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Water-use efficient plantations – separating the wood from the leaves

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Water-use efficient plantations – separating the wood from the leaves

Prepared for

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List of Acronyms and Symbols

Symbol or Acronym	Definition	Units (if applicable)
W_w	Water-use efficiency of wood production or volume growth per unit of evapotranspiration	M^3 ML^{-1}
E_t	Evapotranspiration – the sum of transpiration, soil evaporation and canopy rainfall interception	mm
A	Net carbon assimilation	μmol m^{-2} s^{-1}
E	Instantaneous leaf transpiration	mmol m^{-2} s^{-1}
$A/E=W_i$	Instantaneous leaf scale water-use efficiency - net carbon assimilation per unit transpiration	μmol CO_2 mmol H_2O^{-1}
p_i	CO_2 partial pressure inside the leaf	ppm
p_a	CO_2 partial pressure immediately outside the leaf	ppm
e_s	Vapour pressure inside the leaf	kPa
e_a	Vapour pressure imposed at the leaf surface	kPa
Y	Yield	G of dry matter harvested
E (in Passioura 1977, equation (2))	Water-use (at any scale)	mL water-used
WUE	Water-use efficiency	G mL^{-1}
HI	Proportion of dry matter allocated to the harvestable unit of biomass – Harvest Index	Dimensionless (g g^{-1})
I	Canopy interception	mm
E_s	Evaporation direct from the soil surface	mm
E(stand)	Transpiration by a plantation	mm
P	Rainfall	mm

Symbol or Acronym	Definition	Units (if applicable)
E_0	Potential evaporation	mm
CWI	Climate wetness index, ratio of P to E_0	Dimensionless
W_{max}	Maximum soil water storage	mm
ΔM	Change is soil water storage between measurement times	mm
CAI	Current annual volume increment	M^3 ha^{-1}
K	Crop factor, the ratio of actual evapotranspiration to potential evaporation	Dimensionless

Executive Summary

This report presents current knowledge, including published information and some as yet unpublished data, on the effect of plantation management and climate on the water-use efficiency of wood production (W_w) expressed in m^3 of wood volume per ML of evapotranspiration (E_t, the sum of canopy interception, evaporation from the soil surface and transpiration or direct water-use by the plantation).

Section one defines water-use efficiency at a range of scales and considers the relationship between instantaneous leaf-scale transpiration efficiency and the stand-scale water-use efficiency of wood production (W_w, m^3 ML^{-1}). Most data on water-use efficiency is for the instantaneous ratio of carbon assimilation to transpiration at the leaf scale (W_i). In temperate environments management or breeding to increase water-use efficiency at this scale will almost certainly reduce the water use efficiency of wood production in both *Pinus radiata* and *E. globulus* plantations. This is largely because when plantations are exposed to soil or atmospheric water deficits, there is a reduction in the proportion of assimilated carbon that is allocated to stem wood. For commercial plantations, the ratio of volume growth (or any measure of plantation yield) to total plantation evapotranspiration (E_t, the sum of soil evaporation, canopy interception of rainfall and tree transpiration) is a measure of water-use efficiency that integrates the effect of breeding and management and this measure is subsequently referred to as the water-use efficiency of wood production (W_w).

Section two is a review of the literature on variation in both W_i and W_w and the effect of breeding and plantation management. There is a large body of literature on the variation in W_i between genotypes and the main trends and observations for trees echo the experience with cereal crops and legumes. Instantaneous leaf-scale water-use efficiency is under strong genetic control but in environments with winter dominant rainfall, W_i is often negatively correlated with the water-use efficiency of wood production (W_w). As for cereal crops, genotypes with weak stomatal response to soil and atmospheric water deficits will concentrate production in winter and spring when carbon assimilation is more efficient by virtue of the prevailing conditions. This strategy will grow more wood in average or good years but will increase the risk of tree deaths during drought years

Less has been written about the effects of plantation management on water use efficiency than about variation between genotypes but there is a clear indication that thinning, fertiliser addition, pruning and irrigation all have the potential to dramatically change the water-use efficiency of wood production systems.

Section three explores this potential by bringing together published and unpublished data on growth and evapotranspiration to analyse the effects of climate, species, and management on water-use efficiency under rain-fed and irrigated conditions. The complete data set includes more than 200 estimates of current annual increment, evapotranspiration and W_w. The major observations include:

- W_w varied from 1 to 5 m^3 ML^{-1} for *E. globulus*, *E. nitens* and *P. radiata* plantations from across southern Australia (including SE Australia (Green Triangle), southern Tasmania and SW Australia). There was no clear relationship between W_w and rainfall or potential evaporation.
- For sites where detailed physiological data was also available W_i was negatively correlated with W_w expressed in m^3 ML^{-1}.

- For plantations in Mediterranean environments characterised by winter dominant rainfall and summer drought, any plantation management that increases leaf area index will increase water use during the early part of the growing season and thereby maximise W_w and plantation growth.
- In low rainfall environments, on shallow soils or even in unusually dry years at wetter sites, maximising leaf area to improve W_w and yield may expose the plantation to potentially lethal water stress. Our research suggests that there is no yield penalty for reducing stocking density to as low as 600 stems per hectare and that the risk of drought death is substantially reduced.
- Thus for rain-fed plantations in southern Australia the risk of drought should be managed by varying stocking density. For a given stocking density, W_w should be maximised by ensuring that nutrient supply is non-limiting.
- Establishing plantations where trees can access shallow, fresh groundwater may increase W_w. Similarly in water-limited environments, irrigated plantations will produce wood with greater water-use efficiency than rain-fed plantations.

These results are striking and again echo the experience with cereal and other agricultural crops. In water-limited environments there is an inherent trade-off between rapid, water use efficient wood production and the risk of tree deaths that can be effectively managed using standard, routinely applicable silvicultural techniques.

Contents

Background and scope

There are nearly 1.5 million hectares of commercial eucalypt and pine plantations across southern Australia. Many are in high (>700mm) rainfall catchment areas supplying important surface or ground water-resources. There is considerable pressure from rural communities, other water-users and federal, state and local authorities to quantify and justify water use by these plantations. This is reflected in the National Water Initiative which identified new plantation establishment as an activity that should be accounted for in heavily or over-allocated systems. Policies to restrict plantation development based on water use have already been introduced in southeast SA, with even more severe measures proposed, including issuing all plantations with water licenses.

Maximising the water-use efficiency of new and existing plantations through improved management and genetics is important for water-resource and plantation managers. Plantation growth is largely determined by water availability. There is strong evidence that plantations and tree belts dry out soil profiles and less water may be available in the second rotation than during the first. Plantations near the economic limit of productivity may not be viable during the second rotation, particularly if the current trends of reduced rainfall persist, unless their water-use efficiency is improved.

This report presents current knowledge, including published information and some as yet unpublished data, on the effect of plantation management and climate on the water-use efficiency of wood production (W_w) expressed in m^3 of wood volume per ML of evapotranspiration (E_t, the sum of canopy interception, evaporation from the soil surface and transpiration or direct water-use by the plantation). This information is presented in four sections.

1. A consideration of definitions of water-use efficiency and in particular published information on the relationship between instantaneous leaf-scale transpiration efficiency (W_i) and the water-use efficiency of wood production (W_w).
2. A brief review of the literature on breeding trees and managing plantations for improved water-use efficiency from the leaf to the stand scale.
3. A meta-analysis of published and unpublished data on the effect of species, climate, and plantation management on plantation growth, water use and water-use efficiency.
4. Initial recommendations on best bet approaches for managing the trade-off between water-use efficiency and drought risk in temperate environments. These will be explored more fully in the second stage of this project and a complete analysis included in the final report.

