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The Effect of Elevated [CO_2] on Growth and Photosynthesis of Two Eucalyptus Species Exposed to High Temperatures and Water Deficits

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Two species of eucalyptus (*Eucalyptus macrorhyncha* and *Eucalyptus rossii*) were grown for 8 weeks in either ambient (350 μL L^{-1}) or elevated (700 μL L^{-1}) CO_2 concentrations, either well watered or without water additions, and subjected to a daily, 3-h high-temperature (45°C, maximum) and high-light (1250 μmol photons m^{-2} s^{-1}, maximum) stress period. Water-stressed seedlings of *E. macrorhyncha* had higher leaf water potentials when grown in elevated [CO_2]. Growth analysis indicated that increased [CO_2] may allow eucalyptus species to perform better during conditions of low soil moisture. A down-regulation of photosynthetic capacity was observed for seedlings grown in elevated [CO_2] when well watered but not when water stressed. Well-watered seedlings grown in elevated [CO_2] had lower quantum efficiencies as measured by chlorophyll fluorescence (the ratio of variable to maximal chlorophyll fluorescence [F_v/F_m]) than seedlings grown in ambient [CO_2] during the high-temperature stress period. However, no significant differences in F_v/F_m were observed between CO_2 treatments when water was withheld. The reductions in dark-adapted F_v/F_m for plants grown in elevated [CO_2] were not well correlated with increased xanthophyll cycle photoprotection. However, reductions in the F_v/F_m were correlated with increased levels of nonstructural carbohydrates. The reduction in quantum efficiencies for plants grown in elevated [CO_2] is discussed in the context of feedback inhibition of electron transport associated with starch accumulation and variation in sink strength.

The enhanced greenhouse effect may modify temperature variation as well as the global mean, potentially causing an increase in extreme temperature events (Katz and Brown, 1992). A shift in the distribution or abundance of a species with climate change may be related to the response of seedlings to extreme stress events (Rind et al., 1989). Many studies have predicted an increase in the enhancement of carbon gain associated with elevated [CO_2] at higher temperatures (Long, 1991; Badger, 1992). Although some studies have demonstrated enhanced growth when plants were grown in elevated [CO_2] at temperature extremes (Kriedemann et al., 1976), others (Bassow et al., 1994) have found that shade-tolerant species have an increased susceptibility to heat shock when grown in elevated [CO_2].

Photosynthesis is particularly sensitive to thermal stress, with increased photoinhibition of PSII observed at temperature extremes (Weis and Berry, 1988; Georgieva and Yordanov, 1993). Photoinhibition is a light-dependent reduction in the quantum efficiency of photosynthesis. Photoinhibition can result from photoprotection in which excessive excitation energy is deflected away from PSII and dissipated harmlessly (primarily as heat), as well as from direct photodamage to PSII reaction centers (Osmond, 1994). Leaf temperatures above some threshold (40–50°C, depending on the species tested and the growth temperature) have been shown to cause reductions in PSII activity (Björkman and Powles, 1984; Ludlow and Björkman, 1984), possibly due to thermal denaturation of PSII (Terzaghi et al., 1989). Photoinhibition during high-temperature stress may be an important factor influencing photosynthetic productivity of plants in the field (Bongi and Long, 1987). In previous experiments, we have shown that eucalyptus species exposed to high-temperature (45°C air temperature) and high-irradiance regimes had lower photosynthetic efficiencies when grown in elevated [CO_2] than in ambient [CO_2] (Roden and Ball, 1996). Increased photoinhibition for leaves grown in elevated [CO_2] was associated with an increased concentration of nonstructural carbohydrates.

Sink activity may regulate photosynthetic rates through feedback mechanisms (Farquhar and Sharkey, 1994; Sheen, 1994). The down-regulation of photosynthesis of plants grown in elevated [CO_2] is often associated with starch accumulation (Tissue et al., 1993). Pammenter et al. (1993) found that short-term (4 h) increases in [CO_2] cause a reduction in Φ_{PSII}, indicating that excess carbohydrate synthesis may stimulate mechanisms that reduce photosyn-

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Abbreviations: A, antheraxanthin; Chl, chlorophyll; C_i, intercellular CO_2 concentration; F_m, maximal chlorophyll fluorescence level when PSII centers are closed; F_m', F_m measured after induction of quenching; F_o, minimal chlorophyll fluorescence level when PSII centers are open; F_s, steady-state chlorophyll fluorescence after induction of quenching; F_v, variable ($F_m - F_o$) chlorophyll fluorescence level; g_s, stomatal conductance; LAR, leaf area ratio; NAR, net assimilation rate; PFD, photon flux density; Φ_{PSII}, quantum efficiency of open PSII reaction centers; ψ_w, leaf water potential; RGR, relative growth rate; V, violaxanthin; V + A + Z, total xanthophyll cycle pool size; Z, zeaxanthin.

thetic electron transport capacity. When plants are sink-limited, larger reductions in Φ_{PSII} have been observed when they are exposed to low $[O_2]$ than when they are non-sink-limited (Harbinson, 1994), implying a restriction of electron transport capacity in response to a reduced demand for ATP and NADPH. Thus, photosynthetic activity might be down-regulated if environmental conditions restrict or prevent a plant from responding with growth to elevated $[CO_2]$.

An increase in temperature with climate change may also be associated with other stresses and, in particular, water stress. Some researchers (Rind et al., 1990) have predicted that increases in atmospheric $[CO_2]$ may intensify droughts. Reduced soil moisture may further restrict the growth of a plant in elevated $[CO_2]$ and potentially increase photoinhibition at temperature extremes. Indeed, Ludlow and Björkman (1984) have asserted that water stress may predispose the photosynthetic apparatus to photoinhibition, which may be exacerbated by temperature extremes. However, reduced soil moisture may also shift the carbon allocation patterns, with more carbon going below ground to roots, increasing the sink for carbon in nonphotosynthetic tissues and reducing the carbohydrate buildup in leaves.

In the present study we examined the effect of drying soil and elevated $[CO_2]$ on the growth and photosynthesis of two species, *Eucalyptus macrorhyncha* and *Eucalyptus rossii*, which were exposed to high-temperature and high-irradiance regimes. These two species coexist in mountainous terrain around Canberra, but are dominant on sheltered (*E. macrorhyncha*) and exposed (*E. rossii*) aspects (Pook and Moore, 1966), and have shown differential responses to elevated $[CO_2]$ when exposed to temperature extremes (Roden and Ball, 1996). However, questions concerning the interactive effects of water stress and elevated $[CO_2]$ during extreme temperature events remain unanswered.

