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Elevated [CO₂] effects on crops: Advances in understanding acclimation, nitrogen dynamics and interactions with drought and other organisms

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Key message: In this review we highlight selected areas of plant interactions with elevated CO₂, where recently published experiments challenge long-held, simplified views.

Abstract

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Future rapid increases in atmospheric CO₂ concentration [CO₂] are expected, with values likely to reach ~550 ppm by mid-century. This implies that every terrestrial plant will be exposed to nearly 40% more of one of the key resources determining plant growth. In this review we highlight selected areas of plant interactions with elevated [CO₂] (e[CO₂]), where recently published experiments challenge long-held, simplified views. Focusing on crops, especially in more extreme and variable growing conditions, we highlight uncertainties associated with four specific areas: (1) While it is long known that photosynthesis can acclimate to e[CO₂], such acclimation is not consistently observed in field experiments. The influence of sink-source relations and nitrogen (N) limitation on acclimation is investigated and current knowledge about whether stomatal function or mesophyll conductance (g_m) acclimate independently is summarised. (2) We show how the response of N uptake to e[CO₂] is highly variable, even for one cultivar grown within the same field site, and how decreases in N concentrations ([N]) are observed consistently. Potential mechanisms contributing to [N] decreases under e[CO₂] are discussed and proposed solutions are addressed. (3) Based on recent results from crop field experiments in highly variable, non-irrigated, water-limited environments, we challenge the previous opinion that the relative CO₂ effect is greater under drier environmental conditions. (4) Finally, we summarise how changes in growth and nutrient concentrations due to e[CO₂] will influence relationships between crops and weeds, herbivores and pathogens in agricultural systems.

Introduction

Atmospheric CO₂ concentrations

Mostly driven by fossil-fuel burning and land use change, extensive direct and indirect measurements confirm that the average CO₂ concentration in the atmosphere ([CO₂]) has risen by about ~120 ppm over the past 250 years, to a current global average concentration of ~408 ppm in 2018 (Dlugokencky *et al.* 2018). The rise in [CO₂] has not been constant but the growth rate increased substantially in recent years. For example, the most recent increase by 50 ppm was reached within the last 25 years, from 1994 to 2018, while the first 50 ppm increase from pre-

industrial values required more than 200 years (Hartmann *et al.* 2013). Furthermore, future rapid increases in [CO₂] are expected, with values likely to reach ~550 ppm by mid-century and quite possibly ~1000 ppm by the end of this century, respectively (Hartmann *et al.* 2013). These predicted concentrations go beyond any values that have occurred over the past 20 million years and imply that every terrestrial plant will be exposed to nearly 40% more of one of the key resources determining plant growth by 2050.

In contrast to other atmospheric trace gases such as sulfur compounds, nitrogen oxides or ozone, CO₂ is not directly toxic. Workplace exposure limits for humans are high (the U.S. National Institute for Occupational Health and Safety gives time-weighted averages of 5000 ppm and short-term 30000 ppm as permissible exposure levels; <https://www.cdc.gov/niosh/npg/npgd0103.html>), and although there are reports on CO₂-toxicity on plant function (e.g. on nutrient uptake; Chang & Loomis 1945), such effects occur only under very high concentrations, and are difficult to separate from effects of oxygen displacement. Increasing [CO₂] therefore acts upon plant function through the role of CO₂ as a main plant nutrient and substrate of photosynthesis, affecting trade-offs in resource acquisition and allocation. In principle, there are only two primary effects of increasing [CO₂] on plant function, with all other currently known effects explicable by (often complex) downstream responses. The primary effects are: 1) stimulation of photosynthesis and 2) decrease of stomatal conductance.

Primary effects of elevated [CO₂] on plant physiology

In brief, as a key substrate for photosynthesis, rising [CO₂] directly stimulates photosynthetic carbon assimilation rates in C3 plants, because the key carboxylation enzyme Ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) is not saturated at current [CO₂]. Higher [CO₂] at the site of Rubisco stimulates carboxylation, and inhibits photorespiration, the pathway started by the oxygenation reaction of Rubisco. Photosynthetic stimulation of approximately 31% in C3 plants is usually seen at the concentrations predicted for later in this century, as, e.g., in a meta-analysis by Ainsworth & Rogers (2007) under Free Air CO₂ Enrichment (FACE, 567 ppm) conditions, but with considerable variation across functional groups (e.g. approximately 13% for C3 crops or 45% for trees) and environments. In contrast, in C4 plants, because of their mechanism of concentrating CO₂ in the bundle sheath cells to 2000 ppm, the oxygenation

reaction of Rubisco is completely suppressed whereas the carboxylation reaction is saturated (Hatch & Slack 1968; Poorter & Navas 2003). Because of this mechanism, C4 photosynthesis is not expected to increase under elevated $[\text{CO}_2]$ ($e[\text{CO}_2]$), at least in the first instance.

The second direct effect of $e[\text{CO}_2]$ on plant function is a decrease in stomatal conductance (g_s). At current $[\text{CO}_2]$, the concentration gradient driving H_2O vapour out of a leaf is about 40 times that driving CO_2 into it. Under $e[\text{CO}_2]$, this disparity is reduced, resulting in more favourable conditions for plants. Thus, one widely observed response of plants to $e[\text{CO}_2]$ is the partial closure of stomata. For example, Ainsworth & Rogers (2007), conducting a meta-analysis on results from FACE experiments, reported that $e[\text{CO}_2]$ reduced stomatal conductance by 22% across all plant species ($n = c\ 580$), with significant variability among functional groups. In most cases there was no change in stomatal density in response to CO_2 enrichment, so that changes in stomatal aperture are responsible for decreases. Stomatal closure is also observed in C4 plants, so that they may benefit from $e[\text{CO}_2]$ under conditions of drought (Manderscheid *et al.* 2014; Ottman *et al.* 2001).

Current research fronts

As there are many excellent recent reviews on impacts of $e[\text{CO}_2]$ on plants, and even specifically on crop plants (e.g. Wang *et al.* 2013, Kimball 2016, van der Kooi *et al.* 2016), we do not attempt a detailed quantitative analysis or an encyclopaedic overview, but highlight selected areas of $e[\text{CO}_2]$ -plant interactions, where recently published experiments challenge long-held, simplified views. We concentrate our efforts largely (although not exclusively) on Free Air CO_2 Enrichment (FACE) experiments, especially in highly variable environments. Despite some concerns about ‘unnatural’ short-term CO_2 fluctuations in such systems (Mollah *et al.* 2011; Bunce 2012), the relevance of growing crops in representative environments, and especially in interaction with often highly variable seasonal factors, allow FACE experiments to uncover the variability and uncertainty associated with field conditions.

Current theory posits that all effects of $e[\text{CO}_2]$ on plants are consequences of the changes in photosynthesis and g_s , and a multitude of effects on growth, elemental composition, water relations and interactions with other biotic and abiotic stresses has been described (Long *et al.*

2004). Focusing on crops, especially in more extreme and highly variable growing conditions, we highlight uncertainties associated with four specific areas:

(1) Under which conditions do plants acclimate to growth under $e[\text{CO}_2]$? It has been long known that under prolonged growth photosynthesis can acclimate - e.g. adjust physiologically - to $e[\text{CO}_2]$, so that it becomes less CO_2 -efficient. However, especially in FACE experiments, acclimation is not consistently observed, and a recent analysis suggested that better understanding of acclimation is needed to make current photosynthesis models more realistic (Rogers *et al.* 2017). Whether other physiological properties, such as stomatal function or mesophyll conductance, acclimate independently to $e[\text{CO}_2]$ is currently unknown or recent results are contradictory.

