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

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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

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 CO2. Moreover, the potential to use additionally fixed carbon under elevated CO2 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 CO2 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 CO2. The effect of elevated CO2 on growth of fast- versus slow-growing plants therefore remains controversial. We decided to assess the impact of elevated CO2 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 phylloide production (expanded petioles that form simple lamina) (Maslin 1995). Phylloide production reduces the RGR because phylloides have a smaller area per unit foliage mass than leaves (Atkin et al. 1998). Not surprisingly, phylloide 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 CO2.

**Materials and methods**

Theory

To gain insight into why RGR is increased under elevated CO2, we can factorise RGR into the specific foliage area (SFA, foliage area per unit foliage dry mass, m² kg⁻¹), foliage mass ratio (FMR, the ratio of foliage mass to plant mass, g foliage⁻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:

\[ RGR = SFA \times FMR \times NAR \]  

(1)

In this paper, we use the term ‘foliage’ instead of ‘leaf’, as Acacia species produce leaves and phylloides, 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 (\(\frac{F_p}{F}\), mol N foliage⁻¹ Nplant) and foliar nitrogen productivity (\(\Pi_F\), the amount of dry matter produced per unit of foliar nitrogen and time (g mol⁻¹ N foliage day⁻¹) according to:

\[ RGR = n_p \times \frac{F}{F_p} \times \Pi_F \]  

(2)

The carbon and nitrogen economy approaches can then be combined to describe \(\Pi_F\) according to:

\[ \Pi_F = \frac{(SFA \times FMR \times NAR)}{(n_p \times \frac{F}{F_p})} \]  

(3)

The effect of elevated CO2 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:

\[ RGR = NUR \times RMR \times \frac{n_p}{F} \]  

(4)

Plant material

Ten Acacia species that differ in inherent RGR were chosen for investigation (Atkin et al. 1998; Table I): four species from semi-arid environments that produced leaves in the earliest seedling stage and phylloides 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 phylloides (A. irrorata Sieb. ex Spreng., A. dealbata Link and A. mearnsii De Wild.) and three mesic species that switch to phylloides later in their development (A. inermis 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 CO2 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-CO2 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