GROWTH RESPONSE OF AUSTRALIAN TEMPERATE PASTURE SPECIES TO CO_2 ENRICHMENT

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ABSTRACT
Growth responses to a doubling of the atmospheric CO_2 concentration for 15 species represented in temperate pastures of southern Australia were investigated in a glasshouse experiment. The final dry weight increase due to CO_2 enrichment averaged 34% across species but varied widely. The variation in CO_2 response was greater among species within botanical groups than it was among groups. The CO_2 response of a number of 'desirable', but also a number of 'undesirable' species was greater than the mean response, suggesting that these species may increase their proportion in pastures as atmospheric CO_2 rises. Our results do not support the hypotheses that CO_2 responsiveness is related to nutrient responsiveness or to the species inherent relative growth rates. Thus, knowledge of CO_2 response at the level of the individual species may be necessary to understand, predict or model the response of plant communities to elevated CO_2.

INTRODUCTION
Plant species in temperate pastures of southern Australia fall mainly into 5 principal groups: native perennial grasses, introduced perennial grasses, annual grasses, dicotyledonous herbs, and legumes. Perennial grasses and legumes often decrease over time and are replaced by annual grasses and dicotyledonous herbs. Little is known about how these species or groups may respond to the globally increasing CO_2 concentration or the implications for species botanical composition or productivity of the pastures.

Several studies (Hunt et al. 1991; Poorter 1993; Poorter et al. 1996) have concluded that faster growing species are more responsive to CO_2 enrichment, and this is commonly suggested to be a general response. In a related hypothesis, Loehle (1995) suggested that species responsiveness to CO_2 enrichment is related to responsiveness to resource enrichment in general, whether of nutrients, light or water. The search for generalisation has led to the concept of 'functional types' (Smith et al. 1996), and the expectation that species within functional groups may respond similarly to CO_2 enrichment.

Our aim was to determine growth responses of Australian temperate pasture species to CO_2 enrichment so that we may model and predict elevated CO_2 effects on pasture botanical composition and productivity. We tested the hypotheses of the relationships between CO_2 responsiveness, nutrient responsiveness and inherent relative growth rate, and looked for generalised CO_2 responses within botanical groups.

MATERIALS AND METHODS
Three species from each of 5 botanical groups (Table 1) were studied. The experiment was conducted in a temperature, humidity, and CO_2-controlled glasshouse facility in Canberra, Australia from mid-July to mid-September 1995. CO_2 treatments were 369 mmol mol^{-1} and 725 mmol mol^{-1}. Temperatures averaged 21 ^{o}C by day and 17 ^{o}C at night. Plants were grown in 3 kg of fine sand in 2 litre pots. Seedlings were thinned to one per pot after emergence. Nutrient solution applied 2 and later 3 times each week and distilled water on other days maintained adequate water. Hoagland's solution was used for the high nutrient treatments and quarter-strength Hoagland's solution for the low nutrient treatment. High nutrient plants were harvested four times: at 2, 4, 5 and 7 weeks after emergence. Low nutrient plants were harvested at 5 weeks after emergence. At harvest, plants were separated into leaf , stem, root and reproductive components (when present). The area of harvested leaves was determined with an image processing system (Delta-T). Plant parts were air-dried at 60 ^{0}C (harvests 1 to 3) or freeze-dried for subsequent carbohydrate analysis (harvest 4) and their dry weight determined.

Growth analysis (*cf.* Evans, 1972) yielded relative growth rate (RGR), net assimilation rate (NAR), leaf area ratio (LAR), specific leaf area (SLA) and leaf weight ratio (LWR) over the growth period for each species and CO_2 level. Plant response to CO_2 was expressed as the ratio of each of these factors and of final total dry weight at high CO_2 divided by its value at ambient CO_2. Plant response to nutrients was determined at ambient CO_2 at harvest 3 as the ratio of total plant weight at high nutrients divided by the total plant weight at low nutrients.

RESULTS AND DISCUSSION
The final dry weight increase due to CO_2 enrichment averaged 34% (Fig. 1), similar to values of 30% for 25 British grassland species (Hunt et al. 1991), 35% for 62 'wild herbaceous C_3 species' (principally grassland species) in a meta-analysis by Poorter (1993), and 39% (with a median of 35%) for 108 'wild herbaceous C_3 species' in a more recent meta-analysis by Poorter et al. (1996). However, there was wide variation among species in CO_2 response, which is commonly observed (Poorter et al. 1996). The variation in species response to CO_2 within the botanical groups was larger than the variation in group mean values among groups (Fig. 2). Only the dicotyledonous herb group showed a consistent response in final weight ratio, but this could simply be due to fortuitous species selection.

The CO_2 response of final weight ratio for a number of 'desirable' pasture species such as *Phalaris aquatica*, *Lolium perenne*, *Trifolium subterraneum* and *Danthonia richardsonii* (Table 1) were greater than the mean response (1.34), suggesting that these species may retain or increase their representation in pastures as atmospheric CO_2 concentrations rise. A number of 'undesirable' species such as *Hordeum leporinum* and the dicotyledonous herbs also had CO_2 responses greater than the mean response, suggesting that they too may increase in proportion as atmospheric CO_2 increases. However, these first-order predictions must be treated with caution as community-level responses to CO_2 are not simple linear combinations of individual plant responses on account of competitive effects (Bazzaz et al. 1989). Also, amplification of the dry weight response during the exponential phase of growth (Gifford and Morison, 1993) confounds extrapolation from single plants to swards.

