THE EFFECTS OF ELEVATED CONCENTRATION OF CO_2 ON GAS EXCHANGE OF FIVE COMMERCIALLY IMPORTANT EUCALYPTUS SPECIES

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ABSTRACT

Five *Eucalyptus* species (*Eucalyptus grandis, Eucalyptus urophylla, Eucalyptus torelliana, Eucalyptus camaldulensis* and *Eucalyptus phaeotrica*), which are among the ten most used in large scale plantations, were selected for a study of the effects of elevated concentration of CO_2 on the gas exchange of seedlings. 2.5-month old seedlings of these species, growing in four-liter pots, were put into four pairs of open-top chambers, so 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}. The plants were watered daily with a solution of a 20:20:20 soluble commercial fertilizer and grew in the chambers during a 100 day period, after which gas exchange measurements were taken in at least two fully expanded leaves per plant. Elevated concentration of CO_2 resulted in substantial increases in the rate of photosynthesis of all studied species, with enhancement ratios ranging from 96% (*Eucalyptus urophylla*) to 82% (*Eucalyptus phaeotrica*). Stomatal conductance was not significantly affected by elevated CO_2, even though the overall results showed a slight trend of decreased stomatal conductance with elevated CO_2 concentration. Downregulation, or a decrease in the photosynthetic rate due to acclimation to high CO_2 has not been observed during the study period.

INTRODUCTION

Eucalyptus species have an important role in plantation forestry development. Up to 1973, the total planted area in some 90 countries of the world amounted to approximately four million hectares. In 1987, the area was estimated to be around six million hectares, with a potential productivity of the order of 30 million tonnes of dry wood per year (ELDRIDGE & CROMER, 1987).

The ten most important eucalypt species used in plantations around the world, in terms of current annual increment of wood, are: *Eucalyptus grandis, Eucalyptus camaldulensis, Eucalyptus tereticornis, Eucalyptus globulus, Eucalyptus viminalis, Eucalyptus saligna, Eucalyptus urophylla, Eucalyptus deglupta, Eucalyptus exserta, Eucalyptus citriodora, Eucalyptus paniculata* and *Eucalyptus robusta* (ELDRIDGE & CROMER, 1987). All these species are in the subgenus *Symphyomyrtus*, except for *Eucalyptus citriodora*, which is in the subgenus *Corymbia*.

Questions about the environmental effects of eucalypt plantations persist in many countries and the so called "eucalypt controversy" is far from resolved. Indeed, the debate parallels the increase in planted areas. A major environmental impact inherently associated with eucalypts is related to their water consumption, and their "soil drying power". Speculations about this have been exhaustively explored in most of the countries where eucalypts are planted, as can be inferred from many references (see LIMA, 1993).

Of particular importance in this respect is the quantitative knowledge about the closure of stomata in response to increasing soil water stress and to increasing atmospheric saturation deficit, which has been shown to occur in many tree species, including eucalypts (MCNAUGHTON & JARVIS, 1983, PEREIRA et al., 1986).

In a recent review of the available

evidence, LIMA (1993) concluded that studies related to stomatal responses are much needed for the eucalyptus genus. Such investigations are fundamental but have received little study so far, and this makes it difficult to generalize about canopy resistance, stomatal conductance, and stomatal control of transpiration for the eucalypts. Another interesting aspect of the response of stomata is their response to the rising atmospheric carbon dioxide concentration. Usually, stomata open as the intercellular concentration of carbon dioxide decreases and close as it increases. Clearly, interactions between water use, increased carbon dioxide concentration and stomatal functioning are likely to result in far reaching consequences with regard to photosynthesis, transpiration, and water use efficiency of future plantations forests. The steady build up of atmospheric CO_2 concentration is unquestionable and this is likely to have many direct and indirect effects on plant species (EAMUS & JARVIS, 1989, JARVIS, 1989, HOUGHTON et al, Eds., 1990, GOULDRIAAN & UNSWORTH, 1990, EAMUS, 1991). Therefore, it is important to know where these effects may lead to in terms of survival, acclimation, productivity, water relations, and stomatal behaviour, in order to be able to anticipate significant ecological, socio-economic and management consequences.

In this work, five commercially important *Eucalyptus* species, among the most widely used species for large scale plantations, have been chosen for a study of the effects of elevated CO_2 concentration on gas exchange parameters.

