

VIEWPOINT

Improving ecophysiological simulation models to predict the impact of elevated atmospheric CO₂ concentration on crop productivity

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- **Background** Process-based ecophysiological crop models are pivotal in assessing responses of crop productivity and designing strategies of adaptation to climate change. Most existing crop models generally over-estimate the effect of elevated atmospheric [CO₂], despite decades of experimental research on crop growth response to [CO₂].
- **Analysis** A review of the literature indicates that the quantitative relationships for a number of traits, once expressed as a function of internal plant nitrogen status, are altered little by the elevated [CO₂]. A model incorporating these nitrogen-based functional relationships and mechanisms simulated photosynthetic acclimation to elevated [CO₂], thereby reducing the chance of over-estimating crop response to [CO₂]. Robust crop models to have small parameterization requirements and yet generate phenotypic plasticity under changing environmental conditions need to capture the carbon–nitrogen interactions during crop growth.
- **Conclusions** The performance of the improved models depends little on the type of the experimental facilities used to obtain data for parameterization, and allows accurate projections of the impact of elevated [CO₂] and other climatic variables on crop productivity.

Key words: Acclimation to elevated CO₂, climate change, crop models, impact assessment, model improvement, nitrogen.

INTRODUCTION

World agriculture faces daunting challenges to meet growing demands for food, energy and other agricultural products. Crop production is, however, strongly affected by climate change. Lobell *et al.* (2011) showed that climate trends since 1980 were large enough in many countries to offset a significant proportion of the potential increases in average crop yields due to technological advances, CO₂ fertilization and other factors. By 2100, potentially, atmospheric [CO₂] will rise to 1000 $\mu\text{mol mol}^{-1}$, temperature will rise by 2–4 °C or more, precipitation will become more variable, and episodes of extreme weather will become more frequent and intense and last longer (IPCC, 2007). It is important to assess whether there will be sufficient food and energy production under future climate conditions. Such an assessment can also assist in developing adaptation strategies that improve the resilience of crop systems to stresses induced by climate change.

Numerous studies have assessed the impact of climate change on productivity of major crops. Whilst simple regression analysis can detect a non-linear response of crop yields to warm climate (Schlenker and Roberts, 2009; Lobell *et al.*, 2011), process-based crop simulation models (hereafter ‘crop models’) combined with climate scenario models are considered necessary to assess the impact of climate change on crop production (Porter *et al.*, 1995; Hulme *et al.*, 1999; White *et al.*, 2004; Challinor *et al.*, 2009; Semenov and Halford, 2009; Soussana *et al.*, 2010). Early assessments at the global level (e.g. Rosenzweig and Parry, 1994) often used simple crop models

based on empirical experimental data to define impacts of elevated [CO₂] and other factors on crop processes. More mechanistic ecophysiological models, although not necessarily defined originally for climate change impact assessment, are increasingly used (e.g. Tubiello and Ewert, 2002).

Research on mechanistic crop models, according to Tardieu (2010), has a history of approx. 50 years since the earliest models such as developed by de Wit (1959). These models predict crop productivities based on quantitative functional relationships for underlying processes (photosynthesis, respiration, transpiration, assimilate partitioning, etc.) and their response to environmental variables. Thus, they are believed to be suitable for projecting the impact of future climate scenarios on crop productivity at various (field, regional, national, global) scales (Challinor *et al.*, 2009).

Although crop models have continuously been refined (Weiss, 2003; Priesack and Gayler, 2009), knowledge gaps limit the ability of current crop models to reflect responses to global change factors (White *et al.*, 2004). Many reports emphasize the need to review critically and improve crop models for the assessments of climate change impacts (e.g. Lawlor and Mitchell, 1991; Tubiello *et al.*, 2007a; Ziska and Bunce, 2007; Challinor *et al.*, 2009; Soussana *et al.*, 2010). Rötter *et al.* (2011) indicated that many of the current models used for estimating potential impacts of climate change do not incorporate the latest knowledge about how crops respond to changing climates and management practices. Yet, reports dedicated towards how to improve crop models for climate impact assessment are rare.

The objective of this paper is to outline how models for assessing the impact of elevated [CO₂] can be improved. The current status in using crop models for assessing the impact of elevated [CO₂] is briefly reviewed. I then analyse whether there are differences in quantitative functional relationships for a number of traits between plants grown under the elevated CO₂ and those grown under ambient conditions. Key issues for modelling crop responses to elevated [CO₂] will be discussed.

PERFORMANCE OF EXISTING CROP MODELS

Models for climate change impact assessment need to capture responses of crop growth to all major environmental variables. Much research has focused on crop responses to elevated atmospheric [CO₂] (Long *et al.*, 2004), using various experimental facilities [such as growth chamber, temperature-gradient tunnel, open-top chamber and free-air CO₂ enrichment (FACE) technology]. As a result, the impact of elevated [CO₂] has been a constant focus in modelling. One of the first studies that assessed climate impacts on crop production was conducted by Rosenzweig and Parry (1994). The physiological effects of [CO₂] on crop growth were considered to be mediated through increased rates of net photosynthesis and reduced stomatal openings as reported from early experimental results in enclosure chambers. The ratio of photosynthetic rates at 555 μmol mol⁻¹ to that at 330 μmol mol⁻¹ CO₂ for soybean (*Glycine max*), wheat (*Triticum aestivum*), rice (*Oryza sativa*) and maize (*Zea mays*) were 1.21, 1.17, 1.17 and 1.06, respectively. Stomatal resistance was assumed to increase from 34.4 to 49.7 s m⁻¹ in C₃ crops and from 55.8 to 87.4 s m⁻¹ in C₄ crops with [CO₂] increase from 330 to 555 μmol mol⁻¹. More recently, Tubiello and Fischer (2007) even used the ultra-simple model AEZ to simulate crop response to elevated [CO₂], i.e. as a multiplier of the harvest yield obtained under current [CO₂]. The multiplier was derived from experiments under controlled conditions, which indicated a 25% increase in yield of C₃ crops (such as wheat, rice and soybean), and a 10% increase in the yield of C₄ crops (such as maize and sugarcane) for a doubling of the current atmospheric [CO₂]. Empirical approaches to include impacts of elevated [CO₂] have also been used in other crop models, e.g. CERES (Tubiello *et al.*, 1999).

