The response of fast- and slow-growing Acacia species to elevated atmospheric CO2

4 authors, including:

Owen Atkin
Australian National University
227 PUBLICATIONS   **20,396** CITATIONS

SEE PROFILE

Marcus Schortemeyer
Yara
27 PUBLICATIONS   **1,701** CITATIONS

SEE PROFILE

John R Evans
Australian National University
213 PUBLICATIONS   **24,480** CITATIONS

SEE PROFILE

Owen K. Atkin · Marcus Schortemeyer
Nola McFarlane · John R. Evans

The response of fast- and slow-growing *Acacia* species to elevated atmospheric CO$_2$: an analysis of the underlying components of relative growth rate

Abstract In this study we assessed the impact of elevated CO$_2$ with unlimited water and complete nutrient on the growth and nitrogen economy of ten woody *Acacia* species that differ in relative growth rate (RGR). Specifically, we asked whether fast- and slow-growing species systematically differ in their response to elevated CO$_2$. Four slow-growing species from semi-arid environments (*Acacia aneura*, *A. colei*, *A. coriacea* and *A. tetragonophylla*) and six fast-growing species from mesic environments (*Acacia dealbata*, *A. implexa*, *A. mearnsii*, *A. melanoxylon*, *A. irrorata* and *A. saligna*) were grown in glasshouses with either ambient (~350 ppm) or elevated (~700 ppm) atmospheric CO$_2$. All species reached greater final plant mass with the exception of *A. aneura*, and RGR, averaged across all species, increased by 10% over a 12-week period when plants were exposed to elevated CO$_2$. The stimulation of RGR was evident throughout the 12-week growth period. Elevated CO$_2$ resulted in less foliage area per unit foliage dry mass, which was mainly the result of an increase in foliage thickness with a smaller contribution from greater dry matter content per unit fresh mass. The net assimilation rate (NAR, increase in plant mass per unit foliage area and time) of the plants grown at elevated CO$_2$ was higher in all species (on average 30% higher than plants in ambient CO$_2$) and was responsible for the increase in RGR. The higher NAR was associated with a substantial increase in foliar nitrogen productivity in all ten *Acacia* species. Plant nitrogen concentration was unaltered by growth at elevated CO$_2$ for the slow-growing *Acacia* species, but declined by 10% for faster-growing species. The rate of nitrogen uptake per unit root mass was higher in seven of the species when grown under elevated CO$_2$, and leaf area per unit root mass was reduced by elevated CO$_2$ in seven of the species. The absolute increase in RGR due to growth under elevated CO$_2$ was greater for fast- than for slow-growing *Acacia* species.

Key words *Acacia* · Elevated CO$_2$ · Growth analysis · Relative growth rate · Nitrogen productivity

O.K. Atkin[1] · M. Schortemeyer[2] · N. McFarlane · J.R. Evans (✉)
Environmental Biology Group,
Research School of Biological Sciences,
Australian National University,
Canberra, 0200, A.C.T., Australia
e-mail: evans@rsbs.anu.edu.au,
Tel.: +61-2-62494492, Fax: +61-2-62494919

Present addresses:
[1] Department of Biology,
University of York,
Heslington, York, YO1 5DD, UK
[2] Plant Sciences, Faculty of Agriculture,
University of Western Australia,
Nedlands, WA 6907 Australia

Introduction

It is now well established that elevated atmospheric CO$_2$ increases the final, harvested plant mass of many plant species (e.g. Kimball 1983; Cure and Acock 1986; Poorter 1993; Ceulemans and Mousseau 1994; Lloyd and Farquhar 1996; Poorter et al. 1996). The increase in final mass is often the result of a transient stimulation in the relative growth rate (RGR, increase in mass per unit mass per day) in C$_3$ herbaceous seedlings (Poorter 1993), with longer-term increases in RGR occurring in some longer-lived tree species (e.g. Bazzaz et al. 1993). Annual tree ring width was greater in *Quercus ilex* trees growing near CO$_2$ springs for the first 20 years after coppicing (Hättenschwiler et al. 1997).

The effect of elevated CO$_2$ on plant growth is likely to depend partly on the inherent RGR of the plant species in question. Plant species characteristic of unfavourable environments often have inherently low RGRs compared to species from more favourable environments (Chapin 1980; Lambers and Poorter 1992; Lambers et al. 1998). In woody and non-woody species, an inherently low RGR is often strongly associated with a lower foliage area per unit foliage dry mass (Poorter and Remkes 1990; Garnier 1992; Atkin and Lambers 1998; Atkin et al. 1998). Inherently low RGR values are also

associated with lower concentrations of nitrogen (Poorter et al. 1990; Atkin et al. 1996a; Atkin et al. 1998) and Rubisco (Poorter and Evans 1998; Westbeek et al. 1999) per unit foliage mass, as well as lower rates of photosynthesis per unit mass (Poorter et al. 1990; Atkin et al. 1996b). The proportion of daily fixed carbon that is respired is also substantially greater in inherently slow-growing species than in fast-growing species (Poorter et al. 1990; Atkin et al. 1996b).

The low Rubisco concentration and low rates of photosynthesis per unit foliage mass exhibited by slow-growing species may limit the absolute extent to which carbon acquisition per unit foliage mass can be stimulated by elevated CO_2. Moreover, the potential to use additionally fixed carbon under elevated CO_2 may be limited in slow-growing species that exhibit inherently low rates of cell elongation and/or small numbers of elongating cells (Van Volkenburgh et al. 1998). Consequently, slow-growing species may exhibit a lower absolute increase in growth per unit plant mass than fast-growing species. Poorter (1993, 1998) and Poorter et al. (1996) concluded that inherently fast-growing species do exhibit a greater *absolute* RGR response to elevated CO_2 than their slow-growing counterparts. However, Lloyd and Farquhar (1996) proposed that growth of slow-growing species that respire a greater proportion of daily photosynthesis should be more responsive to elevated CO_2. The effect of elevated CO_2 on growth of fast- versus slow-growing plants therefore remains controversial. We decided to assess the impact of elevated CO_2 on the growth and nitrogen economy of several woody *Acacia* species that differ in maximum inherent RGR (Atkin et al. 1998).

Acacia species from semi-arid environments are inherently slower growing than those characteristic of mesic environments (Atkin et al. 1998). Slow growth in the semi-arid species is not associated with lower net assimilation rates or less plant mass allocated to foliage. Rather, their slow growth is associated with a smaller foliage area per unit foliage mass compared to their faster-growing counterparts. Although all acacias initially produce compound pinnate leaves after germination, most Australian *Acacia* species subsequently switch to phyllode production (expanded petioles that form simple lamina) (Maslin 1995). Phyllode production reduces the RGR because phyllodes have a smaller area per unit foliage mass than leaves (Atkin et al. 1998). Not surprisingly, phyllode production is dominant in inherently slow-growing *Acacia* species from semi-arid Australian environments, with exclusive or dominant leaf production mainly occurring in faster-growing species from mesic environments (Atkin et al. 1998). From a nitrogen economy perspective, fast- and slow-growing acacias exhibit little difference in plant nitrogen concentration or the ratio of foliage nitrogen to plant nitrogen, with foliage nitrogen productivity (dry mass gain per unit foliage nitrogen and time) being directly proportional to differences in foliage area per unit foliage mass and RGR (Atkin et al. 1998). To date, no study has assessed whether fast- and slow-growing acacias that exhibit contrasting foliage characteristics differ in their response to elevated CO_2.

