STOMATAL RESPONSES OF *EUCALYPTUS* SPECIES TO ELEVATED CO_2 CONCENTRATION AND DROUGHT STRESS

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ABSTRACT: Five species of *Eucalyptus* (*E. grandis, E. urophylla, E. camaldulensis, E. torelliana,* and *E. phaeotrica*), among the ten species most commonly used in large scale plantations, were selected for studies on the effects of elevated CO_2 concentration [CO_2] and drought stress on stomatal responses of 2.5-month old seedlings. The first three species belong to the subgenus *Smphyomyrtus,* whereas the fourth species belongs to the subgenus *Corymbia* and *E. phaeotrica* is from the subgenus *Monocalyptus*. Seedlings were grown in four pairs of open-top chambers, arranged to have 2 plants of each species in each chamber, with four replications in each of two CO_2 concentrations: 350 ± 30 μmol mol^{-1} and 700 ± 30 μmol mol^{-1}. After 100 days in the chambers, a series of gas exchange measurements were made. Half the plants in each chamber, one plant per species per chamber, were drought-stressed by withholding irrigation, while the remaining plants continued to be watered daily. Drought stress decreased stomatal conductance, photosynthesis and transpiration rates in all the species. The effect of drought stress on stomatal closure was similar in both [CO_2]. The positive effects of elevated [CO_2] on photosynthesis and water use efficiency were maintained longer during the stress period than under well-watered conditions. The photosynthetic rate of *E. phaeotrica* was higher even in the fourth day of the drought stress. Drought stress increased photoinhibition of photosynthesis, as measured by chlorophyll fluorescence, which varied among the species, as well as in relation to [CO_2]. The results are in agreement with observed differences in stomatal responses between some eucalyptus species of the subgenera *Symphyomyrtus* and *Monocalyptus*.

Key words: eucalyptus physiology, water use efficiency, drought tolerance, CO_2 adaptation

RESPOSTA ESTOMÁTICA AO AUMENTO DA CONCENTRAÇÃO DO CO_2 ATMOSFÉRICO E AO ESTRESSE HÍDRICO DE ESPÉCIES DE *EUCALYPTUS*

RESUMO: Cinco espécies de *Eucalyptus* (*E. grandis, E. urophylla, E. Camaldulensis, E. torelliana* e *E. phaeotrica)*, dentre as dez espécies mais utilizadas em plantações florestais de larga escala, foram submetidas ao aumento do CO_2 e à interação deste com estresse hídrico para avaliar seu comportamento estomático. As três primeiras espécies pertencem ao subgênero *Symphyomyrtus,* a quarta espécie é do subgênero *Corymbia* e o *E. Phaeotrica* pertence ao subgênero *Monocalyptus.* Mudas destas espécies com idade de 2,5 meses foram cultivadas em quatro pares de câmaras de topo aberto, com duas plantas de cada espécie por câmara e quatro repetições em duas concentrações de CO_2: 350 ± 30 μmol mol^{-1} e 700 ± 30 μmol mol^{-1}. Após 100 dias de crescimento nas câmaras, medições de trocas gasosas foram realizadas, após o que metade das plantas em cada câmara foi submetida ao estresse hídrico pela supressão da irrigação, permanecendo as demais plantas sob irrigação diária. O estresse hídrico reduziu a condutância estomática, a fotossíntese e as taxas de transpiração em todas as espécies. O efeito do estresse hídrico no fechamento dos estômatos foi similar em ambas as concentrações de CO_2, embora os efeitos positivos do aumento do CO_2 sobre a fotossíntese e a eficiência do uso da água se mantivessem por um período comparativamente mais longo. A taxa fotossintética do *E. Phaeotrica* permaneceu alta mesmo após o quarto dia do estresse hídrico. O estresse hídrico aumentou a fotoinibição da fotossíntese, medida por fluorescência da clorofila, que variou entre as espécies, assim como em relação à concentração de CO_2. Os resultados mostram diferenças na resposta estomática entre espécies dos subgêneros *Symphyomyrtus* e *Monocalyptus*.

