Field Crops Research xxx (2016) xxx–xxx

Contents lists available at ScienceDirect

Field Crops Research

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

Yield, growth and grain nitrogen response to elevated CO_2 of five field pea (*Pisum sativum* L.) cultivars in a low rainfall environment

Maryse Bourgault[a], Jason Brand[b], Michael Tausz[c], Glenn J. Fitzgerald[b,*]

[a] *Faculty of Veterinary and Agricultural Sciences, The University of Melbourne, 4 Water St, Creswick, VIC 3363, Australia*
[b] *Agriculture Victoria, Grains Innovation Park, 110 Natimuk Rd, Horsham, VIC, 3401, Australia*
[c] *School of Ecosystem and Forest Sciences, The University of Melbourne, 4 Water St, Creswick, VIC, 3363, Australia*

ARTICLE INFO

Article history:
Received 27 January 2016
Received in revised form 7 April 2016
Accepted 8 April 2016
Available online xxx

Keywords:
Climate change adaptation
Genotypic variability
Grain protein
Elevated CO_2

ABSTRACT

Atmospheric CO_2 concentrations have been increasing from about 280 ppm to 400 ppm from the pre-industrial era until now. If intraspecific variability in the response to elevated CO_2 (e[CO_2]) can be found, then it should be possible to select for greater responsiveness in crop breeding programs. Our experiment aimed to determine the effects of e[CO_2] on the yield, biomass, leaf and grain nitrogen content of a range of field pea (*Pisum sativum* L.) cultivars subjected to rainfed and supplemental irrigation conditions. Plants were grown under Free Air CO_2 Enrichment (FACE) at the Australian Grains FACE facility in Horsham, Victoria, Australia under e[CO_2] (550 ppm) or at ambient CO_2 (390–400 ppm) under rainfed conditions and supplemental irrigation during three seasons, 2010–2012. Yields were significantly increased by 26% under e[CO_2] due to an increase in the number of pods per area. Grain size, the number of grains per pod and the harvest index remained unaffected by e[CO_2]. Grain nitrogen concentration ([N]) was slightly, but significantly, decreased by e[CO_2], but this was not consistent across cultivars under all water regimes. The dual purpose cultivar PBA Hayman consistently maintained grain [N] in response to e[CO_2] while the response in grain [N] in the cultivars Sturt and PBA Twilight depended on the irrigation treatment. While there was no evidence for consistent differences in seed yield response to e[CO_2] for the chosen cultivars, understanding the mechanisms for why some cultivars are able to maintain [N] under e[CO_2] would allow breeding programs to develop varieties resistant to decreases in [N] under e[CO_2].

1. Introduction

Atmospheric CO_2 concentrations ([CO_2]) have been increasing from about 280 ppm to 402 ppm from the pre-industrial era until now (December 2015; www.co2now.org). The majority of greenhouse gas emission scenarios considered by the Intergovernmental Panel on Climate Change (IPCC) estimate that atmospheric [CO_2] will continue to increase for at least another hundred years (Bernstein et al., 2007). This increase in the substrate of photosynthesis has direct implications for plant metabolism, such as increased carbon assimilation, growth, and yield (Ainsworth and Long, 2005; Ziska et al., 2012), but often also leads to decreased nutritional value in grains (Fernando et al., 2012; Myers et al., 2014).

The increase in atmospheric [CO_2] also decreases stomatal conductance and transpiration leading to gains in water use efficiency (Leakey et al., 2009). In general, this should lead to relatively greater yield responses to elevated CO_2 in dry areas (Leakey et al., 2009; Gifford, 1979). However, for dryland systems where crops are often subject to increasingly severe water stress conditions post flowering, greater early growth could lead to faster water depletion and more intense terminal stress, thus diminishing the advantage of elevated CO_2 (e[CO_2]). The Australian Grains Free Air CO_2 Enrichment (AGFACE) facility was established in 2007 to address such questions under realistic climatic and field conditions.

