Global Change Biology

Global Change Biology (2015) **21**, 2670–2686, doi: 10.1111/gcb.12830

Response of wheat growth, grain yield and water use to elevated CO_2 under a Free-Air CO_2 Enrichment (FACE) experiment and modelling in a semi-arid environment

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Abstract

The response of wheat crops to elevated CO_2 (eCO_2) was measured and modelled with the Australian Grains Free-Air CO_2 Enrichment experiment, located at Horsham, Australia. Treatments included CO_2 by water, N and temperature. The location represents a semi-arid environment with a seasonal VPD of around 0.5 kPa. Over 3 years, the observed mean biomass at anthesis and grain yield ranged from 4200 to 10 200 kg ha^{-1} and 1600 to 3900 kg ha^{-1}, respectively, over various sowing times and irrigation regimes. The mean observed response to daytime eCO_2 (from 365 to 550 μmol mol^{-1} CO_2) was relatively consistent for biomass at stem elongation and at anthesis and LAI at anthesis and grain yield with 21%, 23%, 21% and 26%, respectively. Seasonal water use was decreased from 320 to 301 mm ($P = 0.10$) by eCO_2, increasing water use efficiency for biomass and yield, 36% and 31%, respectively. The performance of six models (APSIM-Wheat, APSIM-Nwheat, CAT-Wheat, CROPSYST, OLEARY-CONNOR and SALUS) in simulating crop responses to eCO_2 was similar and within or close to the experimental error for accumulated biomass, yield and water use response, despite some variations in early growth and LAI. The primary mechanism of biomass accumulation via radiation use efficiency (RUE) or transpiration efficiency (TE) was not critical to define the overall response to eCO_2. However, under irrigation, the effect of late sowing on response to eCO_2 to biomass accumulation at DC65 was substantial in the observed data (~40%), but the simulated response was smaller, ranging from 17% to 28%. Simulated response from all six models under no water or nitrogen stress showed similar response to eCO_2 under irrigation, but the differences compared to the dryland treatment were small. Further experimental work on the interactive effects of eCO_2, water and temperature is required to resolve these model discrepancies.

Keywords: climate change, elevated CO_2, modelling, radiation use efficiency, transpiration efficiency

Received 27 October 2014 and accepted 28 November 2014

Introduction

Crop simulation models are robust tools to extrapolate likely behaviour under circumstances that are difficult or impossible to experimentally test in the field, such as a changing climate. In agriculture, many studies have employed crop modelling with various future climatic scenarios (e.g. Hoogenboom *et al.*, 1995; Boote *et al.*, 1996; Semenov *et al.*, 1996; Howden & O'Leary, 1997; Amthor, 2001; Howden *et al.*, 2003; Asseng *et al.*, 2004, 2013a; Power *et al.*, 2004; Ludwig & Asseng, 2006; Anwar *et al.*, 2007; Lobell & Ortiz-Monasterio, 2007; O'Leary *et al.*, 2011). The range of crop models available for use in such studies is large because of differences in complexity and function. Models that include some realistic simulation of the effects of elevated atmospheric CO_2 (eCO_2), temperature and water stress on crop growth and development are considered a prerequisite in terms of model function for future climate change studies. Other subcomponents

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involving mineral uptake may also be critical for some applications (e.g. nitrogen in soil C sequestration studies).

Comparison against measured field data is fundamental to improving crop models (Boote *et al*., 1996). Such improvement offers assurance that subsequent simulation scenario studies are the best available. This study tests the performance of six wheat crop models against 3 years of measured crop growth and water use data from the Australian Grains Free-Air CO_2 Enrichment (AGFACE) experiment, located in a semi-arid (seasonal VPD ranging from 0.2 to 1.1 kPa with a mean around 0.5 kPa) environment in southern Australia. Previous studies from other environments that have compared simulations with FACE results have reported response to eCO_2 to be close to the observed response in biomass, yield and water use (Tubiello *et al*., 1999; Jamieson *et al*., 2000; Asseng *et al*., 2004; Ko *et al*., 2010). Seasonal growth responses to eCO_2 for wheat have been in the order of 5–40% (mean ~18%) (Ainsworth & Long, 2005; Sun *et al*., 2009) depending on other growth limiting factors. In general, C_3 cereal crops under water stress responded proportionally more to eCO_2 (~22%) than unstressed crops (~16%), showing the importance of water supply (Kimball, 2011). The lack of observed and consistent high responses (>25%) in field crops is puzzling (Long *et al*., 2006), but one reason proposed might be artefacts of the experimental environment (Long *et al*., 2006; Bunce, 2013). Another aspect needing consideration is the relative dryness of the atmosphere during the season that will affect transpiration efficiency. Previous FACE experiments are not considered representative of semi-arid regions because their annual potential evapotranspiration/rainfall (PET/R) ratio is either less than or close to unity or very high. The PET/R ratio at the AGFACE site in southern Australia is around 3 compared to around 10 in Arizona. Similarly, from a seasonal perspective and despite crops being irrigated in Arizona, the seasonal VPD also remains about three times the Horsham AGFACE site (1.4 kPa cf. 0.5 kPa). Because of the intermediate dryness of the Australian AGFACE experiment and the present view that the relative response to eCO_2 is much higher under conditions of water stress (Leakey *et al*., 2009; Sun *et al*., 2009; Kimball, 2011; Dias De Oliveira *et al*., 2012), this study offers a new opportunity to test the performance of a range of crop models under eCO_2 in a new unirrigated environment. In addition, to testing models in terms of the accumulation of crop biomass, grain yield and water use and subsequent water use efficiency (WUE) in response to eCO_2, we explore whether model components used to calculate these responses need improvement.

Materials and methods

FACE experiment

The AGFACE experiment at Horsham, Australia (36°45′S, 142°07′E, 128 m elev.) (Mollah *et al*., 2009), was used to measure the growth, yield and water use of wheat under various controlled conditions. The experiment included multiple cultivars, but we restricted our study to one popular local cultivar (cv. Yitpi) that was grown under two water regimes (rain-fed and supplemental irrigation), two nitrogen fertilisation regimes (0 and 53–138 kg N ha^{-1}) and two sowing dates (to create two growing season temperature environments) for both daytime ambient (365 μmol mol^{-1}) and elevated (550 μmol mol^{-1}) CO_2 atmospheric conditions. Injection of CO_2 was controlled by wind speed and direction whereby it was injected approximately 150 mm above the crop canopy upwind when wind speed was between 0.3 and 10 m s^{-1} between 2 h after sunrise and 2 h before sunset. The primary design criteria of daytime 550 μmol mol^{-1} CO_2 were achieved 86–94% of time ranging from median 495–605 μmol mol^{-1} (within ±10%) in the centre of 12-m (2007 and 2008) and 16-m (2009) diameter octagonal rings (Mollah *et al*., 2009). Within 1-m downwind of the rings, CO_2 levels ranged from 500 to 1700 μmol mol^{-1}. The agronomic design with the two times of sowing (TOS) over 3 years (2007–2009) comprised a complete randomised block experimental design of four replicates. This equates to 48 crops over the 3 years ($2CO_2$ × 2TOS × 2 irrigation × 2 nitrogen × 3 years). In 2007, plots were split for TOS, where half of each plot was sown to each TOS. In subsequent years, plots were split for irrigation, in which a 0.8-m-deep buried plastic barrier separated the two rain-fed and supplemental irrigated half-plots. Each replication was one 'bay' with two aCO_2 experimental areas and two eCO_2 rings per bay. Sowing time alters biomass partitioning including yield as crops are forced to develop into warmer, less efficient conditions approaching summer (O'Leary *et al*., 1985).

Gravimetric soil water content was measured at sowing and harvest using a hydraulically operated soil sampler where sampling was in increments of 0–0.1, 0.1–0.2 and 0.2 m increments thereafter to 2 m from one core per plot (42 mm diameter). Soil mineral nitrogen (NO_3 and NH_4) was also measured from an additional core taken close to the sampling time of the soil water measurements. Site bulk density was measured from 70 mm diameter × 75 mm deep sampling rings from each octagonal area. We defined seasonal crop water use as the change in soil water content (mm) during the growing season (sowing to harvest) plus rainfall and irrigation between sowing and harvest. This therefore includes losses from soil evaporation, crop transpiration, deep drainage and run-off, with the latter two considered insignificant from an agronomic perspective at this location (i.e. within the error of measurement, after O'Leary & Connor, 1997). For example, seasonal drainage is known to be around 20 mm with typical errors of water use for these soils around 50 mm. We defined WUE as grain yield divided by water used (soil evaporation plus transpiration plus deep drainage plus run-off). Large soil mineral nitrogen content (~300 kg N ha^{-1}) at the site precluded any significant effects of applied N, so soil analyses were pooled across the N treatments.