1. Definitions of Water-use efficiency from leaf to stand scale

The water-use efficiency of trees in plantations may be expressed at a range of scales. In this section we argue that water-use efficiency expressed as volume growth per unit evapotranspiration is a valuable measure of plantation performance and a useful aid to decision making in water-limited environments. The following pages refer to a number of definitions of water-use efficiency. For clarity these are listed and defined in Table 1.

Table 1 – A brief description of some measures and definitions of water-use efficiency

Name	Definition	Symbol	Scale	Units	Examples for trees
Intrinsic water-use efficiency	Assimilation per unit leaf conductance	A/g	Leaf	μmol CO_2 mmol H_2O^{-1}	Dunin and Wong, 1987
Instantaneous water-use efficiency	Assimilation per unit transpiration	A/E and *Wi*	Leaf	μmol CO_2 mmol H_2O^{-1}	Field et al. 1983; Warren et al. 2001
Transpiration efficiency	Dry matter accumulation per unit transpiration	W_d	Tree	g mL^{-1} or g g^{-1}	Olbrich et al. 1993; Osorio et al. 1998; D'Allessandro et al. 2006
Carbon isotope discrimination	Discrimination against 13C in plant tissue relative a standard (usually PDM limestone)	$\delta^{13}C$ or Δ	Leaf to tree	per thousand	Farquhar et al. 1982; Osorio et al. 1998; Warren et al 2001
Water-use efficiency of wood production	Volume growth per evapotranspiration	W_w	Stand	M^3 ML^{-1}	None - but Olbrich et al. 1993 did consider wood per transpiration

1.1. Water-use efficiency of carbon assimilation – leaf scale

Water-use efficiency is most commonly reported as the instantaneous ratio of net carbon assimilation (*A*) to transpiration (*E*) and may be calculated with equation 1 after Farquhar and Richards (1984),

$$\frac{A}{E} = \frac{p_a(1 - {p_i}/{p_a})}{1.6(\Delta e)} \qquad (1)$$

where p_a and p_i are the partial pressure of CO_2 in the atmosphere and inside the leaf and Δe is the vapour pressure difference between the air within and immediately outside the leaf.

The constant 1.6 is the relative diffusivity of water vapour and CO_2 for a given conductance.

Of these variables only the internal CO_2 partial pressure (p_i) is affected directly by leaf responses to growing conditions:

1. If the stomata close in response to either soil drying or increased air saturation deficit i.e. increased dryness of the atmosphere, then photosynthesis will proceed in the presence of light and p_i will decrease resulting in an improvement in the water-use efficiency of carbon assimilation (equation 1).
2. Alternatively any increase in the rate of carbon assimilation for a given conductance will also decrease p_i and improve the leaf-scale water-use efficiency of carbon assimilation (equation 1).

Variation in leaf-scale water-use efficiency in response to soil or atmospheric water deficit is usually the result of stomatal closure (Dunin and Mackay 1982; Wong and Dunin 1987; Osorio et al. 1998). Improved nutrition, particularly addition of nitrogen, can increase carboxylation efficiency and improve instantaneous leaf scale water-use efficiency but these effects are often transient (Warren et al 2001).

1.2 Transpiration efficiency of wood production

The rate of carbon assimilation is strongly correlated with stomatal conductance for all plant species (Cowan 1982) including *Eucalyptus globulus* (Pereira et al 1987; Macfarlane et al 2004). Any increase in water-use efficiency mediated by a reduction in stomatal conductance will therefore be associated with a proportional reduction in the amount of carbon assimilated.

Passioura (1977) observed that crop yield (Y) could be calculated as the product of transpiration (E), water-use efficiency (WUE) and harvest index (HI, the proportion of biomass allocated to the harvested portion of the plant).

$$Y = E \times WUE \times HI \qquad (2)$$

This equation was originally developed for wheat but provides a useful framework for thinking about the relationship between leaf-scale water-use efficiency (WUE) and wood production (given by Y in equation 2) in trees. If we select or manage trees for improved WUE this may increase wood production under water-limited conditions, but only if the harvest index (or allocation of carbon to harvestable stem wood) is positively correlated with leaf-scale water-use efficiency.

Some of the assimilated carbon will be allocated to construction respiration (the cost of converting assimilates into biomass), woody biomass maintenance respiration and dark foliage respiration. Construction respiration costs are $\cong 0.25A$ (Penning de Vries, 1975), maintenance respiration depends on total woody biomass (stem, branch and coarse roots), foliage respiration is proportional to canopy biomass and both foliage and maintenance respiration increase as a function of temperature (Battaglia and Sands 1997). Battaglia and Sands (1997) describe the inclusion of respiration costs in the simple plantation growth model PROMOD and observe that at 20°C the total fraction of assimilation allocated to respiration is $\cong 0.47$ for *E. globulus* and is similar to that reported by Ryan et al. (1996) for *Pinus radiata*.

After accounting for respiratory losses, net canopy production (G) is allocated to biomass pools including coarse roots, fine roots, foliage, branches and stem wood. Cannell (1985) advanced the hypothesis that carbon is allocated preferentially to roots if conditions limit either the supply of water or nutrients and to foliage if light is limiting. Santantonio (1989) found a strong, negative linear relationship between stem and fine root partitioning across a number of *Pinus* species. Battaglia and Sands (1997) summarized existing knowledge on the effects of environment to develop rules for allocating biomass in PROMOD. This model and the more complex CABALA (Battaglia et al. 2004) predict that as either nutrient or water supply becomes limiting the proportion of net canopy production allocated to fine roots and fine root turnover increases from about 0.05 to 0.55 and that this is associated with a decline in allocation to stem wood from 0.55 to 0.2. (Battaglia and Sands 1997).

Thus, when canopy assimilation (*A*) is reduced by stomatal closure, respiratory losses may be considered a fixed cost of *A* for a given temperature (approximately 0.47 at 20°C). Under these conditions net canopy production (*G*) will be allocated preferentially to fine roots rather than stem wood for both *E. globulus* (Battaglia and Sands, 1997) and pines (Santantonio 1989). Thus it is reasonable to hypothesise that improved leaf-scale water use efficiency that results from stomatal closure will be negatively correlated with the harvest index.

1.3 Evapotranspiration efficiency of wood production

Total plantation water use is the sum of transpiration, soil evaporation and canopy rainfall interception and is less sensitive to plantation management than transpiration because changes in transpiration and interception are often offset by opposing changes in soil evaporation. To quantify the effect of plantation management or genetic improvement, the most meaningful measure of water-use efficiency of plantations is yield per unit evapotranspiration (W_w, equation 3). Water-use efficiency expressed in this way allows for the possibility that instantaneous water-use efficiency and harvest index are negatively correlated and integrates the effect of variation in leaf area and function on transpiration, interception and soil evaporation.

$$W_w = \frac{Y}{E_t} = WUE \times HI \tag{3}$$

1. Water-use efficiency of wood production – rationale and definition
Stomatal closure, either in response to soil drying or to rising air saturation deficit, will reduce net carbon assimilation and increase the water-use efficiency with which that carbon is accrued. When the amount of carbohydrate available for conversion to dry matter becomes limiting trees will preferentially allocate carbon for construction and maintenance respiration and fine root production.

Thus in temperate environments, where low summer rainfall coincides with low humidity and high air saturation deficit, there is a risk (likelihood) that intrinsic leaf-scale water-use efficiency will be negatively correlated with harvest index.

Canopy leaf area index is also a major determinant of plantation water use. Thinning, fertiliser addition, pruning and available nutrients and water all affect leaf area index which is in turn a key determinant of all the component fluxes of evapotranspiration

Plantation yield (or financial return) per total water-use or evapotranspiration is the only measure of water-use efficiency that integrates variation in leaf scale water-use efficiency, changes in carbon allocation and the effect of canopy area on transpiration, interception and soil evaporation.