Palavras-chave: fisiologia do eucalipto, eficiência do uso da água, tolerância à seca, adaptação ao aumento da concentração de CO_2

INTRODUCTION

Eucalyptus plantations in the warmer areas of the world amounts to over 10 million hectares. The trend is for a continuous increasing of the planted area to meet growing wood demand and also the need to maintain the balance of the vital ecological processes in the remaining native ecosystems (Brown et al., 1997). However, the value of eucalyptus plantations is not enthusiastically approved by everyone and the question of their environmental effects, particularly water consumption, is far from being resolved. In this regard, it is also important to know where the many direct and indirect effects of increasing atmospheric CO_2 concentration can lead to in terms of survival, acclimation, productivity, water relations and stomatal behavior, to be able to anticipate significant ecological and management consequences (Ceulemans & Mousseau, 1994).

The growth and development of trees on sites experiencing occasional periods of drought stress depends on the ability of stomata to control water loss while maintaining growth. The rate of transpiration can be maintained until a critical amount of soil moisture is reached (Dunin & Aston, 1984), but some studies suggest a linear decline in transpiration with decreasing soil water (Gollan et al., 1985). When leaf water potential declines, stomatal aperture decreases, reducing transpiration and allowing leaf water potential to recover. Leaf water potential *per se* may not be the transducer of stomatal response to drought stress (Gollan et al., 1985; Hinckley et al., 1991) but, in general, there is usually a range of leaf water potential over which stomatal conductance remains unaffected. When a certain threshold value of leaf water potential is reached, photosynthesis declines, internal CO_2 concentration increases and the stomata close in a linear or curvilinear way until stomatal conductance approaches zero (Schulte et al.,1987; Wang et al., 1988; De Lucia & Heckathorn, 1989).

Stomata also respond to CO_2 as stomatal conductance decreases as CO_2 concentration increases (Mott, 1988; Eamus & Jarvis, 1989; Centritto et al., 1999b; Medlyn et al., 2001). This response is related to the intercellular concentration of carbon dioxide (C_i) (Mott, 1988). The stomatal conductance decline in response to increase in CO_2 concentration will, to some extent, compensate for the effect of increased CO_2 on photosynthesis and may also reduce the transpiration rate and the integrated result of these effects is that an increase in atmospheric CO_2 concentration generally increases water use efficiency (WUE) (Morison, 1985; Eamus & Jarvis, 1989, Jarvis, 1989; Drake et al., 1997; Centritto et al., 1999a). A possible beneficial effect of this increase in water use efficiency is a reduction in the rate of water consumption per unit leaf area, but the simultaneous increase in total leaf area as a result of [CO_2] increase may partly offset this increase in WUE. Increase in WUE as a result of increasing CO_2 concentration has been observed in a number of tropical pioneer and climax tree species (*Ochroma lagopus, Tabebuia rosea, Acacia mangium, Myriocarpa longipes, Trichospermum mexicanum, Senna multijuga, Piper auritum, Cecropia obtusifolia)* (Oberbauer et al., 1985; Reekie & Bazzaz, 1989; Ziska et al., 1991), temperate species (*Quercus* sp., *Pinus radiata, Pseudotsuga menziesii, Notophagus* sp.*)* (Norby et al., 1986; Hollinger, 1987), Mediterranean species (Centritto et al., 1999b) and *Eucalyptus* sp. (Wong & Dunin, 1987). It is often assumed that species with high WUE would be favoured in dry environments, but there may be a physiological cost for this. A decrease in stomatal conductance causes a proportionally larger decrease in transpiration than in carbon assimilation, with the net result of a higher WUE. The maintenance of high WUE, by maintaining stomata partially closed, also decreases the rate of carbon assimilation, thus reducing growth (De Lucia & Heckathorn, 1989). Therefore, the main role of this stomatal response may be related to the control of water loss, rather in the sense of preventing tissue damage so as to maximise carbon assimilation in the prevailing circumstances than in the sense of conserving water (Cowan & Farquhar, 1977; Farquhar & Sharkey, 1982; Grace, 1993).

The interactive effects of elevated CO_2 concentration and drought stress on stomatal response may, therefore, have some interesting physiological and practical aspects. It has been assumed that the elevated CO_2–induced increase in WUE may delay the effect of drought, or make it less severe (Tolley & Strain, 1985). Chaves & Pereira (1992), using the model MAESTRO (Jarvis, 1989), parameterised with data from a plantation of *Eucalyptus globulus* in Portugal, observed that the increases in photosynthesis and water use efficiency were still noticeable under moderate drought stress. Even though stomatal restriction to the supply of CO_2 to the chloroplasts is undoubtedly an important factor in this decrease in photosynthesis with drought stress, recent results suggest that other components of the photosynthetic process, unrelated to stomatal response, are also affected by water stress. For instance, water stress may inhibit some steps in the photosynthetic sequence, causing photoinhibition (Bjorkman & Powles, 1984; Ogren & Oquist, 1985; Vu et al., 1987; Ogren, 1988; Scheuermann et al., 1991; Epron et al., 1992; Ogren & Evans, 1992).

