Transpiration by Trees.
A Review of Recent Work Conducted in Western Australia.

by H. Borg and R. Giles

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Water Authority
of Western Australia

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SUMMARY

Studies on transpiration by trees conducted in Western Australia over the past ten years were reviewed. From this review, the following conclusions can be drawn:

1) Over a year tree species transpire more than annual pasture species. Over a year tree species frequently though not always transpire more than other non-tree species, too. Reforestation therefore usually results in an increase in transpiration from a site. However, planting non-tree species may sometimes result in a bigger increase. Also, many areas of south-west Western Australia considered for reforestation are currently under annual pasture. While they may not transpire as much as tree species, annual crops and perennial pastures also transpire more than annual pastures. Changing from annual pastures to annual crops and perennial pastures is likely to be more widely accepted and implemented by farmers than reforestation. Promoting a change in the agricultural system may therefore result in a larger increase in transpiration from a catchment than promoting reforestation. Reforestation should therefore not be regarded as the only option to increase transpiration, but as one of the options. An appropriate mixture of reforestation, changing the agricultural system, and planting suitable non-tree species will yield the largest increase in transpiration from a catchment.

2) There are differences in transpiration between tree species. High water use is associated with a deep and extensive root system, a high stomatal conductance down to very low leaf water potentials, and a large leaf area. However, transpiration by a species also depends on site conditions such as mean annual rainfall and other climatic variables, landscape position, soil water salinity, ground water salinity and depth to ground water. The data available at present are insufficient to select a species for planting at a particular

site for its transpiration characteristics. Therefore, if there are several species which are equally suited to the site to be reforested, the one with the highest aesthetic appeal, commercial value, or other benefit should be chosen.

4) The roots of trees penetrate to a greater depth than the roots of most non-tree species. Trees are therefore more likely to have access to ground water. Several studies have shown that trees can lower the water table. They can achieve this by reducing recharge to the point where ground water outflow from the area planted to trees exceeds ground water recharge, and by transpiring ground water. How much ground water a tree can transpire depends on the depth to ground water, the salinity of ground water, and the amount of soil water available for transpiration.

4) To obtain unambiguous results from studies on transpiration by trees, all species to be compared should be of the same age, exposed to the same site conditions, and sampled on the same day. Measurements should be carried out over at least one year and preferably with a method which accurately measures transpiration by a whole tree. It would be desirable to measure not just transpiration, but also the soil, plant and atmospheric factors which influence transpiration. A description of transpiration in terms of these factors could then be developed, which in turn could be used to assess transpiration by a species under site conditions different from those under which the measurements were carried out.

1. INTRODUCTION

The replacement of perennial and deep-rooted native forest vegetation with annual and less deep-rooted crops and pastures in south-west Western Australia brought about changes in the salt and water balance of the region. Transpiration decreased and ground water recharge increased. The latter raised ground water levels, which mobilised some of the salt stored in the soils of the region. This in turn frequently led to an increase in salt discharge to streams and thus to often large and persistent increases in stream salinity. Large areas of farmland have also become salt-affected due to increased salt discharge to the soil surface. A comprehensive review of the effect of agricultural development on stream salinity is presented by Schofield et al. (1988). The effect on land salinisation is reviewed by Western Australian Department of Agriculture (1988).

Reforestation is one way to tackle the salinity problems in south-west Western Australia as they arose from the replacement of forest with crops and pastures in the first place. The greater transpiration by trees compared to the crops and pastures typically grown in the region can be expected to result in a decrease in ground water recharge. In certain circumstances trees can also transpire some of the ground water which has accumulated since agricultural development. Both of these processes effect a reduction in salt discharge to streams and to the soil surface. Different views on where in the landscape trees should be planted and at what density and areal extent were discussed by Morris and Thompson (1983). How much the tree species selected for planting can transpire in a year has a bearing on planting density. Species which can transpire more water can be planted at a lower density to achieve a desired effect on the salt and water balance. If planted at the same density as species which transpire less, they would achieve the same effect sooner, and a bigger effect in the long term. It can therefore be advantageous to plant the species which can transpire the most water. However, the suitability of a species for planting at a particular site must be the main consideration in its selection. Only if more than one species is suited can transpiration characteristics become a selection criterion. Other characteristics such as the aesthetic or commercial value of a species should also be considered then and, in some cases, may be regarded as more important than transpiration characteristics. Note that differences in transpiration and other characteristics not only exist between species, but also between subspecies and provenances.

This report reviews work conducted in south-west Western Australia over the last ten years on transpiration by trees. Throughout the report transpiration is defined as the loss of water from within living plants to the atmosphere. All other water loss to the atmosphere is called evaporation. Evapotranspiration refers to the sum of evaporation plus transpiration. The amount of water a plant would transpire under a given set of environmental conditions if water availability was not a limiting factor is referred to as potential transpiration. Ground water is defined as subsurface water which occurs in saturated soil and rock formations. Subsurface water held in unsaturated soil and rock formations is referred to as soil water. Saturated soil and rock formations are addressed as saturated zone, and unsaturated soil and rock formations as unsaturated zone. The top of the saturated zone is referred to as the water table, and the process whereby water percolates through the unsaturated zone to the saturated zone is called ground water recharge or simple recharge. Ground water level refers to the distance from the soil surface to ground water in a bore. Leaf area index is the ratio of leaf area to ground area.

2. VENTILATED CHAMBER STUDIES

Since 1976 Greenwood, in association with various co-workers, measured transpiration by pastures and several native and introduced tree species in south-west Western Australia using the ventilated chamber technique. All transpiration data quoted here from these studies are given as transpiration per unit ground area and were derived by dividing the volume of water transpired by the enclosed pasture or trees by the enclosed area of pasture or the planting density of the trees, respectively. Measurements in these studies were usually carried out several times during a day on at least one day each month during the study period. All species to be compared were sampled on the same day. Linear interpolation between measurements was used to obtain a total transpiration for a measurement day and, subsequently, for the study period. Throughout a study transpiration was always measured on the same individual trees.

In their earliest reported study Greenwood and Beresford (1979) measured transpiration rates of a total of 13 *Eucalyptus* species at three different locations with a long-term mean annual rainfall of 850, 500 and 420 mm, respectively. Data were collected for two years in the months of November through April. These months represent a comparatively dry season in south-west Western Australia during which only 20% of the annual rainfall occurs. The other 80% of the annual rainfall occur in a wet season from May through October. During the wet season, rainfall exceeds potential transpiration while during the dry season, potential transpiration exceeds rainfall. In the areas of south-west Western Australia considered for reforestation, potential transpiration for a whole year is also higher than annual rainfall. Potential transpiration for the dry season is typically two to three times higher than for the wet season. Actual transpiration for the wet season is usually close or equal to potential transpiration, but for the dry season it is less than potential transpiration. Actual transpiration for a whole year is therefore also less than potential transpiration.

Greenwood and Beresford (1979) confined sampling to the dry season because they felt that this offered the best opportunity for differences in transpiration between species to be detected. However, unless trees or any other types of plants growing in south-west Western Australia have access to ground water that is within a few metres of the soil surface and of relatively low salinity, their transpiration during the dry season is limited by the availability of water. (The effects of depth to ground water and ground water salinity on the availability of ground water to plants is discussed in more detail later). The lack of available water leads to increasingly greater reductions in transpiration as the dry season progresses. This was demonstrated by measurements of Grieve (1956). How much transpiration is reduced during the dry season depends on how much of the rainfall from the wet season is still available for transpiration. A tree which transpires a lot of water during the wet season may have already used most of the available water by November and thus exhibit low transpiration rates during the dry months. On the other hand, a tree which transpires less during the wet season is likely to have more water left by November and thus exhibit comparatively high transpiration rates during the dry months. This is also evident from the studies of Grieve (1956). He found that in the wet season leaves of Banksia menziesii transpired more than leaves of Banksia attenuata, but in the dry season the situation was reversed. Transpiration measurements from the dry (or the wet) season alone therefore cannot clearly identify the tree species which transpire the most over a one year period. Consequently, the data of Greenwood and Beresford (1979) cannot be used to assess this.

The tree species used in this study cannot be ranked according to the reported dry season transpiration rates either, since these depended on a number of factors. Some species transpired more when planted upslope, others when planted midslope. For a given species, transpiration decreased with mean annual rainfall. At the time of measurement the age of trees ranged from 11 to 27 months. On juvenile trees the leaf area, which is a measure of the transpiring area, increases rapidly with age. Older trees therefore transpired at a greater rate than younger ones.

The water table varied from 2 to 8 m below the soil surface across the three locations in the study. The fact that for a given species transpiration decreased with mean annual rainfall indicates that, at least at the 500 and 420 mm mean annual rainfall sites, transpiration was limited by a lack of available water since in south-west Western Australia potential transpiration generally increases as mean annual rainfall decreases. This in turn indicates that the trees did not utilise much, if any, ground water at this early stage of growth.