2. Opportunities for improving plantation yield though breeding and management

Much of the first crop of the blue gum estate in southern Australia will be harvested before 2010 and the future of the industry depends on sustaining and improving on the productivity of the first rotation. This transition was managed successfully in *Pinus radiata* plantations in the Green Triangle despite an initial decline in productivity in the second rotation. However, since 1970 average annual rainfall in most plantation districts has decreased by more than 20% compared with the previous 80 years and more water-use efficient wood production will be a key to sustaining yield.

This is not intended as an exhaustive review of the literature on the water-use efficiency of trees but rather an attempt to highlight some of the trends apparent in the literature and use published examples to suggest priorities for Australian plantation growers.

2.1 Breeding to improve water-use efficiency and yield under water limited conditions

Screening large numbers of genotypes for intrinsic or leaf-scale water-use efficiency became possible when Farquhar et al. (1982) observed that the carbon isotope composition of plant tissue was related to the partial pressure of CO_2 inside the leaf (p_i) and therefore water-use efficiency. During the fixation of carbon, plants discriminate against the naturally occurring isotope ^{13}C so that plant tissue contains a smaller ratio of ^{13}C to ^{12}C than the surrounding air. The rate of discrimination is inversely proportional to leaf-scale water-use efficiency. A strong correlation between carbon isotope discrimination and instantaneous water-use efficiency measured using portable gas exchange equipment has been demonstrated for a range of plant species including pastures (Bolger and Turner 1999), wheat (Farquhar and Richards 1984), conifers (Aitken et al. 1995), numerous eucalypt species (e.g. Olbrich et al 1993; Hubick and Gibson 1993; Osorio et al 1998; Li 1999; Warren and Adams 2000) and other forest species (Geuhle et al 1994).

Although the relationship between water-use efficiency and carbon isotope discrimination has been understood since 1982, large scale evaluation of water-use efficient wheat cultivars only commenced early in this century (Passioura 2004). Before considering tree breeding for improved water-use efficiency in commercial tree plantations it is worth revisiting the issues confronted by the breeders of cereal and legume crops which are well summarized by Condon et al (2002), Turner (2001) and Passioura (2004).

- Initial yield gains from empirical breeding were slow, leading to attempts to target specific phenological, morphological and physiological traits associated with drought resistance (see Turner, 1997 for a summary). The results of numerous studies were at best equivocal and none of these specific traits were adopted in mainstream breeding programs (Turner et al., 2001).
- The discovery that the isotopic signature of the carbon in plant tissue (especially leaves) could be used to identify variation in transpiration efficiency (Farquhar and Richards 1984) resulted in renewed efforts to select for improved water-use efficiency of wheat and some other crops.
- Backcrossing genotypes of superior transpiration efficiency with local cultivars produced wheat varieties with up to 10% higher yield at low yielding sites with predominantly summer rainfall. In these environments crops grow through winter and spring primarily on stored soil moisture (Condon et al. 2002).
- At sites with winter dominant rainfall the program was less successful initially and Turner (2001) observed this was because in these environments improved

transpiration efficiency was either weakly correlated or even negatively correlated with yield. Moreover, when water-use efficient clones were deployed at wet sites or in high rainfall years there was a yield depression compared with the performance of low water-use efficiency clones that maintained high stomatal conductance and shortened the growing season.
- Recently, water-use efficiency wheat varieties have become available for Mediterranean type low rainfall environments (Passioura 2005). Again there is a yield penalty associated with deploying these varieties in wetter years or on wetter sites.

There is good evidence that instantaneous leaf water-use efficiency is under strong genetic control (Brendel et al 2002; Donovan and Ehleringer, 1992; Osorio and Pereira, 1994) and this is also true for a range of tree species including *E. globulus* (Osorio and Pereira, 1994 and Osorio et al., 1998; Li 1999) and Douglas-fir (Aitken et al 1995). Pita and Pardos (2001) measured the growth, water use and water-use efficiency of selected *E. globulus* clones. Their results, and the results of many other studies, echo the experience with crop species; clones that grew well during water deficit did not perform well under well watered conditions.

The literature on genotypic variation in physiological traits associated with water-use efficiency is voluminous. Although there are exceptions, most published studies are consistent with the following observations.

- In general leaf-scale transpiration efficiency during soil or atmospheric deficit is greatest for species, families or clones selected from low rainfall environments (Field et al. 1993; Stewart et al., 1995; Anderson et al., 1996; Li, 2000).
- In temperate and Mediterranean environments characterised by a winter rainfall peak and summer drought, the relationship between instantaneous or leaf-scale water-use efficiency and larger scale measures is either weak or the correlation is negative (Pita et al 2001; Grossnickle et al 2005)
- Some exceptions to the previous dot points are from studies in summer rainfall environments (tropical or sub tropical) or for measurements made on genotypes from these environments. For example Olbrich et al (1993) and Xu et al (2000) found a positive relationship between leaf-scale measures of water-use efficiency and measures of stand growth (volume and height). In a similar vein, Hubick and Gibson 1993) observed that high rainfall tropical provenances of *E. camaldulensis* were more water-use efficient than dry zone provenances under both well watered and droughty conditions.

In the only study to estimate the water-use efficiency of wood production, Olbrich et al (1993) observed two-fold variation amongst *E. grandis* clones in the amount of wood produced per unit of transpiration.

2.2. Effect of plantation management on leaf- and stand-scale water-use efficiency

There is limited information on the direct effects of management on leaf- or stand-scale water-use efficiency of wood production, but the available data are quite consistent. In summary:

- Thinning tends to increase the instantaneous water-use efficiency of the residual trees (Warren et al. 2001; Welander and Ottossson 2001) both overall and for a given level of water stress. In loblolly pine the rate of carbon assimilation and transpiration in the lower crown rose by 84 and 40% respectively after thinning

(Tang et al 2003). Thus the increase in carbon assimilation in the lower crown of thinned stands was not accompanied by an equi-proportional increase in transpiration. Two mechanisms are probably at play: - i) increased irradiance of lower leaves increased carbon assimilation and ii) partial decoupling of the lower canopy resulting in reduced sensitivity of transpiration to changes in stomatal conductance.

- Where the native supply is limiting, application of nitrogen increases both leaf and stand scale water-use efficiency. In *Pinus pinaster* a transient increase in foliar concentration was associated with increased water-use efficiency at a given level of water stress, suggesting a non-stomatal cause for the improved water-use efficiency. Stand-scale water-use efficiency of *E. grandis* was also improved by nearly 100% by improved nutrition (Olbrich et al 1993).
- Irrigation decreased leaf scale water-use efficiency (stomata stayed open in irrigated trees) and increased the water-use efficiency of dry matter production in *P. taeda* (Choi et al 2005).
- Pruning from below also has the potential to improve water-use efficiency at the stand scale due to up regulation of the carbon assimilation rate of retained foliage (Pinkard 2003) and the small contribution of the removed foliage to total stand transpiration (White et al 2000)
- Stand scale water-use efficiency (W_w expressed in m^3 wood produced per ML of evapotranspiration) also varies with species (Honeysett et al., 1992).

2. Improving the water-use efficiency of plantations by breeding and application of standard plantation silviculture (literature review)

In cereal and legume crops it took nearly thirty years from the first attempts to breed for improved water-use efficiency to the widespread evaluation and success of water-use efficient cultivars. Notwithstanding this success, screening of genotypes is prohibitively expensive and water-use efficiency is not yet part of any commercial breeding improvement program.

Leaf-scale water-use efficiency is under strong genetic control in trees, but in environments with winter dominant rainfall leaf-scale water-use efficiency is often negatively correlated with the water-use efficiency of wood production. As for cereal crops, genotypes with weak stomatal response to soil and atmospheric water deficits will concentrate production in winter and spring when carbon assimilation is more efficient by virtue of the prevailing conditions. This strategy will grow more wood in average or good years but will increase the risk of tee deaths during drought years.

