



Contents lists available at ScienceDirect

Food Research International

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

Impacts of climate changes on crop physiology and food quality

Fábio M. DaMatta^{a,*}, Adriana Grandis^b, Bruna C. Arenque^b, Marcos S. Buckeridge^b^a Departamento de Biologia Vegetal, Universidade Federal de Viçosa, 36570-000 Viçosa, MG, Brazil^b Laboratório de Fisiologia Ecológica de Plantas (LAFIECO), Departamento de Botânica, Instituto de Biociências, Universidade de São Paulo, Caixa Postal 11461, 05422-970 São Paulo, SP, Brazil

ARTICLE INFO

Article history:

Received 8 June 2009

Accepted 5 November 2009

Keywords:

Food quality
 Global climatic changes
 Global warming
 Plant physiology
 Photosynthesis
 Nitrogen

ABSTRACT

Carbon emissions related to human activities have been significantly contributing to the elevation of atmospheric [CO₂] and temperature. More recently, carbon emissions have greatly accelerated, thus much stronger effects on crops are expected. Here, we revise literature data concerning the physiological effects of CO₂ enrichment and temperature rise on crop species. We discuss the main advantages and limitations of the most used CO₂-enrichment technologies, the Open-Top Chambers (OTCs) and the Free-Air Carbon Enrichment (FACE). Within the conditions expected for the next few years, the physiological responses of crops suggest that they will grow faster, with slight changes in development, such as flowering and fruiting, depending on the species. There is growing evidence suggesting that C₃ crops are likely to produce more harvestable products and that both C₃ and C₄ crops are likely to use less water with rising atmospheric [CO₂] in the absence of stressful conditions. However, the beneficial direct impact of elevated [CO₂] on crop yield can be offset by other effects of climate change, such as elevated temperatures and altered patterns of precipitation. Changes in food quality in a warmer, high-CO₂ world are to be expected, e.g., decreased protein and mineral nutrient concentrations, as well as altered lipid composition. We point out that studies related to changes in crop yield and food quality as a consequence of global climatic changes should be priority areas for further studies, particularly because they will be increasingly associated with food security.

© 2009 Elsevier Ltd. All rights reserved.

1. Introduction

Over the past 800,000 years, atmospheric [CO₂] changed between 180 ppm (glacial periods) and 280 ppm (interglacial periods) as Earth moved between ice ages. From pre-industrial levels of 280 ppm, [CO₂] has increased steadily to 384 ppm in 2009, and mean temperature has increased by 0.76 °C over the same time period. Projections to the end of this century suggest that atmospheric [CO₂] will top 700 ppm or more, whereas global temperature will increase by 1.8–4.0 °C, depending on the greenhouse emission scenario (IPCC, 2007). There is growing evidence suggesting that many crops, notably C₃ crops, may respond positively to increased atmospheric [CO₂] in the absence of other stressful conditions (Long, Ainsworth, Rogers, & Ort, 2004), but the beneficial direct impact of elevated [CO₂] can be offset by other effects of climate change, such as elevated temperatures, higher tropospheric ozone concentrations and altered patterns of precipitation (Easterling et al., 2007).

* Corresponding author. Fax: +55 31 3899 2580.

E-mail addresses: fdamatta@ufv.br (F.M. DaMatta), msbuck@usp.br (M.S. Buckeridge).

The temperature response of crop growth and yield must be considered to predict the [CO₂] effects (Morison & Lawlor, 1999; Polley, 2002; Porter & Semenov, 2005; Ziska & Bunce, 1997). The threshold developmental responses of crops to temperature are often well defined, changing direction over a narrow temperature (Porter & Semenov, 2005). High temperatures reduce the net carbon gain in C₃ species by increasing photorespiration; by reducing photorespiration, [CO₂] enrichment is expected to increase photosynthesis more at high than at low temperatures, and thus at least partially offsetting the temperature effects of supra-optimal temperatures on yield (Long, 1991; Polley, 2002). Therefore, yield increases at high [CO₂] should occur most frequently in regions where temperatures approximate the optimum for crop growth. Conversely, in regions where high temperatures already are severely limiting, further increases in temperature will depress crop yield regardless of changes in [CO₂] (Polley, 2002). In fact, results of mathematical modeling suggest that, in mid- to high-latitude regions, moderate to medium local increases in temperature (1–3 °C), along with associated CO₂ increase and rainfall changes, can have beneficial impacts on crop yields, but in low-latitude regions even moderate temperature increases (1–2 °C) are likely to have negative impacts on yield of major cereals (Easterling et al., 2007). Thus, climate change may impair food production,

particularly in developing countries, most of which are located in tropical regions with warmer baseline climates (Tubiello & Fischer, 2007).

