GROWTH AND PHOTOSYNTHETIC RESPONSES TO ELEVATED [CO_2] IN GRASSES FROM TASMANIAN NATIVE PASTURE

by Mark J. Hovenden

(with five tables and two text-figures)

HOVENDEN, M.J., 2003 (19:xii): Growth and photosynthetic responses to elevated [CO_2] in grasses from Tasmanian native pasture. *Papers and Proceedings ofthe Royal Society ofTasmania* 137: 81-86. https://doi.org/10.26749/rstpp.137.81
ISSN 0080-4703. School ofPlant Science, University ofTasmania, Locked Bag 55, Hobart, Tasmania 7001, Australia.

Six species of grass (four C_3 and two C_4) from southeastern Australian native pastures were grown in controlled environment cabinets at current (~370 μmol CO_2 mol^{-1}) and twice current (~750 μmol CO_2 mol^{-1}) cabinet [CO_2]. Photosynthetic gas exchange and above-ground biomass were estimated after seven weeks. Cabinet [CO_2] had a highly significant impact on above-ground biomass ($P<0.0003$) with plants exposed to elevated [CO_2] having on average 78% greater above-ground biomass than the controls. The relative increase of above-ground biomass caused by elevated [CO_2] varied among species. [CO_2] during gas exchange measurements and species had highly significant impacts on carbon assimilation and evapotranspiration rates, stomatal conductance and water-use efficiency. Cabinet [CO_2] had a significant impact on carbon assimilation rate only, for which there was a significant cabinet [CO_2] × species interaction. Carbon assimilation rate was influenced by cabinet [CO_2] only for *Poa labillardierei*, but this may well be related to pot conditions. Three-factor analysis of variance found no interaction between cabinet [CO_2] and [CO_2] during photosynthetic measurements, further supporting a lack of photosynthetic acclimation to elevated [CO_2] in young plants of these temperate Australian grass species.

Key words: Climate change, elevated CO_2, grass, growth, photosynthesis, downregulation.

INTRODUCTION

Native grasslands are one of the most endangered plant communities of southeastern Australia and of Tasmania in particular (Kirkpatrick 1999). Much of the native grassy vegetation in southeastern Australia has been extensively modified through clearing, burning and grazing. As a result, there is little grassy vegetation that now remains in a 'natural' or semi-natural state, with about 90% of grassy woodlands being substantially altered or degraded (Kirkpatrick 1991). The alteration of grassy vegetation is particularly pronounced in southeastern Tasmania, where lowland *Poa labillardierei* Steudel- *Themeda triandra* Forsskal grasslands are described as the most threatened plant community in the state (Kirkpatrick 1999). Much of Tasmania's grassy vegetation is subject to grazing by livestock and is termed 'native pasture', but until recently it has been poorly studied from a management point of view (Garden *et al.* 1995, Mason & Kay 2000). This is despite the fact that native pasture provides grazing for over half of Tasmania's sheep flock. In addition, native pastures are highly significant from a conservation perspective both in their own right and because of the rare and endangered plant species they contain (Gilfedder 1990). There is also much to be gained in terms of improved soil chemistry and stability, improved water-use and a reduction of weeds from effective sustainable management of temperate Australian pastures (Kemp *et al.* 2000).

There is substantial evidence that global climate change, through elevated atmospheric temperature and [CO_2], will alter growth patterns in grassland species (Wand *et al.* 1999a). There is evidence that co-occurring pasture species vary in their response to climate change (Clark *et al.* 1999), which may lead to altered community interactions. Several studies have shown that species composition of grasslands does actually change in response to simulated conditions of climate change (e.g., Owensby *et al.* 1999). There is some information on the responses of tropical Australian grassland species to the changing climate (e.g., Howden *et al.* 1999), but no information concerning the potential impacts on Australian temperate pastures, despite their enormous financial and conservation significance.

Australian southern temperate grasslands differ substantially from more northern Australian grasslands in the relative abundance of C_3 and C_4 species (Hattersley 1983). Despite the large degree of interspecific variation within a functional type, there is evidence that C_3 species are more responsive to a doubling of [CO_2] than are C_4 species (Wand *et al.* 1999a). Tasmanian grasslands are particularly interesting from this point of view, in that they contain among the lowest abundance of C_4 species anywhere in the country (Hattersley 1983). Of the seven native Tasmanian C_4 grasses, only *Themeda triandra* is widespread and relatively abundant. Therefore, if elevated [CO_2] does impact on the growth and abundance of C_3 species, then Tasmanian pastures may be among the most affected.

