IAWA Journal, Vol. 16 (3), 1995: 269–276

RELATIONSHIPS BETWEEN WATER AVAILABILITY AND SELECTED VESSEL CHARACTERISTICS IN EUCALYPTUS GRANDIS AND TWO HYBRIDS

by

Ed C. February[1], W.D. Stock[2], W.J. Bond[2] & D.J. Le Roux[2]

SUMMARY

The primary objective of this study was to determine the relationships between water availability, plant growth and selected vessel characteristics for *Eucalyptus grandis* and two hybrids, so as to ascertain whether these xylem characteristics predict water use efficiency. Cuttings of *Eucalyptus grandis, E. grandis* × *camaldulensis* and *E. grandis* × *nitens* were planted in 220 litre drums from which rainfall was excluded. One half of the individuals received a low watering treatment; one half received a higher watering treatment. Soil moisture depletion through root uptake was monitored weekly and the removed water replaced to maintain 60 and 80 litres in the pots of the low and high watering treatments respectively. Mean values for tangential vessel diameter, vessel frequency and vessel element length were compared for the two treatments. In *E. grandis* and the hybrid *E. grandis* × *camaldulensis* vessel diameter ($P < 0.01$ & $P < 0.05$ respectively) and vessel element length ($P < 0.05$ for both) increased from the dry to the wet treatment as water uptake through transpiration increased. There is no significant correlation between available water and vessel frequency. For *E. grandis* × *nitens,* on the other hand, only vessel frequency was significantly ($P < 0.01$) correlated with water uptake. In all three species / hybrids water availability also had a significant influence on stem diameter ($P < 0.0001$) and transverse sectional stem area ($P < 0.0001$) which increased with increased water consumption. These results suggest that *E. grandis* × *nitens* may be more water use efficient than *E. grandis*, which is commonly grown for timber and thus could potentially be used as a replacement species that is more water conservative in this water limited region.

Key words: *Eucalyptus grandis*, *Eucalyptus* hybrids, vessel diameter, vessel frequency, water use efficiency.

---

1) South African Museum, P.O. Box 61, Cape Town, 8000, South Africa.

2) Department of Botany, University of Cape Town, Private Bag, Rondebosch, 7700, South Africa.

INTRODUCTION

Eucalyptus species, predominantly the Australian *Eucalyptus grandis* Hill ex Maiden, have been planted extensively in South Africa since the beginning of this century. The fast growth of eucalypts and the increased demand for wood and wood products in South Africa has meant a steady increase in the extent of these plantations despite the fact that eucalypts consume large quantities of water (Henrici 1946; Bosch & Von Gadow 1990). Planting these trees in water catchment areas decreases water runoff to a wide area, thus reducing the agricultural viability in these areas. Selecting trees that use water more efficiently than currently exploited species / hybrids, without compromising production, is one possible solution to the problem of maintaining the viability of large agricultural districts in South Africa where rainfall is marginal (Henrici 1946). Improvement of plant water use efficiency (WUE) is not only needed to increase water runoff, but is also necessary for plant survival under water limiting conditions. This was evident during the 1991/1992 drought in which the forest industry in South Africa experienced heavy losses. Such losses have raised concern for improving silvicultural practices by selecting water use efficient species that would not only survive but continue to be productive under restricted water conditions (Olbricht et al. 1993). This study addresses the problem of what techniques are appropriate for breeders to use as selection tools by examining the possibilities for using ecoclimatically significant wood variables in selecting for productive *Eucalyptus* species with lower water demands.

With the introduction of a genetic improvement programme in 1983, many other species and clones besides *E. grandis* have been planted in provenance trails aimed at improving growth rate, stem form and wood quality (Stanger 1991). As a result of these trails two hybrids, *E. grandis* × *camaldulensis* and *E. grandis* × *nitens*, now are being used in commercial forestry although not yet to the same extent as *E. grandis*. The potential importance of these three eucalypts to commercial forestry in South Africa was the major criterion in selection for this study on the relationships between vessel characteristics and water use efficiency.