If intraspecific variability in the response to elevated CO_2 can be found in crops, then it should be possible to select for greater responsiveness in crop breeding, thus taking advantage of the opportunity presented by rising atmospheric [CO_2] (Ainsworth et al., 2008; Ziska et al., 2012; Tausz et al., 2013). There is growing evidence that, to date, plant breeding has not enabled greater responsiveness to e[CO_2], but might have inadvertently selected against it (Ainsworth et al., 2008). For example, in wheat, an older cultivar with low harvest index showed a greater yield response to e[CO_2] than the modern cultivar (Ziska, 2008). In rice, a modern cultivar selected for tiller uniformity in different environments showed a lower yield response than a cultivar that increased tiller-

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* Corresponding author.
E-mail address: glenn.fitzgerald@ecodev.vic.gov.au (G.J. Fitzgerald).

http://dx.doi.org/10.1016/j.fcr.2016.04.011

ing under e[CO_2] (Moya et al., 1998). In soybean, an ancestral line that branched more responded twice as much to e[CO_2] in grain yield than seven other cultivars tested (Ziska et al., 2001). These results suggest that the ability to increase vegetative biomass, often related to a low harvest index, is related to greater CO_2 responsiveness.

However, such results could be confounded by very different genetic backgrounds in the lines used, so that other (less visible) traits might contribute more to genotypic differences in response to e[CO_2]. Ainsworth et al. (2004) addressed this issue in an experiment with single gene substitutions performed in soybean, by comparing an indeterminate cultivar (which continues to grow after flowering) with its determinate mutant (growth is 80% complete at flowering). They demonstrated downward acclimation of photosynthesis under e[CO_2] in the determinate mutant, whereas the normal indeterminate line did not show such photosynthetic acclimation. They suggested that if there are more assimilates than can be used in growing tissues, so-called carbon sink limitation arises and this could then cause photosynthetic downward acclimation and thereby play a role in genetic differences in CO_2 responsiveness (Ainsworth et al., 2004). However, an indeterminate growth habit is not likely to be useful for all crops under large-scale mechanized agriculture if it leads to variable maturity in the crop. Similarly, increased branching or other traits that might lead to a large biomass accumulation but a low harvest index, may therefore still lead to lower yields under e[CO_2] than current cultivars, even if it is related to greater responsiveness to e[CO_2].

For legume crops used as dual-purpose of fodder and grain (such as some field pea cultivars) and grown as a rotation crop, a low harvest index or an indeterminate growth habit might not diminish the crop value and benefits in the agricultural production system. In addition, nitrogen fixation in legumes might be increased under e[CO_2] as the increased carbon available would help feed the nitrogen fixing symbiosis, and thus maintain or increase nitrogen uptake and utilisation by the plant (Rogers et al., 2009). As such, the soil fertility benefits from legumes in crop rotations could become greater with rising atmospheric CO_2 concentrations. In addition, legumes are not susceptible to the same decreases in leaf and grain protein levels that are observed in cereals under e[CO_2] (Jablonski et al., 2002; Myers et al., 2014). Finally, field peas are grown in a wide range of environments, and adapted to many soil types (Coyne et al., 2011), with a worldwide production of almost 11 million tonnes in 2013 (FAOSTAT, 2015).

Our experiment aimed to determine the effects of elevated CO_2 on the yield, biomass accumulation, leaf and grain nitrogen concentration ([N]) of five cultivars of field peas (*Pisum sativum* L.) subjected to rainfed and supplemental irrigation conditions. In this experiment, we were particularly interested in finding one or more cultivars that responded better to e[CO_2] than others to determine if traits identified in previous studies, such as low harvest index, indeterminacy, and sink strength influence the response to e[CO_2] in field peas.