Seedlings of these species were grown in a set of four pairs of open-top chambers, in which controlled CO_2 concentrations were continuously maintained by automated computerized system. Even though most of such studies of the effects of elevated CO_2 concentration on tree species have been done with seedlings in artificial, controlled environments (JARVIS, 1989), it is recognized that there are some limitations involved in this technique (KRAMER, 1981, EAMUS & JARVIS, 1989, LAWLOR & MITCHELL, 1991, ARP, 1991). Nevertheless, WONG & DUNIN (1987), measuring gas exchange of a large *Eucalyptus maculata* tree growing in a weighing lysimeter located within a forest in Australia in relation to a range of CO_2 concentrations, observed that the responses of canopy photosynthesis, transpiration and stomatal conductance were similar to those obtained with a leaf clamped in the cuvette of a portable gas exchange system.

MATERIAL AND METHODS

Species

Five *Eucalyptus* species were selected for the experiment: *Eucalyptus grandis, Eucalyptus urophylla, Eucalyptus camaldulensis, Eucalyptus torelliana* and *Eucalyptus phaeotrica.*

The selection was based, first of all, on the importance of the species with regard to their utilization in large-scale, industrial, plantation forests in tropical and sub-tropical regions.

A second selection criterion was the sub-genus. The first three species belong to the sub-genus *Symphyomyrtus*, whilst *Eucalyptus torelliana* is from the sub-genus *Corymbia*, and *Eucayptus phaeotrica* is one of the few *Monocalyptus* that grows succesfully in plantations outside Australia. As reviewed by NOBEL (1989), there may be contrasting growth responses amongst these sub-genera to environmental factors.

Within the group of *Symphyomyrtus* species, the final selection criterion was their growth habit in their natural environment. Both *Eucalyptus grandis* and *Eucalyptus urophylla* are species of tall forests. However, the former is a Gum type tree species, whereas *Eucalyptus urophylla* is of the Fibrous Bark type. *Eucalyptus camaldulensis*, on the other hand, is a *Symphyomyrtus* species typical of open woodland.

Seeds of these five selected species were obtained from IPEF (Institute of Forest Research and Studies), in Piracicaba, State of São Paulo, Brazil. Seeds from *Eucalyptus grandis, Eucalyptus urophylla, Eucalyptus camaldulensis* and *Eucalyptus phaeotrica* were collected in the Anhembi Forest Experiment Station, of the Forestry Department, University of São Paulo. The seed source of *Eucalyptus torelliana* was Ouriçangas, State of Minas Gerais, Brazil.

Cultivation

Seeds were germinated during the first week of February 1992 in individual plastic containers filled with peat and topped with vermiculite, in the glasshouse. After establishment, the seedlings in each container were thinned periodically to a final density of one plant per container.

The seedlings stayed in the glasshouse for two months after germination, when they were transplanted to 4 dm^3 plastic pots filled with a 7:3:2 mixture of loam soil:sand:peat. To this mixture, 150 g of lime and 75 g of ENMAG 4:19:10 fertilizer was added, which was equivalent to a rate of approximately 20 g of 4:19:10 N:P:K per plant. The potted seedlings remained in the glasshouse for two additional weeks, to allow for adequate adjustment to the new substrate.

The potted seedlings were finally placed in the open-top chambers on the 21st of April, at the age of 2.5 months. Two pots of each species were placed randonly 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 glasshouse outside the open-top chambers, but adjacent to them.

The plants were irrigated daily with a solution (one measure in 9 dm^3 of water, Formula 3 Soluble Plant Food, Chempak Products, UK), containing 20:20:20 N:P:K plus micronutrients. Once a week, the amount of soluble fertilizer added to the irrigation water was doubled.

Open-top chambers

The system of open-top growth chambers consisted of a set of 8 chambers located inside a glasshouse at the University of Edinburgh (55° 31' N, 3° 12' W), at an elevation of 185 m, arranged as four pairs of chambers, one with ambient CO_2 and one elevated CO_2 concentration, giving an experimental layout in which each pair of chambers was replicated four times.

The chambers were made out of transparent polypropylene (about 15% light attenuation) and had dimensions of 1.25 m in diameter, 1.25 m in height, and a total volume of about 1.5 m^3.

Air from outside the glasshouse was constantly blown into the chambers. 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 ambient CO_2 chambers at 350 ± 30 $\mu mol.mol^{-1}$, and at 700 ± 30 $\mu mol.mol^{-1}$ in the elevated CO_2 chambers. The CO_2 concentration in the chambers was continuously monitored by an infra-red gas analyzer (PP Systems, Hertfordshire, UK), which was calibrated regularly.

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

a) Growth in elevated CO_2/ Measured in elevated CO_2 (E/E): prior to the measurements, the air intake fo the gas exchange system was placed in one of the high CO_2 chambers. After equilibration of the chamber, the elevated CO_2 plants were measured. These plants were then transfered to the ambient CO_2 chambers for over one hour, for short-term acclimation.

b) Growth in ambient CO_2/ Measured in ambient CO_2 (A/A): the air intake was now placed into an ambient CO_2 chamber, and measurements wee made on all ambient CO_2 plants. These plants were then placed into the elevated CO_2 chambers for short-term acclimation for a similar period of time.

After acclimation, the measurements were repeated inversely, that is:

c) Growth in elevated CO_2/ Measured in ambient CO_2 (E/A) : elevated CO_2 plants, short-term acclimated to ambient CO_2, were measured with the air intake in an elevated CO_2 chamber.

d) Growth in ambient CO_2 / Measured in elevated CO_2 (A/E) : ambient CO_2 plants, short-term acclimated to elevated CO_2, were measured with the air intake in an elevated CO_2 chamber.

All measurements were made during the period between 9:30 and 14:00 h each time, 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 around 1000 $\mu mol.m^{-2}.s^{-1}$.

Data analysis

First, gas exchange data were analyzed by split-plot analysis of variance, with individual chamber as the main plot, split into five species as sub-plots. The main effect of CO_2 was tested with the CO_2 x Chamber error term. The main effect of species and the interaction Species x CO_2 was tested with the CO_2 x Chamber x Species 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 GLM of SAS (SAS Inst. Inc, 1993). All tests of significance were made at the 0.05 level of probability. The significance of the differences among treatment means was evaluated by Duncan's Multiple Range Test.

RESULTS AND DISCUSSION

Figure 1 shows the average micrometeorological conditions inside the open-top chambers during the week of gas exchange measurements. It can be seen that the prevailing average photon flux density were not adequate for a good set of gas exchange measurements and this was the reason we decided to use an artificial light source attached to the cuvette.

Growth in elevated CO_2 resulted in substantial, statistically significant, increases in the rate of photosynthesis of all species, as well as in the instantaneous water use efficiency (Table 1).

These positive responses to CO_2 enrichment are in agreement with the results found in similar studies with other tree species, including eucalypts (SIONIT et al, 1985, HIGGINBOTHAM et al, 1985, OBERBAUER et al, 1985, NORBY et al, 1986, HOLLINGER, 1987, BARLOW & CONROY, 1989, ZISKA et al, 1991, WULLSCHLEGER et al, 1992, ROUHIER et al, 1992, CONROY et al, 1992, BUNCE, 1992, RADOGLOU et al, 1992, CEULEMANS & MOUSSEAU, 1994, AMTHOR, 1995, DRAKE & GONZALEZ-MELER, 1996). Nevertheless, there have been studies with tree species in which elevated CO2 did not stimulate growth (REEKIE & BAZZAZ, 1989, KORNER & ARNONE, 1992),

Comparative values of photosynthetic rates among the species, in both ambient and elevatged CO_2 concentrations, together with the CO_2 concentration in the cuvette during gas exchange measurements, are shown in Figure 2. Short-term acclimation of ambient CO_2 grown plants to elevated CO_2 concentration also increased photosynthesis, but not to the same extent as was achieved by the plants grown and measured in elevated CO_2 (long-term acclimation).

Conversely, plants grown in elevated CO_2, and which were short-term acclimated to the ambient CO_2 concentration, had about the same photosynthetic rates as plants grown in ambient CO_2. These results indicate that downregulation of photosynthesis in elevated CO_2 did not occur, a result that can also be deduced from analysis of the *A*/Ci curves for the species.

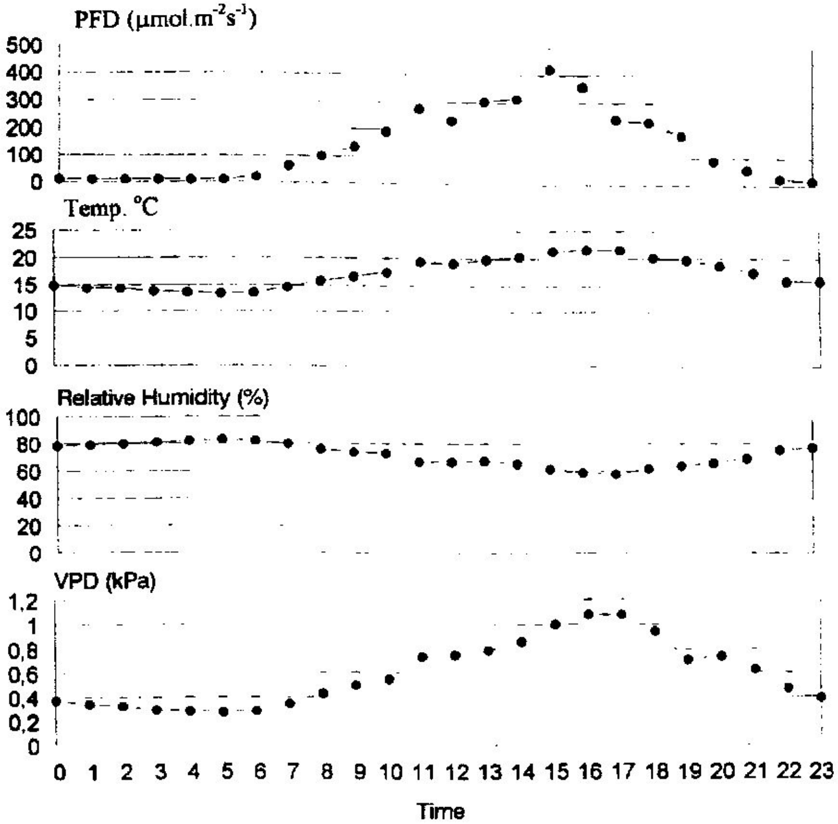

FIGURE 1. Average micrometeorological conditions inside the open-top chambers. Diurnal variations of PFD, air temperature, relative humidity, and vapour pressure deficit are averages for the week of gas exchange measurements (22-31 July, 1992).

TABLE 1. Average increases in photosynthetic rate (enhancement ratio, calculated as the percentage increase above the ambient CO_2) and water use efficiency (also calculated as a percentage increase above ambient CO_2) as a result of doubling the CO_2 concentration.

Species	Enhancement ratio (%)	Increase in WUE (%)
E. grandis	134	62
E. phaeotrica	130	82
E.camaldulensis	122	53
E. torelliana	107	72
E. urophylla	96	36

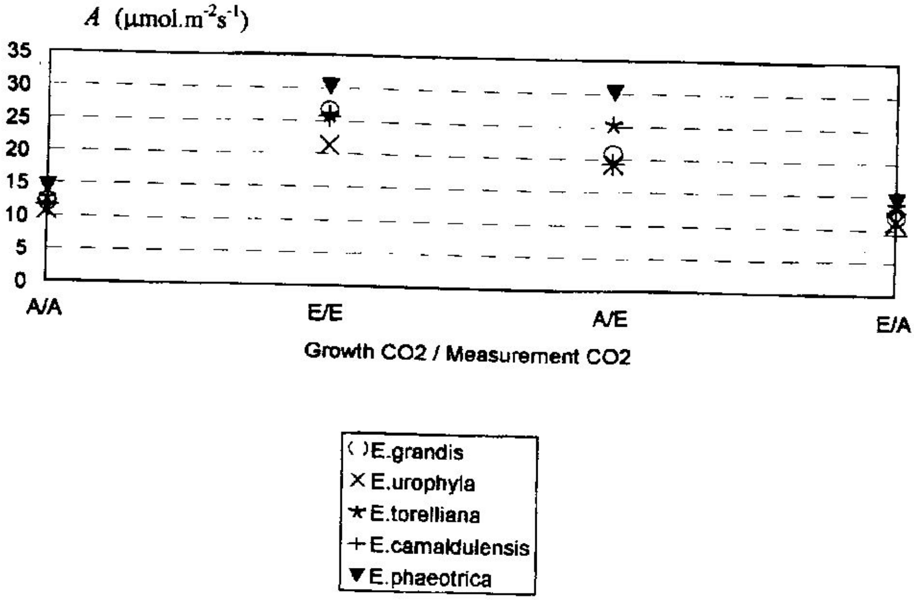

FIGURE 2. Net photosynthetic rate (A) of plants grown and measured in ambient CO_2 concentration (A/A), grown and measured in elevated CO_2 (E/E), as well as plants which were grown in ambient CO_2, but measured in elevated CO_2 after short-term acclimation (A/E), and the reverse (E/A).

However, although significant, these results of elevated CO_2 concentration on photosynthesis should still be seen as a short-term response of seedlings to high CO_2, and not used to make predictions of the likely impacts of increasing atmospheric CO_2 concentrations at the stand scale. Young trees are usually more sensitive to environmental changes than mature tress, and consequently their responses may be larger than in mature trees (EAMUS & JARVIS, 1989).

Nevertheless, long-term studies of the effects of elevated CO_2 concentration, such as those by IDSO & KIMBAL (1992a and 1992b) with sour orange trees growing in elevated CO_2 for four years, as well as modelling of whole canopy responses to elevated CO_2 concentration (REYNOLDS et al., 1992), suggest that these short-term responses may give a general indication of the possible effects of increasing atmospheric CO_2 concentration on tree growth.

Overall, stomatal conductance was not affected by growth in elevated CO_2 concentration. The overall results, however, do show a general downward trend in stomatal conductance with increased CO_2, and short-term acclimation to elevated CO_2 of plants grown in ambient CO_2 gave consistent, similar decreases in stomatal conductance for all species (Figure 3).

Stomatal conductance differed among the species. In general, the stomatal responses to elevated CO_2 varied from no-response (*Eucalyptus urophylla*), increased stomatal conductance (*Eucalyptus grandis* and *Eucalytus camaldulensis*), and decreased stomatal conductance (*Eucalyptus torelliana* and *Eucalyptus phaeotrica*).

The values of measured stomatal conductance are well within the range of values found in the literature for eucalypts (KUPPERS et al, 1986, PEREIRA et al, 1986, WONG & DUNIN, 1987, ITO & SUZAKI, 1990, ROBERTS et al., 1992, DYE & OLBRICH, 1992).

The average values of transpiration for each species in relation to the CO_2 concentration in which they were grown and in which they were measured are given in Table 2. Transpiration rates, taken collectively, are significantly higher for the plants grown in elevated CO_2 than in ambient CO_2.

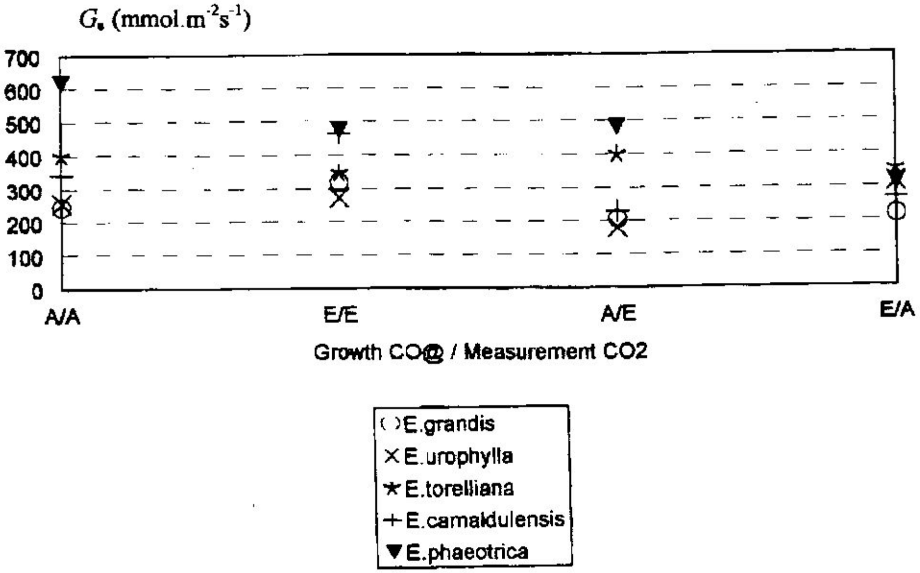

FIGURE 3. Stomatal conductance of plants grown and measured in ambient CO$_2$ concentrations (A/A), grown and measured in elevated CO$_2$ (E/E), grown in ambient but measured in elevated CO$_2$ (A/E), and grown in elevated but measured in ambient CO$_2$ (E/A).

TABLE 2. Average transpiration rate in relation to growth and measurement CO$_2$ concentrations, together with one standard error of the mean (SE) in parentheses.

Growth CO$_2$	CO$_2$ concentration during gas exchange measurements (µmol.mol^{-1})									
	Eucalyptus grandis		*Eucalyptus urophyla*		*Eucalyptus torelliana*		*Eucalyptus camaldulensis*		*Eucalyptus phaeotrica*	
	350	700	350	700	350	700	350	700	350	700
	(mmol.m^{-2}.s^{-1})									
350	2.9 (0.3)	2.9 (0.5)	2.4 (0.2)	2.4 (0.3)	3.2 (0.3)	3.5 (0.4)	3.2 (0.3)	2.9 (0.3)	3.9 (0.3)	4.1 (0.1)
700	3.5 (0.2)	3.9 (0.2)	3.8 (0.5)	3.5 (0.4)	4.0 (0.2)	3.9 (0.3)	3.2 (0.5)	4.7 (0.3)	4.5 (0.3)	4.4 (0.2)

The increases in water use efficiency which have been found in experiments with elevated CO_2 concentrations are usually a result of both increased photosynthesis and reduced transpiration (because of a decrease in stomatal conductance). The proportion of these two effects in eliciting an increase in WUE varies with species (ACOCK, 1990), and some studies on trees have shown an increase in stomatal conductance in elevated CO_2 concentration. A more realistic evaluation of the exact response of stomatal conductance to CO_2 should consider the interactive effects of CO_2 concentration, vapour pressure deficit, temperature, photon flux density and plant water status (EAMUS & JARVIS, 1989).

In this investigation, the observed increases in WUE of the plants grown in elevated CO_2 concentration (Figure 4) were mainly the result of the substantial increase in the photosynthetic rates of the plants.

Nevertheless, when we consider the results of short-term acclimation to elevated CO_2 of the plants grown in ambient CO_2, there was a decrease in transpiration, and, in this case, the resultant increase in WUE was a consequence of both increased photosynthesis and decreased transpiration.

CONCLUSIONS

Elevated CO_2 concentration resulted in substantial increases in the rate of photosynthesis of all five species, with enhancement ratios ranging from 96% (*Eucalyptus urophylla*) to 134% (*Eucalyptus grandis*).

Water use efficiency was also substantially increased in all five species, the increase ranging from 36% (*Eucalyptus urophylla)* to 82% (*Eucalyptus phaeotrica*).

During the 3-month period of growth in elevated CO_2 concentration, there was no indication of downregulation, or a decrease in photosynthetic rate resulting from acclimation to elevated CO_2.

Stomatal conductance was not significantly affected by elevated CO_2 concentration, even though the results, taken collectively, showed a slight trend of decreased stomatal conductance with increased CO_2 concentration.

Most of the observed increase in water use efficiency in all species was primarily a result of the large increase in photosynthetic rate caused by elevated CO_2 concentration.

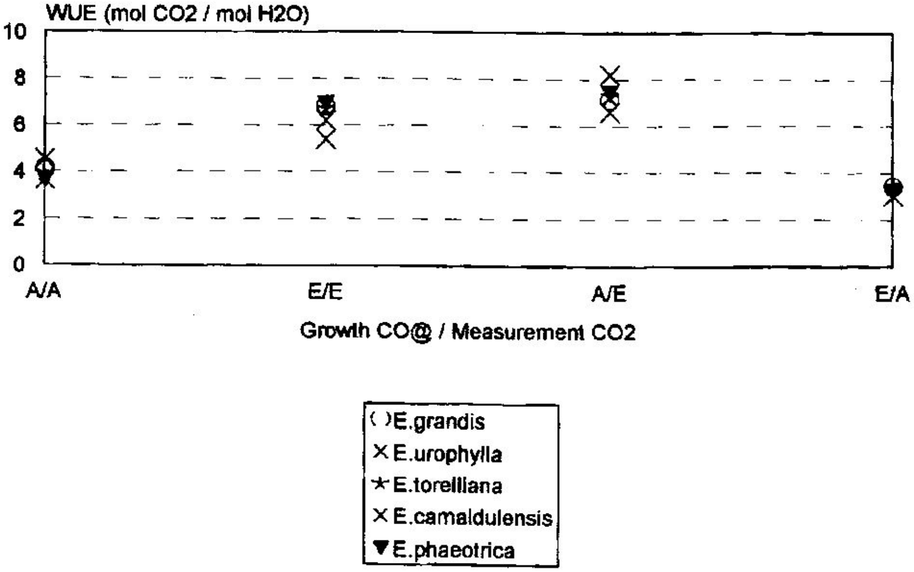

FIGURE 4. Instantaneous water use efficiency of plants grown and measured in ambient CO_2 (A/A), grown and measured in elevated CO_2 (E/E), grown in ambient but measured in elevated CO_2 (A/E) and grown in elevated but measured in ambient CO_2 concentration (E/A).

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