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Grown In Different Climates.**

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# CARBON ISOTOPE DISCRIMINATION OF IRRIGATED AND FERTILISED *EUCALYPTUS GRANDIS* GROWN IN DIFFERENT CLIMATES.

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## ABSTRACT

Previous work suggests that growth of *Eucalyptus grandis* (Hill ex Maiden) grown in plantations in south-eastern Australia was negatively correlated with annual pan evaporation, with a 3-fold increase in growth across six sites corresponding to a 1000 mm decrease in annual evaporation. As both water and nutrients had been supplied in non-limiting quantities at these sites, these growth differences appeared to be caused by a tree response to the aerial environment. It was hypothesised that stomatal closure under the harsher atmospheric conditions might have been responsible for the observed growth suppression. This should have resulted in lower intercellular CO<sub>2</sub> concentrations and lower carbon isotope discrimination at sites with higher evaporation rates.

Wood samples from four locations were, therefore, analysed for their carbon isotope discrimination to identify whether there were differences in stomatal responses across the gradient in pan evaporation rates. The analysis showed that carbon isotope discrimination increased by only about 1‰ as annual pan evaporation increased from 1300 to 2040 mm. This implies that mean effective intercellular CO<sub>2</sub> concentration was about 16 μmol mol<sup>-1</sup> lower at the site with lowest pan evaporation than at the site with highest pan evaporation. This result was the opposite of what had been expected. Stomatal closure in response to higher vapour pressure deficits without direct effects on photosynthetic capacity, therefore, cannot explain the observed differences in growth across these sites. Instead, it appears that the inherent photosynthetic capacity of leaves must have been affected similarly to stomatal conductance by increasing environmental stress.

## INTRODUCTION

*Eucalyptus grandis* (Hill ex Maiden) is an important commercial species that can achieve high growth rates if nutrition and water are not limiting (Cromer et al. 1993). It can also transpire large quantities of water and accumulate a large amount of nutrients, which in effluent-irrigated plantations may be as much a desired trait as a high wood-growth rate. However, we still have insufficient knowledge of the conditions under which rates of growth and water use can be maximised, and to what environmental and/or management conditions these rates are most sensitive.

Myers et al. (1996) reported the growth of *E. grandis* in six irrigated plantations established in different climates in eastern Australia. All these plantations were irrigated at or above their water-use rate and supplied with non-limiting levels of nutrients either through application of municipal sewage effluent or fertiliser. However, growth across the six sites differed more than 3-fold, with highest growth at Gympie in a subtropical climate in southern Queensland, and lowest growth at Robinvale in a semi-arid climate in western Victoria.

When growth was expressed as a function of mean annual pan evaporation, a negative relationship was obtained. Gympie had the highest growth and lowest mean annual pan evaporation rates, and Robinvale had lowest growth and highest pan evaporation rates. Myers et al. (1996) therefore suggested that this might be caused by a tree response to vapour pressure deficit (VPD), with sites with

highest evaporation rates having the highest VPD. Consistent with that view, Leuning (1990) observed strong stomatal closure with increasing VPD in *E. grandis*, which might have reduced potential photosynthetic carbon gain at the sites with highest VPD. Substantial suppression of tree water use of *E. grandis* and *Pinus radiata* has also been recorded at the intensively studied Wagga Wagga effluent-irrigated plantation during periods of high evaporative demand (Benyon et al. 1996a). Myers et al. (1998) showed that daily transpiration of *E. grandis* was highly correlated with mean daily VPD up to about 1.5 kPa, but at higher VPDs, there was no further increase in transpiration. Similarly, Sweeney and Stevens (1997) reported that for another irrigated eucalypt species, *Eucalyptus camaldulensis*, there was no significant correlation between daily water use and potential transpiration on days when potential transpiration was greater than 3 mm d<sup>-1</sup>.

Stomatal closure in response to high VPD would have important implications for the management of effluent-irrigated plantations. One of the key aims in managing such plantations is to avoid oversupplying effluent. When it is oversupplied, excess nutrients might leach below the root zone and eventually contaminate ground water reservoirs. If high VPD during summer months were to lead to stomatal closure, it would reduce trees' water use at a time of the year when potentially the greatest water use is possible and greatly reduce the total amount of water, and consequently nutrients, that trees can utilise over a year.