Tubiello *et al.* (2007a) reported that some models used in impact assessment have not been evaluated against FACE data. Where this has been carried out, Tubiello and Ewert (2002) found that five widely used crop models reproduced well the effects of elevated [CO₂] on wheat in the Maricopa FACE experiment of Kimball *et al.* (1995). However, this statement was challenged by Long *et al.* (2005, 2006) and Ainsworth *et al.* (2008a), who re-analysed modelled CO₂ enhancement ratio compared with experimental response ratio (Fig. 1). They concluded that current crop models over-estimated the CO₂ fertilization effect both under well-watered conditions and under drought-stress conditions. CO₂ enhancement ratios from similar experimental set-ups were also over-predicted by other models, e.g. APSIM (Asseng *et al.*, 2004) and SPASS (Biernath *et al.*, 2011).

The observed CO₂ enhancement ratio on yield and other plant traits is generally lower in FACE than in enclosed chambers (e.g. de Graaff *et al.*, 2006; Ainsworth *et al.*, 2008a). In

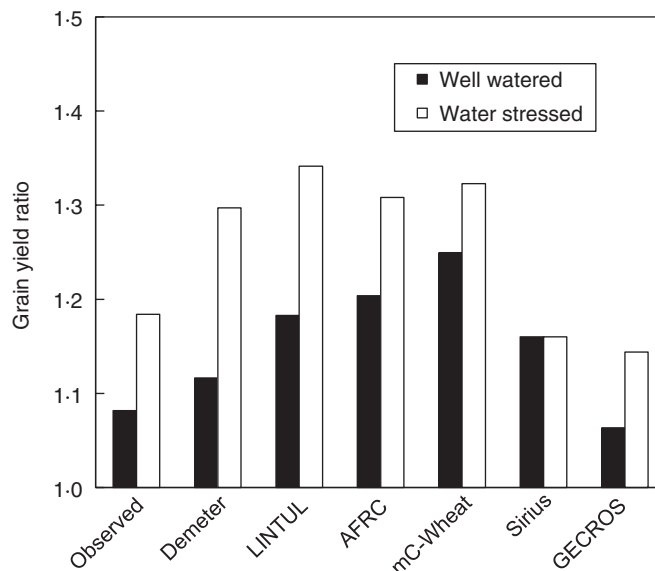


FIG. 1. Observed stimulation of grain yields of well-watered and water-stressed wheat crops grown under ambient CO₂ (370 μmol mol⁻¹) and elevated CO₂ (550 μmol mol⁻¹) for the free-air CO₂ enrichment (FACE) experiment conducted in Maricopa, Arizona, USA (see Kimball *et al.*, 1995). The stimulation ratio was expressed as the average ratio of grain yield under elevated CO₂ to the yield under ambient CO₂ for the two growing seasons 1992–1993 and 1993–1994. The modelled stimulation ratio from five crop models (Demeter, LINTUL, AFRC, mC-wheat, Sirius) previously evaluated by Tubiello and Ewert (2002) and that from model GECROS evaluated by Yin and Struik (2010) were also given. The observed stimulation effects was not over-predicted by GECROS. Other models tended to over-estimate the effects, largely leading Long *et al.* (2006), Ainsworth *et al.* (2008a) and Leakey *et al.* (2009) to conclude that model parameterization based on chamber experiments is inappropriate to project crop response to elevated CO₂ under field conditions. Reproduced from Yin and Struik (2010) with permission.

my opinion, this may be explained by the difference in the scale of experiments (typically plots of >300 m² in FACE vs. <4 m² in enclosure studies). Because of reduced chance of mutual shading, leaves in enclosures tend to receive higher light; under high-light conditions photosynthesis is more likely limited by Rubisco capacity than by electron transport. Rubisco-limited photosynthetic rates are stimulated more by elevated [CO₂] than electron transport-limited rates (Kirschbaum, 2011). The increased photosynthetic rates can result in higher leaf area that will further lead to more light interception and biomass production. However, there have also been doubts about whether the lower enhancement values in FACE reflect a flaw of the FACE technology. For example, in the experiment of Kimball *et al.* (1995) control plots lacked the blowers that were installed in the elevated [CO₂] plots. Such a difference may have resulted in a relatively lower measured response to elevated [CO₂] than if both treatments were similarly equipped (Kimball, 2013). Furthermore, Holtum and Winter (2003) and Bunce (2012) showed that frequent fluctuations in [CO₂], as commonly occurred in FACE, may diminish the response of leaf photosynthesis to elevated [CO₂]. One can predict from the convex nature of the photosynthetic [CO₂] response curve that fluctuations in [CO₂] can lead the FACE systems to an underestimation of steady-state photosynthetic rates at projected future [CO₂] concentrations. If fluctuations are highly irregular and variable, steady-state

photosynthesis may not be achieved and the impact becomes complicated to predict quantitatively. Ainsworth and Long (2004), however, argued that [CO₂] fluctuations seem an unlikely explanation of the lower stimulation in the FACE experiments. First, there was no evidence for the difference in photosynthetic electron transport rate between constant and fluctuating elevated [CO₂] in wheat for oscillations of a half-cycle of 30 s or less, which would include most of the fluctuations observed in the FACE systems (Hendrey *et al.*, 1997). Second, fluctuations in [CO₂] are also observed in open-top chambers, albeit to a lesser extent.

Long *et al.* (2004, 2005, 2006) and Ainsworth *et al.* (2008a) therefore expressed concern that there may be some quantitative differences in how crops respond to elevated [CO₂] in FACE and chamber experiments. They suggested that controlled chamber environments were not the best experimental facilities to parameterize crop models for estimating CO₂ response ratio of crop yield, as FACE has revealed factors in field conditions that were not identified by chamber experiments (e.g. increased herbivory). The need for larger-scale FACE experiments to determine how inter- and intraspecific variations in crop yield are affected by [CO₂] in combination with other aspects of climate change was collectively proposed by a large group of scientists (Ainsworth *et al.*, 2008b). I will examine this controversial issue later.

There have been debates (e.g. Tubiello *et al.*, 2007b) on the statement of Long *et al.* (2005, 2006) and Ainsworth *et al.* (2008a) about quantitative differences in crop response to elevated [CO₂] between FACE and chamber experiments. Ziska and Bunce (2007) analysed a large set of compiled data and found little evidence that relative increases of crop yield in response to future [CO₂] obtained using a number of enclosure methodologies are quantitatively different from those with FACE results for rice, wheat and soybean. They suggested that instead of focusing on methodological disparities per se, improved projection of the impact of future climate could be achieved by better characterization of other biotic/abiotic uncertainties associated with projected changes in [CO₂] and incorporation of these uncertainties into crop models. For example, they highlighted the result of Matsui *et al.* (1997) that at air temperatures above 30 °C, the percentage of filled rice spikelets under elevated [CO₂] was lower than that under ambient [CO₂], a trend that is opposite to the positive interaction between [CO₂] and temperature on leaf photosynthetic rates (Long, 1991). Such a response of spikelet fertility could be explained, at least in part, by the reduction in transpirational cooling, higher panicle temperature and thus increased pollen sterility under elevated [CO₂] conditions.