(2) How do N relations change in response to $e[\text{CO}_2]$? We demonstrate that the response of N uptake to $e[\text{CO}_2]$ is highly variable, even for one cultivar examined within the same field site, although the decrease in N concentration is very consistent. We update the mechanisms potentially contributing to [N] decreases under $e[\text{CO}_2]$ and outline the implications of decreased [N] on nutritional and end product aspects. Proposed solutions to overcome decreases are addressed.

(3) What is the interaction between $e[\text{CO}_2]$ and drought? Recent results from crop FACE experiments in highly variable, non-irrigated, water-limited environments, or from very dry years or rainout treatments in otherwise more humid environments challenge the previous opinion that the relative CO_2 effect is greater under drier conditions.

(4) Finally, we address how changes in growth and nutrient concentrations due to $e[\text{CO}_2]$ will influence relationships between crops and weeds, herbivores and pathogens in agricultural systems.

Acclimation to CO_2

Photosynthetic acclimation

The initial stimulation of C_3 photosynthesis by $e[\text{CO}_2]$ is not always maintained, because plants exposed for a longer period to $e[\text{CO}_2]$ often show photosynthetic down-regulation, also termed CO_2 acclimation. CO_2 acclimation is associated with lower activity of Rubisco, which can either result from reduced Rubisco activation state (Sage *et al.* 1988) or lower amounts of Rubisco

(Drake *et al.* 1997; Stitt & Krapp 1999), or both. Photosynthetic acclimation can be measured *in vivo* as a decrease in maximum carboxylation rate, V_{cmax} , a fundamental parameter in many photosynthesis models. Photosynthetic acclimation limits stimulation of photosynthesis, but generally does not cancel out the effect, at least not under field conditions (Leakey *et al.* 2009). Yet, acclimation may contribute significantly to current uncertainties in projecting the $e[\text{CO}_2]$ effect on plants (Rogers *et al.* 2017).

Source-sink relations influence photosynthetic acclimation

Acclimation is commonly associated with a mismatch between carbohydrate synthesis and carbohydrate utilisation in growing organs, termed ‘sink limitation’. When plants are not able to use the additional assimilates acquired under $e[\text{CO}_2]$, because sink strength of growing organs or metabolic assimilate consumption is insufficient, then assimilates accumulating in the leaves exert feedback inhibition on photosynthesis and Rubisco synthesis (Moore *et al.* 1999). Evidence to support the sink limitation hypothesis includes observations that CO_2 acclimation of photosynthesis is often associated with a significant accumulation of non-structural carbohydrates as shown in leaves of $e[\text{CO}_2]$ grown soybeans (*Glycine max*) (Sims *et al.* 1998) or stems in wheat (*Triticum aestivum*) (Macabuhay *et al.* 2018). Phloem loading strategies may affect the ability to export carbohydrates from leaves and species with different phloem loading strategies may be differently prone to photosynthetic acclimation (Bishop *et al.* 2018).

Further support for the sink-limitation mechanism of photosynthetic acclimation comes from experiments comparing related crop varieties or species with larger or smaller sink sizes. Reekie *et al.* (1998) reported that $e[\text{CO}_2]$ induced acclimation occurred in *Brassica* species with low sink strength (rape, mustard) whereas no acclimation was found for species with well-developed carbon sinks (broccoli, cauliflower). For soybeans, Ainsworth *et al.* (2004) found acclimation in non-nodulating iso-lines, but not in nodulating ones, whose *Rhizobium*-symbiosis is a major carbon sink. However, their comparisons of determinate (producing only a set number of pods) and indeterminate lines (which continue to produce new pods as long as carbohydrate supply continues) was less clear, because one determinate line had apparently large enough sink-capacity to avoid acclimation.

In FACE experiments acclimation is often not evident at all (Tausz-Posch *et al.* 2013a), although targeted comparisons, involving crop varieties with particularly limited (or particularly large) sink sizes, did confirm acclimation in some cases. For example, a tobacco line with limited leaf growth potential (leaves being the main sink in a tobacco crop) showed acclimation in a FACE experiment, but a line that can grow many large leaves did not (Ruiz-Vera *et al.* 2017). Similarly, a wheat line with limited shoot (tiller) production potential showed some symptoms of photosynthetic acclimation compared to a cultivar with high tillering potential, at least when measured during a vegetative growth stage (Thilakarathne *et al.* 2015), but this did not translate to a diminished CO₂-effect on final grain yield of the low tillering cultivar compared to a higher tillering one (Tausz-Posch *et al.* 2015). This latter example highlights the often temporary nature of source-sink relationships, such as during shifts from vegetative sinks to reproductive sinks, aspects that are already well appreciated in crop improvement programs, especially for environments with high within- and between-season variability (Fischer 2011). Accordingly, the extent of photosynthetic acclimation may vary strongly over the crop growth cycle. The change of the source-sink balance over the crop growth cycle is often fine-tuned by modern crop breeding efforts (Reynolds *et al.* 2017), and e[CO₂] will almost certainly affect such trade-offs.

Nitrogen limitation triggering photosynthetic acclimation

Perhaps more importantly from a crop production and quality perspective, acclimation is commonly associated with a decrease in leaf N concentration ([N]). If acclimation is linked to a decrease in Rubisco, which makes up a large proportion of leaf N, this should not be surprising. There is evidence that plants can avoid acclimation under sufficient but not deficient N supply (Ruiz-Vera *et al.* 2017), suggesting a more complex causality. For example, acclimation under low N supply can contribute to a decrease or even lack of CO₂-stimulation as observed in FACE experiments with cereal crops (Wall *et al.* 2000; Dier *et al.* 2018). Low N would also contribute to growth limitation or even prevent production of new organs and thus lead to sink limitation. However cause and effect play out, the changes in plant N metabolism associated with photosynthetic acclimation may be more important for crop quality than the relatively small moderation of the 'CO₂-fertilisation' effect on yields.

Photosynthetic acclimation through mesophyll conductance

A decrease in apparent V_{cmax} , symptomatic for photosynthetic acclimation, could also, or in part, be the result of a decrease in mesophyll conductance (g_m) to CO_2 (Ethier & Livingston 2004). Despite strong current interest in g_m in regards to crop improvement (Flexas *et al.* 2016), very little is known about the long term effects of $e[\text{CO}_2]$ on this process. In the short term, and in some species (e.g. bean) but not others (e.g. soybean, sunflower), g_m increases with decreasing internal CO_2 (C_i), especially at low C_i values, and independent of the method used to assess g_m (Bunce 2018). It has been suggested that ignoring g_m in terrestrial carbon exchange models leads to significant errors (Sun *et al.* 2014). However, traditional photosynthetic models use an ‘apparent’ V_{cmax} whose measured values implicitly include g_m . Carbon exchange estimates are therefore correct if models are re-parameterised with the decreased V_{cmax} values observed under $e[\text{CO}_2]$, even though mechanistic understanding of such changes is lacking (Rogers *et al.* 2017). This traditional approach does not allow to determine whether observed decreases in apparent V_{cmax} are due to decreases in the ‘true’ V_{cmax} (the in vivo activity of Rubisco), or to a decrease in g_m (contained in the commonly measured apparent V_{cmax}), or both, and to which proportion. A better understanding of the responses of g_m to environmental conditions is therefore desirable (Rogers *et al.* 2017), and would even be critical if g_m acclimates independently from the ‘true’ V_{cmax} to prolonged growth under $e[\text{CO}_2]$.