This paper presents a first attempt at assessing responsiveness of biomass and photosynthetic gas exchange to elevated [CO_2] of several dominant grass species of southeastern Australian native pasture.

MATERIALS AND METHODS

Plant Material

Species studied are all native or naturalised in Tasmania according to Buchanan (1999). Four C_3 grasses were studied, namely *Austrodanthonia caespitosa* (Gaudich.) H. P. Linder, *Austrostipa pubinodis* (Trin. & Rupr.) S. W. L. Jacobs & J. Everett, *Dichelachne crinita* (L.f.) Hook.f. and *Poa labillardierei* Steudel, all of which are native to Tasmania. The C_4 grasses used were *Themeda triandra* Forsskal, the only widespread and successful Tasmanian native C_4 grass, and *Sporobolus africanus* (Poir.) Robyns & Tournay, which is native to Africa and is naturalised in Tasmania. All species are caespitose or tufted perennials. *Austrodanthonia* spp., *Poa* spp. and *Themeda triandra* are perhaps the most important native pasture species, all being dominant under different conditions. *Austrostipa* spp. are widespread and can form a major component of grasslands, while *Dichelachne* spp. are occasionally important components. *Sporobolus africanus*, which was included because of the lack of C_4 species in Tasmanian native pasture, is an introduced species occasionally found in coastal grasslands and grassy woodlands. It has a very high growth rate under current conditions and produces seed prolifically and is therefore potentially highly invasive.

Seeds were collected from local wild populations of all species except *Sporobolus africanus*, seeds of which were collected from approximately 20 individuals growing in pots in the glasshouses of the School of Plant Science, University of Tasmania. These plants had been collected approximately six months earlier from a local area where the species is naturalised. Seeds were germinated in a 1:1:1 mix of sand, vermiculite and coconut fibre on a heat bed within a glasshouse at the University of Tasmania. When seedlings were approximately 1 cm high, 10 individuals of each species were planted out into 20 cm diameter pots (pot volume 4 L) containing a mixture of equal quantities of sharp sand and pine bark, to which slow-release fertiliser was added (Osmocote, Scotts-Sierra Horticultural Products, USA).

Five plants of each species were then transferred to each of two controlled environment cabinets (Thermoline, Smithfield, NSW, Australia) with a 14/10 h 25/12°C day/night cycle with daytime illumination of approximately 900 μmol $m^{-2}s^{-1}$ at plant height. The temperature chosen was about 2°C warmer than the average summer maximum temperature in the Midlands area of Tasmania. Cabinet relative humidity remained at approximately 50% throughout the experiment. One cabinet was maintained at a CO_2 concentration of approximately 750 μmol mol^{-1} by injection of pure CO_2 from a cylinder (BOC Gases). CO_2 control was provided by a microprocessor-controlled proportional integrating device (Thermoline, Smithfield, NSW, Australia). The $[CO_2]$ was measured constantly and varied by less than 20 μmol mol^{-1} from the set-point. The second cabinet was maintained at the current ambient CO_2 concentration of approximately 370 μmol mol^{-1}. The $[CO_2]$ of the controls was monitored routinely and varied by only ±10 μmol mol^{-1}. Plants were organised in a random block design within each cabinet and were watered daily, which was sufficient to keep the soil moist at all times.

After seven weeks, photosynthetic gas exchange was measured on each plant using a LI-COR LI-6400 portable photosynthesis system fitted with LI-6400-01 CO_2 gas mixer and LI-6400-04 blue-red LED light source (LI-COR, Ann Arbor, MI, USA). Gas exchange was measured in the middle part of the lamina of a young, well-expanded leaf. Several leaves were used at a time for *Poa labillardierei*, in which leaf width is typically <1 mm. *Austrostipa pubinodis* was not used for gas exchange measurements as it has tightly rolled leaves and proved difficult to measure. Leaf temperature was set at 25°C and the relative humidity in the chamber was kept at between 70–75% throughout all measurements. Leaf area was estimated by measuring the width of the leaf at either side of the chamber and multiplying the mean of the two leaf width measurements by the chamber width. Where more than one leaf was used, the sum of the areas of individual leaves was used. A test of this method using a flat-bed scanner and image analysis software indicated that the technique had an accuracy ±1 mm^2 with these linear leaves.

Gas exchange was measured at a leaf chamber $[CO_2]$ of 370 and 750 μmol mol^{-1} for each leaf, with photosynthetic photon flux density of 1000 μmol m^{-2} s^{-1}. The leaf was measured first at the $[CO_2]$ at which it was grown and then at the other concentration. Once the leaf was sealed into the chamber and again after changing the chamber $[CO_2]$, the leaf was allowed to equilibrate until readings stabilised, which typically took 15 to 30 min. Gas exchange calculations were according to von Caemmerer & Farquhar (1981).

