Agronomic and physiological responses of wheat grown in split-column under elevated CO_2

Shihab Uddin[1 2], Markus Löw[1], Shahnaj Parvin[2 3], Glenn Fitzgerald[1 4], Sabine Tausz-Posch[1], Roger Armstrong[4], Garry O'Leary[4] and Michael Tausz[3]

[1] Faculty of Veterinary and Agricultural Sciences, The University of Melbourne, 4 Water Street, Creswick, VIC 3363, shihab.uddin@unimelb.edu.au.
[2] Department of Agronomy, Bangladesh Agricultural University, Mymensingh-2202, Bangladesh.
[3] School of Ecosystem and Forest Sciences, The University of Melbourne, 4 Water Street, Creswick, VIC 3363
[4] Agriculture Victoria Research, Department of Economic Development, Jobs, Transport and Resources, Private Bag 260, Horsham, VIC 3401

Abstract

Increasing atmospheric CO_2 concentration ([CO_2]) has profound effects on plant growth, yield and water use. Elevated atmospheric [CO_2] (e[CO_2]) increases above- and below ground biomass production of wheat. The increased root growth under e[CO_2] may allow the extraction of subsoil water, which is especially important in hot and dry Mediterranean conditions when the top soil dries off quickly. A glasshouse experiment was conducted with hydraulically separated top and bottom layered soil column to investigate the effect of soil drying at different depths on growth and gas exchange of wheat under e[CO_2]. Drought stress was induced either in the top or the bottom soil layer or both by withholding 33% of the irrigation. Drought treatments started at stem elongation. At the flowering growth stage, net photosynthetic assimilation rate (A_{net}) stomatal conductance (g_s), as well as above- and below ground biomass were measured.

In our study, A_{net} was higher and g_s was lower under e[CO_2] than a[CO_2], which resulted in greater intrinsic water use efficiency (iWUE). Above- and below ground biomass production of wheat under e[CO_2] were higher compared to a[CO_2]. Under e[CO_2], wheat produced more biomass than under a[CO_2] well-watered conditions even if either the top or bottom layer were subjected to drought treatment. In the DW treatment (D = drought, W = well-watered, where the first letter denotes the top layer and second letter denotes the bottom layer) vigorous root growth under e[CO_2] increased the accessibility to the moisture in the bottom layer and resulted in g_s similar to that of the WD. In addition, the reduction of above ground biomass in DW treatment was lower compared to DD conditions under e[CO_2]. Therefore higher below ground production of wheat under e[CO_2] could be able to ameliorate the potential effect of drought by improving accessibility of sub-soil water.

Keywords

Split-column system, biomass production, net assimilation rate, stomatal conductance.

Introduction

Atmospheric carbon dioxide concentration ([CO_2]) has been increasing since the industrial revolution (280 ppm) and recently exceeds 400 ppm. If CO_2 emissions continue to increase at the current rate, atmospheric [CO_2] is predicted to reach 550 ppm by 2050 and to exceed 700 ppm at the end of this century (IPCC 2013). This higher [CO_2] stimulates growth and yield of C3 crops through the so-called CO_2 fertilisation effect. Biomass accumulation in wheat at 550 ppm [CO_2] is about 16.6 to 44% higher compared to ambient CO_2 (a[CO_2]) (Ainsworth and Long 2005; Fitzgerald et al. 2016). With sufficient water supply at 700 ppm of [CO_2] biomass accumulation of wheat can be increased up to 89% (Wu et al. 2004). Apart from the above ground biomass, root growth is also influenced by elevated [CO_2] (e[CO_2]) (Madhu and Hatfield 2013). Roots of plants grown under e[CO_2] grow faster, which results in more numerous, thicker and longer roots (Chaudhuri et al. 1990). In low rainfall regions, such as under Mediterranean climate, top soil wettens (due to sudden precipitation) and dries quickly (due to hot air and high wind speed) compared to the sub-soil. In such environments, vigorous growth of wheat root under e[CO_2] may increase the accessibility of water from different depths. In addition, increases in net photosynthetic assimilation rate (A_{net}) and decreases in stomatal conductance (g_s) under e[CO_2] may lead to an enhanced intrinsic water use efficiency (iWUE) of plants (Tausz-Posch et al. 2013; Houshmandfar et al. 2016). Crops with higher (iWUE) under e[CO_2] would be able to translate the available water into more biomass than crops under a[CO_2], and this could ameliorate the drought effect to some extent. In this study we investigated whether wheat grown under e[CO_2] can maintain its normal agronomic and physiological performance when drought is imposed in different soil layers of the root system. In particular, we investigated whether e[CO_2] leads to changes in root biomass conducive to improving access to available water.