Materials and methods

Theory

To gain insight into why RGR is increased under elevated CO_2, we can factorise RGR into the specific foliage area (SFA, foliage area per unit foliage dry mass, $m^2 \, kg^{-1}$), foliage mass ratio (FMR, the ratio of foliage mass to plant mass, g foliage g^{-1} plant) and net assimilation rate (NAR, the increase in plant mass per unit foliage area and time, $g \, m^{-2} \, day^{-1}$) according to:

$$RGR = SFA \times FMR \times NAR \qquad (1)$$

In this paper, we use the term 'foliage' instead of 'leaf', as *Acacia* species produce leaves and phyllodes, both of which function as foliage.

We can also factorise RGR into its nitrogen economy components (Ingestad 1979; Hirose 1988): the plant nitrogen concentration (n_P, mmol N g^{-1}), the proportion of plant nitrogen allocated to foliage (v_F, mol $N_{foliage}$ mol^{-1} N_{plant}) and foliar nitrogen productivity (Π_F, the amount of dry matter produced per unit of foliar nitrogen and time (g mol^{-1} $N_{foliage}$ day^{-1}) according to:

$$RGR = n_P \times v_F \times \Pi_F \qquad (2)$$

The carbon and nitrogen economy approaches can then be combined to describe Π_F according to:

$$\Pi_F = (SFA \times FMR \times NAR)/(n_P \times v_F) \qquad (3)$$

The effect of elevated CO_2 on the RGR of the acacias can also be assessed in terms of the nitrogen uptake rate per unit root mass (NUR), the proportion of plant mass allocated to roots (RMR, root mass ratio) and n_P, according to:

$$RGR = NUR \times RMR/n_P \qquad (4)$$

Plant material

Ten *Acacia* species that differ in inherent RGR were chosen for investigation (Atkin et al. 1998; Table 1): four species from semi-arid environments that produced leaves in the earliest seedling stage and phyllodes thereafter (*Acacia aneura* F. Muell. ex Benth., *A. colei* Maslin and Thompson, *A. coriacea* DC. and *A. tetragonophylla* F. Muell.), three species from mesic environments that never produce phyllodes (*A. irrorata* Sieb. ex Spreng, *A. dealbata* Link and *A. mearnsii* De Wild.) and three mesic species that switch to phyllodes later in their development [*A. implexa* Benth, *A. melanoxylon* R.Br., and *A. saligna* (Labill.) H. Wendl.]. Seeds of the ten species were generously provided by the Australian Tree Seed Centre (CSIRO Division of Forestry and Forest Products), Canberra.

Plant growth

Seeds of all species were germinated as previously described (Atkin et al. 1998). Germinated seedlings were transferred to 50×9 cm pots (four plants per pot) filled with sterilised washed river sand and placed in one of two parallel glasshouses (approximately 22/17°C day/night in both) that differed in atmospheric CO_2 concentration [ambient (approx. 350 ppm) or 700 ppm]. The glasshouses were located in the Plant Growth Facility at the Research School of Biological Sciences, ANU, Canberra, at an altitude of 600 m. The elevated-CO_2 concentration was automatically monitored and controlled by a combined IRGA and controller. The daylength during the experiment was approximately 10–11 h, with additional lighting extending the photoperiod in both glasshouses to 16 h throughout the experiment. At the beginning of the experiment, the

Table 1 Total dry mass at final harvest, *average* relative growth rates (*RGR*, mg g^{-1} day^{-1}), *average* net assimilation rates (*NAR* g m^{-2} day^{-1}), and the *average* ratio of foliage dry mass to plant dry mass (*FMR*, g g^{-1}) and root dry mass to plant dry mass (*RMR*, g g^{-1}) of ten *Acacia* species exposed to ambient atmospheric CO_2 and elevated atmospheric CO_2 over the 12-week growth period. Species are ranked in order of increasing average RGR when grown under ambient-CO_2 conditions. NAR for each species was calculated by dividing the average RGR value by the average ratio of leaf area to plant dry mass. The r^2 values for the linear regressions used to calculate the RGR values were equal to, on average, 0.951, with the lowest value being 0.903 (*A. coriacea*, ambient CO_2). Significant differences in final dry mass and RGR between the ambient and elevated treatments are indicated next to the elevated-CO_2 value (***$P < 0.01$; **$P < 0.05$; *$P < 0.10$; *n.s.* not significant)

Species	Final total dry mass (g)		RGR (mg g^{-1} day^{-1})		NAR (g m^{-2} day^{-1})		FMR (g g^{-1})		RMR (g g^{-1})	
	Ambient	Elevated	Ambient	Elevated	Ambient	Elevated	Ambient	Elevated	Ambient	Elevated
A. coriacea	0.85 ± 0.10	1.35 ± 0.18**	48.4	55.4*	7.76	10.05	0.50	0.51	0.25	0.24
A. aneura	0.76 ± 0.10	0.60 ± 0.07 n.s.	59.5	64.2 n.s.	7.35	9.11	0.49	0.49	0.33	0.31
A. tetragonophylla	1.16 ± 0.20	1.91 ± 0.20**	64.2	69.5 n.s.	7.29	9.60	0.51	0.52	0.31	0.29
A. colei	1.34 ± 0.18	2.73 ± 0.44***	72.3	81.8 n.s.	7.87	10.49	0.48	0.53	0.36	0.31
A. dealbata	3.82 ± 0.55	8.55 ± 1.54**	82.7	94.6**	7.33	9.09	0.48	0.51	0.34	0.29
A. implexa	7.16 ± 0.47	13.60 ± 1.87***	84.0	90.4*	7.26	9.12	0.46	0.47	0.35	0.33
A. melanoxylon	2.29 ± 0.35	6.68 ± 0.56***	84.9	92.2*	6.45	8.28	0.4	0.42	0.40	0.4
A. irrorata	3.71 ± 0.83	6.46 ± 0.86**	88.1	94.5 n.s.	7.29	8.75	0.49	0.53	0.33	0.29
A. saligna	10.34 ± 1.52	17.00 ± 2.22**	92.7	101.9**	8.10	11.23	0.48	0.5	0.36	0.35
A. mearnsii	7.68 ± 1.50	11.98 ± 2.63**	93.6	104.8**	7.14	10.02	0.49	0.49	0.33	0.31

midday irradiances on a clear day in the two glasshouses were not substantially different, being 600 ± 240 and 660 ± 180 µmol photons m^{-2} s^{-1} ($n = 66$) at plant height in the ambient- and elevated-CO_2 glasshouses, respectively. An automatic irrigation system was used to water the free-draining pots in both glasshouses with UV-sterilised nutrient solution containing 5 mol m^{-3} KNO$_3$ as a nitrogen source. All species remained nodule free throughout the experiment.

Plants in both glasshouses were arranged according to a randomised split block-plot design, with the ten species arranged randomly within eight replicate blocks. For each species and CO_2 treatment, we commenced the experiment with similar-sized plants in all harvest blocks. The first harvest took place 3 weeks after the germinated seedlings had been transferred to the sand-filled pots, with the subsequent five harvests taking place every 2 weeks thereafter. CO_2 enrichment began 10 days before the first harvest. Just prior to the first harvest, plants were reduced to two plants per pot for harvests 1 to 3, where four pots were sampled, and one plant per pot for harvests 4 to 6, where eight pots were sampled at each harvest.

Harvest measurements

Eight plants of each species were sampled from each CO_2 treatment at each harvest and the fresh and dry mass of the roots, stems, leaves and phyllodes (if present) recorded. Leaf and phyllode areas were determined (Li-Cor 3050A/3000A, Lincoln, Neb., USA).