Obviously, the arguments of Ziska and Bunce (2007) were proposed from different perspectives from those of Long *et al.* (2005, 2006) and Ainsworth *et al.* (2008a). According to Long *et al.* (2006) and Ainsworth *et al.* (2008a), most existing crop models are unable to accurately predict the impact of elevated [CO₂] on crop growth and yield, especially considering the interaction of [CO₂] with other climatic factors, unless substantial calibrations of model parameter values are made. One possibility is that major crop models were developed mainly from ambient [CO₂] conditions; when used to assess the impact of climate change, only some parameters were modified from elevated-[CO₂] experiments (Soussana *et al.*,

2010). This raises a question whether elevated [CO₂] alters quantitative functional relationships for plant growth used in crop models.

DOES ELEVATED [CO₂] CHANGE FUNCTIONAL RELATIONSHIPS OF PLANT GROWTH?

This question will be discussed by analysing several physiological processes or traits.

Leaf photosynthesis

Crop models quantify processes related to crop carbon (C) or biomass accumulation in order to predict final seed yield. Many crop models use a simple approach relating daily biomass increase as a function of daily intercepted solar radiation multiplied by radiation use efficiency (RUE) (e.g. Asseng *et al.*, 2004; Ko *et al.*, 2010; also see review of White *et al.*, 2011). Other models quantify specifically crop photosynthesis and respiration. To calculate photosynthesis, often either an empirical light response equation (e.g. Matthews *et al.*, 1997; Tubiello *et al.*, 1999) or a mechanistic biochemical model (Grant, 2001; Rodriguez *et al.*, 2001) is first used to estimate leaf photosynthesis rate, which is then scaled up to the canopy level.

It has been shown theoretically (van Oijen *et al.*, 2004) and experimentally (e.g. van Oijen *et al.*, 1999; Sakai *et al.*, 2006) that RUE varies with [CO₂] concentration. Any RUE-based crop models need to adjust RUE empirically to varying [CO₂] (e.g. Asseng *et al.*, 2004; Ko *et al.*, 2010). In the crop models where leaf photosynthesis is modelled using an empirical light-response equation, an underlying parameter – photosynthetic rate under saturated light (P_{\max}) – was modified to depend on the [CO₂] concentration (Matthews *et al.*, 1997; Tubiello *et al.*, 1999), whereas the other underlying parameter – initial light-use efficiency (ϵ) – was assumed to vary (Matthews *et al.*, 1997) or not to vary (Tubiello *et al.*, 1999) with the [CO₂] concentration. Experimental measurements (e.g. Ehleringer and Björkman, 1977) have long shown that under the ambient O₂ conditions, ϵ does vary with [CO₂] in C₃ plants. Even the parameters V_{\max} (maximum carboxylation rate of Rubisco), J_{\max} (maximum electron transport rate under saturated lights) and TPU (potential rate of triose phosphate utilization) of a biochemical leaf-photosynthesis model proposed by Farquhar *et al.* (1980) and extended by Sharkey (1985) were found to decrease with increasing growth [CO₂] concentrations in cotton (*Gossypium hirsutum*) plants (Harley *et al.*, 1992). All these indicate that elevated [CO₂] will result in changes in parameter values or functional relationships of these traits used in crop models.

Harley *et al.* (1992), however, also showed that photosynthetic parameters V_{\max} , J_{\max} and TPU correlate linearly with leaf nitrogen (N) content, and the relationships between these parameters and leaf N varied little with growth [CO₂] in cotton (Fig. 2). Similar linear relationships between V_{\max} or J_{\max} and leaf N across contrasting [CO₂] were widely reported, for example in ryegrass (*Lolium perenne*) (Nijs *et al.*, 1995) and in rice (Nakano *et al.*, 1997), or across diverse species (Ellsworth *et al.*, 2004). A small deviation of the V_{\max} -leaf N relationship under elevated [CO₂] from that

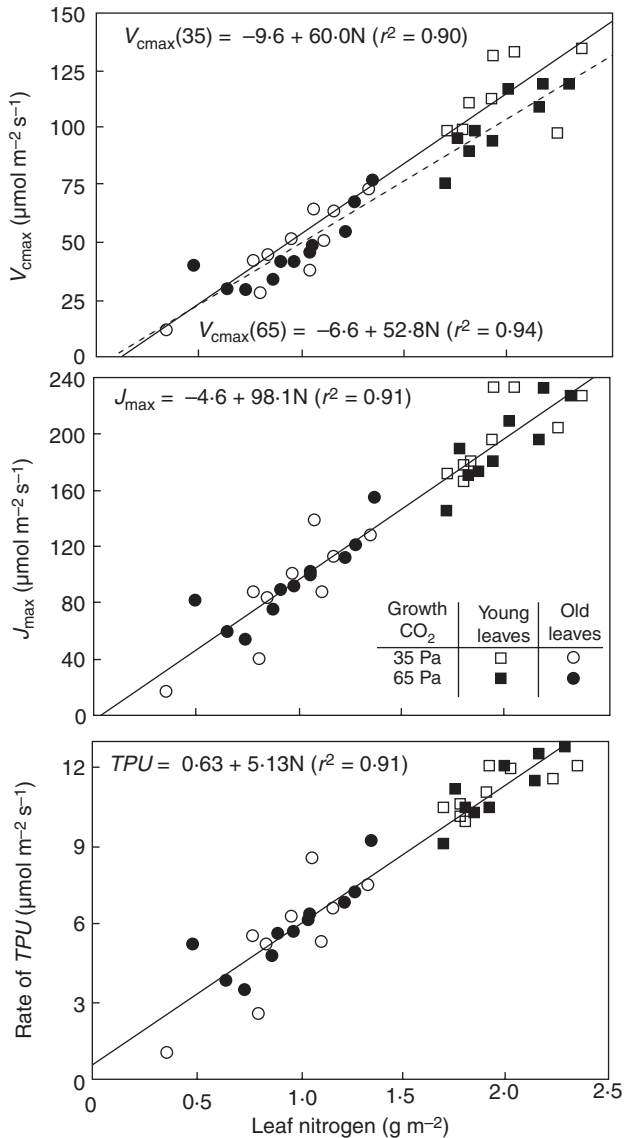


FIG. 2. Estimates of photosynthetic parameters V_{cmax} , J_{max} and TPU plotted as a function of leaf N in cotton plants. Squares, estimates obtained from recently fully expanded leaves; circles, from leaves up to 18 d after full expansion. For V_{cmax} , independent linear regressions were obtained for leaves of plants grown in 35 (open symbols) and 65 Pa CO₂ (filled symbols); regressions for J_{max} and TPU data are based on combined 35 and 65 Pa data (reproduced from Harley *et al.*, 1992) with permission.