In order to meet the overall demand for food as the global population increases from the present 6.6 billion to 8.7 to 11.3 billion in 2050 (Bengtsson, Shen, & Oki, 2006), it is clear that crop production will need to continuously increase by 50% over the next few decades (Ingram, Gregory, & Izac, 2008). Predicting future global food production is rather complex (Challinor, Ewert, Arnold, Simelton, & Fraser, 2009; Tubiello & Fischer, 2007), however, especially because the intended end-of-the-century global effects may be unevenly distributed among regions and decades. Furthermore, this uneven distribution cannot be predicted due to uncertainties related to both regional climate dynamics and crop responses to increased atmospheric $[\text{CO}_2]$ and other associated climatic changes (Tubiello & Fischer, 2007). In fact, scientific publication on the isolated effects of elevated $[\text{CO}_2]$, temperature rise and water supply on crop growth and yield have produced a wealth of valuable information, critically increasing understanding of the dynamics of photosynthesis, biomass accumulation and crop yield that are necessary to forecast impacts of climate change on agriculture (Tubiello, Amthor, et al., 2007). However, a relatively small amount of work has been performed with the combined effects of those variables, which would give a more realistic picture of how crop plants will respond to global climatic changes.

In addition to crop growth and yield, crop quality is also expected to be affected by global climatic changes. Crop quality is thought to be a multi-faceted and complex subject involving growth, assimilate partitioning and storage, and pre- and post-harvest, including nutritional, technological and environmental facets (Hay & Porter, 2006). Elemental (e.g., zinc, iodine) and macromolecular (e.g., protein) composition in plant tissues are expected to change in a future high- CO_2 world (Taub, Miller, & Allen, 2008). In this context, crop physiologists will need to take more account of the interests of breeders and processors by studying, quantifying and modeling the differences not only in increasing yields but also in food quality among crop varieties and species in climate change scenarios (Hay & Porter, 2006).

The efforts to understand the impact of elevated $[\text{CO}_2]$, temperature and other ongoing climatic changes on food crops are crucial to estimate food production in the future. The present review, which is by no means exhaustive, is mainly focused on the current understanding of the consequences of climatic changes (mainly CO_2 enrichment and temperature) on crop physiology and chemistry. This review is organized into sections dealing with methodological concerns about CO_2 fertilization, CO_2 and temperature effects on carbon gain, phenology and crop yield, and the broad consequences of climate changes on food quality.

2. Methodological concerns on CO_2 fertilization

Throughout the late 1970s and 1980s, most high- CO_2 research was limited mainly to greenhouses and Open-Top Chambers (OTC), both of which may produce questionable results (Stafford, 2008) under certain circumstances. If the plants are grown in unrealistic rooting environments (small pots), down-regulation of photosynthesis (see Section 3.1) is to be expected (Arp, 1991; Ronchi et al., 2006), thus impairing the plant's response to CO_2 . In contrast, if the plants are grown in relatively large pots for a length of time that does not lead to root growth limitation, photosynthetic down-regulation does not occur, as demonstrated with sugarcane by De Souza et al. (2008). Nonetheless, results from OTC experiments have been criticized: even in field studies using open-top and transparent-walled chambers, the plants grown in such systems are not exposed to varying environmental conditions such as wind

and normal alterations in temperature and humidity (Long, Ainsworth, Leakey, & Ort, 2006; Stafford, 2008). In fact, OTCs typically create conditions that are warmer than in adjacent unenclosed fields, and the plants within them are subject to pronounced edge effects (Long et al., 2004). In addition, access by pests and diseases is restricted, but if they gain access, high humidity and more shelter may exacerbate epidemics (Long et al., 2006; McLeod & Long, 1999). As an alternative to such limitations, the Free-Air CO_2 Enrichment (FACE) was developed to minimize the microclimatic and edge effects arisen from artificial enclosures and small pots, thus presumably mimicking realistic future agricultural conditions (Ainsworth, Beier, et al., 2008; Ainsworth, Leakey, Ort, & Long, 2008; Leakey, Ainsworth, et al., 2009; Long et al., 2004).

A typical large scale FACE apparatus consists of a number of 15- to 30-m diameter plots within the crop field, in which CO_2 is released just above the crop surface on the upwind side of the plot (Ainsworth et al., 2008; Long et al., 2006; Miglietta & Raschi, 1993). However, the rapidly fluctuating $[\text{CO}_2]$ within FACE rings may underestimate the fertilization effect of enriched CO_2 on plant growth (Holtum & Winter, 2003; Ziska & Bunce, 2006). Regardless of this consideration, the major limitation of FACE technology is the cost of the large amounts of $[\text{CO}_2]$ that must be released (about US\$ 1 million over a year, excluding the additional costs of the investigation; Long, personal communication) to attain the set point $[\text{CO}_2]$. In addition to costs, other key points, such as CO_2 versus temperature interaction evaluations and testing $[\text{CO}_2]$ above 550 ppm, are hardly performed using the current FACE technology (Ainsworth et al., 2008; Tubiello, Soussana, & Howden, 2007; Tubiello et al., 2007).