The average RGR of each species in each CO_2 treatment over the 12-week harvest period was determined as previously described (Atkin et al. 1998). Unless discussing leaves and phyllodes separately, we use the term foliage, regardless of whether phyllodes were produced or not. The average NAR over the 12-week harvest period for each species/CO_2 treatment was determined by dividing the average RGR value by the average foliage area per unit plant mass (i.e. SFA × FMR) over the 12-week growth period. Due to the unequal number of plants in the six harvests over the 12-week growth period, SFA, LMR and RMR values were calculated using the average of the six harvest means. Ontogenetic changes in foliage area per unit plant dry mass were described by a fourth-order polynomial fitted to the individual plant data plotted against the natural log of plant mass and were used to calculate daily RGR for each species/CO_2 treatment, assuming a linear dependence of NAR on daily irradiance (see Results).

Individual plant parts were pooled for subsequent chemical analyses. Total nitrogen and carbon concentration of each pooled root, stem, leaf and phyllode sample from each harvest were determined using a CHN analyser (Carlo Erba Instruments, Model EA 1110, Milan, Italy). Tissue nitrate was determined in water extracts of a random sample of the above harvest material (Cataldo et al. 1975). As little nitrate nitrogen was found in any of the analysed samples (typically less than 5% of total N in leaves; data not shown), we decided to discontinue the nitrate analyses. Total non-structural carbohydrates were determined from 5-mg aliquots of ground dry sample extracted in 80% ethanol and incubated at 80°C for 20 min. After centrifugation, the supernatant was removed and the sample re-extracted twice. The supernatant from leaves and phyllodes was cleared with 20 mg activated charcoal per 600 µl of supernatant. Aliquots (400 µl) of the supernatants were dried at 50°C and resuspended in 100 µl of water. Soluble sugars were assayed after incubation with invertase at 55°C for 20 min by the glucose oxidase/peroxidase method adapted to a titre plate assay read at 500 nm (glucose assay kit, Megazyme, Australia). Total starch was determined on the pellet that remained after soluble sugar extraction, by converting it to glucose using amyloglucosidase and α-amylase (total starch kit, Megazyme).

The effect of elevated CO_2 on RGR was tested by comparing the slopes of dry mass versus time plots using linear regression analysis (GraphPad Prism version 1.03, GraphPad Software). The effect of elevated CO_2 on the final yield of each species (using ln-transformed data) was tested by one-way analysis of variance (Quattro Pro for Windows).

Results

Effect of elevated CO_2 on growth: carbon economy

The increase in the natural logarithm of dry mass over time was relatively constant in both CO_2 treatments for all ten species, as demonstrated for the fast-growing *A. mearnsii* and the slow-growing *A. coriacea* (Fig. 1A). We therefore fitted linear regressions to the data to estimate the *average* RGR for each species and CO_2 treatment over the 12-week growth period (Table 1). Elevated CO_2 increased the average RGR of all species by, on average, 10% (Fig. 2A). Consequently, final total dry masses were substantially greater under elevated CO_2 (Table 1, Fig. 3). *A. aneura* plants grown under elevated CO_2 were smaller at the final harvest than ambient-CO_2-grown plants (Table 1, Fig. 3), despite
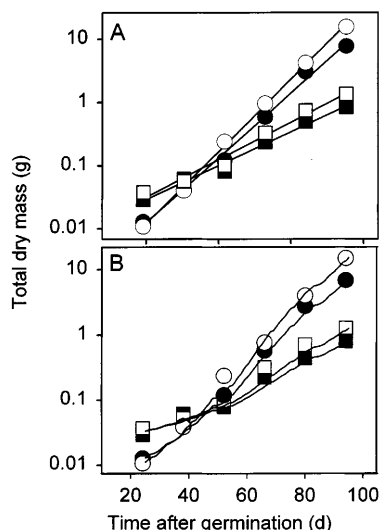
Fig. 1 A Exponential increase in total plant dry mass versus time for two of the ten *Acacia* species: *A. mearnsii* (*circles*) and *A. coriacea* (*squares*). Similar results were observed in the other eight species. The *solid* and *open* symbols represent growth in ambient and elevated CO_2, respectively ($n = 8$). Error bars were smaller than the symbols and therefore not shown. The *lines* are the linear regressions, the slopes of which are the average RGR (see Table 1). **B** Modelled increase in total dry mass through time. Daily increments in growth were calculated from a starting mass as the product of foliage area per unit plant mass and net assimilation rate. Net assimilation rate was dependent on daily irradiance (see text for details)

Fig. 2 Effect of CO_2 treatment on the *average* relative growth rate (*RGR*) (**A**) *average* net assimilation rate (NAR) (**B**), and *average* foliage mass ratio (*FMR*, foliage mass per unit plant mass, *closed circles*) and root mass ratio (*RMR*, root mass per unit plant mass, *open circles*) (**C**) for ten *Acacia* species differing in RGR. Values represent the ratio of elevated to ambient CO_2 in each case (a value greater than 1.0 means that elevated CO_2 was stimulatory) and are plotted against the average RGR (mg g^{-1} day^{-1}) for each species grown under ambient-CO_2 conditions (Table 1). Due to the unequal number of plants in the six harvests over the 12-week growth period, values were calculated using the average of the six harvest means within each treatment. The net assimilation rate for each species was calculated by dividing the average RGR over the 12-week period by the average foliage area per unit plant mass. The species can be identified from the ambient CO_2 RGR values shown in Table 1, as can the absolute values of each parameter

their greater average RGR (Fig. 2A), presumably due to unusually small plants in that final harvest.

Growth under elevated CO_2 resulted in a substantial increase in the *average* net assimilation rate in *all* species, with the lowest increase being 20% in *A. implexa* and the highest 40% in *A. mearnsii* (Table 1). The average increase in NAR for all species was 30%, which was independent of RGR (Fig. 2B).

Little or no change was observed in the allocation of biomass to foliage or roots in seven of the ten *Acacia* species (Fig. 2C, Table 1). For *A. colei*, *A. dealbata* and *A. irrorata*, FMR increased by an average 9% and RMR decreased by an average 13% when grown under elevated CO_2. Despite some variation between species, the *average* proportion of biomass allocated to stems was not affected by growth under elevated CO_2 (data not shown).

The SFA was substantially lower in plants exposed to elevated CO_2 in *all* ten *Acacia* species (Table 2, Fig. 4A). This was not due to any change in the time at which plants switched from leaf to phyllode production (data not shown). Two factors contribute to variation in SFA: foliage thickness (as estimated from the fresh mass per unit area) and the dry matter content (Dijkstra 1989). Foliage that is thicker and/or has a higher dry matter content will have a lower SFA. Direct measurements of leaf and phyllode thickness confirmed that the ratio of fresh mass to foliage area was a good indicator of thickness in our *Acacia* species (data not shown). Lower SFA in the plants exposed to elevated CO_2 was mainly
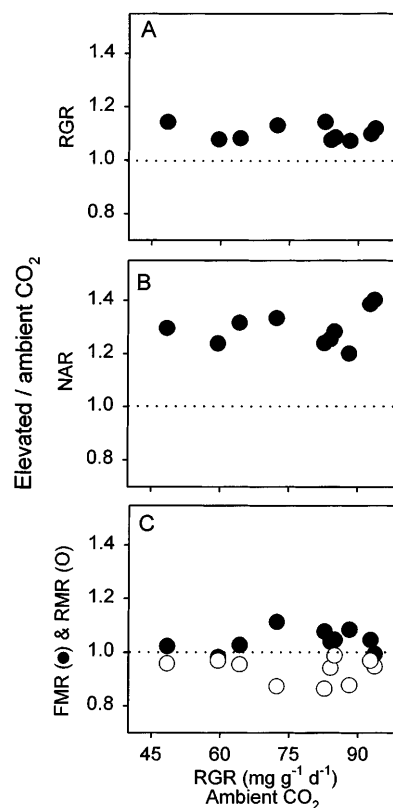
due to an increase in foliage thickness and to a lesser extent increased dry matter content (Table 2, Fig. 4B, C).