MATERIALS AND METHODS

Plant Material and Growth Conditions

Eucalyptus macrorhyncha F. Muell. ex Benth. and *Eucalyptus rossii* R.T. Baker et H.G. Smith (Myrtaceae) were grown from seed collected on Black Mountain (Australian Capital Territory, Australia). After germination, seedlings were transferred to 11-L pots in a 2:1:1 mixture of sand, peat, and soil. The air temperature in the greenhouse was 20°C (± 5°C) and the PFD was 1100 μmol photons m^{-2} s^{-1} (maximum). After 1 month, 44 plants of similar size for each species were randomized and placed in two growth chambers (Thermoline, Wetherill Park, Australia), with each set at 35/20°C (day/night) and a 10-h photoperiod (750 μmol photons m^{-2} s^{-1}) for 4 d so the plants could make a gradual transition to the higher temperatures of the stress treatment.

Chamber conditions were then changed to provide a midday, 3-h stress period when the temperature and light regimes were 45°C and 1250 μmol photons m^{-2} s^{-1}, respectively. CO_2 concentrations were monitored by an IR gas analyzer and maintained at either ambient (350 ± 30 μL L^{-1}) or twice ambient (700 ± 30 μL L^{-1}) $[CO_2]$ by injecting pure CO_2 via a solenoid switch when the CO_2 concentrations in the chamber decreased below the set point. Both the light and temperature regimes were stepped through a 10-h photoperiod (Roden and Ball, 1996), beginning with a 2-h period at 30/300 (air temperature, °C/PFD, μmol photons m^{-2} s^{-1}), followed by a 1.5-h period at 35/800, and then a 3-h stress period at 45/1250. The chamber was then symmetrically stepped down (1.5 h at 35/800, 2 h at 30/300 to the night regime of 25°C) to simulate a natural diurnal cycle of light and temperature. The chamber environment was changed in steps to allow measurements to be taken during stable conditions (for at least 1 h) at discrete intervals in the cycle. An air temperature of 45°C is not an unrealistic extreme for these eucalyptus species to experience with global warming, since temperatures at screen height (1 m) in Canberra can reach 40°C (Commonwealth Scientific and Industrial Research Organization Ginninderra weather records).

In each chamber, 11 plants for each species were watered daily to field capacity and fertilized three times weekly with one-fifth-strength Hoagland solution throughout the experiment. The remaining plants were watered and fertilized for the first 4 d of the 45°C stress treatment and then water was withheld. Since the last watering for the plants experiencing low soil moisture was a drenching with one-fifth-strength Hoagland solution, water taken up from these pots during the experiment had a similar nutrient status as the water taken up by the well-watered plants. The empty pots were weighed, and subsamples of the soil were dried in an oven at 80°C to estimate soil dry weight in each pot. At weekly intervals the pots were weighed to determine gravimetric soil moisture content. By the end of the experiment, the fresh weight of the largest seedlings still contributed less than 1% of the total weight of the pot. Plants were watered if the soil moisture content decreased below 10% or if there were visible signs of wilting. However, the pot was not watered to field capacity but given the same amount of water that had been transpired in the preceding week (Fig. 1). The plants were randomized within each chamber, and at weekly intervals the plants were re-randomized and placed into the opposite growth chamber (with the CO_2 set point switched as well) to account for any differences between growth chambers.

The RH for both chambers was set to 70% and varied by ±20% when the plants were watered or the doors were opened for measurements. Within chamber light, variation for each step change was quantified at plant height with a quantum sensor (model 190s; Li-Cor, Lincoln, NE) using 24 measuring points and was 325 ± 38/290 ± 33 (PFD ± 1 SD for both chambers), 798 ± 42/763 ± 45, and 1259 ± 64/1251 ± 60 for the stress treatment. Light was provided by eight incandescent and five metal halide bulbs. Air temperature was within 1°C of the set point unless the doors were opened for measurements, when the temperature would decrease (at the highest temperatures) by 3 to 4°C.

No significant difference in air temperature between the two chambers was observed. The seedlings grew in these conditions for a total of 60 d.

Growth and Carbohydrate Measurements

Seven plants of each species were harvested for initial biomass and leaf area measures (leaf area meter model LI-3000, Li-Cor). Roots, leaves, and stems were separated and dry weights were determined after 48 h in an oven set at 80°C. RGR, NAR, and LAR were determined as described by Chiarello et al. (1989). Four plants for each treatment combination were harvested at 30 d, and the remaining seven plants were harvested at the end of the experiment.

Total nonstructural carbohydrates in the foliage were determined using a method developed by J. Masle (unpublished data). Leaf discs (0.785 cm^2) were punched during the 45°C stress treatment with a cork borer, immediately frozen in liquid N_2, and then stored at −80°C. The discs were dried and then ground to a fine powder in liquid N_2 and placed in an Eppendorf tube, and the sample weight was determined. The soluble sugars were extracted by heating the sample plus 500 μL of distilled water to 100°C for 15 min (repeated three times). The sample was spun in a centrifuge (model Z230 M; BHG, Gosheim, Germany), and the combined supernatant for all three extractions was collected. A small amount of activated charcoal was added to absorb impurities, and the tube was spun again. Subsamples of the extract were taken for enzymatic assays of soluble sugars by the method of Jones et al. (1977). Starch in the remaining pellet was hydrolyzed with 100 μL of 5% (w/v) dialyzed clarase 900 (Miles Laboratories, Springvale, Victoria, Australia) in acetate buffer (pH 4.6) added to each tube and incubated for 24 h. The Glc content of the digest was assayed enzymatically as described above.

Chl Fluorescence

A plant efficiency analyzer (Hansatech Instruments, King's Lynn, UK) was utilized to measure the F_o and F_m yields of the youngest, fully expanded leaf on seven plants of each species in each chamber. A dark leaf clip was placed on the leaf for 5 min prior to the measurements. A 5-min dark adaptation was sufficient for relaxation of PSII reaction centers while not allowing a complete recovery from the effects of the treatments. A "true" dark-adapted fluorescence yield was obtained prior to the first photoperiod in the morning. The instrument utilized a time-resolved method to determine F_o with light-emitting diodes that also delivered a saturating pulse of 1900 μmol photons m^{-2} s^{-1} to obtain F_m. F_v and F_v/F_m were calculated for the same leaf for both 35°C periods as well as the midday 45°C stress treatment.