Stomatal acclimation

Stomata respond not only to $e[\text{CO}_2]$ but to a number of environmental factors, and their interactions are still unclear. Widely used empirical models of the Ball-Berry type can predict changes in stomatal responsiveness on the basis of a linear, empirical relationship between g_s a parameter combining photosynthetic rate (A) and humidity (h) as well as $[\text{CO}_2]$ ($= A \cdot h / [\text{CO}_2]$; Ball *et al.* 1987). Sensitivity of g_s to the environmental variables air humidity and $[\text{CO}_2]$ is indicated by the slope of the linear relationship in this model. Despite some early results from chamber studies suggesting the possibility of stomatal acclimation, FACE results from high rainfall agro-ecosystems generally found no evidence (Leakey *et al.* 2009). However, more recent results show that this assumption may have to be modified at least for drier conditions: In a semi-arid Mediterranean-type agroecosystem, Tausz-Posch *et al.* (2013b) found that the Ball-Berry slope was significantly different between ambient and $e[\text{CO}_2]$ grown wheat, implying a change in stomatal sensitivity. Similarly, stomata of $e[\text{CO}_2]$ grown soybeans responded more

sensitively to drying soil than ambient $[\text{CO}_2]$ grown plants when drought was more severe (Gray *et al.* 2016), in contrast to previous results at the same site under ample water or moderate drought. In apparent contrast, using a Jarvis-type g_s model, which uses independent empirical response functions to multiple environmental factors, Houshmandfar *et al.* (2015) found that stomata of $e[\text{CO}_2]$ grown wheat responded less sensitively to drying soil, that is, stomatal closure was initiated earlier – at greater soil water content – under ambient $[\text{CO}_2]$ than under $e[\text{CO}_2]$. It is difficult to compare these results directly because the Jarvis-type model employed by Houshmandfar *et al.* (2015) uses relative functions (with values between 0 and 1) to scale a maximum (unstressed) conductance (g_{max}). In accordance with most other studies, $e[\text{CO}_2]$ significantly depressed g_{max} in the first place, so that a less sensitive response from this lower g_{max} to drying soil can lead to similar absolute conductance as a more sensitive (stronger) response starting from a greater g_{max} value under ambient $[\text{CO}_2]$.

Although such discrepancies, especially among studies using comparable Ball-Berry models clearly warrant further investigation, and environmental variability especially in timing of water availability and evaporative demand may play an important role. Mechanisms underlying such changes in stomatal sensitivity are yet unresolved. Increased abscisic acid (ABA) concentrations in leaves are commonly associated with stomatal closure under drought but in one study on soybean in very dry seasons, measurements of xylem and leaf ABA showed that it was stomatal sensitivity to ABA, not ABA concentrations themselves, that changed (Gray *et al.* 2016). Whatever the exact mechanisms, changes in stomatal sensitivity may have effects on plant water balance and carbon acquisition, and these effects would be additional to the general decrease in g_s under $e[\text{CO}_2]$.

Nitrogen relations under elevated $[\text{CO}_2]$

Impacts on nutritional quality

It is well known that growth under $e[\text{CO}_2]$ changes plant stoichiometry, in particular the C/N ratio or N concentration ($[\text{N}]$) in biomass (Loladze 2002). As total $[\text{N}]$ is linked to protein concentrations, such a decrease compromises nutritional quality of plant materials, for human nutrition as well as for feed quality. Of greatest concern are decreases in grains, because they have negative implications for the nutritional quality and end-product uses of important staples.

Conducting a meta-analysis on wheat, rice, maize, sorghum, field peas and soybeans, $e[CO_2]$ was associated with lower protein content in wheat and rice grains and slight decrease in field peas (Myers *et al.* 2014). Implications of decreased grain [protein] are numerous. In countries where the main protein source comes from C3 grains (e.g. India, Swaminathan *et al.* 2012), decreases in grain protein may lead to serious public health concerns (Myers *et al.* 2014). Also, grain protein is directly related to bread-making quality which requires a minimum protein concentration of 11.5 % and a decrease under $e[CO_2]$ might decrease values below the minimum quality standard (Högy & Fangmeier 2008). For example, a study by Panozzo *et al.* (2014) reported of a compromised baking quality of bread when wheat was grown under $e[CO_2]$ with protein composition showing greater glutenin/gliadin ratios as well as reduced starch damage and amylograph peak viscosity. In contrast, for malting barley the lower [N] under $e[CO_2]$ is actually a quality advantage (Erbs *et al.* 2010).

Response of N uptake to elevated $[CO_2]$

N uptake under $e[CO_2]$ is strongly correlated with biomass stimulation indicating the dependency of nutrient foraging on whole-plant sink strength (Tausz *et al.* 2017a). The relative magnitude of the CO_2 response varies greatly across studies with some suggesting unchanged (e.g. Wang *et al.* 2013) and others suggesting greater N uptake under $e[CO_2]$ (e.g. Lam *et al.* 2012a), perhaps partly dependent on developmental stage (Houshmandfar *et al.* 2018). Figure 1 shows the CO_2 response of N uptake in relation to biomass stimulation of one wheat cultivar (*Triticum aestivum* cv. 'Yitpi') grown from 2007 to 2015 at the Australian Grains FACE site. In that highly variable agro-ecosystem, CO_2 response varies greatly even for the same cultivar grown at the same field site over several years. The effect of CO_2 on N uptake and biomass stimulation ranged from negative to highly positive, potentially reflecting the high plasticity of that particular cultivar to adapt to seasonal trends (Tausz *et al.* 2017a). There was no indication that total in-season water supply influenced the magnitude of response (solid vs open symbols) thus timing of in-season rainfall, differences in stored soil water and/or temperature might have driven the results (Figure 1), indicating a strong dependence of CO_2 stimulation on environmental factors.

The figure also reveals that when the effect of $e[CO_2]$ on aboveground biomass is small or zero, N uptake is lower than under $a[CO_2]$ (negative intercept of linear equation) whereas with strong

stimulation of aboveground biomass, N uptake is also stimulated resulting in a positive slope of the linear equation. This slope is not significantly different from the 1:1 line, although the effect of $e[\text{CO}_2]$ on N uptake generally does not match biomass stimulation. Across all years, $e[\text{CO}_2]$ increased aboveground biomass on average by 23% whereas N uptake increased by only 15%, as indicated by the offset (but not changed slope) from the 1 : 1 line (Figure 1). This result is in line with the synthesis by Feng *et al.* (2015), who reported of a 16% biomass stimulation in comparison to an 8% N acquisition stimulation across different ecosystems, including crop- and grasslands as well as forests.

N concentrations and its influencing mechanisms

Independent of the relative magnitude of the CO_2 effect on N uptake and biomass stimulation, biomass N concentration ([N]) is consistently decreased under $e[\text{CO}_2]$; by ~7% as indicated in Figure 1, comparable with the 8% reported by Feng *et al.* (2015) or 5-6% decrease in leaves of C3 species reviewed in Wang *et al.* (2012). With few exceptions (Sinclair *et al.* 2000), such a step-decrease in leaf [N] seems quite conserved across environmental conditions or even N application rates in FACE experiments, as shown in wheat (Tausz *et al.* 2017a; Dier *et al.* 2018). This confirms that although the effect of CO_2 on N uptake and biomass can vary considerably, reductions in [N] are very consistent.