Taken together, the greater growth of plants exposed to elevated CO_2 was the result of an increased rate of carbon gain per unit foliage area (i.e. NAR). Increased NAR was offset by a general reduction in foliage area per unit foliage mass, but this decrease was not sufficient to prevent a greater RGR under elevated CO_2.

Effect of elevated CO_2 on accumulation of total non-structural carbohydrates

Were the lower SFAs of plants grown under elevated CO_2 due to the accumulation of total non-structural carbohydrates (TNCs)? The concentration of foliage TNC increased with RGR, being equivalent to about

50% of the daily growth increment (solid line, Fig. 5A). TNC content varied between harvests, being particularly low in harvest 4 which took place during very cloudy weather which reduced daily irradiance to one-third that of the subsequent three harvests (data not shown). Foliage TNC was higher in nine of the ten *Acacia* species grown under elevated versus ambient CO_2 (on average, 83% higher; Table 2). The proportional increase in foliage TNC concentration under elevated CO_2 was greatest in the fast-growing species (Fig. 5B).

The open circles in Fig. 4 show the effect of subtracting TNC from foliage dry mass on SFA (Fig. 4A) and foliage dry matter content (Fig. 4C) of each species. This correction only altered the ratio of SFA between the two CO_2 treatments by around 5% in five of the ten *Acacia* species. Subtracting TNC had no significant effect on foliage fresh mass per unit foliage area (Fig. 4B). Subtracting TNC revealed that elevated CO_2 increas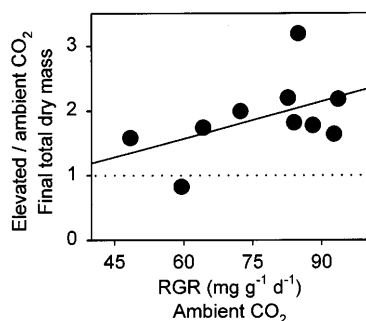ed structural foliage dry matter content by about 4% across all species (Fig. 4C). The difference in SFA between ambient- and elevated-CO_2-grown plants is therefore mainly the result of thicker foliage with a slightly higher structural dry matter content and not due to the accumulation of non-structural carbohydrates.

Modelling the effects of elevated CO_2 on RGR during development

To assess when RGR of the acacias was stimulated by elevated CO_2, growth was modelled in daily increments from a starting mass. NAR was linearly related to the average daily photosynthetically active radiation between the harvest dates (Fig. 6), with the slope being 29% greater for plants grown under elevated CO_2. There was little difference in NAR between the species for a given pair of harvests. Polynomial functions were used that related foliage area per unit plant dry mass to total plant dry mass (Fig. 7A). Foliage area per unit plant mass (foliage area ratio, FAR) increased to a peak before declining again. Growth under elevated CO_2 initially resulted in a lower FAR value, but for *A. coriacea*, there was little CO_2 effect once plants reached 0.3 g. To assess ontogenetic changes in RGR of plants exposed to ambient and elevated CO_2, we calculated the product of foliage area per unit plant mass and NAR (using each daily irradiance integral). Examples of the growth curves are shown in Fig. 1B and the ratio of elevated- to ambient-grown RGR is shown as a function of plant mass in Fig. 7B. The stimulation of RGR by elevated CO_2 was not limited to the early growth stage in any of the ten species, being consistently higher throughout their growth.

Fig. 3 Effect of CO_2 treatment on total plant dry mass of ten *Acacia* species after 93 days growth. Values represent the ratio of the geometric mean of final plant masses (Poorter 1998) from the elevated- and ambient-CO_2 treatments ($n = 8$) plotted against the average RGR (mg g^{-1} day^{-1}) for each species grown under ambient-CO_2 conditions (Table 1). The species can be identified from the ambient CO_2 RGR values shown in Table 1, as can the absolute values. The absolute values used to calculate the elevated to ambient ratios are shown in Table 1

Effect of elevated CO_2 on growth: nitrogen economy

When viewed from a nitrogen economy perspective, increased RGR under elevated CO_2 could occur via an

Table 2 Foliage characteristics of ten *Acacia* species exposed to ambient atmospheric CO_2 and elevated atmospheric CO_2 averaged over the 12-week growth period. *Average* values of specific foliage mass (*SFA*, foliage area, foliage thickness, foliage dry matter content, foliage total non-structural carbohydrates (*TNC*) and whole plant carbon concentration are shown
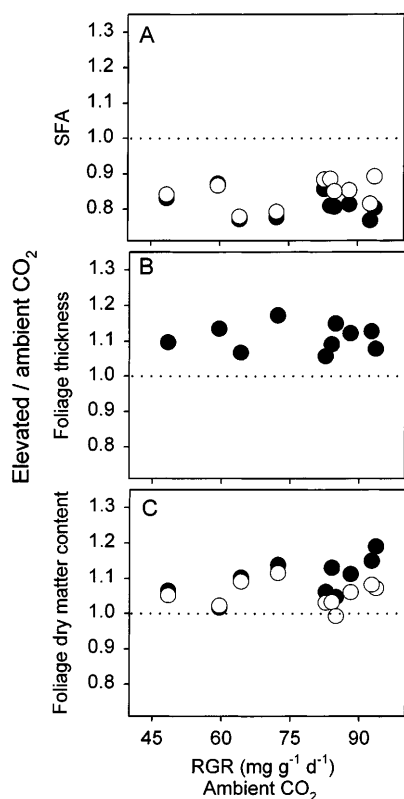
Species	SFA (foliage area/ dry mass) (m^2 kg^{-1})		Foliage thickness (foliage fresh mass/area) (g fresh mass m^{-2})		Foliage dry matter content (dry mass/ fresh mass) (% fresh mass)		Foliage TNC (% dry mass)		Plant carbon concentration (mmol C g^{-1})	
	Ambient	Elevated	Ambient	Elevated	Ambient	Elevated	Ambient	Elevated	Ambient	Elevated
A. coriacea	13.6	11.3	408	444	21.1	22.7	3.0	4.2	35.6	36.1
A. aneura	16.3	14.2	301	337	22.0	22.5	5.6	5.0	35.6	35.9
A. tetragonophylla	18.5	14.3	331	351	19.9	22.2	2.4	3.4	34.3	35.8
A. colei	19.8	15.4	259	300	21.2	24.3	10.5	12.4	34.1	35.1
A. dealbata	23.3	20.0	195	207	23.7	25.7	5.3	8.1	35.7	36.3
A. implexa	25.9	20.9	185	203	22.9	26.4	6.2	14.2	35.2	35.1
A. melanoxylon	32.8	26.4	136	158	23.6	25.3	5.8	10.7	34.5	35.7
A. irrorata	24.8	20.2	170	188	24.8	27.7	6.6	10.9	35.5	36.1
A. saligna	24.7	19.0	288	322	16.0	18.6	3.8	9.4	34.3	34.7
A. mearnsii	26.3	21.1	182	197	21.9	25.7	3.7	13.2	35.2	35.7

Fig. 4 Effect of CO_2 treatment on the *average* specific foliage area (*SFA*, foliage area per unit foliage dry mass) (**A**), *average* foliage thickness (estimated using foliage fresh mass per unit foliage area) (**B**) and *average* foliage dry matter content (foliage dry mass per unit foliage fresh mass) (**C**) for ten *Acacia* species differing in growth rate. The ratio of values from elevated- to ambient-CO_2 treatments are plotted against the average *RGR* for each species grown under ambient CO_2 conditions. The *open circles* show values for foliage area per unit structural foliage dry mass and structural foliage dry matter content per unit foliage fresh mass for each species (i.e. corrected for total non-structural carbohydrates). Due to the unequal number of plants in the six harvests over the 12-week growth period, values were calculated using the average of the six harvest means within each treatment). The species can be identified from the ambient-CO_2 RGR values shown in Table 1. The absolute values used to calculate the elevated to ambient ratios are shown in Table 2