Thinning, fertiliser, pruning and irrigation all have the potential to dramatically improve the water-use efficiency of wood production. Published studies in eucalypts suggest that more intensive plantation management will marginally increase water use but will have a profound effect on the water-use efficiency of our plantation estate.

3. Management effects on the water-use efficiency of wood production in *Eucalyptus* and *Pinus* plantations – some recent case studies.

This section presents data on the water-use efficiency of wood production (W_w) in commercial plantations and variation with species, thinning, fertiliser application, irrigation and access to groundwater. Some of this data has already been published but it has never been used to explore the drivers of variation in the water-use efficiency of wood production (W_w).

3.1 Site descriptions

The data set includes:

- *E. globulus* and *Pinus radiata* sites from the Green Triangle (Benyon et al 2006).
- *E. nitens* and *E. delegatensis* at Esperance in Tasmania (Honeysett et al 1992).
- Irrigated and rainfed *E. globulus* and *E. nitens* at a low rainfall site approximately 30 km east of Hobart, Tasmania (Honeysett et al. 1996).
- A series of four *E. globulus* plantations covering a rainfall gradient across south Western Australia (Hingston and Galbraith 1998; Hingston et al 1998).
- Data from five fully replicated *E. globulus* silvicultural experiments in south Western Australia (White – unpublished data). At each site there is an N by thinning experiment and N-rate trial at 1200 stems per hectare.

The results from our Western Australian silvicultural experiments are as yet unpublished. To allow the results to be included as part of this larger data the following is a brief description of the sites, experiments and measurements. All three sites had a sandy A-horizon, and showed evidence of laterite in the top 2 m of soil with clay sub soils (Figure 1). The sites were selected to cover a range of climate wetness (Table 2). At all sites trees were planted at a nominal spacing of 4 m between and 2 m within rows.

Figure 1. Partially exposed soil profile at Wellstead showing shallow gravely sand and laterite over a clay subsoil.

Table 2. Details of all core and satellite sites including tree farm names, locality, year of planting, year of treatment and key site characteristics including rainfall (P), climate wetness index or ratio of rainfall to potential evaporation (CWI) and the maximum capacity of the soil to store water (W_{max}).

Locality (abbreviation)	Year Planted	Year planted and (treated)	Annual Rainfall (mm)	*CWI*	W_{max} (mm)
Scott River	1996	1998	1100	0.88	~800
Wellstead	1996	1998	616	0.47	~1800
Boyup Brook	1996	1998	620	0.41	~700
Perup	1997	1999	750	0.51	>800
Narrikup	1997	1999	720	0.54	>800

Two experiments, a nitrogen-rate and nitrogen by stand density trial, were established at each site. The nitrogen by stand density trial included three stand densities (nominally 300, 600 and 1200 stems ha^{-1}) and two rates of nitrogen application (0 and 250 kg ha^{-1} yr^{-1}) in a factorial design giving six plots per replicate at the core sites and four plots per replicate at Narrikup and Perup where the 600 stem ha^{-1} treatment was not included. In the N-rate trial nitrogen was applied at four rates (0, 45, 125, 250 kg ha^{-1} yr^{-1}) to the maximum stand density plots at all sites and at Scott River and Wellstead, an additional 400 kg ha^{-1} yr^{-1} treatment was included. Each plot was 40 m x 40 m or 10 rows x ca. 20 trees (8 rows x 20 trees at Rathcaven) with an internal measurement plot of 20 x 20 m.

Application of fertiliser. Nitrogen was applied at 0, 45, 125, 250 and 400 kg N per hectare per year. The nitrogen was applied as urea in split applications; half of the annual rate was applied in early spring (September-October) and the other in autumn (April-May). The 0N and 250N treatments are subsequently referred to, respectively, as low and high nitrogen.

Thinning. In spring of 1998 plots designated as low (300 stems ha^{-1}) and medium (600 stems ha^{-1}) densities were thinned. All felled trees were removed from the trials to prevent preferential immobilization of nitrogen in the thinned plots.

Table 3 is a list and brief description of all sites including the WA silvicultural experiments.

3.2 Approaches used to estimate plantation Evapotranspiration

There are two plot-scale experimental approaches for estimating evapotranspiration.

1. Measure evaporation from the soil surface (E_s), rainfall interception by the canopy (I) and tree transpiration (E) and calculate evapotranspiration (E_t) using equation 4.

$$E_t = E + E_s + I \qquad (4)$$

2. Measure the change in soil water content (ΔM) and rainfall (P) and calculate evapotranspiration using equation 5

$$E_t = \Delta M + P \qquad (5)$$

Table 3. Details for study sites including region, species, rainfall (during period of measurement) and potential evaporation, other treatment details

Region	Reference / Site names	Species	Rainfall (mm)	Potential Evap (mm)	Treatments	Ages at which W_w estimates
Green Triangle	Benyon et al. 2006 – Sites 1-5, 6	*E. globulus*	545 – 732	970 – 1250	Groundwater depth < 6m	4 to 10, age range varies amongst sites
Green Triangle	Benyon et al. 2006 – sites 6, 8 and 9	*E. globulus*	489 - 701		Groundwater depth > 10m	4 to 7
Green Triangle	Benyon et al. 2006 – sites 10 and 12	*P. radiata*	362 – 650	960 – 1340	Groundwater depth < 6m	4 to 7, 27 to 31
Green Triangle	Benyon et al 2006 – sites 11, 13 and 14	*P. radiata*	667 - 747	970 – 1230	Groundwater depth > 10 m	4 to 9 or 14 to 18
Southern Tasmania	Honeysett et al. 1996, Lewisham	*E. globulus* and *E. nitens*	441 - 497	1270 – 1517	Irrigated and rainfed	3 to 5
Southern Tasmania	Honeysett et al. 1992, Esperance	*E. nitens* and *E. delegatensis*	??	??	Species	3 to 4
South West WA	Hingston and Galbraith 1998 – Mumbalup, Manjimup, Darkan and Northcliffe	*E. globulus*	Rainfall range: Northcliffe (~1100) to Darkan (~550)		Climate gradient	4 to 10 (varies between sites
South West WA	Unpublished – Scott River	*E. globulus*	714 - 980	1109 – 1240	Thinning and Nitrogen addition	4 to 10
South West WA	Unpublished - Wellstead	*E. globulus*	370 - 669	1116 – 1244	Thinning and Nitrogen addition	4 to 10
South West WA	Unpublished – Boyup Brook	*E. globulus*	317 - 572	1188 – 1383	Thinning and Nitrogen addition	4 to 10
South West WA	Unpublished – Narrikup	*E. globulus*	945 - 1067	965 – 1162	Thinning and Nitrogen addition	4 to 7

South West WA	Unpublished – Perup	*E. globulus*	492 -866	1132 – 1256	Thinning and Nitrogen addition	4 to 7

3.3 Observed variation in the water-use efficiency of wood production

3.3.1 Overall patterns

When data for most sites, treatments and measurement years were aggregated there was a weak positive correlation between current annual increment (CAI) and annual evapotranspiration[1] (Figure 2). The current annual water-use efficiency of wood production W_w varied from less than 0.5 to 8.3 m^3 ML^{-1}, but except for plots with access to groundwater and one plot at Scott River with very shallow soil, W_w was between 1 and 5 m^3 ML^{-1}.