It seems clear that both systems (OTC and FACE) present advantages and limitations and both will have to be used in order to evaluate the effects of global climate changes on plants. On one hand, OTCs afford a much better evaluation of elevated $[\text{CO}_2]$ on plants, whereas a serious limitation of the FACE system is that the maximum $[\text{CO}_2]$ affordable is 550 ppm. As the effect of elevated $[\text{CO}_2]$ is subtler when compared with the effects of temperature, the FACE systems fail to evaluate clearly how plants are affected. Although FACE systems might be used in experiments with combined changes of CO_2 and temperature, OTCs offer better conditions regarding logistics and affordability to perform a greater number of experiments with a combination of elevated CO_2 and elevated temperature. Thus, the use of OTCs is strategic, as it is much more affordable than FACE, they can be installed in many laboratories at the same time and they produce a large amount of data. These results, when analyzed together, will raise hypotheses that could not be tested in the more expensive FACE systems.

3. Climatic changes: physiological background

Crops sense and respond directly to rising $[\text{CO}_2]$ through photosynthesis and stomatal conductance, and this is the basis for the CO_2 fertilization effect on crop yield (Long et al., 2006). These responses are highly dependent on temperature (Polley, 2002; Ziska & Bunce, 1997). Therefore, understanding how crop species will respond to these environmental changes is crucial for maximizing the potential benefits of elevated CO_2 , for which agronomic practice needs to adapt as both temperature and CO_2 rise (Challinor & Wheeler, 2008b).

3.1. CO_2 and plant carbon balance

For photosynthesis to occur, CO_2 must diffuse from the atmosphere towards the chloroplasts. The main gate of entry of CO_2 into the leaf is via the stomatal pore. The same path is traveled in the reverse direction by water vapor, so that an increase in stomatal

conductance through the opening of stomata, although facilitating higher CO₂ uptake, is inextricably associated with increasing transpiration rates (Taiz & Zeiger, 2006).

In higher plants, virtually all of the carbon is assimilated through the reductive pentose phosphate cycle, often referred to as the Calvin cycle. In the first step of this cycle, one molecule of CO₂ reacts with a molecule of ribulose-1,5-bisphosphate (RuBP) to yield two molecules of 3-phosphoglycerate, a three-carbon compound (the C₃ species derives its name from this three-carbon molecule). This reaction is catalyzed by the RuBP carboxylase/oxygenase, referred to as Rubisco. In addition to its function as a carboxylase, Rubisco may also act as an oxygenase. The latter function initiates a series of physiological events in which light-dependent O₂ uptake is associated with CO₂ evolution, a process known as photorespiration. Such a process works in opposite direction to photosynthesis, causing a loss of the CO₂ fixed by the Calvin cycle.

In C₃ species, which comprise the great majority of plant species, including important food crops such as wheat, rice, soybean and potatoes, CO₂ is exclusively assimilated through the above-mentioned Calvin cycle. In contrast, C₄ plants, including the most productive crop species such as maize, sorghum and sugarcane, use a series of enzymes that initially combine CO₂ (HCO₃⁻) with a three-carbon molecule (phosphoenolpyruvate, PEP), producing oxaloacetate, a four-carbon compound. This reaction is catalyzed by PEP carboxylase, which has a much higher affinity for CO₂ than Rubisco and lacks oxygenation activity. The C₄ plants display an effective mechanism for concentrating CO₂ with Rubisco. As a consequence, Rubisco is CO₂-saturated in C₄ plants and the photorespiratory pathway is largely minimized.

Accumulation of carbohydrates in leaves is one of the most pronounced and universally observed responses of C₃ plants to elevated atmospheric [CO₂], even in field-grown plants where rooting volume is unrestricted (Long et al., 2004), causing subsequent down-regulation (acclimation) of photosynthetic capacity (Ainsworth & Rogers, 2007; Leakey et al., 2009; Long et al., 2004). A reduced or acclimated stimulation of photosynthesis has been mechanistically and quantitatively attributed to decreased maximum apparent carboxylation velocity and investment in Rubisco (Ainsworth & Long, 2005), as suggested for common bean (Socias, Medrano, & Sharkey, 1993) and soybean (Ainsworth et al., 2002). Overall, limited sink strength (rate of CO₂ inflow towards the plant higher than its capacity to use assimilates in sink tissues) predisposes plants to a greater acclimation of photosynthetic capacity, and decreases the stimulation of photosynthesis by growth at elevated [CO₂] (Ainsworth & Rogers, 2007; Arp, 1991; Long et al., 2004). In general, trees, particularly fast-growing individuals, display large sink capacity (root–trunk system) than annuals, which to a great extent explains their higher stimulation in photosynthesis when grown at elevated [CO₂] compared to shrubs and annual crops (Ainsworth & Long, 2005). It follows from the above that it is likely that the increases in photosynthesis induced by high CO₂ will need to be balanced by commensurate increases in sink capacity if maximum yield potential is to be achieved (Ainsworth, Rogers, & Leakey, 2008).