Fig. 5 Effect of CO_2 treatment on the concentration of foliage total non-structural carbohydrates (*TNC*) in ten *Acacia* species differing in RGR. **A** Foliage TNC is shown for each species as a function of the average RGR. The *closed* and *open* circles represent values for the ambient and elevated atmospheric CO_2 treatments, respectively (the absolute values are shown in Table 2). The *solid line* represents a pool size equivalent to 50% of daily dry matter growth. **B** The ratio of foliage TNC from elevated- to ambient-CO_2 foliage, using values of TNC from harvests 3–6. Values are plotted against the average RGR for each species grown under ambient-CO_2 conditions. The species can be identified from the ambient-CO_2 RGR values shown in Table 1

Fig. 6 Relationships between net assimilation rate (*NAR*) and average daily irradiance for plants grown under ambient (*closed circles*) and elevated (*open circles*) CO_2. Each symbol represents a different pair of harvests and is the mean ± SE for all ten species. Average daily irradiance was calculated as the mean for all days between the pair of harvests used to calculate each NAR. The *solid* and *dashed lines* show the functions used to model NAR

increase in the plant nitrogen concentration (n_P), the ratio of foliage nitrogen to plant nitrogen (v_F) and/or the foliar nitrogen productivity (Π_F) (Eq. 3). In no case could the higher RGRs of the ten *Acacia* species be attributed to an increase in n_P or v_F (Table 3). In fact, n_P was unchanged in five species and 10% lower on average for the other five species. Growth under elevated CO_2 resulted in a substantial increase in Π_F (21% on average; Fig. 8, Table 3).

Foliar nitrogen productivity is a function of NAR and several other factors (see Eq. 3). The fact that SFA was substantially lower in all species grown under elevated CO_2 (Fig. 4A, Table 2) means that it was not responsible for the increase in Π_F. There were also only minor changes in the average FMR (increased by 4%), average n_P (decreased by 6%) and average v_F (decreased by 2%). Consequently, the substantial increase in foliar
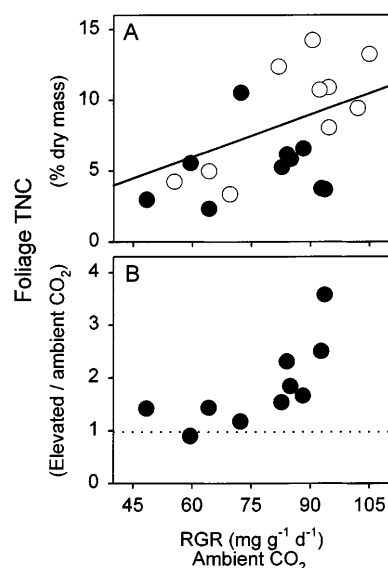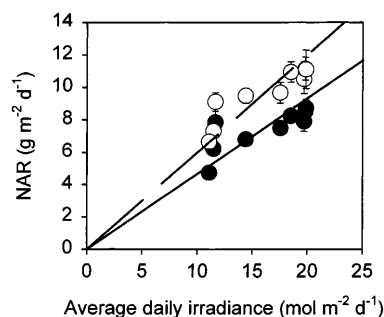
nitrogen productivity due to growth under elevated CO_2 was largely associated with greater NAR.

Effect of elevated CO_2 on nitrogen uptake by roots and the ratio of leaf area to root mass

Elevated CO_2 resulted in a greater demand for nitrogen in all of the selected acacias. In those species which

exhibited little difference in plant nitrogen concentration between the CO_2 treatments (five out of the ten species), the total demand for nitrogen would have been substantially greater compared to the ambient-CO_2-grown plants. In seven species, the rate of nitrogen uptake per unit root mass increased by 6 to 30%, with no significant change occurring in *A. implexa*, *A. saligna* and *A. mearnsii* (Fig. 9A, Table 3). The plant nitrogen concentration was 10% lower under elevated CO_2 for these three species.

The potential flux of water through roots is likely to be highest in plants with a high leaf area per unit root mass and this parameter was found to rise with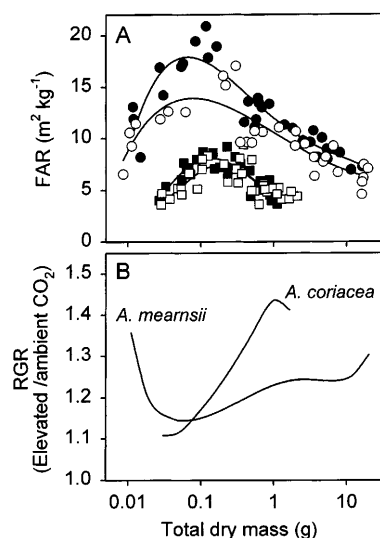 RGR (Table 3). Growth under elevated CO_2 would be expected to reduce this flux due to stomatal closure. Foliage area per unit root mass was reduced by elevated CO_2 in seven of the ten species (Fig. 9B) because foliage area per unit foliage mass declined. In these species, the plants grown under elevated CO_2 would be expected to be less susceptible to water stress. There was no change in foliage area per unit root mass in *A. colei*, *A. dealbata* and *A. irrorata* because in these species, elevated CO_2 also reduced root mass per unit plant mass. The division into these two groups was not related to RGR or foliage type.

Comparing the response of fast- and slow-growing plants to elevated CO_2

To determine whether inherently fast- and slow-growing *Acacia* species systematically differ in their response to elevated CO_2, we plotted the absolute increase in average RGR between the plants grown under elevated and ambient CO_2 (Fig. 10): the increase in RGR between the CO_2 treatments increased with RGR. The line represents the expected relationship when RGR is increased by 10% by growth under elevated CO_2.

Discussion

The results of our study demonstrate that elevated CO_2 increased the average RGR (Fig. 3A, Table 1) of all ten selected *Acacia* species, regardless of their inherent RGR. The increases in RGR were associated with a substantially greater NAR (Fig. 3B), which was offset by a decrease in foliage area per unit foliage dry mass (Fig. 4A). This is essentially the same conclusion reached by Poorter et al. (1996) from a survey of growth analysis experiments for 60 C_3 species. They found an increase in RGR (7%) and NAR (22%) with a decrease in specific leaf area (12%). The averages across our ten *Acacia* species were increases of 10% for RGR and 30%

Fig. 7 Effect of CO_2 treatment on foliage area per unit plant mass (*FAR*) (**A**) and the enhancement of RGR through ontogeny (**B**) for two *Acacia* species: *A. mearnsii* (*circles*) and *A. coriacea* (*squares*) for ambient (*closed symbols*) and elevated (*open symbols*) atmospheric CO_2. The ratio of elevated to ambient RGR is calculated using data from Figs. 6 and 7A for each species and shows enhancement for all plant masses