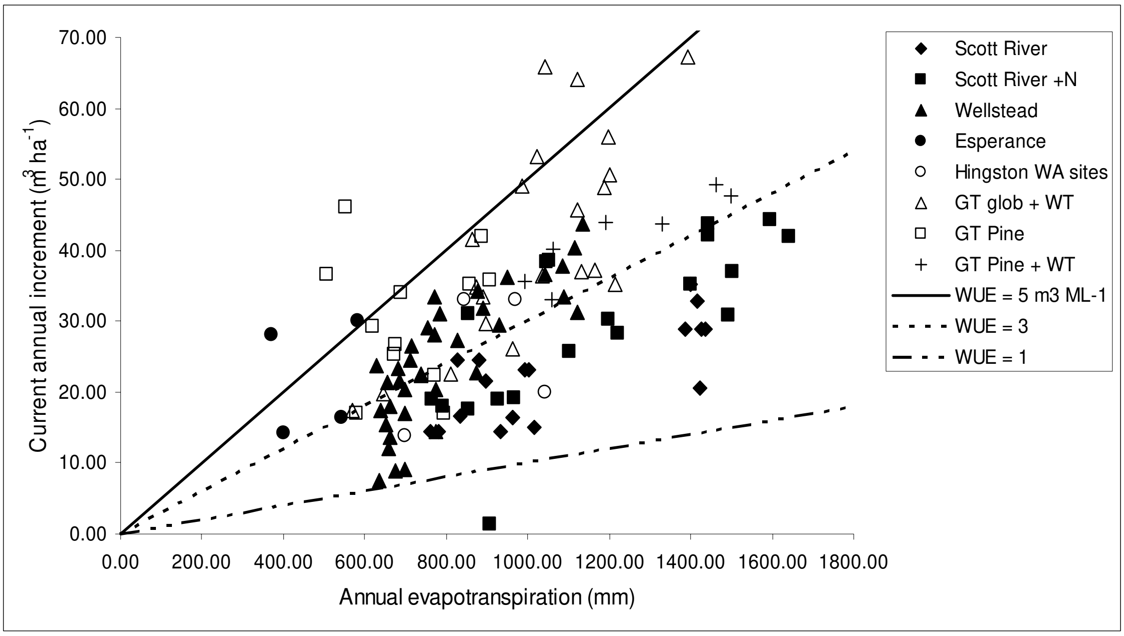

Figure 2. Current annual increment as a function of annual evapotranspiration for a range of species, regions, stand ages, thinning and fertiliser treatments including Scott River (with and without N – all stocking densities included), Wellstead (only high N treatment shown – all stocking densities included), Esperance (both species included), Hingston and Galbraith's (1998) WA sites and *E. globulus* and *Pinus radiata* in the Green Triangle. The lines show the trajectory of the relationship between *CAI* and E_t for *W*w of 1 (broken), 3 (dashed) and 5 (solid) m^3 ML^{-1}

The observed range of variation suggests scope for gains in W_w through improved plantation management. At rain-fed sites (no groundwater or irrigation) W_w peaked at around canopy closure and then decline with increasing stand age. A wide range of stand ages are represented in this dataset and the period of measurement does not always overlap (Table 3) making it difficult to reliably compare sites. Figure 3 shows W_w for the fifth year of growth for sites and groups of sites where measurements were made at this age. Observations that warrant closer investigation include:

- At Scott River W_w increased more than two fold in response to application of nitrogen. A smaller, but still significant, increase in W_w was observed in response to nitrogen at Boyup Brook.
- In the thinning trials at Scott River and Wellstead there was a consistent but non-significant trend towards greater W_w with increased stocking density.

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[1] Evapotranspiration is given both in mm rainfall equivalent and ML. Note that one ML ha^{-1} equates to 100 mm.

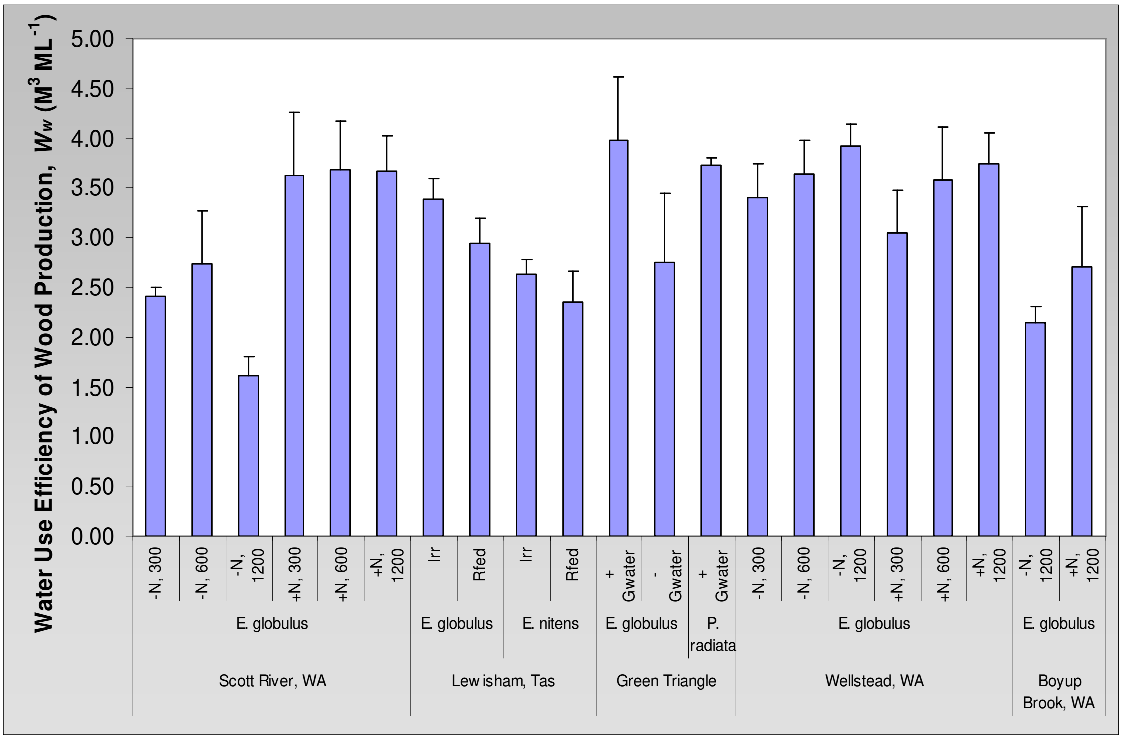

Figure 3. Water-use efficiency of wood production (W_w) during the fifth growth year for a range of sites, species and treatments (including high (+N) and Low (-N) nitrogen, stocking density of 300, 600 and 1200 stems per hectare and irrigation.

- At Lewisham *E. globulus* was more water-use efficient than *E. nitens* under both irrigated and rainfed conditions and there was a significant positive effect of irrigation on W_w.
- Consistent with the observed effect of irrigation at Lewisham, access to shallow groundwater increased W_w for both *E. globulus* and *P.radiata* in the Green Triangle.

3.3.2. Effect of Nitrogen on Water-use Efficiency of Wood Production at Scott River and Boyup Brook.

At Scott River the native Jarrah-Marri forest was cleared less than three years before planting and the surface soil had a high C to N ratio (28). At this site we observed a more than two fold growth response to nitrogen and 125 kg N ha^{-1} was the optimum annual rate of application.

From age 2 to 4 years application of nitrogen significantly increased the water-use efficiency of wood production at Scott River (high rainfall) and Boyup Brook (low rainfall). At Scott River the high nitrogen treatments were more than 100% more water-use efficient than the low nitrogen plots and this effect was independent of thinning intensity (Figure 4 and 5). There are two probable mechanisms for the observed increase in W_w.

Mechanism 1. Increased carboxylation efficiency (based on Ingrid Krockenberger's unpublished data)

At Scott River application of nitrogen initially increased foliar nitrogen concentration expressed on a mass and area basis. This effect was transient and was followed by an increase in specific leaf area so that ultimately nitrogen concentration on an area basis was unaffected by application of nitrogen. Nonetheless both the CO_2- saturated rates of photosynthesis and carboxylation efficiency were elevated for at least two years after the first application of nitrogen. The gas exchange data was equivocal but there was some evidence of increased water-use efficiency at the leaf scale in the high nitrogen treatment (Krockenberger – unpublished data).