under the ambient [CO₂] (Fig. 2) could be explained by elevated [CO₂]-induced decrease in the investment of leaf N in Rubisco (Sage *et al.*, 1989; Leakey *et al.*, 2009); however, the significance of the deviation was only marginal (Harley *et al.*, 1992). This indicates that the aforementioned changes in these parameters with [CO₂] were predominantly due to elevated [CO₂]-induced decrease in leaf N. An eventual decline in leaf N after plants grow for some period of time under elevated [CO₂] is commonly observed (e.g. Wong, 1990; Conroy and Hocking, 1993; Luo *et al.*, 1998; Dijkstra *et al.*, 1999; van Oijen *et al.*, 1999; Kim *et al.*, 2003; Sakai *et al.*, 2006; Zhu *et al.*, 2009). The linear relationships between V_{cmax} (or J_{max} , TPU) and leaf N assume that leaf photosynthetic N is

linearly related to total N, which may generally be the case (e.g. Hikosaka and Terashima, 1995). Macro-scale photosynthesis parameters (e.g. RUE, P_{max} , ϵ), however, even being related to leaf N, are still affected by [CO₂]. Moreover, their relationship with N is often non-linear. For example, Sakai *et al.* (2006) showed the quadratic relationship between RUE and N in rice, with higher RUE under elevated than ambient [CO₂] conditions. Similarly, a hyperbolic relationship between P_{max} and N was shown by Hirose *et al.* (1997) for *Abutilon theophrasti*, with higher P_{max} under elevated [CO₂] conditions.

This also exemplifies an often asked question in crop modelling – how deep, but not deeper, should one go to obtain stable values of a set of parameters in order to model a process in response to environmental variables? A common view of crop modellers is that parameterization of the biochemical model for different crops is difficult and time consuming (Tubiello and Ewert, 2002; Biernath *et al.*, 2011). Given the availability of a wealth of information for the key enzyme constants (see review of Yin and Struik, 2009), which are believed to be conservative among C₃ or C₄ species, the task of parameterization can focus on a few key parameters, estimated from readily available data (e.g. Medlyn *et al.*, 2002) or measurements (e.g. Yin *et al.*, 2009). Yin and Struik (2009) showed that an empirical leaf-photosynthesis model, as used by Matthews *et al.* (1997), incorrectly predicts the interaction of temperature and elevated [CO₂] on parameters P_{max} or ϵ . This problem can be overcome by expressing P_{max} and ϵ based on formulae of the Farquhar *et al.* (1980) biochemical model, as done by Mitchell *et al.* (1995) and van Oijen *et al.* (2004).

Leaf photosynthesis rate and stomatal conductance (g_s) are closely coupled (Wong *et al.*, 1979), and g_s has a profound effect on energy balance and leaf temperature, and hence on water use. An additional advantage of using the biochemical model is that once the model is coupled with an equation for g_s , the coupled model reliably predicts the response of g_s to environmental variables, including [CO₂] (Ball *et al.*, 1987; Leuning, 1995; Yin and Struik, 2009), and performs better than an empirical multiplicative g_s model (Li *et al.*, 2012). A similar argument may apply to modelling mesophyll conductance in response to [CO₂] and light levels (Yin *et al.*, 2009).

Leaf respiration

Besides photosynthesis, respiration has been examined extensively to determine whether it is altered by elevated [CO₂]. Review reports based on meta-analysis of multiple experiments reveal an overall effect of CO₂ on leaf respiration. Such analyses made by Poorter *et al.* (1992; based on published results for 47 species) and by Wang and Curtis (2002; 33 species) revealed that leaf respiration per unit leaf area (R_a) was slightly increased for plants grown at high [CO₂], whereas a small decrease was found when respiration was expressed on leaf weight basis (R_w , also known as ‘specific respiration rate’). Moreover, Wang and Curtis (2002) showed that the longer were plants exposed to elevated [CO₂], the smaller was the increase in R_a and the greater was the reduction in R_w by elevated [CO₂]. Most studies used for the meta-analysis did not measure leaf N content. Wullschleger *et al.* (1992) showed

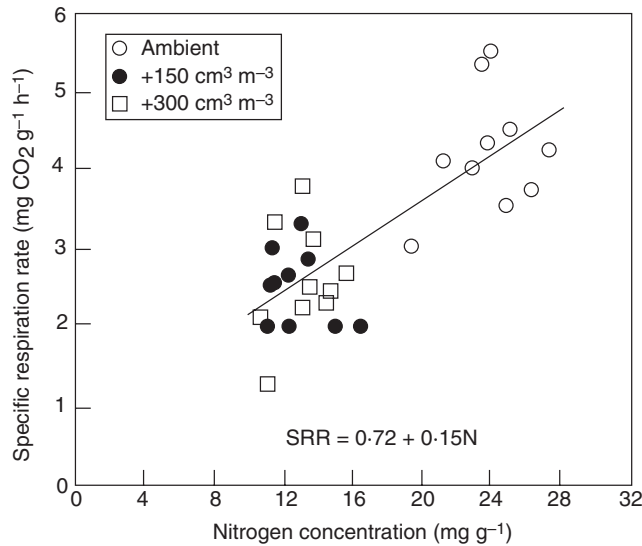


FIG. 3. Leaf respiration rate on a weight basis (or: specific respiration rate – SRR) as a function of leaf nitrogen concentration for 22-d-old yellow-poplar leaves of different ages from sapling grown at each of three CO₂ treatments (ambient, and two elevated [CO₂], increased over ambient by 150 and 300 cm³ m⁻³, respectively). Reproduced from Wullschlegel *et al.* (1992) with permission.

that leaf R_w differed among plants grown in three [CO₂] treatments, and the relationship of R_w values, despite a large scatter within each [CO₂] treatment, with leaf N concentration was shared by plants grown under three [CO₂] values (Fig. 3). This means that leaf respiration, if expressed on leaf N basis, will be affected little by [CO₂]. Ryan (1991) showed a similar linear relationship between R_w and N concentration for a wide variety of species and plant tissues. This relationship can explain the above-mentioned results of meta-analysis of Poorter *et al.* (1992) and Wang and Curtis (2002), as elevated [CO₂] leads to a reduced leaf N concentration (Wong, 1990; Conroy and Hocking, 1993) and an increased leaf mass/area ratio (Lawlor and Mitchell, 1991; Poorter *et al.*, 2009). Cannell and Thornley (2000) noted that maintenance respiration is generically related to total N content, rather than to biomass, because maintenance costs increase with tissue protein content and overall metabolic activity (Barnes and Hole, 1978). When maintenance is related to crop N content (which indirectly represents active protein content), there is little need for empirical correction of the maintenance coefficients for different growing organs or developmental stages (Cannell and Thornley, 2000), whereas such a correction is essential when maintenance respiration is related to biomass (Penning de Vries *et al.*, 1989; Matthews *et al.*, 1997).

