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Leaf temperature of C₄ grasses is increased in elevated CO₂ in a glasshouse

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Introduction

Elevated CO₂ partial pressures lead to enhanced biomass accumulation not only in C₃ plants, but also in C₄ grasses, although to a lesser extent. It has been accepted that in C₃ plants the growth enhancement is primarily due to enhanced CO₂ assimilation rates, which are not CO₂ saturated at present ambient CO₂ partial pressures. In C₄ grasses increase in biomass is not as easily explained since leaf photosynthesis of well watered plants is already CO₂ saturated at present ambient CO₂ partial pressures, when measured under standard gas exchange conditions. Elevated CO₂ reduces stomatal conductance (Wong et al. 1978) and Ghannoum et al. (2001) reported a decreased stomatal conductance as well as increased whole plant water use efficiency for C₄ grasses grown at elevated CO₂. In addition they have shown, that photosynthesis in C₄ grasses is strongly temperature dependent. They suggested that increased leaf temperatures resulting from reduced stomatal conductance at elevated CO₂, might be one of the factors responsible for increased photosynthesis and biomass accumulation observed in C₄ plants when grown at elevated CO₂ partial pressures. We tested this hypothesis in a glasshouse experiment with two C₄ grasses Bothriochloa bladhii and Astrebla lappacea.

Materials and Methods

Plants (*Bothriochloa bladhii* Kuntze and *Astrebla lappacea* (Lindl.) Domin) were grown in 7 L pots with well watered and nutrient supplemented soil in temperature controlled glasshouse compartments (22/26°C min night/max day temperature) at three different CO₂ partial pressures (120/70/35 Pa, average during the light period). The difference between leaf and air temperature (Δ T) was monitored with 7-12 thermocouples (copper-constantan, 0.08mm, AWG 40, Omega Engineering, Stanford CT, USA) per species and glasshouse. Half of the thermocouples measured Δ T, with one junction touching the leaf while the air-reference was suspended 4-7 cm under the leaf. The other half of thermocouples measured the absolute leaf temperature in comparison to the absolute air temperature. Since the differential thermocouples as well as the absolute thermocouples were made from wires of the same material and width and gave very similar results, all measurements were combined and averaged. For data logging we used microloggers and multiplexers (CR23X and AM416, Campbell Scientific, Thuringowa Central, QLD, Australia). The reference for the absolute temperature was measured in a self-built junction box containing a platinum resistor (W 60/3, Degussa AG, Hanau, Germany). Glasshouse humidity was monitored with microprocessor data loggers (Tinytag Plus Dual Channel Internal Temp/RH, Hastings Data Loggers, Port Macquarie, Australia). The measurements were made over three weeks (13th Feb.- 6th Mar. 2001), each week the CO₂ partial pressures of the glasshouse compartments were swapped and plants moved. The average Δ T was calculated for each glasshouse compartment and species and hour of the day. Data around midday (10:40-13:40h) were statistically analysed with a linear mixed effect model (Pinheiro JC, Bates DM, 2000) using the software S-PLUS 2000 (AT&T Bell Laboratories).

Results

Fig. 1 shows the average ΔT of all 21 experimental days for *B*. bladhii and *A*. *lappacea* plants in the three different CO₂ partial pressures. Fig1c shows the photon irradiance measured in one of the glasshouse compartments 1m above plant height. ΔT is greatest at midday when the irradiance is highest and for the plants grown in the highest CO₂ partial pressure. The average ΔT at noon (average between 11:40 and 12:40) was 1.93/1.47/0.97 °C for *B. bladhii* and 1.53/1.23/0.80 °C for *A. lappacea* at 120/70/35 Pa CO₂, respectively. The average ΔT during the full light period was 1.17/0.89/0.54 °C for *B. bladhii* and 1.00/0.77/0.52 °C for *A. lappacea* at 120/70/35 Pa CO₂ respectively. The strong dependence on irradiance can clearly be seen, when ΔT values of the three hours around noon are plotted against irradiance (Fig. 2). Variance in irradiance was generated by cloud coverage. A statistical analysis was performed on the values of Fig. 2 using a linear mixed effect model. It confirmed that ΔT was significantly dependent on irradiance, CO₂ partial pressure and absolute air water vapour pressure (WVP). The effect of CO₂ and WVP was interactive. The CO₂ effect increased with decreasing (WVP). We also found a dependence on air temperature, which we do not interpret, because of the influence of the heat regulation in the glasshouse. The obtained coefficients (not shown) were large relative to the standard errors, showing a high significance of the results. The difference between the two species A. lappacea and B. bladhii was significant (paired students t-test, pvalue $< 10^{-4}$).