Against this general background of stomatal responses to water stress and elevated CO_2 concentration, how does stomatal conductance in *Eucalyptus* species respond to water stress and elevated [CO_2]? In a comprehensive review, Lima (1993) found only a handful of papers related to stomatal responses of *Eucalyptus* species. Results from a number of sources (Grieve, 1956; Langford, 1976; Connor et al., 1977; Carbon et al., 1981;

Florence, 1986; Colquhoun et al., 1984) suggest that *Eucalyptus* species of the subgenus *Monocalyptus* may have developed poor physiological control of water loss, reaching very low leaf water potentials before the stomata begin to close. This characteristic may play a major role in restricting the range of habitats in which species of this subgenus can survive. Species of the subgenus *Monocalyptus* seldom grow well outside Australia, especially in warm temperate or subtropical areas where there is a distinct dry season (Pryor, 1976). By contrast, eucalyptus species of the other subgenera, mainly of the *Symphyomyrtus*, which contains the species most used in large scale plantations around the world (Eldridge & Cromer, 1987), have well developed patterns of stomatal closure in response to water-vapour pressure deficit (Wong & Dunin, 1987; Dye, 1985, 1986; Pereira et al., 1987), soil water shortage (Quraishi & Kramer, 1970; Gindel, 1971; Journet, 1979; Eastham et al., 1990; Harding et al., 1992), and elevated atmospheric [CO_2] (Wong & Dunin, 1987). For instance, Dunin & Aston (1984) showed that *Eucalyptus maculata* growing in a lysimeter in Australia decreased transpiration substantially as soil water content declined below 40% of field capacity.

The main objective of this study was to compare the stomatal responses of some *Eucalyptus* species most representative of the species used in large scale plantations. Variations in net gas exchange and chlorophyll fluorescence characteristics of the subgenera in response to the interactive effects of elevated [CO_2] and drought stress were studied.

MATERIAL AND METHODS

Species

Five species of *Eucalyptus* were selected for the experiment: *E. grandis, E. urophylla, E. camaldulensis, E. torelliana* and *E. phaeotrica.* First selection criterion was the importance of the species in large-scale industrial plantation forests in tropical and subtropical conditions (Eldridge & Cromer, 1987).

A second selection criterion was the subgenus. The first three species belong to the subgenus *Symphyomyrtus*, while *E. torelliana* is from the subgenus *Corymbia*, and *E. phaeotrica* is one of the few *Monocalyptus* that grow succesfully in plantations outside Australia. There may be contrasting physiological responses to environmental variables amongst these subgenera (Noble, 1989). Within the group of *Symphyomyrtus* species, a final selection criterion was related to their growth habit in their natural environment. Both *E. grandis* and *E. urophylla* are species of tall forests. However, the former is a Gum-type tree species, whereas *E. urophylla* is of the Fibrous Bark type. *E. camaldulensis*, on the other hand, is a *Symphyomyrtus* species typical of open woodland.

Seeds of these five selected species were obtained in Piracicaba, SP, Brazil. Seeds from *E. grandis, E. urophylla, E. camaldulensis* and *E. phaeotrica* were collected in open-pollinated seed production areas located in Anhembi, SP, Brazil (23°00'S; 48°21'W). The seeds of *E. torelliana* came from an open-pollinated seed production area located in Oriçanga, MG, Brazil (22°18'S; 47°03'W).

Cultivation

The seeds were germinated in individual plastic containers filled with peat and topped with vermiculite. After establishment, seedlings in each container were selected for uniformity and thinned periodically to a final density of one plant per container, when they were transplanted to 4 dm^3 plastic pots filled with a 7:3:2 mixture of loam soil:sand:peat, to which 150 g of lime and 750 g of the fertilizer 4:19:10 were added, equivalent to a rate of approximately 20 g of 4:19:10 NPK per plant. The pots remained in the greenhouse for two additional weeks, to allow for adequate recovery from transplant.

The potted seedlings were finally placed into open-top chambers in the greenhouse, at the age of 2.5 months. Two pots of each species were placed ramdonly in each chamber. During the study period, they were periodically relocated within each chamber. A set of plants of each species was maintained in the greenhouse outside but adjacent to the open-top chambers.