After gas exchange measurements, the above-ground biomass of each plant was harvested by cutting the plant at soil level. Fresh weight was estimated, material was dried at 70°C for three days and then dry weight was estimated.

Results were analysed by two-way factorial analysis of variance, with $[CO_2]$ during growth and species the two factors examined, with the SAS statistical package (SAS Institute Inc. 2000) using general linear model procedures. Significant results were compared using the Ryan-Einot-Gabriel-Welsch *post hoc* comparison (Day & Quinn 1989).

RESULTS

Above-ground biomass was significantly influenced by $[CO_2]$ ($P<0.0003$) and was dependent upon species ($P<0.0002$) but there was no interaction between these terms. The average above-ground biomass of grasses grown at elevated $[CO_2]$ was 12.5 ± 1.4 g while the mean value for the control plants was 7.0 ± 1.0 g. Table 1 shows the above-ground biomass for each of the six species at elevated and current $[CO_2]$, as well as the average stimulation of above-ground biomass caused by elevated $[CO_2]$ for each species. At 370 μmol CO_2 mol^{-1}, *Sporobolus africanus* plants had the greatest above-ground biomass (table 1). Under elevated $[CO_2]$, *Poa labillardierei* was the largest, with *Austrostipa pubinodis, Austrodanthonia caespitosa* and *Sporobolus africanus* all reaching a similar size. *Dichelachne crinita* and *Themeda triandra* had the lowest above-ground biomass at elevated $[CO_2]$ (table 1).

Results for carbon assimilation rate are shown in figure 1 and all other gas exchange variables are shown in table 2. The results of the analysis of variance are presented in table 3. While it is obvious that both species and the CO_2 concentration during measurements, $[CO_2]_m$, had a highly significant impact on all gas exchange variables, cabinet CO_2 concentration, $[CO_2]_c$, only had a significant impact on net carbon assimilation. However, the significant species × $[CO_2]_c$ interaction ($P<0.01$) indicated that the impact of elevated $[CO_2]$ on carbon assimilation was dependent upon species. This is supported by figure 1, in which it is obvious that cabinet $[CO_2]$ significantly affected assimilation in *Poa labillardierei* only.

If photosynthetic acclimation occurred, then this would be evident in differences in the response to measurement $[CO_2]$ between plants exposed to elevated $[CO_2]_c$ and those exposed to current $[CO_2]_c$. Any impact of $[CO_2]_c$ on the photosynthetic response to $[CO_2]_m$ would be indicated by a significant $[CO_2]_c \times [CO_2]_m$ interaction in the analysis of variance. From table 3, it is evident that the $[CO_2]_m \times [CO_2]_c$ interactions were highly non-significant for all variables, as was the three-way interaction of species × $[CO_2]_m \times [CO_2]_c$.

The short-term responsiveness of gas exchange to $[CO_2]$, as examined by the ratio of measurements made at 750 μmol CO_2 mol^{-1} to those made at 370 μmol CO_2 mol^{-1} for each plant, also indicated no significant differences between

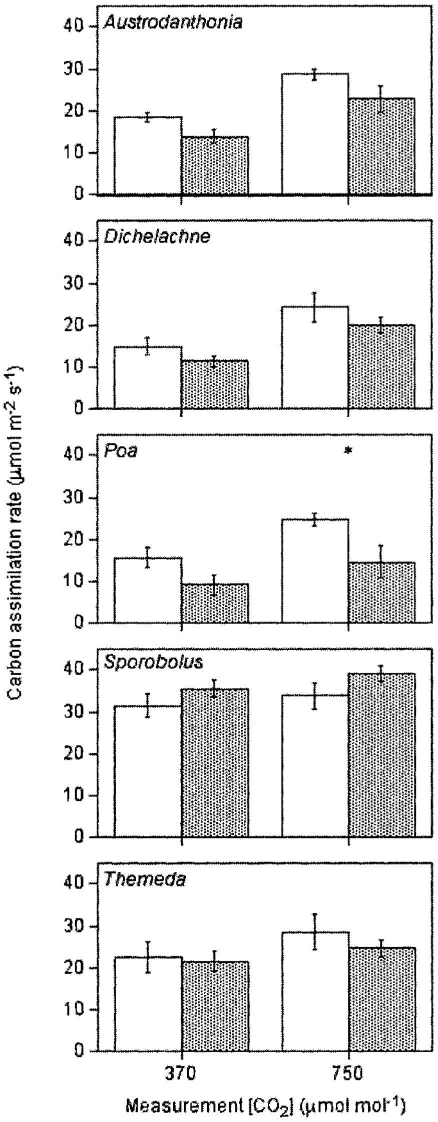

FIG. 1 — Carbon assimilation rates of grass species at 370 µmol mol^{-1} and 750 µmol mol^{-1} CO_2 concentration. Plants were grown at either current (open columns) or twice current (shaded columns) [CO_2]. Error bars indicate ±S.E., n=5.