One of the most straightforward hypotheses proposed for the decrease in [N] is the biomass dilution hypothesis (Poorter *et al.* 1997, Taub and Wang 2008), which posits that the decrease in [N] under $e[\text{CO}_2]$ results when N uptake does not keep up with biomass stimulation. In figure 1, biomass dilution should result in a slope significantly less steep than the 1:1 line, with the relative increase in biomass outpacing the relative increase in N acquisition (Feng *et al.* 2015). However, in line with results synthesised by Feng *et al.* (2015), Fig. 1 shows a decrease in [N] and N uptake even without $e[\text{CO}_2]$ -stimulation of biomass growth, but no decrease in the slope, hence the decrease on a whole plant basis cannot be explained by biomass dilution. This is also supported by earlier studies which showed that leaf [N] remains reduced under $e[\text{CO}_2]$ even after adjusting for increased non-structural carbohydrates (Poorter *et al.* 1997; Taub & Wang 2008).

It is noteworthy that in a similar analysis, but on wheat grain yield versus grain N, Pleijel & Uddling (2012) found a significant decrease of the slope of the relationship compared to the 1:1 line, in addition to a similar offset by about 7% (Figure 1). It seems that in the process of grain formation, but apparently not in the process of whole plant N uptake, there is some effect of biomass dilution detectable. In contrast, in recent wheat studies in dryland agro-ecosystems, where grain N comes primarily from N taken up early in the season and then being remobilised into the filling grains later in the season (Palta & Fillery 1993), there was no clear indication that N remobilisation into grains changed under e[CO₂] when bulk indicators such as N harvest index (the proportion of biomass N that ended up in grains) or loss of N from flag leaves (as the major N source for remobilisation) were reported (Tausz *et al.* 2017b; Macabuhay *et al.* 2018). Changes in relative expression of related genes over the critical grain filling period, however, do suggest alterations in N and C metabolism during the grain filling process (Buchner *et al.* 2015). Those latter results were from a water-limited agro-ecosystem, whereas most of the data synthesised by Pleijel & Uddling (2012) were from higher rainfall or continuously irrigated studies. Without more detailed C and N budgeting studies in different environmental conditions, it is yet unclear how biomass dilution may contribute to the decrease of grain [N] but not total aboveground biomass [N].

What other factors contributing to the reduction in plant [N] under e[CO₂] are emerging? Following the pathway of N from the soil into the plant, the first interface is the root system. Roots generally become more numerous, longer and thicker (e.g. Van Vuuren *et al.* 1997; Madhu & Hatfield 2013) under e[CO₂], which might suggest greater nutrient uptake capacity, which is often assumed to be proportional to root biomass. Commonly observed shifts in the distribution of roots within the soil profile towards the surface (Pritchard & Rogers, 2000) or into greater depth (Uddin *et al.* 2018c), however, might decrease the efficiency of soil exploration (Fitter *et al.* 1996). In environments where soil exploration is important, this could contribute to the decline in [N] under e[CO₂]. Also, a biomass- or root-architecture centred approach does not include uptake rate capacities which may differ significantly between CO₂ treatments.

Uptake of N into roots takes place passively via mass flow in the transpiration stream as well as actively against concentration gradients via specialised transporters (White *et al.* 2012).

Transporters were identified for nitrate, ammonium and organic N (e.g. Hawkesford 2011) and differences in, for example, nitrate transporter activity were related to differences in N uptake capacity and N uptake among genotypes (Melino *et al.* 2015). So far little is known about the effect of $e[CO_2]$ on transporters, but a recent study by Tausz *et al.* (2017a), using a ^{15}N label method on intact roots under FACE, found no evidence that specific root uptake capacity for nitrate, ammonium or glutamine (used as a model organic N source) was affected by $e[CO_2]$. They concluded that N uptake strategies were unrelated to changes in grain or biomass [N] at the investigated field site.

Because $e[CO_2]$ decreases stomatal conductance and therefore may decrease transpiration (e.g. Leakey *et al.* 2009; Tausz-Posch *et al.* 2013b), the mass flow hypothesis suggests that the flow of N to the roots decreases under $e[CO_2]$ contributing to decreases in N uptake (van Vuuren *et al.* 1997; Taub & Wang 2008). Evidence was provided by McGrath & Lobell (2013a) who showed in their meta-analysis that nutrients whose uptake depends significantly on mass flow, including N, are more decreased under $e[CO_2]$ than nutrients driven by diffusion to the roots. Measuring transpiration and nutrient uptake simultaneously within the same field setting, Houshmandfar *et al.* (2018) confirmed the relationship but also showed that nutrient uptake per unit of water transpired was consistently greater under $e[CO_2]$ compared to $a[CO_2]$, including for N. If reduced mass flow were the sole mechanism responsible for decreased nutrients under $e[CO_2]$, then nutrient uptake per unit transpiration would be the same for ambient and $e[CO_2]$ grown crops. The observed difference suggests that mechanisms other than reduced mass flow contribute to nutrient decreases. In addition, Feng *et al.* (2015) noted that the mass flow hypothesis is in conflict with the finding that g_s is decreased under $e[CO_2]$ in C3 and C4 plants, but the negative effect on N at unchanged productivity is mostly observed in C3 plants, pointing to the involvement of other mechanisms, presumably directly related to physiological responses of C3 plants. The analyses in Fig. 1 and previous ones by Feng *et al.* (2015) and Pleijel & Uddling (2012) indicate a step-change in N uptake under $e[CO_2]$ independent of biomass stimulation, consistent with a physiological readjustment of N metabolism to $e[CO_2]$. However, these analyses do not allow to identify such a mechanism.

There are currently two main, not necessarily mutually exclusive, contenders. Firstly, one such mechanism may follow from photosynthetic acclimation discussed previously, as a decrease in Rubisco would be linked to a decrease in total leaf [N]. If downregulation of net Rubisco synthesis occurs, as postulated in the carbohydrate feedback hypothesis (Moore *et al.* 1999), then a knock-on effect on N uptake would be possible. Secondly, there is recent evidence that e[CO₂] directly affects the N metabolism in plants by inhibiting nitrate assimilation (e.g. Bloom *et al.* 2010, 2014). In C₃ plants, nitrate assimilation is linked to photorespiration. Because photorespiration rates are decreased under e[CO₂], there is less reductant available, which could negatively affect nitrate reduction (Bloom *et al.* 2014). In support of this hypothesis, recent FACE studies reported that wheat leaves grown under e[CO₂] had a significantly greater proportion of unassimilated nitrate remaining in the N pool of their leaves than their a[CO₂] grown counterparts (Bloom *et al.* 2014; Bahrami *et al.* 2017). Additionally, the stable isotope ratios of organic N and free nitrate also suggested that nitrate assimilation was slower under e[CO₂] (Bloom *et al.* 2014) and there was a significant correlation with grain protein: The greater the percentage of N remaining as unassimilated nitrate in the tissue, the lower the grain protein concentration, hinting at the negative implications of reduced nitrate assimilation not only for tissue [N] but also grain [N] (Bahrami *et al.* 2017). Considering that e[CO₂] inhibits shoot nitrate assimilation in C₃ but not C₄ plants (Bloom *et al.* 2012), this hypothesis also helps to explain observed differences in [N] between C₃ and C₄ plants. In contrast, a recent study by Dier *et al.* (2018), also investigating wheat under FACE conditions, did not find e[CO₂] effects on nitrate reductase activity or transcript levels and concluded that an inhibition of nitrate assimilation is not the reason for decreases in [N] under e[CO₂] in their study. It is noteworthy that the studies by Bloom *et al.* (2014) and Bahrami *et al.* (2017) were conducted on spring wheat in hot climates (Maricopa, Arizona, and Horsham, Australia, respectively) at N saturation whereas the study by Dier *et al.* (2018) was conducted on winter wheat in a cooler climate (Braunschweig, Germany) at ample N supply. Although Dier *et al.* (2018) investigated the dependency of nitrate reductase activity on photorespiration at moderate (16.7°C) and warm (27.6°C) temperatures and found no differences in nitrate reductase activity, these temperatures are still well below temperatures found in the other two studies, often exceeding 30°C. Furthermore, even without changes in nitrogenase activity or transcript levels, the flux through the nitrate assimilation pathway may still change if concentrations of substrates and co-substrates change, and it is this

overall flux through N reduction that is marked by the ^{15}N method applied in Bloom *et al.* (2014).

