϕ_s itself has to be estimated the probability of significant error increases. The reader is referred to Linacre (1992) for a guide to these estimation procedures.

When equation (A1.8) is to be applied to isolated or scattered trees, we require ϕ_h on a unit leaf area basis, which is more difficult. Thorpe (1978) found, for a hedgerow apple orchard in England, that $\phi_{h,leaf}$ was linearly related to ϕ_h per unit ground surface area; his equations were

$$\phi_{h,leaf} \approx 0.5 \phi_h, \text{ where } \phi_h \text{ was the value for the orchard as a whole, or } \phi_{h,leaf} \approx 0.3 \phi_s.$$

The question of boundary layer conductances is not important, since the P-M equation is not sensitive to them. Raupach (1991; unpublished bulletin) has given an expression for r_a for full canopies based on the wind profile equations which, for stands about 10 m tall and wind speeds of order $2-3 \text{ m s}^{-1}$ gives $g_a \approx 0.2 \text{ m s}^{-1}$. The same value is given by Kelliher et al. (1993) as representative of forest canopies. Where we are dealing with isolated trees we have to use values appropriate to individual leaves. Landsberg and Powell (1973) gave an expression that accounted for the mutual sheltering that occurs in these situations - the foliage elements reduce the airflow through the canopy and so reduce the aerodynamic conductance of the leaves. The general equation is $g_a = 1/r_a = 1/(2(d/u)^{0.5})$, where d here is a linear dimension of an average leaf (e.g leaf width). This gives values of g_a for leaves of similar magnitude to the values for canopies, i.e in the range $3-7 \text{ ms}^{-1}$.

As noted in the main text, there is a range of models that can be used to estimate stomatal conductance g_s ($=1/r_s$) and hence g_v (see equation A1.4). The model used will undoubtedly vary with circumstances and the requirements of particular situations. Leuning (1995) has proposed a model that takes account of the relationship between stomatal conductance and internal (to the leaf) CO_2 concentrations, as well as stomatal responses to humidity.

Applying equation (A1.8) to leaves, if we assume that $g_v = 0.005 \text{ m s}^{-1}$ - a reasonable value for maximum g_s - and $g_a = 0.2 \text{ m s}^{-1}$, with $\phi_h = 250 \text{ W m}^{-2}$ and $D = 1 \text{ kPa}$ (i.e. 10 mb or $6 \times 10^{-3} \text{ kg kg}^{-1}$) we get a transpiration rate of $0.14 \text{ kg m}^{-2} \text{ hr}^{-1}$.² In the main text we consider a tree with a leaf area of 13 m^2 , transpiring at 6, 12 and 18 litres day^{-1} - the rates being based on measurements on a captive tree by Green (1993). $0.14 \times 13 = 1.8 \text{ kg hr}^{-1}$, which is 18 litres over a 10 hr period. If we reduced g_s to 0.0012 transpiration is reduced to $\approx 0.04 \text{ kg m}^{-2} \text{ hr}^{-1}$, giving 6 litres per day for this tree. The calculations are therefore completely consistent with observation, demonstrating that we will be able to use the P-M equation to calculate tree water use in this agroforestry project.

For canopies, Kelliher et al. (1993, 1995) give representative maximum values of canopy conductance for forests in general; the 1995 paper explores the relationship between leaf area index and canopy conductance. Maximum values of g_c are about $0.02 - 0.03 \text{ m s}^{-1}$, i.e less than g_a by a factor of about 10. Raupach, in his 1991 bulletin, gave values for irrigated Eucalypts, based on available literature and the advice of scientists who had worked on these problems, of around 0.03 s m^{-1} ($r_c = 50 \text{ s m}^{-1}$) for fertilized plantations and 0.015 s m^{-1} ($r_c = 75 \text{ s m}^{-1}$) for unfertilized plantations. Values collated by Raupach, and calculations he made for various locations in the Murray-Darling Basin, are given in Tables A1.1 and A1.2.

Table A1.1. Values of the canopy conductance parameters for several Eucalypt species. In the column L/C, L indicates leaf measurements by porometry, C canopy-scale measurements by various methods. (From Raupach, 1991)

Species	L/C	$g_{c,max}$	Reference
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² Since the P-M equation is written in energy units, converted to mass units by λ , calculated transpiration rates are in $\text{kg m}^{-2} \text{ s}^{-1}$, so must be multiplied by the interval of interest (seconds) to give the required mass flux. Leuning (1995; unpublished report) noted that "non-linearities in the P-M equation are relatively weak, so satisfactory estimates of daily evapotranspiration can be obtained using daily time steps and mean values of available energy, humidity deficit, canopy conductance and aerodynamic conductance"

		m s^{-1}	
E. saligna	L	0.023	Hookey et al. (1987), quoted in Leuning et al. (1991a)
E. sideroxylon	L	0.021	
E. microcarpa	L	0.015	
E. woollsiana	L	0.015	
E. resinifera	L	0.018	
E. grandis: fertilized	L	0.037	Leuning et al. (1991b), Leuning et al. (1991c)
unfertilized	L	0.019	
E. maculata	C	0.017	Dunin and Greenwood (1986)
E. maculata	C,L	0.017	Dunin and Aston (1983), Aston (1984)
generic values: fertilized		0.033	
unfertilized		0.017	

An important problem in relation to the calculation of actual transpiration is the estimation of the effects of soil water on g_s . Information relevant to this should be obtained from this project: given (heat flow) measurements of the transpiration rates of trees under various circumstances, in which we have good values for all the other parameters and variables in equation (A1.8), we should be able to solve for g_v (g_c) and relate the values obtained to soil water. There are also various modelling approaches to this problem, but these will not be discussed here.

Table A1.2: Calculated seasonally averaged canopy conductance and evapotranspiration at five sites in New South Wales, for fertilized and unfertilized Eucalyptus plantations.

Site	Month	g_c m s^{-1}	fertilized total E mm day^{-1}	g_c m s^{-1}	unfertilized total E mm day^{-1}
Wagga	Jan	0.0189	9.32	0.0094	7.19
	Apr	0.0254	3.97	0.0138	3.14
	Jul	0.0207	1.47	0.0145	1.24
	Oct	0.0269	5.80	0.0135	4.48
Griffith	Jan	0.0162	9.99	0.0081	7.62
	Apr	0.0261	4.98	0.0180	3.85
	Jul	0.0234	2.07	0.0153	1.71
	Oct	0.0253	6.86	0.0126	5.28
Mildura	Jan	0.0157	9.92	0.0078	7.52
	Apr	0.0254	5.01	0.0127	3.88
	Jul	0.0223	2.11	0.0152	1.78
	Oct	0.0241	7.09	0.0121	5.45
Bourke	Jan	0.0106	10.12	0.0053	7.38
	Apr	0.0221	6.42	0.0111	4.96
	Jul	0.0274	3.50	0.0142	2.70
	Oct	0.0188	8.77	0.0094	6.68
Canberra	Jan	0.0232	8.33	0.0116	6.48
	Apr	0.0266	3.50	0.0145	2.76
	Jul	0.0208	1.35	0.0146	1.13
	Oct	0.0283	5.21	0.0141	3.99

Parameter values

Air density: $\rho = 1.2 \text{ kg m}^{-3}$. Specific heat of air at constant pressure: $c_p = 1010 \text{ J kg}^{-1} \text{ K}^{-1}$

Latent heat of vapourization of water: $\lambda = 2.46 \times 10^6 \text{ J kg}^{-1}$

Saturated vapour pressure at temperature $T^\circ\text{C}$:

$$e_{\text{sat}}(T) = 6.106 \exp\left(\frac{17.27T}{237.3 + T}\right) \text{ (mbs; } 10 \text{ mb} = 1 \text{ kPa)}$$

$$s_a: \frac{de_s(T)}{dT} = \frac{4098.2e_s(T)}{(237.3 + T)^2} \quad (\text{mb } ^\circ\text{C}^{-1})$$

$$D = e_s(T) - e_a,$$

$e_a = e_s(T_w) - \gamma(T - T_w)$ (actual vapour pressure) where T_w is the wet-bulb temperature and γ is the psychrometric constant. For fully ventilated psychrometers $\gamma = 0.066 \text{ kPa } ^\circ\text{C}^{-1}$

Appendix 2: The control of transpiration by soil water: the HYDRUS-2D package

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The HYDRUS-2D software package (Simunek et al., 1995) was used to simulate the uptake of water by a tree root system from a region of wet soil. This package uses the finite element numerical procedure and the soil water flow model of the earlier SWMS_2D FORTRAN programs (Simunek et al., 1994), together with a graphical user interface for data input and output. The simulation region for the present exercise is a cylindrical block of soil with depth 3 m and with a radius of 4 m, with an axisymmetric root length distribution. The soil water distribution is also assumed to be axisymmetric, with water movement governed by a Richards' equation whose independent variables are time t , depth z (measured positive downwards) and radial co-ordinate r . It is assumed that there is no flow across the lateral boundary. For all simulations the soil type "sandy clay" of Simunek et al. (1995) was used. This has a fairly low value of saturated hydraulic conductivity K_s of 0.07 cm hr^{-1} , and a correspondingly low soil water diffusivity. Its properties are specified by values of the van Genuchten (1980) parameters, namely $n = 1.23$, $m = (n - 1)/n$, $\alpha = 0.01 \text{ cm}^{-1}$, with residual water content $q_r = 0.089$ and saturated water content $q_s = 0.43$. At the start of the simulation, the soil is assumed to be close to saturation, with a soil water content of 0.4295. It is assumed that there is no evaporation or precipitation during the period of water uptake, and so a no-flux boundary condition applies at the soil surface. At the lower boundary of the simulation region at a depth of 3 m, it is assumed that there is free drainage, in which water moves downwards under the influence of gravity.

It is assumed that the root length density L_v decreases with depth, and with distance from the central axis in the exponential form

$$L_v(r, z) = L_0 \exp(-k_1 z - k_2 r) \quad , \quad 0 \leq r \leq r_0 \quad , \quad 0 \leq z \leq z_{\max} \quad , \quad (\text{A2.1})$$

where L_0 is the root length density at $(r, z) = (0, 0)$, and k_1 and k_2 are parameters. Two root different root systems were used in the simulations: a deeper root system with parameter values $z_{\max} = 2 \text{ m}$, $r_0 = 1.5 \text{ m}$, $k_1 = 1.5 \text{ m}^{-1}$, $k_2 = 2.0 \text{ m}^{-1}$, and a shallower root system with parameter values $z_{\max} = 0.75 \text{ m}$, $r_0 = 3.0 \text{ m}$, $k_1 = 1.5 \text{ m}^{-1}$, $k_2 = 2.0 \text{ m}^{-1}$.

The program uses the root water uptake model of Feddes et al. (1978), in which the potential root water uptake rate $P(t)$ for the whole root system is specified as a function of time. The root water uptake at any point in the soil is governed by a sink term $S(r, z, h, t)$ in the soil water flow equation, which depends on the position (r, z) , soil water potential h at that point, and on time t . The sink term is assumed to have the product form

$$S(r, z, h, t) = a(h)b(r, z)P(t) \quad , \quad (\text{A2.2})$$

where $a(h)$ is the plant water stress response function and $b(r, z)$ is the normalized water uptake distribution, normalized so that

$$2p \iint b(r, z) r dr dz = 1 \quad . \quad (A2.3)$$

The integral is taken over the volume of soil $0 \leq r \leq r_0$, $0 \leq z \leq z_{\max}$ occupied by the plant root system. In this study the normalized water uptake distribution will be assumed to be proportional to the root length distribution.

According to the model of Feddes et al. (1978), the plant water stress response function $a(h)$ has the value unity for h above the (negative) soil water potential value h_3 and the value zero for h below the value h_4 , with $h_4 < h_3 < 0$. Between h_4 and h_3 the function $a(h)$ is assumed to vary linearly with h . The actual root water uptake rate $A(t)$ for the whole root system is defined by

$$A(t) = 2p \iint S(r, z, h, t) r dr dz = 2p P(t) \iint a(h) b(r, z) r dr dz \quad , \quad (A2.4)$$

Initially, when the potential of the wet soil is above the value h_3 everywhere, the function $a(h)$ is unity everywhere and the actual root water uptake rate $A(t)$ is equal to the potential root water uptake rate $P(t)$ by equations (A2.3) and (A2.4). As time increases, because there is no impermeable layer impeding drainage from the bottom of the profile, soil water flows downwards under gravity and the soil dries out near the upper surface. Because the root length density decreases down through the profile, root water uptake removes more water nearer the surface, where there is little downward flow to replenish it. As soon as the soil water potential falls below h_3 somewhere, the value of the function $a(h)$ falls below unity there, and it can be seen from equation (A2.4) that the actual root water uptake rate $A(t)$ falls below the potential root water uptake rate $P(t)$.

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PAPER NO. 2

DOES LEAF WATER EFFICIENCY VARY AMONG EUCALYPTS IN WATER-LIMITED ENVIRONMENTS?

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Summary

There is a need to generalise eucalypt water use behaviour to facilitate bioengineering and landscape remediation programs in a wide range of Australian environments. A critical question can be stated as a null hypothesis: tree water use per unit leaf area (*leaf efficiency*) is independent of eucalypt species. This is implicitly equivalent to the hydrological equilibrium hypothesis of leaf area as a function of climate, at least in cases where transpiration and growth are limited by soil moisture. Failure to reject this null hypothesis leads to several simplifications: (a) selection of tree species for water balance management, (b) the generation of regional-scale expectations of leaf area index, and (c) simplified estimation (monitoring) of the effectiveness of plantations in controlling site water balance.

The hypothesis was tested with tree water use data collected in natural multi-species stands across Australia, including sites in the wet/dry season tropical woodlands of the Northern Territory, the Mediterranean climate forests of Western Australia, and a woodland system in southern New South Wales subject to an even distribution of rainfall throughout the year. To extend this analysis, we included a test of the hypothesis in a multi-species tree plantation growing on a saline gradient.

In each case, we could not reject the hypothesis of constant leaf efficiency among eucalypts. In every case there was a common, strong, linear relationship between tree leaf area and mean daily water use by all tree species in a sample. No significant differences were detected among the leaf water efficiencies of species, analysed by single factor (species) analysis of variance. The null hypothesis could not be rejected for jarrah forest (*Eucalyptus marginata*, *E. calophylla*) in Western Australia in spring (wet) or autumn (dry) conditions, in the mixed species woodland of New South Wales (*E. macrorhynca*, *E. blakelyi*, *E. polyanthemos*) under summer and autumn conditions, or in the wet/dry tropical woodland (*E. miniata*, *E. tetrodonta*, *E. porecta*) of the Northern Territory. Two other genera (*Erythrophleum chlorostachys*, *Terminalia ferdinandiana*) were examined in the Northern Territory with the same result. Measurements made in a plantation of *E. occidentalis* and in provenances of *E. camaldulensis* growing on a shallow saline watertable gradient, also indicated constant leaf water use efficiency across species and varieties., despite the obvious effects of salinity on the size of individual canopies.

Although there are reports to the contrary, especially from investigations on eucalypt plantations, we conclude that there is little evidence for rejecting the hypothesis that the rate of water use per unit leaf area does not vary significantly among sympatric eucalypt species in rainfall-limited (soil water limited) systems. This conclusion allows useful generalities about the hydrological role of trees in the Australian landscape.

Introduction

When different species of eucalypts coexist in a water-limited landscape, do they come to the same long-term solution to the problem of adjusting their canopy conductance to water vapour? That is, do individual trees of sympatric species transpire the same amount of water per unit area of leaf (*leaf efficiency* as in Greenwood et al. 1985, Hatton and Wu 1995) when subjected to periodic water stress? Or do different species of eucalypts, when faced with the same supply of water and demand by the atmosphere, come to unique solutions to optimising the balance between stomatal conductance and leaf area? In this paper we test the hypothesis that leaf efficiency does not vary significantly among eucalypt species growing together under similar conditions at sites with seasonal water limitations.

The importance of this investigation lies in the search for bioengineering solutions to Australia's land degradation problems, which is to a large degree hampered by uncertainty regarding the role that perennial woody vegetation played in the hydrological cycle prior to land clearance. This uncertainty arises out of the immense spatial scale of the affected systems, and the enthusiasm and energy which European settlers brought to land clearance over the past two hundred years; over 12 billion trees have been removed from the Murray-Darling Basin alone (Walker et al. 1993). It also arises out of the difficulty in understanding the hydrogeological, hydrogeochemical, meteorological and biophysical complexity of these large systems.

A key component of this necessary understanding is knowledge of how vegetation, in particular trees in the genus *Eucalyptus*, affects the local and regional water balances. This knowledge is necessary for the selection of species for revegetation as well for determining the location and extent of the plantations required to achieve stated hydrological aims in any particular area (Morris and Thompson 1983). The need for such information has generated many studies on the water relations of Australian evergreen plants. However, these studies are done at a range of scales and with diverse experimental approaches, and consequently have produced a somewhat confused picture of how transpiration varies among species and sites.

At the leaf scale, porometer studies of eucalypt transpiration often show differences among species with respect to leaf conductance. In the most ambitious of these studies (Hookey et al. 1987), significant differences were found among eucalypt species growing over a shallow, saline groundwater system, with some species estimated to transpire (based on scaled stomatal conductances) at three to four times the rate of other species at the end of summer. Such inferences must be treated with caution when extrapolated to the long-term behaviour of tree canopies in established stands because of the notorious variability of leaf-scale conductance measurements in both time (Turner 1991) and space (Jarvis et al. 1981). It is also inappropriate to translate leaf conductance measurements into estimates of canopy transpiration (Denmead 1984, Meinzer 1993). Knowledge about comparative tree water relations is also not advanced when studies are based on leaf-scale responses of seedlings (e.g., Moreshet 1981), often in pots (e.g., Gindell 1971); the results of such work may have little relevance to transpiration rates and leaf efficiency in established stands of trees in the field. Nevertheless, leaf scale studies have led to the view that large differences exist in stomatal conductance (and hence transpiration rates) among eucalypts and other tree species and that stomata play a dominant role in regulating transpiration and water use efficiency.

At the stand scale, however, a different paradigm has emerged, based on micrometeorological, climatological and hydrological investigations. When different forest systems within the same region are compared on the basis of their annual evapotranspiration, differences are often small (Aussenac 1972, Dunin and Mackay 1982, Roberts 1983). Pomeroy et al. (1988) noted that when photosynthesis, respiration, assimilation and transpiration are measured at the ecosystem level, we see remarkably stable rates in spite of successional changes, at least through forested seres.

In general, in southern Australia, evergreen plant communities in the same rainfall zone evaporate about the same amount of water; only a very small fraction of rainfall escapes evergreen perennial systems as liquid water (runoff, groundwater recharge). This in itself does not translate to similarity in leaf efficiency for two reasons: (1) there are components of evaporation other than tree transpiration and these may differ, and (2) leaf area index (LAI) may vary. Studies at the regional scale, however, suggest that there are broad consistencies in the rainfall-LAI relationship across plant communities. One of the earliest and most revealing of these was by Specht (1972), who hypothesised that the structure of canopies was influenced by the availability of soil water as influenced by climate. He demonstrated that the LAIs of a remarkable range of Australian evergreen plant communities were strongly related to a climatic index of evaporative demand and rainfall. These results were later reinforced with additional data and analyses in Specht and Specht (1989). Hatton et al. (in press) cited this

work as evidence in support of Eagleson's optimality theory of an ecohydrological equilibrium (Eagleson 1982, Eagleson and Tellers 1982, Eagleson and Segarra 1985). Other authors have established an empirical relationship between site LAI and available soil water for evergreen vegetation at regional scales (Grier & Running 1977, Gholz 1982, Nemani and Running 1989, Pierce et al. 1993). These observations imply that leaf efficiency is constant across evergreen species *assemblages* in water-limited environments.

It is difficult to reconcile differences in leaf conductance among eucalypt species with strong similarities in leaf efficiency at the regional scale. Meinzer (1993) explained differences in transpiration across these scales largely in terms of the varying role of boundary layer conductance (*coupling*, as in Jarvis and McNaughton 1986, McNaughton and Jarvis 1991), but also recognised that adjustments in leaf area may compensate for plant water stress. It is clearly difficult and imprecise to assess species differences in leaf efficiency at the canopy scale on the basis of leaf-scale measurements and it is equally difficult to assess species differences on the basis of site or regional water balances and stand LAI. Water balance studies cannot directly isolate the transpiration component of evaporation; lower overstory evaporation in one system may be compensated for by higher soil/understory evaporation, higher rainfall interception or greater runoff. Neither can such regional-scale investigations ascertain leaf efficiencies by species in mixed stands; while two systems may have similar total transpiration and LAI, species within such stands may not be contributing equally to this net response.

