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SAVANNAS FACE THE FUTURE: WINDOWS INTO A FUTURE CO_2-RICH WORLD

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INTRODUCTION

Despite the global importance of tropical C_4 vegetation, we understand little about how it will contribute to the biosphere's response to rising atmospheric CO_2 (Nowak *et al*. 2004; Ainsworth and Long 2005). Plants with the C_4 photosynthetic pathway account for about 23% of global gross primary productivity, largely in tropical grasslands and savannas (Still *et al*. 2003). These ecosystems cover about one sixth of the planet's land surface, are primarily used for extensive livestock production, and support over 400 million people who are amongst the world's poorest and most vulnerable to climate change (White *et al*. 2000; Still *et al*. 2003; IPCC 2007). These regions are also rich in biodiversity (e.g., ungulates in African savannas, and vegetation of the South American Cerrado savannas). Unlike C_3 plants, in which elevated CO_2 (eCO_2) directly stimulates carbon fixation, C_4 plants have a CO_2 concentrating mechanism. C_4 growth responses are therefore likely to be mediated mainly by savings in water use (related to stomatal constriction under eCO_2). Ecosystem models and enclosed environment experiments suggest that C_4 plant growth may be stimulated by eCO_2 but, in the absence of empirical field evidence, it is not certain how strong this stimulation will be, or whether C_4 plants will even respond at all. The Australian Savanna Free Air CO_2 Enrichment (OzFACE) experiment was established to test the ecological responses of a natural community of C_4 savanna grasses to eCO_2 in a tropical environment (Stokes *et al*. 2005). This is the first FACE experiment in the tropics and the first in a C_4-dominated plant community.

METHODS

The OzFACE facility was located in northeast Queensland in a coastal tropical savanna with low fertility soils and a grass layer (all C_4) dominated by *Themeda triandra*. The FACE system consisted of a set of six circular plots, two replicates for each of three CO_2 treatments (ambient ≈370 ppm, 460 ppm and 550 ppm). Each plot was divided into three 120° segments for the application of split-plot treatments: selective defoliation of *Themeda* (at 4-weekly intervals through the growth season); nutrient addition (in $g\ m^{-2}\ yr^{-1}$: 4.7 N, 1.0 P, 2.8 K, 1.2 S, 0.86 Ca, 0.24 Mg, 0.02 Zn, 0.04 Bo); and a control. The experiment spanned five full growth seasons between May 2001 and May 2006.

We measured aboveground net primary production (aNPP: $g\ m^{-2}$) of the grass layer each year at the end of the growing season (about May) using a cut and re-harvest method. Vegetation biomass surveys were also conducted annually at the same time, using a non-destructive, calibrated visual estimation technique (Waite 1994). We took baseline measurements of aboveground biomass prior to the start of the experiment and used these to correct subsequent vegetation measurements for pre-existing differences between plots. ANOVAs were used to analyse the data, according to the split-plot design to test for a main effect of CO_2 and whether CO_2 responses were modified by split-plot treatments. For simplicity, we restrict the presented results and discussion to main effects of CO_2 (and exclude interactions).

RESULTS

Over the five years of the experiment there was a total 36.3 ± 16.3 % stimulation of aNPP (all responses expressed as the % change for a 180 ppm increase in $[CO_2]$ relative to ambient $[CO_2]$). The strongest responses (+95% and +48%) were observed in moderately dry years (2001/02 and 2004/05) with weaker responses observed in wetter years (+33% and +28%) (Fig. 1). But there was no detectable effect of elevated CO_2 (eCO_2) on aNPP during an extreme drought (2002/03, bottom 6th percentile rainfall year), serving as a caution against extrapolating the enhanced growth benefits of eCO_2 under dry conditions to conditions of extreme drought.

Growth responses to eCO_2 were dominated by a single species, *Themeda triandra*, which almost tripled in aNPP (183.3 ± 19.4% increase relative to ambient [CO_2], $p < 0.05$). In contrast, there was no detectable stimulation for the remaining components of the vegetation (3.3 ± 12.5% for other perennial grasses and -2.9 ± 20.0% for annual grasses, also C4). Changes in grass aNPP were similarly reflected in species biomass (Fig. 2). There was complete mortality of *Themeda* during the 2002/03 drought, but by the end of the experiment, *Themeda* had benefited most from eCO_2 (Fig 2a.) Other grass species did not benefit from eCO_2, except during the drought when *Themeda* was low in abundance (Fig 2b). During the drought recovery, grasses established temporarily, but this establishment was suppressed by eCO_2 where perennial grasses were more abundant (Fig. 2c).

