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## Responses of tropical native and invader C<sub>4</sub> grasses to water stress, clipping and increased atmospheric CO<sub>2</sub> concentration

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**Abstract** The invasion of African grasses into Neotropical savannas has altered savanna composition, structure and function. The projected increase in atmospheric CO<sub>2</sub> concentration has the potential to further alter the competitive relationship between native and invader grasses. The objective of this study was to quantify the responses of two populations of a widespread native C<sub>4</sub> grass (*Trachypogon plumosus*) and two African C<sub>4</sub> grass invaders (*Hyparrhenia rufa* and *Melinis minutiflora*) to high CO<sub>2</sub> concentration interacting with two primary savanna stressors: drought and herbivory. Elevated CO<sub>2</sub> increased the competitive potential of invader grasses in several ways. Germination and seedling size was promoted in introduced grasses. Under high CO<sub>2</sub>, the relative growth rate of young introduced grasses was twice that of native grass (0.58 g g<sup>-1</sup> week<sup>-1</sup> vs 0.25 g g<sup>-1</sup> week<sup>-1</sup>). This initial growth advantage was maintained throughout the course of the study. Well-watered and unstressed African grasses also responded more to high CO<sub>2</sub> than did the native grass (biomass increases of 21–47% compared with decreases of 13–51%). Observed higher water and nitrogen use efficiency of invader grasses may aid their establishment and competitive strength in unfertile sites, specially if the climate becomes drier. In addition, high CO<sub>2</sub> promoted lower leaf N content more in the invader grasses. The more intensive land use, predicted to occur in this region, may interact with high CO<sub>2</sub> to favor the African grasses, as they generally recovered faster after simulated herbivory. The superiority of invader grasses under high CO<sub>2</sub> suggests fur-

ther increases in their competitive strength and a potential increased rate of displacement of the native savannas in the future by grasslands dominated by introduced African species.

**Keywords** Drought · Global change · Herbivory · Invasion · Neotropics · Savannas

### Introduction

Climate alteration, promoted by increased atmospheric CO<sub>2</sub>, and the invasion of exotic species are two main drivers of global change (Sala et al. 2000). Both may interact synergistically, as the invasion and spread of exotic plants could be promoted by climate change and increased atmospheric CO<sub>2</sub> (Vitousek et al. 1996; Dukes 2002; Gill et al. 2002; Weltzin et al. 2003; Ziska 2003). This interaction is affected by the biophysical constraints of the regional environment and by land use changes (Hoffmann and Jackson 2000).

In Neotropical savannas, the main biophysical limitations to growth are rainfall seasonality and low fertility. Local land use includes stressors as fertilization to improve pastures, herbivory by domestic ruminants and increased fire frequency. This combination of biophysical and anthropogenic stressors, plus the invasion of exotic grasses, potential climate change, and increasing CO<sub>2</sub>, may alter the structure and function of 2.5×10<sup>6</sup> km<sup>2</sup> of Neotropical savannas. This has already taken place at a large scale (~100 million Ha), where Neotropical savannas were converted into grasslands. These grasslands are dominated by invasive C<sub>4</sub> African grasses which were introduced to improve pasture productivity but escaped cultivation and invaded native savannas (Parsons 1972; Baruch 1996; Williams and Baruch 2000).

Several traits of African grasses contribute to their higher competitive potential compared to native species. Compared to one of the main native grasses, two

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prominent invader African grasses have shown higher carbon assimilation rate and nitrogen use efficiency (NUE) (Baruch et al. 1985), higher opportunistic water use (Baruch and Fernández 1993), greater compensatory regrowth after defoliation (Simoes and Baruch 1991), lower leaf construction costs (Baruch and Gómez 1996) and faster recovery of growth after fire (Baruch and Bilbao 1999). The African grasses are facultatively apomictic (Bogdan 1977; Watson and Dallwitz 1998) which may help explain their rapid and effective colonization and spread.

African grasses have displaced native savanna grasses across broad areas of South America, converting relatively diverse and open savanna communities into monospecific grassland stands with much larger plant cover and standing biomass than the native savannas (Baruch 1996). This conversion has far reaching consequences for ecosystem structure and function. Some of these consequences include (1) reduced light levels reaching the soil surface which could change savanna composition by affecting germination and establishment of other native grasses and trees (Gordon 1998; D'Antonio et al. 2001), (2) High biomass production of African grasses which provides additional fuel for more intense and frequent fires, altering the disturbance regime which facilitates conversion of more savanna to grassland (D'Antonio and Vitousek 1992; Baruch and Bilbao 1999; Rossiter et al. 2003), and (3) higher biomass production which will likely alter savanna biogeochemistry (Baruch 1996; Vitousek 1990; Gordon 1998).

Increasing atmospheric CO<sub>2</sub> concentration has the potential to further the invasion of African grasses by promoting their growth and competitive potential. Until recently, C<sub>4</sub> plants were believed to be less affected by elevated CO<sub>2</sub> than were C<sub>3</sub> plants because of their physiology and leaf anatomy, which concentrates CO<sub>2</sub> in the bundle sheath, saturating photosynthesis and eliminating photorespiration (Lambers et al. 1998). However, research with C<sub>4</sub> grassy weeds has shown that the fertilizing effect of CO<sub>2</sub> can be important (Sionit and Patterson 1984, 1985; Anderson et al. 2001), a fact supported by recent reviews indicating that the growth of C<sub>4</sub> grasses is stimulated by elevated CO<sub>2</sub> from 22% to 33% (Poorter 1993; Wand et al. 1999).

The objective of this study is to compare the growth and ecophysiological responses of two populations of a dominant native C<sub>4</sub> grass and two aggressive African C<sub>4</sub> invasive grasses to increased atmospheric CO<sub>2</sub> concentration interacting with two savanna stressors: drought and herbivory. Our goal is to relate the data to ecological strategies which could help infer the outcome of competition among species and the response of savanna communities to high CO<sub>2</sub>. This, in turn may assist in predicting the direction and magnitude of the effects that African grass invasion will have on Neotropical savannas in a future high CO<sub>2</sub> world.