Although the stimulation of C₃ photosynthesis by growth at elevated atmospheric [CO₂] can be predicted with confidence, the nature of changes in respiration is less certain. The primary reason for uncertainty is that the mechanisms of plant respiratory responses to elevated [CO₂] have not been resolved (Gifford, 2003). In fact, some investigators have concluded that plant respiration may increase as much as 37%, decrease as much as 18%, or not change at all with increased [CO₂] (e.g., Drake et al., 1999; Gifford, 2003; Leakey, Xu, et al., 2009). In a recent FACE study where soybean was grown at elevated [CO₂] (550 ppm), the stimulated (37%) rate of nighttime respiration was associated with the additional carbohydrate available from enhanced photosynthesis at elevated CO₂

(Leakey et al., 2009). Although at the leaf and plant scales, stimulated respiration at elevated [CO₂] may reduce net carbon balance, it is possible, nevertheless, that such stimulation could facilitate increased yield by providing greater energy for export of photoassimilate from source organs to sink tissues.

The biochemical basis for the elevated atmospheric [CO₂] stimulation of C₃ photosynthesis is that high [CO₂] around Rubisco accelerates the carboxylation reaction while suppressing the competing oxygenation reaction and subsequently reducing the CO₂ loss and energy costs associated with photorespiration (Leakey et al., 2009; Long et al., 2004). In fact, theoretical analyses suggest that photosynthetic rates might increase by 38% as atmospheric [CO₂] rises from 380 ppm to 550 ppm (von Caemmerer & Furbank, 2003). In C₄ species, however, photosynthesis is likely to be CO₂-saturated at low concentrations due to the mechanism for concentrating CO₂ around Rubisco and, therefore, C₄ crops would not benefit much from increases in atmospheric CO₂ levels (Ainsworth & Rogers, 2007). However, a number of investigators have reported enhanced photosynthesis and biomass production in some C₄ species (e.g., De Souza et al., 2008; Maroco, Edwards, & Ku, 1999; Vu & Allen, 2009; Wand, Midgley, Jones, & Curtis, 1999; Ziska & Bunce, 1997). Nonetheless, stimulation of C₄ photosynthesis and crop yield at high CO₂ might result from the interaction of water deficit with reduced stomatal conductance at elevated [CO₂]. In this sense, the mechanism by which photosynthesis is stimulated in C₄ species would occur through the mitigation of drought stress rather than a direct effect of high CO₂ on photosynthesis (Ainsworth & Rogers, 2007; Leakey et al., 2009).

Overall, in both C₃ and C₄ species, stomatal conductance is consistently, but not universally, decreased at elevated [CO₂] (Ainsworth & Long, 2005; Leakey et al., 2009; Ziska & Bunce, 2006). Because increasing atmospheric [CO₂] enlarges the gradient needed to ensure adequate diffusion of CO₂ from the atmosphere to the chloroplast, greater photosynthetic rates for a given stomatal conductance paralleling lower transpiration rates are to be expected, thus ultimately improving water-use efficiency in addition to reducing soil moisture depletion and ameliorating stress during periods of drought (Leakey et al., 2009). Nonetheless, increased stomatal closure that is usually observed at elevated CO₂ will be inevitably associated with lower latent heat loss, thereby increasing leaf temperatures (Kimball & Bernacchi, 2006).

3.2. Temperature and temperature interactions

The most significant factors for heat stress-related yield loss in crops include shortening of developmental phases induced by high temperature, reduced light perception over the shortened life cycle and perturbation of the processes associated with plant carbon balance (Barnabás, Järgen, & Fehér, 2008). It has been suggested that higher temperatures reduce net carbon gain by increasing plant respiration more than photosynthesis. In fact, the light-saturated photosynthesis rate of C₃ crops such as wheat and rice is at a maximum for temperatures from about 20–32 °C, whereas total crop respiration shows a steep nonlinear increase for temperatures from 15 to 40 °C, followed by a rapid and nearly linear decline (Porter & Semenov, 2005). Increased temperature could potentially reduce photosynthetic capacity due to the heat lability of Rubisco activase on the one hand and the limitation of electron transport in the chloroplast on the other hand (Sage, Way, & Kubien, 2008). In addition, by increasing the air evaporative demand, higher temperatures are often implicated with stomatal closure, which further decreases photosynthesis due to smaller CO₂ flux into leaves.

