Field Crops Research 224 (2018) 170–181

Contents lists available at ScienceDirect

Field Crops Research

journal homepage: www.elsevier.com/locate/fcr

Water use and growth responses of dryland wheat grown under elevated [CO_2] are associated with root length in deeper, but not upper soil layer

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ARTICLE INFO

Keywords:
Climate change
FACE
Dryland agriculture
Root length
NDVI
Water use
Yield

ABSTRACT

This study investigated crop water use of wheat grown in a dryland Mediterranean-type environment under elevated atmospheric CO_2 concentrations ([CO_2]). Two related cultivars, contrasting in agronomic features (cvs. Scout and Yitpi; Scout has good early vigour and high transpiration efficiency), were grown under ambient [CO_2] (a[CO_2], ~400 μmol mol^{-1}) and elevated [CO_2] (e[CO_2], ~550 μmol mol^{-1}) in the Australian Grains Free Air CO_2 Enrichment (AGFACE) facility for two growing seasons. Each year, an irrigation treatment (rainfed versus irrigated) was imposed within the CO_2-treatments. Normalised difference vegetation index (as surrogate for canopy cover) and root length in the upper (0 cm–32 cm) and deeper (33 cm–64 cm) soil layers were measured at stem-elongation and anthesis.

Elevated [CO_2] stimulated root length of wheat in both upper and deeper soil layers, and this stimulation was modified by cultivars and irrigation regimes. Across cultivars and all treatments, water use, biomass and grain yield were positively associated with root length in the deeper soil layer but not with root length in the upper soil layer. The 'CO_2 fertilisation effect' on biomass and grain yield was of similar magnitude under both irrigated and rainfed conditions. Although e[CO_2] did not increase canopy cover in these experiments, the CO_2 effect on water use depended on cultivars and irrigation regimes. Despite greater e[CO_2]-induced stimulation of tillers and spikes, the cv. Scout did not receive more biomass or grain yield benefit from the 'CO_2 fertilisation effect' compared to cv. Yitpi.

1. Introduction

The concentration of atmospheric CO_2 ([CO_2]) has increased by just over 50% from the start of the Industrial Revolution (270 μmol mol^{-1}) (Long et al., 2004) to the current level (408 μmol mol^{-1}) in 2017 (NOAA, 2017). If CO_2 emissions continue at the current rate, atmospheric [CO_2] will reach 550 μmol mol^{-1} by the middle of this century (IPCC, 2013). As CO_2 is the main substrate of photosynthesis, this increase has direct implications for plant metabolism, such as stimulating net photosynthetic CO_2 assimilation in C_3 crops, leading to greater biomass production and yield through the so-called 'CO_2 fertilisation effect' (Ainsworth and Long, 2005; Ziska et al., 2012; Kimball, 2016).

This 'CO_2 fertilisation effect' on C_3 crops has been demonstrated in various agro-ecosystems (Ainsworth et al., 2002; Kimball et al., 2002; Long et al., 2006; Högy et al., 2009; Lam et al., 2012a,b; Hasegawa et al., 2013; Fitzgerald et al., 2016) but the extent of the fertilisation effect varies considerably across regions, as well as within the same region depending on environmental growing conditions (availability of nutrients and soil water, temperatures) (Leakey et al., 2012; McGrath and Lobell, 2013; Reich et al., 2014; Kimball, 2016). Free Air CO_2 Enrichment (FACE) systems have been established to investigate the plant-atmosphere relationship under future [CO_2]. However, such FACE systems focussing on plant or ecosystems responses to elevated [CO_2] (e[CO_2]) are scarce in arid and semi-arid areas because most are established in high rainfall temperate regions (Leakey et al., 2012; Rosenthal and Tomeo, 2013) or dealt with fully irrigated agro-ecosystems (Wall,

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https://doi.org/10.1016/j.fcr.2018.05.014
Received 23 March 2018; Received in revised form 18 May 2018; Accepted 20 May 2018

2001; Wall et al., 2001). There are strong theoretical reasons to assume arid or semi-arid agro-ecosystems will respond differently to e[CO_2] than the well-studied temperate regions, owing to, for example, low inputs of nutrients, low and very variable water supply, and reliance of crops on soil water reserves during hot and dry periods (Leakey et al., 2012). Modelling studies have identified substantial uncertainty around the magnitude and direction of crop response to e[CO_2] in water-limited Mediterranean-type environments (Ewert et al., 2002). Therefore, assessing the effect of e[CO_2] on crops in such environments is an important area of research.

Wheat (*Triticum aestivum* L.) is one of the most extensively grown grain crops in the world (Shewry, 2009). Approximately 15% of the global wheat producing area are located in low yielding, water limited Mediterranean-type environments (Fischer et al., 2014). In these environments wheat commonly has ample water supply during early growth stages, either from stored soil water or early season rainfall, but the grain filling period is often affected by extensive water shortage, termed terminal drought (Braun et al., 1996; Farooq et al., 2014), which is considered the major cause of grain yield variability of wheat in these regions (Tambussi et al., 2007; Dias de Oliveira et al., 2013). Under these conditions, additional water availability in the form of supplemental irrigation, conserved soil water from the early growth stages or sub-soil water acquisition through increased root length could potentially increase grain yields in wheat (Kirkegaard et al., 2007; Lilley and Kirkegaard, 2011).