## Materials and methods

### Species and sites

Large savanna areas in northern South America are dominated by *Trachypogon plumosus* (Humb. & Bonpl.) Nees. (Blydenstein 1967; Baruch 2005), a caespitose, perennial C<sub>4</sub> grass of medium height (1–1.5 m) of the NADP-ME photosynthetic subtype. It is a relatively drought-tolerant and nutrient-poor forage (Baruch and Fernández 1993; Baruch and Gómez 1996). In Venezuela, its geographic range extends from the lowland savannas [mean annual temperature (MAT) = 27°C, mean annual precipitation (MAP) = 1,400 mm, with a 6-month dry period] up to 2,000 m elevation above sea level in the Andean and Coastal Mountains (MAT = 20°C; MAP = 800 mm, and two rainless months).

In the lowlands, *Trachypogon* savannas are invaded by the African C<sub>4</sub> grass *Hyparrhenia rufa* (Nees.) Stapf. which is also a NADP-ME plant. This perennial, tall (up to 3 m) caespitose grass has a marginally higher leaf nutrient content than *T. plumosus* (Baruch and Gómez 1996). It was introduced to improve pasture quality but quickly spread naturally into native savannas. In Venezuela, *H. rufa* competes and displaces the lowland populations of the native *T. plumosus* (henceforth, called the Calabozo population, due to vicinity of the collection site) (Baruch and Bilbao 1999). Above 600 m elevation, the savannas are invaded by another African grass, *Melinis minutiflora* Beauv., a stoloniferous, perennial, C<sub>4</sub> grass (sub-type PCK), known as “molasses grass.” Here, *M. minutiflora* competes and displaces the local population of *T. plumosus* (henceforth named the USB population). In both cases the invasion is aided by opening of the native community by fire, overgrazing or road building (Baruch et al. 1989; Barger et al. 2002).

### Description of experiment

Seeds from the two populations of *T. plumosus* and the invasive grasses, *H. rufa* and *M. minutiflora*, were collected in 2002 from the lowland and intermediate elevation sites (Calabozo and USB, respectively). They were soaked overnight in water and sown on a sterilized substrate (50% sand; 50% vermiculite) in 15-cm-diameter, 50-cm-tall PVC tubes. A total of 120 tubes were set in walk-in growth chambers at ambient CO<sub>2</sub> (380 Pa). The growth chambers had a 12-h photoperiod and the photosynthetic active radiation (PAR) was 500 μmol m<sup>2</sup> s<sup>-1</sup>, with a combination of incandescent and fluorescent lights. Air temperature and RH were 30°C and 70% during the light period and 25°C and 75% in darkness.

After germination, seedlings were thinned to one per tube and the tubes were randomly distributed to chambers under low (380 Pa) and high (700 Pa) CO<sub>2</sub>. Relative

humidity was changed to 50% in the light period and 60% in darkness. Photoperiod remained at 12 h but PAR was programmed to increase stepwise, in  $250 \mu\text{mol m}^2 \text{s}^{-1}$  increments, from  $0 \mu\text{mol m}^2 \text{s}^{-1}$  to  $1,000 \mu\text{mol m}^2 \text{s}^{-1}$ , where it remained for 4 h, and then decrease stepwise to darkness. Initially, plants were watered twice daily, once with half-strength Hoagland nutrient solution and once with distilled water.

Each species or population comprised 30 tubes, 15 each under low and high  $\text{CO}_2$  growing conditions. The arrangement of the tubes in the chambers was randomized bi-weekly. Throughout the experiment, senescent leaves were collected, dried and weighed. Starting one week after germination, seedling height, tiller number, and leaf numbers were measured weekly for the first month. Six weeks after germination, assimilation rate ( $A$ ), and stomatal conductance ( $g$ ) were measured on the youngest fully expanded leaf of six plants of each species/population per  $\text{CO}_2$  treatment (total = 48 plants) with a LI-6400 gas analyzer (LI-COR, Lincoln, NE, USA). The cuvette conditions of temperature,  $\text{CO}_2$  and RH replicated chamber conditions, and PAR in the chamber was  $1,500 \mu\text{mol m}^2 \text{s}^{-1}$ . Instantaneous water use efficiency (WUE) was calculated as  $A/g$ . At this stage, three plants per  $\text{CO}_2$  treatment per species/population were harvested (24 plants), and the aboveground biomass was separated into leaves and culms. Leaf area was measured with a LI-3000 meter (LI-COR, Lincoln, NE, USA). Specific leaf area (SLA) was determined as the quotient of leaf area and dry mass. Roots were extracted from the tubes and washed. All biomass was oven-dried for 48 h and weighed. Relative growth rate (RGR) was calculated as in Hunt et al. (2002).

For the remaining 12 plants per species/population per  $\text{CO}_2$  treatment, water stress was imposed on seven individuals and five remained as watered controls. The stressed plants were further divided: four water stressed only, and three water stressed with subsequent clipping. Water stress was imposed by suspending watering until the first symptoms were visible (leaf folding, drooping or rolling). At this point leaf water potential, measured with a pressure bomb, ranged between  $-0.9 \text{ MPa}$  and  $-2.0 \text{ MPa}$ , depending on species. After each drying cycle, tubes were watered to field capacity and a new drying cycle commenced. Depending on species, plants went through 2–3 drying cycles. Twelve weeks after germination,  $A$  and  $g$  were again measured on four plants per species/population per each water and  $\text{CO}_2$  treatment (total = 64 plants). Prior to measurement, all plants were watered and recovered full turgor. The subgroups of watered and stressed plants were harvested (five watered and four stressed for each species/population per treatment), and SLA was determined as above. A subsample of leaf biomass from each plant was ground with a ball mill and analyzed for C and N content with an elemental analyzer (CE Instruments NC 2100, ThermoQuest, Milano, Italy). NUE was calculated as the ratio of  $A$  (on a mass basis) to leaf N content.