The plants were irrigated daily with a solution, equivalent to approximately 0,30 g of NPK per plant (one measure in 9 dm^3 of water, Formula 3 Soluble Plant Food, 20:20:20 NPK plus micronutrients, Chempak Products, UK). One day a week, the amount of soluble fertilizer added to the irrigation water of that day was doubled to 0.60 g of 20:20:20 NPK.

Open-top chambers

A set of eight open-top chambers was located inside a greenhouse at the University of Edinburgh (55° 31' N, 3° 12' W), at an elevation of 185 m asl. The eight chambers were arranged as four pairs, one of each pair with ambient CO_2 and one with elevated CO_2 concentration, thus giving an experimental design with four replicates of each pair of chambers. The chambers were made out of transparent polypropylene (about 15% light attenuation) with dimensions of 1.25 m in diameter, 1.25 m in height, and a total volume of about 1.5 m^3.

Outiside air was constantly blown into each chamber. To ensure uniform air distribution over the chamber area, the air was blown into a plastic pillow with a perforated upper surface located below the chamber floor. Before entering the plastic pillow, the air stream was supplemented with pure CO_2 from cylinders, through a computerized control system which maintained the CO_2

concentration in the four ambient [CO_2] chambers at 350 ± 30 µmol mol^{-1}, and at 700 ± 30 µmol mol^{-1} in the four elevated [CO_2] chambers. The CO_2 concentration in the chambers was continuously monitored by an infra-red gas analyzer (PP Systems, Luton, U.K.), which was calibrated regularly.

Micrometeorological conditions inside the chambers were monitored almost continuously throughout the period, using a set of four quantum sensors distributed in two of the four pairs of chambers, and a ventilated psychrometer mounted inside one of the chambers. The quantum sensors and psychrometer were linked to a data logger [Model 7X, Campbell (UK) plc., Loughborough, U.K.]. Average temperature for a 13h photoperiod was approximately 13.4°C. Relative humidity inside the chamber was approximately 62 % during daytime, and approximately 80 % at night. Daily photosynthetic photon flux density (PPFD) at the begining of the experiment was 9.9 mol m^{-2} d^{-1}, with midday maxima circa 0.2 mmol m^{-2} s^{-1}. At the end of the experiment, daily photon flux density was approximately 11.5 mol m^{-2} d^{-1}, with a midday maxima circa 0.4 mmol m^{-2} s^{-1}.

Gas Exchange Measurements

Gas exchange measurements were made on all the chamber plants, as well as on the plants that grew outside the open-top chambers, after 90 days of growth in elevated CO_2, on at least two fully expanded leaves per plant, using a portable gas exchange system (Model LCA3, ADC Co. Ltd., Hitchin, U.K.).

After this set of gas exchange measurements, the plants in the chambers were subjected to a drying cycle, according to the following scheme: half the plants in each chamber (that is, one plant per species) were water-stressed by withholding irrigation, while the remaining (control) plants continued to be watered (and fertilized) daily.

Initially all pots were irrigated as previously until water dripped through the pot. The next day (the first day of the drying cycle), gas exchange measurements were made on both control and water stressed plants. Before measurements, the CO_2 concentration in the cuvette was equilibrated to the concentration prevailing in the chambers. The measurements were repeated daily throughout the four-day drying cycle. All measurements were made between 9:30 and 14:00 h each day, using a 12-V battery operated, artificial light source (Nippon Keiki Works, Ltd., Japan) attached to the leaf cuvette. This provided a constant photon flux density of 1000 µmol m^{-2} s^{-1}.

Two additional variables were also measured during the four days of the drying cycle: soil moisture content and chlorophyll fluorescence kinetics. Soil moisture was measured at the same time as the gas exchange measurements, by taking core samples from the entire depth of each pot. The samples were then weighed and oven-dried for 36 hours. Chlorophyll fluorescence was measured right after the gas exchange measurements, using a Plant Stress Meter (Bio Monitor, Sweden). Measurements of the fluorescence parameters with this instrument is straightforward. After a short period of dark pretreatment, five leaves per plant, on five plants of the control and five of the water-stressed plants, on a different pair of chambers each day of the drying cycle, were illuminated with high intensity light, with the photon flux density of the actinic light set at 200 µmol $m^{-2}s^{-1}$, giving the mininum instantaneous value of fluorescence (F_o), which gradually increased to a peak value (F_m). The difference (F_m - F_o) is called variable fluorescence (F_v) and the ratio F_v/F_m is a measure of the efficiency of the photosystem II reaction center (Jones, 1992).