Table 3 Aspects of the nitrogen economy of ten *Acacia* species exposed to ambient atmospheric CO_2 and elevated atmospheric CO_2 averaged over the 12-week growth period. *Average* foliage nitrogen productivity, plant nitrogen concentration, foliage nitrogen per unit plant nitrogen, nitrogen uptake rate and foliage area per unit root dry mass are shown
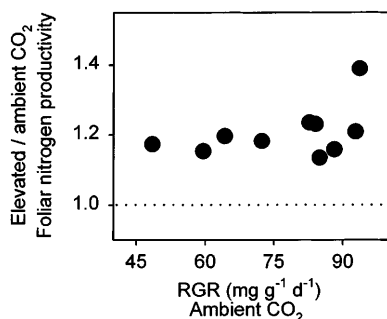
Species	Foliage nitrogen productivity (g mol^{-1} N day^{-1})		Plant nitrogen concentration (mmol N g^{-1})		Foliage N/plant N (mol N mol^{-1} N)		Nitrogen uptake rate (mol N g$_{root}^{-1}$)		Foliage area/ root mass (m^2 kg^{-1})	
	Ambient	Elevated	Ambient	Elevated	Ambient	Elevated	Ambient	Elevated	Ambient	Elevated
A. coriacea	30.3	35.6	2.76	2.73	0.58	0.57	0.53	0.62	24.9	24.3
A. aneura	28.9	33.3	2.95	2.93	0.70	0.66	0.57	0.63	28.4	24.5
A. tetragonophylla	31.2	37.3	2.88	2.83	0.71	0.66	0.61	0.67	30.2	26.2
A. colei	40.3	47.6	2.81	2.65	0.64	0.65	0.57	0.69	25.1	24.9
A. dealbata	44.0	54.4	2.79	2.69	0.67	0.65	0.69	0.88	34.3	35.3
A. implexa	42.0	51.7	3.13	2.81	0.64	0.62	0.75	0.76	33.5	31.2
A. melanoxylon	48.0	54.5	3.09	3.01	0.57	0.56	0.66	0.70	35.4	28.2
A. irrorata	43.8	50.8	3.00	2.71	0.67	0.69	0.81	0.90	37.6	40.0
A. saligna	43.7	52.8	3.35	2.94	0.63	0.66	0.85	0.85	32.7	26.9
A. mearnsii	43.0	59.7	3.17	2.74	0.69	0.64	0.90	0.92	41.4	34.9

Fig. 8 Effect of CO_2 treatment on the average foliar nitrogen productivity of ten *Acacia* species differing in RGR. The ratio of values from elevated- to ambient-CO_2 treatments is plotted against the average RGR for each species grown under ambient-CO_2 conditions. The species can be identified from the ambient-CO_2 RGR values shown in Table 1. The absolute values are shown in Table 3
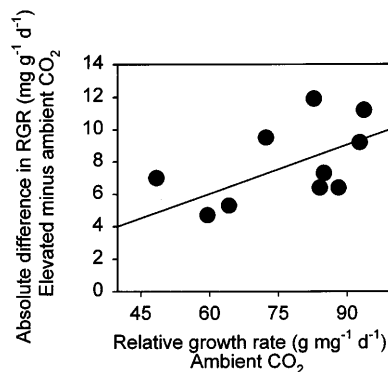

Fig. 10 Effect of CO_2 treatment on the absolute increase in RGR for ten *Acacia* species differing in RGR. All values are plotted against the average RGR for each species grown under ambient CO_2 conditions. The species can be identified from the ambient-CO_2 RGR values shown in Table 1. The line represents a 10% increase in RGR
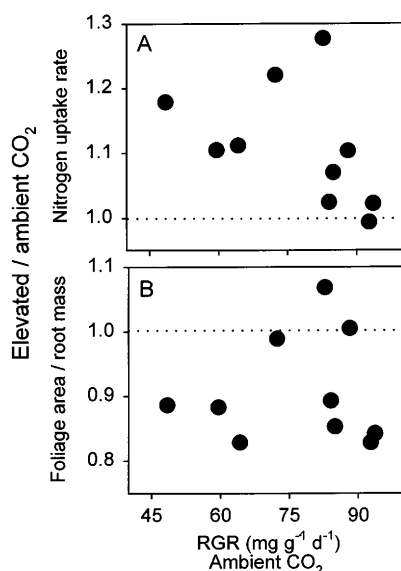

Fig. 9 Effect of CO_2 treatment on average nitrogen uptake rate per unit root dry mass (**A**) and average leaf area per unit root dry mass (**B**) for ten *Acacia* species differing in RGR. The ratio of the values from elevated- to ambient-CO_2 treatments is plotted against the average RGR for each species grown under ambient-CO_2 conditions. The species can be identified from the ambient-CO_2 RGR values shown in Table 1. The absolute values are shown in Table 3

for NAR with a decrease of 19% in foliage area per unit foliage dry mass. For the *Acacia* species, the greater enhancement of NAR by elevated CO_2 was offset by an equally large reduction of foliage area per unit foliage mass.

Effect of CO_2 on NAR

NAR, the dry matter increment per unit foliage area per day, is a function of the daily integral of photosynthesis, the fraction of that consumed in respiration by the plant for growth, ion uptake and maintenance, and the carbon content of the dry matter. Elevated atmospheric CO_2 should increase the daily integral of photosynthesis by stimulating the carboxylation rate of Rubisco and reducing photorespiration (Lloyd and Farquhar 1996; Drake et al. 1997). A survey of photosynthesis in tree species showed that photosynthesis increased by 44% under elevated CO_2 (Gunderson and Wullschleger 1994). Our own photosynthetic measurements confirmed this (data not shown). Poorter (1993) also showed that the CO_2 assimilation rate increased by the same proportion, regardless of inherent RGR. However, there are few data available on the fraction of daily CO_2 assimilation evolved in respiration. Masle et al. (1990) observed a 20% reduction in this fraction for wheat plants grown under elevated CO_2. This would also contribute to greater NAR under elevated CO_2. The carbon content of the *Acacia* species was not affected by CO_2 treatment (Table 2) and is generally not affected by atmospheric CO_2 concentration (Poorter et al. 1992).

For the *Acacia* data, NAR was strongly dependent on daily irradiance and CO_2 treatment (Fig. 6). Increasing atmospheric CO_2 from 350 to 700 ppm increased NAR by 30% on average. NAR was directly proportional to average daily irradiance and not affected by foliage area per unit foliage dry mass. The small variation among species was related to differences in nitrogen content per unit foliage area (data not shown). A strong dependence of NAR on daily irradiance is to be expected, given that the major component of NAR is photosynthesis and a near linear dependence has been observed for many herbaceous species (e.g. Poorter and Van Der Werf 1998). There was no indication in the *Acacia* data of any decline in enhancement of NAR by CO_2 over time, suggesting that photosynthetic acclimation was not occurring.

Effect of CO_2 on foliage area per unit foliage dry mass

Growth under elevated CO_2 resulted in a substantial reduction in foliage area per unit foliage dry mass for all

species. This was mainly due to increased foliage thickness which occurred in both leaves and phyllodes (data not shown). Structural dry matter content per unit foliage fresh mass was also increased by elevated CO_2, as has been observed in many other species (e.g. *Eucalyptus*: Wong et al. 1992; *Q. ilex*: Hättenschwiler et al. 1997; *A. mangium*: Ziska et al. 1991) but not all (e.g. *A. smallii*: Polley et al. 1997; *Q. alba*, Norby et al. 1995). The absence of a change in foliage area per unit foliage mass may well be related to plant age because by the end of our experiment, foliage area per unit foliage mass was no longer affected by CO_2 in *A. coriacea* (Fig. 7A) which possesses very thick phyllodes. Frequently, changes in foliage area per unit foliage mass are influenced by the inclusion of TNC which can accumulate to high concentrations in leaves grown under elevated CO_2 (Wong 1990). However, this was not the case for *Acacia* foliage and the TNC pool size is discussed below.

Effect of CO_2 on RGR

RGR is the product of NAR, foliage area per unit foliage dry mass and foliage mass per unit plant mass. CO_2 treatment does not generally affect foliage mass per unit plant mass (Table 1; Poorter et al. 1996). Consequently, the effect of CO_2 on RGR is the combined result of changes to NAR and foliage area per unit foliage mass. For the *Acacia* species, the effect of CO_2 on both of these parameters was independent of the inherent RGR of the species (Figs. 2B, 4A). The ratio of RGR between the two CO_2 treatments was therefore similar for all species and independent of RGR (Fig. 2A). It follows that the absolute difference in RGR between the two CO_2 treatments increased with inherent RGR (Fig. 10). In his survey of the literature, Poorter (1993) observed that the growth of faster-growing species responded more than that of slow-growing species to elevated CO_2. Subsequently, Poorter et al. (1996) showed that the absolute stimulation in RGR increased with inherent RGR. The *Acacia* data fell very close to the average increase presented by Poorter et al. (1996), confirming their conclusion.