Greenwood et al. (1981) compared transpiration from 16-year old Pinus radiata trees and an annual Trifolium subterraneum pasture in an agroforestry layout where the two are interspersed. The long-term mean annual rainfall at this site is 900 mm. Transpiration was measured throughout a 14 month period during which 1030 mm of rainfall were recorded. Over this period the pasture transpired 90 mm of water while the trees transpired 910 mm of water. The pasture only transpired from May, when it germinated, until November, when it died. During these same months, the trees transpired 460 mm of water. They transpired throughout the study period, but more during the wet months (460 mm from May through October) than during the dry months (350 mm from November through April), even though potential transpiration is much higher in the dry season than in the wet season. This illustrates that in south-west Western Australia transpiration during the dry season is indeed limited by the availability of water, which largely depends on the amount of water left from over from the wet season.

The water table at this site was more than 20 m below the soil surface. Neutron moisture measurements showed there was no significant water extraction beyond a depth of 4.5 m below the soil surface.

A comparison of transpiration from 15-year old Eucalyptus wandoo sucker regrowth and an adjacent annual Trifolium subterraneum pasture was presented by Greenwood et al. (1982). The long-term mean annual rainfall at the location of this study is 750 mm.

Transpiration was measured over 11 months. During these 11 months 520 mm of rainfall were recorded. As in the agroforestry situation described above, the pasture only transpired from germination in May until death in November. The 450 mm of water transpired during this time was exactly equal to the amount of rainfall recorded over this time. The trees transpired about 750 mm of water over this period, and a total of 1100 mm over the full study period. These values are an average for five trees. The higher transpiration by the trees during the wet months relative to the dry months, 750 and 350 mm, respectively, indicates that in this study, too, transpiration during the dry season was limited by a lack of water.

Transpiration by the trees declined as the dry season progressed. This indicates that they were not able to utilise much, if any, ground water. Most of the water transpired in excess of the rainfall recorded during this study must therefore have originated from the unsaturated zone. The water table was 8 m to 10 m below the soil surface at this study site. Only a few roots were found to extend to more than 3 m below the soil surface.

In the study by Greenwood _et_ _al_. (1982) transpiration was measured on five _E. wandoo_ trees whose leaf areas differed. As long as water is not limiting and all other factors are equal, transpiration by a tree increases with its leaf area. If only a limited amount of water is available for transpiration, it is used up faster the greater the leaf area. This is accompanied by an earlier reduction in transpiration by a tree with a greater leaf area due to a lack of available water. In this study the volume of water transpired by the individual trees on the days of measurement in the wet season was proportional to their leaf area. This was still true for the measurement in November. As time progressed, transpiration by the tree with the largest leaf area fell below that of the tree with the second largest leaf area, whose transpiration in turn fell below that of the tree with the third largest leaf area as the dry season progressed further (Figure 1). However, the total transpiration by the trees over a whole year was still proportional to their leaf area. This illustrates again that annual transpiration by trees

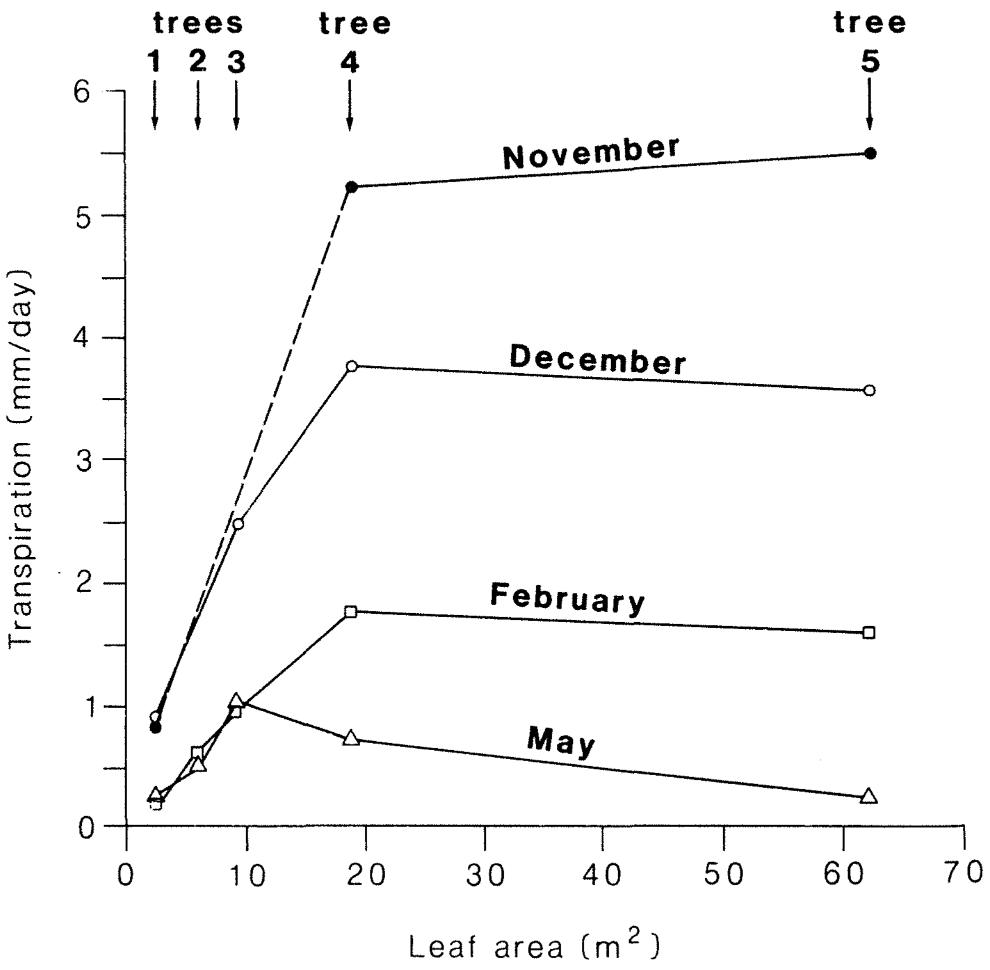

Figure 1

Relationship between leaf area and transpiration by five wandoo trees at different times in the dry season. (Figure redrawn from data by Greenwood _et al_. (1982) with their permission.)

cannot be correctly assessed from transpiration measurements in the dry season only, because the latter is influenced by how much of the wet season rainfall has already been transpired by the onset of the dry season. It also demonstrates that higher transpiration by a tree species can arise from the development of a larger transpiring area and does not have to be due to physiological characteristics such as a high stomatal conductance.

The transpiration from several 6 year old *Eucalyptus* species and adjacent annual clover (*Trifolium subterraneum*) pastures was studied over one year by Greenwood *et al*. (1985) at a location with a long-term mean annual rainfall of 800 mm. During the study 684 mm of rainfall were recorded. Over this period pasture on the upper slopes of the site transpired 370 mm of water, and pasture on the middle slopes of the site transpired 410 mm of water. This corresponds to 54% and 60% of the rainfall recorded over the study period, respectively. As in the two previous studies, the pastures only transpired between germination in May and death in November. About 500 mm of rainfall were recorded over the same months. During these months, the three tree species planted in a plantation on the upper slopes, namely *E. globulus*, *E. cladocalyx* and *E. maculata*, transpired some 1260, 1150 and 1000 mm of water, respectively. The total transpiration by these three species over the study period was 2690, 2660 and 2330 mm, respectively, which is equivalent to 3.4 to 3.9 times the rainfall recorded over the study period. *E. globulus*, *E. leucoxylon* and *E. wandoo*, the three species planted mid-slope, transpired about 990, 950 and 780 mm of water, respectively, from May until November. Over the study period, they transpired 2210, 1840 and 1620 mm of water, respectively, equivalent to 2.4 to 3.2 times the recorded rainfall.

In this study the water table varied from 2 to 8 m below the soil surface. Soil cores recovered from the area planted to *E. cladocalyx* showed that the roots of this species penetrated to 6 m below the soil surface, which is within the range of the water table. The rooting depths of the other tree species in this study were investigated at a later date and were also within the range of the water table (Greenwood, personal communication). Utilisation of ground water is a likely reason why the trees in the study were able to transpire so much more water than the rainfall received.

The trees generally transpired more during the dry season than during the wet season (Table 1). However, in south-west Western Australia potential transpiration for the dry months is typically two to three times higher than for the wet months. The trees in this study transpired only up to 33% more during the dry season than during the wet season, which indicates that they still experienced some water stress during the dry months, despite their access to ground water.