There were 12 subplots per ring in 2007 and 2008, each 1.4 by 4 m. There were 24 subplots in 2009, the additional plots containing cultivars not analysed here. Each subplot was 8 plant rows wide. Row spacing was 0.217 m in 2007 and 0.19 m in 2008 and 2009. Within each subplot, there were three destructive harvests; at maximum tillering/initiation of stem elongation (DC31), anthesis (DC65) and maturity (DC90) (Zadoks *et al.*, 1974). The centre rows were sampled, leaving the outer rows on each side as buffers. In 2007, destructive samples for the DC31 and DC65 samplings were randomly distributed within each subplot as 0.5-m and 1.0-m row segments at maturity (DC90). Beginning in 2008, all samples were collected as quadrats of four rows by 0.5 m (DC31 and DC65) and four rows by 1-m areas at DC90. The DC31 and DC65 samples were collected within a reserved area termed 'growth' subplot, and the DC90 sample was collected from a designated area termed 'maturity' subplot. Biomass samples were oven-dried at 70 °C, and leaf and stem area measurements were made from using an electronic planimeter from subsamples comprising approximately 25% of the collected fresh biomass. Mean sowing plant density measured by plant counts about 3 weeks after the emergence was 120 plants m^{-2} and ranged from 60 to 175 plants m^{-2}. Agronomic management at both sites was according to local practices, including spraying fungicides and herbicides, as needed. Granular phosphorus and sulphur (as 'superphosphate') were incorporated into the soil at sowing at rates between 7–9 kg P ha^{-1} and 8–11 kg S ha^{-1} depending on year.

The experimental site had previously been laser-graded to assist in flood irrigation and had been irrigated with sewage water for over 20 years to assist bulking seed in various plant breeding programmes. This history resulted in extreme variability of critical soil properties at the site, and as a consequence for modelling the response to eCO_2, we pooled the initial soil water content at sowing across the ambient and eCO_2 treatments to be consistent with single soil type parameters for the site (Table S1). This option, as opposed to modelling each ring, provided an effective and simple solution to compare the experimental data with all its site variance, to the modelled data.

Simulation models

Six crop simulation models were tested against the AGFACE data (Table 1). They represent two primary groups of popular models dealing with the effects of eCO_2 and final crop yield by the primary method of daily biomass accumulation: (1) those that primarily use radiation use efficiency (RUE) calculations and (2) those that primarily use transpiration efficiency (TE) calculations. Both approaches are approximations to the real photosynthetic mechanisms, but their utility across diverse environments is well known. Each model was run by the respective modelling groups/authors without adjusting parameters to fit the data apart from the data to define the cultivar phenology. In addition to the selected models, we analysed the median of all the models as an ensemble to explore whether an ensemble result was more accurate than any individual model.

The experimental site is defined by its soil type (Table S1) and daily weather conditions that were measured mostly on site. When on-site measurements were unavailable, locally calibrated calculated values for temperature were made from two nearby meteorological stations approximately 10 km away. Other generic site parameters needed by some of the models are listed in Table S2.

Simulation models – the APSIM-Wheat model. The Agricultural Production Systems Simulator (APSIM) is a farming systems simulation framework that has been designed to allow evaluation of farm decision-making in the face of climatic risk, climate change or changes in policy (Keating *et al.*, 2003). The Wheat model within APSIM has been broadly tested across Australia and internationally in a range of experimental (Holzworth *et al.*, 2011; Zhang *et al.*, 2012) and farm (Hochman *et al.*, 2009; Carberry *et al.*, 2013) conditions. Testing of simulated responses to increasing atmospheric CO_2 has been published for predecessors of the current APSIM-Wheat model (Reyenga *et al.*, 1999; Asseng *et al.*, 2004). Increased atmospheric CO_2 concentration impacts upon simulated crop growth and resource use via changes to RUE, TE and the critical nitrogen concentration (CNC) for crop growth (Reyenga *et al.*, 1999). To capture CO_2 effects on RUE, and interactions with temperature, APSIM-Wheat (v 7.4) scales RUE using the ratio (ϕ_p) of the

Table 1 List of selected models to compare against measured FACE experiment showing the primary biomass accumulation method – radiation use efficiency (RUE) or transpiration efficiency (TE)

Model name	Biomass method	Source	Example climate change analyses
APSIM-Wheat v7.4	RUE	McCown *et al.* (1996)	Ludwig & Asseng (2006) and Asseng *et al.* (2013a)
APSIM-Nwheat v1.55	RUE	Asseng *et al.* (2004)	Asseng *et al.* (2011, 2013a,b)
CAT-Wheat v8.4.5	RUE	Weeks *et al.* (2008) and Christy *et al.* (2013)	O'Leary *et al.* (2011)
CROPSYST v 4.15.24	TE	Stöckle & Nelson (2001)	Anwar *et al.* (2007) and Asseng *et al.* (2013a)
OLEARY-CONNOR v7	TE	O'Leary & Connor (1996a,b)	Howden & O'Leary (1997) and Asseng *et al.* (2013a)
SALUS v1	RUE	Basso *et al.* (2010)	Asseng *et al.* (2013a) and Bassu *et al.* (2014)

These models have all been used in various climate change applications.

light-limited photosynthetic response at the enhanced CO_2 level to that at 350 μmol mol^{-1}:

$$\phi_p = \frac{(Co_2 - \Gamma)(350 + 2\Gamma)}{(Co_2 + 2\Gamma)(350 - \Gamma)}, \tag{1}$$

where the temperature-dependent CO_2 compensation point (Γ) is calculated as:

$$\Gamma = \frac{(163 - t)}{(5 - 0.1t)}, \tag{2}$$

where t is the temperature (°C). The responses of transpiration efficiency (g m^{-2} mm^{-1}) and leaf CNC (%) to increased CO_2 are assumed to be linear with changes of +37% and −7%, respectively, for a doubling of CO_2 concentration to 700 μmol mol^{-1} (Fig. 1). Actual transpiration is indirectly reduced under eCO_2 through the gain in TE. Table S3 lists the salient cultivar parameters for APSIM-Wheat used to simulate the AGFACE experiments.

Simulation models – the APSIM-Nwheat model. The APSIM-Nwheat model (v 1.55) was developed from an earlier version of APSIM. This model has been tested and applied in Australia (Asseng *et al.*, 1998a,b, 2003; Asseng & Van Herwaarden, 2003) and many other growing environments in the world (Asseng *et al.*, 2000, 2002, 2003, 2004; Wessolek & Asseng, 2006; Bassu *et al.*, 2009). It uses the same CO_2 functions by Reyenga *et al.* (1999) as described above for APSIM v7.4 but has accelerated senescence functions and a physiological approach for water-soluble carbohydrate remobilisation, which is critical for terminal drought situations (Asseng & Van Herwaarden, 2003). Table S4 lists the salient cultivar parameters for APSIM-Nwheat used to simulate the AGFACE experiments.

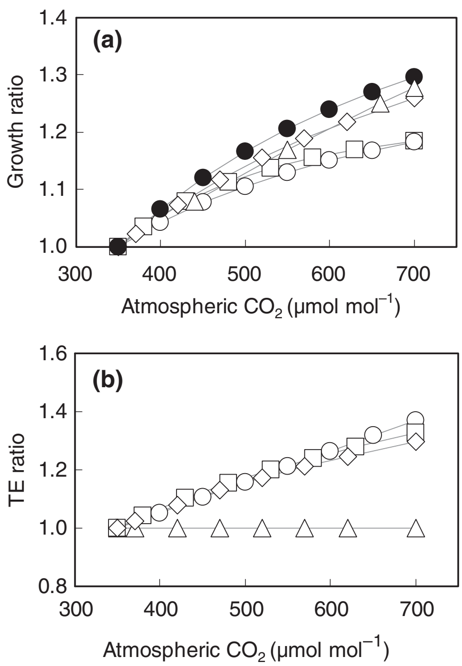

Fig. 1 Correction factors applied to radiation use efficiency (growth ratio, a) for APSIM-Wheat and APSIM-Nwheat at 15 °C (○) and 30 °C (●) and OLEARY-CONNOR & CAT-Wheat (◇), CROPSYST (□) and SALUS (Δ) and transpiration efficiency (TE ratio, b) for the APSIM-Wheat and APSIM-Nwheat (○), CROPSYST (□) and OLEARY-CONNOR (◇) and CAT-Wheat & SALUS (Δ) models. The factors for atmospheric CO_2 of 550 μmol mol^{-1} vary slightly between the models. Note: the various models apply RUE and TE in different ways, and as TE is related to RUE by growth, both correction factors are applied in all these models such that double accounting is avoided (Table 1).