Data analysis

The gas exchange data obtained during the drying cycle were analyzed by a split-split-plot analysis of variance, in which the sub-plots of the first part (species) were now split into sub-sub-plots (control and drought-stressed plants). The main effect of drought stress was tested with the Chamber x Water Stress (Species) as the error term. The interaction CO_2 x Water Stress was tested with the Chamber x CO_2 x Water Stress (Species) as the error term. Some of the gas exchange data were transformed prior to analysis, by taking either the logarithm or the square root of the original values to equalise the variances. The analyses were performed with the ANOVA program in SAS. All tests of significance were made at 5% level. The significance of the differences among treatment means was evaluated by Duncan's Multiple Range Test.

RESULTS AND DISCUSSION

The prevailing average photon flux density was not adequate for light-saturated gas exchange measurements so an artificial light source was attached to the cuvette (Figure 1). There were effects of water stress on stomatal conductance, photosynthetic rate and transpiration rate of all five species at the end of the drying cycle, as well as a significant interaction between species and water stress. However, the interaction CO_2 x Water Stress was not significant for all species, although there were some slight differences between species in relation to the pattern of variation of stomatal conductance with decreasing available soil water (Figures 2, 3 and 4). *E. grandis, E. urophylla, E. camaldulensis* and *E. torelliana* showed similar responses of stomatal conductance throughout the drying cycle in both the ambient and elevated [CO_2] treatments. For these species, stomatal conductance of the drought-stressed plants started to decline when the volumetric soil moisture reached approximately 50% of avail-

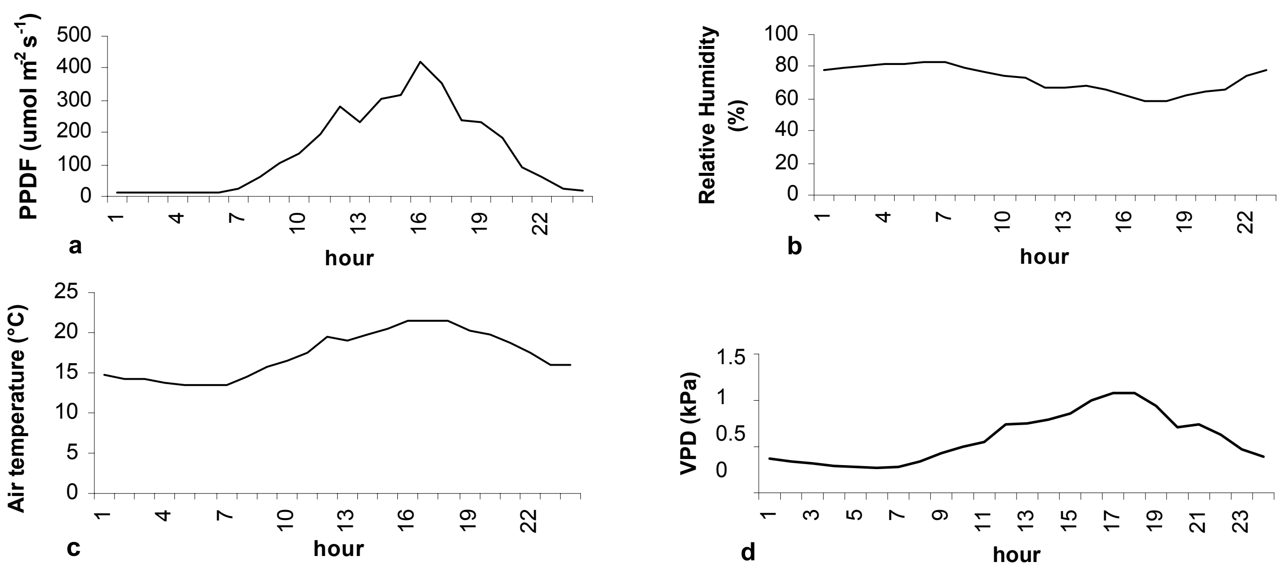

Figure 1- Average micrometeorological conditions inside the open-top chambers: a) photosynthetic photon flux density (PPFD; b) relative humidity; c) air temperature; d) vapor pressure deficit (VPD). Values represent averages for the week of gas exchange measurements (22-31 July 1992).