Wilkes (1988) suggested that wood property variations in eucalypts do not correlate reliably with changes in environment (e.g., rainfall, altitude, soil type). Much of the research on which Wilkes (1988) based this hypothesis was directed toward the pulp and lumber industry. Thus, most research has focused on fibre dimensions and wood density (e.g., Villiers 1968; Taylor 1973; Bamber 1985; Tischler & Heth 1985), both of which show relatively weak ecological trends (Baas 1986). For many genera and species, diameter and vessel element length decrease while vessel frequency increases with decreasing water availability (Carlquist 1975; Baas & Schweingruber 1987; Van der Walt et al. 1988; Zhang et al. 1988; Wilkins & Papassotiriou 1989; February 1993). In the present study we examine the relationship of xylem vessel diameter, vessel frequency and vessel element length with water consumption in *Eucalyptus grandis* and two hybrids.

We also investigate the association between these vessel characteristics and the integrated measure of production per water used (water use efficiency) because it is apparent that plant adaptation to water deficits is a highly coordinated whole-plant process that maintains the structural and functional integrity of the symplastic and apoplastic water transport system (Kolb & Davis 1994). Several physiological traits such as differences in leaf water potential, leaf diffusion resistance, rooting patterns and stomatal frequency have been shown to be associated with increased drought tolerance and water use efficiency (Blum 1974; Burton et al. 1977). Increases in water use efficiency (WUE) may, however, not always be associated with drought tolerance since drought adaptive traits may enable a plant to withstand water shortages but with low biomass accumulation (Hunt 1962; Barnes 1983). Therefore, the drought adaptive traits evident in quantitative wood anatomy may not correspond with WUE.

The objectives of this study are twofold: 1) to determine the relationship between vessel element size, vessel frequency and water uptake in *Eucalyptus grandis* and the two hybrids, *E. grandis* × *camaldulensis* and *E. grandis* × *nitens*; and 2) to establish whether these relationships correlate with water use efficiency. The main purpose is to identify drought tolerant and productive *Eucalyptus* species that will ensure forest production in low rainfall areas. Until recently WUE has not been considered as important in tree breeding in South Africa. In this respect, this study represents the first attempt to ascertain the WUE of eucalypts for possible early selection of suitable hybrids for planting in existing and marginal plantation areas.

MATERIALS AND METHODS

On 21 March 1991, ten-week-old cuttings of *E. grandis* and the hybrids *E. grandis* × *camaldulensis* and *E. grandis* × *nitens*, were planted at 15 cm below soil surface in 220 litre drums. 3 : 2 : 1 NPK fertiliser (100 g) and 2 litres of water were added to each drum at the time of planting. Rainfall was excluded from the drums by fitting specially adapted plastic sheets that only allowed for the protrusion of the plant stem and leaf canopy. The drums were sunk in the soil, in the field at the D. R. de Wet Forestry Research Centre (25° 3' 10" S, 30° 53' 30" E), with only the top 60 cm protruding to simulate, as closely as possible, actual growing conditions and to facilitate water application and measurement. Half of the individuals were subjected to a low watering treatment and the remainder to a relatively high watering treatment where soil moisture in the drums was maintained at 60 and 80 litres respectively on a weekly basis. Soil moisture depletion through root uptake was measured each week with a neutron probe (Troxler Depth Moisture Gauge, model 3300, Troxler Laboratories, North Carolina, USA) and the required amount of water added to maintain the specific watering treatment. For the purpose of using neutron probe count ratios as a measure of soil moisture in the drums, count ratios were calibrated against soil moisture content within the drums according to the methods of Greacen (1981). The amount of water consumed per plant was calculated over the 16 month growth period between planting date (March 1991) and harvest date (July 1992).

The stems were cut off at ground level and oven dried for biomass (80°C for 48 hrs). Roots were harvested by removing the pot contents (by hand) and passing them through a sieve of 10 mm mesh size to separate roots from soil, roots were then oven dried. WUE_{sl} (Water use efficiency, season length, g/l) was calculated as the whole plant dry mass in grams divided by the amount of water used by the plant over the 16 month growth period.

Within a tree, vessel diameters tend to be greater in roots than in stems, and greater in the stem than in the branches. Vessel diameter usually increases from pith to bark (Zimmermann 1978, 1983). To control for this variation, only the main stem wood between ± 50 mm and ± 110 mm above the soil was analysed. This region was roughly one twentieth of the distance from root to crown (Table 1). Measures of xylem vessel size and frequency were always taken 1–2 mm in towards the pith from the cambium. Stem diameters, excluding the bark, were measured at the widest point using dial callipers.

In the laboratory, a 2 cm thick disc was cut from the end of each piece of wood and then split into rectangular sections about 5–8 mm wide, incorporating both the pith and the cambium. These pieces of wood were softened by boiling, before being cut in transverse section (20 μm thick) using a Reichert Jung base sledge microtome. The thin sections were stained over two days in a mixture of alcohol, glycerol and saffranin red. They were then mounted in Kaisers gelatine – glycerine on glass microscope slides. Macerations were prepared using Franklin's method (warm hydrogen peroxide and glacial acetic acid) before being stained and mounted on glass microscope slides. All measures were in accordance with the procedure recommended by the International Association of Wood Anatomists (IAWA Committee 1989). Measurements of vessel elements were made directly from the slide using a Leitz Laborlux K incident light microscope at a magnification of ×40 and the image analysing programme FIPS from the CSIR Pretoria. One transverse section and one maceration per stem was prepared for analysis. Vessel frequencies are the means of five areas per transverse section and were determined by the image analysis programme. Vessel element lengths were measured using macerations and included the tails. Tangential vessel diameters were measured at the widest part of the vessel lumen as viewed in cross section, and did not include the cell wall. Average values for diameters and lengths are based on 30 individual vessel elements. The FIPS programme was also used to measure and calculate transverse sectional area of the stem.

RESULTS

In all three taxa water availability had a significant effect on mean total water consumed ($P < 0.0001$) which in turn had a significant influence on stem diameter ($P < 0.0001$) and transverse sectional stem area ($P < 0.0001$; Table 1). Anatomical responses to water treatment differed between taxa, with vessel diameter and vessel element length in *Eucalyptus grandis* and *E. grandis* × *camaldulensis* being positively correlated with increases in water used (Table 1). However, neither *E. grandis* nor *E. grandis* × *camaldulensis* showed significant correlations between water treatment and vessel frequency. In *E. grandis* × *nitens* only vessel frequency responded to water treatment ($P < 0.01$; Table 1).

Table 1. The differences between plant growth and xylem anatomy of *Eucalyptus grandis*, *E. grandis* × *camaldulensis* and *E. grandis* × *nitens* after cultivation under different watering treatments. Values are means for the number of plants indicated. NS denotes no significant difference between means and *, **, ***, **** indicate significant difference between means at $P < 0.05$, 0.01, 0.001 and 0.0001, respectively.

Variable	Watering treatment				
	dry	std dev	wet	std dev	t-test
grandis					
No of plants	11		14		
Plant mass (g)	1107	233	2055	415	****
Stem diameter (mm)	21	1	26	2	****
Stem area (cm^2)	3.4	0.35	5.3	0.72	****
Vessel diameter (μm)	99	8	115	11	**
Vessel frequency (mm^2)	12	2.5	10	2	NS
Vessel element length (μm)	696	53	743	55	*
Water uptake (l)	349	75	723	130	****
WUE_{sl} (g/l)	3.20	0.33	2.86	0.33	*
Height (m)	1.72	0.10	2.08	0.21	****
grandis × camaldulensis					
No of plants	5		5		
Plant mass (g)	1267	101	2072	353	**
Stem diameter (mm)	22	.6	27	1	****
Stem area (cm^2)	3.5	0.1	5.7	0.5	****
Vessel diameter (μm)	104	8	120	6	*
Vessel frequency (mm^2)	6.9	.7	8.2	1.9	NS
Vessel element length (μm)	625	34	691	36	*
Water uptake (l)	397	47	740	61	****
WUE_{sl} (g/l)	3.21	0.23	2.78	0.27	*
Height (m)	2.14	0.07	2.62	0.18	***
grandis × nitens					
No of plants	8		9		
Plant mass (g)	944	203	1900	267	****
Stem diameter (mm)	19	2	27	3	****
Stem area (cm^2)	2.9	0.6	5.5	1	****
Vessel diameter (μm)	107	15	116	11	NS
Vessel frequency (mm^2)	8.4	1.2	6.7	0.5	**
Vessel element length (μm)	608	39	618	54	NS
Water uptake (l)	252	41	631	113	****
WUE_{sl} (g/l)	3.74	0.38	3.08	0.56	*
Height (m)	1.75	0.18	2.19	0.13	****

There was no significant difference in WUE_{sl} between the three eucalypts in the wet treatment (t-tests). In the dry treatment, however, *E. grandis* ($P < 0.01$) and *E. grandis* × *camaldulensis* ($P < 0.05$) have significantly lower WUE_{sl} than *E. grandis* × *nitens*.

DISCUSSION

There are at least two ways in which a tree may increase transport efficiency. One is by producing more cross-sectional xylem. The other is by changing anatomical features that affect conductivity such as vessel diameter, length and frequency (Ewers 1985). Of these features, vessel diameter is probably the most important anatomical variable in angiosperm wood because hydraulic conductivity is proportional to the radius raised to the fourth power. As a result, even a small increase in vessel radius should result in a large increase in conductivity (Zimmermann 1978, 1983). Previous research has shown that in general vessel diameters and vessel element lengths decrease while vessel frequencies increase with increasing aridity. Based on his observations of the Asteraceae Carlquist (1966) may have been the first to record this relationship. These observations have been supported by further studies such as the following. Zhang et al. (1988) showed a strong positive correlation between rainfall, altitude and element size in *Syringa oblata*, Wilkins and Papassotiriou (1989) indicated a trend towards decreasing vessel diameter with increasing dryness for *Acacia melanoxylon* and February (1993) demonstrated a strong correlation between rainfall, vessel diameter and vessel frequency in *Combretum apiculatum* and *Protea caffra*.

The results for *Eucalyptus grandis* and *E. grandis* × *camaldulensis* show significant correlations between water consumed and vessel diameter that agree with these findings (Table 1). *Eucalyptus grandis* × *nitens*, on the other hand, shows only very weak correlations between quantitative vessel characteristics and the amount of water used (Table 1). Significant correlations between vessel frequency and water in this hybrid suggest that it adapts to increased water use through changes in vessel frequency. This adaptation to increased water use is not as biomass-efficient as increasing vessel diameter because of the r^4 relationship between vessel radius and conductivity versus the additional effort of increasing vessel frequency. As a result, we suggest that *E. grandis* × *nitens* lacks the phenotypic plasticity necessary to optimise use of available water to the same extent as *E. grandis* and *E. grandis* × *camaldulensis*. The latter two are better able to adapt to available water by modifying the most important anatomical variable relevant to conductivity (diameter).

Both *E. grandis* and *E. grandis* × *camaldulensis* have plasticity in vessel morphology that allows them to optimise use of plant-available water. On average in the dry treatment, *E. grandis* and *E. grandis* × *camaldulensis* have a higher biomass accumulation while using between 90 and 140 litres of water more than *E. grandis* × *nitens* (Table 1). These data show that when considering biomass production relative to water used, *E. grandis* × *nitens* is more efficient than the other two eucalypts (Table 1). The increased WUE_{sl} of this hybrid combined with a tendency to use less water than the other two eucalypts in the study is likely to make this hybrid more desirable for planting in low rainfall areas. Planting *E. grandis* × *nitens* would reduce the amount of water extracted in the catchment areas, thereby lessening the impact of silviculture on other agricultural activities downstream.

CONCLUSIONS

Contrary to expectations (Wilkes 1988) wood property variations in these eucalypts are related to specific factors of the environment such as available water. *Eucalyptus grandis* and *E. grandis* × *camaldulensis* are highly plastic in anatomical response to available water whereas *E. grandis* × *nitens* is very much less so (Table 1). On the other hand *E. grandis* × *nitens* has the highest WUE_{SI} of the three species / hybrids. Understanding these differences and significant correlations in anatomy may be useful in developing trees with higher WUE than the currently used taxa. These trees would be better suited to arid environments because lower water use would reduce the impact of silviculture on agricultural activities downstream.

The primary objective of this study was to examine the possibility of using quantitative wood anatomy to select trees that use water more efficiently without compromising on biomass production. We feel that by using vessel diameter and vessel frequency it is possible to select different hybrids or species that are suited for particular ecological situations. We also feel that the findings of this study highlight the need for southern African forestry to diversify the range of *Eucalyptus* species and hybrids planted so that water use efficient hybrids such as *Eucalyptus grandis* × *nitens* rather than poor water use efficient species such as *Eucalyptus grandis* predominate.

ACKNOWLEDGEMENTS

This article was improved considerably by constructive criticism from Dr. D.M. Avery and Dr. B. Gartner. The research was funded by a grant from Division of Forestek, CSIR. The work for this article was conducted in the wood anatomy laboratory at the South African Museum, funded by the Water Research Commission.

REFERENCES

Baas, P. 1986. Ecological patterns in xylem anatomy. In: J. J. Givnish (ed.), On the economy of plant form and function: 327–352. Cambridge Univ. Press, Cambridge, UK.

Baas, P. & F.H. Schweingruber. 1987. Ecological trends in the wood anatomy of trees, shrubs and climbers from Europe. IAWA Bull. n.s. 8: 245–274.

Bamber, R.K. 1985. The wood anatomy of Eucalypts and paper making. Appita 38: 210–216.

Barnes, D.K. 1983. Managing root systems for efficient water use: Breeding plants for efficient water use. In: H.M. Taylor, W.R. Jordan & T.R. Sinclair (eds.), Limitations to efficient water use in crop production: 127–136. American Science of Agronomy, Inc.

Blum, A. 1974. Genotypic responses in sorghum to drought stress: I. Response to soil moisture stress. Crop Science 14: 361–364.

Bosch, J.M. & K. von Gadow. 1990. Regulating afforestation for water conservation in South Africa. South African J. For. 150: 7–17.

Burton, G.W., W.W. Hanna, J.C. Johnson Jr., D.B. Leuck, W.C. Monson, J.B. Powell, H.D. Wells & N.W. Widstrom. 1977. Pleiotropic effects of the trichomeless gene in pearl millet on transpiration, forage quality and pest resistance. Crop Science 17: 613–616.

Carlquist, S. 1966. Wood anatomy of Compositae: a summary, with comments on factors controlling wood evolution. Aliso 6: 25–44.

Carlquist, S. 1975. Ecological strategies of xylem evolution. Univ. of California Press, Berkeley.

February, E.C. 1993. Sensitivity of xylem vessel size and frequency to rainfall and temperature: implications for palaeontology. Palaeontologia Africana 30: 91–95.

Greacen, E.L. 1981. Soil water assessment by the neutron method. CSIRO, East Melbourne, 140 pp.

Henrici, M. 1946. The transpiration of South African plant association. III. Indigenous and exotic trees in the Drakensburg area. Science Bull. No. 247: 1–85. Dept. of Agriculture, Pretoria, Union of South Africa.

Hunt, O.J. 1962. Water requirements of selected genotypes of Elymus junceus Fisch. and Agropyron intermedium (Host) Beauv. and their parent-progeny relationships. Crop Science 2: 97–99.

IAWA Committee. 1989. IAWA list of microscopic features for hardwood identification. IAWA Bull. n.s. 10: 219–332.

Kolb, J.K. & S.D. Davis. 1994. Drought tolerance and xylem embolism in co-occurring species of coastal sage and chaparral. Ecology 75: 648–669.

Olbricht, B.W., D. Le Roux, A.G. Poulter, W.J. Bond & W.D. Stock. 1993. Variation in water use efficiency and ^{13}C levels in Eucalyptus grandis clones. J. Hydrology 150: 615–633.

Stanger, T.K. 1991. Early results in provenance / progeny trails of cold tolerant Eucalyptus in South Africa. In: Intensive Forestry: The role of Eucalyptus 1: 318–329. IUFRO Symposium, Durban, South Africa.

Taylor, F. 1973. Anatomical wood properties of South African grown Eucalyptus grandis. South African For. J. 84: 20–24.

Tischler, K. & D. Heth. 1985. Wood properties of irrigated Eucalypts. In: Procedures of the International symposium 'Forest Products Research International – Achievements and the future', Pretoria. 3, Topic 10–3.

Van der Walt, J.J.A., E. Werker & A. Fahn. 1988. Wood anatomy of the Pelargonium (Geraniaceae). IAWA Bull. n.s. 10: 201–207.

Villiers, A.M. de. 1968. Die verband tussen ouderdom, spesies en sekere houteienskappe van die Eucalyptus grandis/saligna kompleks. Bosbou in Suid Africa 9: 11–44.

Wilkes, J. 1988. Variations in wood anatomy within species of Eucalyptus. IAWA Bull. n.s. 9: 13–23.

Wilkins, A.P. & S. Papassotiriou. 1989. Wood anatomical variation of Acacia melanoxylon in relation to latitude. IAWA Bull. n.s. 10: 201–207.

Zhang, X., L. Deng & P. Baas. 1988. The ecological wood anatomy of the Lilacs (Syringa oblata var. giraldii) on Mount Taibei in North-western China. IAWA Bull. n.s. 9: 24–30.

Zimmermann, M.H. 1978. Structural requirements for optimal conduction in tree stems. In: P.B. Tomlinson & M.H. Zimmermann (eds.), Tropical trees as living systems: 517–532. Cambridge Univ. Press, London, New York, Melbourne.

Zimmermann, M.H. 1983. Xylem structure and the ascent of sap. Springer-Verlag, Berlin.