If stomatal closure occurs in response to high VPD, it is also of interest to know whether this is a response to lowered photosynthetic capacity, or is itself the cause of reduced photosynthetic rates. There are essentially two possibilities: either, stomata respond directly to VPD and reduce photosynthetic rates through lowered intercellular CO<sub>2</sub> concentration, or both stomatal conductance and inherent photosynthetic capacity may be similarly affected by VPD so that photosynthesis is reduced with little change in intercellular CO<sub>2</sub> concentration. If stomatal conductance is more sensitive to VPD than the photosynthetic capacity of leaves then stomatal closure in response to an external condition can force the intercellular CO<sub>2</sub> concentration to low values which restricts photosynthetic carbon gain, but increases transpiration efficiency. This has been observed in *P. radiata* in response to water stress (Korol et al. 1999). On the other hand, if both stomatal conductance and the leaves' inherent photosynthetic capacity were similarly sensitive to external conditions, then any reduced photosynthetic capacity would not be accompanied by altered intercellular CO<sub>2</sub> concentration and transpiration efficiency.

It is possible to distinguish between these possibilities by measuring the carbon isotope discrimination in wood of trees grown under these different conditions. Carbon isotope discrimination of carbon fixed in photosynthesis is directly related to the intercellular CO<sub>2</sub> concentration (Farquhar et al. 1982, 1989). If there are no further discriminations during subsequent biological reactions in the plant, the isotope ratio of carbon laid down in wood is a

direct measure of the intercellular CO<sub>2</sub> concentration at the time when the carbon was fixed. Moreover, by analysing the wood laid down over a whole season, or a number of seasons, an integrated measure of the gas exchange over the whole period and the whole canopy can be obtained. These measures would be weighted by the amount of carbon fixed at different times of the year.

The present study used carbon isotope ratios to infer the average intercellular CO<sub>2</sub> concentration ( $c_i$ ) from four of the plantations reported by Myers et al. (1996). This was done in order to distinguish between the possibilities of reductions in photosynthesis being caused by reduced intercellular CO<sub>2</sub> concentration, or occurring without changes in intercellular CO<sub>2</sub> concentration.

## METHODS

Carbon isotope ratios were measured on wood samples as described in detail by Korol et al. (1999). According to a theoretical relationship, the carbon isotope composition of a C<sub>3</sub> plant ( $\delta^{13}\text{C}$ ) is related to the intercellular CO<sub>2</sub> concentration by (Francey and Farquhar 1982; Farquhar et al., 1982, 1989):

$$\delta^{13}\text{C} (\text{‰}) = \delta^{13}\text{C}_a - a - (b-a) \cdot (c_i/c_a) \quad (1)$$

where  $\delta^{13}\text{C}_a$  is the isotopic composition of CO<sub>2</sub> in the atmosphere, approximately - 8.0‰ for current atmospheric conditions, 'a' is the discrimination associated with diffusion (4.4‰), 'b' is a fitted parameter the value of which is determined primarily by the discrimination of the enzyme Ribulose biphosphate carboxylase/oxygenase (27‰), and  $c_i/c_a$  is the ratio of CO<sub>2</sub> concentrations inside the leaf and that

in the air surrounding the leaf. Carbon isotope discrimination,  $\Delta$ , was calculated as:

$$\Delta = \frac{\delta^{13}\text{C}_a - \delta^{13}\text{C}_p}{1 + \delta^{13}\text{C}_p} \quad (2)$$

## STUDY SITES

Wood samples were collected from *E. grandis* trees in four of the irrigated plantations reported by Myers et al. (1996) representing a range of climates and growth rates. Three of the plantations were irrigated with nutrient-rich municipal sewage effluent at, or above, their rate of water use while one plantation (Gympie) was heavily fertilised and irrigated with bore water. In all four plantations, water and nutrients were considered to have been non-limiting to growth over the first three years, which was the period over which growth was observed.