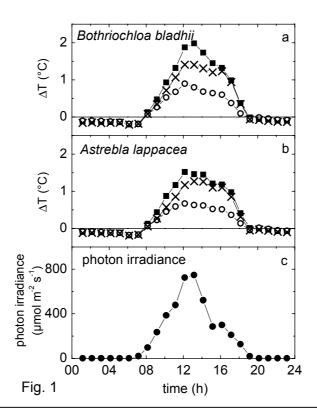


Fig. 1 Average day-profile of leaf-air temperature difference (Δ T) of *B. bladhii* (**a**) and *A. lappacea* (**b**) calculated from the values of three weeks. Plants were in 120 Pa CO₂ (**T**), 70 Pa CO₂ (**X**) or 35 Pa CO₂ (**O**). Average irradiance (**c**) during this three weeks measured 1m above the plants in one glasshouse compartment.

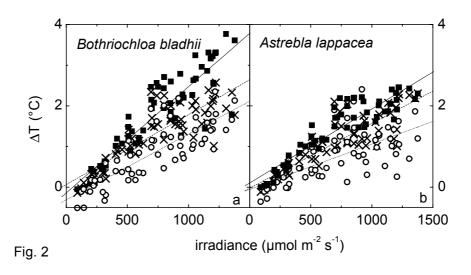


Fig. 2 Average of the leaf-air temperature difference of *B. bladhii* (a) and *A. lappacea* (b), calculated from the values measured during three hours at geographical midday. 120 Pa CO_2 (\blacksquare), 70 Pa CO_2 (X), 35 Pa CO_2 (\bigcirc). The values are plotted against the photon irradiance measured 1m above the plants in one of the glasshouse compartments. The lines show the linear regression for the values at the three CO_2 levels: 120 Pa CO_2 (solid), 70 Pa CO_2 (dashed), 35 Pa CO_2 (dotted).

Discussion

Many glasshouse experiments have reported increased biomass accumulation for C₄ plants grown at elevated CO₂ compared to ambient CO₂. Here we have demonstrated that elevated growth CO₂ can result in increased leaf temperature of C₄ grasses. The increase in leaf temperature is most likely the result of stomatal closure at elevated CO₂ and therefor a decrease in evaporative cooling (Wong et al. 1978, see review Farguhar and Sharkey 1982). This has also been demonstrated to result in improved whole plant water use efficiency in B. bladhii and A. lappacea (Ghannoum et al. 2001). It is interesting to note that leaf temperature continues to increase at CO₂ partial pressures above twice ambient levels. CO₂ assimilation rate of these grasses increases steeply with leaf temperature, approximately 2 μ mol m⁻² s⁻¹ per ^oC between 20 and 36^oC Ghannoum *et al.* (2001). Considering the compound interest of growth, these increases in photosynthetic rate may be sufficient to explain at least some of the growth enhancement which is between 10 to 20% under growth conditions with double ambient CO₂. There is a scarcity of growth data for CO₂ responsiveness of C₄ species to elevated CO₂ in more natural environments (see review Ghannoum et al. 2000). In a natural environments several factors will be different. Firstly, the air temperature is not regulated outside. Therefor on sunny days the air temperature will be warmer, and on cloudy days colder than in our experiment. Second, the air movement was constant. This is different to a natural environment where it varies with for example cloud movements. Although we were not able to measure the wind speed in the glasshouse, partly due to its turbulent nature. We had the subjective impression that it was stronger than outside. Air movement increases the convective heat exchange decreasing ΔT , and increasing evaporative cooling. Evaporative cooling can lead to negative ΔT as for example observed during night and dawn in Fig. 1 and on very cloudy days (lower points in Fig. 2). Third, the infra-red radiation of the sun, which would contribute to the heat input into the leaf beside the light radiation is absorbed by glass and therefore decreased in a glasshouse compartment. Fourth, our plants were well watered and grown in nutrient supplemented soil. This could have had an effect on the evaporative cooling and the leaf size and thickness, which in turn affects ΔT . We have measured a significant difference between B. bladhii and A. lappacea and we attribute this to the fact that B. bladhii has broader leaves than A. lappacea and also some scattered hairs on them. In total, the leaf-air temperature difference in nature might even be higher than what we observed here. Hanson and Sharkey (2001) observed higher ΔT in the field than in a glasshouse in their studies on oaks (personal communication).

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