Fortunately, techniques exist at an intermediate scale which can help resolve this dichotomy. The measurement of transpiration by individual trees by a variety of thermoelectric and tracer techniques (Marshall 1958, Cohen et al. 1981, Edwards and Warwick 1984, Granier 1985, Calder et al. 1986, Baker and Van Bavel 1987, Cermák and Kucera 1987, Hatton et al. 1995), is now common practice, allowing the integration of stomatal and boundary layer conductance behaviours in space and time with good accuracy. A pattern emerging from the large number of observations being made in forest stands using such techniques is the strong generality that transpiration scales linearly and strongly with tree leaf area (Greenwood et al. 1985, Cermák and Kucera 1987, Werk et al. 1988, Vertessy et al. 1994, Hatton et al. 1995). Under very dry conditions the relationship may become curvilinear (Greenwood et al. 1982, Hatton and Wu 1995). A corollary of this linearity between tree leaf area and transpiration within a stand is the constancy of leaf efficiency among trees of different sizes within a species, including *Eucalyptus* species.

In this paper, we examine the question posed earlier as a hypotheses, namely 'does leaf efficiency remain constant among eucalypt species growing together in the same stand?' The hypothesis is tested using tree water use and leaf area data collected in multi-species eucalypt stands growing in (a) a partially-cleared temperate woodland site with an even distribution of monthly rainfall, (b) a natural forest subject to a long summer dry season, and (c) a natural woodland in the wet-dry tropics. We also examined the leaf efficiencies of eucalypts from different natural habitats growing in an experimental plantation on a local saline gradient in a semi-arid climate.

Methods

Tree water use

In all cases, tree water use was measured with the heat pulse method using Greenspan Technology Sapflow Sensors. The sampling and numerical techniques associated with this application were described by Hatton et al. (1995). In each case, sap flow was logged on a 20-30 minute basis, simultaneously for all trees in the sample, throughout the sampling period. Determination of sampling depths into the sapwood and the integration of point estimates of velocity followed Hatton et al. (1990). Wound effects were corrected for on the basis of Swanson and Whitfield's (1981) numerical approach, although these solutions were repeated for stainless steel probes and heaters as employed in the equipment used in this study. Wound diameters were estimated by inspection of the region surrounding probes; previous studies of wound development in eucalypts (Marshall 1992, Moore 1993, Hatton et al. 1995) found good correspondence between the extent of discoloration of the probe region and tyloses formation as estimated from light and scanning electron microscopy. Wound diameters in this study varied between 2.2 and 2.8 mm - within the range reported for eucalypts by Olbrich 1991, Barrett et al. 1995, and Dunn and Connor (1993). Wood and water contents were obtained by the method described in Hatton and Vertessy (1990). The inner boundary of sapwood (conducting wood) was determined by incremental measurement of sap flow with depth as in Hatton et al. (1995). While sensitivity analyses of the heat pulse technique show that the potential error can be as high as 38% (Hatton et al. 1995), tests of the heat pulse method against known transpiration generally show an accuracy of 7 - 15% (Olbrich 1991, Dunn and Connor 1993, Barrett et al. 1995, Hatton et al. 1995). Results were expressed as mean water use per day for each tree over the monitored period.

Leaf area estimation

The leaf area of the trees was measured by the Adelaide (module) technique described by Andrew et al. (1979). Two independent observers estimated the number of eucalypt modules for each monitored tree; the mean of these two estimates was converted to tree leaf area on the basis of the leaf area of a standard module for each species as measured by electronic planimetry (see Hatton et al., 1995). This approach is effectively the same as that applied by Carbon et al. (1979) to the same jarrah forest that we studied. Hatton et al. (1995) tested the method against four trees of varying sizes and known leaf area (determined through destructive sampling of whole tree canopies); linear regression (forced through the origin) of the mean estimated values against known leaf areas yielded a slope of 1.13 ($r^2 = 0.96$). In this study bias between the observers was less than 10% in all cases at all sites. All of the tree leaf areas reported were estimated by the same pair of observers.

Sites and Sampling

Mixed species woodland

This site, a grazed and partially cleared mixed eucalypt woodland site near Goulburn, New South Wales (34° 41' S, 149° 56' E), was described in detail by Kalma and Jupp (1990). The climate is temperate, with an average annual rainfall of 679 mm with no distinct seasonality. Potential evaporation exceeds rainfall for over half of the year. The tree LAI at the landscape scale is less than one, and individual tree canopies are quite open. Over the period 8 - 18 December 1992, two individuals of *E. polyanthemos* Schauer and one of *E. blakelyi* Maiden were monitored for transpiration, at a time when soils were near field capacity. Over the period 12 - 25 March 1993, one *E. macrorhynca* F.Muell. ex Benth individual was added to the set of trees monitored; soil moisture was relatively high at this time as well. These data were originally reported in Hatton and Wu (1995) to test a separate hypothesis related to tree leaf area adjustment to water stress..

Jarrah forest

The jarrah forest of southwestern Australia grows where rainfall exceeds 650 mm per year, but develops into a relatively tall (30 - 40 m) forest despite a prolonged summer drought resulting from a Mediterranean rainfall distribution. This is due to the maintenance of relatively high rates of transpiration through much of the dry season by extraction of water from very deep (>20 m) in the soil profile (Carbon et al. 1980, 1981a, 1981b; Colquhoun et al. 1984). Tree water use was studied at a site (32° 20' S, 116° 05' E) in the Gordon Catchment, in a high rainfall zone (1050 mm) of the forest. This site is in a fifty year old stand with LAI varying between 1.0 - 1.5, and is maintained by ALCOA Pty Ltd as part of a research program on jarrah forest management. Tree water use was monitored over the period 6 - 16 October 1993 in four jarrah (*E. marginata* Donn ex Smith) and three marri (*E. calophylla* R.Br. ex Lindley) trees; at this time surface soil moisture was high following winter rains. Water use was later monitored in four jarrah and four marri trees over the period 10 - 17 March 1994, when soil moisture was relatively low after a very dry summer.

Tropical woodland

The tropical woodland site was near the Howard River east of Darwin in the Northern Territory (12° 30' S, 131° 06' E). The climate is wet-dry tropical, with mean annual rainfall of 1600 mm, almost exclusively between October and March (summer). Tree LAI rarely exceeds 1.5. There is evidence that the woodland persists through the long dry season through access to groundwater in a shallow, unconfined aquifer system, but water stress nevertheless develops toward September (Pidsley et al. 1994). At the end of the wet season, tree water use was monitored over the period 15 - 20 April 1994 in five *E. miniata* Cunn. ex Schauer, four *E. tetrodonta* F.Muell., one *E. porecta* S.T.Blake, two *Erythrophleum chlorostachys* (F. Muell.) Baillon and two *Terminalia ferdinandiana* Exell. trees; the latter species is of a dry season deciduous nature. Toward the end of the dry season (3 - 9 September 1994), four *E. miniata*, four *E. tetrodonta*, two *E. porecta*, and two *Erythrophleum chlorostachys* were monitored.

Saline plantation site

A small (30 × 100 m) experimental plantation was established in 1986 on a sloping edge of a saline lake on the Yorke Peninsula (34° 45' S, 137° 40' E) by the Department of Primary Industries (Government of South Australia) to examine the survival and growth of a selection of eucalypts proposed for revegetation activities in saline landscapes. Annual rainfall at this site is approximately 450 mm, coming mostly in winter. Groundwater is near the surface (0.5 - 2 m below ground level) and quite saline (over 60 dS m⁻¹). The trees included *E. occidentalis*, *E. camaldulensis* (local provenance) and *E. camaldulensis* (provenance: Lake Albacutya). The latter variety has been touted as superior for such applications (e.g., Moreshet 1981). The plantation was laid out

to assess performance of the tree varieties with distance from the saline lake, equivalent to a gradient in depth to the saline water table. Although most trees established and initially grew, after eight years the impact of proximity to saline groundwater was obvious. Trees near the lake were much smaller than those farther back, and their canopies are now dying back (or even dead) as salt accumulates in their (shallow) root zone; there is a clear gradient in size with distance away from the lake (Figure 1). Over the period 17 - 24 October 1996, three *E. occidentalis*, four *E. camaldulensis* (local provenance) and six *E. camaldulensis* (provenance: Lake Albacutya) trees were monitored for water use. This period of the year was selected so that soil matric potentials would be low against the background of the osmotic gradient described above, and that there would be significant atmospheric demand following winter.

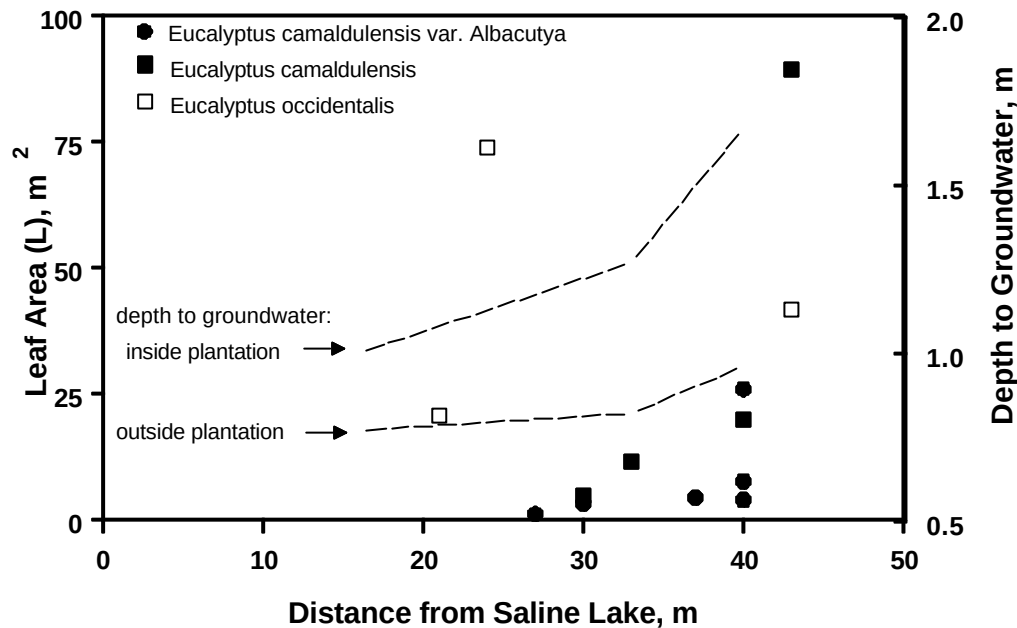


Figure 1. Tree leaf area with distance from the edge of a saline lake, and depth to a saline groundwater table, for an experimental plantation of eucalypts on the Yorke peninsula, South Australia. Note the general trend for larger canopies with deeper water tables and distance from the lake edge, particularly for the two varieties of *E. camaldulensis*. Trees of *E. occidentalis* grew relatively large in relation to the salinity gradient.

For each case, tree water use was regressed on tree leaf area, using a first-order regression model and assuming the independent variable was measured without error. In addition, a one-way analysis of variance was performed where the treatment was the species or provenance and replication was at the tree level. We recognise that no attempt was made to block out other (spatial) sources of variation, due to resource limitations.

Results

There was little evidence of observation bias in the estimates of leaf area made by the two observers. For the jarrah forest in October 1994, the linear regression between these estimates had an intercept not significantly different from zero (-0.31 m^2 , $p > 0.2$) and a slope of 1.06 ($r^2 = 0.97$, d.f. = 6). For the tropical woodland in April 1994, the linear regression between the estimates had an intercept not significantly different from zero (0.02 m^2 , $p > 0.2$) and a slope of 1.00 ($r^2 = 0.94$, d.f. = 12) and in the case of the saline plantation the linear regression between the two observers' estimates for the entire plantation ($n = 101$ trees) had an intercept on the y-axis that was not significantly different from zero (-0.05 , $p > 0.2$) and a slope of 1.035 ($r^2 = 0.99$) over leaf areas ranging from 0.05 to 74 m^2 .

Table 1. Analysis of variance results from tests of the null hypothesis that leaf efficiency does not vary among *Eucalyptus* species. There were too few observations on the mixed woodland for this analysis. Value p is probability of Type I error.

Site, date	F-statistic	p
Jarrah forest, October 1993	6.61	> 0.20
Jarrah forest, March 1994	5.99	> 0.20
Tropical woodland, April 1994	3.71	> 0.20
Tropical woodland, September 1994	4.07	> 0.20
Saline Plantation, October 1996	4.10	> 0.20

At no site, nor for any sampling period, was there a significant difference in leaf efficiency among the eucalypt species examined (Table 1). In the case of the tropical woodland, there was a significant difference in leaf efficiency ($P < 0.05$) between the eucalypts and non-eucalypts in the wet season (thus including *Terminalia*). There was no significant difference in leaf efficiency between the eucalypts and *Erythrophleum chlorostachys* in the dry season ($P > 0.20$). Regressions of the two components of leaf efficiency, leaf area and mean daily transpiration, appear in Figures 2 - 4; none of the y-intercepts in these regressions were significantly different from zero ($P > 0.05$). The slopes of these regressions ranged between 0.86 and 3.80.

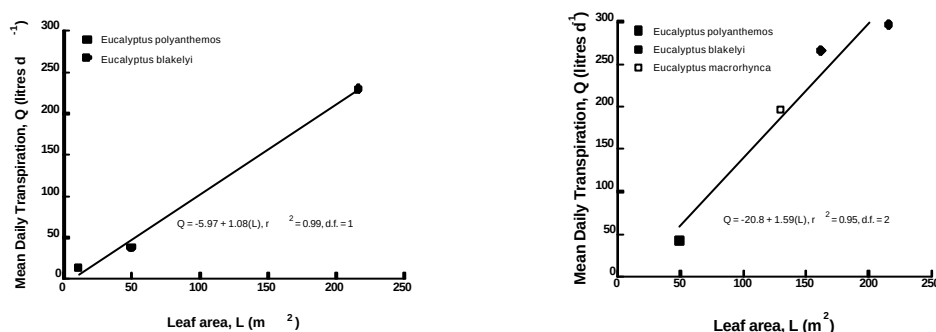


Figure 2. Tree leaf area vs. mean daily transpiration, mixed species woodland, New South Wales (a) 8 - 18 December 1992; (b) 12 -25 March 1993

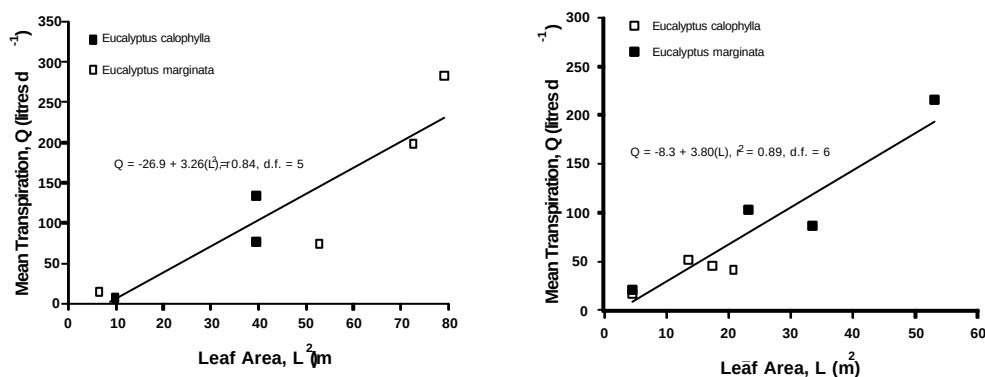


Figure 3. Tree leaf area vs. mean daily transpiration, jarrah forest, Western Australia: (a) 6 -16 October 1993; (b) 10 -17 March 1994.

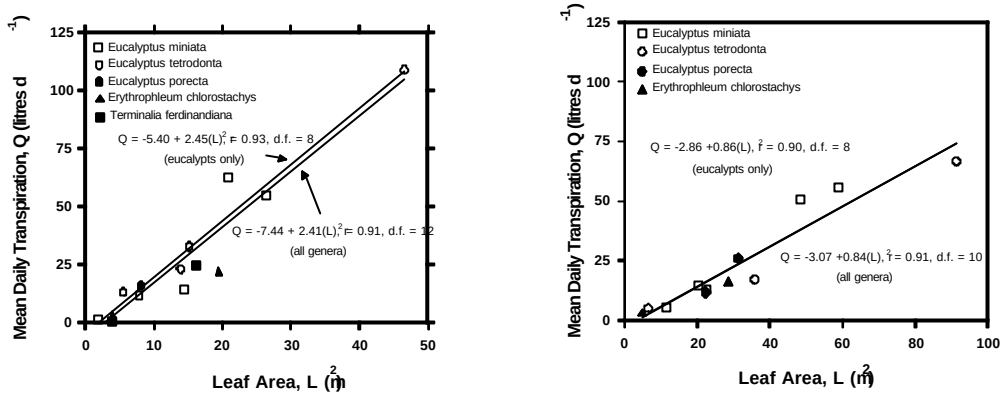


Figure 4. Tree leaf area vs. mean daily transpiration, tropical woodland, Northern Territory (a) 15 - 20 April 1994; (b) 3 - 9 September 1994

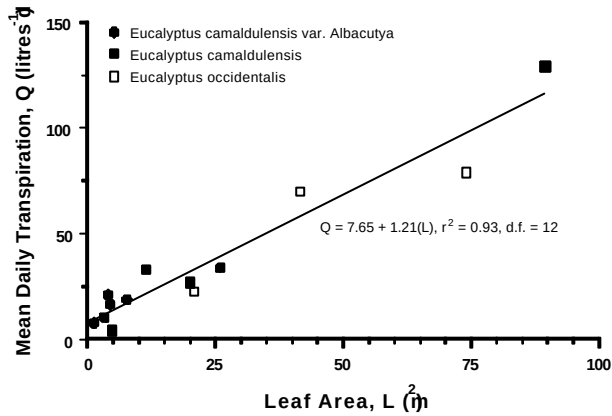


Figure 5. Tree leaf area vs. mean daily transpiration, plantation on saline groundwater gradient, South Australia, 17 - 24 October 1996

Discussion

On the basis of the data presented in this paper, we could not reject the null hypothesis that leaf efficiency - the rate of water use per unit leaf area under particular conditions - does not vary among eucalypts in environments subjected to seasonal water limitations at sites representing very different climates across Australia. Results from the mixed species woodland (Fig. 2) are based on very few data and must be viewed as exploratory; the probability of Type II error (failing to reject a false hypothesis) is high. These results pre-date the other studies, and to a large degree led to the subsequent investigations. Nevertheless, they are consistent with the rest of the results in this paper. We recognise the lack of spatial replication in this set of studies of diverse Australian forests, but we repeated the measurements over time in most cases and the data are consistent.

There are few previous reports on the water relations of the other systems studied. Leaf-scale studies in the jarrah forest (Carbon et al. 1981a) showed little difference in leaf efficiency (or plant water potential) between native *E. marginata* and 6 - 8 year old plantation *E. microcorys* growing nearby in the wet season (winter), but indicated slightly higher values of leaf efficiency for the native forest in summer than for the plantation trees. However, the plantation had a higher LAI than the native forest and Carbon and his colleagues did not scale these results to the whole canopy. In another study Carbon et al. (1981b) found negligible differences between the transpiration rates of *E. marginata* and *E. calophylla* within the same site. Colquhoun et al. (1984) compared leaf-scale conductance and xylem water potential measurements on these two species and found similar behaviour.

There are few comparative studies of eucalypt leaf efficiency at the stand or plantation scale; most of those that have been done have relied on either ventilated chambers or site water balances. In many cases the work was done on plantations that may have been too young to have come into hydrologic equilibrium with rainfall. Some of the work by Greenwood in Western Australia, employing whole tree ventilated chambers (e.g., Greenwood et al. 1985) tends to support our null hypothesis. Using the same technique, however, Greenwood and Beresford (1979) found species differences in leaf efficiencies among very young (1 - 2 years old) plantation trees, although they pointed out that during this experiment there was evidence that some of these trees gained access to a local groundwater table.