The three plants per species/population per  $\text{CO}_2$  treatment selected for the defoliation treatment were clipped to 10 cm above the soil surface, measured for leaf area on a subsample, and then converted to total leaf area. Leaves and culms were separated, dried and weighed. Clipped plants were watered daily with half-strength Hoagland solution and grown for four more weeks, with plant height measured weekly. Before harvesting clipped plants, gas exchange and SLA were measured as above on all individuals. Statistical analysis was performed with several one or two-way ANOVAS that compared pairs of competing species to test species,  $\text{CO}_2$  and treatments effects. These ANOVA results were coupled with a conservative Bonferroni adjustment to correct alpha values for statistical significance (SYSTAT 2003). Multiple analysis of variance would be very difficult to perform and interpret because of the different sampling intervals, unbalanced sample sizes and other complications.

To test for any effects of  $\text{CO}_2$  on germination, five replicates with 25 seeds per species/population were set to germinate on moist filter paper in Petri dishes placed under normal and high  $\text{CO}_2$ . Distilled water was added when necessary and germinated seeds were counted and removed every 2 days. After 14 days, germination percentages were obtained and arcsin transformed before analysis with ANOVA (SYSTAT 2003).

## Results

Elevated  $\text{CO}_2$  promoted germination in general, though responses were similar in magnitude but statistically stronger in invader grasses than in either *T. plumosus* population (from 36.7% to 56.8%;  $P < 0.05$  for invaders; 41.2% to 52.4%;  $P = 0.15$  for native populations). At the first 6-week harvest, elevated  $\text{CO}_2$  had no significant effect on seedling height or leaf or tiller numbers for any species/population. However, the two invader species produced significantly more total biomass and leaf area than either *T. plumosus* population (5–9 times;  $P < 0.05$ ). In addition, under high  $\text{CO}_2$ , introduced grasses were significantly taller than the natives ( $P = 0.02$ ) and grew twice as fast (mean RGR =  $0.58 \text{ g g}^{-1} \text{ week}^{-1}$  vs  $0.25 \text{ g g}^{-1} \text{ week}^{-1}$ ).

For the harvest at 12-weeks, results were compared separately for the highland and lowland pairs of competing native and invader species (*M. minutiflora* vs *T. plumosus*—USB and *H. rufa* vs *T. plumosus*—CAL). Total biomass was significantly higher in both invader species than in either native population (Table 1). This difference was greater at high  $\text{CO}_2$  under both watering regimes: plant biomass increased significantly between 21% and 47% in the invader grasses but decreased in both populations of the native species (between 13% and 51%; Table 1). The mild water stress imposed decreased total dry weight in all species/populations but relatively more in invader than in the native grasses (Table 1). There were no significant interactions between water and  $\text{CO}_2$  treatments (Table 1).

**Table 1** Effect of CO<sub>2</sub> enrichment and water stress on biomass and root/shoot ratio of 12-week-old plants

Species and trait	CO <sub>2</sub> (Pa)	Watered	H/L	Stressed	H/L
<b>Highlands</b>					
<i>M. minutiflora</i>					
Root/Shoot	380	0.269	1.30	0.173	1.02
	700	0.352	NS	0.178	NS
Total weight (g)	380	223.20	1.47	201.17	1.21
	700	328.80	*	243.39	NS
<i>T. plumosus</i> —USB					
Root/Shoot	380	0.175	0.76	0.187	0.72
	700	0.134	NS	0.135	NS
Total weight (g)	380	126.56	0.79	131.28	0.61
	700	100.74	*	80.96	*
<b>Lowlands</b>					
<i>H. rufa</i>					
Root/Shoot	380	0.239	1.45	0.149	1.66
	700	0.347	*	0.248	*
Total weight (g)	380	154.57	1.38	79.68	1.33
	700	213.62	*	106.13	NS
<i>T. plumosus</i> —Calabozo					
Root/Shoot	380	0.307	0.84	0.265	0.78
	700	0.259	NS	0.207	NS
Total weight (g)	380	93.53	0.49	76.91	0.87
	700	46.75	*	67.40	NS
<b>ANOVA</b>					
Source	Total weight		Root/shoot		
	Highlands <i>M. minutiflora</i> vs <i>T. plumosus</i> —USB	Lowlands <i>H. rufa</i> vs <i>T. plumosus</i> —Calabozo	Highlands <i>M. minutiflora</i> vs <i>T. plumosus</i> —USB	Lowlands <i>H. rufa</i> vs <i>T. plumosus</i> —Calabozo	
	<i>P</i>	<i>P</i>	<i>P</i>	<i>P</i>	
Species	0.000*	0.000*	0.024 NS	0.648 NS	
CO <sub>2</sub>	0.146 NS	0.453 NS	0.964 NS	0.393 NS	
Water	0.017*	0.000*	0.081 NS	0.023 NS	
Spp × CO <sub>2</sub>	0.000*	0.001*	0.213 NS	0.013*	
Spp × Water	0.065 NS	0.000*	0.057 NS	0.424 NS	
CO <sub>2</sub> × Water	0.079 NS	0.904 NS	0.529 NS	0.877 NS	
Spp × CO <sub>2</sub> × Water	0.423 NS	0.081 NS	0.647 NS	0.989 NS	

Values are means of 5 and 4 replicates for the watered and stressed treatments, respectively. H/L represents the ratio between the value under high (700 Pa) and low (380 Pa) CO<sub>2</sub> treatments. The two-way ANOVA table indicates the significance of differences between

pairs of invader and native species in the highlands and lowlands, their response to watering and CO<sub>2</sub> treatments and their interaction. Asterisks represent statistical significance corrected according to the Bonferroni adjustment (SYSTAT 2003)