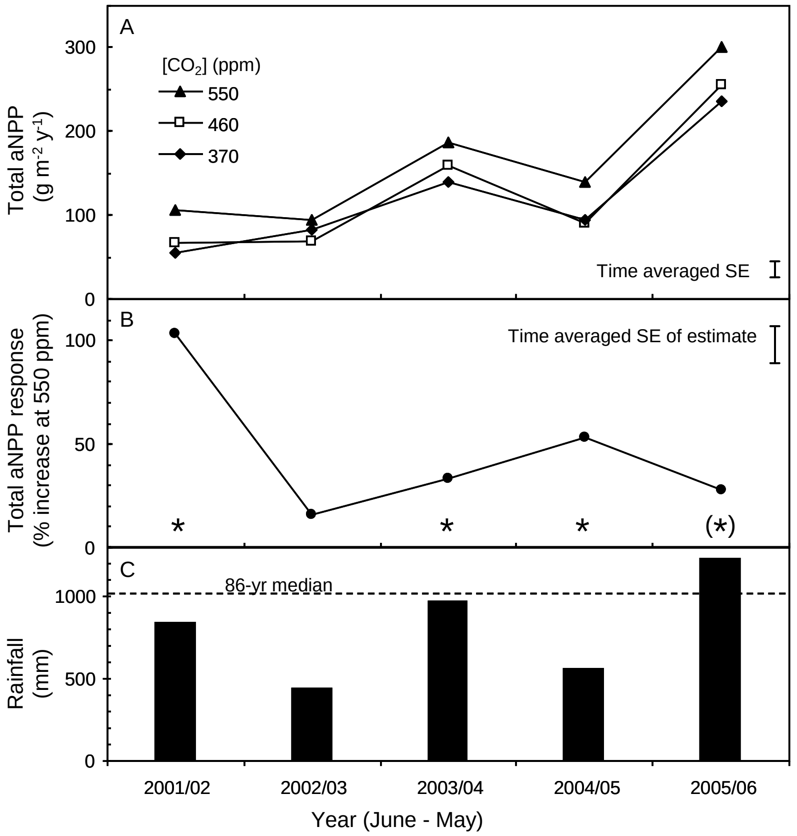

Fig. 1. (*A*) Responses of total aboveground net primary production (aNPP, $n=2$) to elevated individual CO_2 treatments. (*B*) Response strengths, summarised as the percentage increase in aNPP for a 180 ppm increase in [CO_2] relative to ambient [CO_2]. Analyses take pre-existing differences in baseline aboveground biomass into account. Dates for which there was a significant response trend across the three CO_2 treatments are indicated by '*' ($p < 0.05$) and '(*)' ($p < 0.1$). (*C*) Rainfall data is provided for comparison.

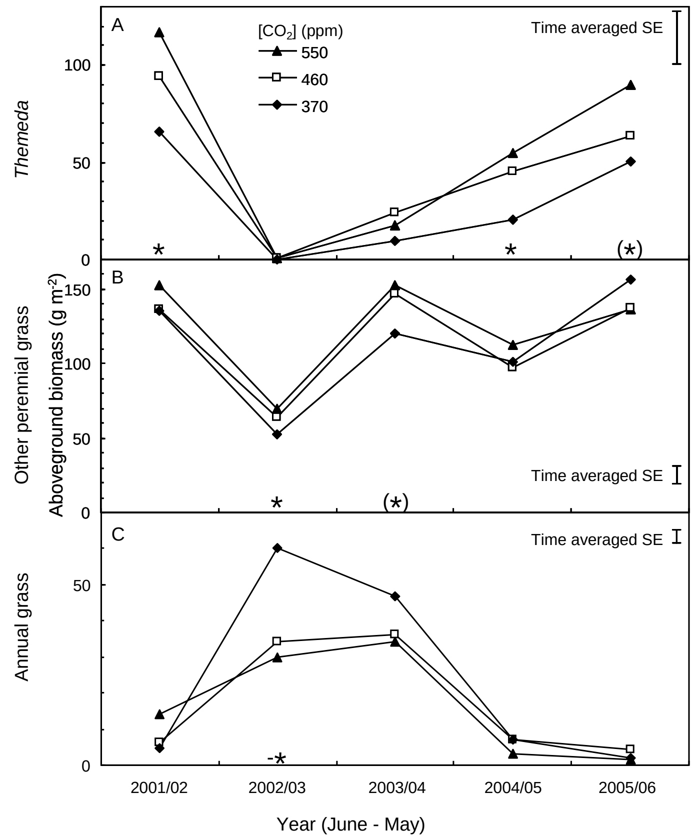

Fig. 2. Changes in aboveground biomass (*n*=2) for (*A*) *Themeda*, (*B*) other perennial grasses and (*C*) annual grasses in response to elevated CO_2 over five years. Analyses take preexisting differences in baseline aboveground biomass into account. Dates for which there was a significant response trend across the three CO_2 treatments are indicated by '*' ($p < 0.05$) and '(*)' ($p < 0.1$).

