Effects of elevated CO_2 and irrigation on gas exchange and water relations among two wheat cultivars

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Abstract

Gas exchange and water relations of two *Triticum aestivum* L. cultivars (Yitpi and H45) were compared under two CO_2 levels (ambient aCO_2 ~380 µmol mol^{-1}, elevated eCO_2 ~550 µmol mol^{-1}) and two water treatments (rain-fed, rain-fed plus irrigated). Yitpi, a high tillering cultivar, was compared to H45, a low tillering cultivar, to study intra-specific variability aspects of responses to a rising atmospheric CO_2 concentration. Measurements were made on flag leaves of plants grown in a Free Air Carbon Dioxide Enrichment (FACE) site during anthesis (DC65-DC68). Both cultivars had increased light saturated net assimilation (A_{sat}) and stomatal conductance (g_s) under eCO_2. When plants grown at either aCO_2 or eCO_2 were measured at a common CO_2 concentration (550 µmol mol^{-1}) to study long-term photosynthetic acclimation, g_s remained greater in eCO_2 grown plants, but A_{sat} was similar. Irrigation increased A_{sat} and g_s as well as decreased cell sap osmolality in Yitpi but there was no irrigation effect in H45. It remains to be seen whether such differences translate into yield variations over a whole growing season.

Key Words

Acclimation, photosynthesis, cell sap osmolality, RWC, climate change

Introduction

Current climate change projections predict a rise in global atmospheric CO_2 concentration (Forster et al. 2007). At the same time, probability and frequency of drought events are expected to increase across an increasing amount of land (Mpelasoka et al. 2008), particularly in dry-land areas important to global wheat production.

In plants, rises in global atmospheric CO_2 concentration commonly increase net assimilation rates (A), while underlying processes of photosynthesis (photosynthetic capacity) are often reduced through continued exposure to elevated atmospheric CO_2 (eCO_2), including a small reduction in A. This reduction in photosynthetic capacity is termed acclimation that occurs over a growing season as plants become so-called acclimatised to the eCO_2 (Ainsworth and Rogers 2007). Acclimation is caused by morphological, biochemical and molecular adjustments to growth under elevated CO_2. Drought-induced decreases in plant productivity and growth are linked to decreased photosynthetic rates, which is caused by the restriction of CO_2 diffusion through closing stomata to the site of carboxylation (Flexas et al. 2006). eCO_2 may counteract negative effects of drought, because drought induced lower stomatal conductance (g_s) becomes less restrictive to photosynthesis. For example, Seneweera et al. (2001) reported that eCO_2 reduces canopy transpiration and improves soil moisture availability, because plants operated at lower g_s and showed increased osmotic adjustment.

To secure global food supply in a changing climate, it will be necessary to breed cultivars best suited to cope with drought under eCO_2. This will be most effective if research is conducted directly within the

production areas under free air CO_2 enrichment (FACE) (Ainsworth et al. 2008). To deepen our understanding of intra-specific physiological responses to potential climate change factors, we specifically investigated photosynthetic responses and water relations of two *Triticum aestivum* L. cultivars (Yitpi and H45) to the combined effects of two CO_2 levels (ambient aCO_2 ~380 µmol mol^{-1}, elevated eCO_2 ~550 µmol mol^{-1}) and two water treatments (rain-fed, irrigated). Yitpi is considered a high tillering cultivar, whereas H45 is considered a low tillering cultivar, a difference that can influences the use of assimilates ('sink strength') and potentially causes different responses to the experimental conditions. Plants were grown within a major dry-land wheat production area of Australia, at the Australian Grains Free Air CO_2 Enrichment (AGFACE) site in Horsham, Victoria (Mollah et al. 2009). The aim of our work was to identify variation among cultivars in response to experimental conditions to identify traits beneficial in a future high CO_2 world.

Materials and Methods

Plant material and growth conditions

Yitpi and H45 were grown in a randomised complete block design with 4 replications. Elevated CO_2 blocks were fumigated to an elevated target CO_2 of 550 µmol mol^{-1}. Each block was split for irrigation ('rain-fed' and 'irrigated'). Sowing date was 23 June 2009.