Lloyd and Farquhar (1996) presented an alternative hypothesis, suggesting that because slow-growing species tend to consume a greater proportion of their daily CO_2 assimilation in respiration, slow-growing species should be more responsive to elevated CO_2. Unfortunately, there is a paucity of whole-plant respiration data. One extensive comparison between 24 herbaceous species clearly showed that a greater fraction of daily carbon assimilation was consumed in respiration by slower-growing species (Poorter et al. 1990). If this were also found to hold true for woody species, Lloyd and Farquhar (1996) predict the opposite to Poorter's observation. Our *Acacia* growth data (Fig. 10) and empirical data from the literature (Poorter 1998) do not support the hypothesis of Lloyd and Farquhar (1996).

Increased RGR was sustained

To what extent can short-term studies be extrapolated to meaningfully predict the long-term consequences of rising atmospheric CO_2? There are several lines of evidence that allow us to conclude that enhanced growth by elevated CO_2 lasts for a considerable period. First, for the duration of this experiment (90 days), the stimulation in NAR by elevated CO_2 remained the same. This means that there was no acclimation of the photosynthetic system. Foliage area per unit foliage mass changed through ontogeny. For most of the *Acacia* species, the effect of CO_2 on foliage area per unit foliage mass at the final harvest was similar to the mean of all harvests. For the three slowest-growing species, which were phyllodinous, there was no CO_2 effect on foliage area per unit foliage mass by the final harvest. Consequently, the observed stimulation of RGR would be expected to continue.

Second, in the literature review by Saxe et al. (1998), growth enhancement by elevated CO_2 increased as exposure duration increased, even after 1000 days. Enhanced *Acacia* growth under elevated CO_2 has previously been reported for *A. mangium* (90 days; Ziska et al. 1991), *A. karroo* (210 days; Wand et al. 1996) and *A. smallii* (390 days; Polley et al. 1997) where one can calculate that RGR was stimulated by about 5% in all three cases. For other species, growth stimulation was still evident in beech trees after 2 years (Mousseau et al. 1996) and for *Q. ilex* over 25 years (Hättenschwiler et al. 1997). In other cases, growth stimulation ceased after 40 days for four *Eucalyptus* species (Wong et al. 1992) and 3.5 months for *Q. alba* (Norby et al. 1995). In these cases, elevated CO_2 gave plants a greater growth rate early on which would result in greater plant size for an extended time.

Significance of foliage TNC pools

Due to the magnitude of the experiment, harvesting took place over 2 days such that foliar TNC values represent approximately the pools present at midday. While diurnal samples were not taken, foliage TNC concentrations were relatively stable for the last three harvests. The lower content observed during harvest 3 was due to dull weather at that time. The foliar TNC pool size was roughly equivalent to half of the daily plant growth increment. This implies that half of the daily photosynthesis is immediately exported while the remaining half is stored in the leaf for export at night to maintain plant growth at night. Of note, however, was the greater TNC pool size for the faster-growing species under elevated CO_2. This may indicate that the early morning minimum TNC pool size was increased by elevated CO_2, or that a greater proportion of photosynthate was exported at night under elevated CO_2. The relationship between TNC pool size and RGR found here for *Acacia* foliage (Fig. 7A) is also evident in the *Eucalyptus* data of Wong et al. (1992).

Körner and Miglietta (1994) found an increase in TNC due to long-term exposure to elevated atmospheric

CO_2. Interestingly, the deciduous *Q. pubescens* had 80% more TNC at the high-CO_2 site compared to the control, while for the evergreen *Q. ilex*, TNC was not affected by CO_2. They also observed similar TNC values on clear and overcast days. Würth et al. (1998) also observed little consequence of shading (up to 75% lower light) under ambient CO_2 on leaf TNC for two tropical tree species. By contrast, TNC content for our *Acacia* species was linearly related to daily irradiance, irrespective of CO_2 treatment or species (data not shown). Würth et al. (1998) found enhanced TNC accumulation due to elevated CO_2 treatment of between 1–8%, but the early morning TNC values were always less than 2.5% of leaf dry mass. This suggests that the TNC is metabolically active and not just a stable pool of excess carbon. Knowing the growth rates in our *Acacia* plants, it is possible to place the TNC pool size in context and show that it is consistent with that required for daily growth.

Water and nitrogen uptake

Growth under elevated CO_2 reduced leaf area per unit root mass in all but three of the ten *Acacia* species (Fig. 9B) due to the reduction in foliage area per unit foliage mass. Combined with reductions in stomatal conductance under elevated CO_2, such changes should reduce the risk of water stress for plants grown under elevated CO_2. Ziska et al. (1991) reported that growth under elevated CO_2 doubled the water use efficiency (determined from gas exchange) of *A. mangium*. Numerous other studies have demonstrated that elevated CO_2 increases the efficiency of water use in plants, with additional growth being achieved without concomitantly higher water use (e.g. Ceulemans and Mousseau 1994; Drake et al. 1997). Consequently, enhanced growth may mean that larger plants end up consuming the same amount of water.

Enhanced growth stimulated nitrogen uptake, both per plant and per unit root dry mass. In this experiment, nutrients were freely available and it is not possible to extrapolate from these results to the field where the additional complication of symbiotic nitrogen fixation occurs. However, nitrogen uptake rate per unit root dry mass was greater for species with higher RGR and increased under elevated CO_2, despite lower foliage areas per unit root mass which would reduce water influx rates per unit root dry mass. Clearly, the capacity for nitrogen uptake could be increased to enable more rapid growth under elevated CO_2, and for half of the *Acacia* species, plant nitrogen concentration was unaltered by growth under elevated CO_2. For the other five species, plant nitrogen concentration was reduced by about 10%.

Response to elevated CO_2 under limiting field conditions

Our results provide some insight into the response to elevated CO_2 by *Acacia* species that differ in inherent

RGR, when grown in the presence of unlimited water and nutrients. Differences in inherent RGR between *Acacia* species are driven by variation in specific foliage area (Atkin et al. 1998) and RGR was enhanced under elevated CO_2 by 10% (Fig. 3A), regardless of species or inherent RGR. In natural habitats, temperature, light, water and nutrient availability (e.g. phosphorus, nitrogen or micronutrients) are likely to reduce growth rates below those measured here. Moreover, the response to elevated CO_2 may differ in N_2-fixing acacias growing on N-deficient soils. The response of *Acacia* species reliant upon N_2 fixation to elevated CO_2 will be reported elsewhere. When experiments have been conducted that combine nutrient and CO_2 treatments, a general conclusion has been that the growth enhancement due to CO_2 is reduced as the nutrient stress becomes more severe (Poorter et al. 1996). This conclusion was not altered if P, N or NPK treatments were considered separately (Poorter 1998). However, while the imposition of nutrient stress reduces the growth response to elevated CO_2, it is not clear whether the size of the effect is dependent on the growth rate of the species. The picture becomes even more complicated when community dynamics are included, as the interaction and relative abundance of different species comes into play and the timescale becomes important, two considerations clearly beyond the scope of the present experiment.