By normalising growth analysis parameters as the ratio of values at elevated and ambient CO_2 levels, the relative response of RGR can be compared to that of its two components: NAR and LAR. There was a small increase in RGR, averaging 3.5% (Fig. 1). This increase in RGR is highly correlated ($r=0.90$, $p<0.01$) with a 27% average increase in NAR, presumably attributable to increased photosynthesis. However, the increase in NAR is offset by an average decrease in LAR of 13%. The LAR in turn can be factorised into SLA and LWR. The decline in LAR is largely the result of a 16% average decrease in SLA, while the LWR increased slightly (3.8%) on average. The consistent decrease in SLA is due in part to the accumulation of non-structural carbohydrates (data not shown). These trends in growth analysis parameters are similar to those reviewed by Poorter et al. (1996) for 60 C_3 species.

Correlation analyses of the results in Table 1 do not support the hypotheses that relative CO_2 responsiveness is related to nutrient responsiveness or to the species inherent RGR. There was no significant correlation between the final CO_2 weight ratio and the RGR of the species at ambient CO_2 ($r=-0.18$, $p>0.05$). Further, the weight ratio response to nutrients was not significantly correlated with the weight ratio response to CO_2 ($r=0.04$, $p>0.05$) or with the species RGRs ($r=0.24$, $p>0.05$). The final weight ratio response to CO_2 was weakly correlated with the RGR response ratio to CO_2 ($r=0.50$, $p<0.05$), and with the initial weight ratio response to CO_2 ($r=0.52$, $p<0.05$) at harvest 1, which had a mean value of 1.11.

The search for generalised responses and functional types may be both necessary and useful for understanding vegetation response to CO_2 at the landscape, regional and global scales. However, given the wide range in CO_2 response among species within a community or botanical grouping as demonstrated here and elsewhere (Hunt et al. 1991; Poorter 1993; Poorter et al. 1996), knowledge at the level of the individual species may be necessary to understand, predict or model the response of plant communities to CO_2.

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Table 1
Botanical groups, species, relative growth rate (RGR) at low CO_2, CO_2 response weight ratio and nutrient response weight ratio.

GROUP	SPECIES	RGR, low CO_2 (mg g^{-1} d^{-1})	CO_2 Weight Ratio	Nutrient Weight Ratio
Native perennial grass	*Danthonia richardsonii*	132	1.70	5.14
	Elymus scaber	138	0.91	3.48
	Microlaena stipoides	101	1.30	1.96
Introduced perennial grass	*Holcus lanatus*	191	0.99	3.05
	Lolium perenne	162	1.57	4.31
	Phalaris aquatica	152	1.75	9.29
Annual grass	*Bromus molliformis*	157	1.05	8.29
	Hordeum leporinum	155	1.82	8.62
	Vulpia bromoides	152	1.07	4.48
Dicot herbs	*Arctotheca calendula*	158	1.40	10.76
	Emex australis	105	1.40	4.47
	Rumex acetosella	155	1.43	3.79
Legumes	*Ornithopus compressus*	145	1.05	7.38
	Trifolium glomeratum	141	1.04	12.93
	Trifolium subterraneum	118	1.67	3.36

Figure 1
Box plot of the relative changes in growth parameters due to elevated CO_2: final weight, relative growth rate (RGR), net assimilation rate (NAR), leaf area ratio (LAR), specific leaf area (SLA) and leaf weight ratio (LWR). The heavy middle line in each box is the mean value of the 15 species. The lighter middle line shown when different from the mean is the median. The lower and upper part of the box give the 25th and 75th percentile, and the lower and upper 'error bars' the 10th and 90th percentile of the observed distribution. Shaded circles outside the bars are extreme values.

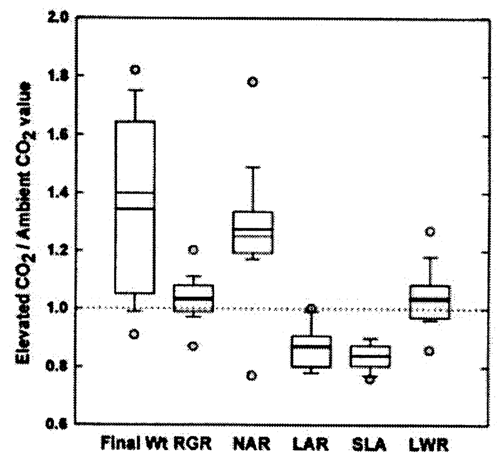

Figure 2
Plot of the final CO_2 weight ratios for each of the botanical groups: native perennial grass (NPG), introduced perennial grass (IPG), annual grass (AG), dicotyledonous herb (DH) and legume (LG). The middle square in each vertical line is the group mean for 3 species. The lower and upper squares for each vertical line are the minimum and maximum values observed for the group.