Gas exchange measurements

Light saturated gas exchange was measured on flag leaves during anthesis (DC65-DC68) using an open gas exchange system (Li-6400, Li-Cor, Lincoln, NE, USA). Measurements were carried out with an air flow rate of 250 µmol s^{-1}, a block temperature of 20 ?C, and at a saturating light intensity of 1800 µmol m^{-2} s^{-1} PPFD. To evaluate gas exchange responses under respective growing conditions (aCO_2 or eCO_2), photosynthesis was recorded at 390 and 550 µmol mol^{-1} CO_2. To evaluate the acclimation effects of growth CO_2, comparisons were made at a common CO_2 concentration of 550 µmol mol^{-1} according to Gutierrez et al. 2009.

Plant water status

Relative water content (RWC) of flag leaves was calculated as (FW – DW) / (TW – DW) where FW is the fresh weight of the leaves recorded immediately after harvesting, TW is the turgid weight after rehydrating leaves to full water saturation, and DW is the dry weight after drying leaves at 70 ?C for 60 hours. For the determination of cell sap osmolality, rehydrated leaves were cut into small pieces and shock-frozen in liquid nitrogen. Cell sap of thawed samples was expressed by centrifugation and its osmolality (osmols kg^{-1}) was measured with an osmometer (Osmomat 030, Gonotec GmbH, Berlin, Germany).

Statistical analyses

Data were processed and analysed using SigmaPlot 11.0 and PASW Statistics 18 software. A three-way ANOVA was conducted with cultivar, CO_2 and water treatment as fixed factors. Homogeneity of variances was checked with the Levene's test. Distribution of residuals was graphically checked for deviations from normality.

Results and Discussion

Growth at eCO_2 significantly increased light saturated net CO_2 assimilation rates (A_{sat}) by up to 60 % in both cultivars (C effect, Figure 1a), whereas irrigation affected Yitpi rather than H45, with Yitpi grown under irrigated and eCO_2 conditions responding with the greatest A_{sat} rates (I x Cu effect, Figure 1a). Growth at eCO_2 also significantly increased g_s (C effect, Figure 1b), whereas irrigation again affected Yitpi rather than H45, with Yitpi grown under irrigated and eCO_2 conditions showing the greatest g_s (I x Cu effect, Figure 1b).

When plants grown at aCO_2 were measured at the common eCO_2 level of 550 µmol mol^{-1} CO_2 to evaluate long-term acclimation, A_{sat} between CO_2 treatments was not different (Figure 2a), whereas the cultivar by irrigation interaction (I x Cu effect, Figure 2a) remained significant, with irrigated Yitpi showing the greatest A_{sat}. There was still a CO_2 effect (C effect) and irrigation x cultivar (I x Cu effect) on g_s when aCO_2 grown plants were measured at 550 µmol mol^{-1}, which again was mostly due to the high values obtained for Yitpi grown under eCO_2 and irrigated conditions (Figure 2b). Cell sap osmolality was significantly greater in rain-fed plants (I effect) as well as in Yitpi compared to H45 (Cu effect, both Figure 1c). There was no significant CO_2 or water treatment effect on the RWC of sample plants (data not shown).

Our results showing increases of A_{sat} in response to growth under eCO_2 are in accordance to a large number of publications, even if the extent of such an increase varies considerably. For example, reported increases in A_{sat} range from ~12% (Sicher and Bunce 1997), ~30% (Garcia et al. 1998), to ~50% (Miglietta et al. 1996) with the latter being in the range of what we found in the present study (60%). Species related differences can be excluded as all these studies were performed on wheat at a similar range of CO_2 and under (Mini)FACE conditions. Garcia et al. (1998) suggested that such differences must result from climate pre-history, differences in soil etc.

Acclimation as a process of optimization of photosynthesis in response to eCO_2 would result in lower rates of A_{sat} if plants are measured at a common CO_2. Such acclimation has been reported widely for wheat systems (e.g. Gutierrez et al. 2009). In contrast, our data give no indication of photosynthetic down-regulation under eCO_2 which agrees with Garcia et al. (1998) or Miglietta et al. (1996) who suggested that under FACE conditions the stimulation of photosynthesis by eCO_2 persists without any evidence of acclimation.
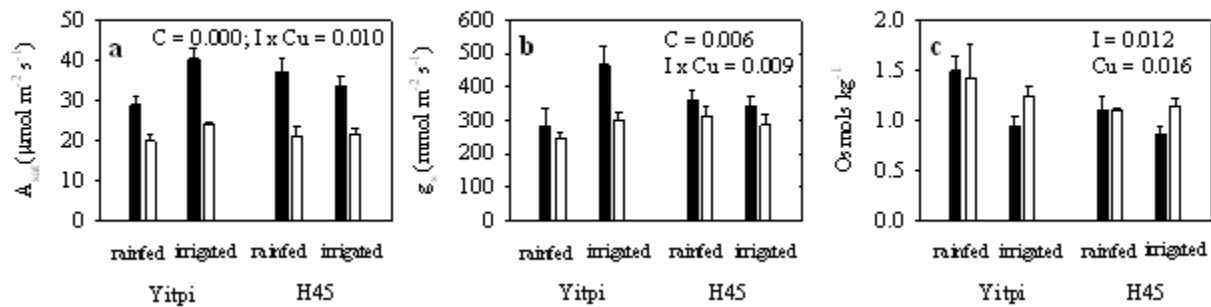