### *Wagga Wagga, NSW*

This plantation was established in mid-1991 at Wagga Wagga in central New South Wales (Myers et al. 1994). The site is moderately arid with a mean annual rainfall of about 550 mm which is slightly winter dominant, ranging from 63 mm in June to 37 mm in December. Annual pan evaporation during the experiment was 1640 mm and was strongly seasonal, ranging from 280 mm in January to 23 mm in June. Mean annual daily maximum temperature was 22°C, ranging from 31°C in January to 12°C in July. The site was formerly an improved pasture. The duplex soils are a mixture of well-drained red earths and red podsolics. The A horizon is a

sandy loam or sandy clay-loam overlying sand to medium clays in the B horizon. Trees were planted at a spacing of 3x2 m for a total of 1667 trees ha<sup>-1</sup>.

### *Adelaide, South Australia*

This plantation was established in early 1990 at the Bolivar sewage treatment works north of Adelaide in eastern South Australia (Hanna et al. 1992). This is the most arid of the four sites with the lowest annual rainfall of 440 mm and the highest annual pan evaporation during the experiment of 2040 mm. Evaporation was strongly seasonal, ranging from 320 mm in January to 55 mm in June. Mean annual daily maximum temperature was 22°C, ranging from 29°C in January to 15°C in July. The site is located 2 km from the coast and is exposed to strong on-shore salt-laden winds. The duplex soils comprise 15-25 cm of loamy sand overlying a calcareous clay sub-soil. The sub-soil is saline and sodic and overlies a shallow watertable less than 2 m deep with salinity in excess of 1500 mS m<sup>-1</sup>. Trees were planted at a spacing of 3x1.5 m or 2222 trees ha<sup>-1</sup>.

### *Gympie, South Queensland*

This plantation was established at Toolara State Forest near Gympie in south-eastern Queensland in early 1987 (Cromer et al. 1993). This sub-tropical site is the most mesic of the four sites with the highest mean annual rainfall of 1150 mm and the lowest mean annual pan evaporation of 1300 mm. Mean annual daily maximum temperature was 27°C, ranging from 31°C in January and February to 21°C in July. The site had grown pine

plantations for more than 35 years before the current trees were established. The soil is a well-drained, sandy yellow earth with no impeded drainage above 1.5 m. Trees were planted at a spacing of 3.4 x 2.6 m. Total stand density was 1131 trees ha<sup>-1</sup>.

### **Wodonga, Victoria**

This plantation was established in mid 1980 on the Murray River flood plain near Wodonga in north-eastern Victoria (Stewart et al. 1988). The site has a moderately mesic climate with a mean annual rainfall of 713 mm which is winter dominant, ranging from 82 mm in June to 38 mm in January. Average annual pan evaporation during the experiment was 1572 mm. Mean annual daily maximum temperature was 22°C, ranging from 32°C in January to 13°C in July. The site was formerly an improved pasture. The soil is a pale loam. Trees were planted at a spacing of 3x1.5 m; stand density was 2222 trees ha<sup>-1</sup>.

## **DATA COLLECTION AND ANALYSIS**

Stemwood samples were collected from nine trees at breast height at each site using an increment borer. Tree diameters had been recorded annually since plantation establishment. The rings representing the first three years of growth were separated and bulked for isotopic analysis. For analysis of the effect of tree size on carbon isotope discrimination, samples from trees grown at Gympie were used. Nine trees were selected, and for each tree, the stem was divided into four concentric sections with equal diameters. *E. grandis* grown in irrigated plantations in south-eastern

Australia does not form recognisable annual growth rings so that an analysis based on annual rings was not possible. Carbon analyses were therefore done separately on each of the four sections, and the mean diameter for each section was recorded.

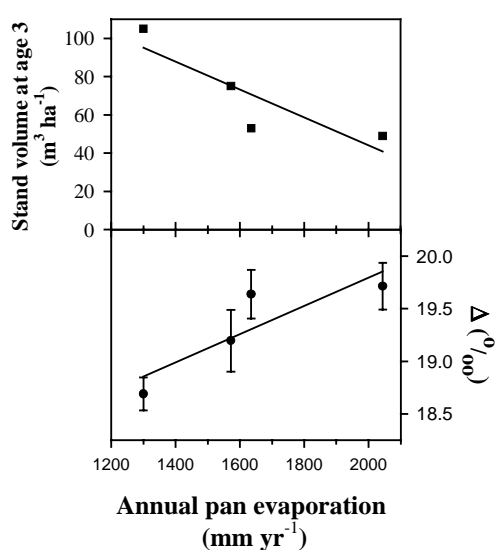
Between-plot differences were analysed using standard t-tests or an ANOVA. The statistical tests were done at the 95% confidence level ( $\alpha = 0.05$ ), and the probabilities (p) that the average plot  $\Delta$  are from the same population are presented.