In situ measures of Φ_{PSII} were estimated with a portable pulse-modulated fluorometer (PAM-2000; Walz, Effeltrich, Germany). Dark-adapted values of F_o, F_m, and F_v/F_m were obtained in the morning prior to the first light period. The gain and the intensity of the measuring beam were adjusted in combination to yield a stable F_o reading between 300 and 400 mV and were not changed for the duration of that day's measurements. The intensity of the saturating pulse was 3000 μmol m^2 s^{-1} and the position of the fiber-optic was fixed. Measurements of Φ_{PSII} were estimated during the 45°C stress treatment. Once F_s was obtained, a 0.8-s saturating pulse was given to obtain estimates of F_m'. From these data Φ_{PSII} ($\Delta F/F_m'$) was calculated as described by Genty et al. (1989). Measurements were made on d 38 and 46 of exposure to the stress treatment to quantify Φ_{PSII} for leaves that had grown and developed within the high-temperature treatment.

Measurements of Carotenoids

Since pigments of the xanthophyll cycle have a role in protecting PSII reaction centers from photodamage by increasing nonradiative energy dissipation (Demmig-Adams and Adams, 1992), carotenoid pigments were assayed using an HPLC method described previously (Gilmore and Yamamoto, 1991). Leaf discs (0.785 cm^2) were punched during the 45°C stress treatment with a cork borer and immediately frozen in liquid N_2 and then stored at −80°C. The leaf disc was ground, and the carotenoid and Chl pigments were extracted as described by Roden and Ball (1996). The pigments were analyzed with a variable wavelength detector (model 490, Waters) at 440 nm as described previously (Roden and Ball, 1996).

Gas-Exchange Measurements

Photosynthetic CO_2 assimilation rates at saturating irradiance (1600 μmol photons m^{-2} s^{-1}) and 30°C (±3°C) leaf temperature were determined with a portable photosynthesis apparatus (model LI-6200, LiCor). The youngest, fully expanded leaves were utilized in all cases. Within the cuvette, RH was maintained at 40% (± 10%). Since stomatal conductance differed widely between treatments, photosynthetic capacity was determined at similar values of C_i. The CO_2 concentration in the cuvette was elevated and then scrubbed to a level that would give a C_i value of approximately 300 or 600 μL L^{-1} (±30 μL L^{-1}), and the assimilation rate and C_i were recorded. A plot of assimilation versus C_i for each plant was made, a line was drawn between the two points measured, and the photosynthetic capacity at a C_i of exactly 300 and 600 μL L^{-1} was estimated. The error in the estimate of assimilation (A) by assuming a linear increase with C_i rather than a curvilinear relationship was estimated to be less than 5%, since the measurements were made at a C_i of approximately the desired estimate.

Stomatal conductances were measured at 1- to 2-week intervals for the duration of the experiment with a diffusion porometer (model AP4; DeltaT Devices, Cambridge, UK). Measurements were made on the youngest, fully expanded leaves of seven plants in each treatment combination approximately 1 h after the start of the first light period at 30°C.

ψ_w values at the end of the experiment were measured both prior to the first light period and during the 45°C

stress treatment on cut branches with a pressure chamber (Soil Moisture Equipment, Santa Barbara, CA).

Data were analyzed with a fully factorial analysis of variance test (Systat, Evanston, IL). Unless otherwise noted, treatment differences were assessed as significant at $P \leq 0.05$.

RESULTS

Water Deficits

Gravimetric soil moisture content was greater than 30% in well-watered pots of both species throughout the experiment (Fig. 1). However, there were interspecific differences in rates of soil moisture depletion when watering was withheld under ambient and elevated [CO_2]. Under ambient [CO_2], soil moisture content decreased to 10% within 45 and 52 d of withholding water from pots of *E. rossii* and *E. macrorhyncha*, respectively. Elevation of [CO_2] enhanced the rate of decrease in soil moisture content in pots of *E. rossii*, but had no effect on soil moisture depletion in pots of *E. macrorhyncha*. Thus, *E. rossii* depleted soil moisture more rapidly than *E. macrorhyncha*, with the differences being greater under elevated [CO_2].

Stomatal conductance was affected by both the watering regime and [CO_2] (Fig. 2). Under ambient [CO_2], well-watered plants maintained the highest stomatal conductances, which varied little during the experiment. In contrast, stomatal conductance in well-watered plants under elevated [CO_2] declined for 35 d to minimal values of approximately 30% less than those in ambient [CO_2]. When water was withheld, stomatal conductance declined with time, with the rate of decrease being more rapid in plants grown in elevated than in ambient [CO_2]. Although decline in stomatal conductance was, in general, more rapid than reduction in soil moisture, estimates of soil moisture (Fig. 1) are whole-pot measurements and roots may deplete the water supply locally long before there is a significant reduction in whole-pot water content. By the end of the experiment, stomatal conductance of these water-stressed plants converged to similar values under ambient and elevated [CO_2].

ψ_w was affected by both the watering regime and [CO_2] (Fig. 3). By the end of the experiment, ψ_w was significantly higher, both predawn and during the 45°C stress treatment, in well-watered plants than in plants growing in drying soil. The [CO_2] had no effect on ψ_w in well-watered plants. However, leaves of *E. macrorhyncha* seedlings grown in drying soil had higher ψ_w under elevated than under ambient [CO_2].

Growth

Plant growth was significantly affected by both the watering regime and [CO_2] (Table I). Both species attained similar biomasses under ambient [CO_2], with growth being greater under well-watered than drying conditions. However, growth of *E. rossii* exceeded that of *E. macrorhyncha* under elevated [CO_2]. Plants grown in elevated [CO_2] had greater leaf, stem, and total biomass than plants grown in ambient [CO_2], with growth again being greater under well-watered than drying conditions. However, plants grown in elevated [CO_2] under a drying soil regime achieved a similar total biomass to well-watered plants grown in ambient [CO_2]. Thus, increasing [CO_2] from 350 to 700 $\mu L\ L^{-1}$ eliminated reductions in growth associated with decreasing soil moisture under ambient [CO_2].

A similar trend was seen in RGR (Table I), with well-watered plants grown in elevated [CO_2] showing the highest RGR and plants grown in drying soil under ambient [CO_2] having the lowest RGR. In general, lower RGR in plants grown in drying soil was attributable largely to lower LAR than in well-watered plants. In contrast, an increase in RGR with elevated [CO_2] was mainly associated with an increase in NAR.

Carbon allocation was significantly affected by plant growth under different water and [CO_2] regimes (Table I). There were no interspecific differences in root:shoot ratio when plants were grown under well-watered conditions. In contrast, *E. macrorhyncha* had a greater root:shoot ratio and more root mass per unit of leaf area than *E. rossii* when plants were grown in drying soil. These interspecific differences were accentuated under elevated [CO_2].