Figure 1. Flag leaf gas exchange (1a and 1b) and water relations (1c) of two *Triticum aestivum* cultivars (Yitpi and H45) grown under two CO_2 levels (closed bars, eCO_2 550 µmol mol^{-1}, open bars, aCO_2, 390 µmol mol^{-1}) and two water treatments (rain-fed/irrigated). Measurements were taken at growth CO_2 concentrations (390 vs 550 µmol mol^{-1} CO_2). ANOVA effects: I irrigation, C CO_2, Cu cultivar, I x Cu irrigation x cultivar interaction
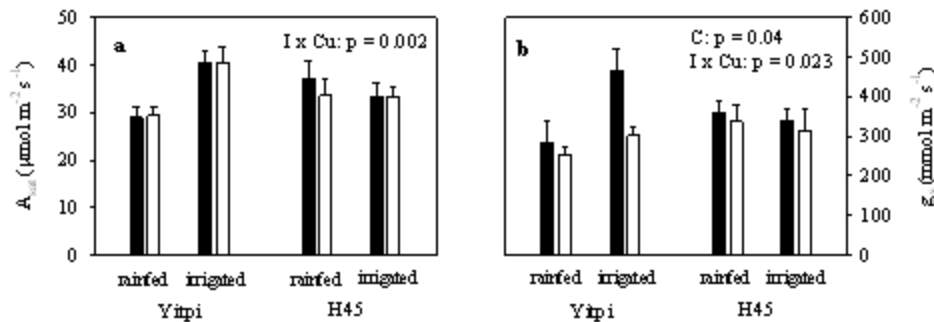
Figure 2. Acclimation responses of Yitpi and H45 to growth under eCO$_2$. Gas exchange measurements of A$_{sat}$ (2a) and g$_s$ (2b) were made at a common CO$_2$ concentration of 550 µmol mol^{-1} CO$_2$. Closed bars: eCO$_2$ 550 µmol mol^{-1}; open bars: aCO$_2$, 390 µmol mol^{-1}. The same experimental conditions as described in Figure 1 apply.

It is overwhelmingly evident from FACE and non-FACE experiments that g$_s$ decreases in eCO$_2$ (Ainsworth and Rogers 2008), however, there are exceptions due to environmental interactions. For example, Leakey et al. (2006) studied acclimation of g$_s$ under FACE conditions on *Glycine max* by measuring g$_s$ throughout the growing season. They found considerable variation of the CO$_2$ effects on g$_s$ and they speculated that soil water content becomes less depleted during dry periods under elevated CO$_2$, thereby potentially minimizing a drought induced decrease in g$_s$. Similar results were reported by Seneweera et al. (2001). In the present study, we have no direct evidence of greater soil water retention under eCO$_2$ and there were no differences in RWC of the crop. However, wheat growing under rain-fed conditions showed greater cell sap osmolality than wheat grown with additional irrigation, an indication of osmotic adjustment under dryer conditions (Zivcak et al 2009). Furthermore, there was also a (nearly significant) trend in osmolality towards a CO$_2$ x irrigation interaction (C x I effect: p = 0.075, data not shown) with eCO$_2$ grown irrigated plants having lowest values in osmolality possibly indicating greater soil moisture retention within the respective plots.

Conclusion

Overall, we saw substantial stimulation of A$_{sat}$ under eCO$_2$ and no indication of photosynthetic acclimation. Differences between the investigated cultivars come into play in their responses to different water supply levels, less so in their response to eCO$_2$. It remains to be seen how such differences reflect on full season growth and yield.

Acknowledgements

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