Elevated [CO_2] might benefit water relations in wheat for two reasons in such Mediterranean-type environments: (1) through reducing stomatal conductance (g_s) and (2) through increasing root length. Reduced g_s under e[CO_2] increases instantaneous leaf level water use efficiency (Ainsworth and Long, 2005; Bernacchi et al., 2007), which may lower crop water use (Leakey et al., 2009; Kimball, 2016) during the early growth stages. This is hypothesised to increase available soil water during the grain filling period (Burkart et al., 2011; Hussain et al., 2013). Greater water availability under e[CO_2] reaching into the grain filling period may prolong physiological processes such as photosynthesis and thus result in greater growth (Wall et al., 2001). In contrast, excessive stimulation of early growth due to 'CO_2 fertilisation' may deplete soil water more quickly despite greater leaf level water use efficiency, and combined with reduced rainfall during grain filling as part of predicted future climates (CSIRO and Bureau of Meteorology, 2015; Watson et al., 2017), increase the risk of 'haying-off', where large early biomass production exhausts soil water and the crop dies off before grains are filled (van Herwaarden et al., 1998; Nuttall et al., 2012).

The second effect of e[CO_2] on water relations of crops particularly relevant to Mediterranean-type environments, is increased root length (Chaudhuri et al., 1990; VanVuuren et al., 1997; Benlloch-Gonzalez et al., 2014a,b; Bahrami et al., 2017), which may improve access to sub-soil water. Under water-limited conditions, access to sub-soil water provides an important buffer to unreliable in-season rainfall. Furthermore, the conversion efficiency of sub-soil water into grain yield is higher than that of in-season rainfall because it is taken up late in the crop growth cycle, during the critical grain-filling period when roots reach deeper layers (Kirkegaard et al., 2007; Wasson et al., 2012). Therefore, grain yield may respond strongly to even small amounts of additional sub-soil water that becomes accessible post-anthesis, because its uptake coincides with grain development when crops are vulnerable to terminal drought (Passioura, 1983).

Superior leaf level transpiration efficiency has been suggested as a promising trait for adapting wheat to semi-arid environments (Condon et al., 2004). It is defined as photosynthetic net CO_2 assimilation (A_{net}) divided by stomatal conductance (g_s) and higher transpiration efficiency is accomplished by either increased A_{net} and/or decreased g_s (Farquhar and Richards, 1984; Condon et al., 2004). A higher transpiration efficiency trait has been successfully implemented in commercial wheat cultivars (Condon et al., 2004). Transpiration efficiency is positively correlated with [CO_2], because rising [CO_2] increases A_{net} and decreases g_s, which ultimately improves transpiration efficiency (Ainsworth and Long, 2005; Ainsworth and Rogers, 2007; Bernacchi et al., 2007; Tausz-Posch et al., 2013). Even though e[CO_2] increases transpiration efficiency generally in wheat, a cultivar with a superior transpiration efficiency trait was shown to take greater advantage of the 'CO_2 fertilisation effect' than a near-isogenic cultivar with low transpiration efficiency (Tausz-Posch et al., 2012, 2013; Christy et al., 2018). Selection of traits, such as superior transpiration efficiency or deeper rooting for breeding CO_2-responsive crops may allow crops to take advantage of increased water use efficiency (WUE), biomass and yields of increasing atmospheric [CO_2].

Meta-analyses reported mean grain yield increases for wheat under e[CO_2] from 15 to 17% compared to a[CO_2] (Ainsworth and Long, 2005; Wang et al., 2013; Kimball, 2016). Most of these results were derived from FACE experiments in high yielding, high rainfall or continuously irrigated wheat growing systems where mean yields are commonly > 5 t ha^{-1} (Fitzgerald et al., 2016). The magnitude of relative yield stimulation by e[CO_2] is frequently predicted to be greater under drier than well-watered conditions (Leakey et al., 2009; McGrath and Lobell, 2013; Kimball, 2016), but a recent meta-analysis could not confirm this for drought stressed compared to well-watered crops (van der Kooi et al., 2016). Similarly, a recent long term evaluation of FACE results that included rain-out shelters to manipulate precipitation in the world's most productive agro-ecosystems showed that more intense drought diminished grain yield stimulation by e[CO_2] to zero (Gray et al., 2016). In a water limited agro-ecosystem, Houshmandfar et al. (2016) reported inter-seasonal variability of the 'CO_2 fertilisation effect' depending on the amount of rainfall, whereby grain yield stimulation of wheat by e[CO_2] was greater in a high rainfall than in a low rainfall year. However, because direct experimental evidence with side-by-side well-watered and drought treatments have not yet been conducted in dryland agro-ecosystems, it is not clear to what extent such previous results are direct consequence of water supply or related to possible other aspects of season-by-season variability.

To close this gap in current knowledge and also investigate the potential differences in water acquisition strategies between wheat cultivars under e[CO_2], we selected two commercial wheat cultivars with common genetic background but with contrasting agronomic features (vigour, grain size and transpiration efficiency). The experiments were conducted in the Australian Grains FACE (AGFACE) facility in the southeast Australian wheat belt, representative of Mediterranean or semi-arid, water limited, low yielding wheat cropping systems (Fitzgerald et al., 2016). This facility allowed us to study crops in the field and assess changes due to increased atmospheric [CO_2]. We tested the following hypotheses:

- Elevated [CO_2] will stimulate root growth and this greater root growth will be associated with better access to soil water in deeper layers.
- The 'CO_2 fertilisation effect' will be greater under irrigated than under rainfed conditions.
- Increased canopy cover caused by stimulation of biomass growth may nullify the benefit from greater leaf level water use efficiency under e[CO_2].
- A cultivar with a superior transpiration efficiency trait will capitalise more from the 'CO_2 fertilisation effect'.

2. Materials and methods

2.1. Plant materials

Wheat (*Triticum aestivum* L.) cultivars Scout and Yitpi were selected for their similar genetic background but contrasting agronomic (early vigour, grain size, transpiration efficiency) features (Houshmandfar et al., 2016; Bahrami et al., 2017). Yitpi is adapted broadly to most soil types and rainfall regions in southeast Australia, while Scout is a high