Trees can transpire ground water by extracting it from the saturated zone or, if there is flow from the saturated into the unsaturated zone, by extracting it from the unsaturated zone. The former process requires that a tree's roots extend into the saturated zone, while the latter operates with or without roots in the saturated zone. To transpire ground water it is therefore not necessary for a species to have roots below the water table. Also, a species with roots below the water table does not always transpire more ground water than one without roots below the water table as this not only depends where the roots are in relation to the water table, but also on the resistance in the flowpath from the saturated zone to the leaves, which in turn depend on the hydraulic properties of the soil and the species in question. Furthermore, the roots of many species do not function below the water table and may even die if they are water-logged for more than a few days.

Transpiration of the E. globulus trees in the midslope plantation was 0.82 of those in the upslope plantation. The difference in transpiration was due to the smaller leaf area of the midslope trees. As both plantations were established at the same time and in the same manner it is not clear what caused the smaller leaf area at the midslope site. Whatever caused the reduction in leaf area in E. globulus probably had the same effect on E. leucoxylon and E. wandoo, the other two species planted at the midslope site. Due to

Table 1 : Annual and seasonal transpiration of the species at the upslope and midslope site in the study by Greenwood *et al*. (1985).

Site	Species	Transpiration [mm]		
		May-October	November-April	whole year
Upslope	E. globulus	1260	1430	2690
	E. cladocalyx	1150	1510	2660
	E. maculata	1000	1330	2330
	T. subterraneum	370	-	370
Midslope	E. globulus	990	1220	2210
	E. leucoxylon	950	890	1840
	E. wandoo	780	840	1620
	T. subterraneum	410	-	410

this site effect, transpiration by species planted upslope cannot be directly compared with transpiration by those planted midslope.

Greenwood et al. (1985) also presented a transpiration per unit leaf area for the species in the upslope and midslope plantation which they calculated by dividing the measured transpiration by the leaf area of the trees. These data are reproduced here in Table 2 and show that, based on this transpiration per unit leaf area, the ranking of the species is virtually reversed from the ranking based on total transpiration by a tree shown in Table 1. In dividing the total transpiration by leaf area it is implicitly assumed that all leaves are equally effective in transpiring water. This is unlikely to be correct. Data presented by Grieve (1956), Doley (1967) and Morris and Wehner (1987) demonstrate that not all leaves in a canopy transpire equally. The degree of stomatal opening, and hence stomatal conductance, is sensitive to light. Stomata on shaded leaves are therefore often at least partially closed. Furthermore, stomatal conductance varies with leaf age (Grieve 1956, Doley 1967, Watts et al. 1976). Also, the atmospheric conditions that affect transpiration vary throughout the canopy.

As the number of leaves on a tree increases, the proportion of leaves which will not transpire at the full potential for the above reasons increases. This proportion is also affected by the distribution of the leaves in the canopy (Morris and Wehner 1987). This is confirmed by the data in Table 2 which show an increase in transpiration per unit leaf area with decreasing leaf area. These data do therefore not reflect the transpiration which could be attained by a leaf of a species that is not shaded and fully exposed to the prevailing atmospheric conditions. The above factors are also the reason why the proportionality between leaf area and transpiration implied several times in the previous and following discussion does not hold in stands with more than 3 to 5 m^2 of leaf area per unit ground area, that is a leaf area index greater than 3 to 5. In such stands there is little change in transpiration with a change in leaf area (Ritchie and Burnett 1971, Kristensen 1974).

Table 2 : Annual and seasonal transpiration per unit leaf area of the species at the upslope and midslope site in the study by Greenwood *et al*. (1985).

Site	Species	Leaf area index	Transpiration [mm]		
			May-October	November-April	whole year
Upslope	E. globulus	4.3	293	333	626
	E. cladocalyx	3.2	359	472	831
	E. maculata	3.4	294	391	685
	T. subterraneum	.9			
Midslope	E. globulus	3.4	291	359	650
	E. leucoxylon	1.3	731	685	1416
	E. wandoo	1.0	780	840	1620
	T. subterraneum	1.0	410	-	410

This also points to some problems with transpiration estimates for trees arrived at from measurements on leaves as done in porometer studies, for example. How much a species can transpire not only depends on how much an individual leaf can transpire, but also on how many leaves there are, which means the leaf area. A leaf from one species may transpire more than a leaf from another species, but the latter may compensate for that with a larger leaf area and hence have the higher transpiration on a per tree basis. Therefore, a direct comparison of transpiration measured on single leaves cannot be used to identify the species which transpires most on a per tree basis. To do that the measurements from individual leaves must be extrapolated to correctly account for all leaves in a tree and the differences in transpiration among the leaves in a tree.

It is interesting to note from an ecological point of view that in the study of Greenwood et al. (1985) where water availability was not as serious a limitation as in earlier studies by Greenwood and co-workers, E. globulus transpired significantly more than E. wandoo as a result of its greater leaf area. The variety of E. globulus planted originated from Tasmania. In its natural habitat rainfall usually exceeds potential transpiration so that it is rarely exposed to a lack of water for transpiration. Hence, this species evolved with little need for water conserving characteristics such as a small leaf area. E. wandoo on the other hand is native to areas in south-west Western Australia where potential transpiration during summer far exceeds rainfall. In its natural habitat ground water is also usually too far below the soil surface or too saline to be utilised in significant quantities. During the dry season this species must therefore rely on stored soil water left over from the winter rains. Copious transpiration during the wet season when water is available would thus leave it without water during the dry season which could lead to death as a consequence of desiccation. E. wandoo therefore evolved with a need for water conserving characteristics such as a small leaf area. If water availability was limiting, the situation might have been different as E. globulus may then not have had enough water to build up or maintain a large leaf area.

The studies discussed so far show that the tree species *P. radiata*, *E. globulus*, *E. cladocalyx*, *E. maculata*, *E. leucoxylon* and *E. wandoo* transpire more over a year than the annual pasture species *T. subterraneum*. This is due to two factors. Firstly, the trees transpire throughout the year while the pasture transpires only during part of the year. Secondly, during the times when the pasture is transpiring, the trees transpire more than the pasture. The 90 mm annual transpiration by pasture in the agroforestry layout (Greenwood *et al*. 1981) compared to 370 to 520 mm for pasture in open fields (Greenwood *et al*. 1982, 1985), may have been due to shading of the pasture by the trees since radiation is the main driving force for transpiration from short crops such as pasture. However, in an agroforestry layout trees and pasture compete for the same water. More rapid use of water by the trees compared to the pasture would leave less water for the pasture and could thus have caused the low transpiration of the pasture in the agroforestry layout. Differences in leaf area could also have been the reason. The data reported by Greenwood *et al*. (1981, 1982, 1985) are insufficient to ascertain the correct explanation.

Rooting depths in excess of 5 m can be expected from most tree species. The roots of several eucalyptus species have been found at depths greater than 20 m (Campion 1926, Dell *et al*. 1983). Most annual pasture species rarely exceed a rooting depth of 1 m. Trees are therefore more likely to access ground water. Their ability to transpire ground water and potentially lower the water table in this way was alluded to in the study by Greenwood *et al*. (1985). That trees can indeed lower the water table was demonstrated by Engel (1986) and Bell *et al*. (1988). They can achieve this not only by transpiring ground water, but also by reducing recharge to the point where ground water outflow from the area planted exceeds recharge plus lateral ground water inflow. A decline in the water table below a reforested area therefore does not necessarily imply that the trees transpired ground water. However, Johnston *et al*. (1983) presented evidence that, in certain circumstances, most of the ground water recharge can occur via root channels from removed or still existing trees. Water moves very rapidly through such preferred pathways so that there is little opportunity for trees to transpire it as it flows to the saturated zone. Hence, in areas where most of the ground water recharge is via preferred pathways trees can only lower the water table substantially by transpiring ground water.

Because the environmental conditions at the various measurement sites and the age (and hence leaf area) of the trees measured were different, the transpiration data from the various ventilated chamber studies reviewed here cannot be compared. Only in the study by Greenwood et al. (1985) was transpiration measured on several species of the same age, at the same time, and at the same site so that a ranking according to their transpiration over the study period was possible. However, only three species were compared at each of the two sites in this study and it is not certain that the same ranking would have been achieved had these species been planted at another location with different site conditions. The various studies by Greenwood and his co-workers therefore yield very little information on which species to plant to maximise transpiration from a site.

There were several faults in the design and operation of the ventilated chambers in the studies by Greenwood and his various co-workers. Due to these faults there is some doubt about the numerical accuracy of the transpiration data presented in their paper and in the data reproduced here. Comparisons between species were probably not seriously affected by these faults. Because they are of a technical nature, these faults are discussed in detail in an appendix rather than in the main text.