The CO₂:O₂ ratio at the active site of Rubisco is about 0.024, and therefore the relative rate of carboxylation to oxygenation is ca. 2.2 at 25 °C, implying that about every third molecule of RuBP is consumed in photorespiration. Rising temperature modifies the

kinetic constants of Rubisco, increasing the rate of oxygenation more than that of carboxylation, in addition to lowering the solubility of CO₂ relative to O₂. As a consequence, the rate of carboxylation to oxygenation is reduced (increased photorespiration rates) even further, about 1.4 at 35 °C (Ainsworth & Rogers, 2007), thus further compromising the plant carbon balance at elevated temperatures.

Some evidence indicates that elevated [CO₂] can offset the negative impacts of high temperatures on photosynthesis and crop growth and production (Polley, 2002), depending on warmer baseline climates. Nevertheless, it must be emphasized that the effects of high [CO₂] and temperature on plants often are not additive, implying that the combined effects of these changes cannot be predicted from knowledge of their individual effects (Long, 1991). In addition, it seems that the magnitude and even direction of crop responses to elevated [CO₂] and temperature change are species- and even cultivar-specific (Polley, 2002).

In summary, the predicted increase in average global temperature will accelerate crop development rates, and the negative effects tend to be larger for grain yield than for total biomass (Fuhrer, 2003). These constraints associated with other ongoing climatic changes such as more frequent and severe droughts and more intense precipitation events will probably offset gains in carbon assimilation associated with elevated CO₂ (Challinor & Wheeler, 2008a; Sage et al., 2008).

3.3. Nitrogen and other nutrients

Nitrogen availability to plants, more than any other environmental factor, determines their responses to elevated [CO₂] (Ellsworth et al., 2004). This has been associated with the fact that elevated CO₂ results in decreased N content (typically by 13–16%) in plant tissues regardless of the CO₂-enrichment technology (Ainsworth & Long, 2005; Curtis & Wang, 1998). Although the mechanisms by which elevated CO₂ decreases tissue concentrations of N (and proteins) are not yet fully understood, such decreases exceed what would be expected if a given amount of N were diluted by additional biomass (Bloom, 2006). It is likely that decreases in tissue N result to some extent from (i) the accumulation of carbohydrates and other organic compounds as a consequence of CO₂ stimulation of photosynthesis (Idso & Idso, 2001), (ii) reduced uptake of N from the soil under high CO₂ due to lower transpiration rates resulting from decreased stomatal conductance (Kimball & Bernacchi, 2006), and (iii) impaired nitrate assimilation associated with decreases in the photorespiration pathway at elevated CO₂, as found in C₃ species such as wheat and tomato (Bloom, 2006). In contrast, leguminous plants such as soybean, which can largely acquire reduced N through its N-fixing ability, display much smaller changes in leaf N at elevated CO₂ than non-leguminous crops (Ainsworth et al., 2002). In any case, it should be noted that decreases in the concentrations of Rubisco and other photosynthetic enzymes are found at elevated [CO₂] without negatively compromising carbon acquisition (Drake, Gonzalez-Meler, & Long, 1997). Therefore, decreased leaf protein may lead to reduced sink (e.g., grains and tubers) protein concentration as the N supply to sinks during filling is largely from translocation from catabolized proteins in senescing photosynthetic tissues (Hay & Porter, 2006).

Apart from N, most of the other nutrients in grains also originate from mobilization from vegetative pools during grain-filling (Hay & Porter, 2006). In photosynthetic tissues, for example, increases in photosynthesis induced by high CO₂ may be associated with increased plant requirements for P but decreased for N (Loladze, 2002). Accordingly, CO₂ effects on primary carbon fixation may also alter the concentrations of different elements that respond similarly to N, such as Ca, S, Mg, Zn and K (Fangmeier

et al., 1999). Furthermore, mass flow, which is generally more important for uptake of mobile elements such as N, and diffusion, which is more important for immobile elements such as P, are both predicted to be changed under elevated CO₂ (Loladze, 2002) due to alterations in transpiration and soil moisture. From the above, tissue nutrient concentrations, and thus the nutritional value of crops, are also expected to be affected, at least on a theoretical basis, under high CO₂.

4. Consequences of climatic changes for phenology and crop yield

4.1. Temperature and interactions

With regard to warmer temperatures, crop yield can be affected at any time from sowing to grain maturity, but it is the time around flowering, when the number of grains per land area is established, and during the grain-filling stage, when the average grain weight is determined, that high temperatures have the most impact on the final harvestable crop, as found in cereals (Barnabás et al., 2008; Morison & Lawlor, 1999). Thus, understanding how environmental factors signal phenological processes such as flowering will be extremely relevant for future food production, since a large part of food comes as grains/seeds. In this context, any change in flowering time could affect not only seed production but also food composition (Springer & Ward, 2007).