Simulation models – the CAT-Wheat model. CAT-Wheat model (v 8.4.5) (Weeks *et al.*, 2008) was selected as a simple model with respect to biomass accumulation (see below) but has high utility in spatial analyses across landscapes (O'Leary *et al.*, 2011; Christy *et al.*, 2013). It includes modules for phenological development, crop growth and yield, together with dynamics of water and nitrogen in the crop and soil. Photosynthetic area (includes leaf and stem) is determined by above-ground biomass. The model was based on a generic annual crop model to enable the simulation of any crop and is based on extensively used contemporary models (Williams *et al.*, 1989; Littleboy *et al.*, 1992). Biomass accumulation is determined from intercepted radiation, RUE, water and nutrient stress factors and a photoperiod factor (Williams *et al.*, 1989). The minimum value of these factors (i.e. the most limiting) is always used to reduce RUE. The fertilisation effect of eCO_2 is achieved by multiplication of RUE by a factor (RUECC) from (Stöckle *et al.*, 1992).

$$\begin{aligned} \mathrm{RUECC} = &(-1.7/(350 \times (1 - 1.7)) \times CO_2 \times 1.7)/ \\ &(-1.7/(350 \times (1 - 1.7)) \times CO_2 + 1.7), \end{aligned} \tag{3}$$

where CO_2 is the atmospheric CO_2 concentration (μmol mol^{-1}) such that RUECC = 1, 1.18 and 1.23 at 350, 550 and 650 μmol mol^{-1}, respectively (Fig. 1). Potential or actual crop transpiration is not reduced by eCO_2. Grain yield is determined using the harvest index approach that is modified by water and nitrogen stress. Components of the water balance include crop interception, soil evaporation, transpiration, run-off and drainage that provide daily soil water content. Table S5 lists the salient cultivar parameters for CAT-Wheat used to simulate the AGFACE experiments.

Simulation models – the CROPSYST model. The CROPSYST model (Stöckle *et al.*, 1994, 2003) is a popular systems model that has been well tested and used in USA and Mediterranean environments in Europe and the Middle East (Stöckle *et al.*, 1994, 1997; Pala *et al.*, 1996; Donatelli *et al.*, 1997; Stöckle & Debaeke, 1997; Pannkuk *et al.*, 1998; Stöckle & Jara, 1998; Ferrer-Alegre & Stöckle, 1999; Tubiello *et al.*, 2000; Sadras, 2002; Díaz-Ambrona *et al.*, 2005).

We used CROPSYST (v 4.18.27) which calculates dry matter accumulation as a function of daily intercepted solar radiation and daily crop transpiration, using constant coefficients of RUE (Monteith 1981), and variable coefficients of TE (Kremer *et al.*, 2008). The minimum of the two calculations each day of the growing season determines the dry matter production for the day. For unstressed wheat, a ratio (r) of 1.134 for a CO_2

change between 360 and 560 μmol mol^{-1} was used in this study. The value of this ratio as a function of CO_2 is given by a nonrectangular hyperbola (NRH) fitted to three points: $r = 1$ at $CO_2 = 360$ μmol mol^{-1}, $r = 1.134$ at $CO_2 = 560$ μmol mol^{-1} and $r = 0.95 \times$ NRH maximum ratio at $CO_2 = 900$ μmol mol^{-1} (CO_2 approaching saturation for C3 species). The ratio for any given CO_2 of interest is applied directly to RUE. In the case of TE, the effect of CO_2 on canopy conductance for water vapour (and therefore on crop transpiration) is accounted for following Allen (1990). Thus, both TE (increase) and crop transpiration (reduction) are adjusted to obtain the expected value of r. Table S6 lists the salient cultivar parameters for CROPSYST used to simulate the AGFACE experiments.

Simulation models – the OLEARY-CONNOR wheat model. The OLEARY-CONNOR (v7) model calculates biomass primarily by transpiration and transpiration efficiency (TE, kg ha^{-1} mm^{-1}), which is modified by temperature and nitrogen functions via an algebraic equivalent radiation use efficiency (RUE, g MJ^{-1}) (O'Leary & Connor, 1996a,b). It has been successfully tested and used in southern Australia in unirrigated conditions (O'Leary & Connor, 1998; Latta & O'Leary, 2003). The fertilisation effect of eCO_2 is achieved by multiplication of TE by a factor (TECC) that is derived from a RUE factor (RUECC) (Stöckle *et al.*, 1992; Stöckle & Nelson, 2001) with simplifying assumptions of aerodynamic resistance of crop canopy 300 s m^{-1} and canopy resistance of 36 s m^{-1} at 350 μmol mol^{-1} CO_2:

$$\mathrm{TECC} = \mathrm{RUECC}/\{[\delta + (\gamma \times (36+300)/300)]/[\delta + \gamma \times ((36 \times \mathrm{CO_2})/(350 \times \mathrm{RUECC}) + 300)/300]\}, \tag{4}$$

$$\mathrm{RUECC} = (-1.7/(350 \times (1-1.7)) \times \mathrm{CO_2} \times 1.7)/(-1.7/(350 \times (1-1.7)) \times \mathrm{CO_2} + 1.7), \tag{5}$$

where CO_2 is the atmospheric CO_2 concentration (μmol mol^{-1}) and δ (kPa °C^{-1}) and γ (kPa °C^{-1}) are the psychrometric constant and slope of saturated vapour pressure–temperature curve, respectively, such that RUECC = 1, 1.18 and 1.23 at 350, 550 and 650 μmol mol^{-1}, respectively. Potential crop transpiration is reduced by eCO_2 in proportion to the ratio of RUECC/TECC that provides a TECC of 1.30 at 700 μmol mol^{-1} CO_2 (Fig. 1). The RUE correction is almost identical to APSIM at 25 °C, but no temperature correction is applied (Fig. 1). Photosynthetic area (includes leaf and stem) is determined by above-ground biomass and its nitrogen concentration. Table S7 lists the salient cultivar parameters for OLEARY-CONNOR used to simulate the AGFACE experiments.

Simulation models – the SALUS model. The Systems Approach to Land Use Sustainability (SALUS) (Basso *et al.*, 2006, 2010) is an evolution of the CERES models (Ritchie *et al.*, 1988). When perceived improvements in CERES models became available after 2002, those were included in SALUS. The primary purpose of SALUS is to do long-term simulation cropping systems with emphasis on simulating yields along with environmental consequences of various the management strategies. SALUS has been tested for crop yield (e.g. Basso *et al.*, 2007, 2009, 2010, 2012; Asseng *et al.*, 2013a; Rosenzweig *et al.*, 2013; Dzotsi *et al.*, 2013), soil C dynamics (e.g. Senthilkumar *et al.*, 2009), plant N uptake and phenology (e.g. Basso *et al.*, 2010, 2011a), nitrate leaching (e.g. Giola *et al.*, 2012; Syswerda *et al.*, 2012), and tillage effects on soil properties (Basso *et al.*, 2006, 2011b). Growth is primarily determined by the RUE approach and is then reduced based on the transpiration and nitrogen limitations. The effects of eCO_2 are simulated by adjusting RUE as a function of CO_2 with a corresponding increase in the amount of transpiration use efficiency (Fig. 1). The effect of temperature on RUE and transpiration is made by applying a multiplier to both whereby the factor varies nonlinearly from 1.25 to unity below or above the optimum temperature for photosynthesis. The advantage of this model is its utility in soil management across diverse landscapes. Table S8 lists the salient cultivar parameters for SALUS used to simulate the AGFACE experiments.

Statistical analyses

Comparisons of simulated data against the observed data were made by simple regression of treatment means (arithmetic) of the form $y = a + bx$ where y is the observed and x is the simulated data ($n = 48$). The regression coefficients (a, b), their standard errors (SE), 95% lower and upper confidence intervals of b, residual degrees of freedom (df), coefficient of determination (R^2), significance of regression (P) and root mean square error (RMSE) are reported and listed in Table S9.

The response of a number of variables to eCO_2 was analysed by simple regression of treatment means (arithmetic) of the eCO_2 treatments against the ambient treatments, forced through zero. The classical method of determining the response to eCO_2 by dividing the elevated measurement (e.g. grain yield) by the ambient measurement is, by default, a fit forced through the origin with the slope (eCO_2/aCO_2 ratio) above unity indicating positive response to the level of CO_2 elevation. One of the problems of measuring response to eCO_2 for each treatment is the problem of increasing or decreasing response as the absolute growth or yield approaches zero (Amthor, 2001). The method of fitting a single slope that we employed weights the response against such sensitivity because the mean slope is forced through zero over the wide range of absolute growth or yield. This relative approach provided a robust and simple way to reduce experimental noise and obtain gross estimates of the effects of eCO_2 on observed and simulated yield, water use and WUE rather than by differences through classical ANOVAs. This method then allows both graphical and statistical comparison of the experimental data against the simulated data in an efficient way. For this comparison, the resultant degrees of freedom are halved ($n = 24$).

Results

FACE experiment

FACE experiment – wheat response to elevated CO_2. The AGFACE field data have shown that early growth, yield and WUE of wheat increased under eCO_2. At stem elongation (DC31) and anthesis (DC65), biomass under ambient CO_2 was 1200 and 6200 kg ha^{-1}, respectively, but increased by 21% and 23% under eCO_2 (Table 2). There was also a corresponding increase in crop leaf area index of 21% and photosynthetic area index of 25% due to eCO_2. The increases in vegetative growth under eCO_2 resulted in a 26% increase in grain yield. For these crops, the WUE of producing biomass increased 36% (21.3–28.9 kg ha^{-1} mm^{-1}) and for grain increased 31% (7.2–9.6 kg ha^{-1} mm^{-1}) under eCO_2 with a corresponding small reduction (6%, $P = 0.1$) in total accumulated water use from 320 to 301 mm during the growing season.