2. Materials and methods

2.1. Experimental site and growing conditions

The Australian Grains Free Air CO_2 Enrichment (AGFACE) facility is located near Horsham, Victoria (36°45′07″S 142°06′52″E, 127 m above sea level) on a cracking clay (Vertosol) soil. A detailed description of the site and the CO_2 exposure equipment is given in Mollah et al. (2009). Briefly, the study site has approximately 35% clay content at the surface increasing to 60% at 1.4 m depth. Elevated CO_2 levels (target 550 mmol mol^{-1} air) were maintained during daylight hours by injecting pure CO_2 into the air on the upwind side from horizontal stainless-steel tubes positioned about 150 mm above the canopy and following the growth of the crop. Concentrations were maintained within 90% target (495–605 mmol mol^{-1} air) for 93–98% of the time.

The region has a Mediterranean climate, but with drier and cooler winters. The average rainfall based on the last 15 years is 269 mm during the winter growing season (from May to November inclusive); average maximum and minimum temperatures are 17.6 °C and 5.7 °C respectively (Bureau of Meteorology, 2014). Maximum and minimum temperatures as well as rainfall data during the 2010–2012 growing seasons were recorded by an on-site weather station (MEA Premium Weather Station 103, Measurement Engineering Australia, Magill, SA, Australia; Fig. 1). Plots were sown on 26 May 2010, 26 May 2011 and 31 May 2012. Superphosphate was drilled with the seed at sowing at 9 kg P ha^{-1} and 11 kg S ha^{-1} each year. No N fertilizer was added. Initial nitrate levels prior to sowing were 280 kg ha^{-1} in 2010, 125 kg ha^{-1} in 2011, and 80 kg ha^{-1} in 2012. Plots were treated with pre-emergence herbicides (trifluralin, isoxaflutole, and glyphosate) prior to sowing and with haloxyfob approximately 4 weeks after emergence. In 2011, insecticides (methidathion and alpha-cypermethrin) were also used to control aphids.

Supplemental irrigation was applied with sprinklers. A plastic barrier was dug in the middle of the rings to a depth of 1 m to prevent water movement from the supplemental irrigation side to the rainfed side. Supplemental irrigation plots received an additional 80 mm of water in 2010, 100 mm in 2011 and 120 mm in 2012 as indicated in Fig. 1.

2.2. Experimental design

Within the site, field peas were grown in eight octagonal ‘rings’ in a complete randomised block design with four blocks. Within each block, there were one ambient (a[CO_2] ~ 390–400 mmol mol^{-1} air) and one elevated (e[CO_2] ~ 550 mmol mol^{-1} air) ring. Peas were grown in rotation with wheat. Rings were 16 m in diameter, and split for a plus/minus supplemental irrigation treatment described above. Within each rings, cultivars of field peas were grown in sub-plots (4 by 1.4 m).

2.3. Plant material

Five field pea cultivars were selected for their contrasting agronomic characteristics such as growth habit, seed size, time to flowering, etc. In particular, the cultivar PBA Hayman is a dual purpose, high biomass, small seeded cultivar (with low grain harvest index) that represented an interesting contrast for evaluating potential sink limitations. Other varieties included Bohatyr, a historical variety in the Australian breeding program, Kaspa and Sturt, both industry standards for Australian dun type (tan seed coat) and white type (white seed coat) grains respectively, as well as a high-yielding, early flowering Kaspa-type modern cultivar PBA Twilight (released by Pulse Breeding Australia in 2010) well adapted to low rainfall environments. Seeds were inoculated with the appropriate peat-based rhizobial inoculum (Inoculaid, Group E, Becker Underwood (now BASF), Southbank, VIC, Australia) as per industry practice. A few plants were sampled at the vegetative stage to verify the levels of root nodulation and these were found adequate in all three years.

2.4. Measurements

There were three destructive above-ground biomass samplings: at the vegetative growth stage (GS) with 7 nodes (GS107), at the first open flower (GS203), and at physiological maturity (GS210) accord-

Please cite this article in press as: Bourgault, M., et al., Yield, growth and grain nitrogen response to elevated CO_2 of five field pea (*Pisum sativum* L.) cultivars in a low rainfall environment. Field Crops Res. (2016), http://dx.doi.org/10.1016/j.fcr.2016.04.011