Canopy leaf area index

Not only can leaf photosynthesis or respiration be affected by elevated [CO₂] but so too can canopy-scale traits such as leaf area index (LAI). As LAI determines the proportion of incoming radiation that is intercepted by a canopy, an accurate quantification of LAI is important for modelling crop response to elevated [CO₂] (Ewert, 2004).

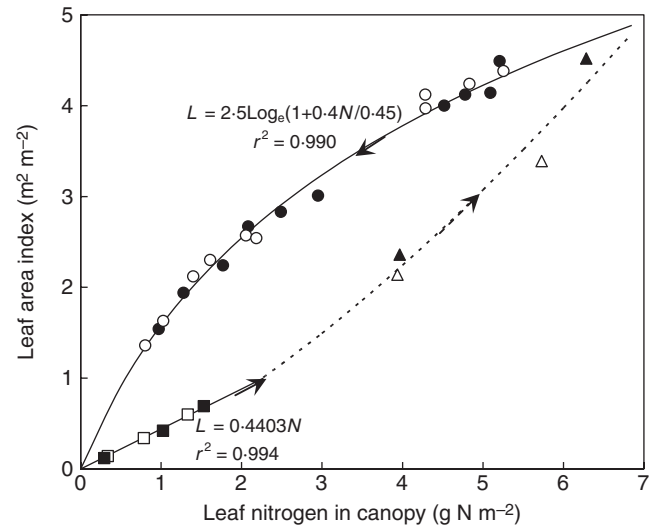


FIG. 4. Canopy leaf area index (L) plotted against canopy leaf-nitrogen (N) for rice plants grown under ambient (open symbols) and elevated (i.e. 200 $\mu\text{mol mol}^{-1}$ above ambient, filled symbols) CO₂ levels in a FACE experiment of Kim *et al.* (2003) with three nitrogen supply levels, for the early tillering phases if $L < 1$ (squares), for the late phase from panicle initiation to maturation (circles), and for the intermediate phase (triangles). The solid line and curve represent a linear equation and a logarithmic equation, fitted to the combined data of the two CO₂ levels, for the first phase and the third phase, respectively. The dotted curve was drawn from the expected transitional trajectory from the first to the third phase. Arrows indicate the temporal direction of L or N in each of the three phases.

LAI varies significantly with [CO₂] (e.g. Dijkstra *et al.*, 1999; Kim *et al.*, 2003; Sakai *et al.*, 2006) and, generally, elevated [CO₂] results in slightly higher LAI (see the review of Ainsworth and Long, 2004). Most models assume that this effect on LAI is indirect, via increased photosynthesis and leaf mass, which means a higher LAI under elevated [CO₂]. But for the same measurement times, the increased LAI under elevated [CO₂] was not always observed, and LAI could sometimes be even lower (Miglietta *et al.*, 1998; Dijkstra *et al.*, 1999; Kim *et al.*, 2003; Sakai *et al.*, 2006). Leaves usually become thicker under elevated [CO₂] (Thomas and Harvey, 1983), which limits an increase of LAI. These results suggest that LAI is not determined only by C supply. Experimental data have shown that LAI is in fact highly related to the amount of leaf N in the canopy (Yin *et al.*, 2003). Sakai *et al.* (2006) showed that the ratio of LAI under elevated to ambient [CO₂] increases linearly with the ratio of canopy leaf N under elevated to ambient [CO₂]. By plotting LAI against canopy leaf-N using the data of Kim *et al.* (2003) for rice, linear and logarithmic relations can be obtained for the early tillering phase and for the phase from panicle initiation to maturity, respectively (Fig. 4). Data points that did not follow either linear or logarithmic trends were those measured in the intermediate phase. These relationships coincide with the theoretical analysis of Yin *et al.* (2003) using a generic equation for LAI in relation to canopy leaf N. Note that in neither phase did elevated [CO₂] alter the relationships (Fig. 4). Limited data points for wheat (e.g. Dijkstra *et al.*, 1999; van Oijen *et al.*, 1999) showed a similar pattern for the relationship. These suggest

that the functional relationship for the canopy-size LAI, once being related to canopy-N status, is not altered by a change in [CO₂]. The LAI–N relationship also generates a robust method for predicting leaf senescence in the canopy (Yin *et al.*, 2000).

Crop sink size

Leaf photosynthesis, respiration and LAI are traits related to the source of net photosynthetic assimilates for crop production. Often crop yields can be limited by sink size, and some crop models simulate a number of ‘sink’-related traits, such as the number of grains per unit area, in addition to the traits of ‘source’ activity. Crop sink size responds to elevated [CO₂] (Lawlor and Mitchell, 1991; Mitchell *et al.*, 1993).

It has been frequently observed that grain number increases with N accumulation in crops (see review of Makino, 2011). Horie *et al.* (1997) found a close relationship between the number of spikelets per m² in rice and the amount of N accumulated through to the early reproductive stage (i.e. the critical period for forming spikelets), using data collected across locations of widely varied climate and edaphic conditions (Fig. 5A). Analysing data from FACE experiments (e.g. Kim *et al.*, 2001), Kobayashi *et al.* (2006) found a similar relationship for the fertile spikelets per m² and N accumulation through to the panicle initiation stage, which held across [CO₂] and N supply rate (Fig. 5A). The difference in the two relationships could be due to the genetic difference in average grain weight between cultivars used: 22.6 mg for ‘Koshihikari’ (Horie *et al.*, 1997) vs. 24.7 mg for ‘Akitakomachi’ (Kim *et al.*, 2001). If the spikelet number is multiplied by average grain weight to fully represent the sink size, the difference in the relationships of Horie *et al.* (1997) and of Kobayashi *et al.* (2006) virtually disappears (Fig. 5B). The plots in Fig. 5 support that the empirical relationship for sink size, once being related to crop N status, was unaltered by elevated [CO₂]. Limited data points from van Oijen *et al.* (1999) suggested that the conclusion also holds for wheat.

