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The effect of elevated CO_2 on photochemistry and antioxidative defence capacity in wheat depends on environmental growing conditions – A FACE study

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ABSTRACT

The present study examines photosynthesis, photochemistry and low weight molecular antioxidants (ascorbic acid and glutathione) of two *Triticum aestivum* L. cultivars (H45 and Yitpi) in response to growth under two CO_2 concentrations (elevated CO_2, e[CO_2] *vs.* ambient CO_2, a[CO_2]), two sowing times (time of sowing 1, TOS1, less stressful growing conditions *vs.* time of sowing 2, TOS2, more stressful growing conditions) and two water treatments (rain-fed *vs.* irrigated). The objective was to evaluate (1) if growth under e[CO_2] will alleviate climate stresses such as higher temperature and/or limited water supply thereby reducing the need for photoprotection and concentrations of low weight molecular antioxidants and (2) cultivar-specific responses to combined climate change factors which may be useful to identify intra-specific variation in stress tolerance for future breeding. We compared gas exchange, chlorophyll fluorescence and antioxidative defence compounds (ascorbic acid, glutathione) of flag leaves of Australian Grains Free Air Carbon dioxide Enrichment (AGFACE) grown wheat. When plants were grown under the less stressful growing conditions of TOS1, e[CO_2] increased light saturated net assimilation rates (A_{sat}) and quantum yield of PSII electron transport (ΦPSII) but decreased thermal energy dissipation (indicated by increased efficiency of open PSII centres, Fv′/Fm′), while antioxidant concentrations did not change. Under the more stressful growing conditions of TOS2, e[CO_2] also increased A_{sat} (like at TOS1), however, photochemical processes were not affected while antioxidant concentrations (especially ascorbic acid) were decreased. Cultivar specific responses also varied between sowing dates: Only at TOS2 and additional irrigation, antioxidant concentrations were lower in e[CO_2] grown H45 as compared to Yitpi indicating decreased photo-oxidative pressure in H45. These results suggest a photo-protective role of e[CO_2] as well as some intra-specific variability between investigated cultivars in their stress responsiveness, all strongly modified by environmental growing conditions.

1. Introduction

Global atmospheric CO_2 concentration ([CO_2]) is continually increasing and will reach 550 μmol mol^{-1} by 2050, according to the IPCC (Intergovernmental Panel on Climate Change) emission scenario A1B (Carter et al., 2007). This is a more than 40% increase over about 390 μmol mol^{-1} in 2011. Such a large change in a key resource for plant growth will have significant direct effects on its own (Ziska, 2008a). In addition, increasing [CO_2] causes an increase in mean global temperature (Houghton, 2001) leading to climate change with perturbations such as more frequent and more severe drought events across an increasing area of land (Mpelasoka et al., 2008). Plant growth and metabolism, and, consequently, global crop production will be profoundly affected by such changes. Future global food security will depend on understanding how primary crop physiological processes will be affected by combined climate change factors including elevated [CO_2] (e[CO_2]).

The current investigation deals with wheat, which is one of the three main cereal crops, with over 600 million tonnes harvested annually and providing one fifth of the total calorific input of the world's population (Amthor, 2001; Shewry, 2009). Wheat is currently also successfully grown under limited water supply ('rain-fed agriculture'), with the semi-arid Australian wheat-belt being a good example. In rain-fed agriculture, high temperatures and drought episodes occur frequently during the crop growing season (Nicolas et al., 1984), and are predicted to increase in the

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future (Mpelasoka et al., 2008; Saxe et al., 2001). It is widely recognised that selection of promising cultivars will be an important aspect of adaptation of wheat production in the face of a changing climate (Semenov and Halford, 2009). Such considerations must take into account the direct effects of e[CO_2], which are significant and can moderate responses to other climate change related stress factors (Ainsworth et al., 2008).

Leaf-level gas exchange measurements show that wheat generally responds to e[CO_2] with increased photosynthetic net assimilation rates (*A*) (Ainsworth and Rogers, 2007; Garcia et al., 1998). These increases are brought about by a stimulating effect of e[CO_2] on the carboxylation reaction of Rubisco and, at the same time, a suppressing effect on photorespiration (Ghannoum et al., 2007; Long et al., 2006). Garcia et al. (1998), for example, reported that wheat grown under Free Air Carbon dioxide Enrichment (FACE) had an increase in midday A of 28% compared to plants grown as control under ambient [CO_2] (a[CO_2]). Long-term exposure to e[CO_2], however, can reduce stimulation of carboxylation (manifested in a decrease in V_{cmax}, a surrogate for *in vivo* activity of Rubisco) through a process called photosynthetic acclimation (Ghannoum et al., 2007; Seneweera et al., 2002). In wheat, for example, a decline of A was reported when acclimation effects of photosynthesis were assessed (Gutierrez et al., 2009; Martinez-Carrasco et al., 2005; Sicher and Bunce, 1997).