plants grown at current $[CO_2]_c$ and those grown at elevated $[CO_2]_c$ (table 4). There was, however, a significant effect of species on short-term gas exchange responsiveness to [CO_2] (table 4). This was due to the carbon assimilation rate of the C_4 species, *Themeda triandra* and *Sporobolus africanus*, being less responsive to $[CO_2]_m$ than that of the C_3 species. In contrast, elevated $[CO_2]_m$ caused a larger reduction in both stomatal conductance and evapotranspiration rate in C_4 species than it did in C_3 species.

Analysis of the photosynthetic characteristics at each plant's $[CO_2]_c$ (each plant's 'home' [CO_2]), shows that significant differences existed in the steady state gas exchange of plants growing at current compared to elevated $[CO_2]_c$ (table 5). The only measured gas exchange variable that did not vary between current and elevated $[CO_2]_c$ treatments was the ratio of intercellular to ambient [CO_2], c_i/c_a, indicating a consistent stomatal response to $[CO_2]_m$ between the treatments (table 5). There was an impact of species on all gas exchange variables, but a significant species × CO_2 interaction only for instantaneous WUE ($P<0.04$) (fig. 2). Hence, the carbon assimilation rate of plants growing at current $[CO_2]_c$ was significantly less than that of plants growing at elevated $[CO_2]_c$ (table 5). Stomatal conductance, and hence evapotranspiration rate, was lower in plants growing at elevated $[CO_2]_c$. Together, these differences lend the plants growing at elevated [CO_2] a significantly higher intrinsic WUE (fig. 2, table 5).

DISCUSSION

These results demonstrate that substantial differences in the potential growth response to elevated [CO_2] occur among Tasmanian grasses. This variation is partly related to photosynthetic pathway, since *Sporobolus africanus*, the least responsive species, is C_4 while *Poa labillardierei* and *Austrostipa pubinodis*, the most responsive species, are C_3. Photosynthetic pathway is not, however, sufficient to explain the variation in the growth response to elevated [CO_2], since *Themeda triandra* (C_4) responded similarly to *Dichelachne crinita* (C_3) (table 1). There is little evidence of photosynthetic acclimation to elevated [CO_2], as indicated by highly non-significant $[CO_2]_c$ × $[CO_2]_m$ interactions.

Instantaneous photosynthetic rates were approximately 21% higher and evapotranspiration rates 17% lower in plants growing at elevated [CO_2] than in those growing in current conditions (table 5). Furthermore, intrinsic

TABLE 1

Above-ground dry weight (g) of each species grown at current (370 µmol CO_2 mol^{-1}) or elevated (750 µmol CO_2 mol^{-1}) CO_2 concentrations

Species	C_3/C_4	Current CO_2	Elevated CO_2	Growth enhancement
Austrodanthonia caespitosa	C_3	6.3 ± 1.2	12.4 ± 1.8	95%
Austrostipa pubinodis	C_3	5.1 ± 1.9	13.8 ± 3.0	169%
Dichelachne crinita	C_3	4.0 ± 1.2	6.5 ± 1.5	65%
Poa labillardierei	C_3	6.5 ± 1.9	19.7 ± 4.6	201%
Sporobolus africanus	C_4	15.9 ± 3.0	15.5 ± 3.2	–2%
Themeda triandra	C_4	3.6 ± 1.0	6.8 ± 1.9	90%

Biomass values are means ± SE, n = 5. Growth enhancement is the percentage change in mean above-ground biomass for each species caused by elevated CO_2.