BALANCED QUANTIFICATION OF CARBON–NITROGEN INTERACTIONS TO MODEL PHOTOSYNTHETIC ACCLIMATION TO ELEVATED [CO₂]

The above analyses indicate that elevated [CO₂] changes little the functional relationships of plant growth if these relationships are expressed as a function of plant N status. This is in line with the early modelling concept of functional balance based on C–N interactions (e.g. Brouwer, 1962) and with early approaches of Thornley (e.g. Thornley, 1998) for grass modelling, although most of the classical work did not consider the effect of [CO₂]. Therefore, it is necessary to couple above-ground C assimilation with below-ground N uptake in crop models if the models are able to predict crop yields under any [CO₂] without much calibration needed. This echoes the suggestion of Stitt and Krapp (1999) that interpretation of experiments in elevated [CO₂] requires monitoring the N status of the plants.

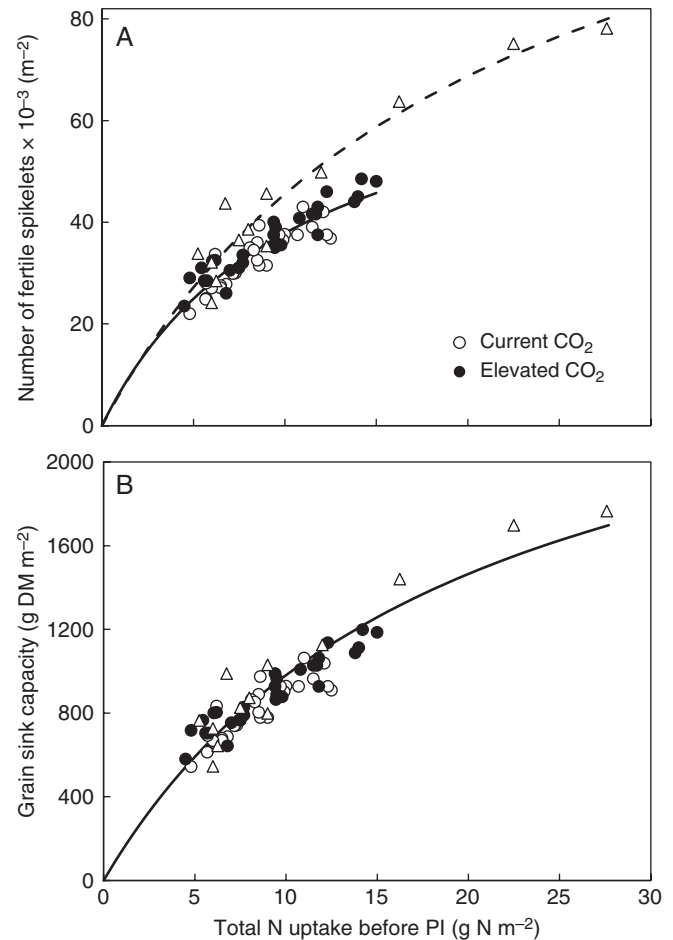


FIG. 5. (A) Relationships shown by Kobayashi *et al.* (2006) between the number of fertile spikelets at harvest and nitrogen (N) accumulated through to panicle initiation (PI), in which observations in a rice FACE experiment for current CO₂ and elevated are shown (as indicated in key), with the curve fitted to the FACE data (solid line) and the relationship (dashed line with triangles) reported by Horie *et al.* (1997). (B) Data re-analysed by correcting for the difference in average grain weight between the variety used in the FACE and that used by Horie *et al.* (1997) in such a way that the y-axis is represented as the full sink capacity i.e. number of fertile spikelets × average single grain dry-mass (DM) weight.

Based mainly on the concepts of the C–N interaction during crop growth, the crop model GECROS was developed (Yin and van Laar, 2005; see Supplementary Data). Compared with most existing crop models, GECROS has a more complex structure but requires fewer input parameters, because many of those used in more empirical models can be considered to be emergent properties of the mechanisms modelled by GECROS on the interactions of physiological processes.

Using data from a FACE experiment of Kimball *et al.* (1995) for wheat – the same data set that Tubiello *et al.* (1999), Tubiello and Ewert (2002), Long *et al.* (2006) and Ainsworth *et al.* (2008a) used to evaluate other models – Yin and Struik (2010) evaluated GECROS (v2.0) in estimating the impact of stimulation of yield by elevated [CO₂]. The analysis did not consider the experimental flaw as pointed out by Kimball (2013). Like most previous models, GECROS

correctly showed that the ‘CO₂-fertilization’ effect was larger under drought than non-stress conditions (Fig. 1), although underlying physiological mechanisms simulated differ among the models. However, whereas earlier crop models tended to over-estimate yield responses to elevated [CO₂], GECROS did not (Fig. 1) when standard parameters for instantaneous leaf photosynthesis and other growth processes of wheat were used. GECROS also simulated well absolute yields and total biomass across the treatments (Yin and Struik, 2010).

Yin and Struik (2010) attributed the good performance of GECROS without over-estimation to its ability in capturing the photosynthetic acclimation to elevated [CO₂]. This acclimation refers to an observation that initial enhancement of photosynthesis by elevated [CO₂] cannot be sustained over a longer term (e.g. Xu *et al.*, 1994; Vandermeiren *et al.*, 2002; Sakai *et al.*, 2006), which has been considered as a general rule although the extent of acclimation depends on species (Sage *et al.*, 1989; Bowes, 1993). Photosynthetic acclimation is probably not due to acclimation of g_s to elevated [CO₂] (Leakey *et al.*, 2006) but can be explained by mechanisms at various biological scales (e.g. Stitt and Krapp, 1999; Long *et al.*, 2004). Under elevated [CO₂] conditions, the enhancement in N uptake may not keep pace with that of C gain (Kim *et al.*, 2003). As a result, N dilution may occur as a result of increased C accumulation in plant materials (Skinner *et al.*, 1999), and N and organic-N concentration of plants and leaves under elevated [CO₂] may eventually be lower, irrespective of N availability (Wong, 1990; Conroy and Hocking, 1993; Pleijel and Uddling, 2012). One direct consequence of this effect is the previously discussed decrease of N content and photosynthesis at the leaf level, and an indirect consequence is faster senescence and reduced LAI at the canopy level for later stages, as observed experimentally (e.g. Miglietta *et al.*, 1998; Kim *et al.*, 2003). This effect of acclimation at both leaf and canopy levels is most evident under limited N conditions (e.g. Mitchell *et al.*, 1993; Stitt and Krapp, 1999). Photosynthetic acclimation could reduce the positive effect of elevated [CO₂] on crop yield by 50 % (Schapendonk *et al.*, 2000). To simulate this acclimation effect, a crop model has to appropriately quantify the C and N interaction. GECROS captures this acclimation at both leaf and canopy levels. At the leaf level, the photosynthetic advantage of plants grown under elevated [CO₂] will decrease with developmental stage as a result of a stronger decreasing leaf N content, compared with those under ambient [CO₂]. At the canopy level, there is an additional contributory mechanism: C-determined LAI is initially higher and leaves will soon senesce faster under elevated than ambient [CO₂] for a given canopy N content. As a result, LAI may eventually become smaller, compared with the canopy at ambient [CO₂] (Yin and Struik, 2010).