Photosynthesis

Rates of photosynthetic CO_2 assimilation were measured under saturating irradiance at two different C_is. Both spe-

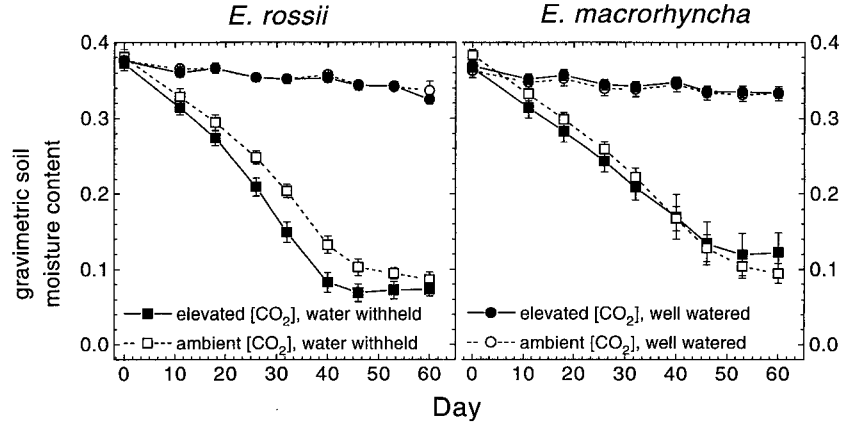

Figure 1. Gravimetric soil moisture content of pots containing two species of eucalyptus growing in either elevated or ambient [CO_2] for 60 d. Pots were either watered daily or no water additions were given until the soil moisture content decreased to less than 10%. Values are means ± SE (n = 7).

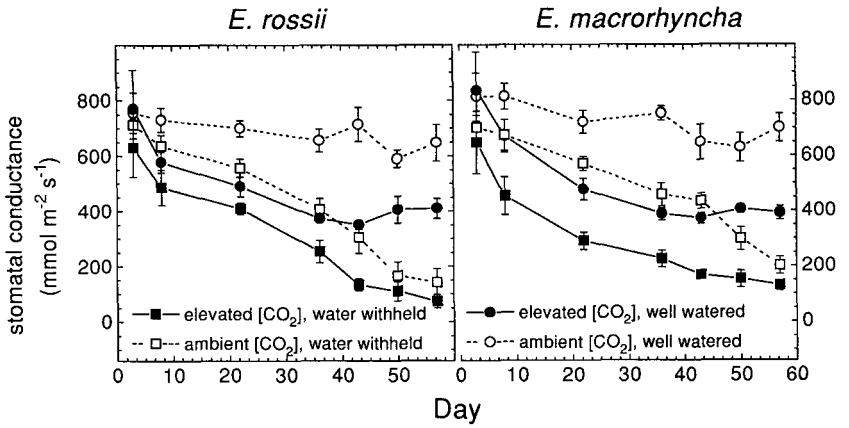

Figure 2. Stomatal conductance of two species of eucalyptus growing in either elevated or ambient [CO_2] for 60 d with or without water additions. Measurements were made on the youngest, fully expanded leaves approximately 1 h after the start of the first light period at 30°C. Values are means ± SE (n = 7).

cies had similar photosynthetic capacities at a C_i of 300 μL L^{-1}. However, *E. rossii* tended to have higher photosynthetic capacities at a C_i of 600 μL L^{-1} than did *E. macrorhyncha* (Fig. 4). Although well-watered plants showed a reduction in photosynthetic capacities when grown in elevated [CO_2], there was no evidence of photosynthetic down-regulation in plants grown in elevated [CO_2] when water was withheld. Indeed, there was a tendency for photosynthetic capacity to be higher in plants grown in drying soil than under well-watered conditions.

Chl Fluorescence

For both species, the 45°C stress period caused a midday depression in photosynthetic efficiency as measured by reductions in F_v/F_m (Fig. 5). However, *E. macrorhyncha* had deeper depressions in F_v/F_m than *E. rossii*. Recovery of F_v/F_m in the afternoon was not symmetrical with the decline in the morning, indicating a carryover effect of the midday depression in F_v/F_m, although recovery of F_v/F_m was complete by the next morning. For well-watered seedlings, midday values of F_v/F_m were generally lower for plants grown in elevated [CO_2] than in ambient [CO_2], with F_v/F_m being lower in *E. macrorhyncha* than in *E. rossii*. The differences in F_v/F_m between species and CO_2 treatments were associated with increases in the F_o. However, when plants were grown in drying soil, the differences in F_v/F_m and F_o between CO_2 treatments disappeared (Fig. 5). These responses were similar for all of the days tested, although for brevity, diurnal fluorescence data have been presented for d 45 only (Fig. 5).

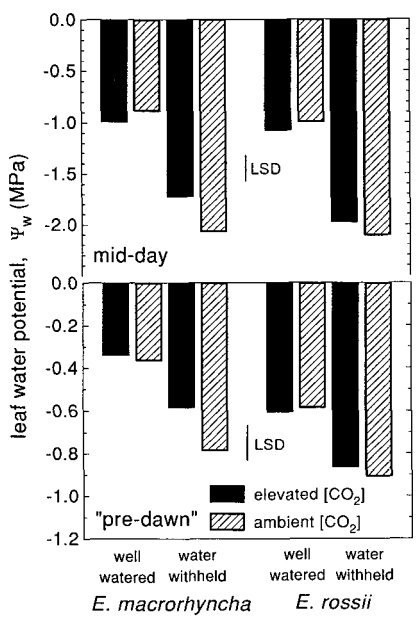

Figure 3. Midday (during the 45°C stress period) or "predawn" (prior to the first light period) ψ_ws measured (on d 59) for two species of eucalyptus growing in either elevated or ambient [CO_2] with or without water additions. The bar indicates the LSD between any two means in each chart (n = 7).

Time-dependent changes in values of F_v/F_m obtained during the midday 45°C stress treatment are shown in Figure 6. In all treatments, values of F_v/F_m declined during the first 10 d of the experiment and then tended to stabilize. When plants were well watered, midday F_v/F_m was greater in seedlings grown under ambient than under elevated [CO_2], with *E. rossii* maintaining higher values of F_v/F_m than *E. macrorhyncha*. In contrast, there were no significant effects of [CO_2] on midday F_v/F_m for plants grown in drying soil. Withholding water seemed to have less effect on the F_v/F_m values for *E. rossii* than for *E. macrorhyncha*. Any chamber differences would have had little effect on these patterns, since the plants were switched between growth cabinets (and randomized) on a weekly basis. Measurements were confined to horizontally displayed leaves to minimize effects of different leaf angles. The juvenile leaf form of these eucalyptus species tends to be displayed horizontally, and by the end of the experiment little change in leaf angles was observed.