At a first glance, the effects of elevated [CO₂] on flowering time seem rather inconsistent, as noted by Springer and Ward (2007), who evaluated 33 papers that included several CO₂-enrichment technologies dealing with the matter. Earlier flowering in response to increased [CO₂] was reported in most crop species, but delayed and unchanging flowering time at elevated [CO₂] have also been reported (Springer & Ward, 2007). These inconsistencies might in part be associated with experimental approaches used, i.e., OTC and FACE technologies (e.g., Hesketh & Hellmers, 1973, Leakey et al., 2006). Nonetheless, according to Craufurd and Wheeler (2009), it is more likely that [CO₂] has little or no effect on flowering time; probably changing flowering time is more directly associated with side effects of elevated temperatures linked to CO₂ enrichment, as particularly noted in controlled-environment experiments.

Taking into account the apparent lack of direct effect of [CO₂] on the rate of crop development, then temperature and interactions with temperature will be the most important aspects of climatic change for crop development (Craufurd & Wheeler, 2009; Morison & Lawlor, 1999). Moreover, at elevated [CO₂], tissue temperatures are often increased due to lower evaporative cooling. In fact, results from Matsui, Namuco, Ziska, and Horie (1997) on rice show that elevated [CO₂] (+300 ppm over ambient concentration) may even increase sterility and thus depress crop yield at high temperatures, possibly by further increasing temperature within the plant canopy. However, seed yield response to CO₂ may depend on the sensitivity of individual cultivars to temperature, especially during the reproductive development stage, as demonstrated in peanut by Bannayan, Tojo Soler, Garcia y Garcia, Guerra, and Hoogenboom (2009). Nonetheless, some evidence suggests that elevated [CO₂] might counteract the negative effect of higher temperatures, as in the case of cool-temperate grasses (Fuhrer, 2003). In fact, modeling studies suggest that climate change without CO₂ fertilization could reduce rice, maize and wheat yields by up to 37% in the next 20–80 years (Erda et al., 2005).

At warmer temperatures, the yield of wheat may decline up to 10% per 1 °C rise in mean seasonal temperature (Mitchell, Mitchell, Driscoll, Franklin, & Lawlor, 1993). The timing of wheat flowering and grain maturity may be considerably earlier at warmer

temperatures, thus shortening the time for carbon fixation and biomass accumulation before seed set [see Morison and Lawlor (1999) for a review]. Hot temperatures (>32–36 °C) can also greatly reduce seed set in many annual crops if elevated temperatures coincide with a brief critical period of only 1–3 days around the time of flowering (Craufurd & Wheeler, 2009). In groundnut, for example, Vara Prasad, Craufurd, Summerfield, and Wheeler (2000) noted that, from between 32 and 36 °C and up to 42 °C, the percentage fruit set fell from 50% of flowers to zero and the decline in rate was linear, illustrating the sharpness of response of crop plants to temperatures between 30 and 35 °C during the flowering and fruiting periods. Similar patterns have been identified for other food crops; for example, in maize, pollen viability is reduced at temperatures above 36 °C, while grain sterility is brought on by temperatures in the mid-30 °C in rice (Porter & Semenov, 2005). In fact, the reproductive limits for most crops are narrow, with temperatures in the mid-30 °C representing the threshold for successful grain set (Porter & Semenov, 2005).

4.2. Elevated [CO₂] and interactions

Jablonski, Xianzhong, and Curtis (2002) evaluated 79 crop and native species at elevated CO₂. They found, on average, increases in the numbers of flowers (19%) and fruits (18%), in biomass per seed (4%), in total seed biomass (25%), and in total plant biomass (31%). The number of seeds increased much more in rice (42%) than in other important crops such as soybean (29%), wheat (15%) and maize (5%). In a recent FACE study with rice, Yang et al. (2009) found at elevated atmospheric [CO₂] (ca. 570 ppm) increased numbers of panicles per unit area (8%), numbers of spikelets per panicle (10%), and grain biomass (4%), which taken together led to increased (ca. 30%) grain yield. However, in a rice variety less responsive to elevated [CO₂], grain yield increased by 13% only (Yang et al., 2009). This is not surprising, since there seems to be sufficient intraspecific variation among cultivars as demonstrated in glasshouses by Ziska, Manalo, and Ordonez (1996), who showed that the response to high [CO₂] of 17 different rice cultivars varied between 30% and 400%.

