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Can elevated CO_2 buffer the effects of heat waves on wheat in a dryland cropping system?

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ABSTRACT

Increasing atmospheric CO_2 concentration [CO_2] drives the rise in global temperatures, with predictions of an increased frequency of heat waves (short periods of high temperatures). Both, CO_2 and high temperature, have profound effects on wheat growth and productivity. We tested whether elevated [CO_2] (eCO_2) has a potential to ameliorate the effects of simulated heat waves (HT) on wheat in a dryland cropping system. Wheat was field-grown at the Australian Grains Free Air CO_2 Enrichment (AGFACE) facility under ambient [CO_2] (~390 ppm) or eCO_2 (~550 ppm) for two growing seasons, one with ample water supply and one of severe drought. Using heated chambers, heat waves (3-day periods of high temperatures) were imposed at critical growth stages before anthesis (HT1) or post-anthesis (HT2, HT3). Gas exchange, chlorophyll content and concentration of nitrogen (N) in mainstem flag leaves, as well as concentrations of stem water-soluble carbohydrates (WSC) in mainstems were monitored throughout the season. Yield, biomass and thousand kernel weights (TKW) were measured at maturity. Elevated [CO_2] moderated the effect on net CO_2 assimilation rates of pre-anthesis (HT1), but not of post-anthesis heat waves (HT2, HT3). Growth under eCO_2 increased stem WSC both, with and without experimental heat waves, but remobilisation decreased significantly under heat indicating that a greater WSC pool does not necessarily translate into greater remobilisation into the grain. Grain yield (g m^{-2}) was greater under eCO_2 and especially pre-anthesis heat stress decreased grain yield in the wetter season, and this decrease was stronger under eCO_2 (up to 20%) than under aCO_2 (up to 10%). Grain N decreased under eCO_2, but less so under heat stress. We conclude that eCO_2 may moderate some effects of heat stress in wheat but such effects strongly depend on seasonal conditions and timing of heat stress.

1. Introduction

Atmospheric carbon dioxide concentration [CO_2] has rapidly increased from a steady ~280 µmol mol^{-1} prior to the Industrial Revolution to currently ~405 µmol mol^{-1}, and is predicted to reach ~550 µmol mol^{-1} by the middle of this century (IPCC, 2014; Pearson and Palmer, 2000). This rise in [CO_2] drives an increase in global mean temperatures by 1.0 to 3.7 °C by the end of the 21st century. In addition, heat wave events (short periods of high temperatures) are likely to become more frequent and more severe (IPCC, 2014). Changes in global climate are already adversely affecting yield and quality of important food crops, such as wheat (*Triticum aestivum* L.), and are predicted to have more severe impacts in future climate scenarios (IPCC, 2014).

Aside from driving climate change, the increase in [CO_2] alone affects all plant systems (Ziska, 2008). CO_2 enrichment studies, in particular Free Air CO_2 Enrichment (FACE) experiments, have shown the following effects of elevated [CO_2] (eCO_2) on C_3 crops such as wheat: Greater net CO_2 assimilation rate but lowered stomatal conductivity and photorespiration (Ainsworth and Long, 2005; Kimball et al., 2001; Long et al., 2004); increased leaf and canopy water use efficiency and decreased transpiration (Drake et al., 1997; Leakey et al., 2009; Tausz-Posch et al., 2013a) as well as increases in dry matter accumulation and grain yield, mostly derived through increased fertile tiller numbers and sometimes also through increased single kernel weight (Ainsworth and Long, 2005; Dubey et al., 2015; Tausz-Posch et al., 2015). Elevated CO_2 can also lead to an increased accumulation of water-soluble

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carbohydrates (WSC), such as starch and total non-structural carbohydrates in leaves and, in particular, fructans in the stems (Nie et al., 1995; Sild et al., 1999; Smart et al., 1994). In contrast, the concentration of mineral nutrients, particularly of nitrogen (N), is universally reduced under eCO_2 in vegetative and reproductive plant parts, translating directly to lower protein concentrations in vegetative tissues and grains, adversely affecting the nutritional and economic value of crops (Cotrufo et al., 1998; Taub and Wang, 2008).

With optimum growing temperatures between 17 and 23 °C (Shanmugam et al., 2013), wheat is very sensitive to heat (Farooq et al., 2011; Slafer and Rawson, 1995). Heat stress occurs when a plant is exposed to temperatures above an upper threshold for long enough to cause irreversible damage (Wahid et al., 2007). For wheat, threshold temperatures impacting growth and yield, are most commonly given between 31–35 °C (Barnabas et al., 2008; Ferris et al., 1998; Fischer, 2011), although some studies have reported high temperature impacts already above a threshold as low as 26 °C (Stone and Nicolas, 1994).

Heat stress decreases net CO_2 assimilation rates resulting in decreased photo-assimilate production as well as reduced dry-matter accumulation and yield (Bergkamp et al., 2018; Narayanan et al., 2015; Tahir and Nakata, 2005). When photosynthesis is constrained by heat stress, carbon (C) reserves, such as stem WSC (fructans) in wheat, can be used to fill the grains (Dreccer et al., 2013; Fokar et al., 1998). For example, the contribution of remobilised stem WSC to grain weight can increase from 10 to 20% under non-stress conditions to 30–50% under stress conditions (van Herwaarden et al., 2003; Wang et al., 2012). Similar trends were shown by Zamani et al. (2014) and Tahir and Nakata (2005) who reported that high temperature stress was correlated with increased WSC remobilisation from the mainstem into grains. Nevertheless, grain size and quality are affected by heat stress, with starch deposition into the grain being generally reduced under heat stress resulting in smaller kernels and more N per unit of starch (Stone and Nicolas, 1994; Farooq et al., 2011). Heat stress also induces phenological responses such as accelerated development, thus shortening the duration for the critical grain-filling period (Bergkamp et al., 2018; Stone and Nicolas, 1996).