Can decreases in plant [N] under e[CO₂] be ameliorated by increased N fertilisation?

If declines in plant [N] under e[CO₂] are caused by changes to N metabolism rather than N availability in the soil, then it would not be expected that N application above optimum growth requirements would ameliorate this decrease. Whilst most previous studies in crop FACE systems compared sub-optimum with optimum N supply, some recent results with higher N rates confirmed such an expectation. In a dryland FACE system limited by water but not by N, Tausz *et al.* (2017b) found no evidence for amelioration of decreases in plant [N]. Although there were small increases in [N] with N addition, the increases were not sufficient to offset e[CO₂]-induced declines in [N]. Similarly, Feng *et al.* (2015), categorising data of their study into groups of very high, high and intermediate/no external N supply, found that e[CO₂] most strongly affected N acquisition (at unchanged productivity) at very high N supply, also implying that simply increasing N fertilisation will not offset decreases in plant [N] under e[CO₂]. Promising might be the exploitation of genotypic variability in the ability to maintain grain [N] as found in field pea (*Pisum sativum* L.) cultivars (Bourgault *et al.* 2016) but a similar response has yet to be confirmed for wheat.

Interactions of elevated [CO₂] and drought

Interactions of e[CO₂] with water availability contribute significantly to regional variability and uncertainty in modelled predictions of crop production in a changing climate (McGrath & Lobell 2013b). Even where models include functions to estimate interactive effects, they commonly assume that relative CO₂ effects on yields are greater towards the drier end of the water availability spectrum (McGrath & Lobell 2013b). However, recent experimental results discussed in the following section show that these simple functions must be revised, and first model extrapolations of e[CO₂] responses with a more realistic representation of factors give different results (Jin *et al.* 2018). Only with better understanding of CO₂ x water interactions will it become possible to extrapolate potential adaptive strategies, such as water saving traits, to larger regions (Christy *et al.* 2018).

Water use efficiency

The conviction that the effect of $e[\text{CO}_2]$ on growth and yield is greater under drought is widely reported (Kimball *et al.* 1995; Leakey *et al.* 2009; Kimball 2016). The nearly paradigm status appears fundamental because the two direct effects of $e[\text{CO}_2]$ on leaf physiology (increased assimilation rate and decreased stomatal conductance) logically result in greater leaf level water use efficiency, *i.e.* more carbon assimilated per unit of water lost (Leakey *et al.* 2009; Tausz-Posch *et al.* 2013b). Many results from FACE experiments not only confirmed greater leaf level water use efficiency (Bernacchi *et al.* 2007; Tausz-Posch *et al.* 2013b), but often also showed that leaf level effects translated to canopy scale reductions in transpiration (Kimball *et al.* 1995; Bernacchi *et al.* 2007), which in turn can lead to soil water savings throughout the season (Erbs *et al.* 2009; Manderscheid *et al.* 2018). Such greater water reserves could sustain yield formation processes for longer through drought periods, and would be of particular benefit for grain crops during the later reproductive growth stages, when yield formation depends on sufficient carbon supply to the filling grains.

C4 crops

The water x CO_2 interaction is relatively straightforward in C4 crops, whose photosynthesis operates at CO_2 -saturation already at current ambient CO_2 concentrations. Therefore, C4 plants generally show $e[\text{CO}_2]$ -stimulation of productivity only under drought conditions, when gains in transpiration efficiency allow photosynthesis to be maintained for longer (Leakey *et al.* 2006; Ghannoum, 2000). This was demonstrated by Leakey *et al.* (2006) and Manderscheid *et al.* (2014) in maize. Even in a relatively high rainfall agro-ecosystem, drought years saw $e[\text{CO}_2]$ -stimulation of biomass and grain yield, but no such stimulation was observed in years when soil moisture was adequate (Manderscheid *et al.* 2014). In sorghum, Ottman *et al.* (2001) showed yields were increased by 15% with $e[\text{CO}_2]$ under the dry treatment, but no change was observed under irrigation. Similarly, a meta-analysis that synthesised only CO_2 experiments where drought-stressed and well-watered crops were compared side by side, confirmed that C4 crops only benefited from $e[\text{CO}_2]$ under drought conditions (van der Kooi *et al.* 2016). Also, Leakey *et al.* (2006) showed that a 34% decrease of g_s in maize led to higher soil moisture throughout most of the season. Although such greater soil moisture can be responsible for $e[\text{CO}_2]$ -

stimulation of C4 crop yields if drought is otherwise limiting yield, in some high rainfall areas it might also lead to greater deep percolation and nitrate leaching (van Ittersum *et al.* 2003).

C3 crops

For C3 crops, an increasingly complex picture of CO₂ x water interactions emerges. Now that more results from field experiments conducted over a wider range of environmental conditions have become available, the notion that the e[CO₂] effect is generally greater under drier conditions cannot be upheld for C3 crops (Gray *et al.* 2016; Houshmandfar *et al.* 2016; Parvin *et al.* 2018). For example, although Fitzgerald *et al.* (2016) found that across two water-limited, low yielding agro-ecosystem FACE sites relative wheat yield response to e[CO₂] was greater in the more arid location and sometimes greater in drier than higher rainfall seasons, paradoxically within one and the same agro-ecosystem, responses were consistently greater when some supplemental irrigation was applied. Similarly, there was no difference in the CO₂ effect between well-watered and drought treated C3 crops in side by side experiments (van der Kooi *et al.* 2016), contrasting earlier reviews synthesising predominately results from high rainfall or continuously irrigated FACE experiments.

Effect size metric

One formal aspect must be considered when evaluating relative effect sizes among experiments in different agro-ecosystems: The common choice of the response ratio as the effect size metric in many meta-analyses over-emphasises e[CO₂]-effects in situations where growth and yield is very low in absolute terms. At the extreme end, the response ratio would become infinitely large if e[CO₂] led to some grain yield where crops failed completely under ambient CO₂ (Gifford, 1979). For example, the very high response of wheat yield to e[CO₂] (up to 79%) reported in Fitzgerald *et al.* (2016) and pointed out in the meta-analysis by Kimball (2016) occurred in a particularly low yielding, semi-arid agro-ecosystem. In terms of mean difference (an alternative effect size measure), the response is less impressive, as it amounts to a yield increase of about 0.8 t wheat grains ha⁻¹ (Fitzgerald *et al.* 2016), similar or less than in many cases with lower response ratios. Similarly, Bourgault *et al.* (2017) found dramatic responses of lentil (*Lens culinaris*) yields (up to 138%) in a very low yielding season in a dryland agro-ecosystem, but the same effect in terms of yield difference was only 0.5 t ha⁻¹.