Similar patterns were found when the overall Φ_{PSII} was measured in situ during the 45°C stress treatment with a portable pulse-modulated fluorometer (PAM-2000, Walz) near the end of the experiment (Fig. 7). Values of Φ_{PSII} were higher in *E. rossii* than in *E. macrorhyncha* in all treatments. When plants were well watered, values of Φ_{PSII} were lower under elevated than under ambient [CO_2], with *E. macrorhyncha* being the more sensitive species. However, when water was withheld, there were no significant differences in Φ_{PSII} between CO_2 treatments.

Table I. *Effect of elevated [CO_2] on biomass, dry matter partitioning, and growth characteristics of seedlings of E. macrorhyncha and E. rossii grown in well-watered or drying soil for 60 d*

LSD is between any two means in the same row ($P < 0.05$).

Parameter	*E. macrorhyncha*				*E. rossii*				LSD
	Well Watered		Water Withheld		Well Watered		Water Withheld		
	Elevated [CO_2]	*Ambient* [CO_2]	*Elevated* [CO_2]	*Ambient* [CO_2]	*Elevated* [CO_2]	*Ambient* [CO_2]	*Elevated* [CO_2]	*Ambient* [CO_2]	
Dry wt (g)									
Leaf	6.46	4.17	3.98	2.89	7.78	4.66	5.69	3.46	1.13
Stem	1.98	1.45	1.09	0.73	2.54	1.34	1.52	0.94	0.46
Root	1.82	1.93	1.89	1.37	2.54	2.27	1.95	1.15	0.78
Total	10.26	7.55	6.96	4.99	12.85	8.27	9.16	5.54	1.98
Leaf area (cm^2)	913.71	695.11	474.09	330.03	1155.56	734.92	695.75	470.31	178.80
Specific leaf area ($cm^2\ g^{-1}$)	139.7	170.8	116.6	112.7	147.7	156.1	122.0	134.8	17.1
Root:shoot ratio ($g\ g^{-1}$)	0.217	0.354	0.407	0.387	0.247	0.381	0.266	0.261	0.144
Root wt:leaf area ($g\ m^{-2}$)	20.47	27.97	47.40	42.36	22.84	31.79	27.46	25.39	17.85
RGR ($mg\ g^{-1}\ d^{-1}$)	55.3	50.2	48.8	43.1	63.2	55.7	57.5	49.0	
LAR ($m^2\ kg^{-1}$)	8.91	9.20	6.81	6.62	8.99	8.89	7.60	8.49	
NAR ($g\ m^{-2}\ d^{-1}$)	6.21	5.46	7.16	6.51	7.03	6.27	7.57	5.77	

Carotenoids and Carbohydrates

Leaf tissue samples were collected near the end of the experiment for analysis of carotenoid pigments and carbohydrate concentration (Table II). *E. macrorhyncha* had a significantly greater V + A + Z as well as a greater concentration of A + Z relative to the total V + A + Z pool than *E. rossii*. Although there were no significant differences between [CO_2] treatments for either V + A + Z or its composition during midday, there was a consistent increase in pool size and conversion for plants grown in ambient [CO_2]. There were few significant differences between species or CO_2 treatments in total carotenoids or Chls. The concentrations of total carotenoids and Chls were greater in plants grown in drying soil than under well-watered conditions. These increases in pigment concentrations per unit of leaf area might be explained by a decrease in specific leaf area in plants grown in drying soil (Table I). Finally, no significant differences in the Chl *a/b* ratio (approximately 2.9) were observed between species or treatments (data not shown).

By the end of the experiment, the concentration of starch and total nonstructural carbohydrates in leaves of both species were lower in plants grown in drying soil than under well-watered conditions (Table II). Growing plants in elevated [CO_2] tended to increase leaf level starch and total nonstructural carbohydrates. Plants grown in drying soil and elevated [CO_2] had similar leaf level starch concentrations as did well-watered plants grown in ambient [CO_2].

DISCUSSION

During summer in the natural habitat of *E. macrorhyncha* and *E. rossii*, air temperatures can reach 40°C (screen height) and plants can experience prolonged drought. Seedlings could experience even higher temperatures than 45°C, particularly if growing in bare or sparsely covered soil when exposed to direct sunlight and low wind speeds, which occurs in forest gaps. Thus, it is not surprising that both species were able to survive and grow in the high-temperature and low soil moisture treatments. Bassow et al. (1994) found substantial leaf damage and mortality of birch and maple seedlings due to a single 4-h heat stress of 45°C. However, the plants tested were not acclimated to higher temperatures as in the present study. In nature, it is unlikely that seedlings would experience 45°C without being exposed to air temperatures above 35°C for at least 1 or 2 d prior to the extreme event.

Because large pots were used, the soil moisture content decreased slowly, making the results more comparable to the field, where water stress usually develops gradually (Luo and Strain, 1992). The reduced soil moisture for *E. rossii* when grown in elevated [CO_2] as compared with ambient [CO_2] when water is withheld is due to increased growth rates, which causes a more rapid depletion of the soil moisture reserves. Withholding water clearly reduces the water status of both species, which was evidenced by reduced ψ_w and stomatal conductance by the end of the experiment. Many studies have found reductions in stomatal conductance for plants grown in elevated [CO_2], as well as even further reductions in g_S when water deficits are imposed (Tyree and Alexander, 1993; Samarakoon et al., 1995). Reductions in g_S are associated with reduced transpiration rates and increased water use efficiency for plants grown in elevated [CO_2] (Johnsen, 1993; Tyree and Alexander, 1993); however, increased leaf area production often results in similar rates of whole canopy water loss despite reductions in g_S (Prior et al., 1991; Samarakoon et al., 1995).