Previous research has placed much emphasis on mechanisms of photosynthetic acclimation to e[CO_2], particularly with regard to decreased V_{cmax} and the role of Rubisco, although theoretical considerations suggest that the regeneration of RuBP, rather than Rubisco activity itself, may become more limiting under e[CO_2] (Zhu et al., 2010). RuBP regeneration is determined by the activity of Calvin cycle enzymes other than Rubisco, and by photochemical reactions determining light driven electron transport rates. Elevated [CO_2]-induced long and short-term changes in A will require modifications in photochemical activity, because photosynthetic electron transport destined for CO_2 assimilation will increase proportionately with increasing A while photorespiratory flux to oxygen will be inhibited (Aranjuelo et al., 2008; Habash et al., 1995; Hymus et al., 2001). The net result of these changes will determine how total electron transport rates will adjust (Gutierrez et al., 2009; Hymus et al., 2001). Previous studies on effects of e[CO_2] on photochemical processes reported inconsistent results. For example, quantum yield of photosystem II (PSII) electron transport (ΦPSII), one determinant of electron transport, has been reported to variously increase under e[CO_2] (Habash et al., 1995; on wheat, Hymus et al., 2001; on high N *Dactylis glomerata*), not to change (McKee et al., 1995; on wheat) or to decrease (Aranjuelo et al., 2008; on *Medicago sativa*). Habash et al. (1995) related the increases in ΦPSII to increases in open PSII centres, estimated by the coefficient of photochemical quenching of fluorescence (qP), rather than to changes in the efficiency of light harvesting and energy transduction of open PSII centres (measured as the fluorescence parameter Fv′/Fm′), while Hymus et al. (2001) reported of simultaneous increases in qP and Fv′/Fm′.

Changes in photochemical parameters can affect the extent to which plants experience excess excitation pressure. Excess excitation pressure is the result of plants absorbing light at a faster rate than they can use in photosynthesis, which is particularly common under stress conditions (Asada, 1999; Murchie and Niyogi, 2011). Excess excitation pressure is problematic because it can lead to electrons supplied in excess of the requirements for CO_2 fixation resulting in the formation of reactive oxygen species (ROS). ROS are potentially harmful as they degrade pigments and proteins of the thylakoid membranes, most notably the D1 protein subunit of the PSII reaction centre (Asada, 1999; Murchie and Niyogi, 2011). Protection against oxidative damage caused by excessive ROS production is possible via thermal dissipation of excess excitation energy, a process which avoids ROS formation altogether (Murchie and Niyogi, 2011), and the activity of antioxidants, such as ascorbic acid or glutathione, which keep ROS under control (Foyer and Shigeoka, 2011). It is noteworthy that some ROS ‘leakage’ is important to enable stress related signalling processes, and perhaps ‘prime’ metabolism for responses to sudden stress exposure (Foyer and Shigeoka, 2011).

Elevated [CO_2] may alleviate the formation of ROS, because for a given electron transport rate, relatively more electrons can be consumed in carbon fixation, and fewer are channelled into ROS producing pathways, such as photorespiration or the Mehler reaction (Asada, 1999). This would protect against the formation of ROS, thereby reducing the need for antioxidative defence capacity (Badiani et al., 1998; di Toppi et al., 2002). Previous studies addressing oxidative stress and antioxidative defence responses to growth under e[CO_2] have reported that plants grown under e[CO_2] compared to a[CO_2] had decreased photooxidative stress (Aranjuelo et al., 2008) as well as significantly lower concentrations of ascorbic acid (Aranjuelo et al., 2008; Gillespie et al., 2011; Robinson and Sicher, 2004) and glutathione (Aranjuelo et al., 2008; Robinson and Sicher, 2004). Contrasting results, however, were reported by Badiani et al. (1998), di Toppi et al. (2002), Jia et al. (2010), and Rao and De Kok (1994) with some indication that growth under e[CO_2] can increase the level of oxidative stress (Qiu et al., 2008).

Increasing global temperature and drought events are major stress factors expected to limit crop production in the future. The two stress factors are commonly coincident and crop responses to one stress can be altered by the level of the other stress (Machado and Paulsen, 2001) and the combination can be more severe than the effects of the individual stresses alone (Nicolas et al., 1984). Plant responses to combined temperature and drought, as with virtually all plant stress responses, involve thermal energy dissipation and ROS metabolism (Foyer and Shigeoka, 2011; Murchie and Niyogi, 2011). Hence, temperature and drought responses may change under e[CO_2]. For example, Qaderi et al. (2006) reported for *Brassica napus* that high temperature and drought decreased A and ΦPSII in plants when grown under a[CO_2] but not when grown under e[CO_2]. They concluded that physiological and biochemical modifications arising from e[CO_2] concentrations may ameliorate some of the effects of high temperature and water stress. Similar suggestions were made by Aranjuelo et al. (2008) and Erice et al. (2007).

Intra-specific variability in responses to e[CO_2] (Ziska, 2008b) or in photoprotective and antioxidative responses to stress (Lascano et al., 2001) may provide selection traits for breeding programmes. In this study we therefore investigated two wheat cultivars, contrasting in their tillering capacity and reproductive sink strength. Sink strength is thought to increase the utilisation capacity of assimilates, thereby potentially reducing the risk of photosynthetic acclimation to e[CO_2]. A number of mechanisms have been put forward to explain this phenomenon, such as a suppression of key photosynthetic related genes which are mediated by the sugar induced hexokinase signalling pathway (Moore et al., 1999). That variability in sink strength can affect photosynthetic acclimation to e[CO_2] was demonstrated for contrasting soybean cultivars (Ainsworth et al., 2004).

The current study was conducted in the AGFACE (Australian Grains Free Air Carbon dioxide Enrichment) facility within the major wheat production area of Australia (Mollah et al., 2009). Wheat plants were grown under a[CO_2] (~390 μmol mol^{-1}) and e[CO_2] (~550 μmol mol^{-1}), and two sowing dates (time of sowing 1, TOS1, less stressful growing conditions *vs.* time of sowing 2, TOS2, more stressful growing conditions) and two water treatments (rain-fed only *vs.* rain-fed plus irrigation). This created a combination of different environmental growing conditions. Simultaneous measurements of chlorophyll fluorescence and gas