The low measured stimulation of elevated [CO₂] in the FACE experiments could be due to the aforementioned artefacts of the FACE system (Holtum and Winter, 2003; Bunce, 2012; Kimball, 2013). The GECROS-based analysis, however, suggests that the low stimulation of elevated [CO₂] for wheat in the FACE system was at least partly due to photosynthetic acclimation at both leaf and canopy level. Most existing crop models are unable to simulate the photosynthetic acclimation to elevated [CO₂], therefore tending to

overestimate the stimulation of elevated [CO₂], especially when model parameters for [CO₂] response are calibrated from enclosure studies.

The evaluation of GECROS by Yin and Struik (2010) demonstrated that a robust crop model requiring minimum inputs does translate input information at the single-organ level over a short timescale (e.g. photosynthetic rates on single leaves in $\mu\text{mol m}^{-2} \text{s}^{-1}$) to crop performance in a continuously changing field environment. Lenz (2007) and Lenz-Wiedemann *et al.* (2010) also showed good performance of GECROS in representing the growth of various crops and the interplay of water, C and N fluxes under field conditions. The separate evaluation of the model by Yin and Struik (2010) and Lenz-Wiedemann *et al.* (2010) confirms a well-recognized principle (e.g. Penning de Vries *et al.*, 1989) that a good model should be able to extrapolate the results from one to another experiment. Thus, to accurately predict CO₂ response of crop yield, one should not place emphasis on the type of experimental facilities to obtain data for parameterization, but on how the model is structured and how it is parameterized from available data. With a robust crop model, there is no need to seek for untested hypotheses (e.g. increased herbivory in FACE fields as compared with growth enclosures) for the failure to predict the CO₂ response ratio of crop yield using data of controlled enclosure environments. Similarly, the reliance on a large-scale FACE experimentation, as emphasized by Ainsworth *et al.* (2008b), could be considerably reduced. This latter assertion is especially true if the FACE facilities, due to the impact of [CO₂] fluctuation (Holtum and Winter, 2003; Bunce, 2012), cannot exactly mimic the real [CO₂] environment of future climate.

CONCLUDING REMARKS

Both statistical modelling (e.g. Schlenker and Roberts, 2009; Lobell *et al.*, 2011) and ecophysiological modelling approaches are currently used to assess the impact of climate change on crop production. Compared with statistical modelling, ecophysiological modelling research should play a greater role in facilitating the design of genetic and agronomic strategies of adaptation to climate change (Challinor *et al.*, 2009; Semenov and Halford, 2009). Algorithms in current ecophysiological crop models to simulate [CO₂] effects are, however, often empirical. Long *et al.* (2005, 2006) and Ainsworth *et al.* (2008a) indicated that when parameterized from controlled chamber environments, current crop models tend to overestimate the observed response of crop yield to elevated [CO₂] in the FACE experiments. They further argued that controlled chamber environments were not the best experimental facilities for estimating CO₂ response ratio of crop yield, as FACE has revealed factors in field conditions that were not identified by chamber experiments (e.g. increased herbivory). However, the lower than expected response to elevated [CO₂] could actually be explained by: (1) the different size between enclosure and FACE experiments (see earlier discussions), (2) the impact of the flaw in FACE technology, e.g. the ‘blower artefact’ (Kimball, 2013) and more [CO₂] fluctuation in FACE experiments (Holtum and Winter, 2003; Bunce, 2012) and (3) the inability of most crop models to accommodate photosynthetic acclimation to elevated [CO₂]. Although

further studies are needed to quantify the relative importance of the three explanations, the present paper discussed how to improve crop models to deal with the acclimation given that this acclimation is recognized as a general rule.

My analysis suggests that elevated [CO₂] alters quantitative functional relationships only little if they are expressed as a function of plant N status (Figs 2–5), suggesting that fundamental expressions of plant performance can be captured in relatively simple models. This viewpoint has been supported by the success in modelling root–shoot partitioning using functional balance theory (Brouwer, 1962) and in modelling stomatal and mesophyll conductance using phenomenological equations (e.g. Ball *et al.*, 1987; Leuning, 1995; Yin *et al.*, 2009; Li *et al.*, 2012). The analysis also showed that photosynthetic acclimation to elevated [CO₂] can be an emerging property of an appropriate quantification of interactions between C- and N-related processes. Crop models with such functionalities for C–N interactions have a sophisticated structure, but require few empirical input parameters – an important property of the models when used to extrapolate both in time and in space for assessment of climate change impact (Lenz-Wiedemann *et al.*, 2010). Their performance in projecting the impact of elevated [CO₂] will depend little on the type of experimental facilities used to obtain data for parameterization.

Such a robust crop model is a basis for developing a general framework that models critical physiological processes and traits in response to all climatic factors, including extreme events (Rötter *et al.*, 2011). It is also the basis to further improve the models based on new physiological understandings. Notably, my viewpoint stresses the need to model C–N relationships. However, photosynthesis and respiration should be related to active protein, whereas significant amounts of plant N can accumulate as nitrate (Cárdenas-Navarro *et al.*, 1999). [CO₂] enrichment was recently found to inhibit shoot nitrate assimilation into protein compounds, and this inhibition might alter the partitioning between leaf nitrate and protein and be responsible for photosynthetic acclimation to elevated [CO₂] (Bloom *et al.*, 2010; Pleijel and Uddling, 2012). This phenomenon might also be relevant to the differences in the [CO₂] response between controlled-environment chambers and FACE experiments where crops may have different access to nitrate relative to ammonium as an N source. Once the mechanisms for nitrate-assimilation inhibition are elucidated, an approach that models individual pools for inorganic and organic N may enhance mechanistic prediction of elevated [CO₂] effects on crop productivity.

In this paper I have discussed only generic aspects of crop responses to elevated [CO₂], especially those related to photosynthesis and respiration. Other processes also respond to [CO₂]. For example, early flowering was often associated with a higher canopy temperature induced by elevated [CO₂] (Craufurd and Wheeler, 2009). Direct phenological (Springer and Ward, 2007) and morphogenetic (Thomas and Harvey, 1983) responses to elevated [CO₂] are species-specific and need to be addressed differentially when developing models for specific crops. Finally, crop models should be combined with soil and pest models in order to account for indirect impacts on crops resulting from climate-induced changes in soil moisture and nutrient availability and in weed, insect and disease pressures (Soussana *et al.*, 2010; Hatfield *et al.*, 2011).

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SUPPLEMENTARY DATA

Supplementary data are available online at www.aob.oxfordjournals.org and consist of a detailed summary of the GECROS crop model.

ADDITIONAL NOTES IN RESPONSE TO THE COMMENTS OF KIMBALL (2013)

Following the online publication of this paper ahead of print, Kimball (2013) has noted several important points related to FACE experimentation and model projection of crop responses to elevated [CO₂]. In particular, he points out the flaw (i.e. the ‘blower artefact’) of the FACE experiment reported in Kimball *et al.* (1995), conducted in 1992–93 and 1993–94.

It would have been more timely if this particular comment had been published earlier following publications such as Ainsworth *et al.* (2008a), who commented on the over-estimation of yield response to elevated [CO₂] by existing crop models, based on data from the experiments of Kimball *et al.* (1995). I thank Dr Kimball for pointing out this experimental flaw explicitly, and as a result I have already made some small adjustments to several parts of this paper. To further respond to his comments, I put forth additional notes below.

The higher [CO₂] response ratio from the 1995–96 and 1996–97 FACE experiments (see Kimball, 2013) cannot be entirely attributed to the removal of the experimental artefact that existed in the 1992–93 and 1993–94 experiments. Besides the possible difference in climates between the years, actual nitrogen fertilizer application was appreciably higher in the 1995–96 and 1996–97 experiments (350 kg ha⁻¹) than in the 1992–93 and 1993–94 experiments (260–276 kg ha⁻¹; see Ko *et al.*, 2010). It is well known that plants generally respond more to elevated [CO₂] in high-nitrogen than in low-nitrogen environments (e.g. de Graaff *et al.*, 2006; also shown by the 1995–96 and 1996–97 experiments).

The water stress treatment was not repeated in the 1995–96 and 1996–97 experiments. Although the 1992–93 and 1993–94 experiments had a technical flaw, the ratio in the relative [CO₂] response between the two water treatments or the responses to water stress under either [CO₂] environment should still be quite representative of the real values. Such information would be very useful to test crop models in reflecting underlying biological mechanisms of [CO₂] × drought interactions, e.g. elevated [CO₂] reduces the loss due to higher photorespiration under drought (Long *et al.*, 2004). Relative to most other models, GECROS still predicts these ratios well (Fig. 6). Of course, it is necessary to use a wider range of FACE data to critically parameterize and evaluate the models, given the wide range of variation in reported crop responses to elevated [CO₂] (Ainsworth *et al.*, 2008a).

Kimball (2013) also discusses genotype-specific responses, and mentions a few Chinese FACE experiments that have

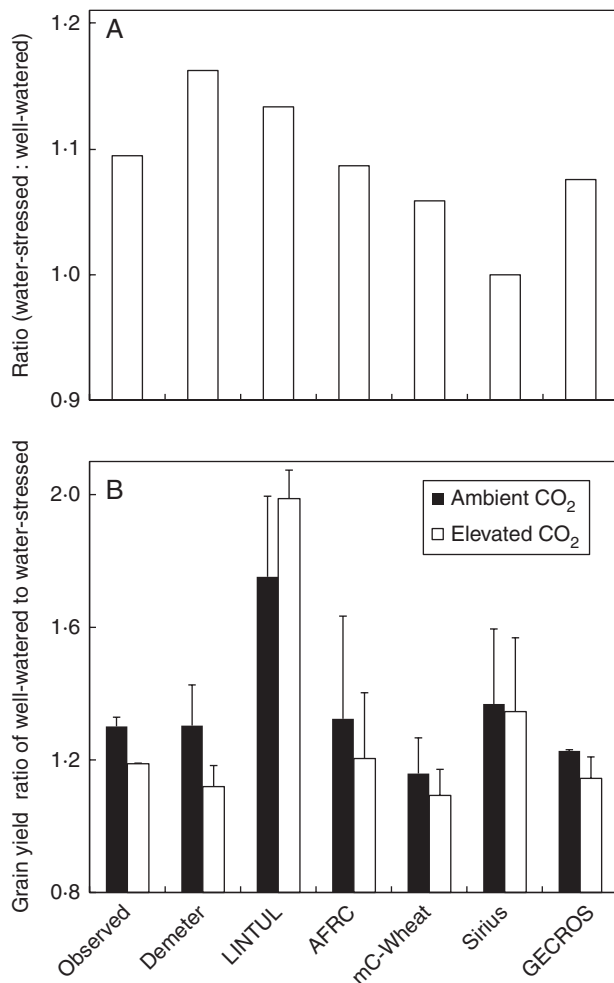


FIG. 6. (A) The ratio in stimulation of grain yield by elevated [CO₂] (relative to ambient [CO₂]) in the water-stressed treatment to that in the well-watered treatment for a wheat crop grown in the experiment reported by Kimball *et al.* (1995). This ratio was calculated from data as shown in Fig. 1. (B) The ratio of grain yield in the well-watered treatment to that in the water-stressed treatment under two different [CO₂] environmental conditions for the same crop. For further details see Fig. 1. The error bars represent standard errors for variation between two growing seasons.

reported a high response ratio to elevated [CO₂] in hybrid rice cultivars (see references therein). However, no inbred rice cultivar was used as a control in these FACE experiments. So, this higher value may simply add to the inconsistency already known in the literature on crop response to [CO₂], and not necessarily reflect an intrinsically higher response of hybrid rice. As mentioned in the Concluding Remarks above, my paper addresses only generic aspects of crop response to CO₂. Crop- (or genotype-) specific responses need to be addressed differentially for specific crops or genotypes.

Kimball (2013) emphasizes respective advantages of FACE and non-FACE in climate change research. However, my current paper never really questions the merits of these experimental facilities and their value in supporting modelling. In addition, Kimball (2013) stresses the importance of both relative and absolute responses to elevated [CO₂]. This is again not very different from the discussions in this current paper, where

I also indicate model performance in simulating absolute values for yield and biomass, although not in the format of a figure. In addition, models should also be evaluated in terms of intermediate physiological variables (such as time course of LAI and canopy transpiration), rather than only end-of-season yield traits.

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