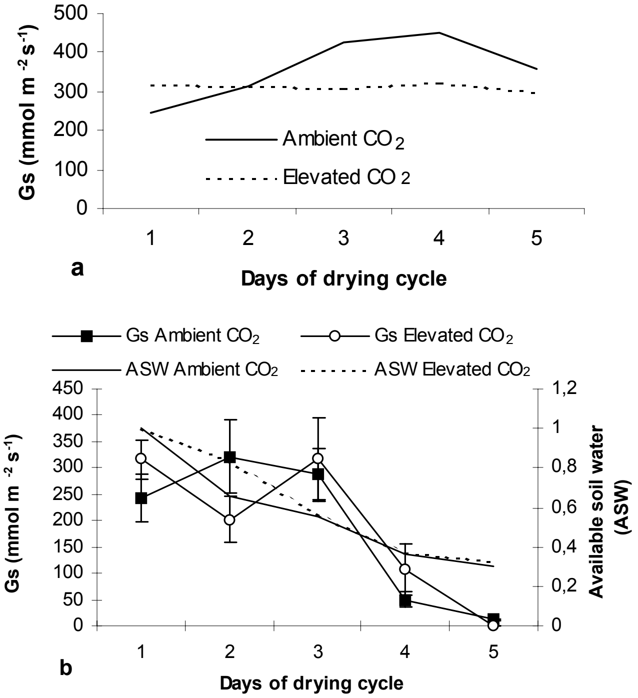

Figure 2 - Variation of stomatal conductance (G_s) in relation to CO_2 concentration and to available soil water (ASW) of *E. grandis* during the four days of the drying cycle. In day 1 all plants were watered to the dripping point: a) well-watered plants; b) droughted plants. Vertical bars indicate standard error.

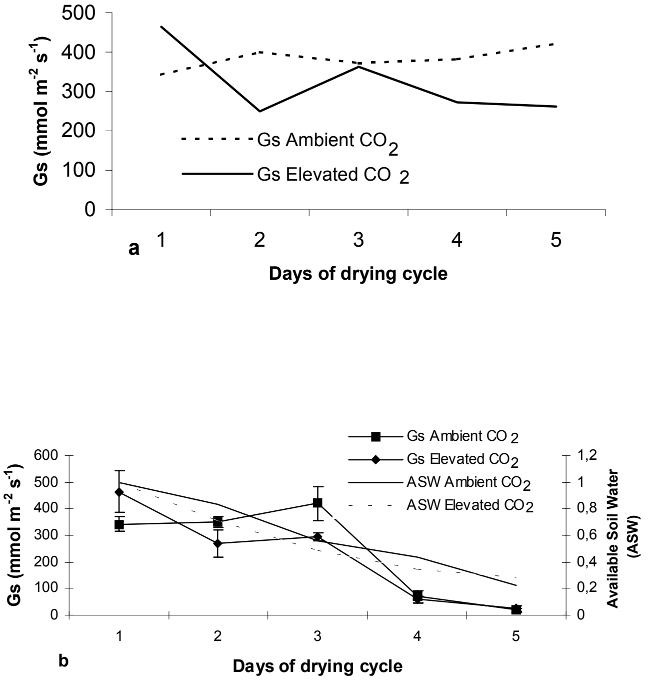

Figure 3 - Variation of stomatal conductance (G_s) in relation to CO_2 concentration and to available soil water (ASW) of *E. camaldulensis* during the four days of the drying cycle: a) well-watered plants; b) droughted plants. Vertical bars indicate standard error.

able capacity. These results are similar to the results obtained by Dunin & Aston (1984) for *E. maculata*. For *E. phaeotrica,* stomatal conductance was higher (P<0.01) (Lima & Jarvis, 1997), and the pattern of decline in stomatal conductance along the drying cycle appeared to be linear (Figure 4). Root dry mass and root:shoot ratio of the plants of this *Monocalyptus* subgenus were much smaller than in the other species, which would lead to a higher sensitivity of stomata to soil drought. A prolonged, comparative study of the biology of root development and water status in relation to drought stress between species of these two subgenera might contribute to a better understanding of these observed differences (Rhizopoulou & Davies, 1991).