The timing of heat stress during plant development is important because certain damage mechanisms only apply during particularly sensitive growth stages (Wollenweber et al., 2003). For example, in wheat heat stress shortly before or at anthesis will decrease grain numbers through floret abortion (Fischer, 1985), while stress episodes during the grain-filling stage will decrease grain weight by interfering with carbohydrate supply and translocation into the grains (Telfer et al., 2013).

Most previous research has focused on eCO_2 or heat stress separately, and those studies that investigated eCO_2 in combination with higher temperature commonly used moderate, continuous warming, not exceeding heat stress thresholds (e.g. de Oliveira et al., 2015). Little is known about the effects of heat waves, short periods of high temperatures, during critical developmental stages, in combination with eCO_2, despite the potential of eCO_2 to mitigate or interact with heat stress. For example, Shanmugam et al. (2013) reported that heat stress decreased net CO_2 assimilation rates in wheat, but when heat-stressed crops were grown under eCO_2, assimilation rates remained higher. Also, greater WSC pools under eCO_2 (Sild et al., 1999; Smart et al., 1994; Winzeler et al., 1990) may provide greater reserves for C remobilisation into grains, thereby ameliorating the negative effects of heat stress on grain weights.

The present study investigated whether growth under eCO_2 protects wheat from effects of heat waves in a dryland cropping system. Immediate and long-term responses to heat waves were recorded from pre-anthesis to maturity, and the experiment was replicated over two seasons. To account for different sensitive growth stages (Wollenweber et al., 2003), separate heat wave treatments were applied pre-anthesis (HT1) and during the grain-filling period (post-anthesis, HT2 and HT3). The experiment was conducted under ambient $[CO_2]$ (~390 ppm, aCO_2) and eCO_2 (~550 ppm) at the Australian Grains Free Air CO_2 Enrichment (AGFACE) facility in Horsham, Victoria. This location is part of the semi-arid cropping region of the south-eastern Australian wheat belt, representative of globally important water-limited dryland wheat cropping areas, which are at particular risk from increased incidence and severity of climate change driven heat stress events (Sadras and Dreccer, 2015). Heat waves were simulated with mobile heat chambers (Nuttall et al., 2012), and treatment effects on grain yield assessed. Physiological (gas exchange and leaf chlorophyll) measurements were conducted in conjunction with assessments of stem WSC and leaf N concentrations from pre-anthesis through the grain-filling period and related to grain yield and grain N. These investigations were done on mainstems, because of their stable and relatively high contribution to grain yield as opposed to late-forming tillers which are affected by depleting photoassimilate supply (Darwinkel, 1978; Gan and Stobbe, 1995), even without environmental stresses.

In this study, we critically assess whether eCO_2 has the potential to ameliorate heat stress effects in wheat when grown in water-limited dryland wheat cropping systems. We determine if eCO_2-induced increases in net CO_2 assimilation will lead to a greater WSC pool in stems and, if yes, this helps to ameliorate the negative effects of heat stress on grain weights. Add-on effects for grain N are also investigated. In detail, we tested the following hypotheses:

1) Crops grown under eCO_2 have greater net assimilation rates than crops grown under aCO_2, both pre- and post-anthesis. Heat waves decrease net assimilation rates in crops grown under aCO_2, but eCO_2 buffers heat wave effects by maintaining net assimilation rates.
2) Increased net assimilation rates in crops grown under eCO_2 result in greater stem WSC concentrations. A greater pool of C reserves (WSC concentration) allows greater remobilisation to grains and this results in the maintenance of greater grain yield of eCO_2 grown crops subjected to heat waves.
3) Any reduction in grain N under eCO_2 is less in crops subjected to heat waves, because grains of heat stressed crops commonly have less carbohydrates relative to nitrogen.

2. Materials and methods

2.1. Site description

This experiment was conducted within the AGFACE facility during the 2013 and 2014 growing seasons. The research site of 7.5 ha is located 7 km west of Horsham, Victoria, Australia (36°45′07″S latitude, 142°06′52″E longitude, 128 m elevation); a semi-arid region of the Australian wheat belt. The average annual rainfall for the site is 435 mm with growing season (June-November) rainfall averaging 274 mm. The long term mean temperature is 16.5 °C. The soil type is classified as a Vertosol under the Australian Soil Classification (Isbell, 2002). This type of soil is characteristically pedal and non-dispersive on the surface. A detailed specification of the experimental facility can be found in Mollah et al. (2009). Local practices were the basis for agronomic management, including spraying of fungicides and herbicides, as needed.

2.2. Experimental setup

Eight rings (= experimental plots), arranged in four complete blocks, four under ambient CO_2 (aCO_2, ~390 $\mu mol\,mol^{-1}$) and four under elevated CO_2 (eCO_2, targeted concentration of ~550 $\mu mol\,mol^{-1}$), were used in both seasons. Ring diameters were 16 m in 2013 and 12 m in 2014. For the eCO_2 treatment, rings were surrounded with octagons of horizontal stainless steel tubes adjusted to about 0.15 m above the plant canopy at any given developmental stage. Pure CO_2 gas was injected in upwind direction through 0.3 mm laser-drilled holes facing outward of the ring. Using automated control