FACE experiment – wheat response to water availability. Early growth of wheat up to stem elongation was not affected by irrigation, but by anthesis, supplemental irrigation increased biomass and LAI by 10% and 37%, respectively, compared with the rain-fed crops (Table 3) showing the more sensitive nature of LAI to water stress. This translated through to a 19% increase in yield and 17% greater water use under irrigation treatments. There was no effect of water regime on wheat WUE for biomass or grain.

FACE experiment – wheat response to time of sowing. Early growth up to stem elongation was greater (50%) with late sowing, but this pattern reversed at anthesis where late sowing caused a 42% and 60% reduction in biomass and leaf area compared with early-sown wheat (Table 3). This translated to a 43% reduction in yield where crops were sown late due to crop exposure to increased temperature. Additionally, late sowing reduced water use and WUE of grain production by 10% and 37%, respectively, compared with early-sown crops.

FACE experiment – combined effect of elevated CO_2, water and time of sowing. For early growth of wheat up to stem elongation, the increase in growth (relative and absolute) due to eCO_2 was greatest (30%) for crops sown late under rain-fed conditions (Table 3). At anthesis, this pattern changed to the greatest growth response due to eCO_2. Late-sown crops under supplemental irrigation had the greatest absolute increases in growth due to eCO_2 (40%) (Table 4). For grain yield, both least and greatest response to eCO_2 occurred for rain-fed and irrigated crops, respectively, when crops were late sown, although the greatest absolute increases in yield due to eCO_2 occurred in combination when wheat was sown early under supplemental irrigation. The WUE of grain production was reduced under eCO_2 (−50%) when crops were sown late under rain-fed condition; however, when these crops were irrigated, there was a 34% increase in WUE due to eCO_2. Increases in WUE due to eCO_2 of early-sown wheat were 41% and 27% for rain-fed and irrigated crops, respectively. There were no effects of applied N on growth due to the high levels of soil mineral nitrogen content at the site (see Materials and methods).

The timing of emergence, anthesis and maturity were not affected by eCO_2 (Table 5) despite the expectation of accelerated development through raised canopy temperatures under eCO_2 (Kimball, 2011). In simulating phenological development, there were, however, larger than expected unexplained errors (6−8 days) in all of the models in simulating time to anthesis and maturity (Table 5). Despite this variation in phenological performance, all the models were able to simulate the response of biomass, yield and water use to eCO_2.

Table 2 Observed gross response to elevated carbon dioxide (b) of wheat (cv. Yitpi) biomass at stem elongation (DC31) and anthesis (DC65), leaf area index at DC65 (LAI65), leaf + stem area index at DC65 (PAI65), yield, water use and water use efficiency for biomass (WUEb) and grain (WUEg) under FACE (free-air carbon dioxide enrichment) conditions

	Ambient CO_2 (365 μmol mol^{-1})	Elevated CO_2 (550 μmol mol^{-1})	b	SE	Low b	High b	R^2
DC31 (kg ha^{-1})	1248 (91)	1504 (122)	1.209	0.0357	1.135	1.283	0.85
DC65 (kg ha^{-1})	6169 (405)	7762 (452)	1.232	0.0391	1.151	1.313	0.69
LAI65 (m^2 m^{-2})	1.3 (0.1)	1.6 (0.2)	1.213	0.0730	1.065	1.360	0.67
PAI65 (m^2 m^{-2})	2.0 (0.2)	2.6 (0.3)	1.254	0.0630	1.124	1.384	0.73
Grain yield (kg ha^{-1})	2289 (154)	2872 (214)	1.255	0.0372	1.178	1.332	0.82
Water use (mm)	320 (9)	301 (10)	0.936	0.0243	0.886	0.986	0.36
WUEb (kg ha^{-1} mm^{-1})	21.3 (1.3)	28.9 (2.0)	1.357	0.0407	1.273	1.441	0.79
WUEg (kg ha^{-1} mm^{-1})	7.2 (0.5)	9.6 (0.7)	1.311	0.0483	1.211	1.411	0.72

Data are from the AGFACE experiment for 3 years (2007–2009) and pooled across time of sowing and watering regime treatments. The fitted slope (b) of the model $y = bx$ where y is the parameter under eCO_2 and x is the parameter under ambient CO_2 is shown together with its standard error (SE) and 95% lower and upper confidence intervals of b and its coefficient of determination (R^2). The total residual degree of freedom was 23.

Table 3 The observed treatment-mean performance of wheat (cv. Yitpi) growth at stem elongation (DC31) and anthesis (DC65), leaf area index at DC65 (LAI), yield, water use and water use efficiency for biomass (WUEb) and grain (WUEg) under ambient (aCO_2) and elevated carbon dioxide (eCO_2) under FACE (free-air carbon dioxide enrichment) conditions

		aCO_2		eCO_2	
	TOS	Rain-fed	Irrigated	Rain-fed	Irrigated
Biomass (DC31) (kg ha^{-1})	N	1028 (132)	1004 (131)	1219 (182)	1159 (190)
	L	1393 (140)	1567 (226)	1815 (219)	1823 (279)
Biomass (DC65) (kg ha^{-1})	N	7901 (370)	8059 (392)	9119 (581)	10 170 (531)
	L	4171 (113)	4546 (276)	5383 (122)	6376 (269)
LAI (DC65) (m^2 m^{-2})	N	1.7 (0.2)	2.1 (0.1)	1.9 (0.2)	2.6 (0.4)
	L	0.6 (0.1)	0.8 (0.1)	0.7 (0.1)	1.2 (0.1)
Grain yield (kg ha^{-1})	N	2777 (109)	3046 (202)	3391 (222)	3972 (269)
	L	1565 (188)	1768 (172)	1704 (180)	2420 (274)
Water use (mm)	N	316 (6)	354 (18)	280 (12)	357 (9)
	L	272 (10)	339 (20)	278 (23)	290 (13)
WUEb (kg ha^{-1} mm^{-1})	N	26.4 (2.0)	26.1 (2.3)	38.9 (4.1)	33.7 (2.4)
	L	16.7 (0.8)	16.2 (1.1)	19.1 (0.6)	23.9 (0.9)
WUEg (kg ha^{-1} mm^{-1})	N	8.8 (0.5)	8.8 (0.9)	12.4 (1.4)	11.2 (1.0)
	L	5.8 (0.8)	5.5 (0.9)	6.2 (0.6)	8.3 (0.9)

Data are from the AGFACE experiment for 3 years (2007–2009) for normal (N) and late time (L) of sowing (TOS) and watering regime (rain-fed and irrigated). Standard errors of mean are in parentheses.

Table 4 The observed and simulated treatment-mean performance of wheat (cv. Yitpi) growth at anthesis (kg ha^{-1}) (DC65) under ambient and elevated carbon dioxide under FACE (free-air carbon dioxide enrichment) conditions

		Rain-fed			Irrigated		
	TOS	Ambient	Elevated	%	Ambient	Elevated	%
Observed	N	7901 (370)	9119 (581)	15.4	8059 (392)	10 170 (531)	26.2
	L	4171 (113)	5383 (122)	29.1	4546 (276)	6376 (269)	40.3
APSIM-Wheat	N	7145 (1002)	8758 (1124)	22.6	8031 (689)	9831 (660)	22.4
	L	5342 (710)	6463 (848)	21.0	6421 (158)	7931 (142)	23.5
APSIM-Nwheat	N	7086 (2558)	8622 (2372)	21.7	8042 (159)	9843 (410)	22.4
	L	3892 (915)	4480 (1156)	15.1	5244 (259)	6445 (258)	22.9
CAT-Wheat	N	6232 (654)	7449 (722)	19.5	7310 (426)	8787 (463)	20.2
	L	4435 (559)	5301 (652)	19.5	6074 (316)	7241 (433)	19.2
CROPSYST	N	6405 (929)	8202 (1032)	28.0	7080 (338)	9012 (343)	27.3
	L	4857 (482)	6195 (637)	27.5	5273 (94)	6755 (104)	28.1
OLEARY-CONNOR	N	6768 (1143)	8332 (1213)	23.1	6979 (716)	8818 (960)	26.3
	L	4742 (744)	5841 (1192)	23.2	5438 (667)	6815 (516)	25.3
SALUS	N	7087 (201)	8181 (199)	15.5	7056 (275)	8199 (478)	16.2
	L	5679 (395)	6451 (453)	13.6	6031 (800)	7038 (800)	16.7

Data are from the AGFACE experiment for 3 years (2007–2009) for normal (N) and late time (L) of sowing (TOS) and watering regime (rain-fed and irrigated). Standard errors of mean of the observed data and standard deviation of simulated data are in parentheses.

Simulation performance

Simulation performance – biomass and yield. Despite large variation in the data, the simulated biomass and grain yield showed no serious bias, and all models provided a similar mean error (Table S9). There were, however, some differences between the models in the absolute simulation of early biomass and LAI. Comparison of modelled growth over time at the early growth stage of DC31 is somewhat difficult without observations from multiple sampling dates, because the cause of mismatch may not be clear from a single DC31 measurement. Nevertheless, the overall response to eCO_2 was similar among the models (Table S10).