523
524 *Interactions of elevated [CO₂] with water use over the crop growing cycle: Possible scenarios*

525 Most of the complexity in the interaction between water and e[CO₂] is independent of the
526 chosen effect size metric and arises in environments with highly variable and limiting water
527 availability. Figure 2 illustrates different possible scenarios of how e[CO₂] can affect wheat
528 water use and related growth and yield in water-limited agro-ecosystems such as those studied in
529 the Australian Grains FACE programme (Tausz-Posch *et al.* 2015). In such Mediterranean-type
530 semi-arid agro-ecosystems, crops are sown in autumn and mature during spring and early
531 summer under increasing evaporative demand and commonly develop terminal drought (Turner
532 2004). Depending on the highly variable in-season rainfall amount, crops rely to a variable extent
533 on soil water reserves during the important grain-filling period (Fischer 2011; Fig. 2A). Due to
534 the high within- and between-season variability in such agro-ecosystems, extent and possibly
535 even direction of e[CO₂] effects on growth and yield may be different from season to season
536 (Tausz-Posch *et al.* 2012; Tausz-Posch *et al.* 2015; Houshmandfar *et al.* 2016; Fitzgerald *et al.*
537 2016). For example, in e[CO₂] scenario 1 (Fig. 2B), where gains in leaf level water use
538 efficiency translate to soil water savings during earlier growth, the additional soil water reserve
539 is available after flowering to sustain grain-filling. In water-limited growing environments, such
540 additional water available later in the season has a very high conversion efficiency into grain
541 yield (Kirkegaard *et al.* 2007). Elevated [CO₂] Scenario 1 thus represents the mechanism
542 commonly cited to explain a greater e[CO₂] effect under drought (Leakey *et al.* 2009) and
543 experimental evidence supporting this comes mainly from high rainfall or continuously irrigated,
544 high yielding environments, especially seen during moderate and transient droughts (Kimball *et*
545 *al.* 1995; Bernacchi *et al.* 2007; Erbs *et al.* 2009).

546
547 In more water-limited environments, it is well known that water savings during earlier growth
548 can be productively used to boost yields (Condon *et al.* 2002). Irrespective of e[CO₂],
549 transpiration efficient wheat cultivars selected for dryland agro-ecosystems can save soil water
550 during early growth, and this soil water can be exploited later in the season. Such a transpiration
551 efficiency trait has been shown to be particularly beneficial in systems where stored soil moisture
552 is relatively important (Rebetzke *et al.* 2009). As e[CO₂] increases transpiration efficiency of all
553 cultivars, one might expect the advantage of such a transpiration efficiency trait to be diminished

under $e[\text{CO}_2]$, yet experimental FACE results showed the opposite (Tausz-Posch *et al.* 2012), and extrapolation of these results to a larger cropping region confirmed this trend (Christy *et al.* 2018). The explanation may be that $e[\text{CO}_2]$ changes the water use dynamics of the agro-ecosystems, possibly shifting timing and extent of water use in a way that amplifies the benefit of greater transpiration efficiency during early growth.

Growth under $e[\text{CO}_2]$ may change the seasonal water balance of crops more drastically, as illustrated in $e[\text{CO}_2]$ Scenario 2 (Fig. 2C). Scenario 2 sees overly vigorous growth stimulation by $e[\text{CO}_2]$ early in the season, and despite decreased stomatal conductance this greater biomass may transpire more and deplete soil water faster (e.g. Samarakoon *et al.* 1995), which causes a shortage of available soil water during the critical grain-filling stages. In extreme cases, wheat plants may produce many and large tillers that can then not be converted into grain yield during a dry seasonal finish. Such ‘haying off’ phenomena have been characterised in response to excess N application, which can stimulate early growth too much for a dry season finish (van Herwaarden *et al.* 1998), and $e[\text{CO}_2]$ may play a role analogous to that of N fertiliser. Symptoms of ‘haying off’ might include a decrease in harvest index (the ratio of grain yield over total biomass), possibly even in combination with a negative absolute effect of $e[\text{CO}_2]$ on yield. Only under the most extreme conditions ‘haying off’ resulted in loss of CO_2 -stimulation of yield in FACE (Fitzgerald *et al.* 2016), but less extreme indications of shifting trade-offs between biomass production and yield formation were observed more consistently. For example, consistent with early stimulation of biomass and tillering, a freely tillering wheat cultivar exhibited poor ‘tiller economy’ under $e[\text{CO}_2]$ in a dryland agro-ecosystem (Tausz-Posch *et al.* 2015), even though it still produced yield increases. Poor tiller economy implies that more tillers were ‘unproductive’, that is, they ended up without heads and grains.

Although the likelihood of either $e[\text{CO}_2]$ Scenario 1 or 2 or any response in between is determined by the relative timing of water availability and effects of $e[\text{CO}_2]$ on growth and water use, the probability of $e[\text{CO}_2]$ reducing rather than conserving soil water appears greater under drier conditions. In a highly productive and high rainfall soybean agro-ecosystem, very dry years resulted in a sparser canopy (Gray *et al.* 2016). Stimulation by $e[\text{CO}_2]$ of sparse leaf area can have a greater effect on canopy transpiration than the same relative stimulation of an already

very dense canopy, because at high leaf area index (dense canopies), small leaf area increases do not increase transpiration further. Wheat breeders targeting rainfed, semi-arid agro-ecosystems are already focusing on traits that fine tune trade-offs between biomass growth and yield formation (e.g. restricted tillering traits; Moeller & Rebetzke 2017), leaf level transpiration (e.g. high transpiration efficiency traits; Condon *et al.* 2002) or canopy closure (e.g. early vigour traits; Rebetzke *et al.* 2004), and such trade-offs will be directly affected by $e[CO_2]$. However, as these trade-offs are highly crop- and site-specific, quantitative extrapolation from the relatively few FACE sites is difficult and uncertain and highlights the lack of experimental data for many important agro-ecosystems.

Root growth is an additional factor that can complicate the interaction of $e[CO_2]$ with water availability. Interest of crop breeders in root systems is already high, because bigger and deeper roots were linked to improved access to water in dryland agro-ecosystems (Palta *et al.* 2011). As $e[CO_2]$ generally stimulates both above- and belowground biomass (Benlloch-Gonzalez *et al.* 2014), larger root systems may allow access to additional water during critical grain-filling stages, as represented by scenario 3 (Fig. 2D). Although glasshouse experiments suggested that $e[CO_2]$ may facilitate access to deeper water resources (Uddin *et al.* 2018a,b), direct evidence for such a scenario in the field is equivocal. Whilst a recent study on wheat in a dryland agro-ecosystem indicated that yield stimulation by $e[CO_2]$ is associated with root growth stimulation in deeper, but not in shallow soil (Uddin *et al.* 2018c), there was no evidence that $e[CO_2]$ mitigated drought through better or deeper water extraction in soybean FACE experiments (Gray *et al.* 2016). Such results may depend on soil structure and water holding capacity, especially whether deeper roots would increase the size of the ‘bucket of water’ accessible to each plant.

The extent to which such uncertainties are interspecific differences, between-site differences, or differences due to other factors that might be interacting with drought and $e[CO_2]$ is unclear. However, as $e[CO_2]$ is likely to coincide with warmer temperatures (hence greater evaporative demand) and changes in precipitation patterns, and many food production regions are likely to see longer or more severe periods of drought stress, it is of great importance to better understand in what conditions drought negates the benefits of $e[CO_2]$.

Biotic Interactions in Agricultural Systems: Weeds, Insects and Diseases

Understanding the effects of $e[CO_2]$ on the biotic interactions present in agricultural systems is a topic that represents an important knowledge gap, in particular as the effects of $e[CO_2]$ and broader climate change impacts can be specific to species involved and how they interact, and might not extrapolate to other localities. Of practical importance to agricultural communities are questions related to the following: Will weeds be more competitive in a high $[CO_2]$ world? Will insect and disease pressure increase? If the disease is insect-transmitted, how will biochemical changes in plants grown under $e[CO_2]$ affect feeding behaviour and disease transmission and severity?