The highland competing pair of grasses differed more in root/shoot ratios than did the lowland pair, but the among-species differences were not significant. Water stress decreased root/shoot ratios in all species except in *T. plumosus*—USB (Table 1). As with total biomass, high CO<sub>2</sub> increased the root/shoot ratio in both invader grasses but decreased it in both *T. plumosus* populations (Table 1). After 12 weeks, invader grasses had produced 53 to 92 times more senescent leaf biomass than either native population (invasives = 26.3–64.5 g vs natives = 0.5–0.7 g;  $P < 0.001$ ), which attests to their shorter leaf life span. CO<sub>2</sub> treatment did not affect senescent leaf biomass in either species ( $P = 0.44$ ). Only the unstressed *H. rufa* developed reproductive tillers and inflorescences; the reproductive effort (estimated as the

number of reproductive tillers/plant) was significantly higher under high CO<sub>2</sub> ( $19 \pm 2$  vs  $5 \pm 3$ ;  $P < 0.01$ ).

Leaf properties also differed significantly among species. Under both CO<sub>2</sub> and water stress treatments, invader grasses had higher SLA than either species of *T. plumosus* (Table 2). In all species/populations and under both water treatments, high CO<sub>2</sub> promoted the development of leaves with increased SLA (Table 2), though this response was significant only in the highland species (Table 2). Higher SLA of invader grasses contributed to 8–31% higher leaf area under both CO<sub>2</sub> and watering treatments (data not shown). Leaf N was significantly higher in *M. minutiflora* than in the local highland population of *T. plumosus* but the invader *H. rufa* had a lower leaf N than its competing native population (Table 2).

**Table 2** Effect of CO<sub>2</sub> enrichment on SLA and leaf nitrogen concentration of plants subjected to water stress and harvested 12 weeks after germination

Species and trait	CO <sub>2</sub> (Pa)	Watered	H/L	Stressed	H/L
<b>Highlands</b>					
<i>M. minutiflora</i> SLA (cm <sup>2</sup> g <sup>-1</sup> )	380	237.04	1.26	344.10	1.03
	700	298.89	NS	354.99	NS
Leaf N (%)	380	2.47	0.83	2.25	0.83
	700	2.07	NS	1.87	*
<i>T. plumosus</i> —USB					
SLA (cm <sup>2</sup> g <sup>-1</sup> )	380	163.04	1.31	137.56	1.32
	700	213.97	*	182.59	NS
Leaf N (%)	380	1.92	0.99	1.97	0.93
	700	1.95	NS	1.84	NS
<b>Lowlands</b>					
<i>H. rufa</i> NS					
SLA (cm <sup>2</sup> g <sup>-1</sup> )	380	186.66	1.02	249.35	1.01
	700	191.70	NS	253.95	NS
Leaf N (%)	380	1.69	0.89	1.99	0.97
	700	1.52	NS	1.95	NS
<i>T. plumosus</i> —Calabozo					
SLA (cm <sup>2</sup> g <sup>-1</sup> )	380	164.97	1.17	171.47	1.03
	700	194.44	NS	177.76	NS
Leaf N (%)	380	1.71	0.98	1.67	0.87
	700	1.68	NS	1.46	NS

## ANOVA

Source	SLA		Leaf N	
	Highlands <i>M. minutiflora</i> vs <i>T. plumosus</i> —USB	Lowlands <i>H. rufa</i> vs <i>T. plumosus</i> —Calabozo	Highlands <i>M. minutiflora</i> vs <i>T. plumosus</i> —USB	Lowlands <i>H. rufa</i> vs <i>T. plumosus</i> —Calabozo
	<i>P</i>	<i>P</i>	<i>P</i>	<i>P</i>
<i>Species</i>	0.000*	0.000*	0.001*	0.032 NS
CO <sub>2</sub>	0.010*	0.279 NS	0.004*	0.125 NS
Water	0.091 NS	0.010*	0.091 NS	0.117 NS
Spp × CO <sub>2</sub>	0.704 NS	0.530 NS	0.024 NS	0.951 NS
Spp × Water	0.001*	0.003*	0.199 NS	0.002*
CO <sub>2</sub> × Water	0.355 NS	0.571 NS	0.629 NS	0.862 NS
Spp × CO <sub>2</sub> × Water	0.462 NS	0.585 NS	0.504 NS	0.289 NS

The ANOVA table indicates the significance of watering and CO<sub>2</sub> treatments and their interaction. Symbols and statistics as in Table 1

High CO<sub>2</sub> decreased leaf N in all species/populations but this effect was significant only in *M. minutiflora*.

Clipping differentially affected the regrowth of native and invader grasses (Table 3). High CO<sub>2</sub> significantly increased tiller regrowth in clipped plants in *M. minutiflora* but decreased it in the other species (Table 3). Few morphological and architectural effects of clipping were evident after 4 weeks of regrowth; both introduced grasses produced greater leaf areas than either population of the native species (data not shown) and high CO<sub>2</sub> promoted leaf area only in *M. minutiflora* ( $P < 0.05$ ).