3. POROMETER STUDIES

Hookey et al. (1987) reported on measurements of stomatal conductance on a total of 23 eucalyptus species and provenances after 5 years of growth at a site with 750 mm long-term mean annual rainfall. The measurements were carried out from November 1984 to May 1985, and from mid-October 1985 to April 1986. From November 1984 through April 1986 some 843 mm of rainfall were recorded at the site.

On average, conductances for a species or provenance were measured every ten days during the measurement periods. (In the remaining discussion of this study any reference to species shall include provenances). Measurements were then taken three to six times per day. During each of the three to six daily samplings conductances were measured either on 20 leaves at the top of the canopy or on 60 leaves throughout the canopy, depending on the species. The leaves were randomly selected and no attempt was made to use the same leaves for each set of measurements. However, all measurements for a species were done on the same trees. Because of the large number of measurements taken on a species during a measurement day, only two to three species could be sampled on a given day. The combination of species measured on a given day was varied during the study so that virtually no two species were measured on the same day twice.

For each of the three to six sets of daily measurements the conductances were averaged and then used in conjunction with the Penman-Monteith equation (Monteith 1965) to compute daily transpiration from a leaf, expressed in mm of water per day per unit leaf area. The weather data required for the computations were collected at a climate station some 7 km south-west of the study site. Total transpiration from a unit leaf area for various periods during the study as well as for the total study period from November 1984 through April 1986 was then obtained by interpolation. Three interpolation methods were used. The first method, chosen for its simplicity, was a linear interpolation between the transpiration values computed for the days of measurement. In the second method a relationship between vapour pressure deficit and stomatal conductance was derived for each species from measured data. This relationship was then used to estimate stomatal conductances for all days without measurements, which in turn were used to compute transpiration for these days. This method was chosen because several researchers had previously reported a causal relationship between vapour pressure deficit and stomatal conductance. At this stage, however, it is still a matter of scientific debate whether such a relationship really exists. Recent evidence suggests that it is an experimental artefact associated with the use of porometers (Meyer et al. 1985, Idso and Allen 1988). In the third method a relationship was derived for each species between the actual transpiration, calculated for the measurement days with the observed conductances, and a potential transpiration, calculated for the measurement days with a fixed, arbitrarily selected conductance value. Then a potential transpiration was calculated with this fixed conductance value for every non-measurement day. Finally, an actual transpiration for each non-measurement day was estimated from the derived relationship between actual and potential transpiration. No rationale for using this interpolation method was given by the authors. It does not have a scientific basis.

The interpolated transpiration values were summed for a specified period and the species ranked according to the total transpiration per unit of leaf area obtained for the period. Several periods were considered and for each period a ranking was presented for each of the three interpolation methods. After considering the various rankings, Hookey et al. (1987) highlighted several species from the study which they considered to be able to transpire the most. However, their results are questionable for a variety of reasons. Firstly, there are problems with the approach taken because, as explained above,

- measurements taken only during summer cannot accurately identify the annual transpiration by a tree, and

- the amount of water transpired by a leaf does not unambiguously reflect the amount of water transpired by a tree. If all the trees in this study would have had a similar leaf area and canopy structure this would not necessarily be a serious problem. However, the leaf areas were quite different as indicated by the estimated leaf area indices which ranged from 0.6 to 3.5.

One of the main objectives of this study was to identify the tree species which can transpire the most ground water. Conductance measurements were therefore confined to the dry season since the authors felt that high transpiration in the dry season would clearly identify such species. High transpiration by a species in the dry season can indeed reflect its ability to utilise ground water as alluded to in the study by Greenwood et al. (1985). However, as illustrated in the study by Greenwood et al. (1982), it can also indicate that a species has used less water in winter than others and therefore has more water available to sustain a higher transpiration in summer than others.

Apart from the problems with the approach, there are also some faults in the design of this study.

- Site conditions were not the same for each species. For example, at planting the depth to the water table ranged from 5 to 20 m and ground water salinity ranged from 1,000 to 14,000 mg/l TSS (total soluble salts). Also, some species were planted in discharge areas, others in recharge areas.

- The sampling strategy was not the same for all species. For some only 20 leaves at the top of the canopy were sampled, for others 60 leaves throughout the canopy were sampled.

- Measurements on the various species were not taken on the same day so that the results cannot be compared directly.

- The porometer used did not function properly. Its humidity sensor could not be calibrated accurately and once calibrated as well as possible, the calibration changed with time.

- The methods used to interpolate between measurement days are questionable. The linear interpolation procedure misrepresents transpiration if the data include a day of unusually low or high transpiration. This is especially serious for estimating transpiration during the wet months when no measurements were taken. The interpolated results then depend very strongly on the last measured value before, and the first one after the wet season. In the second method the relationship between vapour pressure deficit and stomatal conductance derived for each species were poorly defined at best, and in some cases virtually non-existent. Also, throughout the measurement seasons all species had partially closed stomata, at least during the midday hours, which indicates water stress. Any correlation developed from data collected under these conditions is unlikely to hold during the wet season when the trees would not experience much water stress. The third method is put into doubt for similar reasons. The derived relationships between actual and potential transpiration were poorly defined to virtually non-existent and were equally applied to the dry and wet season even though they were only based on data from dry season when the trees suffered water stress. The ranking of several species was markedly affected by the interpolation method used.

- The weather data used for the computation of transpiration were collected at a site some 7 km away. It is not certain how applicable these are to the study site.

In light of these problems it is unlikely that the data presented by Hookey _et_ _al_. (1987) and their ranking of the species resemble the true transpiration and ranking of the species in this study. If they do, it must be considered fortuitous.

In addition to the problems with the approach and the design of the study, the data presented by Hookey et al. (1987) also contain several calculation errors which arose from mistakes in the use of the Penman-Monteith equation.

- A reflectance coefficient of 0.1 was substituted into the Penman-Monteith equation, even though measurements on eucalypts suggest a value of 0.19 (Stanhill 1970).

- The fact that some leaves have stomata on one side only, but others on both sites was not accounted for. The latter requires the measured conductances to be multiplied by two when they are inserted into the Penman-Monteith equation.

- Tree height was taken as 7.3 m for all species when in fact it ranged from 4 to 12 m. Tree height is required for the calculation of aerodynamic resistance of leaves to water loss, a term in the Penman-Monteith equation.

- Zero plane displacement and roughness length, two other parameters needed in the calculation of aerodynamic resistance, were estimated wrong. The former was estimated as 0.9 times tree height, the later as 0.1 times tree height. Experimental data suggest 0.63 times tree height and 0.13 times tree height, respectively (Monteith 1973). Apart from the wrong coefficients, a tree height of 7.3 m was used for all species.

These calculation errors could be corrected retrospectively, but it is pointless because this does nothing to overcome the fundamental flaws with the approach and the design of the study. It would not make the results any more credible.

4. GROUND WATER MONITORING

It has been suggested to obtain a qualitative comparison of transpiration by various tree species by comparing the change in ground water level below each species. This is theoretically possible if the plots of each species are large enough or far enough apart that the water level change observed under one species is not affected by the water level change under a neighbouring species. How large or how far apart the plots have to be to prevent this interference depends on the hydraulic properties of the aquifer. Also, for this approach to be useful the initial depth to ground water and all other site conditions must be the same for each species.

Ground water levels were monitored at the site of the study by Hookey et al. (1987) with a network of bores. Since reforestation the ground water levels declined under each of the planted tree species, though not by the same amount. At this site the plots for the various species were typically 80 by 100 m wide and adjacent to each other. Analysis of the ground water data showed that declines in the water level could only be differentiated on a scale much larger than individual plots. This indicates that the plots in this study were too small and too close together to prevent interference.

The site conditions in this study were not the same for each species as detailed previously. The importance of equal site conditions is illustrated in Figure 2 which shows that the decline in ground water level in the bores at the study site was related to the initial ground water level. This invalidates any attempt to compare transpiration by the species in this study from the decline in ground water level.