TABLE 2

Photosynthetic gas exchange variables measured at a $[CO_2]$ of 370 and 750 μmol mol^{-1} for five grass species grown at either current (370 μmol CO_2 mol^{-1}) or double (750 μmol CO_2 mol^{-1}) $[CO_2]$

Species	$[CO_2]$	E ($mmol\ H_2O\ m^{-2}\ s^{-1}$)		g_s ($mmol\ H_2O\ m^{-2}\ s^{-1}$)		c_i/c_a		A/g_s ($mmol\ CO_2\ mol\ H_2O^{-1}$)	
	Treatment	370	750	370	750	370	750	370	750
Austrodanthonia	Current	2.39 ±0.19	2.03 ±0.22	277 ±26	227 ±30	0.627 ±0.031	0.655 ±0.027	69 ±6.1	133 ±13.3
caespitosa	Double	3.13 ±0.57	2.67 ±0.54	266 ±54	227 ±54	0.684 ±0.039	0.691 ±0.044	59 ±9.0	121 ±22.0
Dichelachne	Current	2.67 ±0.18	2.61 ±0.17	269 ±23	257 ±15	0.697 ±0.022	0.750 ±0.022	55 ±4.0	93 ±9.5
crinita	Double	2.19 ±0.47	2.17 ±0.30	212 ±28	207 ±15	0.712 ±0.013	0.746 ±0.013	54 ±3.3	97 ±3.9
Poa	Current	2.44 ±0.29	2.32 ±0.32	263 ±57	259 ±62	0.668 ±0.023	0.705 ±0.047	64 ±6.8	113 ±22.4
labilliardierei	Double	1.68 ±0.41	1.46 ±0.38	170 ±59	137 ±49	0.694 ±0.041	0.683 ±0.068	61 ±10.8	127 ±29.6
Sporobolus	Current	2.95 ±0.29	2.05 ±0.29	317 ±37	211 ±37	0.438 ±0.015	0.538 ±0.039	100 ±4.7	173 ±21.3
africanus	Double	3.43 ±0.39	2.73 ±0.42	341 ±33	250 ±45	0.412 ±0.024	0.529 ±0.085	105 ±5.8	183 ±39.0
Themeda	Current	2.50 ±0.45	1.70 ±0.12	188 ±29	140 ±19	0.409 ±0.031	0.476 ±0.050	118 ±5.5	219 ±47.7
triandra	Double	2.17 ±0.32	1.40 ±0.21	174 ±15	102 ±10	0.390 ±0.033	0.442 ±0.036	123 ±6.1	247 ±22.9

Figures shown are means ± S.E., n=5. Abbreviations are defined in the text.

TABLE 3

Results of three-way ANOVA (P>F) for gas exchange variables for five cool temperate Australian grass species

Source of variation	A	E	g_s	c_i/c_a	A/g_s	A/E
Species	**0.0001**	**0.003**	**0.0001**	**0.0001**	**0.0001**	**0.0001**
$[CO_2]_c$	0.01	0.69	0.06	0.91	0.63	0.11
$[CO_2]_m$	**0.0001**	**0.007**	**0.008**	**0.006**	**0.0001**	**0.0001**
Species × $[CO_2]_c$	**0.01**	**0.01**	0.14	0.68	0.88	**0.04**
Species × $[CO_2]_m$	0.30	0.42	0.46	0.41	0.1	0.28
$[CO_2]_c$ × $[CO_2]_m$	0.54	0.97	0.91	0.61	0.59	0.58
Sp. × $[CO_2]_c$ × $[CO_2]_m$	0.97	0.99	0.99	0.99	0.99	0.96

$[CO_2]_c$ = cabinet $[CO_2]$ during growth, $[CO_2]_m$ = $[CO_2]$ during gas exchange measurements. Bold figures indicate significant results (P<0.05).

TABLE 4

Results of ANOVA (P>F) on short-term responsiveness to $[CO_2]$

	CO_2	Species	CO_2 × species
Net Assimilation Rate (A)	0.75	**0.0001**	0.38
Evapotranspiration rate (E)	0.97	**0.003**	0.58
Stomatal conductance (g_s)	0.34	**0.005**	0.31
c_i/c_a	0.54	**0.05**	0.98
Instantaneous water-use efficiency (A/E)	0.95	0.28	0.91
Intrinsic water-use efficiency (A/g_s)	0.41	0.57	0.98

Bold figures indicate significant results (P<0.05).

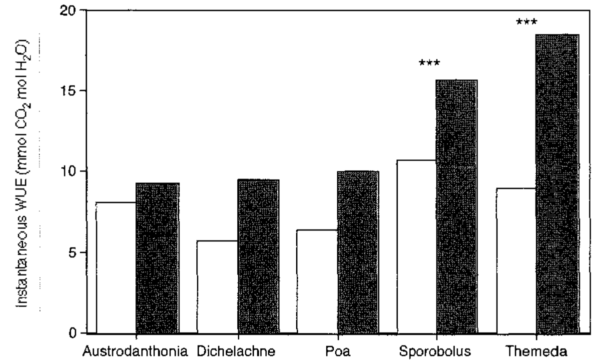

*FIG. 2 — Instantaneous water-use efficiency (A/E) measured at 370 μmol CO_2 mol^{-1} for plants grown in current $[CO_2]$ (open columns) and at 750 μmol CO_2 mol^{-1} CO_2 for plants grown at twice current $[CO_2]$ (shaded columns). *** indicates significant differences between means (P<0.001).*