Honeysett et al. (1992) examined the water balance of fertilised 4-5 year old plantations of *E. delegatensis* and *E. nitens* at a site naturally supporting wet sclerophyll forest (annual rainfall 916-1132 mm during study). Soil water content was monitored down to 1.2 m. These authors had evidence that, at least during the measurement period, deep drainage had ceased, but they could not account for soil evaporation or runoff. *E. nitens* developed approximately twice the LAI as *E. delegatensis*, but used only 7% more water. This result would seem to contradict the null hypothesis proposed in this paper, unless (a) the trees on the site were not water stressed (potential evaporation is probably not much more than 1100 mm per year, i.e about the same as rainfall), (b) the experimental procedures could not accurately isolate the transpiration component of the water balance of these plantations, or (c) the leaf areas were not yet in equilibrium with rainfall.

The last of these possibilities deserves comment. The hypothesis that evergreen vegetation will adjust its LAI in response to long term water availability (Specht 1972, Grier & Running 1977, Gholz 1982, Eagleson 1982, Eagleson and Tellers 1982, Eagleson and Segarra 1985, Nemani and Running 1989, Pierce et al. 1993, Hatton and Wu 1995) seems compelling. Studies based on young plantations may violate this condition if they either do not yet fully occupy the site in a hydrological sense, or if they initially mine soil water stored in the profile prior to their establishment. This is not a consideration in the natural stands studied in this paper. There was evidence that the saline plantation studied here had clearly reached limits to its productivity based on the availability of water, in this case dominated by osmotic constraints.

The plantation case in this paper is significant in two aspects. The first of these is that while there are differences between species in the effects of salt on the growth of the trees, the leaf efficiencies are still the same (Fig. 5). It may well be that in the longer term, the absence of any significant salt leaching or diffusion phenomenon at this site will start to affect the health (e.g. Jolly et al. 1993) of the *E. occidentalis* trees to the same extent as *E. camaldulensis* and they will thus share a similar fate. Nevertheless, despite the current differences in growth response to a salinity gradient, tree water use still scales similarly with canopy leaf area across species and provenances within species.

The second key aspect of the plantation case is that the species and provenances involved do not occur naturally together. In contrast to the other cases examined in this paper, the possibility of equivalent leaf efficiency arising from either recent co-evolution or local co-adaptation is eliminated. In a major review of controls on the distribution of *Eucalyptus* in Australia, Adams (1995) challenged the dominant paradigm, traced back to Beadle (1954), that nutrients delimit vegetation types and plant development on the continent. Adams argued that nutrient recycling supplies most of the nitrogen and phosphorus (and other nutrients) required for tree growth in Australian forest and woodlands, and that water availability is the dominant control on vegetation in geologically-old landscapes. If eucalypts in general have adapted so that nutrients do not in general limit the extent of their canopy development or function to the degree that water ultimately does, then this might in part explain the uniformity of leaf efficiencies among allopatric species.

It must be emphasised that the hypothesis is not proposed to hold for situations in which plant-available water is unlimited. Lack of at least seasonal water stress due to abundant and well-distributed rainfall or access to fresh groundwater may reveal significant differences in stomatal control and leaf area among eucalypts, as implied by Greenwood et al. (1982) and Morris and Thomson (1983). We also note that the LAIs of the systems examined in this report were all relatively low (< 1.5), and thus all leaves in the canopy might be considered as effective with respect to energy interception. In a sense, at low LAI, transpiration is controlled more by energy interception than leaf conductance.

There are clear limitations to the resolution of the analyses reported in this (and most other) papers of this type, at least with respect to testing a general hypothesis. There were relatively few observations. The errors of measurement, of order $\pm 10\%$ for both leaf area and transpiration, were large enough to (possibly) mask ecologically and physiologically significant differences in detail. Nevertheless, there are strong empirical and theoretical arguments in favour of small differences in leaf efficiencies among evergreen trees in water-limited environments. The empirical arguments have been discussed. Hatton et al. (1997) reviewed some of the more theoretical ones. For example, if one adopts the simple model of canopy conductance proposed by Sziecz and Long (1969):

$$r_c = \frac{\bar{r}_s}{LAI}$$

where r_c is canopy conductance and $\bar{r}_s$ is the mean stomatal resistance, then we see two levers on the control of transpiration in plants. In water limited environments, we know that evergreen plants employ both strategies to regulate water use, but adjusting the numerator comes at a price: higher leaf-air vapour pressure gradients, lower net carbon assimilation per unit leaf area, and potentially fatal leaf temperatures (e.g., Pook 1986). Adjustment of LAI can help maintain lower resistances in the remaining leaves during stressful periods. That evergreen plant communities in Australia do this is, we believe, beyond question. In this paper, we have presented evidence that sympatric eucalypts tend to come to the same solution to the above dilemma.

If the hypothesis of similar leaf efficiencies among eucalypts holds, then the selection process for species for revegetation work is somewhat simplified. This is useful given the plethora of criteria brought to bear on this selection: drought tolerance, salinity tolerance, frost tolerance, disease resistance, wood quality and quantity. From the viewpoint of revegetation aimed at water balance control in a seasonally water-limited environment, it may well be that a similar result will follow from a plantation of any species of eucalypt as long as it is fully stocked and survives. Further, the possibility that the extent of canopy development can be used as an indicator of the hydrological behaviour, regardless of eucalypt species, could offer an intriguing and efficient way of assessing the effectiveness of tree plantations and natural stands in maintaining the landscape water balance.

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PAPER NO. 3

RELATIONSHIPS BETWEEN WATER USE EFFICIENCY AND TREE PRODUCTION

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Summary

This paper is concerned with the Water Use Efficiency (WUE) of trees, with a view to assessing the value of this parameter as a criterion for species selection or a basis for the management of stands in an agroforestry context. WUE may be defined as the amount of dry matter produced by a plant per unit of water transpired. It can be considered at the leaf, plant or stand level, and over a range of intervals. The paper focuses on the stand level, over periods up to a season.

Data in the literature suggest that mean values of WUE from different tree species are similar. Analysis of data from eucalypt plantations in Western Australia gave values at the higher end of the range, but there are significant uncertainties associated with the results, and the way they are derived, so these values cannot be taken as definitive. The use of a well-validated tree growth model to analyse the influence of growing conditions on tree growth patterns, particularly in relation to the allocation of assimilate to above- and below-ground components of tree, indicates that estimation of WUE on the basis of above-ground growth does not provide a useful basis for the evaluation of tree performance.

It is concluded that, although WUE may provide useful insights into the responses of trees to varying environmental conditions, it is unlikely to be of primary value as an index of tree performance for use at the relatively applied level of the design and management of agroforestry systems.

Introduction

Water Use Efficiency (shortened to WUE for convenience in the text, but denoted q for algebraic purposes) may be defined as the amount of dry matter produced by a plant per unit of water transpired. The phrase has been used to describe a range of processes, from gas exchange by individual leaves, over time periods as short as a few minutes, to dry matter accumulation over a growing season. (Water use by a stand of trees - or a crop - could also be defined as total water use, i.e. transpiration plus interception, run-off and drainage, but this is not helpful for present purposes and will not be considered further in this paper.)

Since photosynthesis - the fundamental growth process - and transpiration are inextricably linked by their dependence on stomatal behaviour, it is reasonable to expect that WUE will be relatively conservative and might be a useful biological parameter for analysing the interactions and relative significance of CO_2 uptake and transpiration. However, it does not seem likely that WUE values are sufficiently stable to be useful as measures of tree performance in different environments, nor is it likely that the values associated with particular species are consistent enough to be useful as a basis for selecting trees for particular uses, or for management. This paper examines the way WUE varies in trees, and the reasons for these negative assertions about the usefulness of this parameter.

Background

Values of WUE at the leaf/gas exchange level are more useful for interpreting the influence of growing and current environmental conditions on leaf physiology than for predicting growth. There is no evidence that there exist definitive values, associated with particular species or provenances. For reference we note that Küppers, (1984)

gave values ranging from 0.88 to 2.95 g (dry biomass equivalent) kg^{-1} (water transpired) for a selection of woody species in Europe, while Pereira et al. (1986) found that WUE of *E.globulus* leaves (in Portugal) was highest in spring (ca. 13 g kg^{-1}), falling to low values in autumn. WUE also varied through the day. Pereira et al. cite a WUE range from 4.3 to about 7 for other woody species measured by other scientists.³

WUE measurements on leaves are always made over short periods and reflect short-term variations in environmental conditions and the physiological state of the leaves. WUE can be estimated for stands from canopy flux measurements, which integrate spatially but still reflect short-term variation caused by environmental conditions. Values estimated for stands over longer periods, on the basis of growth measurements and average transpiration rates are likely to be more stable. These points are illustrated by results from Baldocchi et al. (1987) and Dewar (1997). Baldocchi et al. made CO_2 and water vapour flux measurements over a mixed stand of oak and hickory in Tennessee. From these they obtained WUE values between 3.6 and 13 g kg^{-1} . Extensive growth data for crops show that WUE is approximately inversely proportional to mean vapour pressure deficit (D), so Dewar derived a ratio between WUE normalised for the effects of humidity ($\text{WUE} \times D = q_0$) and a 'light' utilization coefficient⁴ (α_c). He obtained values for α_c/q_0 of about 0.27 kg $\text{H}_2\text{O MJ}^{-1} \text{kPa}^{-1}$ for *Pinus radiata*, where α_c was calculated in terms of total incoming short-wave (solar) radiation. Baldocchi et al. give radiation utilization efficiency values of 2.4 - 4.7 g $\text{MJ}^{-1} \text{PAR}$ which, combined with their WUE values, give $\alpha_c/q_0 \approx 0.36 - 0.7 \text{ kg MJ}^{-1} \text{PAR}$, i.e. about 0.16 - 0.36 kg MJ^{-1} for total radiation, with a mid-range value of

³ WUE values tend to be reported in a variety of units - e.g. mol $\text{CO}_2 \text{ kmol}^{-1}$ water transpired, g $\text{CO}_2 \text{ kg}^{-1}$ water transpired and g dry mass kg^{-1} water transpired. I will use g (dry biomass) kg^{-1} (water transpired) - i.e. g kg^{-1} - since this is the most easily understood unit when we are considering tree growth and transpiration, which is generally calculated in mass flux units in relation to trees in the field. The data from Küppers and Pereira have been converted to these units.

⁴ Dewar used the symbol ϵ for light utilization efficiency; the same symbol used by Landsberg and Hingston for the radiation utilization efficiency of above-ground growth. As suggested by Landsberg and Waring (1997) I will use the symbol α_c to denote radiation utilization efficiency - or canopy quantum efficiency - applied to total growth, and the symbol ϵ for above-ground growth. In both cases it is important to specify whether the calculations were made in terms of total short-wave radiation or photosynthetically active radiation (PAR). There is (approximately) a difference of a factor of two between them. Dewar's use of the term 'light' utilization efficiency is, technically, incorrect: PAR is the same as light; total short-wave radiation is not. I will use radiation utilization efficiency here.

0.24 (cf Dewar's 0.27). The similarity of these values indicates that α_c/q_0 may be a useful parameter for modelling tree growth in general, but the similarity of the values obtained by Dewar, and from Baldocchi's data, provides no support for the idea that there are significant differences between the WUE values of different species.

The Dewar (1997) and Baldocchi (1987) data considered above applied to stands and included above and below-ground dry mass production. This highlights one of the problems with WUE as a parameter that might be used for tree selection for particular areas or ecological situations: it is determined by above and below-ground growth, and we cannot assume that below-ground growth is a constant fraction of above-ground dry mass production. The point is explored in some detail later in this paper.

At the whole tree level WUE depends not only on leaf (stomatal) characteristics, and on D, but also on factors such as the leaf area of trees relative to the volume of soil exploited by the roots, and the amount of water in that soil. If trees are to be used to control water tables, the requirement may be for maximum possible growth and water use rates, which are not necessarily correlated with high WUE: a tree which grows rapidly, producing a large leaf area, is likely to transpire rapidly, although its WUE may be low. Alternatively, if trees are to be used for wood production in areas where rainfall is likely to limit their growth, it may be important that they should have high WUE. The most useful approach to evaluating variations in WUE will be to analyse in some detail the data that are available, and to use an appropriate model to simulate tree growth and water use, and hence provide a range of WUE values. These should provide a basis for considering the implications of the variations in this parameter, and the relative importance of the factors that influence it.

Analysis of West Australian data

Hingston et al. (1995) produced a detailed and very valuable report from three years of measurements, and the subsequent analysis, of the effects of soil and climate on the productivity of *E.globulus* at five sites in Western Australia (WA). The data presented allow the calculation of WUE for each site. Hingston et al. measured only above-ground productivity, but they used McMurtrie's BIOMASS model (McMurtrie et al., 1990a,b) to simulate total dry mass productivity, and matched the results to stem and leaf mass production. The 'residual' material was assumed to have gone to root production. Since the amounts of material that had to be allocated to roots were well within the range and variation observed in various studies (on other tree species) where roots had been excavated, Hingston et al. were able to indicate the proportion of material allocated to roots (f_r). From these estimates, and above-ground production (W_{a-g}) it is a simple matter to estimate total biomass production, as follows:

$$\text{if } \Delta W_{\text{tot}} = \Delta(W_{a-g} + W_{\text{roots}}), \text{ and } W_{\text{roots}}/W_{\text{tot}} = f_r,$$

$$\text{then, since } W_{a-g} = W_{\text{tot}}(1 - f_r),$$

$$\Delta W_{\text{tot}} = \Delta W_{a-g}/(1 - f_r)$$

Above-ground production includes stems, branches and leaves. Table 1, below, is derived from data provided by F.J. Hingston (the complete set of above-ground biomass values does not appear in the Hingston et al. report). The seasonal transpiration rates (ΣE , mm) are provided in the report. They were based on a complete hydrologic analysis, which included consideration of run-off, interception and drainage, and gave results consistent with neutron probe measurements of soil water content in the rooting zones of the plantations (although the values of 1-2 mm day⁻¹ are surprisingly low).

Table 1. WUE values (g biomass kg⁻¹ water transpired) calculated for *E.globulus* for two seasons for five study sites in Western Australia from data of Hingston et al.(1995).

	1991- 1992			1992-1993		
Site	DW _{tot} /(1-f _r) (kg ha ⁻¹)	SE (mm)	WUE (g kg ⁻¹)	DW _{tot} /(1-f _r) (kg ha ⁻¹)	SE (mm)	WUE (g kg ⁻¹)
Darkan 84	9.7/0.72	262	5.14	9.4/0.72	397	3.29
Darkan 87	15.0/0.75	339	5.90	15.8/0.75	401	5.25
Mummbalup	22.5/0.85	476	5.56	20.4/0.85	484	4.96
Manjimup	15.8/0.73	595	3.64	28.9/0.73	595	6.63

Norhtcliffe	35.6/0.82	1195	3.63	32.7/0.82	1104	3.61
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The data in Table 1 show a twofold range of WUE values, i.e. between 3.3 and 6.6, with an average value of 4.76.

Landsberg and Hingston (1996) obtained radiation conversion efficiency values for the WA eucalypt data (above-ground production). Correcting these to represent total dry matter production, from which we can calculate α_c , gave a range between 1.29 and 2.72 g (dry biomass) MJ⁻¹ PAR and α_c/q ratios which ranged from 0.23 to 0.75, with a mean of 0.48. If the α_c values had been calculated using total short-wave radiation they would have been about half the values obtained, so this range and mean is exactly consistent with Dewar's results for *P. radiata*. However, note that WUE (q) has not been normalised by D - average D over the year for these sites is less than 1 kPa, so normalising would give q_0 values higher than q and α_c/q_0 commensurately lower. (The usefulness of this procedure, on the basis of annual average D, is open to argument.)

Analysis of WUE using a model

The model used to analyse WUE and the way it varies when different environmental conditions cause different patterns of tree growth is called 3-PG. It is a generalised model of forest productivity based on the physiological processes that govern tree growth - hence the name 3-PG (**Physiological Principles in Predicting Growth**). The model was developed and initially tested by Landsberg and Waring (1997). It calculates total carbon fixed (gross primary production; P_G) from utilizable, absorbed photosynthetically active radiation ($\phi_{p,a,u}$), obtained by correcting the photosynthetically active radiation absorbed by the forest canopy ($\phi_{p,a}$) for the effects of soil drought, atmospheric vapour pressure deficits and stand age. P_G is obtained from $\phi_{p,a,u}$ and the canopy quantum efficiency (α_c), values of which are becoming available for a number of forest types. The ratio of net (P_N) to gross primary production is emerging as relatively constant for trees. This eliminates the need to calculate respiration and is used to estimate P_N - the net amount of carbon (assimilate) converted to biomass. 3-PG uses a simple relationship based on growing conditions to estimate the amount of carbon allocated below ground (see Fig. 1), and a procedure based on allometric ratios - widely available for many species and situations - to determine the allocation of carbon to foliage and stems and constrain tree growth patterns. The model includes a procedure for dealing with sub-optimal nutrition (Fig. 1), and routines that deal with stem mortality, but these are not needed for the analysis presented here. It is currently configured for stands; a version to deal with single trees is under development.

3-PG allocates carbohydrates to roots on the basis of a simple equation which reflects the accumulating evidence that trees allocate increased amounts of carbon to their roots when growing conditions deteriorate - a strategy that seems intuitively 'sensible' in terms of the need to survive adverse conditions. It imposes limits to the proportion of carbon allocated to root growth, maintenance and turnover that are consistent with many studies and observations and are physiologically plausible (see Keyes and Grier, 1981; Landsberg, 1986 (for a review), Sanantonio, 1989, Beets and Whitehead, 1996). The equation describes the curves shown in Fig.1.

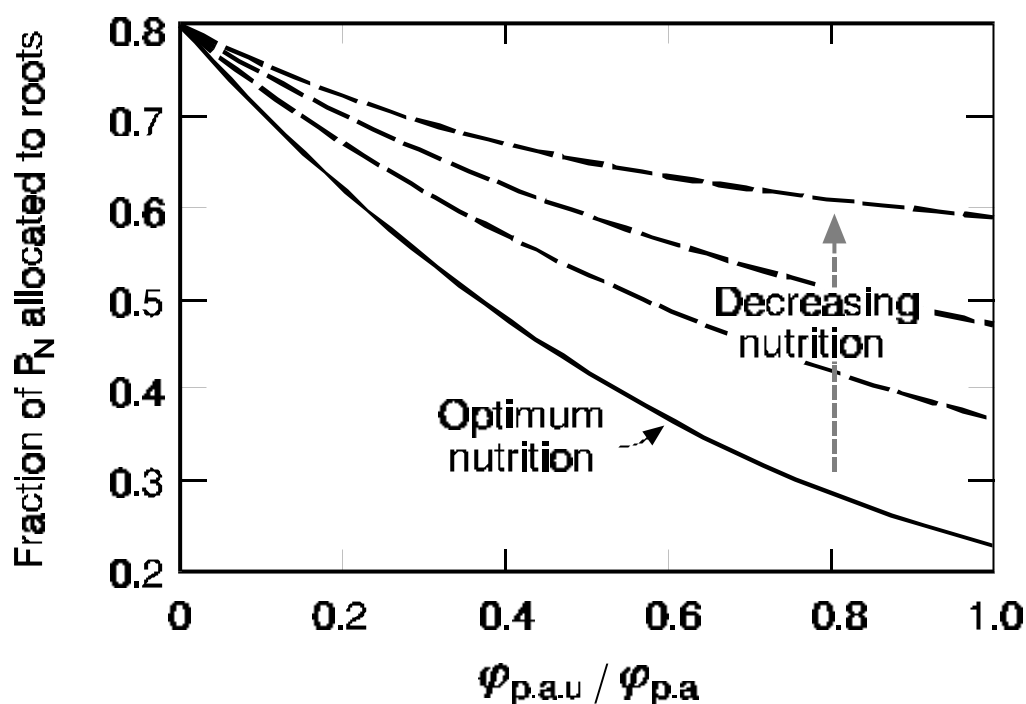


Figure.1 Variation of the carbon allocation coefficient with site nutritional status, or nutrient availability. Nutrition is altered by a modifier based on soil fertility. The x-axis is the ratio of utilizable absorbed photosynthetic radiation to absorbed photosynthetic radiation, which provides an index of growing conditions - under good conditions the index tends towards unity and the fraction of assimilate allocated to roots tends to a minimum. Available soil water at any time, and atmospheric conditions determined by VDP, are the major factors affecting $\phi_{p.a.u}/\phi_{p.a}$. (from Landsberg and Waring, 1997)

3-PG requires weather data as inputs, works on monthly time steps and has been run for periods up to 120 years, producing realistic patterns of stem growth and stem diameter increments.