Mechanism 2. Increased leaf area and spring water-use
At Scott River, application of nitrogen rapidly increased the leaf area index (LAI) at all stocking densities. After six months LAI was significantly greater in the high nitrogen compared to the low nitrogen treatments. Application of nitrogen also significantly increased LAI at Boyup Brook but not at any of the other sites. The magnitude of this effect peaked at age 5 years but persisted throughout the rotation (Figure 6).

The observed increase in LAI was associated with a growth response of similar magnitude. Evapotranspiration also increased but this increase was concentrated early in the growing season. For example in 2000-2001, the fifth year of growth, the high nitrogen treatment used about 135 mm more water than the low nitrogen treatment and nearly all of this additional water was used between mid October and mid December (Figure 7a) when air saturation deficit was moderate compared to later in the season (January, February or March).

This observation is consistent with the experience in cereal crops for which Turner (2001) and others observed that early season water-use increased both water-use efficiency and yield. This is because air saturation is a major determinant of water-use efficiency at both the leaf and stand scale (equation 1). Any strategy that reduces the average air saturation deficit during periods of water use will markedly increase water-use efficiency. Thus optimising nutrition to maximise early season LAI will maximize the water-use efficiency of wood production and yield of plantations, particularly in the Mediterranean type environments that dominate the southern Australian Plantation estate.

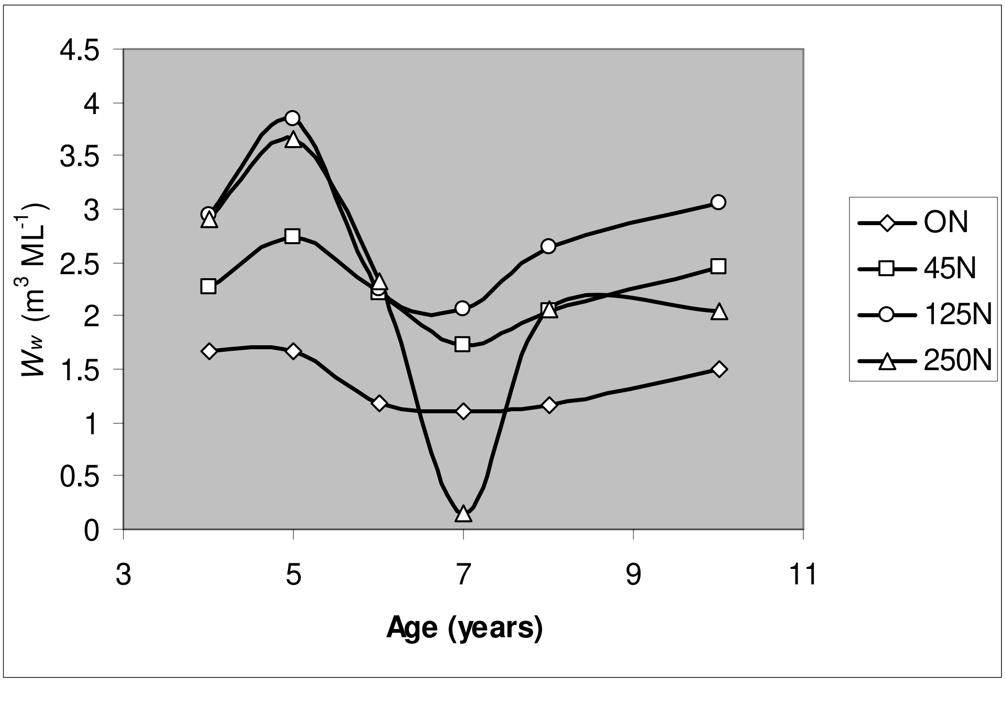

Figure 4. Water-use efficiency of wood production (W_w) at Scott River as a function of stand age for high stocking density stand at four annual rates of nitrogen application (0, 45, 125 and 250 kg ha^{-1}).

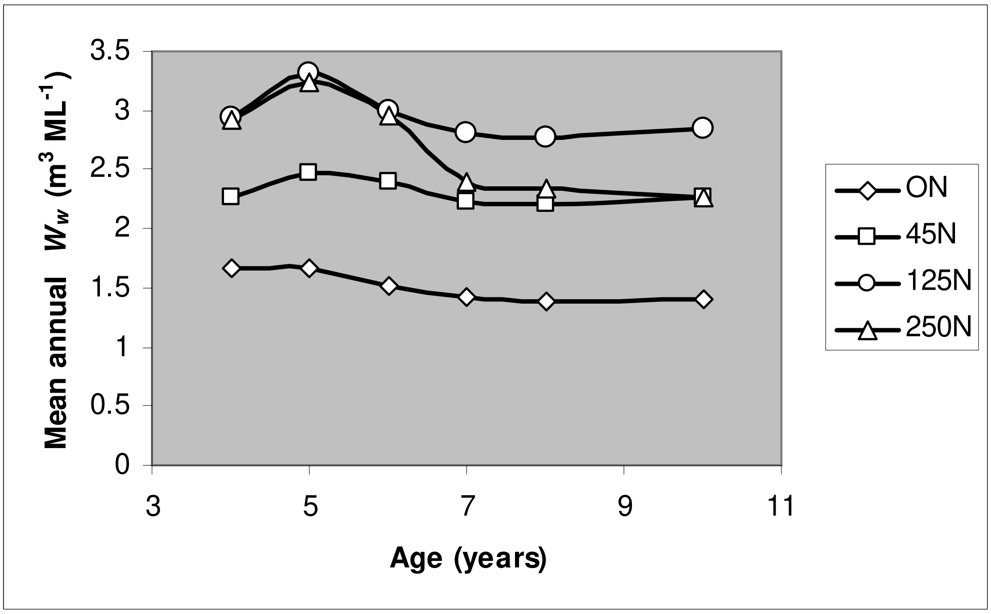

Figure 5. Mean annual water-use efficiency of wood production (W_w, analogous to mean annual increment) at Scott River as a function of stand age for a high stocking density plots at four annual rates of nitrogen application (0, 45, 125 and 250 kg ha^{-1}).

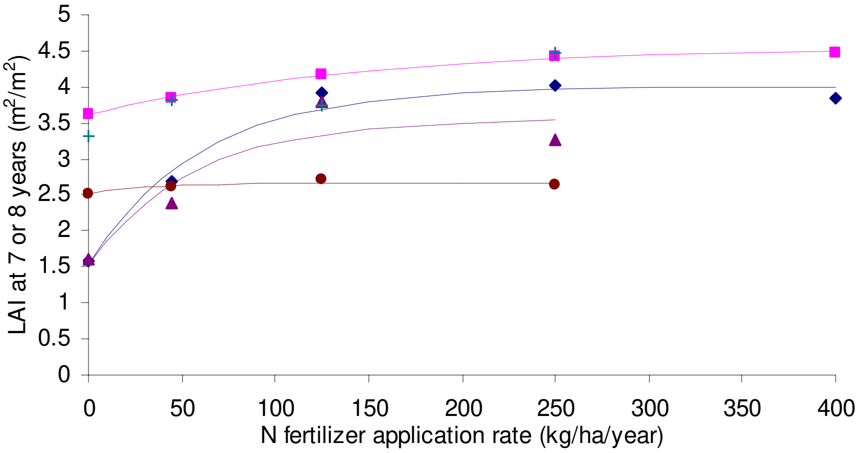

Figure 6. Leaf area index as a function of the annual rate of N application for four of the WA drought risk sites. Note that application of nitrogen significantly increased LAI at Scott River (Avery tree farm, Blue) and Boyup Brook (Loton tree farm, Brown) but not at the other sites.