Plants exposed to reduced soil moisture and grown in elevated [CO_2] often have higher ψ_w than plants grown in ambient [CO_2] (Sionit et al., 1981; Prior et al., 1991; Luo and Strain, 1992; Johnsen, 1993; Tyree and Alexander, 1993), as found with *E. macrorhyncha* in the present study. Increased ψ_w for plants grown in elevated [CO_2] has been associated

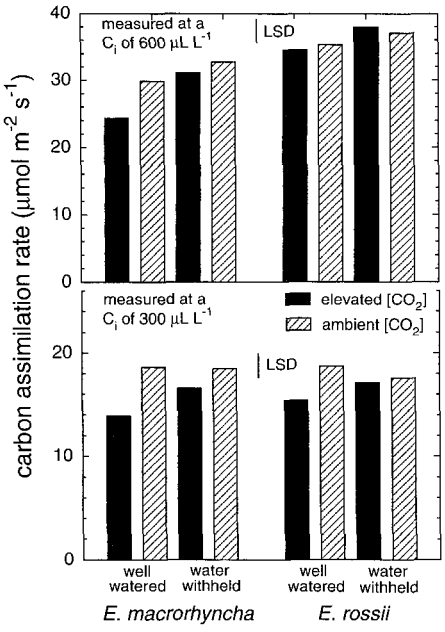

Figure 4. Carbon assimilation rates measured using an open steady-state gas-exchange system at a C_i of either 300 or 600 μL L^{-1} and saturating irradiance (1600 μmol photons m^{-2} s^{-1}) at a leaf temperature of 30°C for *E. macrorhyncha* and *E. rossii* grown for more than 4 weeks in either elevated or ambient [CO_2] and with or without water additions while exposed to a daily high-light and high-temperature (45°C) stress. The bar indicates the LSD between any two means in each chart (n = 6).

with reduced osmotic potentials and/or reductions in the elastic modulus (Sionit et al., 1981; Morse et al., 1993; Tyree and Alexander, 1993).

Withholding water reduces the relative growth rates, total biomass, and leaf area production of both species; however, increased [CO_2] tend to compensate for the reduced soil moisture (Table I). The increase in RGR with increased [CO_2] is due to increased NAR, since LAR remains unchanged or is reduced. In the present study growth enhancement for plants exposed to elevated [CO_2] was 1.36 and 1.40 for *E. macrorhyncha* and 1.55 and 1.65 for *E. rossii* grown in the well-watered and water-withheld treatments, respectively. The growth results for well-watered plants agree with those from previous experiments performed on these same species (Roden and Ball, 1996); however, the magnitude of the enhancement is lower in the present study. The fact that the growth enhancement increases when plants are grown in drying soil implies that the increased sink for carbon in the roots may alleviate some of the feedback limitations for plants grown in elevated [CO_2]. Many studies have shown or predicted increases in root allocation for water-stressed plants grown in elevated [CO_2] (Rogers et al., 1992; Tyree and Alexander, 1993), whereas other studies (Sionit et al., 1981) have found no increase in root:shoot ratios, similar to our findings with *E. rossii* when water was withheld.

The results of the present study agree with predictions (Sionit et al., 1981; Conroy et al., 1986; Gifford, 1992; Luo and Strain, 1992; Johnsen, 1993; Tyree and Alexander, 1993; Samarakoon et al., 1995) that increased atmospheric [CO_2] could enable seedlings to perform better under drought stress. However, it is also clear that species may have different capacities to respond to elevated [CO_2] in stressful environments. *E. rossii* grown in elevated [CO_2] has a greater growth enhancement as well as greater RGR and NAR increases than *E. macrorhyncha* when water is withheld. These results are consistent with the observations that *E. rossii* tends to inhabit the more exposed slopes, which would generally be drier than the sheltered slopes where *E. macrorhyncha* is more prevalent.

Exposure to the 45°C stress treatment (producing leaf temperatures of approximately 40°C) clearly causes a depression in quantum efficiency as measured by reductions in F_v/F_m (Fig. 5). Many studies have demonstrated abrupt increases in photoinhibition above a threshold leaf temperature (usually greater than 40°C, Björkman and Powles, 1984; Ludlow and Björkman, 1984; Terzaghi et al., 1989). The reduction in F_v/F_m is associated with an increase in F_o, obtained after a 5-min dark adaptation, which may be associated with thermal damage of the PSII reaction center (Björkman and Powles, 1984; Weis and Berry, 1988; Terzaghi et al., 1989). The two species respond differently to the

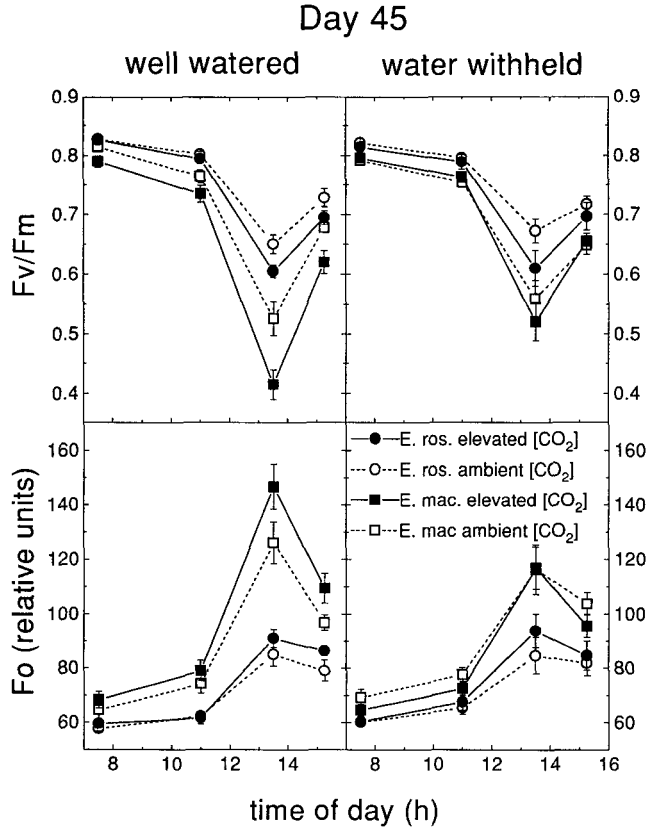

Figure 5. The diurnal time course of F_v/F_m and F_o for *E. macrorhyncha* (E. mac.) and *E. rossii* (E. ros.) grown in either elevated or ambient [CO_2] and with or without water additions while exposed to a daily high-light and high-temperature (45°C) stress. Measurements were made on d 45 with a plant efficiency analyzer meter using a 5-min dark adaptation. The observations prior to 8 AM were measured before the first light period. Values are means ± SE (n = 7).