In soybean, from a meta-analysis in which 111 papers were used to evaluate photosynthesis, growth responses and grain yield at elevated atmospheric [CO₂], Ainsworth et al. (2002) found that leaf photosynthesis increased by ca. 39%, along with a decrease in stomatal conductance of about 40%. They also found increases in leaf area (18%), in net assimilation rate (59%), in total biomass (37%), and seed yield (24%). The above results suggest that food crops such as rice and soybean that have been selected to partition photoassimilates to their seeds will still proceed in this way in a high-CO₂ environment.

In some OTC studies, crop yield has been shown to be highly responsive to elevated [CO₂]. For example, De Souza et al. (2008) performed a 1-year experiment with sugarcane plants growing under 380 and 740 ppm [CO₂] and found an increase in biomass of ca. 50%, paralleling a 29% sucrose accumulation, which resulted from higher photosynthetic rates in elevated CO₂. Experiments with potato showed that higher [CO₂] increased the number of tubers per plant (1.5 tubers every 100 ppm increase in atmospheric CO₂), leading to 40% increased tuber yield at 660 ppm [CO₂] (Miglietta et al., 1998). In sour orange (*Citrus aurantium*) plants grown for 17 years in elevated [CO₂] (at 300 ppm CO₂ above ambient), Kimball, Idso, Johnson, and Rillig (2007) showed that instead of acclimation, the plants continued to respond by increasing fruit production by 70%. During the last years of the experiment, increased wood growth resulted in extra (70%) biomass accumulation. These results suggest that at least in orange trees, the

positive effect on biomass production can be sustained by a higher [CO₂] for many years.

The estimates of the CO₂ fertilization effect on crop yield vary depending on which experimental approach is used (Ainsworth et al., 2008; Fuhrer, 2003; Long et al., 2006; Tubiello et al., 2007; Ziska & Bunce, 2007). It has been argued (Ainsworth et al., 2008; Long et al., 2006) that enclosure experiments overestimate the effect of [CO₂] on plant growth and yield. However, the relative yield estimates in response to future [CO₂] obtained using a number of enclosure technologies seem to be quantitatively consistent with FACE results, at least for three crops of global importance: rice, soybean and wheat (Ziska & Bunce, 2007). Furthermore, there is growing evidence that crop models, largely based on enclosure experiments, are able to reproduce the observed crop responses in the FACE experiments (Challinor et al., 2009; Tubiello et al., 2007).

The examples mentioned above are consistent with the possibility that increased atmospheric [CO₂] will probably be positive, inducing higher growth rates and crop yield as a result of higher photosynthetic rates. The concomitant increase in temperature will likely strongly affect these responses, and this effect will depend on the species. It is possible, however, that when (if) temperature crosses the optimal conditions for photosynthesis and grain production, the positive effects will be reverted, with great losses for agriculture. Thus, experimental studies with a combination of elevated [CO₂] under different ranges of temperatures for main food crops will be of crucial and strategic value to forecast what gains or losses humanity will have with global climatic changes. In the long run, these experiments will have to be repeated with different water availabilities so that the results can be examined in comparison with expected local changes in rainfall.

5. Consequences for food quality

A major omission of the effects of a globally altered environment on crops is concerned with food quality (Högy & Fangmeier, 2008; Loladze, 2002; Porter & Semenov, 2005). Apart from an overall decrease in N and protein concentrations, as shown under elevated CO₂, the nutritional value and the quality of the edible products of most food and forage crops are largely unknown. Moreover, the available information is somewhat contradictory, rendering insufficient knowledge to draw firm conclusions on how the current and ongoing climatic changes will affect food quality for either human or animal nutrition. Furthermore, while it seems that temperature differences of only a few degrees have more pronounced overall effects on quality than increased [CO₂], our ability to assess the effects of temperature and CO₂ interactions on food quality is currently quite limited, since little is known about how CO₂ and temperature determine the linkages between assimilate supply and assimilate demand (Morison & Lawlor, 1999).

5.1. Carbohydrates

The effects of temperature and elevated CO₂ on carbohydrate composition of food crops are mixed and probably reflect differences in experimental conditions (e.g., CO₂ enrichment technologies and rooting volume) in addition to being species- or even cultivar-dependent. However, the preponderance of evidence suggests that increases in temperature should have a larger effect than elevated [CO₂] on carbohydrate composition, as can be seen below.