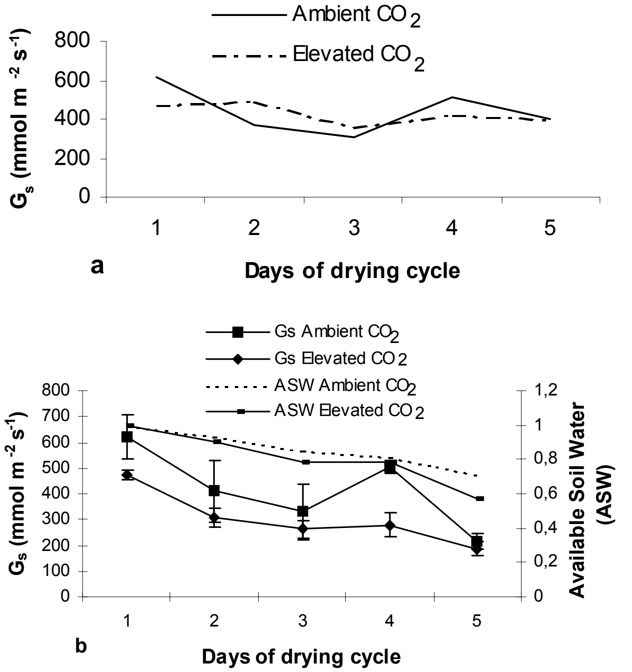

Figure 4 - Variation of stomatal conductance (G_s) in relation to CO_2 concentration and to available soil water (ASW) of *E. phaeotrica* during the four days of the drying cycle: a) well-watered plants; b) droughted plants. Vertical bars indicate standard error.

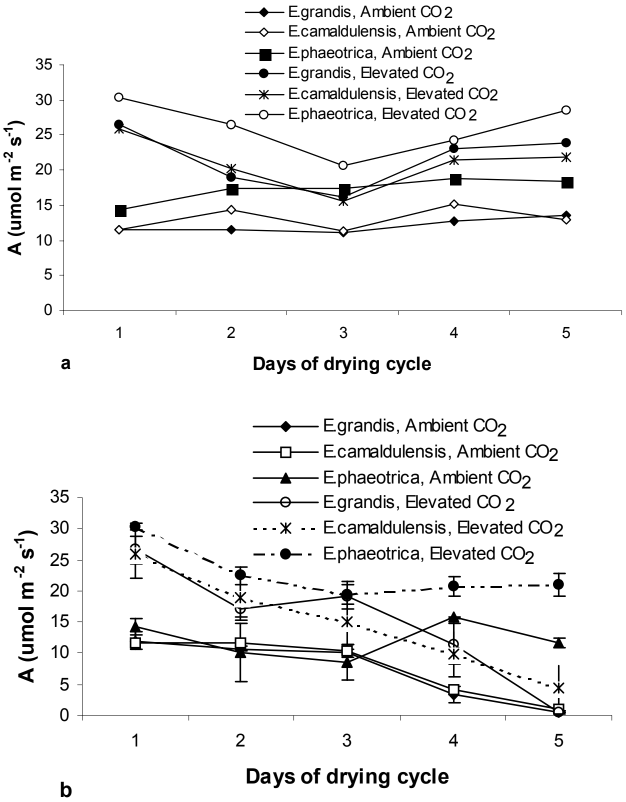

Figure 5 - Variation of net photosynthetic rate (A) in relation to CO_2 concentration during the drying cycle for *E. grandis*, *E. camaldulensis* and *E. phaeotrica*. a) control, well-watered plants; b) water stressed plants: Vertical bars indicate standard error.

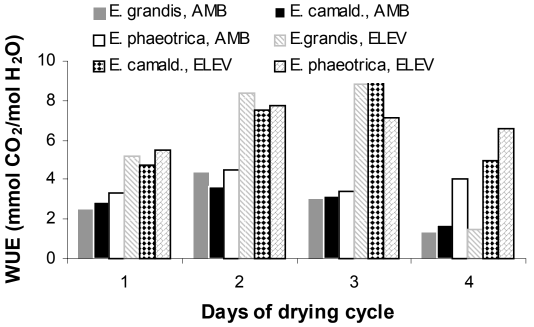

Figure 6 - Instantaneous values of water use efficiency (WUE) in relation to elevated CO_2 and to water stress during a four-day drying cycle.