## Gas exchange

Assimilation rates for 12-week-old plants ranged between 25  $\mu\text{mol m}^{-2} \text{s}^{-1}$  and 33  $\mu\text{mol m}^{-2} \text{s}^{-1}$  in all species/populations, slightly lower than for 6-week-old plants (see below). High CO<sub>2</sub> promoted *A* in both unstressed invader grasses but depressed it in both native

populations, though this effect was statistically significant only in *H. rufa* (Fig. 1a, Table 4). Mild water stress significantly decreased *A* only in the invader *M. minutiflora* (Fig. 1a). In all species/populations, *g* ranged between 0.1  $\text{mmol m}^{-2} \text{s}^{-1}$  and 0.3  $\text{mmol m}^{-2} \text{s}^{-1}$  which was similar in natives and invaders (Table 4). High CO<sub>2</sub> decreased *g* in all species/populations (Fig. 1b), though more in unstressed than in watered plants (Fig. 1b). Instantaneous WUE ranged between 0.1  $\mu\text{mol}$  and 0.3  $\mu\text{mol CO}_2 \text{ mmol H}_2\text{O}^{-1}$ . As a consequence of the responses of *A* and *g* to high CO<sub>2</sub>, WUE was significantly higher in all species/populations under high CO<sub>2</sub>, although this response was more marked in the unstressed plants (data not shown). NUE ranged between 1.1  $\mu\text{mol}$  and 1.8  $\mu\text{mol CO}_2 \text{ g N}^{-1} \text{ s}^{-1}$ . Due to the decrease of leaf N concentration at high CO<sub>2</sub>, NUE was always larger in high CO<sub>2</sub> grown plants, but this was more evident in water stressed plants (Fig. 1c, Table 4). The unstressed plants of the invader *M. minutiflora* showed the largest NUE response to high CO<sub>2</sub> (Fig. 1c).

**Table 3** Effect of CO<sub>2</sub> enrichment on the biomass regrowth (excluding roots) after clipping of native and introduced grasses

	CO <sub>2</sub> (Pa)	Wt (g)	H/L
Highlands			
<i>M. minutiflora</i>			
Total	380	11.08	4.38
Regrowth	700	48.60	*
<i>T. plumosus</i> —USB			
Total	380	13.96	0.75
Regrowth	700	10.60	NS
Lowlands			
<i>H. rufa</i>			
Total	380	13.25	0.31
Regrowth	700	4.11	NS
<i>T. plumosus</i> —Calabozo			
Total	380	12.10	0.50
Regrowth	700	6.10	*

## ANOVA

Source	Highlands			Lowlands		
	<i>M. minutiflora</i> vs <i>T. plumosus</i> —USB			<i>H. rufa</i> vs <i>T. plumosus</i> —Calabozo		
	Biomass regrowth	<i>A</i>	<i>g</i>	Biomass regrowth	<i>A</i>	<i>g</i>
Species	0.018*	0.000*	0.000*	0.265 NS	0.000*	0.062 NS
CO <sub>2</sub>	0.168 NS	0.912 NS	0.000*	0.293 NS	0.002*	0.006*
Species × CO <sub>2</sub>	0.172 NS	0.034 NS	0.003*	0.561 NS	0.950 NS	0.747 NS

Values are means of three replicates. The ANOVA table indicates the significance of differences between pairs of invader and native species in the highlands and lowlands and their response to CO<sub>2</sub> clipping. Includes total regrowth, assimilation rate (*A*) and stomatal conductance (*g*). Symbols and statistics as in Table 1

Assimilation rates of leaves grown after clipping were similar to those measured on 6-week-old plants (31–39 μmol m<sup>-2</sup> s<sup>-1</sup> in invaders vs 21–30 μmol m<sup>-2</sup> s<sup>-1</sup> in native populations). Defoliation had different effects on *A*. Except in *M. minutiflora*, clipping increased the response of *A* to high CO<sub>2</sub> (Fig. 2a, Table 3). As in the previous measurements, the leaves grown after clipping showed significantly lower *g* under high than under low CO<sub>2</sub> (Fig. 2b). Consequently, in all species/populations, intrinsic WUE was significantly higher in plants under high CO<sub>2</sub> (data not shown).

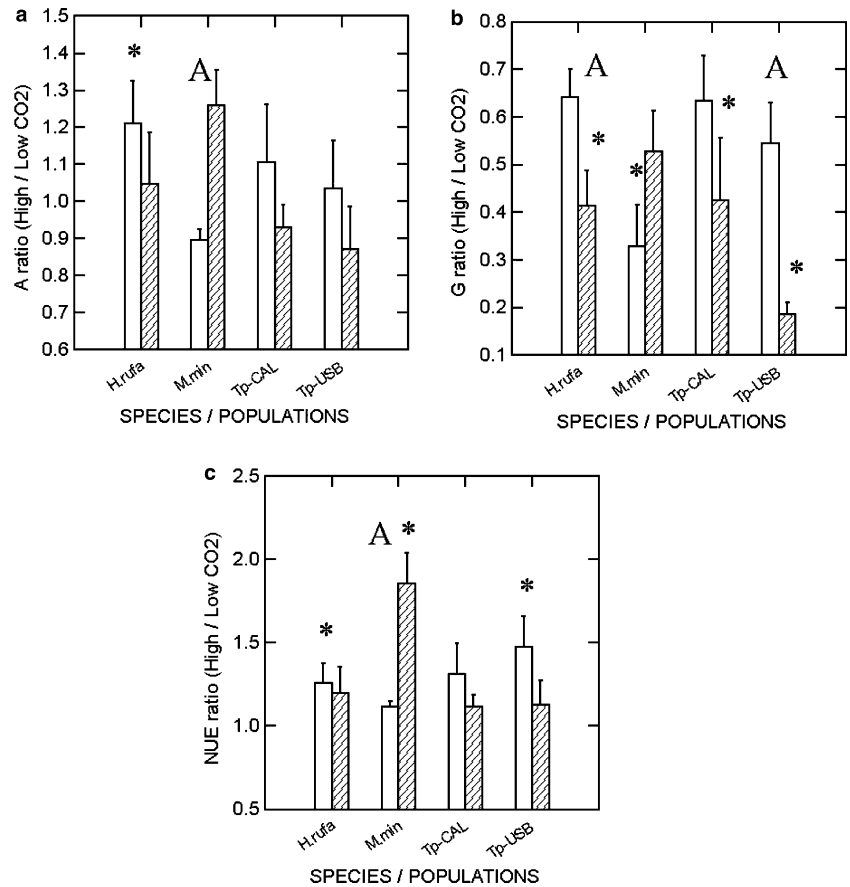
## Discussion

Native and introduced grasses differed in their responses to elevated CO<sub>2</sub>, which interacted with water stress and defoliation. Previous work at low CO<sub>2</sub> showed higher growth capacity in introduced African grasses, which helped explain their success as invaders in Neotropical savannas (Baruch et al. 1985). Here, invader grasses also outperformed natives under all CO<sub>2</sub> levels and experimental conditions. These results mark the high competitive potential of invaders and suggest a likely future increased rate of displacement of the native grasses of Neotropical savannas by African grasses. At a large scale, this displacement could change the present savanna to a grassland biome.