With increasing depth below the soil surface, roots become fewer as a result of decreasing oxygen concentration, lower soil temperature and other increasingly unfavourable environmental conditions (Taylor 1983). In addition, there is a resistance to water flow in roots which increases with the distance water travels inside the roots

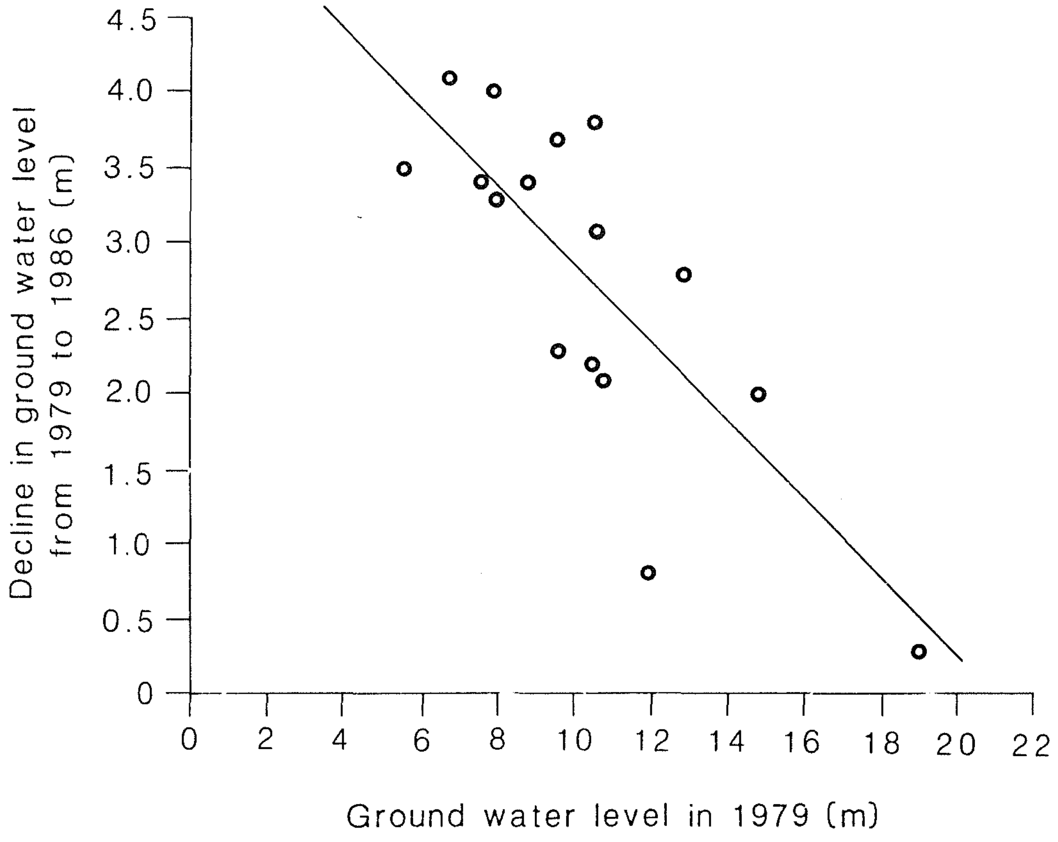

Figure 2

Relationship between the ground water level at planting in 1979 and the decline in ground water level from 1979 to 1986 in bores at the site of the study by Hookey _et_ _al_. (1987).

(Taylor and Klepper 1978). Hence, the further water is below the soil surface, the more difficult it becomes for plants to extract it. The amount of ground water a tree can utilise therefore decreases with the depth to ground water. The data in Figure 2 could be interpreted as an illustration of this fact.

Trees and all other terrestrial plants transpire water in the top of the soil profile first because it is easier to extract. Only when most of the available water there has been removed do they begin to use significant amounts of water from lower parts of the soil profile (Gardner 1983). Hence, since ground water is typically several metres below the soil surface, trees transpire considerable amounts of soil water before they transpire a significant amount of ground water, if any. Since soil water which has been transpired cannot recharge ground water, the higher transpiration by trees compared to annual crops and pastures can be expected to reduce ground water recharge in reforested areas. (Note that this would not apply in areas where most of the ground water recharge is via preferred pathways). Trees are not likely to transpire much ground water unless it is within reach of their roots, of relatively low salinity, and the demand for transpiration cannot be fully met by water from the unsaturated zone. The more soil water there is available to the trees, the less ground water they transpire.

Salinity also affects the availability of water to a plant. For a salt composition typical for south-west Western Australia, every 1000 mg/L TSS lowers the water potential by .75 bars. Soil water and ground water salinities of 10,000 mg/L TSS are common in agricultural areas and salinities in excess of 30,000 mg/L are not unusual. These salinity levels lower the water potential by 7.5 and 22.5 bars, respectively. To extract soil water or ground water and transport it to the leaves from where it is transpired into the atmosphere, the leaf water potential must typically be several bars lower than the soil water or ground water potential. This difference is required to overcome the resistance to water flow along the flowpath from the soil to the leaves. To transpire water the stomata in the leaves must at least be partially open, that is leaf conductance, a measure of the degree of stomatal opening on a leaf, must be greater than zero. Relationships between leaf water potential and leaf conductance for five Eucalyptus species are shown in Figure 3. To utilise water with a salinity of 10 000 mg/L TSS requires lowering the leaf water potential by 7.5 bars plus several bars to overcome the resistances in the flowpath. All species shown in Figure 3 could use such water and maintain leaf conductances reasonably close to the highest possible value for each species. To utilise water with a salinity of 30,000 mg/L TSS requires lowering the leaf water potential by 22.5 bars plus an additional amount to overcome the resistances in the flowpath. At a leaf water potential of 22.5 bars, the stomata of E. saligna are completely closed. This species would therefore not be able to utilise any water of such very high salinity. The other four species mentioned in Figure 3 could utilise it, but not at the same rate as water with 10,000 mg/L TSS since the leaf water potentials required to do so are much lower and result in much lower leaf conductances and, hence, transpiration rates.

Besides its effect on water potential, salt can also have toxic effects on plants. The concentration at which salt becomes toxic varies between species and also depends on the type of salt involved. Toxic effects can remove the advantage a species might have had due to its leaf water potential - leaf conductance relationship or other adaptations to overcome the osmotic effects of salinity. For a discussion of toxic effects of salts on plants, the reader is referred to Bernstein (1974).

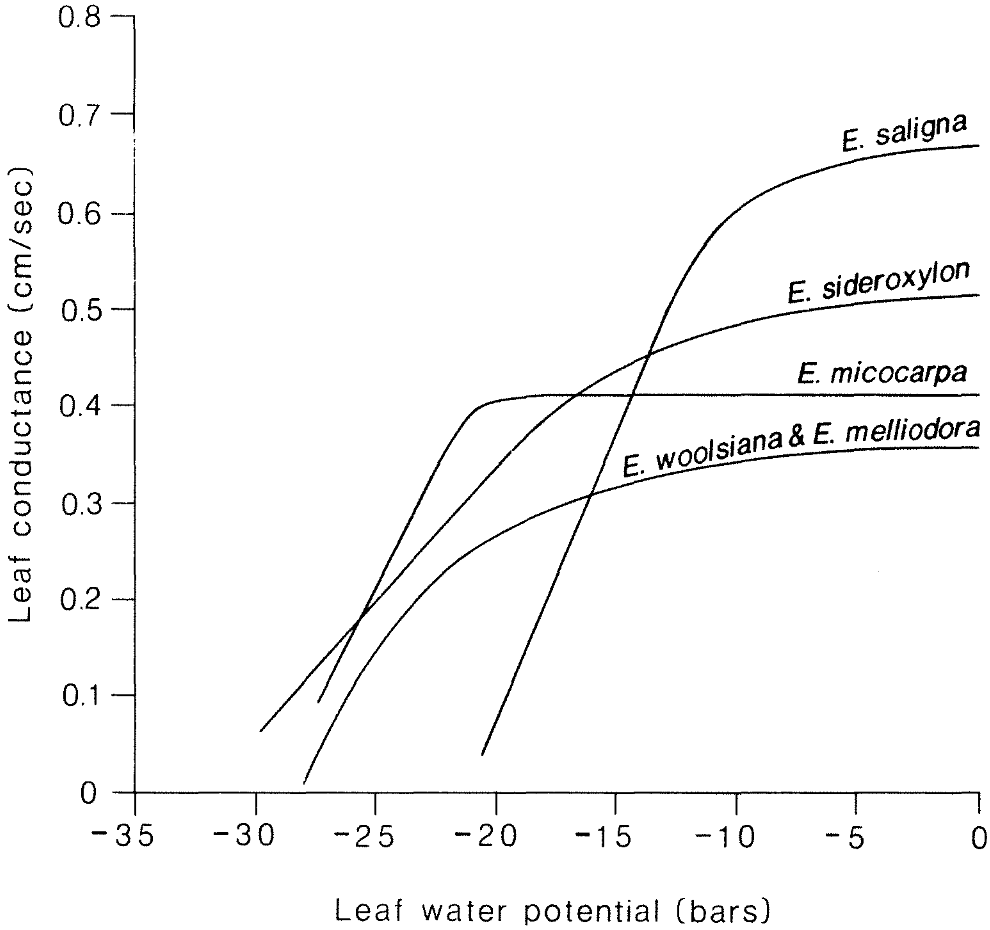

Figure 3

Relationship between leaf water potential and leaf conductance for five Eucalyptus species. (Figure redrawn from data by Hookey et al. (1987) with their permission.)