Photosynthetic rates of the plants in elevated [CO_2] were consistently higher than those on ambient [CO_2] throughout the drying cycle (Figure 5). Moreover, the photosynthetic rate of both ambient and elevated [CO_2] plants declined steadily with increasing drought stress during the drying cycle, as in other cases (Sharkey, 1990). The photosynthetic rate of *E. phaeotrica* was higher even in the fourth day of the drought stress (Figure 5). Although the stomata began to close early during the drought stress period, water use efficiency remained relatively higher in the plants grown in elevated [CO_2], (Figure 6). Elevated [CO_2] elicited an improvement in photosynthetic uptake of [CO_2] by all species, and this was maintained throughout the drought stress period. These findings are in agreement with some inferences in the literature, that suggest that elevated [CO_2] may partly compensate for the negative effects of drought stress (*e.g.*, Tolley & Strain, 1984, 1985; Chaves & Pereira, 1992).

Drought stress led to a fall in the F_v/F_m ratio in all five species, but the degree of response varied among the species (Figures 7, 8 and 9). The pattern of decrease was in general similar in plants grown under both ambient and elevated [CO_2] conditions, although there were some slight differences among the species. *E. camaldulensis* and *E. phaeotrica* responded similarly in both ambient and elevated [CO_2], whereas ambient [CO_2] plants of *E. grandis* showed a higher susceptibility to photoinhibition than did the elevated [CO_2] plants. Ogren & Evans (1992) observed photoinhibition, or depression of the quantum yield of photosystem II, which is given by the decrease in the F_v/F_m ratio, to be a common phenomenon in six *Eucalyptus* species.

The percentage decrease in the F_v/F_m ratio of the stressed plants was compared to the control plants; *E. camaldulensis* appeared to be a little more sensitive to photoinhibition, what is in agreement with the results of Ogren & Evans (1992). A well developed mechanism of protection against permanent photoinhibition overall decline in the F_v/F_m ratio with stress, can be seen as an important component of a strategy of tolerance to drought stress (Scheuermann et al., 1991).

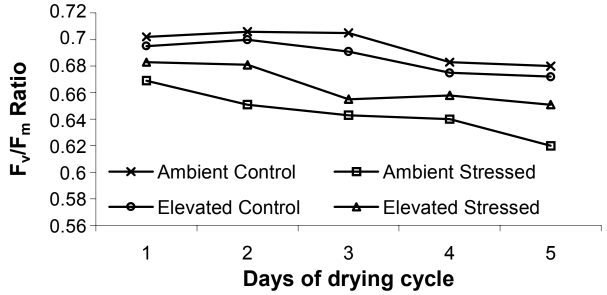

Figure 7 - Variation of the F_v/F_m ratio of *E.grandis* in relation to CO_2 concentration during the drying cycle.

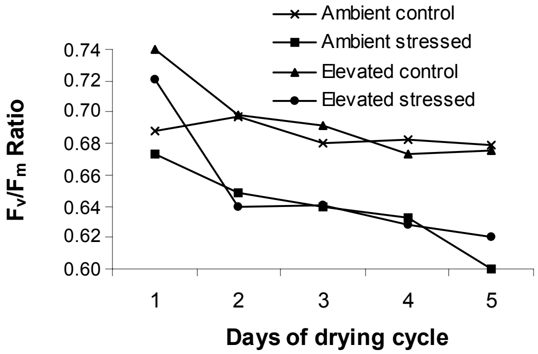

Figure 8 - Variation of the F_v/F_m ratio of *E. camaldulensiss* in relation to CO_2 concentration during the drying cycle.

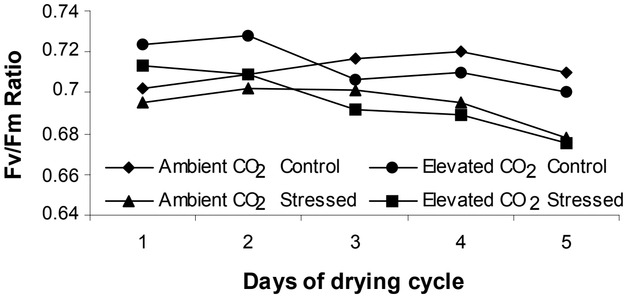

Figure 9 - Variation of the F_v/F_m ratio of *E. phaeotrica* in relation to CO_2 concentration during the drying cycle.

CONCLUSIONS

The stomatal responses to elevated CO_2 concentration and drought stress, in terms of stomatal conductance, photosynthesis, transpiration, water use efficiency and photoinhibition of photosynthesis of the studied *Eucalyptus* species were similar to results obtained with other tree species. Observed differences in stomatal responses between *Monocalyptus* and *Symphyomyrtus* were also verified.

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