For crop growth up to anthesis, RMSE between observed and simulated biomass ranged from 1400 to

Table 5 The observed mean time to emergence, stem elongation, anthesis and maturity and root mean square error (RMSE) for six crop models

	Sowing to emergence (days)	Sowing to stem elongation (days)	Sowing to anthesis (days)	Anthesis to Maturity (days)
Observed	13.3	68.7	109.0	40.2
RMSE				
APSIM-Wheat	3.3	11.1	8.7	8.3
APSIM-Nwheat	3.7	12.9	8.8	9.1
CAT-Wheat	3.3	6.5	7.8	6.6
CROPSYST	1.7	na	6.4	11.2
OLEARY-CONNOR	1.6	10.6	7.9	9.2
SALUS	3.0	7.7	8.6	13.7

No differences were observed under elevated CO_2, so data were pooled across CO_2 levels. CROPSYST does not simulate stem elongation. na, not available.

1500 kg ha^{-1} across the six models (Table S9). All the models tended to simulate biomass until anthesis reasonably well, despite over prediction of LAI. Both APSIM-Wheat (R^2 = 0.24 and RMSE = 0.70 m^2 m^{-2}) and APSIM-Nwheat (R^2 = 0.39 and RMSE = 1.18 m^2 m^{-2}) simulated LAI closer to the observed data than the other models simulating PAI. No differences in model performance in simulating biomass to anthesis occurred between the ambient and eCO_2 treatments. For crop yield (Table S9), comparison of RMSE between observed and predicted ranged from 600 to 1300 kg ha^{-1}. The SALUS model had the highest R^2 (0.69) and the lowest RMSE (600 kg ha^{-1}) with CAT-Wheat and OLEARY-CONNOR models exhibiting typical means errors around 750 kg ha^{-1} and the APSIM-Wheat and APSIM-Nwheat >1000 kg ha^{-1}. This variation among the models highlights the extent of accuracy that can be expected using such models without fitting the models to the data and is considered sufficiently accurate to test the relative response of eCO_2.

Simulation performance – water use and water use efficiency. The average water use across all treatments was 310 mm during the growing season and ranged from 272 to 357 mm (Table 3). All the models simulated water use with a relatively high degree of accuracy and consistency with R^2 ranging from 0.58 to 0.31 and RMSE from 31.3 to 67.6 mm (Table S9). No differences in model performance in simulating water use occurred between the ambient and eCO_2 treatments. There was some variation between the models in simulating WUE for biomass and grain yield. For the accumulation of biomass, the water use efficiency (WUEb) was simulated with varied accuracy by APSIM-Wheat, APSIM-Nwheat, CAT-Wheat, CROPSYST and SALUS with R^2 ranging from 0.18 to 0.84 and RMSE from 6.63 to 9.69 kg ha^{-1} mm^{-1}). For grain yield, the water use efficiency (WUEg) R^2 ranged from 0.03 to 0.51 and RMSE from 2.48 to 4.12 kg ha^{-1} mm^{-1} (Table S9).

Biomass and leaf area response to eCO_2

The observed increase in growth of wheat, up to stem elongation, due to eCO_2 was 21% (using regression) (Table S10). This early growth response was not captured well by all the models where APSIM-Wheat, APSIM-Nwheat, CAT-Wheat, CROPSYST, OLEARY-CONNOR and SALUS produced a predicted response to eCO_2 of 29%, 18%, 25%, 40%, 45% and 9%, respectively (Fig. 2 and Table S10). The models: APSIM-Wheat, CAT-Wheat and SALUS substantially oversimulated early biomass (stem elongation), whereas the OLEARY-CONNOR model undersimulated the amount of biomass but oversimulated the response to eCO_2 for the same period. Wheat growth up to anthesis increased on average (using regression) by 23% due to eCO_2 (Fig. 3 and Table S10). In comparison, simulated response was 22%, 21%, 20%, 28%, 25% and 16% for the APSIM-Wheat, APSIM-Nwheat, CAT-Wheat, CROPSYST, OLEARY-CONNOR and SALUS models, respectively. All the six models performed within or close to the 95% confidence limits of observed slope. However, in contrast to the oversimulation of early growth, SALUS was not able to capture the observed range of biomass. The simulated increase in LAI at DC65 from eCO_2 was 19% for both APSIM-Wheat and APSIM-Nwheat and 13%, 7%, 24% and 8% for PAI for CAT-Wheat, CROPSYST, OLEARY-CONNOR and SALUS models, respectively (Fig. 4 and Table S10). For both APSIM models, the range of both observed and simulated data matched, whereas the CAT-Wheat, CROPSYST, OLEARY-CONNOR and SALUS

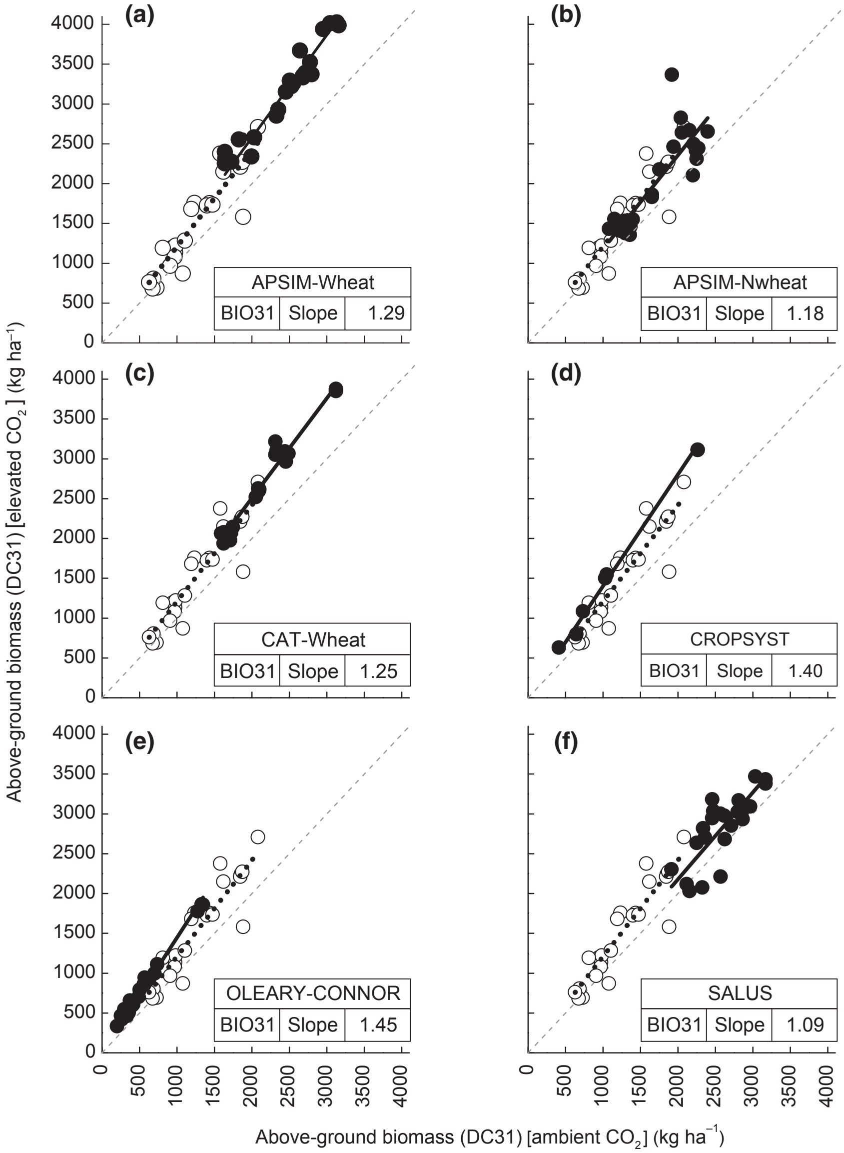

Fig. 2 Response of biomass at stem elongation (DC31) to elevated CO_2 compared to daytime ambient conditions (365 μmol mol^{-1}) from six crop models; APSIM-Wheat (a), APSIM-Nwheat (b), CAT-Wheat (c), CROPSYST (d), OLEARY-CONNOR (e) and SALUS (f). The simulated response to elevated CO_2 (● and solid fitted lines) compared to the observed response to elevated CO_2 (○ and dotted fitted lines slope = 1.21). The 1 : 1 unity dashed line is the line of zero response to elevated CO_2. CROPSYST does not simulate stage DC31, but simulated biomass was outputted on the observed date of DC31 for comparison.

did not match well the observed range of PAI. The observed and simulated biomass and LAI response to eCO_2 at DC65 (50% anthesis) under irrigation was generally increased despite irrigation not fully preventing stress (Table S10). Under irrigation, the effect of late sowing on response to eCO_2 to biomass accumulation at DC65 was substantial in the observed data (~40%), but the simulated response ranged from 17% from SALUS to 28% from CROPSYST (Table 4). Simulated response from all the six models under no water or nitrogen stress showed similar response to eCO_2 under irrigation, but the differences compared to the dryland treatment were small.