By maximising early season leaf area index and water use it is possible to increase the water-use efficiency of wood production, and therefore yield, in water limited environments. However, this strategy will also increase the risk of drought deaths in low rainfall areas, on shallow soils or in extremely dry years on wetter sites. At Scott River, by age 5 the high nitrogen treatments had dried the soil profile to a depth of 8 m and this deficit was only partially recharged each winter. The soil water deficit under the less efficient low nitrogen treatment was less than half that developed under the high nitrogen treatment and completely the soil refilled completely each winter. In the 7th year (2002-2003) some trees (about 25%) died in the high nitrogen treatment. This is illustrated in Figure 7 which shows the relationship between current annual increment and the minimum predawn leaf water potential (maximum water stress) observed during that season. The low current annual increment of the high nitrogen, high stocking density treatment was the result of drought deaths in two plots. This relationship between growth and cumulative water stress was also noted by (Myers 1988) and shows that maximum yield will be achieved by early season depletion of the soil water store but that this must be weighed against the potential for drought deaths.

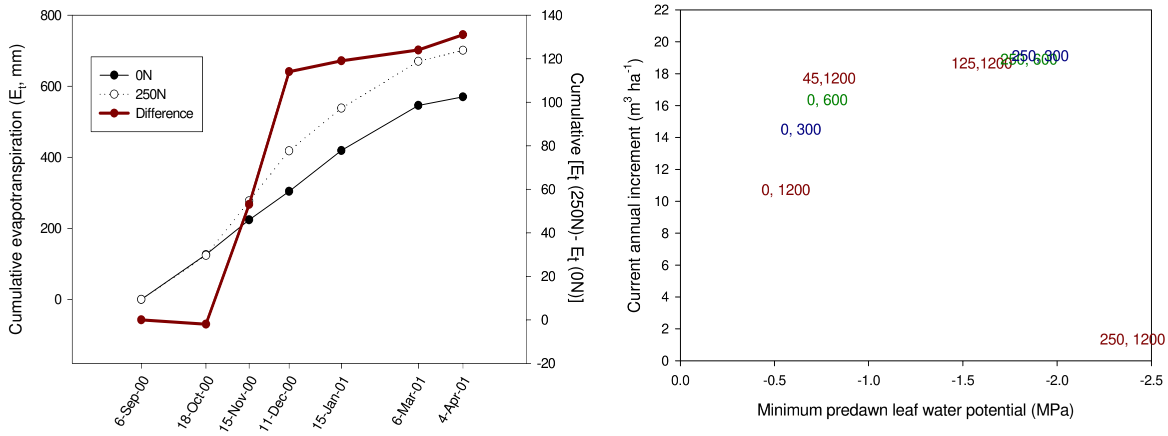

Figure 7. a) Cumulative evapotranspiration during the 2000 to 2001 growing season for the high and low nitrogen treatments (the heavy line is the cumulative difference in water use between the treatments). b) Current Annual Increment in relation to minimum predawn water potential. Data labels are (annual rate of N application, stocking density).

3.3.3 Water-use efficiency of wood production under limiting and non-limiting water supply

Results from an irrigation experiment in Tasmania and from sites with and without groundwater in the Green Triangle indicate that under non-limiting water supply, plantations not only grow faster but convert water to wood with greater efficiency. In an irrigation experiment at a low rainfall site in Tasmania (Lewisham) (W_w) was greater for *E. globulus* than *E. nitens* and for irrigated than rain-fed trees (Figure 8). At the same site White et al. (1999) showed that during water stress the average stomatal conductance of *E. nitens* was lower than for *E. globulus* and that in the rainfed treatment both species suffered growth limiting water stress between November and May (White et al. 1996). These patterns of water stress and stomatal response confirmed that average leaf-scale water-use efficiency was greatest for rainfed *E. nitens* and lowest for irrigated *E. globulus*. The observed ranking for water-use efficiency of wood production indicated a negative correlation between leaf and stand scale water-use efficiency.

For both *Pinus* radiata and *E. globulus* in the Green Triangle average water-use efficiency of wood production (W_w) was greater at sites with shallow groundwater than for sites with deep or inaccessible groundwater but the differences were not huge and there was significant overlap in the range of W_w for sites with and without groundwater.

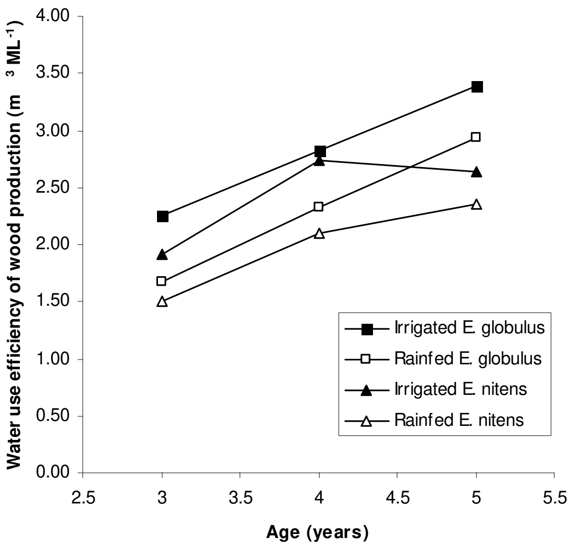

Figure 8. Water-use efficiency of wood production (W_w) for irrigated and rainfed *E. globulus* and *E. nitens*

Mechanisms for greater water-use efficiency of wood production when water is non-limiting might include reduced soil evaporation, higher absolute rates of carbon assimilation and greater allocation to stem wood.

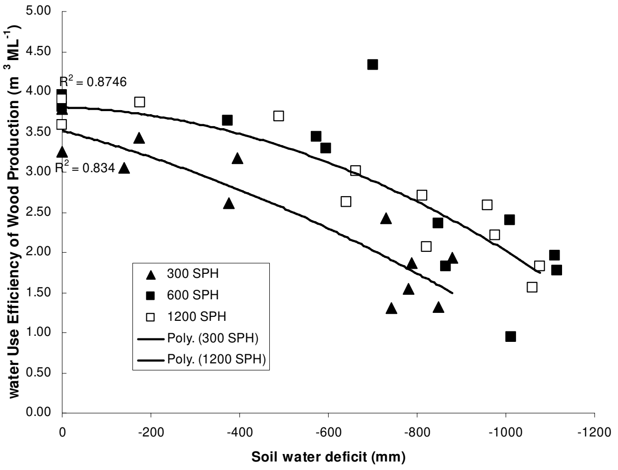

Figure 9. Water-use efficiency of wood production as a function of soil water deficit for three stocking densities at Wellstead

3.3.4 Variation in water-use efficiency of wood production with stocking density and the effect of stand age

Under water-limited conditions W_w tended to decline with stand age. When rainfall exceeds potential evaporation, well-managed plantations progressively dry out soil profiles. The thinning by nitrogen experiment at Wellstead was established in a 580 mm rainfall zone and on a very deep (>18 m) soil and provided an ideal opportunity to test the hypothesis that decline in W_w with stand age was due to a resource (probably water) limitation that was correlated with stand age.

W_w declined with increasing soil water deficit and the rate of decline increased with soil water deficit. More than 80% of the variation in W_w at Wellstead could be explained by a non linear (second order polynomial) relationship with soil water deficit (Figure 9). Moreover, the rate of decline was greater for the 300 stem per hectare plots than for either the 600 or 1200 stem per hectare plots (Figure 9). Closer examination of the comparative seasonal pattern of water use early (small soil water deficit) and late (large soil water deficit) in the rotation provided an insight into the mechanism of W_w decline (Figure 10). The crop factor is the ratio of actual evapotranspiration to potential evaporation (from a free water surface) and integrates changes in leaf area index and stomatal responses to environment. For a given leaf area index a high crop factor indicates that stomata are open while a rapid reduction in crop factor shows that stomata have closed. For both years the crop factor was approximately one during July and August but much lower during spring and summer when soil water deficit increased later in the rotation (Figure 10). Again the rate of water-use during spring was an important determinant of annual W_w.