The stable carbon isotope composition was determined on finely ground wood samples using a VG Isomass isotope ratio mass spectrometer, using an internal standard that was related in turn to PDB as the usual reference (Farquhar et al. 1989). Whole-wood samples were used for analyses because research has shown that the same trends in  $\delta^{13}\text{C}$ , and subsequently  $\Delta$ , occur in whole wood as in the cellulose component, or in leaf material (Leavitt and Long 1982, 1986; Francey 1986).

## **RESULTS AND DISCUSSION**

Figure 1 shows that there was a positive relationship between  $\Delta$  and evaporative demand, with Gympie having the lowest discrimination ( $18.69 \pm 0.16\text{‰}$ ; mean  $\pm$  standard error), and Adelaide having the highest ( $19.71 \pm 0.22\text{‰}$ ). While the difference between sites of approximately 1‰ is not large, the value of  $\Delta$  at Gympie was significantly different from that at Wagga Wagga ( $19.64 \pm 0.23\text{‰}$ ;  $p = 0.003$ ) and Adelaide ( $p = 0.002$ ), but not significantly different from the value at Wodonga ( $19.20 \pm 0.29\text{‰}$ ;  $p = 0.15$ ). The Adelaide, Wagga Wagga and

**Figure 1:** Stand volume (upper panel) and carbon isotope discrimination,  $\Delta$ , (lower panel) at age 3 for four sites in south-eastern Australia, expressed as a function of annual pan evaporation rate. For Gympie, this is the mean annual pan evaporation rate, and for the other three sites, it is the amount recorded in the relevant years. Error bars given for carbon isotope discrimination refer to the standard error of the data. Lines drawn in the Figure are regression lines fitted to the data.



Wodonga sites had mean  $\Delta$  values that were not significantly different from each other ( $p = 0.31$ ).

More important than the between-plot differences observed was the direction of the change; it was opposite of what had been expected. Gympie, with the most mesic climate and lowest salinity, had the lowest carbon isotope discrimination and therefore the lowest inferred intercellular  $\text{CO}_2$  concentration. Consequently, the data suggest that the high VPDs (from a correlation with high pan evaporation rate) at Wagga Wagga and Adelaide did not lead to stomatal closure independent of any

reduction in photosynthetic capacity. Had the high VPD led to stomatal closure without affecting the leaves' inherent photosynthetic capacity, then the sites with high VPD should have had lowest intercellular  $\text{CO}_2$  concentrations and lower carbon isotope discrimination, which is the opposite of what was observed.

One possible explanation for this surprising result relates to the influence of tree size on stomatal responses. Panek and Waring (1995), for example, found that carbon isotope discrimination can decrease with tree size, suggesting lower intercellular  $\text{CO}_2$  concentrations as trees age. As trees in the present study were all sampled over 3 years of growth, and as there were significant differences in growth, any size induced differences in stomatal responses might possibly have contributed to the observed pattern.

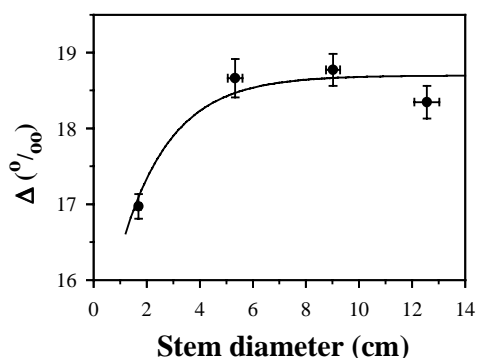
An analysis of the Gympie trees by quarter sections showed that for very young trees, when diameters were below 3 cm,  $\Delta$  averaged  $16.97 \pm 0.16\text{‰}$ , while for samples taken when trees were older with diameters between 3-7 cm, average discrimination had increased to  $18.66 \pm 0.25\text{‰}$  but changed little with further growth within the observed range (Fig. 2). The 1.7‰ difference in  $\Delta$  between the two smallest size classes was highly significant ( $p < 0.001$ ). Once diameters were greater than 3 cm, there was no further significant difference in  $\Delta$  ( $p = 0.85$ ).

The effect of tree size on carbon isotope discrimination was not investigated at the other sites. However, trees were largest at Gympie, and if the same size dependence of carbon isotope discrimination occurred at all four sites,

then it would have marginally increased the

**Figure 2:** Carbon isotope discrimination ( $\Delta$ ) as a function of stem diameter for trees from Gympie. Four samples were taken from each of nine trees at different positions within the stem. Data were pooled for the ranges <3 cm, 3-7 cm, 7-10 cm and >10 cm. Data show means and standard errors. The curve is a relationship fitted to all individual data and given by:

$$\Delta = 18.70 - 3.96 \exp(-0.535 d); r^2 = 0.489.$$



trend apparent in Figure 1 even further.

### INFERRED INTERCELLULAR CO<sub>2</sub> CONCENTRATION AND TRANSPIRATION EFFICIENCY

The observed carbon isotope discrimination implies that the difference of  $c_a - c_i$  was about  $16 \mu\text{mol mol}^{-1}$  greater at Gympie than at Adelaide, which is the opposite of what might have been expected on the basis of observed leaf-level responses to VPD. The fact that trees at Gympie operated at a lower  $c_i$  should have reduced photosynthesis and consequently growth. Therefore, the inferred low  $c_i$  can, therefore not explain the higher growth

rates observed at Gympie. The data imply that trees had higher transpiration efficiency at Gympie, but that would have been no advantage as water was available in non-limiting quantities.

In addition to the gradient in VPD across the four sites, there was a gradient in salinity. This gradient, however, is more difficult to quantify. The Gympie plantation would have experienced the lowest salinity because it was irrigated with low salinity bore water and benefited from soil leaching from the high annual rainfall of 1150 mm. The Wodonga plantation also would have experienced low-salinity conditions. Despite being irrigated with effluent averaging  $70 \text{ mS m}^{-1}$  EC, the rate of application generally exceeds the rate of tree water use (Stewart et al. 1988). Therefore, salt would have regularly been leached below the root zone and trees would have generally been exposed to salinities not much higher than that of the effluent. The Wagga Wagga plantation was irrigated with slightly lower salinity effluent (average  $60 \text{ mS m}^{-1}$ ), but because it was irrigated at or below the water use rate of the plantation, salt accumulated in the root zone to the extent that soil salinity rose to between  $250$  and  $300 \text{ mS m}^{-1}$  in mid summer of the fourth year (Benyon et al. 1996b). The Adelaide plantation experienced the highest salinity because of salty effluent ( $230 \text{ mS m}^{-1}$ ), salt-laden air from the coast and a very saline water table at 1.5 m depth.

It might be expected that trees experiencing higher salinity may have reduced stomatal conductance. This could then lead to reduced  $c_i$  and increased transpiration efficiency. Hence, the



differences in salinity between sites, just like the differences in climatic conditions, would lead to the expectation that trees at Gympie should have operated at the highest  $c_i$  and trees at Adelaide at the lowest. This trend is again the opposite of what was observed (Fig. 1), and leaves open the question why trees in these environments showed such marked differences in growth response. Our analysis would exclude reduced stomatal conductance leading to reduced photosynthesis as a possibility.

This has important implications for the management of water application on effluent-irrigated plantations. Myers et al. (1996) showed that plantation water use could not be calculated as a simple fraction of pan evaporation rates, and that growth of plantation trees was severely reduced in climates with higher VPD. The present study shows that these reductions in growth were accompanied by only small differences in intercellular  $CO_2$  concentration. The reduced growth under conditions of high VPD presumably was accompanied by reduced water use, but water use was not further reduced by trees operating at lower intercellular  $CO_2$  concentration, which would have increased the efficiency with which water was used.

## CONCLUSIONS

Our results imply that there were only small changes in carbon isotope discrimination across four sites with widely differing climates, and that those changes indicated trees to operate at highest intercellular  $CO_2$  concentration on sites where their growth was poorest. They can therefore not help to explain the observed 3-fold differences in growth, with sites with

highest annual evaporation rates having highest intercellular  $CO_2$  concentration, but poorest growth. These results were surprising and inconsistent with other lines of evidence that suggest strong effects of the aerial environment on stomatal behaviour.

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