Yield response to eCO_2

The observed mean wheat yield response to eCO_2 was 26% (using regression) (Fig. 5 and Table S10). Similarly, simulations match well the response with simulated

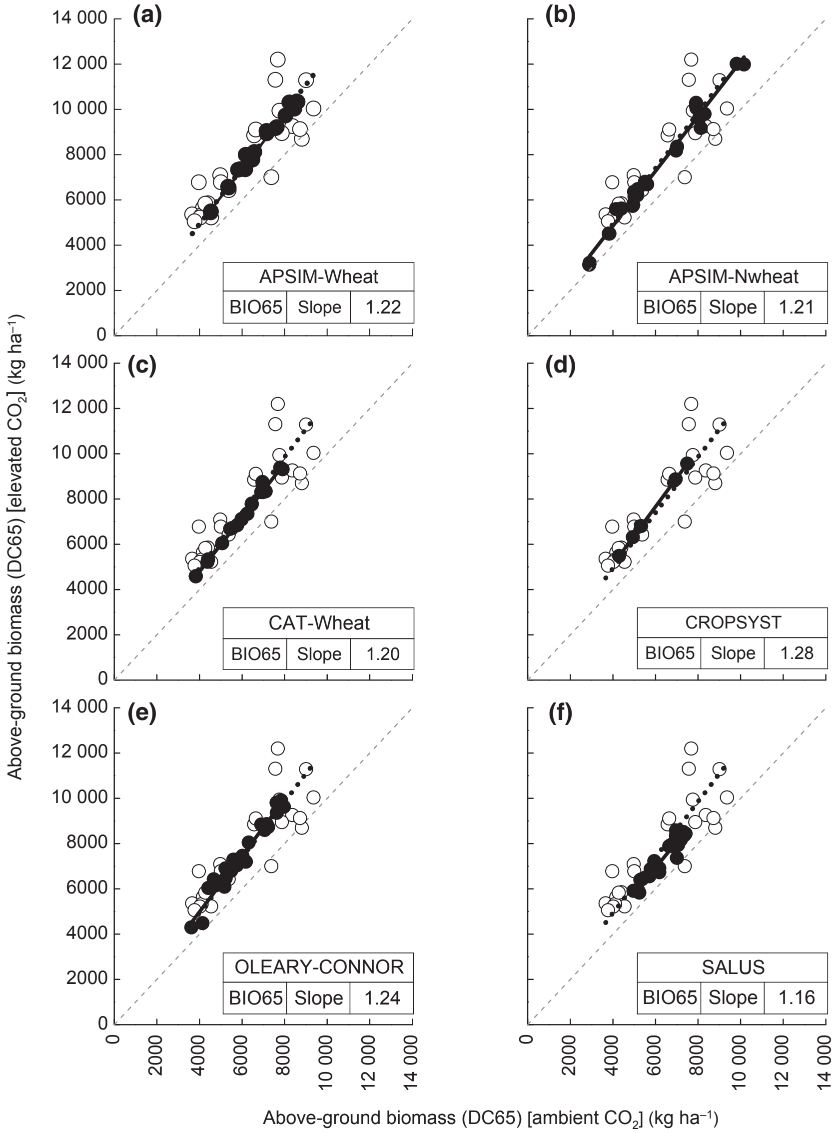

Fig. 3 Response of biomass at anthesis (DC65) to elevated CO_2 compared to daytime ambient conditions (365 μmol mol^{-1}) from six crop models; APSIM-Wheat (a), APSIM-Nwheat (b), CAT-Wheat (c), CROPSYST (d), OLEARY-CONNOR (e) and SALUS (f). The simulated response to elevated CO_2 (● and solid fitted lines) compared to the observed response to elevated CO_2 (○ and dotted fitted lines slope = 1.23). The 1 : 1 unity dashed line is the line of zero response to elevated CO_2.

increases of 19%, 28%, 20%, 27%, 21% and 25% for the APSIM-Wheat, APSIM-Nwheat, CAT-Wheat, CROPSYST, OLEARY-CONNOR and SALUS models, respectively. There was a tendency for APSIM-Wheat to slightly oversimulate the range of yields, but all the other models simulated the response to eCO_2 and range well (Fig. 5).

Water use and water use efficiency response to eCO_2

The water use during the growing season of wheat was slightly reduced by eCO_2, but simulated water use from all the models showed no consistent reduction (Table S10). Some models actively reduce daily transpiration under eCO_2 conditions (e.g. CROPSYST and OLEARY-CONNOR), but the accumulated WU (Table S10) and T (data not shown) were near 1 : 1 with respect to eCO_2. Of all the parameters, simulated water use gave the most consistent nonresponse to eCO_2 (Table S10). The observed water use efficiency of biomass (WUEb) and wheat yield (WUEg) increased by 36% and 31% (using regression) under eCO_2, respectively (Tables 2 and 4). In comparison, simulations tended to underestimate the effect of eCO_2 on WUEb and WUEg but were closest for APSIM-Nwheat (22% and 27%) and CROPSYST

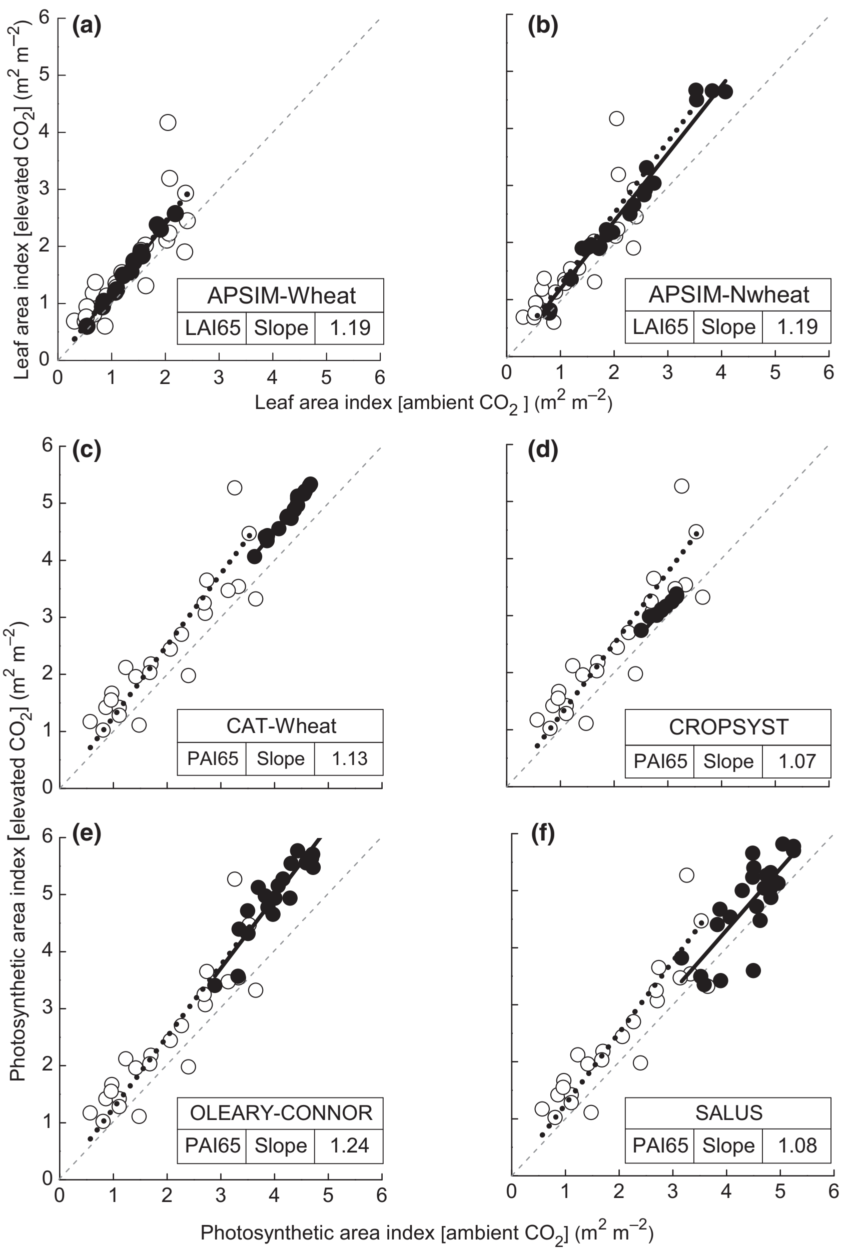

Fig. 4 Response of leaf area index (LAI) at anthesis (DC65) to elevated CO_2 compared to daytime ambient conditions (365 μmol mol^{-1}) from two crop models; APSIM-Wheat (a) and APSIM-Nwheat (b) and response of stem and leaf area index (PAI) at anthesis (DC65) from four crop models; CAT-Wheat (c), CROPSYST (d), OLEARY-CONNOR (e) and SALUS (f). The simulated response to elevated CO_2 (● and solid fitted lines) compared to the observed response to elevated CO_2 (○ and dotted fitted lines LAI slope = 1.21 and PAI slope 1.25). The 1 : 1 unity dashed line is the line of zero response to elevated CO_2.

(29% and 29%), respectively. Given the large variance in WUEb and WUEg data, differences between the models are not considered significant (Tables 4 and S9).

Discussion

The measured response of wheat cv. Yitpi to eCO_2 over the 3 years was strong and consistent for all above-ground biomass at DC31 and DC65, and LAI/PAI at DC65 and grain yield. The response is considered large but not necessarily indicative of some future climate because the experimental conditions evaluated CO_2 response under ambient temperature and VPD conditions and did not consider likely future elevated temperature or increased VPD. Nevertheless, an interactive effect of temperature was seen

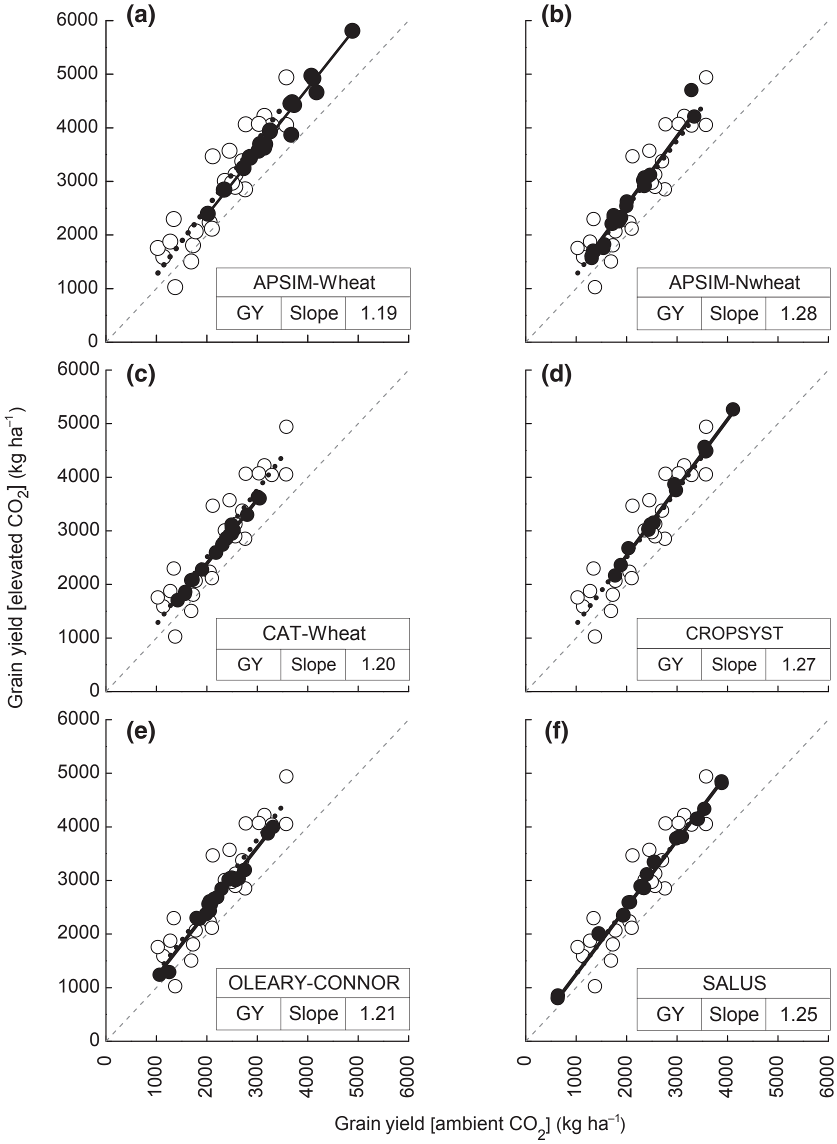

Fig. 5 Response of harvested grain yield to elevated CO_2 compared to daytime ambient conditions (365 μmol mol^{-1}) from six crop models; APSIM-Wheat (a), APSIM-Nwheat (b), CAT-Wheat (c), CROPSYST (d), OLEARY-CONNOR (e) and SALUS (f). The simulated response to elevated CO_2 (● and solid fitted lines) compared to the observed response to elevated CO_2 (○ and dotted fitted lines slope = 1.26). The 1 : 1 unity dashed line is the line of zero response to elevated CO_2.

in the observed data where the late-sown crops consistently responded proportionally greater to eCO_2 than the normal time of sowing (Table 4). All the six models did not match this observed interaction, and a closer focus on such response is needed in future experiments.

The overall observed response to eCO_2 (~550 μmol mol^{-1}) of around 21–23% in biomass, LAI and yield was slightly higher than reported meta-analysis means around ~18% (Ainsworth & Long, 2005; Sun *et al.*, 2009), but near identical expected for dry environments (cf. ~22% in Arizona, USA, Kimball, 2011). The assumption that there is a larger response under water-stressed conditions of the experiment is, however, not supported by the experimental data nor modelling data. Indeed, the measured response to eCO_2 of biomass accumulation by anthesis was higher under irrigation (28% cf. 18%). This response was contrary to that observed in Arizona whereby unstressed conditions had a lower response to eCO_2 (cf. ~16% Kimball, 2011). The reasons are unclear and warrant further investigation.

This magnitude of response to eCO_2 was also close to the findings of Yang *et al.* (2007a) that reported an average increase of 24.8% in wheat grain yield across various N levels over 2 years in Nanjing, China. These two FACE experiments were conducted under near-identical CO_2 concentrations (365 vs. 550 μmol mol^{-1} for AGFACE; 350 vs. 550 μmol mol^{-1} for China FACE). The response in biomass to eCO_2 was reported to be an average of 13.6% across key growth stages (Yang *et al.*, 2007b). The extent of the increase in biomass from China FACE is relatively small compared with our findings. This was partly due to their reported negative impact of eCO_2 on biomass accumulation from heading to maturity (−5.5%) even though positive effects were found in the pre-anthesis growth phases ranging from 11% to 41% (Yang *et al.*, 2007b). It is possible that excess pre-anthesis storage and translocation resulted in greater yield gain.

The modelled gross response to eCO_2 was similar among all models despite their different primary mechanism of computing daily growth. None of the models were specifically fitted to the data and thus show a robustness that should allow confident application to climate change scenarios involving eCO_2 in combination with varying water and N supply and growing season temperatures. Despite the good overall performance of each model with respect to response to eCO_2 against the measured data at Horsham, differences were evident. This was particularly noted by growth stage DC31 where without temperature corrections to the TE-RUE functions OLEARY-CONNOR and CROPSYST appear to overpredict the response to eCO_2 (45% and 40%, respectively, Fig. 2 and Table S10), but this is a relatively small error occurring so early in the season that this apparent discrepancy did not affect later growth. APSIM-Nwheat followed the early observed response data more closely than all the other models. We concur with Ewert (2004) regarding the need to improve LAI simulation to achieve the correct CO_2 response in all the models except the APSIM-Nwheat model. Nevertheless, despite the poorly modelled early growth by anthesis, all the models matched the seasonal biomass production quite well. Because the grain yield response to eCO_2 was simulated well by all models, the consequences of poor early simulation were not detectable by maturity at this location. This is a particularly critical finding for the applicability of these models to other similar dryland areas where incomplete cover is a dominant feature of the growing season.

Another potential uncertainty is the artefacts of high frequency changes in CO_2 concentration in FACE raised by Bunce (2013). As the modelled response does not contain any physiological mechanisms that might mimic such processes, and the modelled crop response at 550 μmol mol^{-1} was within the experimental error for all models for biomass at DC65, we consider the pulse CO_2 injection artefact to likely be small and within the experimental error of our experiment. However, whilst the mean response to eCO_2 was consistent across the range of treatments and years, results from individual crops did exhibit large variability. The effect of such variability was reduced by the forcing of the regression through the origin (Table S10). Similarly, the 6-model ensemble generally reduced the modelled variability, but some models matched the observed data better than the ensemble (e.g. SALUS in grain yield). This is not unexpected because the ensemble represents a statistical outcome rather than an explanatory outcome represented by each model. Careful application of such ensemble data is therefore needed.

Despite the modelled response being within or close to the experimental error, an obvious issue of FACE experiments is the spatial and temporal variation in CO_2 concentrations. The destructive samples for the three growth stages were collected at least 1 m away from CO_2 delivery rings, thus avoiding the areas of highest CO_2 concentrations, at times over 1200 μmol mol^{-1} within 1 m of the ring (Mollah *et al.*, 2012). Median plot CO_2 concentrations varied in 2009 from 524 to 640 μmol mol^{-1}, depending on prevailing winds, and were as high as 722 μmol mol^{-1} in one plot in 2007. Whilst the equipment maintained its designed 550 μmol mol^{-1} in the centre, no crops were grown at the centre and we suggest that a 650-μmol mol^{-1} level is probably more realistic for majority of the area within the rings for the measured crops, as noted in the standard deviation ring map in Mollah *et al.* (2012).

The lack of a phenological response to eCO_2 is an interesting result because of the strong growth response; however, the differences of <2 days may not have been noted in the AGFACE experiment. At Nanjing in China, eCO_2-accelerated phenological development was reported by 1.3 days to heading and another 1.3 days between heading and maturity (Yang *et al.*, 2007a). Such very small changes in phenology are unlikely to gain any large benefit in terms of water savings that might ultimately occur in high-VPD environments. Future FACE experiments should consider measuring canopy temperatures throughout the day and night to better explain water fluxes with canopy temperature and crop development. The performance of all the models in terms of predicting anthesis date with RMSE's over 6 days provides room for improvement; however, notably only one crop in 2008 was responsible for the large error. Interestingly, uncertainties in simulating the impact of increasing global temperature and temperature by eCO_2 interactions have been recently pointed out as the largest shortcomings in wheat models for simulating future climate change impacts, with additional experimental research required for targeted model improvements (Asseng *et al.*, 2013a). Our analyses support that view.