5. SOIL WATER MONITORING

Carbon *et al*. (1982) monitored changes in soil water storage under native, mixed species forest of *Eucalyptus marginata*, *Eucalyptus gomphocephala* and *Banksia grandis*, a 14 year old *Pinus pinaster* plantation, the pernennial legume *Medicago sativa*, the perennial pasture grasses *Eragrostis curvula* and *Hyparrhenia hirta*, and the annual pasture grass *Bromus mollis* using the neutron scattering technique. The age of *M. sativa* and the perennial grasses was not given. The long-term annual rainfall at the site of this study is 900 mm. Measurements were taken at 30 cm depth intervals to a maximum depth of 6 m every six weeks for 17 months. Over this period 703 mm of rainfall were recorded. No mention was made of the depth to ground water in any of the studies reported by Carbon *et al*. (1982).

Evapotranspiration (ET) by the various types of vegetation was computed as

$$ET = R - WS - D \tag{1}$$

where R = rainfall, WS = change in soil water storage, and D = drainage below a depth of 6 m. Due to the deep sandy soils runoff hardly ever occurs at this site and was not observed during the study. Table 3 lists the evapotranspiration data presented by Carbon *et al*. (1982) for the various vegetation types. They did not attempt to separate evaporation and transpiration. Also, they summarised the data for the three periods shown in Table 3 and did not provide sufficient data in their paper to work out evapotranspiration for November through April and May through October. In the discussion of their work the periods of November 9 to March 30 and September 22 to March 13 are therefore referred to as dry periods, and the period of March 30 to September 22 as wet period.

Table 3 : Seasonal evapotranspiration of the species in the study by Carbon *et al*. (1982) and seasonal rainfall at the site.

Species	Evapotranspiration [mm]			
	September-March	April-September	October-March	total
Native forest[1]	176	286	277	739
P. pinaster	107	513	118	738
M. sativa	158	430	206	794
H. hirta	157	325	195	677
Er. curvula	107	363	173	643
B. mollis	91	376	90	557
Rainfall	33	578	90	703

[1] consisting mainly of *Eucalyptus marginata*, *Eucalyptus gomphocephala* and *Banksia grandis*

Table 3 shows that native forest and the *P. pinaster* plantation used more water over the study period than *Er. curvula*, *H. hirta* and *B. mollis*, but less than *M. sativa*. This illustrates that tree species do frequently, but not always use more water than non-tree species. Whether they use more water than non-tree species depends on site conditions and the species involved. *B. mollis* was the only annual species monitored in this study. In south-west Western Australia this species is usually only alive and transpiring from May to November. Judging from the values in Table 3, *B. mollis* probably consumed a similar amount of water during the wet period as some of the perennial species in the study. However, it consumed the least amount over the study period. This illustrates again that annual species can generaly be expected to consume less water over a year than perennial ones because they transpire only part of the year. The same observations can be made from data comparing the water use by the perennial species *Er. curvula* and the annual species *T. subterraneum* collected at a later date but also reported by Carbon *et al*. (1982).

According to Carbon *et al*. (1982) *B. mollis* depleted the available soil water to a depth of 1 m, *E. curvula* to a depth of 3 m, and native forest, *P. pinaster* and *M. sativa* to a depth of at least 6 m, the maximum depth to which soil moisture was monitored. Comparing this information with the water use data in Table 3 shows that water use increased with the depth of soil water depletion. The depth of soil water depletion is a reflection of rooting depth, which in turn affects the amount of water accessible to a plant. This indicates that the differences in water use between the vegetation types in this study were largely due to differences in rooting depth and, hence, the supply of water. However, differences in leaf area and other plant characteristics such as stomatal conductance properties certainly had an influence, too. How much of an influence, though, cannot be said since Carbon *et al*. (1982) did not present data which would allow such an assessment.

Native forest used less water during the wet period than the other vegetation types in this study. As a result it had more water available for transpiration in the dry season and was able to consume more water in the dry season than the other vegetation types (Table 3). This shows yet again that measurements during the dry or wet season only cannot clearly identify the species which consumes the most water over a year. The native forest evolved with the need for conservative water use in the wet season to have enough water left to guard against dessication in the dry season. Species which do not possess this trait are susceptible to drought damage or death if they are planted in south-west Western Australia, especially after years of below average rainfall and where they are planted in dense stands (Butcher 1979). Many species currently used for reforestation in the region, among them _P. radiata_ and _E. globulus_, do not. This should be considered in future reforestation plans. Drought death of _P. radiata_, _E. globulus_ and other non-native species has been observed in south-west Western Australia.

A substantial portion of the areas of south-west Western Australia considered for reforestation are currently under annual pastures such as _T. subterraneum_. Although they may not consume as much water as tree species, perennial pasture species do consume more water than annual ones as evidenced by the data in Table 3. Annual crops have also been found to use more water than annual pastures (Nulsen and Baxter 1982, Schofield _et al_. 1989). Changing from annual pastures to annual crops or perennial pastures would increase transpiration. Such a change in the agricultural system is likely to be more widely accepted and implemented by farmers than reforestation. At a given site, reforestation may yield a bigger increase in transpiration than changing the agricultural system, but because it is likely to be less widely implemented, encouraging reforestation on its own may result in a smaller increase in transpiration from an entire catchment than encouraging a change in the agricultural system on its own. An appropriate mixture of these options will yield the best result.

The pine water use data in Table 3 were collected in a stand with 1200 trees/ha and the data for native forest in a stand with 820 trees/ha. Both stands used the same amount of water. Carbon _et al_.

(1982) also reported water use data for a 14-year old P. pinaster plantation and native forest at a site with 800 mm mean annual rainfall. The density of the pine plantation again was 1200 trees/ha, but the trees were smaller than at the higher rainfall site. The density of the native forest was less than at the higher rainfall site, namely 640 trees/ha, and trees were smaller, too. A reduction in plant size and plant density is a typical adjustment of vegetation to drier conditions since it usually results in a smaller leaf area and thus more conservative use of the available water. Measurements at the 800 mm rainfall site were carried out concurrently with those at the 900 mm rainfall site. As at the higher rainfall site, the native forest used less water during the wet period than the pine plantation, but more during the dry period. Over the entire study period the pine plantation consumed 627 mm of water and the native forest 471 mm. There were 669 mm of rainfall at this site over this period.

The pine trees at the lower rainfall site used less water than those at the higher rainfall site. This was also the case for native forest and can be attributed to the drier conditions and the smaller leaf area of the plants, the latter being a response to the drier conditions itself. This demonstates again that transpiration not only depends on the species involved, but also on the environmental conditions it is exposed to. Transpiration data obtained for a species at one site therefore cannot be applied to another site unless the differences in environmental and plant conditions between the sites are properly accounted for. Also, at the lower rainfall site the pine plantation used more water than the native forest, while at the higher rainfall site they used the same amount. This shows that a ranking of species according to water use obtained at one site may not hold at another site.

Due to differences in canopy structure between species, a difference in tree size and stand density between species does not necessarily imply a difference in leaf area. The tree size and stand density information given by Carbon et al. (1982) therefore cannot identify whether the pine plantation or the native forest had the larger leaf area. However, this information can be used to assess the leaf areas of the two vegetation types at the lower rainfall site relative to those at the higher rainfall site. It suggests that relative to the 900 mm rainfall site, the leaf area of the native forest at the 800 mm rainfall site was probably more reduced than that of the pines. This would explain why at the lower rainfall site native forest used less water than the pine plantation, even though they used the same amount at the higher rainfall site. It also highlights that transpiration data presented without some complementary information on the experimental conditions can be ambiguous since on their own they provide no insight why a particular value of transpiration was observed. This in turn makes any reliable extrapolation of the results to another site virutally impossible. Without the information on stand density on tree size the reader would have been left with conflicting data on the water use of P. pinaster in relation to native forest.

Carbon et al. (1982) compared the water use of a 14-year old P. pinaster plantation and native forest at a third site. The long-term mean annual rainfall at this site was also 800 mm, but the fertility of this site was less than at the other 800 mm rainfall site. The composition of the native forest was therefore different from that at the other two sites and was dominated by Banksia attenuata and Banksia menziessii. Its average density was 340 trees/ha and the trees were smaller than at the other 800 mm rainfall site. However, it cannot be ascertained whether the lower density and smaller plants were mainly due to the difference in site conditions or species composition. The pines were again planted at a density of 1200 trees/ha and responded to the poorer fertility by developing into smaller trees than at the other 800 mm rainfall site. Measurements at this third site were taken at the same time as at the other two sites. Here the pine plantation used more water than the native forest in the dry period as well as in the wet period. Over the full study period the pine plantation consumed 643 mm of water, the native forest 326 mm. Total rainfall over the study period was 669 mm. The large difference in stand density suggests that the higher water use by the pine plantation may have been due to a greater leaf area. However, for reasons given above it is not certain if there was in fact a difference in leaf area.

As a response to the less favourable site conditions, stand density and the size of the native forest was less at the two 800 mm rainfall sites than at the 900 mm rainfall site. The pines were planted at the same stand density at all three sites so that at the time the studies by Carbon et al. (1982) were undertaken a smaller tree size was the only reported response to the poorer site conditions. However, while the native forest at these sites had many centuries to adjust itself to the different site conditions, the pines had only been there for 14 years. It is quite likely that with time some of the pine trees will die and the stand density will thus adjust to the various site conditions. This has been observed in other pine plantations in Western Australia.

Young trees are likely to transpire more water per unit leaf area than old trees (Borg 1988), and a greater number of trees per hectare often results in a larger leaf area. In the studies of Carbon et al. (1982) the pines were much younger than the trees in the native forest, and there were more trees per hectare in the pine plantations than in the native forest. It is therefore not surprising that in this study the pine plantations were found to consume at least as much or more water than native forest. However, it cannot be determined from these results whether P. pinaster or native tree species would consume more water given the same number of trees per hectare, the same age of the trees and all other conditions being equal.

The water use data of Carbon et al. (1982) must be viewed with caution. Drainage was computed from Darcy's Law, combined with one relationship between soil water content and soil water potential, and one between soil water content and soil hydraulic conductivity. Over the range of water contents observed in their studies the hydraulic conductivity of the soil at the study site changes markedly with a small change in soil water content. A small error in the measurement of soil moisture content can therefore lead to a substantial error in the computed drainage value and thus the water use calculated from equation 1. Because there are always some inaccuracies in the measurement of soil water content with the neutron scattering technique, the numerical accuracy of the data presented by Carbon _et al_. (1982) is questionable. The use of the same single relationship between soil water content and soil water potential and the same single relationship between soil water content and soil hydraulic conductivity for all measurement sites and depths also casts doubt on the accuracy of their data because such relationships typically vary significantly over distances of less than one metre. It is not clear for which location these relationships were obtained in the first place. How much all this affected the water use data is uncertain. Nevertheless, the general conclusion drawn here from these data are consistent with the physical principles which govern transpiration.

6. CONCLUDING REMARKS

All studies reviewed here presented data on transpiration by plant species at selected sites over selected periods. The data from one of these studies were rejected as wrong. The data from the other studies, as far as they are reliable, illustrated that there are differences in transpiration between species. However, the transpiration values obtained in the various studies are subject to the experimental conditions under which they were obtained. A proper comparison of the results would require that the experimental conditions were the same or at least similar, or that sufficient complementary information on the experimental conditions is given to transpose results from one site to another. This was not the case in these studies. A valid comparison was therefore not possible. In addition, only few species were compared in any one study and it is likely that their ranking according to water use would have been different under different experimental conditions. Consequently, a list of species ranked according to their transpiration cannot be compiled from the studies discussed here.

Soil and ground water salinity, soil hydraulic properties, soil and ground water storage, extent of the root system, plant age, leaf area, and weather are some of the experimental conditions which affect transpiration. In future studies it would be desirable to measure not just transpiration, but also the soil, plant and atmospheric factors which influence it. A description of transpiration in terms of these factors could then be developed, which in turn could be used to assess transpiration by a species under conditions different from those under which the measurements were carried out. Data collected under different experimental conditions could thus be compared, or data extrapolated to a situation of interest for which no experiments have been conducted.

It is unfortunate that all the studies discussed here were mainly concerned with quantifying transpiration by selected species at selected sites and therefore collected few data on the factors which affect transpiration. This made the interpretation of the results difficult. Nevertheless, a deep and extensive root system, a high stomatal conductance down to very low leaf water potentials, and a large leaf area were identified as characteristics associated with high water use.

6. ACKNOWLEDGEMENTS

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Appendix A

Design and operation of ventilated chambers

The ventilated chamber is used to determine transpiration by a whole plant, or sometimes several whole plants. The plant (or plants) in question is completely enclosed inside the chamber. The volume of airflowing through the chamber (V) and the vapour pressure of the air entering and leaving the chamber (e_{in} and e_{out}, respectively) are measured. Transpiration (T) is then calculated as

$$T = kV(e_{in} - e_{out}) \qquad (2)$$

where k is a temperature dependent factor. A detailed derivation of this equation and the factor k is available upon request from the authors. If the chamber is not sealed at the soil surface, as in case of the various studies by Greenwood and his co-workers, then the calculated transpiration can include evaporation of water from the soil surface. Also, if the chamber is open at the top, again as in the case of the studies conducted by Greenwood and co-workers, the calculated transpiration can include evaporation of free water on leaf surfaces from dew or intercepted rain. Strictly speaking, the data extracted from the various studies of Greenwood and co-workers and presented in chapter 2 therefore represent evapotranspiration from the enclosed area.

In the ventilated chamber technique the plants are enclosed in plastic. There is some question how well the atmospheric conditions inside the chamber reflect the conditions outside. Greenwood et al. (1979, 1981, 1985) noted that they were different, but how much this affected water use is not clear.

The type of chamber used by Greenwood and Beresford (1979) and Greenwood et al. (1981, 1982) was completely open at the top and air was drawn through the chamber from its top to the bottom by fans in outlet ducts at the base of the chamber (Figure 4). Airflow through this type of chamber is strongly influenced by wind across the top of the chamber. Fluctuating wind leads to fluctuating air pressure and, thus, to fluctuating airflow through the chamber. Because airflow and vapour pressure are sampled at discrete intervals, this leads to fluctuating transpiration readings. Also, due to

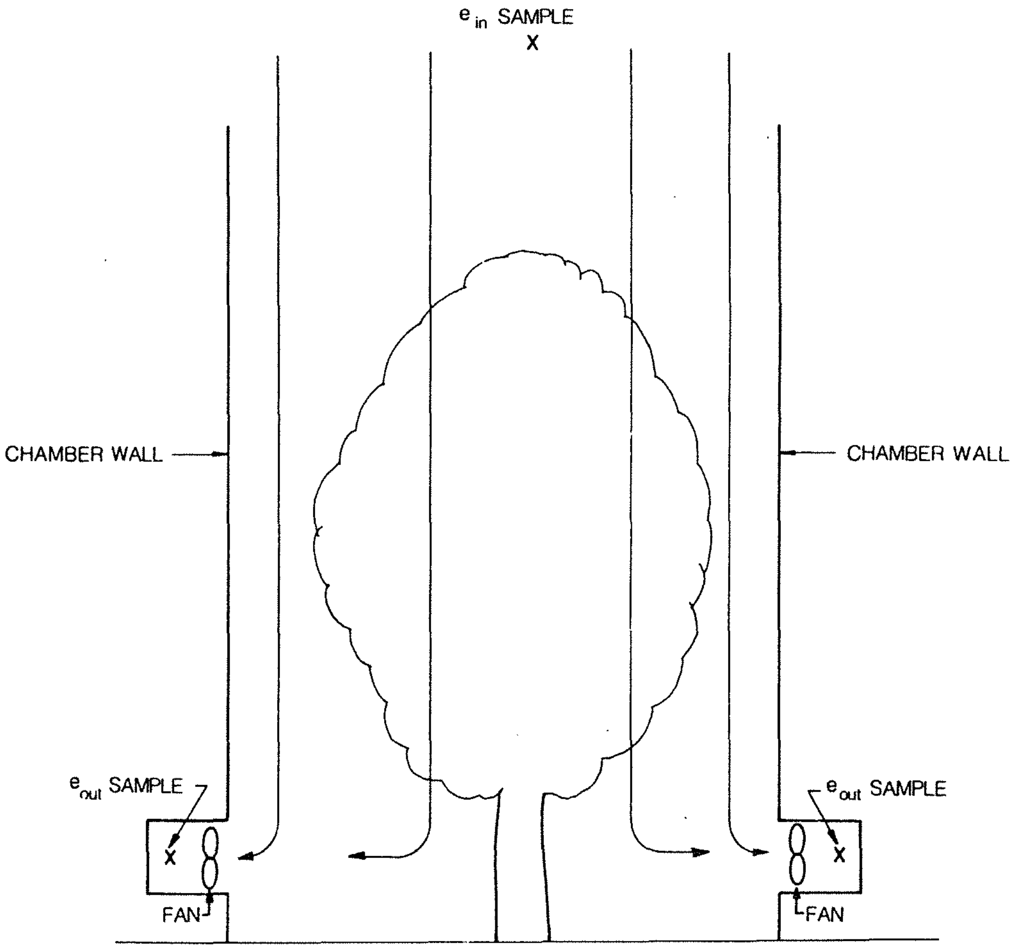

Figure 4

Sketch of the type of ventilated chamber used in the studies of Greenwood et al. (1979, 1981, 1982).

turbulence created by wind across the chamber top, air, and with it water transpired by the enclosed plants, left through the open chamber top rather than through the outlet ducts at the bottom. Some of the transpired water was therefore not measured. Air entering the chamber was prone to flow down along the sides, largely bypassing enclosed tree crowns. Hence, not all of the recorded airflow through the chamber carried transpired water to the outlets. Airflow through the chamber was measured at the top of the chamber using a vane anemometer. This type of anemometer reacts to the fastest wind speed across its arms and therefore overestimates the actual flow rate.