To give confidence in the capacity of the model to simulate forest growth I present, in Fig. 2, simulated and measured values of cumulative stem biomass (*P. radiata*) for sites in Australia and New Zealand, and tabulate results of tests against the Western Australia eucalypt data (Table 2).

The age of the plantations studied by Hingston et al. varied from 2 to 6 years at the start of the 3-year measurement period. Model runs were made for four of the plantations, using the weather data provided, from the age of the plantation a year before measurement period to a year past the age of the plantation at the end of the period; eg. if the plantation was 4 years old at the start of measurements the run would be from Yr 3 to Yr 8. Soil water storage values were given. Starting biomass values (stems, leaves and roots) were set to values estimated one year before the start of the measurement period and the stem populations used were those given for the plantations. Specific Leaf Area, which is a variable in 3-PG, but usually set to a default value of $6 \text{ m}^2 \text{ kg}^{-1}$, was set to the values given, which were on the very low end of normal, but consistent with trees

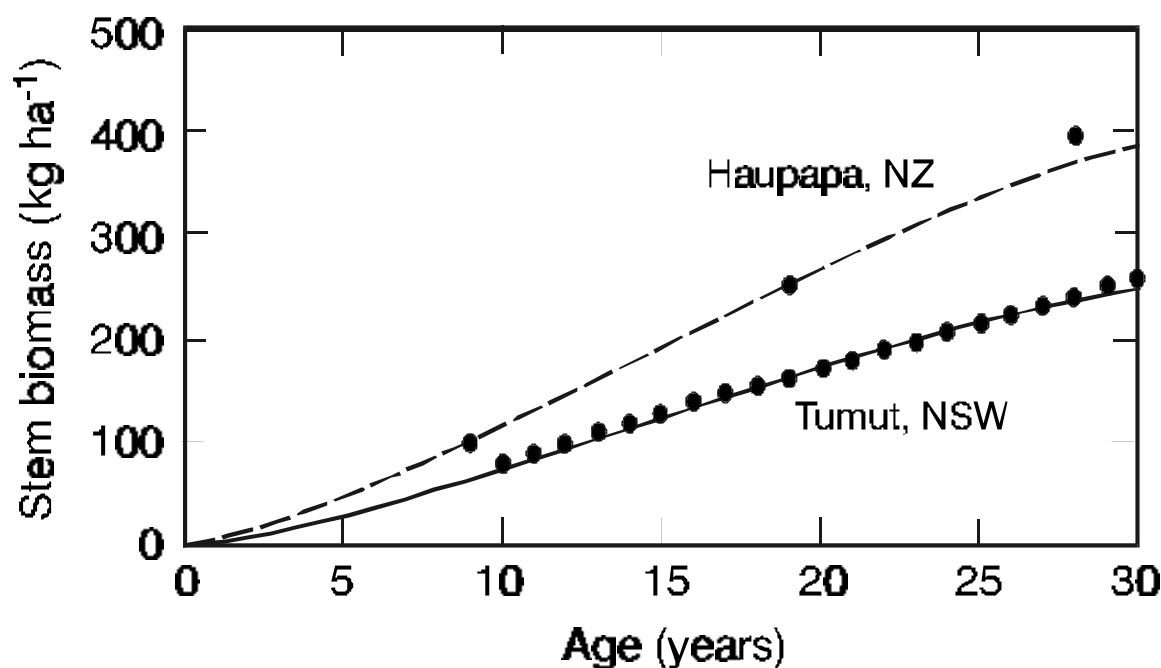


Figure 2. Simulated (lines) vs measured values (points) of cumulative stem biomass (*P. radiata*) at Haupapa, New Zealand, and Tumut, New South Wales, over 30 years. The simulated values were calculated with 3-PG, using appropriate weather data and values for available water in the root zone and fertility modifiers. Initial stem populations were taken as 1500 ha⁻¹. No fitting procedures or adjustments were used. (From Landsberg and Waring, 1997)

growing in dry areas. Since all the plantations were fertilised nutrition was assumed optimal. For the Northcliffe plantation, where the trees apparently had access to a water table, the model could not produce growth rates to match those observed unless the restriction on growth imposed by the soil water content in the root zone was ‘switched off’. On the other hand the Manjimup plantation may also have had access to a water table, yet simulated growth rates were higher than those observed. The results of these, and other tests of the model, will be discussed in detail elsewhere, but for present purposes they suffice to show that the model performs well enough to provide a sound and acceptable tool for the analysis of WUE and the way it varies under different conditions. The results obtained are presented in Table 2.

To explore the variation in WUE caused by environmental conditions I simulated the growth of hypothetical plantations using a standard set of radiation data (approximately the radiation regime of south Western Australia) and varying VPD and rainfall. Rainfall regimes were :

- (1) 600, (2) 900 and (3) 1200 mm year⁻¹, evenly distributed through the year, associated with average monthly VPD varying from
- (1) 1.5 (summer) to 0.5 kPa (winter), (2) 1.2 to 5 kPa and (3) 0.9 to 5 kPa, respectively.

Table 2. Comparisons between observed and simulated growth of and LAI of *Eucalyptus globulus* at four sites in Western Australia. The ‘observed’ (measured) values are from Hingston et al. (1995); the simulated values were obtained with the model 3-PG, provided with weather data, stem numbers and Specific Leaf Area values. There was no fitting procedure.

Stem biomass (t ha ⁻¹)				Mean LAI		Mean CAI	
Start		Finish				(t ha ⁻¹ yr ⁻¹)	
Observed	Simuld	Observed	Simuld	Observed	Simuld	Observed	Simuld
Site: DARKAN 84 (Start: end Yr 6; Finish: end Yr 9)							
33	30	55	59	3	2.5	8.4	9.5
Site: MANJIMUP (Start: end Yr 6; Finish: end Yr 9)							
100	102	132	138	5	4	11	12

Site: MUMMBALUP (Start: end Yr 2; Finish: end Yr 5)							
12	21	50	55	3.5	3.2	15.2	11
Site: NORTHCLIFFE (Start: end Yr 4; Finish: end Yr 7)							
98	94	182	165	6	7	30	24

Starting stem populations were standard at 1250 ha⁻¹ and soil moisture storage capacity was 150 mm (lower than the values at the sites studied by Hingston et al.). Other parameters took default values. Each run was 20 years. The results, in terms of the time course of LAI and on WUE are shown in Figs 3 and 4.

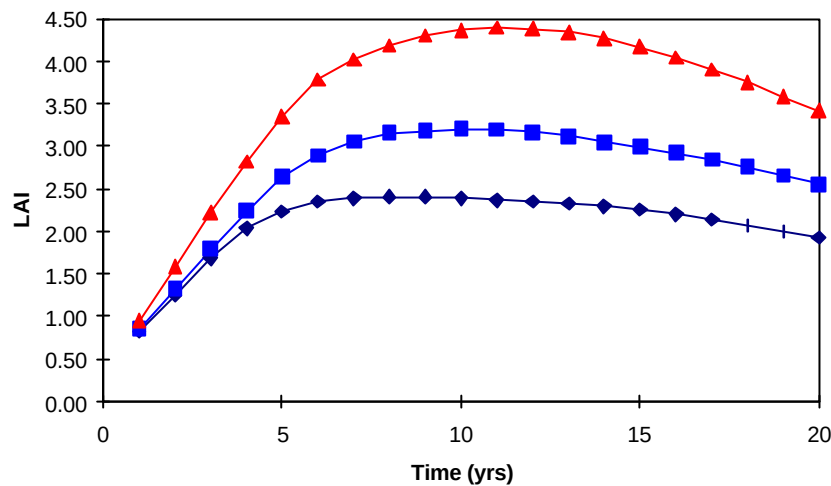


Figure 3. Time course of plantation LAI under 3 climatic regimes. The curves reflect the increasing dryness of the environment: top - high rainfall, low average VPD; bottom - low rainfall, higher average VPD.

The WUE values in Fig. 4 apply to total dry mass production. They are lower than those obtained for WA from the Hingston et al. data (Table 1), largely because the transpiration rates calculated by 3-PG are higher than those obtained by Hingston et al. from their water balance in WA. The α_c value used by 3-PG is 1.8 g C MJ⁻¹ (PAR) (1 g C $\approx$ 2 g dry

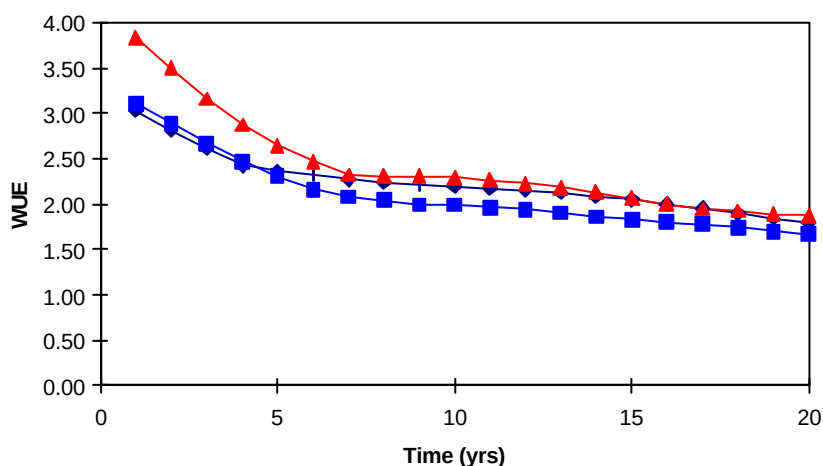


Figure 4. The time course of WUE of plantations under the three climate regimes. WUE under the wettest regime (1200 mm rain, relatively low VPD) was slightly higher throughout the growth period; markedly so in the first 5 years.

biomass). Of the carbon fixed 0.45 is assumed lost by respiration so the effective value of α_c , in terms of dry biomass, is about 2 g MJ^{-1} ; correcting for the difference between PAR and total short-wave reduces this to about 1, so to get α_c/q ratios of the order of those cited earlier we would need $q \approx 4 \text{ g kg}^{-1}$.

For reference, the dry mass of stems in each of the three climatic regions represented in Fig. 4, after 10 and 20 years, was

- (1) 55 tons ha^{-1} at 10 years, 99 tons ha^{-1} at 20 years
- (2) 71 tons ha^{-1} at 10 years, 129 tons ha^{-1} at 20 years
- (3) 96 tons ha^{-1} at 10 years, 167 tons ha^{-1} at 20 years.

(Stem mass in 3-PG includes branches, which will normally be 10-15% of total above-ground mass.)

The differences in LAI and stem growth, which are not reflected in WUE (Fig. 4), must be caused by changes in the pattern of carbon allocation, as indicated by the curves in Fig. 2. This can be illustrated quantitatively by calculating the time course of WUE for total biomass production (q_{tot}) and topgrowth ($q_{\text{t-g}}$) (stems and foliage), separately, under two different moisture regimes. These were

- (1) rainfall 900 mm year^{-1} , VPD moderate (1.2 to 0.5 kPa)
- (2) rainfall 600 mm year^{-1} , same VPD regime.

Other conditions were as for Figs 3 and 4.

The results are shown in Fig. 5, where the two upper lines show the time course of LAI and the lower lines show the ratio of $q_{\text{tot}}/q_{\text{t-g}}$. We see that, in the higher rainfall regime, the ratio $q_{\text{tot}}/q_{\text{t-g}}$ remains constant, while under the lower rainfall regime the ratio falls steadily as the trees allocate increasing amounts of assimilate to their root systems in response to the steadily increasing moisture stress. WUE values, derived from total biomass production, were similar to one another. These results illustrate clearly the influence of growing conditions on the distribution of dry mass, and the dangers of deriving WUE values from top growth measurements alone; they may indicate large differences in WUE, while in fact the real differences are small and the data reflect differences in the physiological response of trees to water stress.

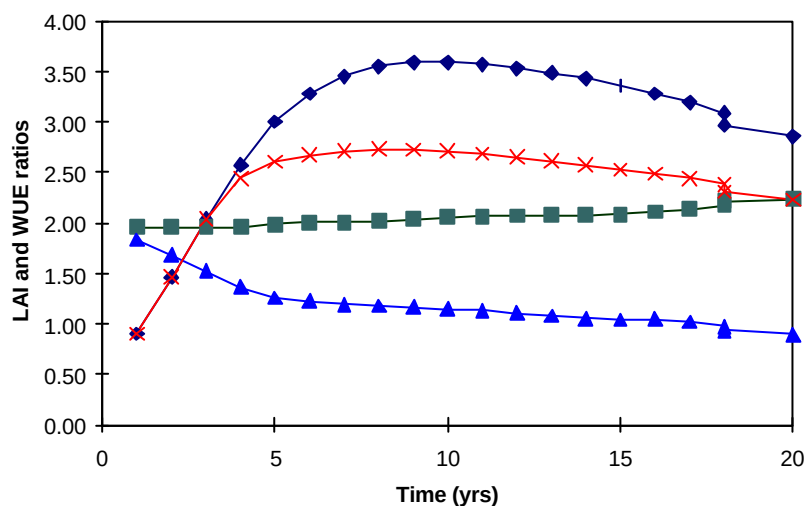


Figure 5. Time course of LAI with relatively high and low rainfall (upper curves), and the associated changes in the ratio of the WUE of the whole tree to that of the top growth alone. Under the low rainfall regime the increasing proportion of assimilate allocated to roots causes the ratio to fall steadily over time.

Discussion and conclusions

An objective of this paper has been to present information about WUE and, on the basis of that information, to evaluate whether this parameter may be valuable as a criterion for the selection of trees for agroforestry purposes, or for management or yield prediction - which implies concern with above-ground productivity. For WUE to be of any value for the selection of species for particular purposes (wood production, water

extraction...) it would have to be (demonstrably) significantly different between species. It would also have to be relatively easy to measure. WUE does not appear to fulfil either of these criteria.

We know that there are large differences in the capacity of trees to withstand drought, or to respond to favourable water regimes, and therefore it is highly probable that there are real inter-species differences in WUE. These may be reflected in a number of ways: for example different assimilate partitioning strategies may result in differences in leaf area as well as in root mass and turnover. Such differences cause feed-back effects which will be difficult to identify and quantify and Fig. 5 illustrates the extent to which the allocation of assimilates to root growth and turnover can affect above-ground growth. Factors such as varying ability to withstand desiccation without losing leaves or, alternatively, rapid loss of leaves under stress and rapid re-growth of new ones when the water regime improves, will also affect WUE. In general, a great deal of subsidiary information on processes such as leaf growth and longevity, and stomatal behaviour, will be required to ensure that efforts to interpret varying tree growth patterns in terms of WUE will provide useful and reliable information. I would argue that it is likely to be more useful to try to interpret the tree growth patterns observed under different conditions in terms of conventionally studied factors such as water regimes, fertility or soil salinity than to try to determine differences in WUE.

Determination of WUE is complicated by the fact that it is a ratio of two quantities - growth rate and transpiration rate - both of which generally have significant uncertainty associated with them. Even if consideration was confined to above-ground growth - which may be tempting from a pragmatic point of view - estimates of growth rates, if made by conventional means such as stem measurements, incorporate the uncertainties at the beginning and end of the measurement interval. These estimates should include foliage dynamics (litterfall). Water use by transpiration must either be estimated from a complete water balance (as was done by Hingston et al. or at Pearce's Creek - the data used by Dewar (1997)) or calculated, in which case the calculation should include an estimate of stomatal conductance, which is an important factor in WUE, so may itself bias the results.

Even where very detailed data are collected, and an effort is made to account for below-ground growth, Table 1 of this paper, which shows a two-fold range in WUE derived from a detailed, high quality data set for a single species, suggests that it would be difficult to demonstrate significant differences between tree species from field studies. This is supported by the correspondence between the results obtained by Baldocchi et al. (1987) from a deciduous forest in Tennessee and Dewar (1997) from *Pinus radiata* in Australia. It would be easier to identify species differences from studies in pots in controlled environments, but if such studies did show real inter-species differences it would remain very doubtful whether the results could be extrapolated to the field.

WUE may have more value for yield prediction (growth modelling) than for species selection if we could assume that it is constant. This seems to be a reasonable assumption for grain crops (see references cited by Jones, 1992), where it seems the ratio between root and top mass is less variable than in trees. Dewar's (1997) model explicitly assumes that normalised WUE is a constant, and he gets almost identical values of the ratio α_c/q_0 for the control treatment and a fertilised treatment in the *P. radiata* stand. He argues (personal communication) that since CO_2 uptake and transpiration are inextricably linked through stomatal behaviour, WUE reflects environmental conditions (through D) and the biology of the system (through q_0), and therefore reflects the conservative nature of the ratio between internal (c_i) and external (c_a) CO_2 concentrations. This does not solve the problem of assimilate partitioning and root growth but takes account of the link that there must be between growth and transpiration.

In summary, I would argue that WUE is not a particularly useful parameter for evaluating the effects of trees on the landscape, in relation to agro-forestry, for selecting trees or for predicting their above-ground growth rates. The values are variable, difficult to determine and, although they may reflect the influence of environmental conditions on total growth, the influence of those conditions on growth patterns is likely to confuse matters. Nevertheless, it will remain important to improve our ability to calculate transpiration accurately, and of course to measure or model dry mass production. Estimates of WUE will emerge from studies aimed at these objectives and will, almost certainly, provide interesting insights into the eco-physiological responses and behaviour of trees.

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PAPER NO. 4

ROOT DISTRIBUTIONS AND WATER UPTAKE PATTERNS IN EUCALYPTS AND OTHER SPECIES

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Summary

This paper reviews what is known about the structure and function of tree root systems in relation to the uptake of water and competition with other species. A large number of studies confirm that deeper root systems enable Eucalypts and other trees to access water not available to shallow rooted trees and crops, and to maintain their relatively high transpiration rates over dry summer periods. Information on the size and shape of Eucalypt root systems is critically reviewed.

From the observations made in several continents of trees at different stages of growth, a consistent picture emerges that Eucalyptus trees have a dimorphic root system. A typical system has a widely spreading lateral root system just below the soil surface, with a deep tap root in young trees and deep vertical sinker roots in mature trees. The roots are opportunistic in their search for water and nutrients, and will follow moisture gradients up to 20 m into adjacent fields. It appears that even the vertical roots will move horizontally towards sources of water. Many agroforestry workers recommend controlling competition by restricting the lateral spread of roots into crops by root pruning, or digging ditches.

The single root model for plant water uptake can be used to model relative water uptake by trees and crops or pasture, and the way that transpiration is reduced as the soil dries. The model requires that root length density distributions of the two species must be measured, or else estimated using a function such as the negative exponential. The single root model commonly overestimates soil water uptake, but can be modified to take account of factors such as poor root-soil contact, clumping of roots, and anaerobic conditions near saturation.

Introduction

To design a successful agroforestry system, it is necessary to examine below-ground interactions between the tree root systems and the roots of the associated crop or pasture in order to assess the degree of competition or complementarity between trees and the crop (van Noordwijk et al., 1996). Until recently, Australian studies of the desirability of planting trees on farms (Brown and Hall, 1968; Hall, 1972) considered principally the above ground effects of improving shade and shelter. For many Australian sites, it is desirable that an agroforestry system increase the overall water use, to reduce the amount of water reaching the deep water table. At the same time, it is desirable that the tree roots do not compete too strongly with the crop roots, and cause a reduction in the yield of the crop or pasture. Because of their longer lifetime, trees have the opportunity to explore larger soil volumes and to use their deeper root systems to access water or nutrients that may be inaccessible to annual crops.. However, a tree with a deep root system may also have a large number of roots close to the surface, and if water and nutrients are available there, may take up most of its water from the soil zone shared with the crop root system, and may greatly reduce the productivity of the associated crop. As pointed out by Ong et al. (1996), there are many philosophical and practical difficulties in measuring or estimating water uptake and use by agroforestry systems and their component species. The study described by Eastham and Rose (1988, 1990) was designed to address these questions, and is the main source of field information under Australian conditions. As there is a paucity of experimental data, a natural approach is to use theoretical models of soil water flow and root water uptake to predict the water use of agroforestry systems of different designs.