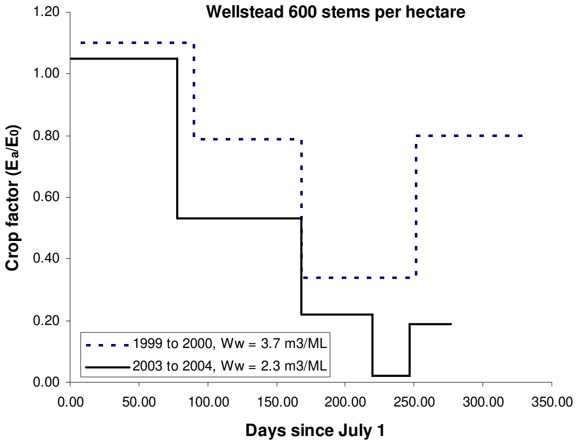

Figure 10. The crop factor (ratio of observed evapotranspiration to potential evaporation) for the 600 stem per hectare, high nitrogen treatment at Wellstead – one year early (dotted line) and a second late in the rotation (solid line).

3.1. Management options for managing the trade-off between water-use efficient wood production and drought risk in water-limited environments?

The water-use efficiency of wood production (W_w) varied from 1 to 5 m^3 ML^{-1} for *E. globulus*, *E. nitens* and *P. radiata* plantations in SE South Australia (Green Triangle), southern Tasmania and SW Western Australia. There was no clear relationship between W_w and rainfall, potential evaporation or the climate wetness index.

For sites where detailed physiological data was also available (Lewisham, the WA drought risk sites) instantaneous leaf-scale water-use efficiency was negatively correlated with the water-use efficiency of wood production expressed in m^3 ML^{-1}.

For plantations in Mediterranean environments characterised by winter dominant rainfall and summer drought, any plantation management that increases leaf area index will increase water use during the early part of the growing season and thereby maximise W_w and plantation growth.

Using nutrition and spacing to trade-off W_w and drought risk
In low rainfall environments, on shallow soils or even in unusually dry years at wetter sites, maximising leaf area to improve W_w and yield, may expose the plantation to potentially lethal water stress. Our research suggests that there is no yield penalty for reducing stocking density to as low as 600 stems per hectare but that the risk of drought death is substantially reduced.

Thus for rain fed plantations in southern Australia the risk of drought should be managed by varying stocking density. For a given stocking density, W_w should be maximised by ensuring that nutrient supply is non-limiting.

Irrigation and groundwater
Establishing plantations where trees can access shallow, fresh groundwater may increase W_w. Similarly in water limited environments irrigated plantations will produce wood with greater water-use efficiency than rain fed plantations.

4. Observations and next steps

Based on a review of the literature and meta-analysis of stand scale data the following general observations seem to apply in Mediterranean environments:

- Genetic improvement based on leaf-scale responses or their expression in the carbon isotope composition of plant tissue is unlikely to lead to improved water-use efficiency of wood production.
- Responses to soil and atmospheric deficit that increase leaf-scale water-use efficiency of carbon assimilation can often make the stand-scale conversion of water to wood less efficient.
- The water-use efficiency of wood production varied from 1 to more than 5 m^3 ML^{-1}.
- In Mediterranean-type environments, where there is sufficient soil stored water, any strategy that maximizes leaf area index will maximize the water-use efficiency of wood production.

The final output from this project will be a Decision Support System for quantifying the water-use efficiency of a range of silvicultural options. We will now test and if necessary modify CABALA to predict water-use efficiency from leaf- to stand-scale and then run scenarios and quantify the effect of plantation management options on the water-use efficiency of plantations in a changing climate.

4. Managing the inherent trade-off between water use efficient wood production and the risk of drought death in Mediterranean type environments

Measurements of the stand the scale water use efficiency of wood production in Eucalyptus plantations show that intensively managed, fast growing plantations are water use efficient but there is an inherent trade-off between production, water use efficiency of wood production and the risk of drought death in Mediterranean type environments with winter dominant rainfall and summer drought.

The crop factor (*k*), a ratio of actual water use (*E*) to potential, provides a means for comparing the relation of *E* to soil water content for different plant communities. When *k* is related to the relative soil water store in the rooting zone, there are two phases to the resultant relationship. The first phase, at high values of relative soil water is a plateau where *k* is unrelated to the level of the water store. In the second phase, which starts below a threshold relative soil water store, *k* declines in a linear fashion as the water store in the root zone is depleted (Figure 1). These relationships define the well-watered upper bound to water use, the (threshold) soil water content at which plants exert stomatal control over transpiration, and the rate of decline in water use as the soil dries (Figure 11).

As annual rainfall increases from environments supporting mallee to those supporting *E. globulus* plantations, the value of *k* that defines the plateau increases and the relative soil water store at the threshold decreases. These changes are also associated with an increase in leaf area index. (Specht 1972) observed that for a range of native forests in southern Australia, leaf area index increased as a linear function of available water. This observation underpins the view that in order to survive, trees must maintain a rate of water use that is in equilibrium with long-term rainfall (Eagleson 1982; Hatton et al. 1998). Higher leaf areas and growth are possible where the trees may access water sources other than current rainfall. However, these will only be maintained where the supply of additional water can be also be maintained.

The high plateau values of *k* for major plantation species reflect high values of optimum leaf area and maximum stomatal conductance. These traits confer high rates of growth under well-watered conditions but also increase the risk of death during drought. This trade-off may be managed by optimizing nutrition and reducing the risk of drought deaths by varying stocking density. For individual trees this increases the value of W_{max} and reduces risk without compromising stand scale volume growth.

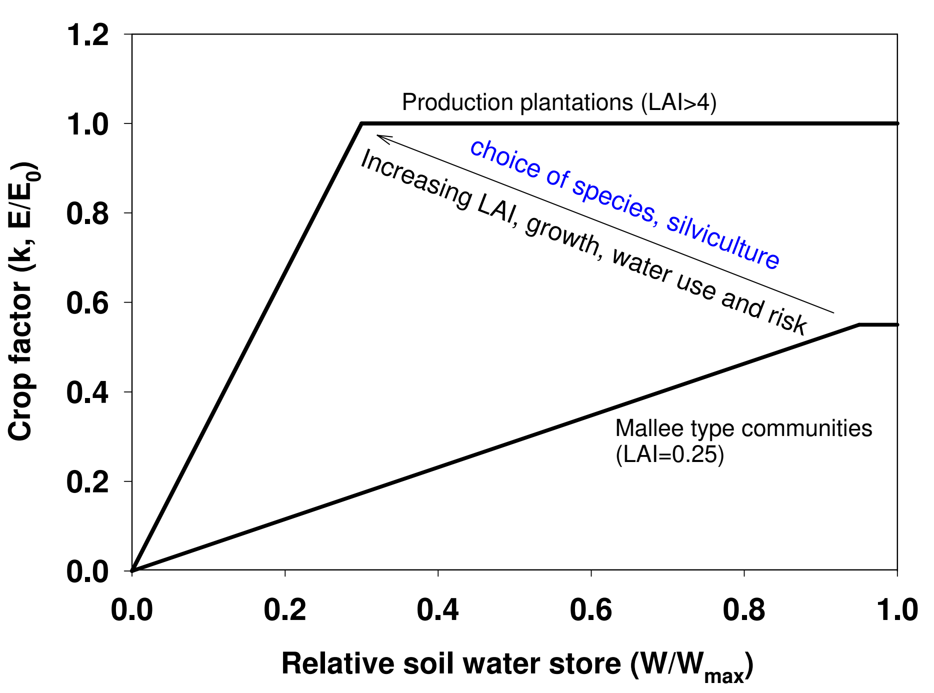

Figure 11. Crop factor (k) as a function of relative soil water store for a fast growing plantation and a more conservative ecosystem. More intensive plantation management will increase growth, W_w and drought risk.

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