Weeds

Attempts have been made to predict weed pressure changes with $e[CO_2]$ based on crop and weed photosynthetic pathways. Most crop plants have the C3 photosynthetic pathway and many of their problematic weeds have the C4 photosynthetic pathway. Because C4 plants generally do not capitalise on $e[CO_2]$, it was thought that weed pressure might be less severe in a high $[CO_2]$ world. However, C4 weeds might be advantaged under $e[CO_2]$ x drought (through water savings caused by decreased stomatal conductance, details above) and higher temperatures (Alberto *et al.* 1996), so the overall outcome is not easy to predict. In contrast, C4 crops such as maize, sugarcane and sorghum represent large cropping areas worldwide, and can have problematic C3 weeds, which would be expected to become relatively more competitive under $e[CO_2]$ (Ziska 2001). Furthermore, there are also numerous problematic C3 weeds in C3 cropping systems. Some studies have shown a greater competitiveness of the crop, for example of sugarbeet against *Chenopodium album* (Houghton & Thomas 1996). Others studies found greater competitiveness of the weed species, for example with alfalfa and *Taraxacum officinale* (Bunce 1995), with pasture grasses and *Plantago lanceolata* (Newton *et al.* 1996), or with pasture grasses and both *Taraxacum* and *Plantago* weeds (Potvin & Vasseur 1997). There are other factors that influence competition between crops and weeds that can be critical to the overall response (Bunce & Ziska 2000), and that can be modified with climate change, but also with management.

One of the important factors that will determine weed pressure in the future is how much access to chemical control options farmers will have and how effective these will be. In theory,

systemic herbicides might show greater efficacy from the faster growth under e[CO₂], however, there are some reports which rather show less control under e[CO₂] (Ziska & Teasdale 2000; Ziska *et al.* 2004; Manea *et al.* 2011). For example, Canada thistle (*Cirsium arvense*) is a creeping perennial weed that reproduces through seeds and rhizomes. Under e[CO₂], the weed allocated a greater proportion of its biomass to the root system, thus diluting glyphosate to the extent that weed control was incomplete despite similar above-ground damage (Ziska *et al.* 2004). Recommended rates might need to be adjusted upwards for some products and weeds. Predicted climatic changes associated with e[CO₂], such as higher temperatures and more intense rainfall events, might also make it more challenging to apply pesticides at the optimal timing (Ziska 2016).

An increasingly important problem in conventional agriculture is herbicide resistance in weed species, so regardless of [CO₂], weed pressure in agricultural systems is increasing. Changes in [CO₂] can exacerbate this problem by improving the synchronicity of reproduction between the crop and closely related species. For example, in rice cultivation, outcrossing between cultivated herbicide-resistant rice and wild rice can lead to hybrid weedy and herbicide-resistant rice progeny. Ziska *et al.* (2012) have shown that e[CO₂] advanced the flowering time of wild rice, but not the cultivated rice, improving outcrossing opportunities. Elevated [CO₂] also increased reproductive organs proportionally more in wild rice, thus creating conditions to enhance and perpetuate weedy, but herbicide-resistant, rice populations.

There are further concerns that weeds might be evolving more quickly to take advantage of e[CO₂] than we are able to achieve in crop breeding programs, and might thus represent a greater problem in the future (Ziska 2017). Weed populations generally show high genetic diversity compared to crop plants and are subject to natural reproductive processes and selection pressures. As such, weed populations have access to a greater number of alleles to adapt to the e[CO₂]. This has raised the question whether weed adaptation to e[CO₂] might already be happening (Ziska 2017). Obviously, evolutionary processes take time, but these early indications, in addition to other concerns raised previously, point to weed problems becoming potentially more important in many cases.

Herbivory

Changes in host plant biochemistry and morphology are likely to impact the nutritional quality of crops to herbivores. Several investigations have reported that herbivorous foliage-feeding insects respond by consuming more foliage, presumably to ingest the same amount of protein as under ambient [CO₂]. These insects show lower survival, fecundity and abundance (see reviews by Coviella & Trumble 1998 and Robinson *et al.* 2012). By contrast, the impact of e[CO₂] on phloem feeders, aphids for example, appears to improve insect survival rates, fecundity, and abundance (Robinson *et al.* 2012).. The mechanism for this improved fitness is not clear as we have little information about possible differences in phloem chemical composition between host plants grown in ambient versus e[CO₂]. For example, O'Neil *et al.* (2011) found no differences in the concentrations of amino acids in the phloem, and suggested increased leaf temperatures under e[CO₂] from lower stomatal conductance were responsible for the doubling of the population of soybean aphids observed under FACE. On the other hand, Oehme *et al.* (2013) found changes to phloem sugars and amino acids, but these changes were different between wheat and canola, and effects on associated phloem feeding aphids were different in direction.

The C:N ratio is not the only change in biochemistry that might impact herbivorous insects. There are indications that e[CO₂] also impacts the biochemistry of secondary compounds involved in the plant chemical defence against herbivores and pathogens. In particular, e[CO₂] appears to down-regulate genes related to the jasmonic acid and ethylene pathways, which appears to increase the susceptibility of plants to insects (Guo *et al.* 2014a,b; Sun *et al.* 2013; Zavala *et al.* 2008). Another report showed increased concentrations of phenols, condensed tannins and defensive enzymes, which would rather improve resistance to insects (Sharma *et al.* 2016). Interestingly, Guo *et al.* (2014a) found that e[CO₂] induced greater morphological defences in greater trichome density, but these were not enough to prevent greater infestation due to the lower biochemical defences. There have been relatively few studies on this topic, and it remains to be seen if these responses can be generalized.

Diseases

Disease pressure in agricultural systems appears to be sometimes worse, sometimes better, and many of these responses appear to be related to infection mechanisms of the individual pathogen

and the interaction with changes in the host plant under e[CO₂]. For example, some pathogens become more prevalent with the larger biomass and denser canopy of plants grown under e[CO₂]. This was the mechanism suggested by Chakraborty *et al.* (2000) when they investigated the incidence and severity of the anthracnose pathogen *Colletotrichum gloeosporioides* in the tropical pasture legume *Stylosanthes scabra*; greater growth at e[CO₂] led to a higher relative humidity in the plant canopy, thus encouraging disease development. Similarly, Kobayashi *et al.* (2006) found that the greater number of tillers under FACE in rice contributed to more contact points for the development of *Rhizoctonia solani*. Melloy *et al.* (2010) also showed greater wheat biomass under FACE was related to greater *Fusarium pseudograminearum* biomass. On the other hand, the severity of other diseases that infect plants through stomata may decrease due to changes in stomatal aperture under e[CO₂], although Eastburn *et al.* (2010), investigating two diseases in soybean that use stomata for entry into the plant, showed contradictory results with downy mildew (*Peronospora manshurica*) decreasing in incidence, whereas brown spot (*Septoria glycines*) increased slightly. The authors suggested that perhaps the number and density of stomata were more important in reducing disease incidence than stomatal aperture.

Vaughan *et al.* (2016) also hypothesised that changes in primary metabolism in plants grown under e[CO₂], and in particular a greater C:N ratio, might benefit fungal diseases, although there are very few studies that investigated this (but see Plessl *et al.* 2005). Changes in secondary metabolites and defence pathways in the host plants grown under e[CO₂] also show similarities with herbivory, and appear to point towards greater disease pressure in the future. For example, Vary *et al.* (2015) found that the susceptibility of wheat to *Fusarium* head blight was increased under e[CO₂], especially for a moderately resistant cultivar, and for pathogens acclimated to growth under e[CO₂]. Resistance to *Fusarium* head blight in wheat occurs through the salicylic acid pathway, the jasmonic acid pathway and through the accumulation of metabolites related to the phenylpropanoid pathway (Vaughan *et al.* 2016). Zavala *et al.* 2008; Casteel *et al.* 2012 Based on the genetics of the moderately resistant cultivar used by Vary *et al.* (2015), Vaughan *et al.* (2016) suggested that the effect of e[CO₂] might be to compromise the phenylpropanoid metabolism. Unfortunately, defence metabolites were not investigated in the Vary *et al.* (2015) study, so it is unclear whether e[CO₂] might have also changed salicylic acid and jasmonic acid biosynthesis as has been observed in soybean (Zavala *et al.* 2008; Casteel *et al.* 2012). The rapid

acclimation of the pathogen to e[CO₂] in this experiment also points to serious gaps in knowledge concerning the possible response mechanisms in fungal pathogens to e[CO₂].

Insect-transmitted viral diseases

The effects of e[CO₂] and warmer temperatures on diseases that are transmitted by insects are particularly complex as there are several organisms involved. All are directly affected by meteorological factors, but they can also be affected indirectly in ways that might be counteracted or amplified by changes in other organisms. Studies of e[CO₂]-effects on plant-vector-disease systems are still rare, report variable effects, and are nearly all studies conducted on crops grown under controlled conditions in glasshouses or climate chambers (Chakraborty et al. 2008; Guo et al. 2016). One such system that has been comparably well studied under FACE conditions is the barley yellow dwarf virus (BYDV). Barley yellow dwarf virus (BYDV), an important disease of wheat in Australia, is a plant-aphid-virus system, where aphids become infected by feeding on infected plants. Natural incidence of the BYDV in wheat was shown to increase under e[CO₂] between 14 and 34% in high-incidence years in AGFACE despite pesticide applications (Trebicki *et al.* 2017). Virus incidence was high in three of the four years investigated, and tends to be high across the region, particularly in growing seasons with relatively high rainfall and mild temperatures (Trebicki *et al.* 2017). In a complementary study, changes in the C:N ratio and [N] in wheat leaves due to e[CO₂] reduced aphid fecundity and increased feeding rate in non-infected plants, but infection with the BYDV increased [N], with no differences observed in the fecundity and feeding behaviours. This led Trebicki *et al.* (2016) to conclude that e[CO₂] will not delay or reduce BYDV spread, but if aphids show a preference for infected plants, this might increase BYDV spread. It is also conceivable that shifts in population genetics in one or several of the plant-aphid-virus components could change the impact of e[CO₂] on wheat-based cropping systems in unforeseeable ways.

Summary and outlook

In this review we highlighted uncertainties in how crops respond to e[CO₂] in association with four specific areas: Acclimation, nitrogen dynamics, interactions with drought and interactions with other organisms. Evidence was provided that reprogramming of plant metabolism is taking place in response to e[CO₂]. Altered sink-source relationships contribute to photosynthetic

acclimation under $e[CO_2]$, commonly in association with a diminished N demand for the photosynthetic machinery in C3 crops. Knock-on effects of reduced N demand on N uptake are suggested, consistent with the observed decreases in [N] under $e[CO_2]$. Recent studies also suggest the involvement of reduced nitrate assimilation to [N] decreases under $e[CO_2]$, at least in C3 crops when grown in hot climates under N saturation.

Across the four research areas investigated it is obvious that crop responses to $e[CO_2]$ are not uniform but strongly modified by environmental conditions. Responses vary across agro-ecosystems but also between seasons within the same agro-ecosystem. Developmental dynamics including the change from vegetative to reproductive growth also strongly interact with $e[CO_2]$. To better understand these temporal and environmental aspects of crop responses to $e[CO_2]$, it will be critical to holistically investigate the functioning and performance of crops in realistic field settings across model agro-ecosystems in various climates. Deeper understanding of $e[CO_2]$ x environment interactions will underpin the fine-tuning of trait selection and crop management to fully capitalise on the additional carbon. Also, looking at interactions between crops and other organisms, it is rare to find data on more than two or three organisms simultaneously. Systems-based approaches are also rare in $e[CO_2]$ research, so we are still in the dark as to what might be the most important threat(s). Similarly, although we have data on many isolated interactions between crops and other organisms, we have yet to draw wider inferences from various multi-species studies.

Specific key areas to consider in future research could include: (1) Interactions of crop traits and environmental conditions that eliminate photosynthetic acclimation under $e[CO_2]$. (2) Scanning of genotypes with enhanced root nitrate assimilation to compensate for decreased shoot nitrate assimilation under $e[CO_2]$ and the performance of such a trait in various agro-ecosystems. (3) Fine-tuning of plant metabolism not only in response to $e[CO_2]$ but also in interaction with other climate change factors such as increasing temperature, heat stress events or changing precipitation patterns. (4) Interactions between crops and other organisms in various multi-species studies.

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Legends

Figure 1

Response of N uptake (% difference to ambient [CO₂], blue symbols), N concentration ([N], %, green symbols) and biomass accumulation (%) to e[CO₂] for wheat (*Triticum aestivum* L. cv. ‘Yitpi’). Data were collected over nine years (from 2007 to 2015; O’Leary *et al.* 2015, Fitzgerald *et al.* 2016, Tausz *et al.* 2017a, Houshmandfar *et al.* 2018) at three different developmental stages (DC30/31, DC65 and DC90, Zadoks *et al.* 1974) at the Australian Grains Free Air CO₂ Enrichment (AGFACE) facility, Horsham, Australia, a Mediterranean agro-ecosystem where crops grew either under ambient [CO₂] (~400 μmol mol⁻¹) or elevated [CO₂] (~550 μmol mol⁻¹) under non-limiting N supply. Open symbols and corresponding regression (dashed lines) represent data from seasons with below average (178 mm) to average (274 mm) in-season water supply, whereas closed symbols and corresponding regression (solid lines) indicate average (274 mm) to above average (436 mm) in-season water supply (either rainfall only or a combination of

rainfall and supplemental irrigation). Each data point represents the mean value of $n=4$. In addition, the grey dotted line represents the 1:1 line which would indicate matching biomass and N uptake stimulation, whereas the black solid line represents the equation ($y = 1.08x - 10.6$) for the relationship between the response of whole plant net primary production and corresponding N acquisition of croplands reported in Feng *et al.* (2015). The equations and values for r^2 are: Blue solid line: $y = 1.01x - 8.38$, $r^2 = 0.90$; blue dashed line: $y = 1.00x - 8.23$, $r^2 = 0.77$; green solid line: $y = 0.04x - 7.84$, $r^2 = 0.02$; green dashed line: $y = 0.04x - 7.77$, $r^2 = 0.01$

Figure 2

Possible scenarios how $e[CO_2]$ and water interact on wheat growth in a Mediterranean-type agro-ecosystem. A. Current $[CO_2]$ Scenario: Under current $[CO_2]$ conditions crops use winter rainfall and stored soil water until flowering and then commonly experience high evaporative demand and seasonal drought during grain-filling. B. Elevated $[CO_2]$ Scenario 1: Gains in leaf level water use efficiency translate to soil water savings that can support grain filling for longer during the late season drought. This scenario is commonly cited to explain a greater $e[CO_2]$ effect under drought (Leakey *et al.* 2009). C. Elevated $[CO_2]$ Scenario 2: Strong stimulation of early growth by $e[CO_2]$ depletes soil water faster, leaving little reserves to support grain filling during seasonal drought. As a result grain filling is incomplete. D. Elevated $[CO_2]$ Scenario 3: Root growth stimulation facilitates access to deeper soil water to support grain filling during the seasonal drought.

Figure 1

Figure 2

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