High CO<sub>2</sub> favors invader grasses beginning at the earliest life cycle stages. Germination was promoted by high CO<sub>2</sub>, relatively more in the introduced than in the native grass, though literature reports for other species are inconsistent; (Farnsworth and Bazzaz 1995; Yoshioka et al. 1995; Baskin and Baskin 1998). Six-week-old African grasses grew twice as fast as the natives and accumulated significantly more biomass at both CO<sub>2</sub> concentrations. *M. minutiflora* produced the largest plants, with massive stoloniferous culms. However, these young plants did not show consistent effects of high CO<sub>2</sub> on biomass or leaf morphology. The initial differences of faster growth rates, larger biomass accumulation and size and higher germination of introduced grasses were nonetheless augmented by high CO<sub>2</sub>. If these early life differences are maintained under field conditions, they may have marked effects on community regeneration and composition after disturbance, favoring invaders over native grasses and other taxa, as found by *M. minutiflora*'s invasion in Hawaii (D'Antonio et al. 2001).

Older African grasses maintained their initial advantage in biomass production under all CO<sub>2</sub> levels and water availability. This was more prominent in *M. minutiflora* than in *H. rufa* and could be attributed to their larger and more rapidly developed leaf area. The leaves of the African grass appear to be shorter lived than those of *T. plumosus*, as evidenced by their large necromass. In nature, this deposition carpets the soil and may serve to reduce the growth of other taxa (Gordon

**Fig. 1** Mean and standard error of the ratio between values measured at high and low CO<sub>2</sub> **a** assimilation rate (*A*), **b** leaf stomatal conductance (*g*) and **c** NUE in 12-week-old plants. Values > 1 indicate the promoting effect of high CO<sub>2</sub>. Asterisks denote significant differences between the variable values measured under high and low CO<sub>2</sub>. Letter *A* denotes significant differences between watered and stressed treatments. Significance was corrected for multiple comparisons after Bonferroni (SYSTAT 2003). Open bars represent values obtained under the water stressed treatment and stapled bars those obtained under the watered or control treatment. All variables were measured at their respective CO<sub>2</sub> growth concentration. (M.min *M. minutiflora*; Tp-CAL *T. plumosus*—Calabozo or lowland population; Tp-USB *T. plumosus*—USB or highland population)



1998) and increase the fuel base for fires (D'Antonio and Vitousek 1992). Both effects may contribute to the dominance of invader grasses.

In contrast to younger plants, older African grasses respond more to elevated CO<sub>2</sub> than either native grass. The average increase in total biomass for both introduced species at high CO<sub>2</sub> was 34%, well in the range reported for other C<sub>4</sub> grasses (Poorter 1993; Ghannoum

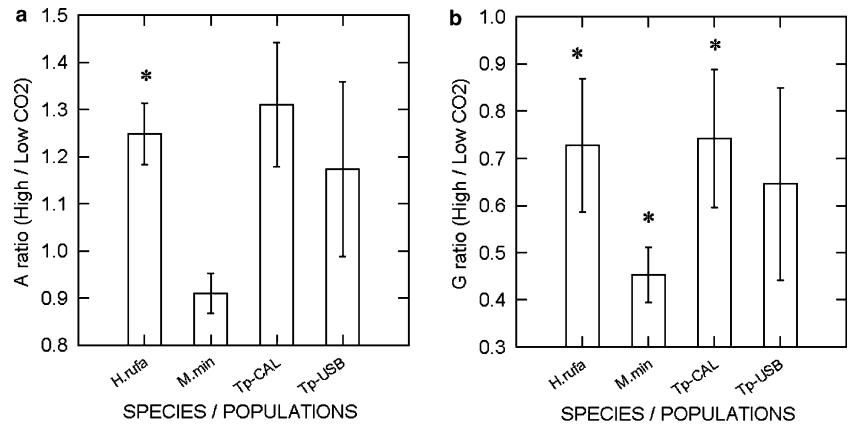
et al. 1997; Wand et al. 1999; Poorter and Navas 2003). As compared to natives, in both African grasses the effect of high CO<sub>2</sub> on biomass accumulation was reduced in young plants and increased with age. Several possible causes of this ontogenetic drift have been proposed: (1) the proportional increment in leaf area (Wulff and Strain 1982), (2) Start of reproductive stage (as in *H. rufa*) (Coleman and Bazzaz 1992) and (3) Root constraints

**Table 4** Two-way ANOVA table indicating the statistical significance of the differences between native and invader species or populations, high and low CO<sub>2</sub> growth conditions and the watering treatments (watered and stressed) and their interaction for three variables obtained by gas exchange measurements

Source	Assimilation rate		Stomatal conductance		NUE	
	Highlands <i>M. minutiflora</i> vs <i>T. plumosus</i> —USB	Lowlands <i>H. rufa</i> vs <i>T. plumosus</i> — Calabozo	Highlands <i>M. minutiflora</i> vs <i>T. plumosus</i> —USB	Lowlands <i>H. rufa</i> vs <i>T. plumosus</i> — Calabozo	Highlands <i>M. minutiflora</i> vs <i>T. plumosus</i> — USB	Lowlands <i>H. rufa</i> vs <i>T. plumosus</i> — Calabozo
	<i>P</i>	<i>P</i>	<i>P</i>	<i>P</i>	<i>P</i>	<i>P</i>
Species	0.000*	0.009*	0.586 NS	0.795*	0.000*	0.000*
CO <sub>2</sub>	0.936 NS	0.284 NS	0.000*	0.000*	0.000*	0.002*
Water	0.431 NS	0.230 NS	0.330 NS	0.453 NS	0.000*	0.011*
Spp × CO <sub>2</sub>	0.125 NS	0.319 NS	0.382 NS	0.657 NS	0.002*	0.603 NS
Spp × Water	0.606 NS	0.036 NS	0.026 NS	0.262 NS	0.000*	0.014*
CO <sub>2</sub> × Water	0.150 NS	0.127 NS	0.212 NS	0.188 NS	0.046 NS	0.237 NS
Spp × Water × CO <sub>2</sub>	0.002*	0.855 NS	0.002*	0.672 NS	0.000*	0.980 NS

Symbols and statistics as in Table 1

**Fig. 2** Mean and standard error of the ratio between values measured at high and low CO<sub>2</sub> of **a** the assimilation rate (*A*) and **b** leaf stomatal conductance (*g*) of 4-week-old leaves grown after the clipping treatment. Values > 1 indicate the promoting effect of high CO<sub>2</sub>. Statistical and species symbols as in Fig. 1. All variables were measured at their respective CO<sub>2</sub> growth concentration



due to pot size reduce sink stress which feedbacks to restrict *A* (Coleman and Bazzaz 1992). This last proposal appears relevant here; in both invaders, roots responded more than any other organ to high CO<sub>2</sub>, perhaps attributable to accumulation of excess carbohydrates (Potvin and Strain 1985).

In contrast, biomass of both populations of the native grass decreased considerably under high CO<sub>2</sub> (mean = 31%). This growth depression has been credited to either photosynthetic acclimation or downregulation (Lecain and Morgan 1998; Ziska et al. 1999; Poorter and Navas 2003) or a reduced sink strength of the slow-growing native grass (Roumet and Roy 1996; Wand et al. 1999; Poorter and Navas 2003). In *T. plumosus*, the lower biomass may be associated with decreased *A*, at least in well-watered plants. This suggests that photosynthetic acclimation was more prevalent in the longer lived leaves of *T. plumosus*, which possibly had enough time to acclimate.

High CO<sub>2</sub> affected reproductive period and output. The earlier flowering of *H. rufa* under high CO<sub>2</sub> parallels results from other C<sub>4</sub> grasses (Potvin and Strain 1985; Ziska and Bunce 1997). Also, high CO<sub>2</sub> increased reproductive biomass as a probable consequence of increased total biomass. These reproductive changes have a potentially large demographic consequence by increasing the invasive potential of *H. rufa* under high CO<sub>2</sub>.

Specific leaf area explains a large proportion of the RGR differences found between slow and fast growing plants (Lambers and Poorter 1992; Roumet and Roy 1996). In our study, *T. plumosus* had consistently lower SLA than the introduced grasses. Its leaves are > 50% thicker with a lower proportion of photosynthetic tissue (Baruch et al. 1985), contributing to its lower *A* and biomass production. In all species/populations, SLA increased or was unaffected by high CO<sub>2</sub> which deviates from some literature reports (Ghannoum et al. 1997; Wand et al. 1999). The potential accumulation of non-structural carbohydrates, promoted by high CO<sub>2</sub>, did not decrease SLA. However, Sionit and Patterson (1984), also report increased SLA under high CO<sub>2</sub>. Higher SLA of African grasses contributed to their higher total leaf area and faster growth at high CO<sub>2</sub>.

Previous work showed that invader grasses had lower leaf construction costs (CC) than native species (Baruch and Gómez 1996). Leaf CC decreases as C content increases and/or N content decreases (Poorter and Bergotte 1992; Griffin 1994). Here, high CO<sub>2</sub> promoted both higher leaf C content and lower leaf N content. This response was proportionally higher in invader than in native grasses. This change in leaf chemistry implies that leaf CC of invader grasses grown at high CO<sub>2</sub> is even lower than that of the native grass. A similar result was reported comparing invader and native grasses grown under high CO<sub>2</sub> under arid conditions (Nagel et al. 2004). This reduction in the energetic cost of leaf construction may also underlay the higher growth potential of invader grasses under high CO<sub>2</sub> and further favor their dominance in invaded savannas.

Herbivory by native or domestic grazers is an important stressor in savannas, and coping efficiently can provide a considerable competitive advantage. The largest effect of high CO<sub>2</sub> on defoliated plants was for *M. minutiflora*, whose regrowth increased by 338%. This contrasts with results obtained from another stoloniferous African grass whose regrowth after clipping was unaffected by high CO<sub>2</sub> (Wilsey et al. 1994). Under ambient CO<sub>2</sub>, defoliated *H. rufa* showed partial compensatory regrowth whereas *T. plumosus* was severely affected by defoliation (Simoes and Baruch 1991; Baruch and Bilbao 1999). Therefore, it was expected that *T. plumosus* would be negatively affected by clipping even under high CO<sub>2</sub> but unexpected that *H. rufa* did not respond to clipping and CO<sub>2</sub>. The meristems of *H. rufa* might have been damaged by clipping, slowing its regrowth; this is an erect caespitose grass, in contrast with the stoloniferous and prostrate *M. minutiflora*, whose meristems are close to the soil surface and could have escaped clipping.

#### Gas exchange

As in a previous study (Baruch et al. 1985), *A* was consistently higher in the invaders than in either population of the native grass. However, there was not a clear-cut response of *A* to high CO<sub>2</sub> which separated

invaders from native grasses. An ontogenic shift occurred in the invaders but not in native grasses, as leaves of young plants (or regrown leaves) had higher  $A$  than those from older plants. Such ontogenetic effects of high  $\text{CO}_2$  on  $A$  are not fully understood but have been attributed to biochemical changes in the photosynthetic machinery (Bazzaz 1990).

Only *H. rufa* showed consistently higher  $A$  under high  $\text{CO}_2$ . In  $\text{C}_4$  plants, this response is attributed to bundle sheath chloroplast fixation due to leaky cell walls (Lambers et al. 1998). Leakiness and  $\text{CO}_2$  response are related to photosynthetic subtype: NADP-MEs leak less and are generally less responsive to high  $\text{CO}_2$ , NAD-MEs leak more and respond more, whereas PCK plants are intermediate (Hattersley 1982). Although this might explain the low response of  $A$  to high  $\text{CO}_2$  in the NADP-ME *T. plumosus* and the relatively high response in the PCK *M. minutiflora*, it is inconsistent with the relatively high response found in *H. rufa*, which is also NADP-ME. However, several exceptions have been found to the proposed correlation between  $\text{CO}_2$  response and photosynthetic subtype (Ziska et al. 1999; Ghannoum et al. 2001; Wand et al. 2001; Poorter and Navas 2003). Some common species as *Sorghum bicolor* and *Andropogon glomeratus* (both also NADP-ME and Andropogoneae) were adversely affected by high  $\text{CO}_2$  (Carter and Peterson 1983; Bowman and Strain 1987). Even species from the genus *Setaria* (also of the NADP-ME sub-type) diverged in their responses to elevated  $\text{CO}_2$ , with some decreasing biomass accumulation by more than 50% under high  $\text{CO}_2$  (Kellogg et al. 1999).

The contrasting response to high  $\text{CO}_2$  between *H. rufa* and *T. plumosus* is interesting as both belong to the tribe Andropogoneae. The lack of and even the negative response to high  $\text{CO}_2$  is still poorly understood. Several explanations have been proposed for this growth depression: (1) either photosynthetic acclimation or downregulation (Lecain and Morgan 1998; Ziska et al. 1999; Poorter and Navas 2003) or (2) internal regulatory changes related to accumulation of end products which inhibit carbon fixation due to reduced sink strength in the slow growing grasses (Roumet and Roy 1996; Kellogg et al. 1999; Wand et al. 1999; Poorter and Navas 2003). Also, it has been attempted to attribute differences in  $\text{CO}_2$  response among grasses to phylogeny and climate (Taub 2000) but this seems not appropriate here. An alternative explanation to this difference in photosynthetic and growth capacity may lay in the different biogeographic origin of both grasses (Palaeo- and Neotropics) where evolution of different genetic stocks may have selected for metabolic routes that differ in carbon fixation and use.

In contrast to  $A$ ,  $g$  and  $E$  showed consistent decreases at high  $\text{CO}_2$  and increased intrinsic WUE in all species. This seems to be a general response of herbaceous  $\text{C}_3$  and  $\text{C}_4$  plants (e.g., Jackson et al. 1994; Field et al. 1995; Wand et al. 1999; Maherali et al. 2002). There were no consistent differences in WUE between native and introduced grasses under either  $\text{CO}_2$  treatment. Photo-

synthetic NUE was also increased by high  $\text{CO}_2$  in all species, more as consequence of reduced leaf N than increased  $A$ . Our values are in the range of previous results (Baruch et al. 1985) where invader grasses showed higher NUE than the native species. This difference was further promoted under high  $\text{CO}_2$ . This response, in savanna systems where N is frequently limiting, may be another competitive advantage of invader grasses in a future high  $\text{CO}_2$  world.

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## Conclusions and perspectives

By virtue of higher growth potentials, African grasses have displaced many species from Neotropical savannas, converting them into less diverse and treeless grasslands. The prospective global changes predicted for the next century include the doubling of atmospheric  $\text{CO}_2$  concentration and alteration of the rainfall regime. For Neotropical savannas, some models also predict a warmer and drier climate accompanied by an increase in fire frequency (Hoffmann et al. 2002).

This study provides several pieces of evidence that suggest the invasive and competitive potential of African grasses may be magnified in the future:

1. High  $\text{CO}_2$  promotes germination and seedling size in introduced grasses. This could tilt seedling competition in their favor by early occupation of space. Early reproduction and apomixis would also accelerate the invasion of African grasses.
2. Under high  $\text{CO}_2$  the RGR of young introduced grasses is twice that of the native grass. This initial advantage is maintained as the plants age, further aiding their competitive potential.
3. Well-watered introduced grasses respond more to high  $\text{CO}_2$  than native grasses, making them formidable competitors in the relatively wet and fertile savannas. In the drier and less fertile sites, high  $\text{CO}_2$  would aid invader grasses to establish and compete by virtue of their high WUE and NUE. This advantage would also apply if the climate becomes drier.
4. High  $\text{CO}_2$  increases leaf C and decreases leaf N. Both effects decrease leaf construction costs, but even more in invader than in native grasses. This lower energy investment in leaf biomass contributes to the potential success of invasive African grasses.

The above list of possible effects of high  $\text{CO}_2$  on the ecophysiology of invader grasses suggests an increased competitive potential and increased rate of displacement of the native savannas by introduced African grasses in the future. Higher biomass production may increase fire frequency and intensity (Rossiter et al. 2003), further favoring invasive species and opening new sites for their expansion. (Baruch 1996; D'Antonio and Vitousek 1992; Williams and Baruch 2000). Savanna functioning and stability would also likely be affected. The large biomass of African grasses may alter food webs by offering more biomass but lower

quality forage due to the lowered C/N ratio which could also depress decomposition rates, further affecting ecosystem function. Nevertheless, the opposing responses to high CO<sub>2</sub> of the native and invader grasses (which share taxonomic tribe and photosynthetic subtype) cautions against general predictions of the effect of global change in communities dominated by C<sub>4</sub> plants. The magnitude and extent of future changes accompanying the invasion of Neotropical savannas by invasive grasses appears to be large, and their effects will not be fully known for decades.

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