The loss of water from plant leaves is an inevitable consequence of the process by which a plant acquires carbon dioxide from the atmosphere, and the rate of water loss at any time is determined by the interaction of the plant and its environment. Variables such as temperature, humidity, wind and light govern the loss of water by the leaves. The rate at which this water can be replenished by the root system depends on the ability of the root system to transmit water to the leaves, and on the ability of the soil to store water, and to transmit water to the roots. If the rate at which the roots can take up soil water does not match the potential evapotranspiration determined by atmospheric factors, then the plant will dry out, and will close its stomata to reduce the transpiration rate. As the amount of water stored in the soil decreases, so does the rate that water can flow through the soil to the roots, and the actual evapotranspiration decreases. Originally there was a widespread belief among agronomists that soil water was freely available to the plant root system until the soil became so dry that the “wilting point” was reached, whereupon the transpiration stopped. (See for example Viehmeyer and Hendrickson, 1955.) The view that there would be a gradual reduction in actual transpiration as the soil water was depleted was a result of the successful application by Philip (1957) and others of modern theory of water movement through soils.

The size and shape of plant root systems and the uptake of water and nutrients have been studied by agriculturalists and foresters seeking to improve productivity, and by ecologists wishing to observe plant competition and explain relative abundances of species at different sites. It is only in recent times that agroforesters have been investigating competition or complementarity between trees and crops or pasture, and climatologists have been seeking information about root systems and root water uptake in order to model soil water variation on a regional (Katul et al., 1997) or global (Canadell et al., 1996) scale. The qualitative observations and the number and kinds of measurements that have been made depend on the aims of the experimenter, and may be not shed much light on the design of agroforestry systems. Dabral et al. (1985) reviewed the mainly Australian material then available on Eucalypt root systems, and commented on the lack of information relevant to the design of agroforestry systems in India.

In the field, excavation of root systems is time consuming and labour intensive, and destroys or badly disturbs the normal functioning of the root system. Methods of studying root systems are described in detail by Bohm (1979). However, root presence does not necessarily imply root activity, and it is much more challenging to investigate actual water and nutrient uptake. Indirect methods can be used in the laboratory to observe water uptake and transmission by root systems (See for example Hainsworth and Aylmore, 1989; Bottomley et al. 1986.) Field water uptake distribution has usually been inferred from soil water depletion patterns, but to calculate an accurate estimate it is necessary to perform a proper water balance and to correct for the simultaneous flow and drainage of soil water (Wilcox, 1960; Rose and Stern, 1967). Traditionally, neutron moisture meters have been used to measure soil water content, but Time Domain Reflectometry (TDR) is now being used to give better resolution in both space and time (Katul et al., 1997). Recently, analysis of the stable isotope composition of plant water has become an important technique to infer the source of water taken up by the root system. (See for example White et al. 1985.) This provides qualitative information, and must be combined with another technique such as the heat pulse method to measure actual evapotranspiration.

This paper reviews what is known about the size and shape of root systems of Eucalypts in particular and other species in general, and how the morphology of root systems is related to their water uptake function and rates of evapotranspiration, particularly in competition with other species. Although many of the general principles that relate root system design to water uptake patterns and competition with other species for water and nutrients are part of the “conventional wisdom”, there have been few rigorous studies performed to unambiguously confirm them (Franco and Nobel, 1990). A number of studies which have examined patterns of soil water uptake and depletion, and the associated reduction in evapotranspiration in Eucalypts and other species will be described. Finally, various theoretical models for soil water uptake by roots will be critically examined.

Important sources of information have been a number of review articles. I have used the review by Gardner (1983) on soil properties and efficient water use, and the survey by Passioura (1988) of water transport in and to roots, as well as the review by Molz (1981) of models of water transport in the soil-plant system. Ong et al. (1991) review the effects of competition between species. Ong et al. (1996) give an account of various methods for measuring water use in tree-crop systems. Ehleringer and Dawson (1992) review the use of variations in the composition of stable isotopes to infer water uptake patterns. Stone and Kalisz (1991) list what is known about the maximum extent of root systems of many species, but their data on Eucalypts is sparse. The influence of root distribution of trees and crops on competition or complementarity is surveyed by van Noordwijk et al. (1996), and van Noordwijk and van de Geijn (1996) discuss the parameters required for process-oriented models of soil water uptake. Jackson et al. (1996) summarise 250 studies of rooting patterns of a wide variety of species, and Canadell et al. (1996) tabulate the maximum rooting depth of vegetation types at the global scale. Clothier and Green (1997) give an account of root water uptake modelling, and recent improvements in the techniques for observing root activity. Other sources of information have been keyword searches in the Science Citation Index and the CAB Abstracts databases.

Morphology of root systems related to water uptake

This section reviews the known information from studies of the extent and density of Eucalypt root systems, and how the morphology of root systems is related to their water uptake function, especially in competition with other species. Although the general principles relating root system design to water uptake patterns are widely assumed to be true, there are not many studies which actually confirm or disprove them.

Root systems and rainfall

It is a matter of observation that plants in drier environments usually have deeper root systems. A survey of global patterns of root distribution was given by Jackson et al. (1996), and Canadell et al. (1996) collected known information on rooting depth. On a global average, desert vegetation reaches a maximum rooting depth of 13.4 m, with 37% of the total root biomass below 0.3 m soil depth, while temperate forests have a maximum rooting depth of 3.7 m, with 35% of the root biomass below the 0.3 m soil depth. The root systems of temperate grasses reach a maximum depth of only 2.4 m, and have only 17% of the total root biomass below 0.3 m.

As discussed by Barbour (1973), there has long been an assumption among ecologists that plants in deserts or other drier environments have higher root/shoot ratios and deeper root systems to enable them to access water deeper in the soil profile. To test this assumption, Schulze et al. (1996) conducted an extensive study to examine vegetation patterns, rooting depth and water extraction levels along an aridity gradient in Patagonia, in South America. At the end of a dry season, they tested the hypothesis that decreasing precipitation would lead to increasing depths of rooting and of the horizons from which roots extract water. They were surprised to find that there was no correlation between rooting depth and rainfall in their study areas, that soil water was available at a depth of 2-3 m at all sites, and that roots reached that depth at all sites. However, their conclusions were based on a single “snapshot” in one season of the soil water status along their aridity gradient. It is extremely likely that the optimum rooting depth, particularly for perennial species, is determined by an interaction between the local soil type and the expected frequency of rainfall events of a particular intensity, and by the occurrence of intermittent droughts. The ability to withstand droughts is of particular importance in Australia, which has a greater rainfall variability than other continents.

Patterns of water use

Different rooting depths and the ability of plants to extract soil moisture are likely to influence competition or complementarity between species in the same natural or artificial ecosystem, as discussed by van Noordwijk et al. (1996). As they point out, this can be quantified by comparing the crop production on control plots and plots where there has been trenching to control roots, or the roots have been pruned. However, this method includes

effects caused by water uptake and also by nutrient uptake and cycling. Ehleringer et al. (1991) studied the differential utilisation of summer rains by different species of desert plants. They found that roots of annual species were limited to the upper soil layers, and that in summer annuals and succulent perennials used only the summer precipitation. Roots of perennials occurred in all of the soil zones likely to be recharged on an annual basis, and herbaceous and woody perennial species utilised both the summer precipitation and the remaining winter-spring precipitation stored deep in the profile. They found differences between the ability of the roots of different perennial species to take up water, and considered that some species would be better equipped to survive episodic droughts occurring up to 10 years apart.

Eissenstat and Caldwell (1988) compared the water extraction rates and competitive abilities of two species of aridland tussock grasses, *Agropyron desertorum* and *Agropyron spicatum*, chosen because they have similar root biomass and rooting depth, but *A. desertorum* has thinner roots and about twice the root length as *A. spicatum*. They measured rates of water depletion under plots of both species, and found that *A. desertorum* extracted water more rapidly from the soil profile. They conducted separate experiments to measure the competitive abilities of the two species, and found a substantially greater competitive ability of *A. desertorum* under conditions in which soil water was limiting.

Ehleringer and Dawson (1992) reviewed the results of a number of stable isotope studies of deep water utilization by perennial plants. In some cases, trees used water from deep in the profile almost exclusively, even at those times when surface water was readily available. Ehleringer and Dawson (1992) suggest a possible explanation for some plants not taking advantage of intermittent and unreliable supplies of moisture near the surface. They proposed that, where summer moisture is a small fraction of annual precipitation, plants will not develop many roots near the surface. However, where summer rains are still low but more reliable, plants will develop a dimorphic root system with two zones of active roots, one near the surface to capture summer rains and take up nutrients, and another at depth to use more reliable groundwater..

Dimorphic root systems

Dodd et al. (1984) studied native species on the Swan coastal plain of Western Australia with a Mediterranean climate and deep sandy soils. They found a number of species with dimorphic root systems consisting of substantial lateral roots near the surface and a deep tap root. These plants were able to draw at times on the water table and its associated capillary fringe, and at other times to rely on moisture stored in the soil profile. The results of Dawson and Pate (1996) for seasonal water uptake in *Banksia prionotes* in Western Australia were similar. They found that during the dry summer the deep tap root supplied most of the plant's water, whereas during the wet winter the plant used its lateral roots to acquire water by uptake of recent precipitation from the upper soil layers. Parallel studies of other native species and two plantation-grown species of *Eucalyptus* all demonstrated similar behaviour to *Banksia prionotes*. Lamont and Bergl (1991) studied the water relations and shoot and root architecture of three co-occurring *Banksia* species in the same area, and found similar results for all three.

In his monograph on the growth of eucalypts, Jacobs (1955) discussed the extent and morphology of *Eucalypt* root systems. He observed that most eucalypts growing in savanna woodlands in Australia have dimorphic root systems, with a layer of shallow roots which spread out possibly 30 m from the trunk in sandy soils, and deep tap roots which enable the tree to survive dry seasons. He cautioned against assuming that the root systems observed in trees blown over by wind were necessarily typical, and emphasised the large amount of labour involved in measuring the root system of a large eucalypt. It is presumably for this reason that not many such measurements are available in Australia, but recently a number have been performed in countries with lower labour costs. He gave typical values of the variation of root length density with depth for a mature *Eucalypt* tree in a forest, which are shown in Table 1, converted to approximate metric equivalents. His diagram of the features of a typical *Eucalypt* tree root system is given in Figure 1.

Table 1: Typical root length variation with depth in a *Eucalypt* forest soil

Depth range in cm	Root length density in cm cm ⁻³
0 - 7.5	0.54
7.5 - 15	0.19
15 - 22.5	0.06
22.5 - 30	0.03
30 - 37.5	0.02
37.5 - 45	0.01
45 - 52.5	0.01

52.5 - 60	0.01
67.5 - 75	0.01
75 - 82.5	0.005
82.5 - 90	0.005

Perhaps the most extreme form of dimorphic root system was reported by Kimber (1974) for Jarrah trees growing in lateritic soils in south-western Australia. He found that jarrah has a dense lateral root system confined to the gravel zone in the top 0.9 m above the massive laterite layer. Beneath this a well-developed sinker root system penetrates down to the water table, and develops into a secondary fine root system in the clay above the water table, which may be from 15 m to 20 m below the soil surface. Figure 2 shows a typical Jarrah root system as observed by Kimber (1974).

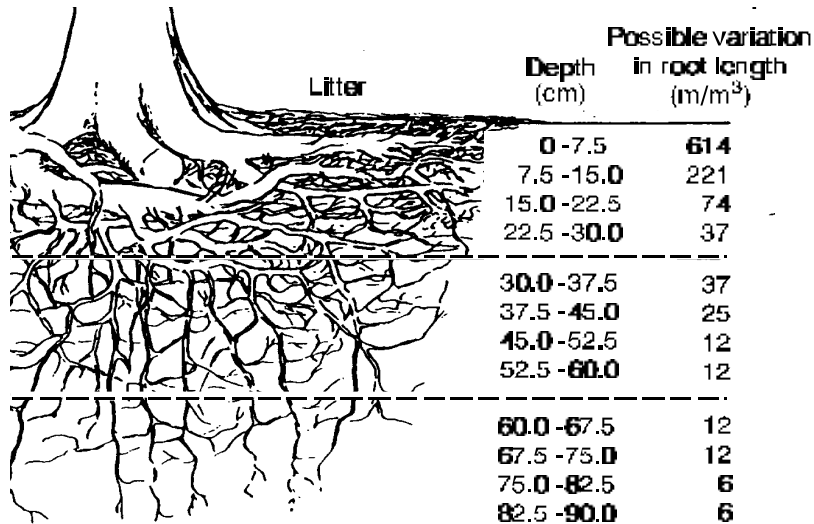


Figure 1: Features of the root system of a Eucalypt (from Jacobs, 1955)

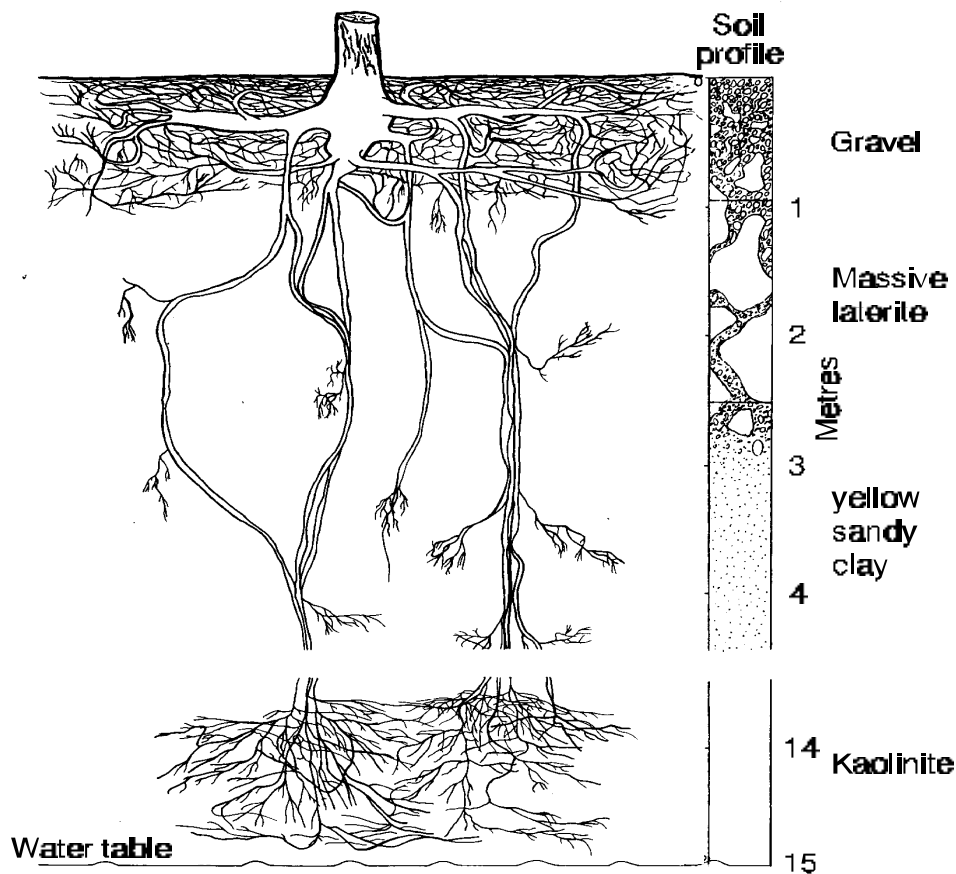


Figure 2: Dimorphic root system of Jarrah (from Kimber, 1974)

Root spread and density

Carbon et al. (1980) measured root length densities for jarrah trees on sites without a permanent water table, and on sites with root access to a water table as described by Kimber (1974). In the top 10 cm of the soil, root length density was 7.0 cm cm^{-3} , and declined rapidly with depth. In the rest of the sandy loam horizon to about 4 m, root length density was about 0.2 cm cm^{-3} . In the clay horizon below that, root length density was about 0.7 cm cm^{-3} , and no roots were found below the water table.

Dell et al. (1983) studied the role of root channels in the occupation of deep soils by jarrah roots. In profiles derived from dolerite, they found no root channels, and roots spread throughout the clay. In profiles derived from granite, they found that roots occupied well defined channels, which were a permanent feature of the soil and occupied by successive generations of trees. In this soil type, only fine roots penetrated the clay matrix.

Zimmer and Grose (1958) measured the root systems of seedlings of 14 different species of Victorian eucalypts grown under controlled conditions. They found that species from drier areas developed a higher root/shoot ratio than those from moister areas. The species native to drier areas developed a longer tap root with only a few lateral roots. Chilvers (1972) sampled the lateral distributions of fine roots in the top 20 cm of the soil, for two Eucalypt trees of different species, growing about 12 m apart in a forest in the Australian Capital Territory. He found that approximately equal numbers of the roots of two species were intermingled in the surface soil between and around the trees, and that proximity to a particular trunk was no guide to the identity of a root sample. Westman and Rogers (1977) measured the biomass in a subtropical eucalypt forest growing on infertile sands on North Stradbroke Island off the Queensland coast, and found that 42% of the total was below ground. In a study of nutrient cycling, Feller (1980) measured the root biomass for different species in two eucalypt forest ecosystems, and concluded that both forests had a relatively low proportion of their biomass below ground. He commented on the different maximum depths sampled by different workers, making it difficult to compare their results.

Neave and Florence (1994) measured the distribution with depth of the root length densities of the fine roots of three different competing tree species in a regrowth forest in south coastal New South Wales. They found significant differences, which they concluded may explain observed differences in the abundance of the three

species along the slope. Table 2 shows the root length densities that they found for the three species - *Eucalyptus maculata*, *Eucalyptus pilularis*, and *Acacia mabellae* respectively.

Table 2: Root length densities from Neave and Florence (1994)

Soil Depth (cm)	Species		
	<i>E. maculata</i>	<i>E. pilularis</i>	<i>Acacia</i>
0 - 10	0.47	0.89	1.86
10 - 20	0.27	0.20	0.66

Ashton (1975) measured the root development of *Eucalyptus regnans* trees in natural forests at a wide range of ages. He found that *E. regnans* develops a strong tap root early and then produces a system of lateral roots. Figure 3(a) shows a profile of 3 year old seedlings, with a tap root descending to at least 1.7 m, and lateral roots. In the sapling stage at about 7-10 years, the root system changes from a “juvenile” type to an “adult” type by development of sinker roots downwards from the laterals. Figure 3(b) shows a root profile of 8 year old trees at the sapling stage. Later the sinker roots become branched and the tap root dies back. Mature trees have a network of fine roots in the surface 0.25-0.5 m of the soil. Figure 3(c) shows a root profile of a 23 year old tree, with many sinker roots descending to 2-3 m.

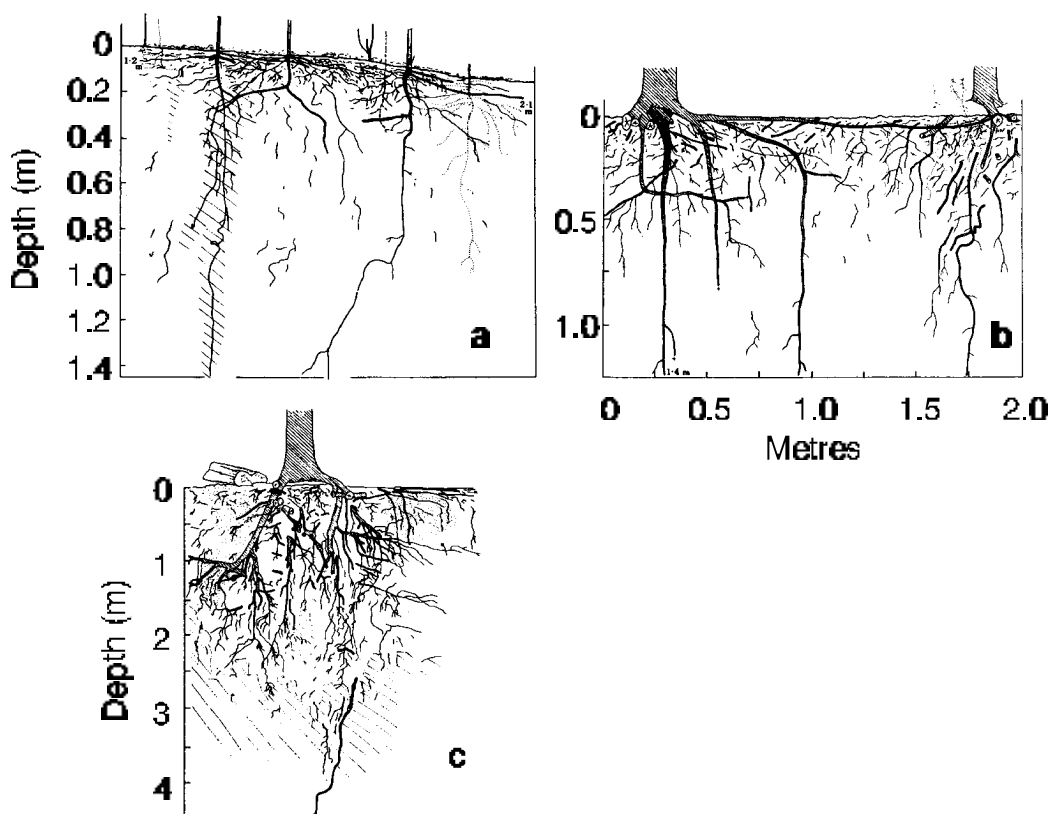


Figure 3: (a) Root profile of 3-year -old seedlings. (b) Root profiles of 8-year-old trees at the sapling stage. (c) Root profile of a 23-year-old tree (from Ashton, 1975)

Baldwin and Stewart (1987) measured the distribution, length and weight of roots in young plantations of *Eucalyptus grandis* irrigated with recycled water. They found that root concentrations were highest in the top 0.3 m of the soil, and declined sharply with depth. Table 3 shows the root length distributions in cm cm^{-3} measured at 6 year old plantations at Mildura and four year old plantations at Robinvale.