The simulated WUE was quite poor particularly for grain yield despite significant performance in WU and biomass and yield (Table S9). This probably reflects the problem of compounding of errors in both the numerator and denominator in calculating WUE. A way to dampen such effects would be to fit regressions through the prime data with various sources of variance reduced such as removing soil evaporation and examining the TE dynamics. Nevertheless, the modelled response matches the observed first-order processes sufficiently well with acceptable absolute errors (Table S10).

The gross response to eCO_2 was simulated satisfactorily; however, on close examination, there are aspects requiring model improvement. For APSIM-Wheat, CAT-Wheat, OLEARY-CONNOR and SALUS models, the primary focus should be on early growth in terms of biomass and leaf and stem components and water relations under drought and unstressed conditions. Despite simple temperature reduction via RUE in CROPSYST and OLEARY-CONNOR, a temperature interactive term with eCO_2 might be needed. This would allow very high responses to eCO_2 to be reduced early in the season when mean temperatures are typically below 10 °C and TE is high because of the low VPD. Similarly, the failure of all models to simulate the eCO_2 response under late sowing might be indicative of a poorly understood eCO_2 response under such conditions. For CAT-Wheat and SALUS, the simple RUE approach with no TE or temperature reduction and a simple harvest index method simulated the gross response reasonably well, but its interaction of eCO_2 and water supply conditions warrants further experimentation because of the relatively high early growth. New field experiments are needed focusing on early growth and water relations. The phenological development should also be scrutinised in future experiments with a focus on canopy heating and cooling as water fluxes change under FACE conditions.

The FACE experiment was conducted under ambient temperature and VPD conditions that are unlikely to be directly representative of future climates. It remains to be seen what the effect of high temperatures and VPD when combined with eCO_2 will be on leaf area development, tiller number, above-ground biomass and grain yield. Certainly, the large response to eCO_2 under late sowing shows that the interactive effects will be of continuing interest. It was recently shown that biomass and particularly grain yield of vigorous and nonvigorous wheat genotypes increased when grown under eCO_2 and a mean temperature of 1.0 °C above the mean ambient temperature (Dias De Oliveira *et al.*, 2012). However, when grown under eCO_2 and mean temperatures of 2.0 and 3.0 °C above the mean ambient temperature, grain yields tended to decrease linearly, mainly because the combination of eCO_2 and high temperature reduced the time between anthesis and physiological maturity (Dias De Oliveira *et al.*, 2012). Consequently, it is expected that the predicted increments in the temperature for the Mediterranean climatic region of Australia (Christensen *et al.*, 2007) will reduce the grain yield response of wheat to eCO_2 unless wheat cultivars with high tolerance to temperature are developed. We suggest field experimentation using open air heating for heating the air around field-grown crops be explored (Kimball & Conley, 2009).

This experiment at Horsham has allowed for the first time the testing of several crop models to eCO_2 under semi-arid unirrigated conditions. At this Mediterranean-type climatic site, the response to eCO_2 was higher under irrigation. However, no elevated temperature treatments were explicitly applied in our FACE experiment, and the models did not fully match the observed interaction of the late-sown crops; therefore, some caution is required when applying the models to some future climate. These findings can therefore be cautiously used as representative of semi-arid environments, and the models used here can equally be applied in eCO_2 impact and adaptation studies for other similar semi-arid regions of the world.

Overall, without any amendment, six different crop models were able to simulate gross response to eCO_2 at Horsham, Australia – notwithstanding some second-order deviations at the early growth stage for APSIM-Wheat, CAT-Wheat, CROPSYST, OLEARY-CONNOR and SALUS models. Whilst APSIM-Nwheat performed well across many variables, it was not the better performer for all of them. General improvements in all the models are expected with future local calibration, but the RUE and TE methods of biomass accumulation represented in the models were sufficient in reproducing the main responses in the FACE experiment and therefore applicable for future climate change analyses in similar dry environments where increased water supply increases the response to eCO_2 at around 550 μmol mol^{-1}.

Acknowledgements

The research at the Australian Grains Free-Air Carbon Dioxide Enrichment (AGFACE) facility was jointly managed by the Victorian State Government Department of Environment and Primary Industries and The University of Melbourne with additional funding from the Australian Grains Research and Development Corporation and the Australian Government

Department of Agriculture, Fisheries and Forestry. Technical and engineering support was provided by Mahabubur Mollah, Russel Argall, Peter Howie, Janine Fitzpatrick, Justine Ellis, Jennifer Briggs and Jason Ellifson. At the outset of the project, we invited guest collaborators to join the team (O'Leary & Anwar, 2008; O'Leary *et al.*, 2010). Participation of CS and CROPSYST simulations was supported by the project of Regional Approaches to Climate Change for Pacific Northwest Agriculture (REACCH-PNA) which is funded through award #2011-68002-30191 from the US National Institute for Food and Agriculture. We acknowledge helpful discussions during the project from Doug Arbrect, Jeanphilippe Aurambout, Craig Beverly, Hamish Brown, Deli Chen, Kithsiri Bandara Dassanayake, Andrew Fletcher, Peter Grace, Bruce Kimball, Robert Norton, Eduardo Dias de Oliveira, David Stephens, Humaira Sultana, Michael Tausz, Gerard Wall and Jeff White. The experimental data set comprising meteorological observations and treatment crop and soil data from the 48 crops presented here are available upon request from the senior author. Helpful comments were made by an anonymous referee on an earlier manuscript.

Author contribution

The various contributions from the authors were as follows: concept, primary author: GOL; modelling data contributions: GOL, BC, JN, NH, DC, CS, BB, IS and SA; and discussion contributions with respect to other published data: GF, QL, IFC and JP.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Soil profile data describing the mean air dry, crop lower limit (LL), drained upper limit (DUL), saturation (SAT), bulk density (BD), pH, organic carbon (OC) and organic nitrogen (ON) content of the experimental site used by all models. APSIM-Wheat used additional water availability coefficients (KL and XF).
Table S2. Additional generic site specific and soil type parameters defining the experimental site including some APSIM-Wheat specific parameters (APSIM).
Table S3. Key parameters used to define wheat growth in APSIM-Wheat for cultivar Yitpi.
Table S4. Key parameters used to define wheat growth in APSIM-Nwheat for cultivar Yitpi.
Table S5. Key parameters used to define wheat growth in CAT-Wheat for cultivar Yitpi.
Table S6. Key parameters used to define wheat growth in CROPSYST for cultivar Yitpi.
Table S7. Key parameters used to define wheat growth in the OLEARY-CONNOR model for cultivar Yitpi.
Table S8. Key parameters used to define wheat growth in SALUS for cultivar Yitpi.
Table S9. Comparison of simulated and observed data showing regression coefficients (a, b), their standard errors (SE), 95% lower and upper confidence intervals of b, coefficient of determination (R^2), significance of regression (P) and root mean square error (RMSE) for the linear model $y = a + bx$ where y is the observed and x is the simulated data of biomass at DC31 (BIO31 kg ha^{-1}), biomass at DC65 (BIO65 kg ha^{-1}), leaf area index (LAI at DC65 m^2 m^{-2}), leaf and stem area index (PAI at DC65 m^2 m^{-2}), grain yield (GY kg ha^{-1}), water use (WU mm), water use efficiency for biomass (WUEb kg ha^{-1} mm^{-1}) and water use efficiency for grain (WUEg kg ha^{-1} mm^{-1}) for the APSIM-Wheat, APSIM-Nwheat, CAT-Wheat, CROPSYST, OLEARY-CONNOR, SALUS wheat models and the 6-model ENSEMBLE. The residual degrees of freedom was 46. [a]CROPSYST does not simulate stage DC31 but simulated biomass was output on the observed date of DC31 for comparison.
Table S10. Regression coefficients of the mean response to elevated CO_2 on biomass at DC31, biomass at DC65, leaf area index at DC65 (LAI at DC65), leaf + stem area index (PAI at DC65), grain yield, water use and water use efficiency for biomass and grain for the observed experimental data (OBS) and APSIM-Wheat, APSIM-Nwheat, CAT-Wheat, CROPSYST, OLEARY-CONNOR, SALUS models and the 6-model ENSEMBLE. The response under dryland and irrigated conditions and simulated unstressed conditions showing the varied general effect of added water to the response to eCO_2. The fitted slope (b) of the model $y = bx$ where y is the parameter under eCO_2 (550 μmol mol^{-1}) and x is the parameter under ambient CO_2 (365 μmol mol^{-1}) is shown together with its standard error (SE) and 95% lower and upper confidence intervals of b for the observed data. The residual degrees of freedom was 23. [a]CROPSYST does not simulate stage DC31 but simulated biomass was output on the observed date of DC31 for comparison.