An improved chamber design (Figure 5) was used in later studies (Greenwood et al. 1985). Three to four fans were used to introduce air into the bottom of the chamber and to push it upwards through the chamber and out into the atmosphere through a restricted outlet at the top of the chamber. This resulted in a small positive pressure inside the chamber which inflated the chamber and thus made it structurally more stable. Furthermore, positive pressure inside the chamber and the restricted outlet led to high velocities of the exhaust air and made the airflow through the chamber independent of the wind velocity across the top of the chamber.

To measure airflow into the chamber, Greenwood et al. (1985) placed a duct with an airflow straightener at the intake end in front of the fans. Flow in the duct was then measured with pitot tubes. Only one duct was used which was moved around the fans at the base of the chamber. Flow rates measured with the duct in place were assumed to be the same as flow rates without the duct. However, this assumption is most likely wrong since the airflow straightener in the duct imposed a significant resistance to airflow.

An analysis of the airflow through this type of chamber showed that these were two distinct pathways. Along one pathway, air moved upwards along the chamber wall, by-passing the enclosed tree crown, and left through the outer parts of the exhaust. In the other, air moved upwards through the enclosed tree crown and left the chamber

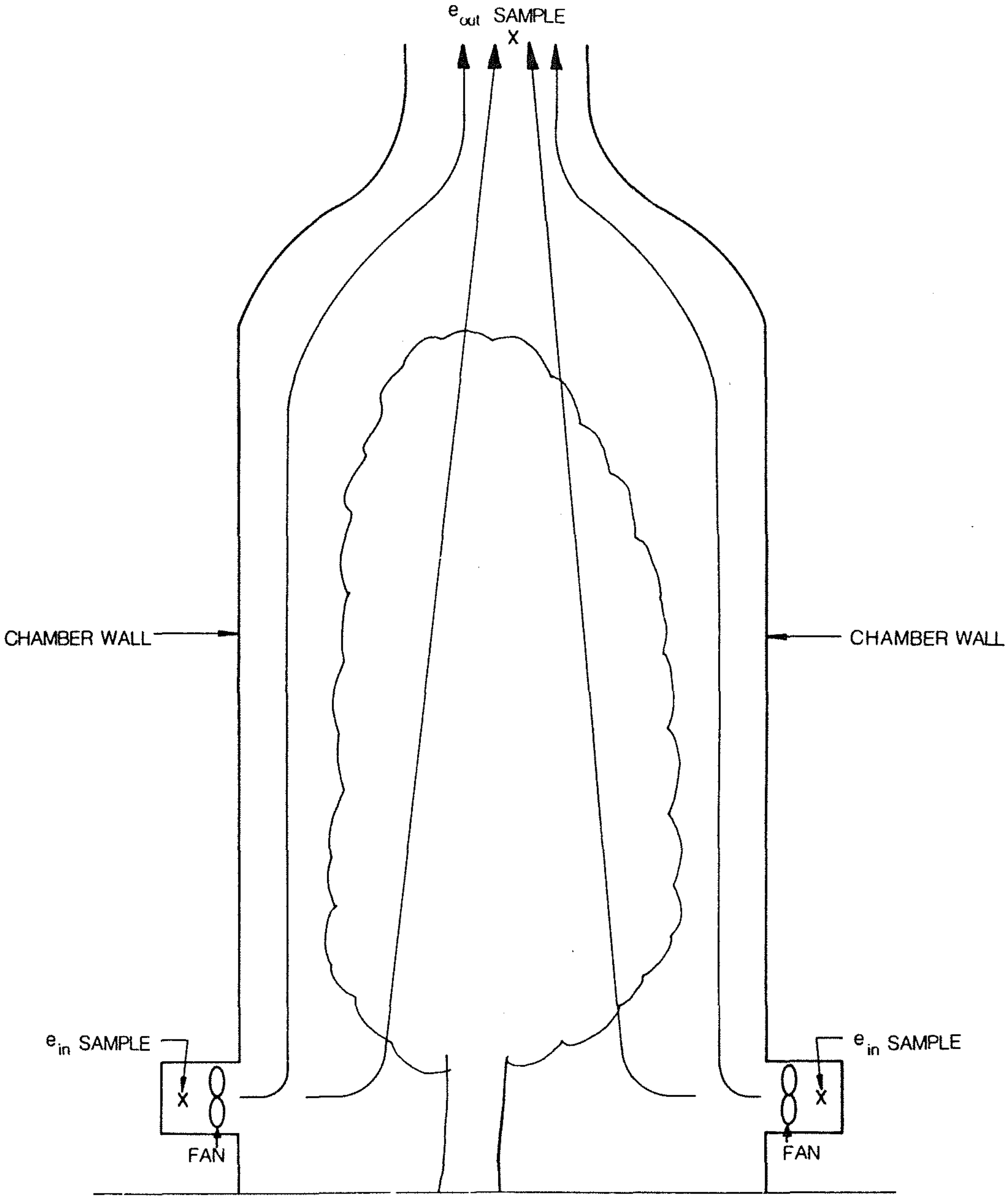

Figure 5

Sketch of the type of ventilated chamber used in the studies of Greenwood *et al*. (1985).

through the inner area of the exhaust. The air from these two pathways did not mix effectively and air moved faster through the first pathway than through the second one. Greenwood _et al_. (1985) initially sampled for e_{out} at the center of the exhaust. This value was then used in equation (2), together with the total flow through the chamber. However, the way the e_{out} sample was obtained it only reflected the vapour pressure of the air which passed through the tree crown along the second pathway described above. The air which by-passed the tree crown along the first pathway would have been much drier so that the e_{out} representative of the total flow would have been less than the measured value. The transpiration computed using the measured e_{out} and the total flow volume is therefore too high. Greenwood _et al_. (1985) later modified their sampling strategy and collected e_{out} samples at several points of the exhaust. An arithmetic average of these samples was then used in equation (2) in conjunction with the total flow volume. This is more realistic than the initial approach, but it is still not correct. Air flowing along the first pathway has a higher velocity than air flow along the second pathway. Hence, to obtain a correct average value of e_{out}, each sample must be weighted by the flow volume it is associated with, or the sample points must be spaced such that each point is associated with a similar flow volume. Neither was the case. Recall that the trees in the study by Greenwood _et al_. (1985) transpired 2.4 to 3.9 times more than the rainfall recorded during the study. In light of the sampling techniques described above it is quite conceivable that some of this high transpiration was in fact an artefact caused by improper sampling.

An infrared gas analyser (IRGA) is used to measure the vapour pressure of the air entering the ventilated chamber and of the air leaving the chamber. An IRGA can only measure the difference in vapour pressure between two samples by comparing the sample of interest to a reference sample with a known vapour pressure. Greenwood _et al_. (1981, 1982) used the samples form the chamber intake as reference samples to which the samples from the exhaust were compared. The sensitivity of an IRGA varies with the vapour pressure of the reference sample. The vapour pressure of the air entering the chamber varied throughout the day. The use of the intake air as the reference sample was therefore incorrect. In subsequent studies Greenwood and his co-workers compared inlet and outlet samples to a constant reference sample.

The material the air sample lines are made of can also have an effect on the IRGA readings. Plastic air lines can absorb water from and later release it to the airflow through the lines. The ethyl vinyl acetate lines used by Greenwood et al. (1981, 1982, 1985) did absorb water. To prevent condensation the lines were heated at night. This apparently released water absorbed by the tubes during the day and gave the impression of substantial transpiration at night. An attempt to resolve this problem by using polythene tubing was unsuccessful because this material released organic vapours into the airflow. An IRGA cannot distinguish between water vapour and OH-groups from organic vapours. Copper tubing cleared of milling oils does not pose either of these two problems and is therefore well suited for air sampling lines.

Between measurement days the chambers were usually folded up on the ground. Rain and condensation water often accumulated in the folds. When the chambers were raised water was sometimes spilled onto the enclosed plants and the soil surface within the chambers. Evaporation of this water was included in the transpiration measurements.

It is not clear how much these problems affected the studies of Greenwood and his co-workers, but they cast some doubt on the numerical accuracy of the data though the comparisons made in the various studies may not have been affected seriously. The ventilated chambers used to measure transpiration from pasture (Greenwood et al. 1981, 1982, 1985) were different from those used for trees. We are not familar enough with these chambers to comment about their design and operation in detail.