Table 3: Root length distributions in cm cm^{-3} at Mildura and Robinvale.

Soil Depth in cm	Mildura	Robinvale
0 - 10	0.57	0.35
10 - 20	0.43	0.21

20 - 30	0.20	0.11
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Eucalypts have been extensively planted in India, where serious concerns have been raised about the role of their deep roots in lowering water tables. Dabral et al. (1985) excavated the root systems of a number of trees in a 16 year old hybrid *Eucalyptus* plantation. They found that the roots had not been able to penetrate the soil beyond a depth of about 3.75 m, but that lateral roots extended up to 18 m between a soil depth of 0.3 to 0.6 cm. Because of concerns that Eucalypts would lower water tables, Mathur et al. (1987) excavated *Eucalyptus globulus* trees of ages up to 20 years at Nilgiri Hills, and found their root systems to be confined to the upper 3 m of the soil and to have a large lateral spread. Table 4 shows the root system characteristics at ages 1, 3, 10 and twenty years of age.

Table 4: *Eucalyptus globulus* root system parameters from Mathur et al. (1987).

Parameters	Age of trees (years)			
	1	3	10	20
Lateral extension (m)	3.12	5.12	6.40	9.52
Depth of root system (m)	1.02	2.21	3.08	2.46
Total volume (m ³)	7.80	47.16	99.03	160.78
Length of tap root (m)	1.49	2.31	3.94	5.52

Competition between roots

Bi et al. (1992) investigated competition from “weeds” of *Eucalyptus obliqua* in a plot of *Pinus radiata*. As an indicator of below ground competition they measured the rooting density of both species. They found that most of the root density was in the top 0.2 m of the soil. The root length density of the fine roots of *P. radiata* was about 0.7 cm cm⁻³ in the absence of competition, and decreased to about 0.3 cm cm⁻³ in the presence of fine roots of *E. obliqua* at a density of about 0.4 cm cm⁻³. They emphasised the importance of measuring the root length density when investigating competition between species. However, their study of the relative abundance of the roots and stems of the two tree species does not provide information on the actual mechanism of competition.

In an agroforestry experiment, Eastham and Rose (1988, 1990) studied the effects of competition between pasture and eucalypt trees planted at different densities on the root length densities of both species. Nine concentric rings of *Eucalyptus grandis* trees were planted in a Nelder design into a previously established pasture, and root length densities were measured at various depths and distances from each of three trees at different equivalent planting densities. The high, medium and low densities were the equivalent of 2150, 304 and 82 stems per hectare respectively. They measured total (tree plus pasture) root densities and tree root densities, found that proximity to trees and increase in tree density reduced pasture root density. Tree root systems were deeper and denser at high tree densities, although increased tree density reduced the number of roots per tree. Densities of pasture roots were considerably higher than those of tree roots near the surface, but tree roots penetrated deeper than pasture roots, allowing the trees to access subsoil water. For each tree planting density, Table 5 shows the total root length density in cm cm⁻³ at various depths at each of the sampling points.

Eastham and Rose (1990) fitted their root length distributions $R_T(Z)$ for trees and $R_P(Z)$ for pasture to exponential functions of depth Z of the form

Table 5: Total root length densities (cm cm^{-3}) at various depths at each of the sampling distances and planting densities, from Eastham and Rose (1990).

Sampling radius (m)	Soil depth range (m)				
	0.0 - 0.2	1.0 - 1.2	2.4 - 2.8	4.0 - 4.4	5.6 - 6.0
High density					
1.2	2.93	0.3	0.09	0.07	0.0
Medium density					
0.6	9.42	0.08	0.03	0.01	0.0
1.2	5.83	0.04	0.03	0.01	-
3.25	4.47	0.0	0.0	0.0	-
Low density					
0.6	10.85	0.03	0.03	-	-
1.2	7.80	0.08	0.06	-	-
3.25	10.36	0.03	0.0	-	-
6.2	17.31	0.06	-	-	-

$$R_T(Z) = a_T \exp(-b_T Z) \quad , \quad 0 \leq Z \leq Z_T \quad ,$$

and

$$R_P(Z) = a_P \exp(-b_P Z) \quad , \quad 0 \leq Z \leq Z_P \quad ,$$

respectively. Table 6 gives their values of the fitted parameters a in cm cm^{-3} , b in m^{-1} , and Z in m, for trees and pasture, for each of the sampling distances and planting densities.

Table 6: Fitted values of the parameters a in cm cm^{-3} , b in m^{-1} and Z in m for trees and pasture, for each of the sampling distances and planting densities, from Eastham and Rose (1990).

Sampling radius (m)	a_T (cm^{-2})	b_T (m^{-1})	Z_T (m)	a_P (cm^{-2})	b_P (m^{-1})	Z_P (m)
High density						
1.2	0.93	0.91	5.8	2.19	9.34	1.07
Medium density						
0.6	0.16	0.53	5.3	9.67	11.48	1.00
1.2	0.14	0.59	4.7	6.28	13.99	0.79
3.25	0.001	0.16	4.7	8.93	8.09	1.41
Low density						
0.6	0.22	1.04	3.7	10.16	13.10	0.88
1.2	0.34	1.09	3.7	13.67	14.25	0.83
3.25	0.002	0.26	2.7	11.13	6.96	1.67
6.2	-	-	1.7	44.69	13.01	1.70

As tree spacing decreased, competition between the trees caused the development of deeper and denser rooting systems, and the rooting density did not depend strongly on lateral distance from the tree. The rooting patterns of trees planted at lower densities were more like those of isolated trees, with root density decreasing with distance from the stem. Pasture root concentrations were lowest at high tree planting densities, and at greater distances from the stems at low planting densities. Bowen (1985) suggested on both theoretical considerations and experimental evidence that a root length density of about $1\text{-}2 \text{ cm cm}^{-3}$ was adequate for rapid uptake of water and nutrients from most soils, when soil water content was not limiting. Tree root densities were found to be below this value everywhere, and pasture root densities were well above this value near the surface. Eastham and Rose (1990) suggested that the tree root system could successfully deal with this competition by having a deeper root system. The presence of tree roots reduced the pasture root densities, potentially reducing their ability to compete. The greatest total mass of roots per tree was produced where tree planting densities were the lowest. The implications of the measured root distributions for transpiration will be discussed in a later section.

Zohar (1985) examined the root systems of *Eucalyptus camaldulensis* trees planted as windbreak at the edge of a cotton field in Israel, and found that most roots were concentrated in a layer between 0.4 and 0.8 m in the soil. The eucalypt roots tended to develop towards the moisture gradient and spread laterally up to 20 m into the cropped area, and he recommended that the roots be frequently severed close to the trees to reduce competition

with the crop. In Egypt, El-Lakany and Mohamed (1993a) mapped the root characteristics of 6 year old trees of *E. camaldulensis* and three other tree species being assessed for their suitability for shelter belts alongside fields of crops, under both sprinkler and drip irrigation. The spread of the majority of the horizontal roots and their maximum lateral extension were generally higher in the sprinkler irrigated trees. Figures 4 and 5 show the horizontal and vertical distributions of the root system of *E. camaldulensis* under sprinkler irrigation. On the other hand, the vertical thickness of the layer occupied by the majority of the horizontal roots, the depth of the majority of vertical roots, and the maximum depth of vertical roots were greater for the drip irrigated trees. Figures 6 and 7 show the horizontal and vertical distributions of the root system of *E. camaldulensis* under drip irrigation, and the greater depth of the roots is evident. It is also evident that the vertical roots are spreading laterally towards the wetted soil region under the drippers, at a depth of between 2 and 3 m. Table 7 shows the root system characteristics for *E. camaldulensis* with the two methods of irrigation. Generally similar results were obtained by El-Lakany and Mohamed (1993b) for windbreaks consisting of two of the tree species in combination. They recommended against the planting of *E. camaldulensis* as windbreaks alongside fields in sandy soils, unless ditches can be dug to minimise the extension of the tree roots into the (better watered) crop fields.

Ghosh et al. (1989) grew rows of eucalyptus trees in conjunction with intercropping of cassava and other plants. They found that competition with cassava reduced the maximum spread of the roots of 32 month old eucalyptus trees from 4.8 m to 2.7 m. Dhyani et al. (1990) studied the root distribution of five tree species being considered for intercropping in the Doon Valley in India. They reported that roots of 28 month old *Eucalyptus tereticornis* reached the greatest depth of the five species, although the majority of its roots were in the upper layer of the soil and could be expected to compete with the crop. The eucalyptus trees were planted at a density of 1,111 stems per hectare, and had reached a height of 4.1 m and a stem diameter of 5.4 cm. The root depth was 4.15 m, with a maximum lateral spread of 1.25 m under these plantation conditions. Similarly, Toky and Bisht (1992) investigated the root architecture of 12 species of 6 year old trees in an arid region of north-western India. All species had most of their roots in the top 0.3 m of the soil; *E. tereticornis* roots reached the greatest depth of 2.3 m, and had close to the greatest lateral spread of 4.15 m. Dhyani et al. (1996) found that *E. tereticornis* trees grown on poor quality bouldery riverbed soils had highly coiled roots, and a higher proportion of their biomass below ground, compared to a similar plantation on a deep soil.

Table 7: Root system characteristics of *E. camaldulensis* with drip and sprinkler irrigation, from El-Lakany and Mohamed (1993a).

Parameters	Irrigation method	
	Drip	Sprinkler
Spread most horizontal roots (cm)	700	840
Max extent horizontal roots (cm)	850	1450
Thickness of layer occupied by horizontal roots (cm)	125	80
Depth most vertical roots (cm)	250	200
Max depth vertical roots (cm)	300	250
Dry weight root system (kg)	20.38	18.90
Tree height (cm)	1680	1740
Stem diameter (cm)	42	25
Crown diameter (cm)	475	550

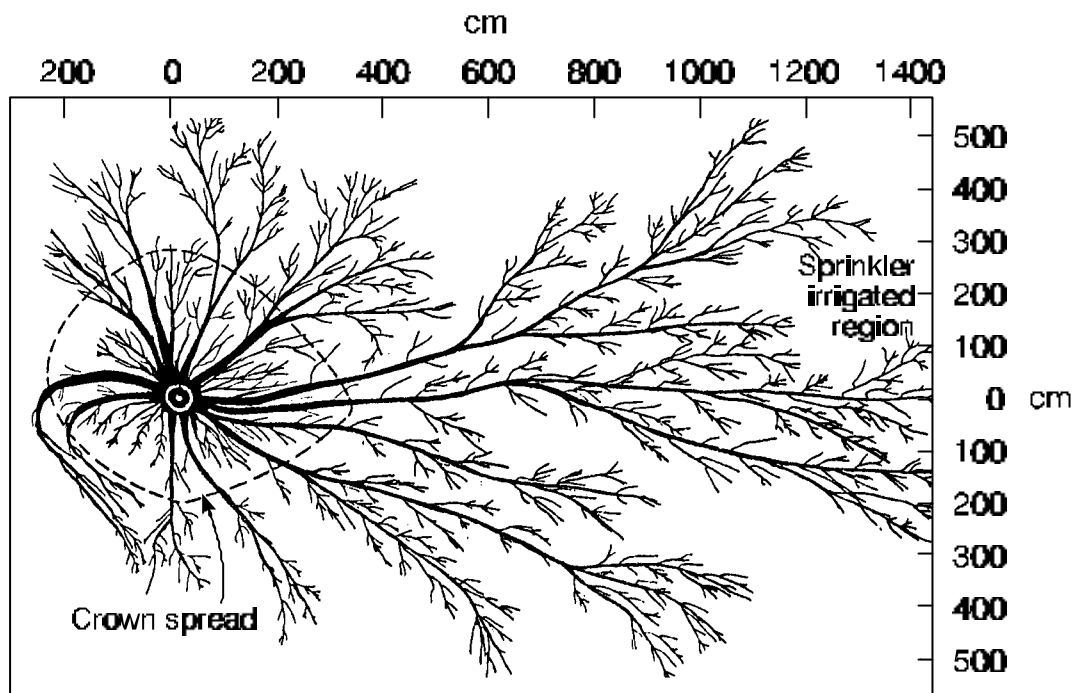


Figure 4: Horizontal distribution of the root system of *E.camaldulensis* grown under a sprinkler irrigation system (from El-Lakany and Mohamed , 1993a)

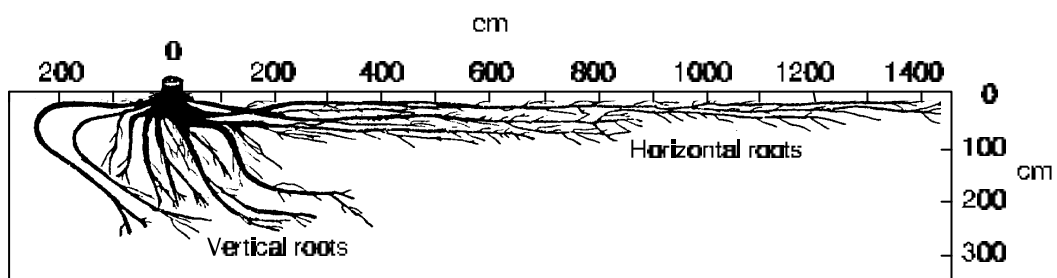


Figure 5: Vertical distribution of the root system of *E.camaldulensis* grown under a sprinkler irrigation system (from El-Lakany and Mohamed , 1993a)

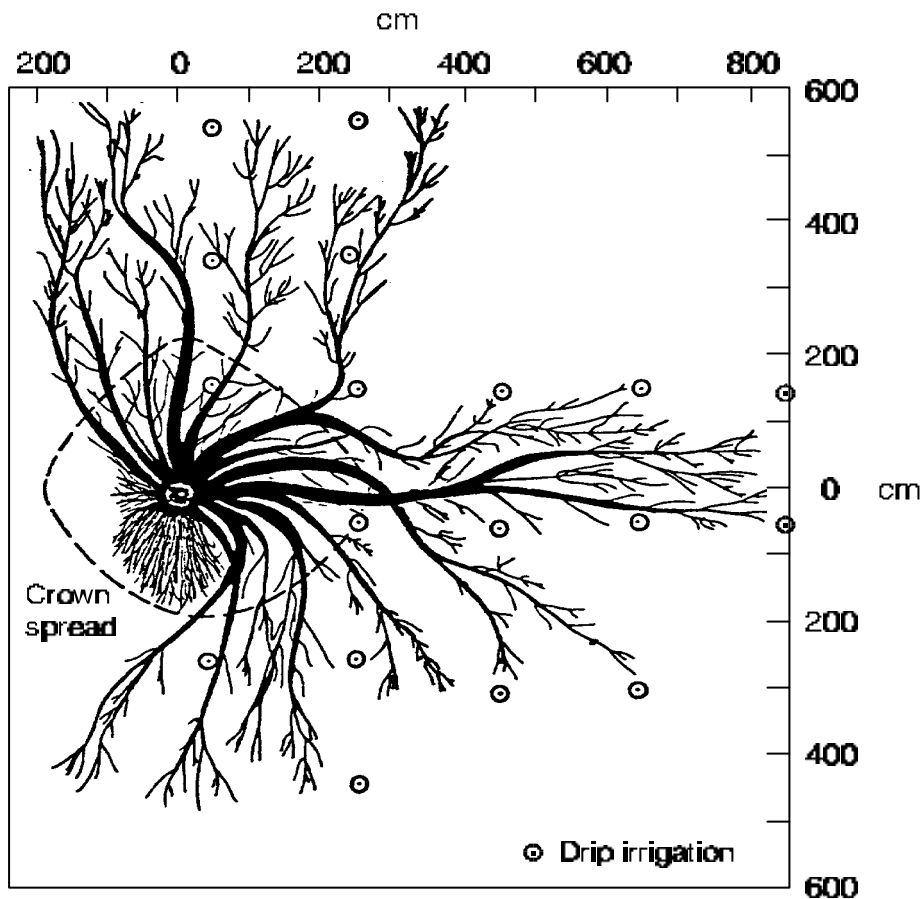


Figure 6: Horizontal distribution of the root system of *E.camaldulensis* grown under a drip irrigation system (from El-Lakany and Mohamed , 1993a)

Ogigirigi and Igboanugo (1985) investigated root growth characteristics of some eucalypt and indigenous tree species in the Nigerian savanna, at a site where there was a hard crust at a depth of 0.4 m to 0.6 m in the soil. They observed that the roots of most of the native species spread out along the top of the crust, whereas the eucalypt roots were mostly able to penetrate the crust and access the water stored below it. Under these circumstances the eucalypts would be ideal species for complementarity with other species.

Jonsson et al. (1988) compared the vertical distributions of the fine roots of five tree species to that of maize roots in Tanzania. They found that the vertical distributions of the roots of *E. camaldulensis* and *E. tereticornis* decreased with depth less rapidly

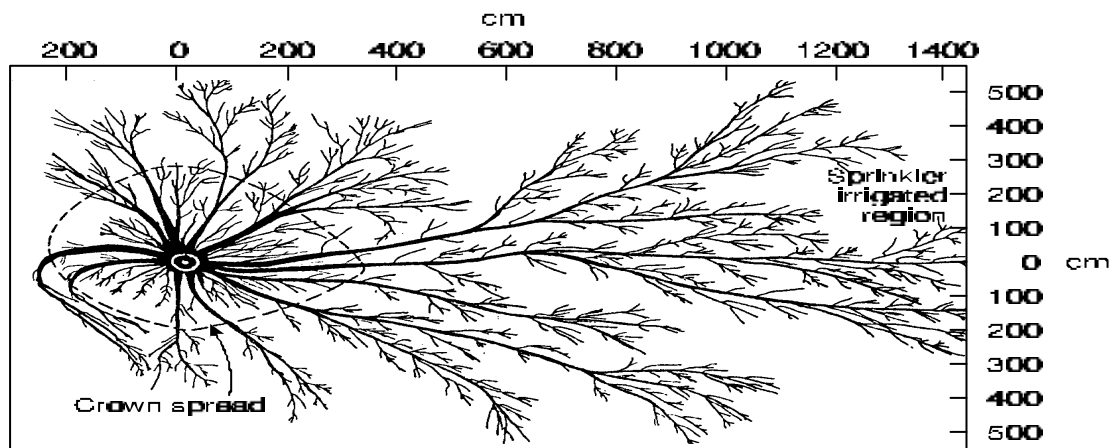


Figure 7: Vertical distribution of the root system of *E.camaldulensis* grown under a sprinkler irrigation system (from El-Lakany and Mohamed , 1993a)

than those of the other tree species and the maize, and that *E. camaldulensis* roots were evenly distributed over the top 1 m of the soil. They pointed out that while many tree species being considered for agroforestry are commonly referred to as deep rooted, such trees still have the bulk of their roots near the soil surface.

In northern Nigeria, Onyewotu et al. (1994) and Onyewotu and Stigter (1995) measured tree root densities at different depths around a *E. camaldulensis* shelterbelt. They found that tree roots spread laterally up to 18 m into the adjacent millet crop and that most tree roots occurred in the top 0.7 m of the soil, competing with the millet roots which were mainly in the 0.05 m - 0.3 m soil layer. When the eucalypt roots were pruned to a depth of 1 m at a distance 3 m from the trees, competition between the trees and the crop was virtually eliminated.

Karejah et al. (1994) reported root length density distributions for six year old eucalyptus trees in an agroforestry drainage management project in California, USA. The root zone had a maximum depth of 2.1 m, with the proportions of the root length density in successive quarters of the root zone, being 42%, 34%, 18% and 6% respectively, from the surface down to the bottom of the root zone.

From all of these observations made in several continents of trees at different stages of growth, a consistent picture emerges that Eucalyptus trees have a dimorphic root system. A typical system has a widely spreading lateral root system just below the soil surface, with a deep tap root in young trees and deep vertical sinker roots in mature trees. The roots are opportunistic in their search for water and nutrients, and will follow moisture gradients up to 20 m into adjacent fields. It appears that even the vertical roots will move horizontally towards sources of water. Many agroforestry workers recommend controlling competition by restricting the lateral spread of roots into crops by root pruning, or digging ditches.

Soil water status and its effects on transpiration

When a plant transpires under controlled conditions, it is generally observed that the transpiration rate is relatively unaffected by the soil water content or the soil water potential over a considerable range. It is only when the water content falls below a given value (which depends on soil type and on root length density) that the transpiration rate is reduced, and decreases approximately linearly with water content. A soil with high values of soil water diffusivity and a plant with high root length density will be able to transmit water from soil to roots at a higher rate. Figure 8 shows a graph given by Gardner (1983) for the variation of the transpiration rate of birdsfoot trefoil with soil water content under controlled conditions, for three different soil types. Gardner and Ehlig (1963) found that the position of the breakpoint in the curve depended on the unsaturated hydraulic conductivity of the soil, but usually occurred in the range of soil water potential from -100 to -1,000 kPa. This general dependence of transpiration rate on soil water content is commonly observed for most species and soil types.

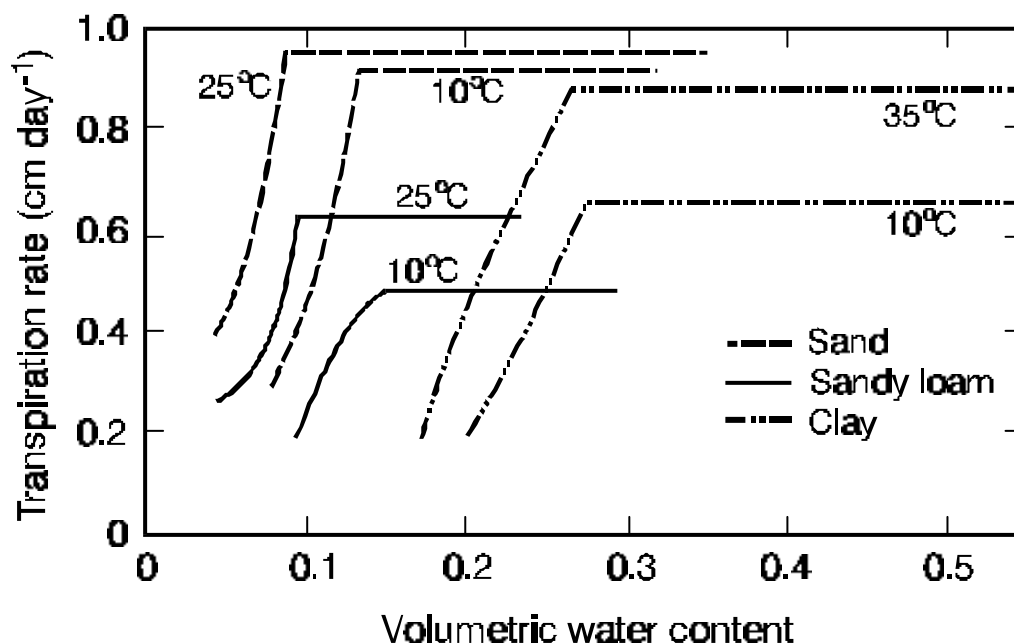


Figure 8: Transpiration rate as a function of soil water content for birdsfoot trefoil in three different soils at two different root temperatures. Data from experiments described by Gardner and Ehlig (1963), plotted by Gardner (1983)

For large plants such as trees, it is difficult to perform such controlled experiments. Most studies of the spatial distribution of soil water uptake have been performed in laboratories, or on field crops. If the soil profile is initially uniformly wet, as the soil dries a zone of soil water deletion appears near the soil surface and then moves downwards. As pointed out by Rose and Stern (1967), to determine the root water uptake distribution accurately, it is necessary to perform a detailed water balance which accounts for evaporation from the surface and drainage from the bottom of the root zone, as well as downward movement of soil water under gravity. In order to calculate these quantities, it is necessary to know the unsaturated soil hydraulic properties. Scholl (1976) used this method to calculate soil water uptake distributions and evapotranspiration from a stand of Chaparral shrubs with a root zone depth of about 4.2m. After rain, he found that a zone of root water uptake occurred first in the top 30 cm of the soil, and then moved downwards to the next layer extending from 30 cm to 180 cm. Total evapotranspiration then declined as the soil dried out.

Nnyamah and Black (1977) made a detailed study of the water balance and soil water uptake patterns in two Douglas-fir forests with root zone depths of 0.65 m and 0.8 m respectively. They calculated water extraction rates and uptake patterns over a four week drying period, and found a gradual downward movement of the zone of maximum root water uptake as the soil dried, as shown in Figure 9. They found a good correlation between water uptake rate and rooting density, and their calculated value of evapotranspiration agreed well with the value measured using micrometeorological methods. They found that evapotranspiration decreased as the soil dried. At site 1 the evapotranspiration decreased from 2.8 to 1.0 mm day⁻¹ over about 30 days, and on site 2 it decreased from 3.6 to 1.2 mm day⁻¹. The amount of water extracted from any soil layer depended on both rooting density and on soil water content.

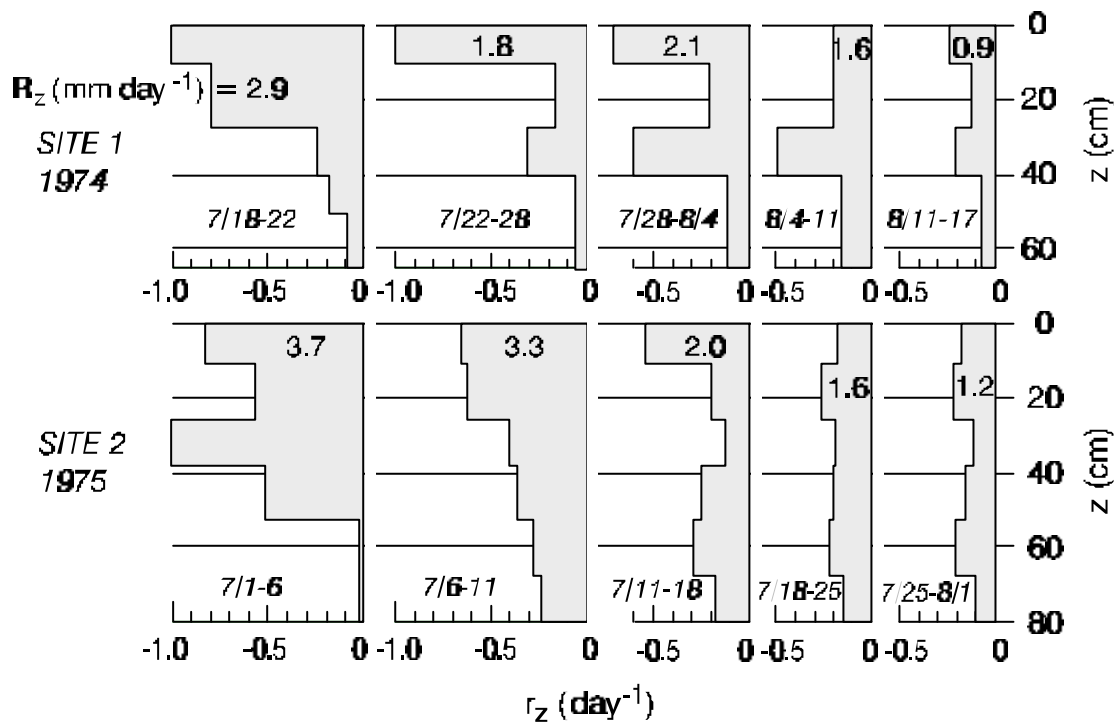


Figure 9: Depth distribution of water uptake by Douglas fir roots at two sites over five time periods, as found by Nnyamah and Black (1977)

Over seven years, Rambal (1984) studied the water balance of a *Quercus coccifera* evergreen scrub in a Mediterranean climate in the south of France. Using similar methods to Nnyamah and Black (1977), he calculated soil water uptake patterns over a depth of 4.5 m, and observed the reduction in evapotranspiration as the depletion zone moved downwards through the soil. When the soil water reserve was exhausted, the plants settled down with closed stomata to consume small quantities of water.

Similar patterns of soil water uptake and depletion were observed by Taylor and Klepper (1973) on corn, by Arya et al. (1975) on soybeans and by Taylor and Klepper (1975) on cotton. Gardner (1983) summarised data from about 40 different root water uptake measurements on a wide range of species, mainly crops but including the Douglas-fir data of Nnyamah and Black (1977). He scaled the data taken at day of first wilt with respect to both root zone depth and total soil water uptake, and plotted it on the same graph for all 40 experiments. His fitted curve is reproduced in Figure 10, showing that it is close to being a “universal curve” for all the 40 uptake functions. The data can be fitted approximately by a curve which is constant over the upper fifth of the root zone, and then decreases linearly to take the value zero at a depth of 0.8 of the scaled root zone depth. This curve gives approximately 40% of the uptake in the top fifth of the root zone, and then 33%, 20%, 7% and zero in successive fifths of the root zone.

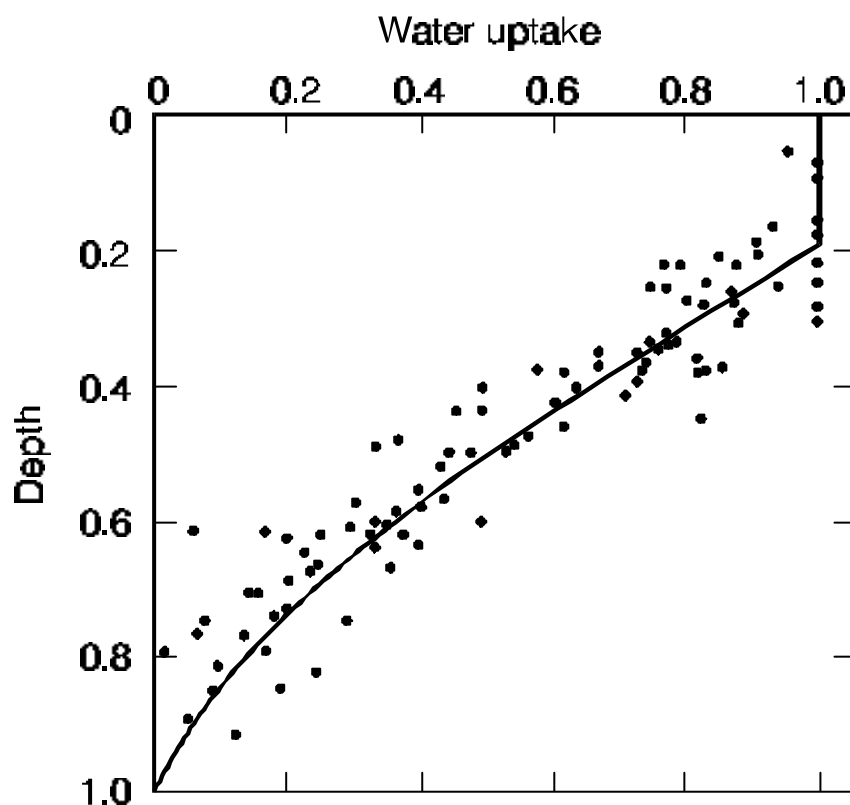


Figure 10: Normalised soil water uptake curves for 40 different experiments from the literature, as scaled and plotted by Gardner (1983)

Clothier et al. (1990) found that apple trees seemed to prefer to extract water from near the soil surface, in a manner that could not be explained merely by the greater proportion of roots near the surface. Heat pulse methods have enabled accurate measurement of sap flow in the trunks and individual roots of trees, leading to accurate observations of water uptake by individual trees or even individual roots. Green and Clothier (1995) used heat pulse methods and Time Domain reflectometry to determine the ability of kiwifruit vines to alter their pattern of root water uptake in response to differential wetting of the root zone. Prior to irrigation there was a broad correspondence between the pattern of water uptake and the distribution of root length density. Following localised irrigation they observed a preferential uptake of water from the wetter regions, and a corresponding decrease in uptake from the drier regions. They also observed a strong preference for near surface water, if available. These authors believed that a rapid flush of new root growth after irrigation led to increased root activity after a rewetting. Green et al. (1997) found similar results with localised irrigation of apple tree roots. They showed that apple roots have the capacity to transfer water from local wet areas at much higher rates than normally occurs when the entire root zone is well supplied with water. The roots were able to shift their water uptake pattern rapidly in response to localised irrigation. Their results led them to conclude that the soil-to-root pathway represents a major resistance to water uptake by apple roots, even when the tree is not under any water stress.

Moreno et al. (1996) compared water use by a regularly irrigated olive tree, and water use by a neighbouring unirrigated tree. Following an irrigation, the well-watered tree was able to maintain a transpiration rate of 1.65

mm day⁻¹ for three days, after which transpiration and the flow of sap in a near-surface root were reduced. At the same time, the unirrigated tree was using water at less than half of the maximum rate of the irrigated tree.

Richards and Caldwell (1987) found evidence of a kind of “reverse uptake” which they called “hydraulic lift”. When this occurs, water is taken up at night from a deep but moist part of the soil profile, and raised to dry soil near the surface. This enables the plant to increase its transpiration rate during the day, as well as to take up nutrients near the surface. Caldwell and Richards (1989) discuss the phenomenon further, and Dawson (1993b) explores the implications for water balance and for interactions between plants. Wan et al. (1993) observed hydraulic lift in a relatively shallow rooted North American species, *Gutierrezia sarothrae*.

It is a common observation that flooding a plant’s roots with water causes partial or total inhibition of transpiration, and paradoxically may lead to wilting. (See for example Glinski and Stepniewski, 1986, p. 147). Controlled experiments have revealed that a sufficient supply of oxygen is necessary for root water uptake. Although roots can absorb some dissolved oxygen from soil water, they generally can not take up water unless there is enough pore space for oxygen to be able to diffuse to the roots. The submerged roots of plants such as mangroves and rice are specially adapted to obtain oxygen while they are functioning under water. Willey (1970) flushed the root systems of tobacco plants with nitrogen or a nitrogen and carbon dioxide mixture, and found that the transpiration rate rapidly decreased. Likewise, the experiments of Holder and Brown (1980) showed a strong correlation between soil oxygen uptake and soil water uptake in bean plants, unless the roots had been in anaerobic conditions long enough to permanently affect their functioning. The effect of soil saturation on root water uptake has been incorporated into the root water uptake models of Feddes et al. (1978) and Dirksen et al. (1993), and will be discussed further in relation to the observations of Gardner (1991).

Soil water uptake patterns inferred from stable isotope composition

Ehleringer and Dawson (1992) and Dawson (1993a) review the use of variations in the composition of stable isotopes to infer water uptake patterns of a number of species. Water from different parts of the soil profile may have different isotopic signatures due to preferential evaporation of particular isotopes near the surface, or due to seasonal variations in isotopic composition of rainfall. When water is extracted from the plant and analysed, its composition gives an integrated response of the root system to the sources of water of different isotopic composition.

Thorburn and Ehleringer (1995) analysed data on plant water isotopic composition from three field experiments, and conclude that some perennial trees and plants gain most of their uptake from deep water sources, even at times when water is readily available nearer the surface. For these trees, water uptake patterns do not necessarily match the root distribution and the soil water content profile. Flanagan et al. (1992) found different rates of uptake of summer precipitation among co-occurring species in the same ecosystem. This general proposition is supported by the results of Mensforth et al. (1994) and Thorburn and Walker (1993, 1994) for riparian trees. A water use pattern of this type would be of advantage for a tree to be used in agroforestry. However, most of these observations have been in systems where the supply of water to the top layers is unreliable and unpredictable, and so the plant may not have time to develop the fine roots needed to take advantage of intermittent water availability near the surface. In a system with sufficient water available from rainfall or irrigation in the upper soil layers to meet the requirements of a crop or pasture, the associated tree can be expected to develop a pattern of uptake that includes the crop root zone.

Other workers have found that trees do use their near-surface roots to take up water from seasonally available water. Dawson and Pate (1996) used stable isotopes to investigate seasonal water uptake and movement in root systems of the native tree *Banksia prionotes* in Western Australia. They found that during the dry summer the deep tap root supplied most of the plant’s water, whereas during the wet winter the plant used its lateral roots to acquire water by uptake of recent precipitation from the upper soil layers.

Dawson (1996) measured water use by individual trees in a sugar maple forest in New York State, USA, where there was a hard pan layer in the soil at about 50 to 80 cm deep. The roots of large trees penetrate this layer and access the water table which is at about 3 m. He measured very different transpiration rates in trees of different sizes. Using stable isotope composition to infer the depth of water uptake in the soil profile, he found that larger trees had relatively higher transpiration rates, and used a higher proportion of groundwater. On the other hand, smaller trees showed more variation in their transpiration rates and were apparently more sensitive to soil water deficits in the upper soil layer. Overall, stands composed of small trees had from 20% to 50% of the evapotranspiration rates of stands composed of large trees over the growing season from May to September. In

mixed size stands, water raised by large trees through hydraulic lift could be expected to contribute to transpiration by neighbouring small trees. Jackson et al. (1995) found similar results for water use by trees of different species and sizes in a lowland tropical forest on Barro Colorado Island in Panama during the dry season. They found that species using deeper, more abundant water resources had both higher rates of water use determined using a heat flux method, and also more favourable leaf water status.

Soil water uptake patterns inferred from soil water depletion

For agroforestry, there are a number of important questions when selecting species suitable for mixed tree/crop systems. It is desirable to know where the tree roots go, from what zones in the soil they will extract water, and how much they can extract over the summer when the surface is dry. Ideally, the trees should be able to use their deep root systems to extract water from the subsoil at high rates through dry periods, while not taking too much water or nutrients from the shallow rooted crop or pasture with their lateral roots. The combined system should have higher water use rates than the crop or pasture alone. There are a number of studies which give some information on these questions.

For large trees such as Eucalypts with extensive root systems, there are considerable practical difficulties in making detailed measurements of transpiration rates and soil water uptake patterns. It is necessary to correct for soil water movement and drainage, to get accurate estimates of uptake distribution from observed depletion patterns. The study by Eastham et al. (1988, 1990a, 1990b) was specifically designed to measure soil water use by trees planted at different densities in a pasture, but there is a general shortage of data on actual water uptake by competing species in mixed systems. There are a number of other field experiments that have been designed to provide evidence of increased water use by eucalypts compared to pasture, which also provide some evidence of soil water depletion under eucalypts during a dry season, and associated seasonal reduction in transpiration. Such results are often dependent on the subsurface hydrology and soil type at one particular site, and may be difficult to generalise. In this section we describe some of these studies of water use by Eucalypts.

Doley (1967) investigated the water relations of a deep rooted Jarrah forest in South Western Australia. He measured the transpiration rates of individual leaves, and separately assessed the evaporation due to environmental conditions with an evaporimeter. He found that there was a close linear relation between his measured values of transpiration and evaporation, which was independent of observed soil water depletion in the upper part of the root zone. This relation between evaporation and transpiration continued through summer, even though the upper 0.45 m of the soil was dry. He concluded that the trees were able to obtain adequate water from the subsoil using their deep rooting system.