Methods

The experiment was conducted from June to December 2016 in a glasshouse facility of the University of Melbourne, located in Creswick, Victoria, Australia. Wheat (*Triticum aestivum* L. cv.Yitpi), was grown in a[CO_2] (~ 400 µmol mol^{-1}) and e[CO_2] (~ 700 µmol mol^{-1}) chambers. [CO_2] treatments and whole experimental units were swapped fortnightly between chambers. Specially designed segmented columns (Abdelhamid et al. 2011) were used to split the wheat root system into top and bottom layers. This allows controlling soil water independently at the two layers. Each soil column consisted of two polyvinylchloride (PVC) pipes of 15 cm diameter, 30 cm long, mounted on top of one another to give a soil column of 60 cm depth. A ~4 mm thick wax-coated layer (Figure 1a) prepared by melting paraffin wax pellets and petroleum jelly (1:4) was placed in between the two soil layers to separate them hydraulically. This wax layer allows root growth (Figure 1b) but prevents water movement between the layers (Abdelhamid et al. 2011). A plastic wire mesh was embedded into the wax layer to increase its strength. The columns were hand-watered twice per week to maintain the water content close to field capacity until the plants were at the stem elongation growth stage -DC31 (Zadoks et al. 1974). A 150 ml syringe was used to water the bottom layer through a previously inserted 5 mm diameter hose.

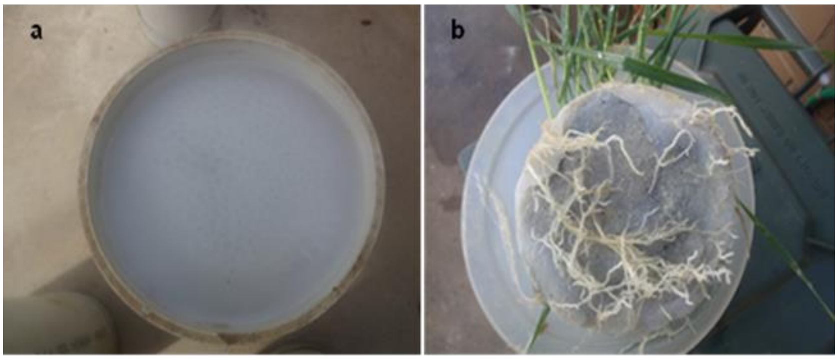

Figure 1. (a) Wax layer at the top of bottom soil layer to hydraulically separate it from the top layer. (b) Wheat roots penetrating the plastic wire mesh embedded in the wax layer during a preliminary trial.

After DC31 columns were randomly assigned to four groups (3 replicates in each group) and drought stress was induced by withholding 33% of the irrigation to some soil layers as follows: in the first group, both layers of each column were well-watered (WW). In the second group, drought was induced at the bottom layer only and the top remained well-watered (WD). In the third group, drought was induced at the top layer only (DW) and in the fourth group (DD) drought was induced at both layers. A_{net} and g_s of the flag leaf were measured at DC65 (anthesis) using an open path infrared gas analyser with a standard leaf chamber (clear-top with a maximum leaf area of 2 × 3 cm, illuminated by prevailing natural light, IRGA, Li-6400, Li-Cor, Lincoln, NE, USA). iWUE was calculated as A_{net} divided by g_s (Huang et al. 2017). Columns were harvested at DC65 and plants were oven dried for 72 h at 70˚C and their dry masses were recorded. Roots in each layer were collected from the soil by repeated washing and sieving with a 2 mm sieve and oven dried. Above- and below ground biomass of all the treatments were cross compared with a[CO_2] WW considering it as control treatment.

Results

[CO_2] significantly ($p<0.001$) affected A_{net} of wheat measured at DC65 (Figure 2a). Wheat grown under e[CO_2] had 19% higher A_{net} compared to a[CO_2]. Water treatments also showed a significant ($p<0.001$) effect on A_{net}. Values were 21 and 34% lower ($p<0.001$) for DW and DD respectively, compared to WW. Stomatal conductance of wheat decreased 14% ($p<0.01$) under e[CO_2] compared to a[CO_2] (Figure 2b). Application of drought stress in different layers also decreased g_s by 17 ($p<0.01$), 32 ($p<0.001$) and 48% ($p<0.001$) for WD, DW and DD respectively, compared to WW. Compared to WD decrease of g_s under e[CO_2] was not as prominent ($p=0.943$) for the DW treatment as DD ($p<0.01$). Higher A_{net} and lower g_s of wheat under e[CO_2] resulted in 33% greater ($p<0.001$) iWUE. At DC65 above- and below ground biomass production of wheat under e[CO_2] were increased ($p<0.001$) by 63 and 65% respectively, compared to a[CO_2]. Stimulation of root growth under e[CO_2] was higher (74%) in the top layer than bottom layer (38%, Table 1).