DISCUSSION

Our results provide the first field evidence showing that natural tropical grass communities (C_4) can respond strongly to eCO_2, comparing favourably with the strongest C_3 plant responses reported from other FACE experiments (Nowak *et al.* 2004; Ainsworth and Long 2005). The strong grass growth (aNPP) responses were likely influenced by the occurrence of an extreme drought during the experiment. Responses of C_4 plants to eCO_2 have usually been considered in terms of moisture-mediated feedbacks, whereby plant water savings under eCO_2 accumulate in the soil and stimulate plant growth (Stokes and Ash 2006). But our results show that besides the stimulating effect on growth, eCO_2 also has an important additional effect in reducing the adverse ecological impacts of drought on C_4 grass communities and enhancing post-drought recovery. C_4 plants typically grow in harsh, periodically-dry environments, conditions which have been poorly represented in past CO_2 experiments. Important ecological interactions between eCO_2 and episodic climatic stresses have therefore not been experimentally captured or fully appreciated. Such interactions will take on added relevance in understanding how eCO_2 might offset the impacts of climate change, particularly if the frequency and/or severity of stress events increases in the future.

A key advantage of FACE, particularly for ecosystem experiments, is that treated areas are large enough to capture the natural complexity of ecological interactions and feedback processes in whole plant systems. For example, in moisture-mediated growth responses of C_4-dominated vegetation to eCO_2, there is no guarantee that water 'saved' by a given plant will necessarily benefit only that plant. In multi-species vegetation in particular, this suggests that there is strong potential for responses to CO_2 to be modified by competition for 'saved' soil moisture. The approximate tripling in aNPP of *Themeda* cannot be explained by a direct physiological response to a 50% increase in $[CO_2]$ alone, but demonstrates important contributions of ecological feedback processes: 1) *Themeda* is likely exploiting water saved by other grass species (species that were unable to use the saved water to enhance their own growth); and 2) the initial advantage of *Themeda* was compounded over time as *Themeda* increased in relative abundance in the grass community.

Results from the first FACE study in a tropical environment show that eCO_2 can strongly affect C_4 plant communities. Two ecological processes likely enhanced the strength of this response: interactions between eCO_2 and a climatic event (drought) and positive feedbacks that altered community composition, both of which would be difficult to accurately predict or detect without directly measuring plot-scale field responses. This suggests a need for a greater understanding of ecosystem responses to eCO_2 in natural and semi-natural vegetation. Strong increases in tropical grass production would be expected to benefit livestock and other herbivores, alter fuel loads for fires and change nutrient and carbon cycling (although these responses to eCO_2 will also depend on changes in climate and land management practices). *Themeda triandra* is an important grass across the tropics so, if its strong response to eCO_2 is duplicated in other ecosystems, this would have widespread ramifications for the humans, livestock and wildlife they support.

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REFERENCES

Ainsworth, E. A., and Long, S. P. (2005). What have we learned from 15 years of free-air CO_2 enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy. *New Phytologist* **165,** 351-371.

IPCC (2007). 'Climate change 2007 - impacts, adaptation and vulnerability - contribution of Working Group II to the Fourth Assessment Report of the International Panel on Climate Change'. (Cambridge University Press, Cambridge.)

Nowak, R. S., Ellsworth, D. S., and Smith, S. D. (2004). Functional responses of plants to elevated atmospheric CO_2 - do photosynthetic and productivity data from FACE experiments support early predictions? *New Phytologist* **162,** 253-280.

Still, C. J., Berry, J. A., Collatz, G. J., and DeFries, R. S. (2003). Global distribution of C-3 and C-4 vegetation: Carbon cycle implications. *Global Biogeochemical Cycles* **17**.

Stokes, C. J., and Ash, A. J. (2006). Special example 1: Impacts of climate change on marginal tropical animal production systems. *In*: 'Agroecosystems in a changing climate'. (Eds P.C.D.Newton, R.A.Carran, G.R.Edwards and P.A.Niklaus) pp. 323-328. (CRC Press, London.)

Stokes, C. J., Ash, A. J., Tibbett, M., and Holtum, J. A. M. (2005). OzFACE: the Australian Savanna Free Air CO_2 Enrichment facility and its relevance to carbon cycling issues in a tropical savanna. *Australian Journal of Botany* **53,** 677-687.

Waite, R. B. (1994). The application of visual estimation procedures for monitoring pasture yield and composition in exclosures and small plots. *Tropical Grasslands* **28,** 38-42.

White, R., Murray, S., and Rohweder, M. (2000). 'Pilot analysis of global ecosystems: grassland ecosystems'. (World Resources Institute, Washington, D.C.)