Story (1967) investigated circular patterns in pasture around trees in partially cleared woodland in drier areas of the Hunter Valley, which indicated that pasture growing within the lateral root zones of large trees was sparser than grass outside the root zones. This phenomenon was much more common in drier areas, where soil water could be expected to be limiting. To test the hypothesis that the trees and pasture were competing for water, he used neutron moisture measurements of soil water at a number of positions to compare soil water profiles near trees, under pasture and under bare land. He expected to find that the soil profiles were drier within the tree root zones. Although there were differences between soil water content in the three locations over time, he found no systematic correlation between tree roots and soil water status. In fact, his measurements revealed that the soil was driest where the grass was densest. He cautioned against applying his findings indiscriminately to other locations in Australia.

Stibbe (1975) calculated the water balance for a *Eucalyptus occidentalis* grove in a desert area in Israel, with a root zone about 2 m deep, and most of the roots in the range 30 to 90 cm. He calculated the reduction in transpiration rate with soil water content in the zone to 2.1 m, by measuring soil water content and performing a soil water balance. The ratio of transpiration to evaporation remained constant at about 1.35 as long as the soil water suction was above about -300 cm (-30 kPa). As the soil dried further, he found that the total root water extraction rate decreased approximately linearly with the logarithm of the absolute value of the soil moisture suction in that zone, for a wide range of soil water content, as shown in Figure 11. At the end of the summer when the soil was driest, the ratio of transpiration to evaporation had fallen to about 1% of its maximum value. The difference between his results and those of Doley (1967) is due to the great difference in the depths of the root zones.

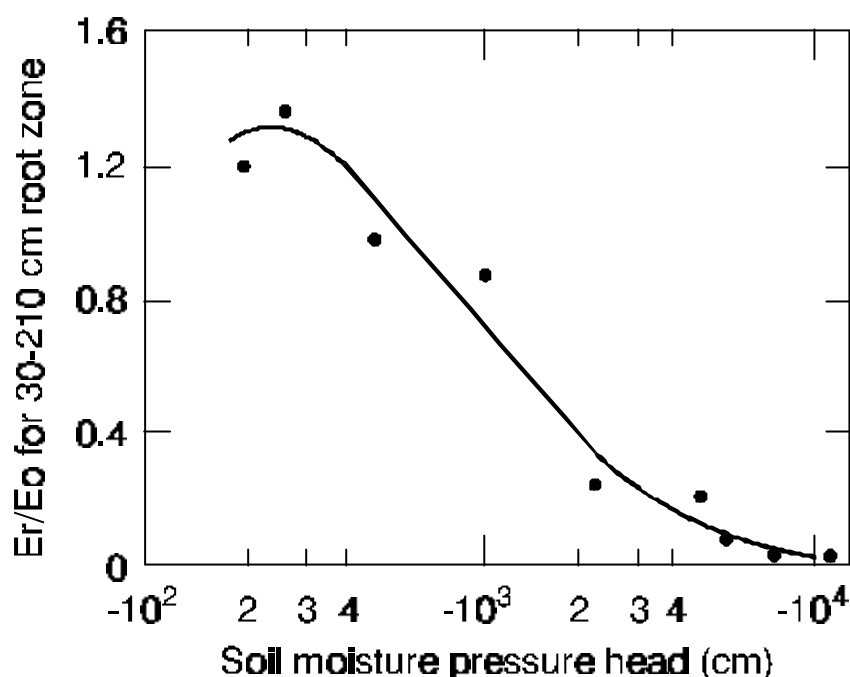


Figure 11: The ratio of water extraction in the zone 30 -210 cm to free-water evaporation, as a function of the soil water pressure head in cm (from Stibbe, 1975).

Carbon et al. (1980, 1981) found that the deep rooted Jarrah forests in Western Australia, with roots up to 18 m deep, were using stored water in the deep heavy clay subsoil over the dry summer, when the upper sandy layer was very dry. They measured the transpiration rates of individual leaves, and found that transpiration rates were generally lower in winter than in summer, but did not compare transpiration rates to evaporation. Their observations supported those of Doley (1967).

Greenwood et al. (1982) measured daily evaporation from five individual regenerating *Eucalyptus wandoo* trees in Western Australia, and from pasture near them, at a site with deep groundwater at about 9 m. The tree roots were believed not to reach the groundwater, with few roots observed below about 3m. They found that transpiration was greatly reduced from mid summer to late autumn, at the same time that soil water content was depleted in the upper 2 m. There was variation between trees, but the overall transpiration for all the trees was reduced to about 20% of its maximum value. When the evaporation rate for each tree was converted to a rate for the appropriate area of soil surface, the trees were found to transpire at a higher rate than the pasture. The authors concluded that soil water was limiting over the dry summer, and that the trees were not able to access the deep groundwater.

Talsma and Gardner (1986) studied Eucalypt trees growing in deep soils near Canberra with a water table at a depth of 8 m. They found that the trees were able to access water deep in the soil profile, while soil water was depleted to a depth of 4 m during a dry period. They did not measure evaporation, but calculated from a soil water balance that the trees used about 3.8 mm day^{-1} during the period October 1981 to March 1982, and about 2.6 mm day^{-1} for the corresponding period a year later which had a much lower rainfall, when the trees mainly used stored soil water rather than rainfall.

Sharma et al. (1987) observed that a significant amount of soil water extraction under Eucalypt forests in Western Australia occurs to a depth of at least 6 m. They measured soil water contents under trees and under pasture, and found that a significant increase in soil moisture storage had occurred with two years of clearing forest for pasture. They measured rainfall, but not evaporation or transpiration.

Crombie et al. (1988) investigated the water relations of tree and understorey species in the Jarrah forest of south-western Australia, and found that seasonal patterns of predawn leaf water potential were connected to rooting depth. The dawn water potentials fell most rapidly and by the greatest amount in plants with the shallowest roots, and so were consistent with a top-to-bottom drying of the soil profiles. Crombie et al. (1992) reported that both tree and understorey species developed substantial water deficits in summer on both higher and lower rainfall sites.

Honeysett et al. (1992) demonstrated a close correspondence between evapotranspiration rates and soil water content during two drying cycles for 4 year old *Eucalyptus nitens* and *Eucalyptus delegatensis* in plots in Tasmania, with all the roots in the top 2 m of the soil. During the first period evapotranspiration for the two species was estimated to be 3.5 and 3.2 mm day⁻¹ respectively, which was only slightly less than the potential evapotranspiration. During the second period the soil was much drier, and the corresponding rates were only 2.2 and 2.4 mm day⁻¹.

Eastham and Rose (1988, 1990) and Eastham et al. (1988, 1990a, 1990b) describe an experiment designed to measure soil water uptake at an experimental site in south east Queensland, in which trees were planted at different densities in a pasture. They found a close connection between root density, soil moisture content and root water uptake. As the drought period progressed, the tree transpiration rates decreased as soil water contents in upper soil layers decreased, and a larger proportion of water was extracted from deeper soil layers. At higher tree densities there was a larger proportion of water uptake at depth in the soil, because the more densely planted trees had developed deeper and denser root systems. Consequently there was a greater depletion of near surface water near the more densely planted trees. Figure 12 is taken from Eastham et al. (1988), and shows the total transpiration from their systems at different tree densities, compared to pan evaporation. Transpiration at the high tree density was close to the open pan evaporation during the wetter year of 1985, but was consistently lower than evaporation in the drier year of 1986.

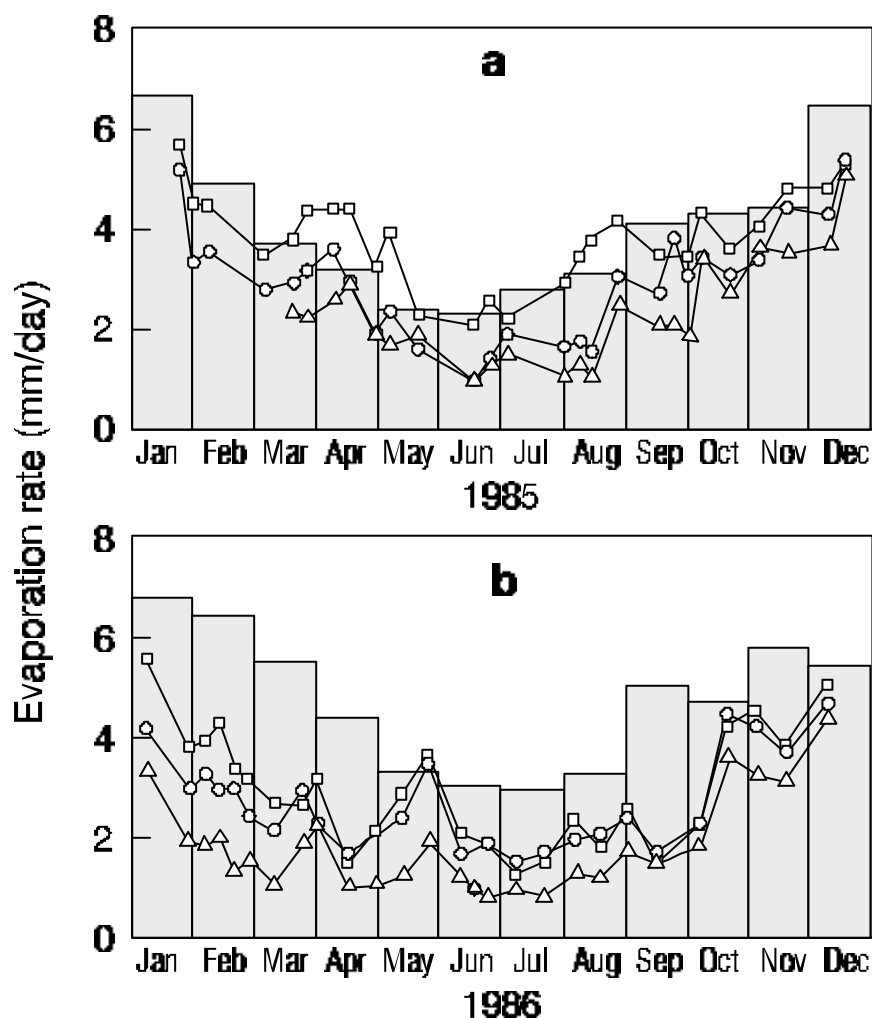


Figure 12: Transpiration during 1985 (a) and 1986 (b) at high ($\square$), medium ($\circ$) and low (Δ) tree densities. The histograms show monthly mean open pan evaporation (figures from Eastham et al. 1988).

Boden (1991) measured soil water content profiles to a depth of 1.4 m at varying distances from a plot of *Eucalyptus grandis* in South Africa. He found that the soil was consistently drier under the largest trees than under the smallest trees, and that the soil profiles were driest closest to the trees. The soil water depletion patterns were found to mirror the tree root systems both laterally and with depth. He measured soil water status, but did not assess transpiration or evaporation.

At a site in Western Australia, Eastham et al. (1994) found generally higher evaporation rates from trees than from pasture, with differences between species. Higher water use by trees was due to their ability to exploit stored soil water, and was associated with soil water depletion under trees, and with upward movement of soil water from below the root zone. They concluded that a number of the species studied would be beneficial in lowering water tables.

The studies reviewed in this section have consistently found that deep rooted Eucalypts are able to access water stored in the soil profile, and to maintain their transpiration rates during dry periods at levels which allow the trees to function. Some deep rooted trees used subsoil water at times when surface water was freely available. However, the transpiration rates of shallow rooted trees can be strongly affected by soil water deficits in the top 2 m of the soil over dry periods. Most of the above studies were not designed to test the theory of soil water uptake by tree roots. Nevertheless, the observations are generally consistent with the hypothesis that soil water uptake is governed by an extraction term in the Richards equation, with the uptake term depending strongly on soil water content and root length density.

Theoretical models of root water uptake

To avoid the need for expensive and time consuming laboratory and field experiments, agronomists frequently simulate water flow in soil and crop systems using idealised mathematical models of the processes involved. Feddes (1981) surveys a number of models used for water movement in the root zone. For the agricultural crops surveyed by Gardner (1983), the concepts of soil water flow theory have given a consistent theory of root water uptake, with an extraction term depending on soil water content and on root distribution, and also on soil type. More recently, Gardner (1991) raised concerns about the ability of models of this type to reproduce the downwards moving extraction pattern often observed in practice. We will address these concerns later in this section.

Macroscopic models of soil water uptake by roots usually consist of the Richards equation governing soil water movement, together with an extraction term which expresses the assumed dependence of soil water uptake rate on root distribution and soil water status (Molz and Remson, 1970). The form of the extraction term may be empirical, or it may be derived from a microscopic model of soil water flow to a single plant root.

Most models of flow to a single root are based on the original ideas of Philip (1957) and Gardner (1960) for water flow to a root from a surrounding cylinder of soil. An account of the assumptions inherent in this model is given by Taylor and Klepper (1975), by Passioura (1988) and by Ehlers et al. (1991). It is assumed that each root has exclusive access to a cylinder of soil of radius b , which is half of the average distance between roots. This radius can be calculated from the measured root length density L , which is given by

$$L = 1 / (p b^2) \quad .$$

When the steady state Richards equation for radial flow to the root is solved, a formula for the soil water flow to the root results. This gives the soil water uptake rate S at a position in the soil in terms of the root length density L , the water potential difference $\Psi_r - \Psi_s$ between the root and the soil, and the soil hydraulic conductivity

$K(\Psi)$ which depends on the water content, and the root radius r_1 as

$$S = \frac{4p L K (\Psi_s - \Psi_r)}{\log[1/(p L r_1^2)]} \quad .$$

It is evident that the soil water uptake rate increases with increasing root length density and with increasing soil hydraulic conductivity. According to the single root model, the specific uptake per length of root also increases with increasing root length density. Ehlers et al. (1991) discuss the way that uptake depends on both root length and on root length density. Molz (1981) reviews the different forms of the soil water extraction term proposed and used by various workers. Most have a similar dependence on water potential difference between root and soil and on the soil hydraulic conductivity, but have a root activity function $A(Z)$ depending on depth Z , which may be empirical or may have a different dependence on root length density,

$$S = A(Z) K(\Psi_s - \Psi_r) \quad .$$

Feddes et al. (1978) and Dirksen et al. (1993) model the effect of poor aeration close to soil saturation by an additional factor which is zero when the soil is at saturation, and reduces uptake near saturation.

Passioura (1985) calculated an approximate expression for the drying of the soil water content q with time around a root as

$$q(t) = q_0 \exp(-Dt / (2b^2))$$

where q_0 is the initial value of soil water content and D is an average value of the soil water diffusivity.

Passioura (1980), Hainsworth and Aylmore (1986) and Stirzaker and Passioura (1996) successfully tested the single root model for their systems. Other workers such as Herkelrath et al. (1977) and Ehlers et al. (1991) have found that it overestimates flow to a root. There are several factors which may cause the model to overestimate actual root water uptake. As pointed out by Thorburn and Ehleringer (1995), root presence in the soil does not necessarily indicate actual root activity. Drying roots may shrink away from the soil and give rise to areas of poor contact between root and soil and a resultant high contact resistance. Herkelrath et al. (1977) invoked a contact resistance between root and soil to explain their measured low rates of water flow from soil to roots. Hainsworth and Aylmore (1989) observed non-uniform uptake along a root, which was modelled by Aura (1996). Nobel and Cui (1992) investigate water vapour transport across gaps between soils and roots. Passioura (1991) and Tardieu et al. (1992) calculate the decrease in effective root length density due to clumping, or non-uniform spatial distribution of the roots. Passioura (1991) shows how various forms of clumping affect the time constant for soil drying. Caldwell and Richards (1986) discuss the effects of suberized roots in limiting water uptake by root systems.

An account of the parameters that are required to be known or estimated for process-oriented models for water and nutrient uptake is given by van Noordwijk and van de Geijn (1996). They distinguish between four levels of complexity in root uptake models, and the parameters required for each. Models of type A predict uptake on the basis of observed root development, and use measurements of root length density with depth and root pattern as input. Models of type B use descriptive functions or curve fits for root growth in space and time, and may assume that the root length density is a negative exponential function of depth, for example. Canadell et al. (1996) give values of a fitted parameter b for a large number of such root distributions. Models of type C include predictions of overall root growth in relation to shoot growth, often based on the concept of “functional equilibrium”. Models of type D attempt to predict the local growth of roots from soil conditions such as soil water content, aeration and nutrient status in each soil zone.

As pointed out by Molz (1981), in many cases the assumed form of a root water uptake function is incorporated into a larger model, and the uptake function is not tested independently of the rest of the model. There have been a number of apparently successful soil water uptake simulations for agricultural crops. It has been applied to tree water uptake in several studies. Carbon et al. (1980) used the single root model and measured root length distributions to perform a detailed theoretical analysis of the limits of flow of soil water to the roots of Jarrah trees, in the deep lateritic soil described earlier. They calculated that the surface layer of sandy soil would not be able to supply sufficient water to the jarrah roots in the dry summer, and that the water would need to come from the deeper clay layer, as was observed in practice. Hunt and Nobel (1987) used a single root model to predict water uptake by desert succulents. Karajeh et al. (1994) and Karajeh and Tanji (1994) successfully used a soil water uptake model as part of an agroforestry drainage management model. They measured actual root length distributions in a type A model and also used a “curve fit” of type B to predict soil water distributions, and found that the second method gave better results.

In South Africa, Dye (1996) studied soil water use by two stands of *Eucalyptus grandis* trees under soil water deficits, with a view to modelling the reduction of evapotranspiration with soil drying. He found that trees at one of his sites were obtaining most of their soil water from depths below 8 m. He decided that it was not practical to obtain the necessary information about the depth of the root system, the soil water recharge mechanism and the hydraulic characteristics of the soil from that depth, in order to model the evapotranspiration reduction.

Gardner (1991) asserted that an uptake model based on the single root model would not be able to model an uptake pattern which was frequently observed, namely a fairly narrow uptake zone moving downwards through the soil. The above dependence of the extraction term on water potential predicts that the roots will withdraw

water from the complete root zone when the soil is uniformly wet. However, a narrow pattern of depletion is frequently associated with a lowering water table and saturated soil. Reicosky et al. (1972) found that water was being extracted from a narrow zone above a water table by soybean roots, and attributed this to poor aeration in and near the saturated zone. On the other hand, Wilcox (1959, 1960) studied drainage and uptake after irrigation in a deep and well-drained soil, and found root water uptake greater nearer the surface, but significant at all depths in the upper 1.2 m of the root zone of alfalfa.

If the uptake function is modified to take account of reduced uptake due to anaerobic conditions near saturation as done by Feddes et al. (1978) and Dirksen et al. (1993), then depletion patterns like those described by Gardner (1991) can be produced. The tendency for non-uniform uptake across the root system will be increased by any significant resistance to longitudinal flow within roots, as discussed by Fowkes and Landsberg (1981). In a soil with a shallow watertable or an impermeable layer, redistribution of irrigation water will cause the lower part of the profile to be saturated, and the roots to be inactive there. The uptake pattern will be similar to that above a water table, but moving downwards at an approximately constant rate as water is removed from the soil. On the other hand, in a deep well drained soil redistribution and drainage after irrigation will cause the soil to become unsaturated over a wide depth range, and roots will be able to take up water over a large part of the root zone. The soil water profile will become drier over the whole root zone, as observed by Wilcox (1960).

Conclusions

This paper has reviewed the known information on the structure and function of plant root systems in relation to the uptake of water and competition with other species. The conventional wisdom that deeper root systems enable Eucalypts and other trees to access water not available to shallow rooted trees and crops has been confirmed. Deep rooted trees are usually able to maintain their relatively high transpiration rates over dry summer periods. Information on the size and shape of Eucalypt root systems has been critically examined. Young Eucalypts have a deep tap root and a lateral root system. Most naturally occurring Eucalypts in savanna woodlands or forests have dimorphic root systems with widely spread lateral roots near the surface and deep sinker roots which grow down from the laterals as the trees mature. The lateral roots may spread for large distances (up to 20 m) into adjacent crop or pasture, particularly if water or nutrient supplies are more readily available there. Pruning or trenching is recommended to control lateral roots in agroforestry. Nazer and Clark (1982) discuss how to control Eucalypt roots by trenching.

The single root model for root water uptake is able to provide a basis for modelling relative water uptake by trees and crops in the same soil volume. It can be used to predict the reduction in transpiration rate as the soil dries. For this model, soil hydraulic properties must be measured or estimated, and root length densities of the two species must be measured or estimated using a distribution such as the negative exponential. The single root model usually overestimates soil water uptake, but has been successfully modified by various authors to take account of factors such as poor root-soil contact, clumping of roots, and anaerobic conditions near saturation.

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