References

Atkin OK, Lambers H (1998) Slow-growing alpine and fast-growing lowland species: a case study of factors associated with variation in growth rate among herbaceous higher plants under natural and controlled conditions. In: Lambers H, Poorter H, Van Vuuren MMI (eds) Inherent variation in plant growth: physiological mechanisms and ecological consequences. Backhuys, Leiden, pp 259–288

Atkin OK, Botman B, Lambers H (1996a) The relationship between the relative growth rate and nitrogen economy of alpine and lowland *Poa* species. Plant Cell Environ 19:1324–1330

Atkin OK, Botman B, Lambers H (1996b) The causes of inherently slow growth in alpine plants: an analysis based on the underlying carbon economies of alpine and lowland *Poa* species. Funct Ecol 10:698–707

Atkin OK, Schortemeyer M, McFarlane N, Evans JR (1998) Variation in the components of relative growth rate in ten *Acacia* species from contrasting environments. Plant Cell Environ 21:1007–1017

Bazzaz FA, Miao SL, Wayne PM (1993) CO_2-induced growth enhancements of co-occurring tree species decline at different rates. Oecologia 96:478–482

Cataldo DA, Haroon M, Schrader LE, Youngs V (1975) Rapid colorimetric determination of nitrate in plant tissue by nitration of salicylic acid. Comm Soil Sci Plant Anal 6:71–80

Ceulemans R, Mousseau M (1994) Effects of elevated atmospheric CO_2 on woody plants. New Phytol 127:425–446

Chapin FS (1980) The mineral nutrition of wild plants. Annu Rev Ecol System 11:233–260

554

Cure JD, Acock B (1986) Crop responses to carbon dioxide doubling: a literature survey. Agric For Meteorol 38:127–145

Dijkstra P (1989) Cause and effect of differences in SLA. In: Lambers H, Cambridge ML, Konings H, Pons TL (eds) Causes and consequences of variation in growth rate and productivity of higher plants. SPB, The Hague, pp 125–140

Drake BG, Gonzàlez-Meer MA, Long SP (1997) More efficient plants: a consequence of rising atmospheric CO_2? Annu Rev Plant Physiol Plant Mol Biol 48:609–639

Garnier E (1992) Growth analysis of congeneric annual and perennial grass species. J Ecol 80:665–675

Gunderson CA, Wullschleger SD (1994) Photosynthetic acclimation in trees to rising atmospheric CO_2: a broader perspective. Photosynth Res 39:369–388

Hättenschwiler S, Miglietta F, Raschi A, Körner C (1997) Morphological adjustments of mature *Quercus ilex* trees to elevated CO_2. Acta Oecol 18:361–365

Hirose T (1988) Modelling the relative growth rate as a function of plant nitrogen concentration. Physiol Plant 72:185–189

Ingestad T (1979) Nitrogen stress in birch seedlings. II. N, K, P, Ca and Mg nutrition. Physiol Plant 45:145–157

Kimball BA (1983) Carbon dioxide and agricultural yield: an assemblage and analysis of 430 prior observations. Agron J 75:779–788

Körner C, Miglietta F (1994) Long term effects of naturally elevated CO_2 on Mediterranean grassland and forest trees. Oecologia 99:343–351

Lambers H, Poorter H (1992) Inherent variation in growth rate between higher plants: a search for physiological causes and ecological consequences. Adv Ecol Res 23:187–261

Lambers H, Poorter H, Van Vuuren MMI (eds) (1998) Inherent variation in plant growth: physiological mechanisms and ecological consequences. Backhuys, Leiden

Lloyd J, Farquhar GD (1996) The CO_2 dependence of photosynthesis, plant growth responses to elevated atmospheric CO_2 concentrations, and their interaction with soil nutrient status. I. General principles and forest ecosystems. Funct Ecol 10:4–32

Masle J, Farquhar GD, Gifford RM (1990) Growth and carbon economy of wheat seedlings as affected by soil resistance to penetration and ambient partial pressure of CO_2. Aust J Plant Physiol 17:465–487

Maslin BR (1995) Systematics and phytogeography of Australian species of *Acacia:* an overview. IFA Newsl 36:2–5

Mousseau M, Dufrêne D, El Kohen A, Epron D, Godard D, Liozon R, Yves Pontailler J, Saugier B (1996) Growth strategy and tree response to elevated CO_2: a comparison of beech (*Fagus sylvatica*) and sweet chestnut (*Castanea sativa* Mill.). In: Koch GW Mooney HA (eds) Carbon dioxide and terrestrial ecosystems. Academic Press, San Diego, pp 71–86

Norby RJ, Wullschleger SD, Gunderson CA, Nietch CT (1995) Increased growth efficiency of *Quercus alba* trees in a CO_2-enriched atmosphere. New Phytol 131:91–97

Polley HW, Johnson HB, Mayeux HS (1997) Leaf physiology, production, water use, and nitrogen dynamics of the grassland invader *Acacia smallii* at elevated CO_2 concentrations. Tree Physiol 17:89–96

Poorter H (1993) Interspecific variation in the growth response of plants to an elevated ambient CO_2 concentration. Vegetatio 103/104:77–97

Poorter H (1998) Do slow-growing species and nutrient-stressed plants respond relatively strongly to elevated CO_2? Global Change Biol 4:693–697

Poorter H, Evans JR (1998) Photosynthetic nitrogen-use efficiency of species that differ inherently in specific leaf area. Oecologia 116:26–37

Poorter H, Remkes C (1990) Leaf area ratio and net assimilation rate of 24 wild species differing in relative growth rate. Oecologia 83:553–559

Poorter H, Van Der Werf A (1998) Is inherent variation in RGR determined by LAR at low irradiance and by NAR at high irradiance? A review of herbaceous species. In: Lambers H, Poorter H, Van Vuuren MMI (eds) Inherent variation in plant growth: physiological mechanisms and ecological consequences. Backhuys, Leiden, pp 309–336

Poorter H, Remkes C, Lambers H (1990) Carbon and nitrogen economy of 24 wild species differing in relative growth rate. Plant Physiol 94:621–627

Poorter H, Gifford RM, Kriedemann PE, Wong SC (1992) A quantitative analysis of dark respiration and carbon content as factors in the growth response of plants to elevated CO_2. Aust J Bot 40:501–513

Poorter H, Roumet C, Campbell BD (1996) Interspecific variation in the growth response of plants to elevated CO_2: a search for functional types. In: Körner C, Bazzaz FA (eds) carbon dioxide, populations, and communities. Academic Press, San Diego, pp 375–412

Saxe H, Ellsworth DS, Heath J (1998) Tree and forest functioning in an enriched CO_2 atmosphere. New Phytol 139:395–436

Van Volkenburgh E, Stahlberg R, Bultynck L (1998) Physiological mechanisms controlling the rate of leaf growth. In: Lambers H, Poorter H, Van Vuuren MMI (eds) inherent variation in plant growth: physiological mechanisms and ecological consequences. Backhuys, Leiden, pp 41–56

Wand SJE, Midgley GF, Musil CF (1996) Physiological and growth responses of two African species, *Acacia karroo* and *Themeda triandra*, to combined increases in CO_2 and UV-B radiation. Physiol Plant 98:882–890

Westbeek MHM, Pons TL, Cambridge ML, Atkin OK (1999) Analysis of differences in photosynthetic nitrogen-use efficiency of alpine and lowland *Poa* species. Oecologia 120:19–26

Wong SC (1990) Elevated atmospheric partial pressure of CO_2 and plant growth. II. Non-structual carbohydrate content in cotton plants and its effect on growth parameters. Photosynth Res 23:171–180

Wong SC, Kriedemann PE, Farquhar GD (1992) $CO_2 \times$ nitrogen interaction on seedling growth of four species of eucalypt. Aust J Bot 40:457–472

Würth MKR, Winter K, Körner C (1998) Leaf carbohydrate responses to CO_2 enrichment at the top of the tropical forest. Oecologia 116:18–25

Ziska LH, Hogan KP, Smith AP, Drake BG (1991) Growth and photosynthetic response of nine tropical species with long-term exposure to elevated carbon dioxide. Oecologia 86:383–389