TABLE 5
Mean photosynthetic gas exchange characteristics of plants grown at current or elevated [CO_2]

Variable	Current CO_2	Elevated CO_2
Net assimilation rate (A) (μmol m^{-2} s^{-1})	20.6^b	25.0^a
Evapotranspiration rate (E) (mmol m^{-2} s^{-1})	2.59^a	2.14^b
Stomatal conductance (g_s) (mmol m^{-2} s^{-1})	263^a	189^b
c_i/c_a	0.568^a	0.612^a
Intrinsic WUE (A/g_s) (mmol CO_2 mol H_2O^{-1})	81^b	157^a

Figures are the means for pooled data of all species. In each row, numbers with a different superscript are significantly different ($P<0.05$).

WUE (as estimated by A/g_s) of plants growing at elevated [CO_2] was approximately double that of plants growing in current conditions. These differences in carbon assimilation and transpiration would doubtless allow plants to grow significantly more quickly at elevated [CO_2] than they do in current conditions. Other than *Sporobolus africanus*, species used in this experiment were all caespitose and therefore the above-ground biomass was almost exclusively leaf material. Since the plants exposed to elevated [CO_2] had a greater above-ground biomass, they would also have had a greater leaf mass and hence the total carbon assimilation rate for the plant would have been greater than just the area-based measurements of CO_2 exchange. Further work should relate the relative growth rate of these species to instantaneous carbon assimilation and canopy leaf area. Only above-ground growth was estimated in this experiment, so it is entirely possible that root growth and whole-plant growth was different from the results shown here.

Photosynthetic downregulation, or acclimation, in response to elevated [CO_2] has been observed in many cases and mechanistic models developed to explain the results (e.g., van Oosten & Besford 1996). However, there is still no agreement that photosynthetic downregulation is a universal response to elevated [CO_2] (Sage 1994). The lack of photosynthetic acclimation to [CO_2]$_c$ in the C_4 species presented here agrees with the results for *Panicum coloratum* grown in pots for six weeks (Ghannoum 1998), as well as for *Paspalum dilatatum* grown in a pasture exposed to free-air CO_2 enrichment (von Caemmerer *et al.* 2001), in which there was little evidence for photosynthetic downregulation. The lack of significant photosynthetic downregulation in the C_3 species *Austrodanthonia caespitosa* and *Dichelachne crinita* disagrees with the results for *Panicum laxum* (Ghannoum 1998), *Lolium perenne* (von Caemmerer *et al.* 2001), as well as many other C_3 grass species reported to display photosynthetic downregulation. There is, however, contrasting evidence such as that for *Avena barbata*, in which no significant downregulation was observed in grasslands exposed to elevated [CO_2] (Jackson *et al.* 1995). Recent results from a free air CO_2 enrichment study showed a significant downregulation of photosynthesis in each of 13 grassland species, irrespective of photosynthetic pathway (Lee *et al.* 2001). The results presented here indicate a significant photosynthetic downregulation in response to elevated [CO_2] in *Poa labillardierei* only. It is possible, however, that the downregulation observed here is due to pot size or nutrient limitations, since the *P. labillardierei* plants grown at elevated [CO_2] were relatively large compared to the other plants in this study and 4 L pots were used (Sage 1994).

The length of this experiment (seven weeks) was short in comparison to some other experiments (e.g., Roumet *et al.* 2000), but significant photosynthetic acclimation to elevated [CO_2] has been noted for other grass species in less time (e.g., Ghannoum 1998). The results here indicate that during the establishment period when the plant is young, photosynthetic downregulation is not a significant factor in the response of these species to elevated [CO_2]. However, the photosynthetic characteristics of the species may have varied over time and with developmental stage.