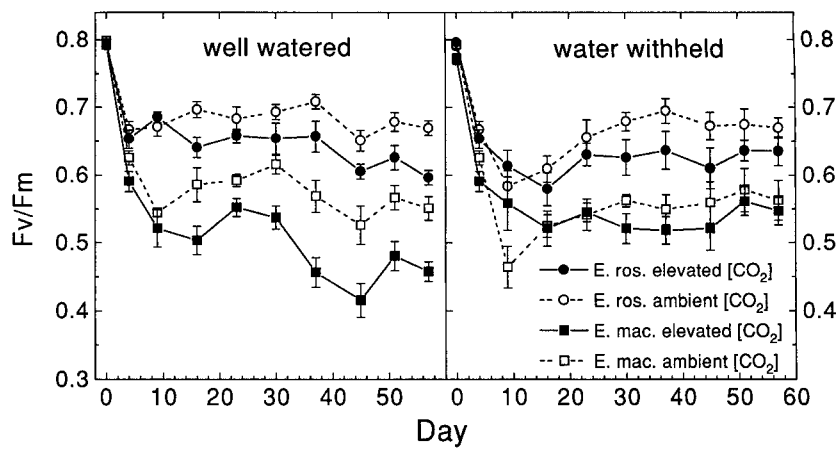

Figure 6. The time course of F_v/F_m for *E. macrorhyncha* (E. mac.) and *E. rossii* (E. ros.) grown at either ambient or elevated [CO_2] for 60 d and with or without water additions. Values are means ± SE (n = 7) taken during the 45°C stress period only.

high-temperature and high-light treatments, with *E. macrorhyncha* having lower F_v/F_m and higher F_o values than *E. rossii*.

For well-watered plants, a reduction in F_v/F_m and an increase in F_o are observed in both species when grown in elevated [CO_2], although the magnitude of the differences is greatest in *E. macrorhyncha*. These results essentially replicate and agree with previous reports of the effects of elevated [CO_2] on high-temperature photoinhibition (Roden and Ball, 1996). However, in this experiment the effect of elevated [CO_2] was sustained for the duration of the experiment, whereas before there were no significant differences in F_v/F_m by the end of the experiment. Other studies have also found reductions in the quantum efficiency of photosynthesis when plants are exposed to both short-term (4 h, Pammenter et al., 1993) and long-term (more than 5 months, Conroy et al., 1986) increases in [CO_2].

When water is withheld from these plants, the differences in F_v/F_m and F_o between CO_2 treatments disappear for both species. Withholding water does not reduce the quantum efficiency for these eucalyptus species, which would seem to differ from the findings of some studies, which demonstrated that water stress may exacerbate photoinhibition because of both stomatal and nonstomatal factors (Björkman and Powles, 1984; Ludlow and Björkman, 1984; Ögren and Öquist, 1985). However, there are seldom significant reductions in quantum efficiency until complete stomatal closure, and many researchers have concluded that photochemistry is not affected until extreme drought (Björkman and Powles, 1984; Ögren and Öquist, 1985; Sharp and Boyer, 1986; Stuhlfauth et al., 1990; Valentini et al., 1995). Since water stress was imposed gradually, the eucalyptus species in the present study never completely closed their stomata and leaf relative-water contents never decreased to less than 80%; therefore, the lack of reduction in F_v/F_m for these plants is not surprising.

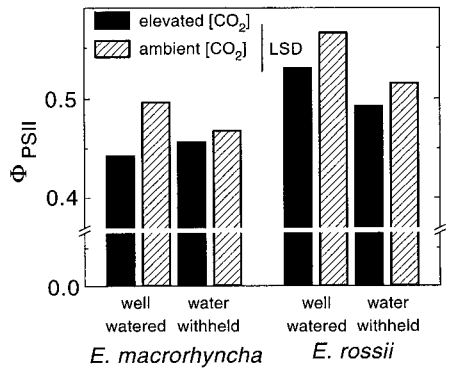

Figure 7. Φ_{PSII} values obtained in situ with a portable fluorometer for leaves of *E. macrorhyncha* and *E. rossii* grown for more than 4 weeks in either ambient or elevated [CO_2] and with or without water additions. Measurements were made during the 45°C stress period. The bar indicates the LSD between any two means in the chart (n = 7).

A reduction in the overall Φ_{PSII} is also observed when well-watered plants are grown in elevated [CO_2], but disappear when water is withheld. *E. rossii* has a higher value of Φ_{PSII} than *E. macrorhyncha*, a finding similar to measures of F_v/F_m. These in situ measures of Φ_{PSII} can be directly related to electron transport rates when the amount of incident light absorbed by the leaf is known. We found no differences in leaf absorptance (data not shown) between treatments; therefore (assuming similar light levels and leaf angles), we may assume that plants grown in elevated [CO_2] have lower electron transport rates than plants grown in ambient [CO_2], even though they have higher carbon assimilation rates. However, electron transport is utilized in photorespiration as well as carbon fixation and, at high temperatures, photorespiration can make large demands on electron transport capacity (as much as 50%, Valentini et al., 1995). Thus, in an elevated [CO_2] environment, a greater carboxylation efficiency may reduce electron transport requirements.

However, if reductions in photorespiration were the whole story, then plants grown in drying soil should also show a significant reduction in Φ_{PSII} and electron transport when grown in elevated [CO_2]. Excessive excitation of PSII during severe water stress and stomatal closure can be avoided through many mechanisms of energy dissipation, including photorespiration (Sharp and Boyer, 1986), cyclic electron transport (Katona et al., 1992), CO_2 recycling (Stuhlfauth et al., 1990), leaf movement (Ludlow and Björkman, 1984), alternative electron acceptors (Osmond, 1995),

Table II. *The effect of elevated [CO_2] on the pigment and carbohydrate concentration of mature leaves of E. macrorhyncha and E. rossii grown in well watered or drying soil for 60 d*

LSD is between any two means in the same row ($P < 0.05$).

Parameter	*E. macrorhyncha*				*E. rossii*				LSD
	Well watered		Water withheld		Well watered		Water withheld		
	Elevated [CO_2]	Ambient [CO_2]	Elevated [CO_2]	Ambient [CO_2]	Elevated [CO_2]	Ambient [CO_2]	Elevated [CO_2]	Ambient [CO_2]	
Carotenoids									
V + A + Z (mmol [mol total Chl]$^{-1}$)	66.8	70.1	60.5	71.8	47.5	49.9	43.6	45.9	10.1
A + Z/(V + A + Z (mol mol^{-1})	0.467	0.508	0.475	0.533	0.149	0.170	0.200	0.291	0.114
Total carotenoids (μmol m^{-2})	167.8	180.7	228.2	262.5	138.4	167.7	182.5	206.7	33.7
Chl *a* + *b* (μmol m^{-2})	693.3	714.8	941.6	1109.0	600.9	688.4	915.8	935.4	149.5
Carbohydrates									
Leaf starch concentration (mg g^{-1})	49.79	42.34	42.04	22.07	34.74	25.52	25.33	13.86	10.51
Leaf total nonstructural carbohydrates (mg g^{-1})	72.77	66.43	68.92	53.80	60.99	36.71	50.61	35.88	15.15

and increased nonphotochemical quenching (Valentini et al., 1995) including increases in xanthophyll cycle carotenoids (Demmig-Adams et al., 1989). However, these mechanisms may not entirely make up for the loss in energy dissipation due to increased carboxylation efficiency in elevated [CO_2] at these high temperatures.