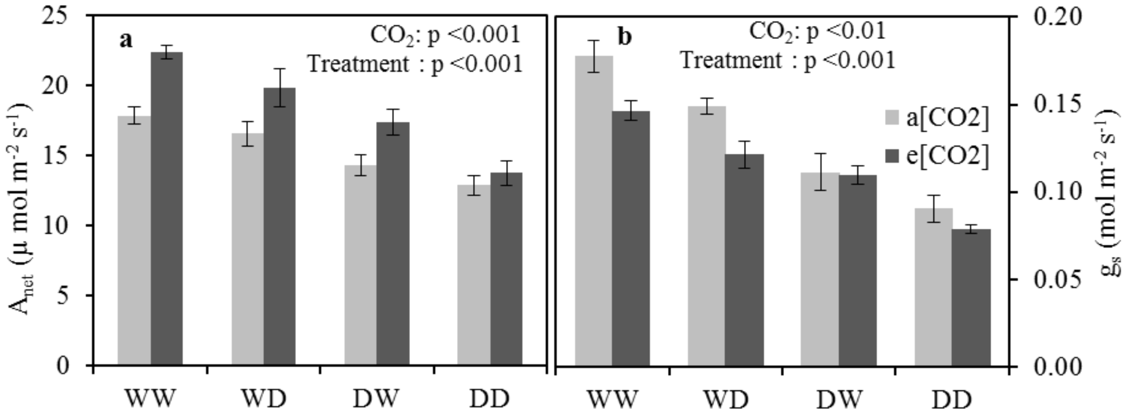

Figure 2. (a) Net photosynthetic assimilation rate (A_{net}) and (b) stomatal conductance (g_s) of wheat cv. Yitpi grown in different water regimes (see methods) measured at growth stage DC65. Plants grown under a[CO_2] and e[CO_2] were measured at 400 ppm (light grey bars) and 700 ppm (dark grey bars) of [CO_2], respectively. Each bar represents mean values and standard error of four samples.

In addition, water treatments had a strong effect ($p<0.001$) on above- and below ground biomass production of wheat. Interaction between CO_2 and water treatment is significant for above- ($p=0.061$) and below ground biomass ($p<0.05$). Induction of drought in either or both of the layers under a[CO_2] reduced the above- and below ground biomass production of wheat compared to a[CO_2] WW condition. Whereas under e[CO_2] above- and below ground biomass of all the treatments (except DD) were higher compared to a[CO_2] WW condition.

Table 1. Above (A) and below (B) ground biomass production of wheat cv. Yitpi at growth stage DC65. Below ground biomass (R) is the sum of root biomass in top and bottom layers. Values are presented as percent [%] relative to the a[CO_2] WW (actual values are given) conditions set as 100%. T is water treatment. Sample size n = 3.

Response parameters	WW			WD		DW		DD		P-value		
	aCO2		eCO2	aCO2	eCO2	aCO2	eCO2	aCO2	eCO2	CO2	T	CO2 xT
A biomass	22.8 (g)	100.0	166.5	88.3	142.2	75.8	128.5	62.3	96.0	***	***	.
B biomass	3.4 (g)	100.0	169.4	77.7	112.1	86.5	150.7	83.1	139.8	***	***	*
Top R	2.5 (g)	100.0	181.0	93.9	129.2	77.7	151.0	80.9	152.0	***	**	ns
Bottom R	0.9 (g)	100.0	137.6	33.5	65.5	110.4	149.7	89.3	106.6	***	***	ns

Significance levels are indicated by the P value: ns, P > 0.1; ., P < 0.1; *, P < 0.05; **, P < 0.01; ***, P < 0.001.

Discussion

The 19% increase of A_{net} under e[CO_2] as compared with a[CO_2] is in agreement with earlier glasshouse (Bourgault et al. 2013) and Free Air CO_2 Enrichment experiments (Wall et al. 2006; Tausz-Posch et al. 2012; Houshmandfar et al. 2016), where A_{net} of wheat was stimulated by 15 to 28% depending on growth conditions. Consistent with earlier findings, g_s in our study was lower under e[CO_2] resulting in greater iWUE.

Wheat grown under e[CO_2] benefited from the CO_2 fertilisation effect and produced more above ground biomass compared to a[CO_2]. Due to increased iWUE this advantage was maintained under e[CO_2] even after withholding water from different layers. Under e[CO_2] wheat receiving well-water in either of the layers also produced more above ground biomass compared to a[CO_2] WW. Elevated [CO_2] increased the below ground biomass production in both layers (except WD) but this increase was higher for the top layer than the bottom similar to the results reported by Madhu and Hatfield (2013). Under e[CO_2], withholding water from the top layer increased the root growth at the bottom layer (Table 1). Deeper roots of wheat are more efficient in extracting and supplying water (Gregory et al. 1978) and therefore wheat grown under e[CO_2] maintained similar g_s of WD treatment when water was withheld from the top layer (DW). Imposing drought in either layer under e[CO_2] did not substantially affect above ground biomass production.

This suggests that e[CO_2] could mitigate drought stress at the top soil if sufficient water is available in the sub-soil and vice-versa. Increased root growth under e[CO_2] might be able to maintain the physiological processes and biomass production of wheat by improving water accessibility from different soil layers.

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