The growth enhancement caused by elevated [CO_2] seen here is large compared with other studies. Wand *et al.* (1999a) showed through a meta-analysis that the average response of wild C_3 and C_4 grasses to elevated [CO_2] was an increase in whole plant dry weight of 44% and 33% respectively. The shoot growth response of *Themeda triandra* to elevated [CO_2] seen here is very similar to the results of Wand *et al.* (1999b) for the same species grown under similar conditions. The comparative maximum seen here was an increase of shoot dry mass of 190%. This could be because plants in this experiment were provided with ample nutrients, which allowed the full potential of growth increase to be realised. Also, the cabinets used in this experiment operated at a relative humidity of approximately 50%, giving a relatively large vapour pressure deficit. Since elevated [CO_2] has a direct effect on stomatal conductance, those plants in the elevated [CO_2] chamber may have had significantly higher shoot water potential than those in the control chamber and this could have directly affected their growth. Large vapour pressure deficits have been seen to increase the growth enhancement caused by elevated [CO_2] in other species (Seneweera 1998). The biomass of *Sporobolus africanus* was least affected by elevated [CO_2] (table 1). This supports previous work in which *Sporobolus cryptandrus* (Torr.) A. Gray was shown to have a slight reduction in biomass under elevated [CO_2] compared to controls (Kellogg *et al.* 1999).

The variation in responsiveness of above-ground biomass to elevated [CO_2] among the six species studied here has important implications for the future management and conservation of southeastern Australian grasslands. While competitive interactions in grasslands involve such processes as fecundity and stress tolerance among others, initial growth rate is very important in southeastern Australian grasslands, where rapid establishment in bare areas after the summer drought is an important facet of a species' success (Garden *et al.* 2000). The extremely high responsiveness of *Poa labillardierei*, which showed the potential for a tripling of above-ground growth with a doubling of [CO_2], and *Austrostipa pubinodis* have particularly important ramifications for the sustainable management of native pasture in Tasmania. Native pasture in Tasmania is largely dominated by *Austrodanthonia* spp. at altitudes below 600 m and by *Poa labillardierei*/*Poa rodwayi* above 600 m because of their tolerance of heavy grazing (Garden *et al.* 1995). *Themeda triandra* becomes dominant in drier areas where *Poa labillardierei* appears to be limited by low water availability (Kirkpatrick 1999). Doubling the [CO_2] causes an increase in the water-use efficiency of all grass species in this study, since there is little evidence of stomatal acclimation to growth at elevated [CO_2]. This may allow *Poa labillardierei* to extend its current dominance into drier areas at the expense of the more drought tolerant *Themeda triandra.*

This study used only a few of the species from native grasslands, and plants were all grown singly, in relatively small pots, in controlled environment cabinets and given an adequate supply of water and nutrients. The performance of plants in natural soils and environmental conditions may well differ substantially from that reported here. However, the experiment was designed to investigate the effects of elevated [CO_2] on the growth potential of several species and to generate hypotheses to test under more realistic environmental conditions, and, as such, has been successful. This study shows that differences do occur in the CO_2-responsiveness of important dominant species in grasslands and native pasture of southeastern Australia, but that this responsiveness is not easily explained by short-term photosynthetic gas exchange measurements. This study provided little evidence that significant downregulation of photosynthesis occurs in young plants in response to elevated [CO_2]. Variation in the growth response of southeastern Australian grassland species to elevated [CO_2] is an area requiring further investigation, including detailed experiments into the competitive interactions of important pasture species and the investigation of botanical composition, productivity and palatability of pastures exposed to simulated future climates.

ACKNOWLEDGEMENTS

This research was supported by the ARC Small Grants Scheme. Technical assistance was provided by Christiane Smethurst and Lisa Schimanski. Ian Cummings and Tracey Jackson provided great help in the glasshouse. Lisa Nelson and Oliver Hovenden helped with collection of grasses.

REFERENCES

BUCHANAN, A. M., 1999: *A Census of the Vascular Plants of Tasmania.* Tasmanian Herbarium, Hobart.

CLARK, H., NEWTON, P. & BARKER, D., 1999: Physiological and morphological responses to elevated CO_2 and a soil moisture deficit of temperate pasture species growing in an established plant community. *Journal of Experimental Botany* 50: 233–242.

DAY, R. W. & QUINN, G. P., 1989: Comparisons of treatments after an analysis of variance in ecology. *Ecological Monographs* 59: 433–463.

GARDEN, D., JONES, C., FRIEND, D., MITCHELL, M. & FAIRBROTHER, P., 1995: Regional research on native grass-based pastures. *In* Reid, R. (Ed.): *Perennial Grasses 1995.* Land and Water Resources Research and Development Corporation: Launceston, Tasmania: 32–49

GARDEN, D. L., LODGE, G. M., FRIEND, D. A., DOWLING, P. M. & ORCHARD, B. A., 2000: Effects of grazing management on botanical composition of native grass based pastures in temperate south east Australia. *Australian Journal of Experimental Agriculture* 40: 225–245.

GHANNOUM, O., 1998: Nitrogen deficiency precludes a growth response to CO_2 enrichment in C_3 and C_4 *Panicum* grasses. *Australian Journal of Plant Physiology* 25: 627–636.