In soybean seeds, carbohydrate composition significantly changed with increasing temperature from 18/13 °C to 33/28 °C (day/night). Whereas sucrose concentration increased, stachyose decreased slightly; other sugars, such as glucose, raffinose and

fructose did not change significantly with rising temperature (Wolf, Cavins, Kleiman, & Black, 1982). More recently, Thomas, Boote, Allen, Gallo-Meagher, and Davis (2003), studying the combined effects of temperature and $[\text{CO}_2]$ on the composition of soybean seeds, found that total soluble sugars and starch decreased as temperature increased from 28/18 °C to 44/34 °C (day/night), while the proportion of soluble sugars to starch decreased, with the effects of elevated $[\text{CO}_2]$ (700 ppm) being comparatively negligible. In wheat, small increases in temperature (2–4 °C) may also have more than twice the effect of $[\text{CO}_2]$ on grain quality, as shown by Williams, Shewry, Lawlor, and Harwood (1995), who noted that starch content, starch grain size and number, and gelatinization were all altered in complex ways with temperature, but with little effect of increased $[\text{CO}_2]$. Thomas, Prasad, Boote, and Allen (2009), studying the combined effects of temperature (28/18 °C and 34/24 °C; day/night) and $[\text{CO}_2]$ (350 and 700 ppm) on the composition of red kidney beans seeds, also found that seed composition was unaffected by elevated $[\text{CO}_2]$, but seeds produced at 34/24 °C showed decreased glucose concentration (44%) and significantly increased concentrations of sucrose (33%) and raffinose (116%) compared to the 28/18 °C treatment. These changes may have important consequences for food quality; for example, Sebastian, Kerr, Pearlstein, and Hitz (2000) reported that increases in raffinose amounts create digestive problems in both non-ruminant animals and humans, where the intestinal mucosa does not contain the galactosidase enzyme necessary to digest raffinose.

High temperature (37/17 °C) from flowering to grain maturity caused a significant reduction in the starch accumulation period in developing wheat grains compared with plants grown under control (24/17 °C; day/night) conditions. When extremely high temperatures (37/28 °C; day/night) were applied, starch incorporation was completed 21 days earlier than in the control, with an increased proportion of A-type starch granules (10–50 µm diameter) and a decreased proportion of B granules (5–10 µm diameter). This result is consistent with shorter starch accumulation, as observed at high temperatures in wheat and barley (Barnabás et al. (2008) and references therein). In barley, loss of fermentable sugars in the form of degraded starch, associated with high temperatures during grain-filling, might represent a considerable financial penalty in terms of commercial malting production. However, it is possible that some exposure to elevated temperatures during grain-filling may have beneficial effects for malting, as the increased mealiness observed in heat-treated endosperms has been associated with increased susceptibility to enzymatic attack (Wallwork, Jenner, Logue, & Sedgley, 1998).

Fangmeier et al. (1999) found that elevated $[\text{CO}_2]$ caused small increases in starch content of grains from crops receiving low levels of N fertilizer. Högy and Fangmeier (2008) concluded that the observed increases in starch concentration due to elevated $[\text{CO}_2]$ would be more restricted to OTC experiments. Nonetheless, Porteus et al. (2009) recently examined two wheat cultivars grown under two N applications in a FACE system (elevated $[\text{CO}_2]$ = 550 ppm) and found increased starch concentration at high $[\text{CO}_2]$ regardless of the N nutrition and cultivars. In any case, Porteus et al. (2009) noted only minor alterations in carbohydrate composition in wheat grains in response to $[\text{CO}_2]$ enrichment – e.g., slight increases in hemicellulose concentration but unaltered concentrations of water soluble carbohydrates, cellulose and lignin. In contrast, Behboudian and Tod (1995) found that CO_2 enrichment was linked to improved quality of tomato fruits by increasing their concentrations of sucrose, glucose and fructose.

Conflicting information also exists on the effects of elevated $[\text{CO}_2]$ on sucrose accumulation in the two most important crops for sugar production. For example, while Demmers-Derks, Mitchell, Mitchell, and Lawlor (1998) found that elevated $[\text{CO}_2]$ (as well as +4 °C above ambient temperature) did not alter sucrose concen-

tration in sugar beet, De Souza et al. (2008) reported a 29% increase in sucrose concentration in sugarcane plants grown in large pots at $[\text{CO}_2]$ = 740 ppm.

In rice, the content of amylose as well as the rheological properties and temperature of gelatinization largely determine the grain quality. The available information on amylose content at elevated $[\text{CO}_2]$ is contradictory, however. Amylose content and palatability were both unresponsive to elevated $[\text{CO}_2]$, as shown by Terao et al. (2005) in FACE studies. In contrast, Yang et al. (2007), also under FACE conditions, found lower amylose content (3.6%), decreased hardness of the rice grains, and improved palatability. However, elevated $[\text{CO}_2]$ caused serious deterioration of processing suitability (decreased milled rice percentage and head rice percentage – 2.0% and 23.5%, respectively) and appearance quality (increased chalky grain percentage and chalkiness degree – 16.9% and 28.3%, respectively). Genotype-dependent effects of elevated $[\text{CO}_2]$ on grain quality might in part explain the inconsistencies between the two above-cited studies. In any case, increased amylose concentration at warmer temperatures has been associated with increased “stickiness” of rice grains (Ziska, Namuco, Moya, & Quilang, 1997).

5.2. Minerals

Manderscheid, