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Research article

The increase of current atmospheric CO_2 and temperature can benefit leaf gas exchanges, carbohydrate content and growth in C4 grass invaders of the Cerrado biome

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ABSTRACT

Leaf gas exchanges, carbohydrate metabolism and growth of three Brazilian Cerrado invasive African grasses were evaluated after growing for 75 days under doubled CO_2 concentration and temperature elevated by 3 °C. Results showed that although the species presented photosynthetic C4 metabolism, they all had some kind of positive response to increased CO_2. *Urochloa brizantha* and *Megathyrsus maximus* showed increased height for all induced environmental conditions. *Urochloa decumbens* showed only improvement in water use efficiency (WUE), while *U. brizantha* showed increased CO_2 assimilation and *M. maximus* presented higher biomass accumulation under doubled CO_2 concentration. The most significant improvement of increased CO_2 in all three species appears to be the increase in WUE. This improvement probably explains the positive increase of photosynthesis and biomass accumulation presented by *U. brizantha* and *M. maximus*, respectively. The increase in temperature affected leaf carbohydrate content of *M. maximus* by reducing sucrose, glucose and fructose content. These reductions were not related to thermal stress since photosynthesis and growth were not harmed. Cellulose content was not affected in any of the three species, just the lignin content in *U. decumbens* and *M. maximus*. All treatments promoted lignin content reduction in *U. brizantha*, suggesting a delay in leaf maturation of this species. Together, the results indicate that climate change may differentially promote changes in leaf gas exchanges, carbohydrate content and growth in C4 plant species studied and all of them could benefit in some way from these changes, constituting a threat to the native Cerrado biodiversity.

1. Introduction

The Brazilian Cerrado is the second largest phytogeographical domain in area, surpassed only by the Amazon rainforest, and one of the richest savanna biomes of the world, with high levels of endemism, being considered an extremely important area for conservation (Myers et al., 2000). However, much of this biodiversity is being lost because of biological invasions. Species of African grasses used as forage are spreading rapidly in the Cerrado fragments, probably displacing native species and therefore constituting a threat to the native biodiversity (Pivello et al., 1999). This problem is likely to be aggravated by other factors, such as climate change with simultaneous increases in atmospheric carbon dioxide (CO_2) concentration and in average global temperature (Baruch and Jackson, 2005).

Temperature and atmospheric CO_2 are important environmental drivers affecting plant growth, development and function, what can potentially change the composition and functioning of communities and ecosystems (Díaz et al., 2004), and both have changed in the recent past (Eller et al., 2012), due to the burning of fossil fuels and change in land use, among other causes (IPCC, 2013). In November 2017, mean atmospheric CO_2 concentration was 405.14 μmol mol^{-1} in Mauna Loa, Hawaii (USA) (ESRL, 2017) and 936 μmol mol^{-1} is expected at the end of the 21st century, considering the most pessimistic emission scenario (IPCC, 2013). At the same time, the last three decades has been successively warmer at the Earth's surface than any preceding decade since 1850 and it is predicted that global temperatures will continue to rise, reaching increases between 1.1 and 4.8 °C by 2100 (IPCC, 2013).

Therefore, concerns about how plants and natural ecosystems will respond to such changes are relevant to the current scientific agenda, since climate change is already responsible for changes in species distribution (Lenoir et al., 2008). Many groups have focused on studying the effects of increasing CO_2 and temperature, together or separately, in

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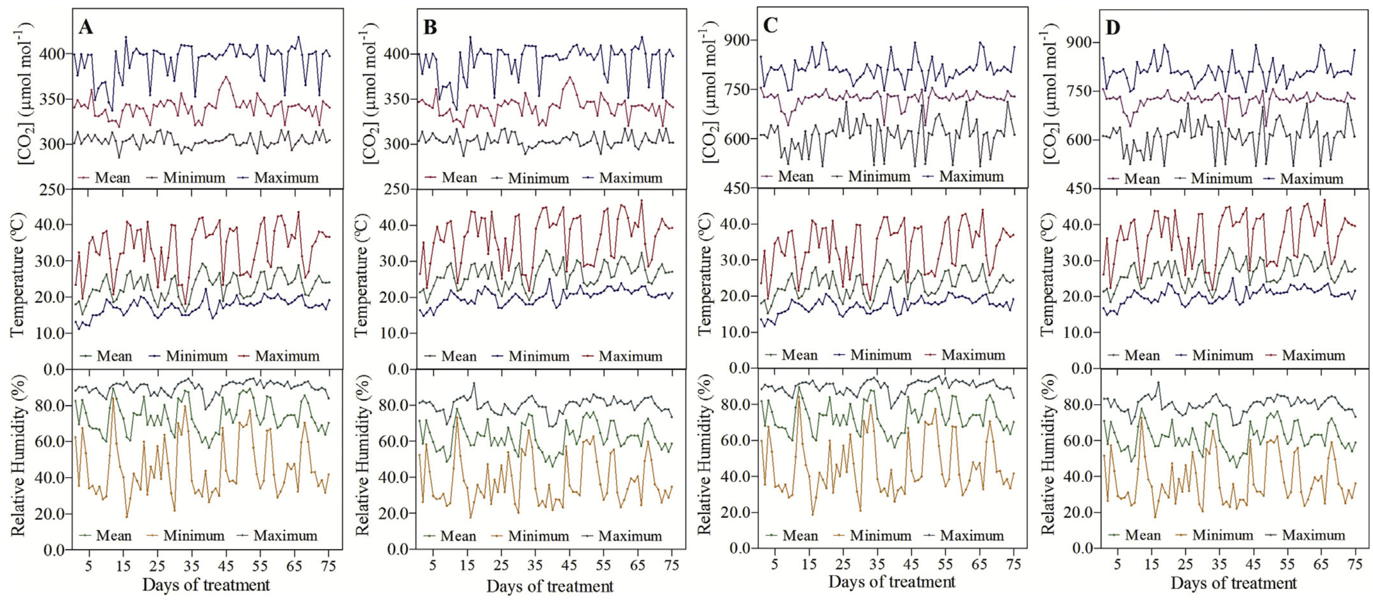

Fig. 1. Environmental conditions (CO_2 concentration, temperature and relative humidity) during 75 days of exposure to different environmental conditions. Each environmental condition is identified as a set of figures: A – Ctrl (Control: current CO_2 concentration and room temperature); B – ET (Elevated temperature: current CO_2 concentration and room temperature + 3 °C); C – EC (Elevated CO_2: doubled CO_2 concentration and room temperature) and D – ECT (Elevated CO_2 + temperature: doubled CO_2 concentration and room temperature + 3 °C), respectively.

plants and ecosystems, especially regarding photosynthetic and growth performance (Eller et al., 2012; Grombone-Guaratini et al., 2013; Souza et al., 2013; Kimbal, 2016; Runion et al., 2016).

Climate change may affect the productivity of the biota not only in relation to growth and resource allocation, but also changing the chemical composition of plant tissues (IPCC, 2013). Most source-sink hypotheses assume that high CO_2 concentration promotes a relative increase in carbon availability, which is accumulated on total non-structural carbohydrates and carbon-based secondary metabolites, provided that carbon values exceed growth requirements (Peñuelas and Estiarte, 1998). Carbon allocation for growth and partition should, by competition for internal resource of limited availability, reduce carbon allocation to secondary metabolism (Ibrahim and Jaafar, 2012). Among the works that investigated the influence of climate change on carbon metabolism in plants, some of them found that higher CO_2 concentration increased production of non-structural carbohydrates as starch (Ibrahim and Jaafar, 2012), and fructans (Oliveira et al., 2010). For sucrose, both increase and decrease of its content have been reported (Ibrahim and Jaafar, 2012; Grombone-Guaratini et al., 2013). For structural carbohydrates, Schädel et al. (2010) found that the increased CO_2 concentration had no significant effect on total hemicellulose concentrations in leaves and woody tissue in 14 of 16 species. Körner et al. (2005) have analyzed the litter composition of a temperate deciduous forest exposed to 530 ppm of CO_2 during 4 years in a FACE system (Free Air CO_2 Enrichment). They observed an increase of 21% in non-structural carbohydrate content and a decrease of 11% on lignin content. As for the increase of temperature, some studies report less accumulation of non-structural carbohydrates such as fructose and glucose in tomato leaves (Jie et al., 2012) and in grasses (Naudts et al., 2014).

Since the effects of CO_2 and temperature on plant metabolism may counteract each other, the combined effects can be different from any factor separately (Morison and Lawlor, 1999). As these climatic factors will change simultaneously, to understand how plants will respond and adapt to a new environment is an essential first step to understand the full impact that multiple climate change factors will have on terrestrial ecosystems (Díaz et al., 2004; Leakey et al., 2009; Eller et al., 2012). Thus, the present study aimed to investigate the effects of increases in CO_2 concentration and temperature predicted for 2100 by the Intergovernmental Panel on Climate Change (IPCC, 2013). The hypothesis is that these environmental changes can differentially affect gas exchanges, leaf carbohydrate content and growth of three of the most invasive species in the Brazilian Cerrado: *Urochloa brizantha*, *Urochloa decumbens* and *Megathyrsus maximus*, cultivated in a CO_2 enriched atmosphere and temperature elevated in 3 °C above room temperature.

2. Materials and methods

2.1. Plant material and environmental conditions

Plants of three grass species, *Urochloa brizantha* (Hochst. ex A. Rich.) RD Webster cv Marandu, *U. decumbens* (Stapf) RD Webster cv Basilisk and *Megathyrsus maximus* (Jacq.) BK Simon and S.W.L. Jacobs cv Tanzania were used in this study. Seeds of the all species were germinated in chambers at 30 °C, 12 h light and 12 h dark photoperiod. Three days after germination, seedlings were placed in 1.7 L plastic pots containing a mixture of sand and vermiculite (2:1) as substrate and grown for 75 days between October and December 2015 in open-top chambers (1.53 m^3 each), inside a glasshouse, designed according to Oliveira et al. (2010). Plants were irrigated with Hoagland and Arnon (1950) nutrient solution every three days and with distilled water on the other days. Four environmental treatments based on IPCC (2013) predictions for 2100 were imposed to the growing plants: (1) Control (Ctrl) – current CO_2 concentration (345.43 ± 38.59 μmol mol^{-1}) and room temperature (minimum 11.2 °C; mean: 22.9 °C and maximum: 43.5 °C); (2) Elevated temperature (ET) – current CO_2 concentration (345.55 ± 38.47 μmol mol^{-1}) and 3 °C above room temperature; (3) Elevated CO_2 (EC) – doubled CO_2 concentration (714.63 ± 89.40 μmol mol^{-1}) and room temperature; and (4) Elevated CO_2 + temperature (ECT) – double CO_2 concentration (724.56 ± 88.85 μmol mol^{-1}) and 3 °C above room temperature. The experiments were conducted under natural photoperiod and relative air humidity (RH). The environmental conditions (CO_2 concentration, temperature, RH and light intensity) were monitored throughout the experimental period (Fig. 1).