Pammenter et al. (1993) found that a buildup of carbohydrates in the leaves of plants exposed to short-term increases in [CO_2] (4 h) can lead to a down-regulation of electron transport capacity. However, Betsche (1994) did not find any inhibition of electron transport at very high (4000 μL L^{-1}) [CO_2]. Reductions in photorespiration produced by reducing [O_2] rather than increasing [CO_2] produced a much larger decrease in Φ_{PSII} when plants were sink-limited than non-sink-limited, even when assimilation rates were well below saturating values (Harbinson, 1994). With excess carbohydrate content and reduced sink strength, phosphate levels in the stroma may be reduced if they are bound to sugar phosphates, thus inhibiting the coupling factor and restricting electron transport (Pammenter et al., 1993).

Photosynthetic capacity was also reduced (Fig. 4) for plants grown in elevated [CO_2] when well watered but not when water stressed. Other studies (Conroy et al., 1986; Johnsen, 1993) have failed to find substantial down-regulation of photosynthesis for water-stressed plants grown in elevated [CO_2]. The down-regulation of photosynthesis for well-watered plants grown in elevated [CO_2] for extended periods may be due not only to a reduction in Rubisco content and/or activity (Sage et al., 1989; Socias et al., 1993; Tissue et al., 1993), but also to limitations on triose-P use, which may be correlated with reduced Suc synthesis (Sage et al., 1989; Socias et al., 1993). Increased levels of leaf starch for plants grown in elevated [CO_2] are often associated with the observed down-regulation of photosynthesis (Tissue et al., 1993; Roden and Ball, 1996), and sink limitations may act to regulate photosynthesis in many plants (Stitt, 1991; Gifford, 1992). Therefore, an increase in the sink strength of the roots may be partially responsible for the lack of significant differences in photosynthetic capacity between plants grown in elevated versus ambient [CO_2] when soil moisture is reduced (Fig. 4).

In the present study, plants grown in elevated [CO_2] had a higher concentration of carbohydrates in their leaves, and plants grown in drying soil had lower carbohydrate levels (Table II). Thus, plants growing in elevated [CO_2] and low soil moisture had leaf starch concentrations similar to well-watered plants grown in ambient [CO_2], which agrees with the results from other studies (Hendrix et al., 1994). By the end of the experiment, the mid-stress F_v/F_m value taken immediately before sampling the leaf for carbohydrate content shows a strong negative correlation, both between and within species, with starch concentration (Fig. 8). The combination of watering regimes and CO_2 treatments (the four data points for each species) produced a substantial range of starch concentrations. It would appear that the relationship of leaf starch concentrations and F_v/F_m is not linear within a species, but curves over such that below some lower threshold a reduction in starch would have little effect on quantum efficiencies. It is also apparent that different species may have different sensitivities to starch concentrations, with *E. macrorhyncha* having lower F_v/F_m values at any given starch concentration than *E. rossii*.

Alternatively, much of the reduction in F_v/F_m might be explained by increases in nonphotochemical quenching. Xanthophyll cycle carotenoids are a very important component of nonphotochemical quenching, which allows dissipation of excess excitation energy during drought stress (Demmig-Adams et al., 1989). The larger the proportion of the xanthophyll cycle carotenoids that are in the Z and A form ([A + Z]/[V + A + Z]), the more photoprotection is provided. Although nonphotochemical quenching depends on the pH gradient, which relaxes with darkening, there was a general trend for the lower values of dark-adapted F_v/F_m, observed for *E. macrorhyncha*, to be associated with greater values of (A + Z)/(V + A + Z). However, plants grown in elevated [CO_2] have consistently lower values of (A + Z)/(V + A + Z) as well as a lower pool size of carotenoid pigments (Table II).

These results would seem to be at odds with previous work (Roden and Ball, 1996) in which the same species grown in elevated [CO_2] and high temperatures had increased levels of photoprotective pigments. However, in the previous study, we found that differences in xan-

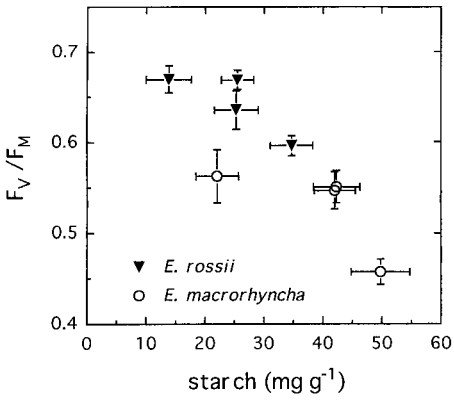

Figure 8. The relationship between the mid-stress F_v/F_m and the proportion of the V + A + Z in the A and Z form as well as the relationship between F_v/F_m and the starch concentration for leaves for two species of eucalyptus grown at either elevated or ambient [CO_2] and with or without water additions. The four data points for each species are the four treatment combinations. Leaf discs for carbohydrate analysis were sampled shortly after (on d 58) the measurements of Chl fluorescence (made during the 45°C stress period). Values are means ± SE (n = 7).

thophyll cycle carotenoids were expressed within the first 15 d of stress. Later in the experiment, when new leaves expanded that had developed under the high-temperature environment, no differences in xanthophyll cycle photoprotection between CO_2 treatments were observed. Therefore, pigments that provide photoprotection may be very important for developed leaves as they are exposed to a new environmental stress (Demmig-Adams and Adams, 1992), but further leaf production may produce leaves that are better acclimated to the new environment in which they develop and potentially become less dependent on photoprotection.

CONCLUSIONS

Well-watered plants may have more difficulty dissipating excess excitation energy when exposed to elevated atmospheric [CO_2] if environmental stresses prevent the utilization of increased carbohydrate production. A down-regulation of photosynthetic electron transport associated with feedback limitations caused by excess carbohydrates (Pammenter et al., 1993) may be the principal cause of reduced quantum efficiencies for plants grown in elevated [CO_2]. However, drought stress may reduce the carbohydrate buildup in leaves, because of an increase in the sink strength of belowground tissues, potentially eliminating the reductions in F_v/F_m observed for plants grown in elevated [CO_2]. It is interesting to note that the magnitude of change in F_v/F_m seems to be unaffected by reduced soil moisture in *E. rossii* (Fig. 6), which is the species that does not increase its allocation to roots (Table I). The differential response of *E. macrorhyncha* and *E. rossii* to the treatment conditions is consistent with their distribution on sheltered and exposed aspects, respectively. Thus, the predicted response of a species to extreme stress events in an elevated [CO_2] world would be dependent on the severity of the stress and the sensitivity of the species to that stress.

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