GILFEDDER, L., 1990: Threatened species from Tasmania's remnant grasslands. *Tasforests* 2: 129–132.

HATTERSLEY, P. W., 1983: The distribution of C_3 and C_4 grasses in Australia in relation to climate. *Oecologia* 57: 113–128.

HOWDEN, S., MCKEON, G., WALKER, L., CARTER, J., CONROY, J., HALL, W., ASH, A. & GHANNOUM, O., 1999: Global change impacts on native pasture in south-east Queensland, Australia. *Environmental Modelling and Software* 14: 307–316.

JACKSON, R. B., LUO, Y., CARDON, Z. G., SALA, O. E., FIELD, C. B. & MOONEY, H. A., 1995: Photosynthesis, growth and density for the dominant species in a CO_2-enriched grassland. *Journal of Biogeography* 22: 221–225.

KELLOGG, E., FARNSWORTH, E., RUSSO, E. & BAZZAZ, F., 1999: Growth responses of C_4 grasses of contrasting origin to elevated CO_2. *Annals of Botany* 84: 279–288.

KEMP, D., MICHALK, D. & VIRGONA, J., 2000: Towards more sustainable pastures: lessons learnt. *Australian Journal of Experimental Agriculture* 40: 343–356.

KIRKPATRICK, J., 1991: The magnitude and incidence of land clearing in Tasmania in the nineteen eighties. *Tasforests* 3: 11–14.

KIRKPATRICK, J., 1999: Grassy vegetation and subalpine eucalypt communities. *In* Reid, J., Hill, R., Brown, M. & Hovenden, M. (Eds): *Vegetation of Tasmania.* Australian Biological Resources Study, Canberra: 265–285.

LEE, T. D., TJOELKER, M. G., ELLSWORTH, D. S. & REICH, P. B., 2001: Leaf gas exchange responses of 13 prairie grassland species to elevated CO_2 and increased nitrogen supply. *New Phytologist* 150: 405–418.

MASON, W. & KAY, G., 2000: Temperate pasture sustainability key program: an overview. *Australian Journal of Experimental Agriculture* 40: 121–123.

OWENSBY, C., HAM, J., KNAPP, A. & AUEN, L., 1999: Biomass production and species composition change in a tallgrass prairie ecosystem after long-term exposure to elevated atmospheric CO_2. *Global Change Biology* 5: 497–506.

ROUMET, C., GARNIER, E., SUZOR, H., SALAGER, J. & ROY, J., 2000: Short and long-term responses of whole-plant gas exchange to elevated CO_2 in four herbaceous species. *Environmental and Experimental Botany* 43: 155–169.

SAGE, R., 1994: Acclimation of photosynthesis to increasing atmospheric CO_2: the gas exchange perspective. *Photosynthesis Research* 39: 351–368.

SAS INSTITUTE INC. 2000 *SAS/STAT user's guide, version 8.* SAS Publishing: Cary, NC.

SENEWEERA, S. P., GHANNOUM, O. & CONROY, J. 1998: High vapour pressure deficit and low soil water availability enhance shoot growth responses of a C_4 grass (*Panicum coloratum* cv. Bambatsi) to CO_2 enrichment. *Australian Journal of Plant Physiology* 25: 287–292.

VAN OOSTEN, J.-J. & BESFORD, R. T., 1996: Acclimation of photosynthesis to elevated CO_2 through feedback regulation of gene expression: climate of opinion. *Photosynthesis Research* 48: 353–365.

VON CAEMMERER, S. & FARQUHAR, G. D., 1981: Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves *Planta* 153: 376–387.

VON CAEMMERER, S., GHANNOUM, O., CONROY, J. P., CLARK, H. & NEWTON, P. C. D., 2001: Photosynthetic responses of temperate species to free air CO_2 enrichment (FACE) in a grazed New Zealand pasture. *Australian Journal of Plant Physiology* 28: 439–450.

WAND, S., MIDGLEY, G., JONES, M. & CURTIS, P., 1999a: Responses of wild C_4 and C_3 grass (Poaceae) species to elevated atmospheric CO_2 concentration: a meta-analytic test of current theories and perceptions. *Global Change Biology* 5: 723–741.

WAND, S., MIDGLEY, G. & STOCK, W., 1999b: Predicted responses of C_4 grass-dominated southern African rangelands to rising atmospheric CO_2 concentrations. *In* Eldridge, D. & Freudenberger, D. (Eds): *People and Rangelands: Building the Future. VI International Rangelands Conference Inc,* Townsville, Australia: 922–923.

(accepted 24 November 2003)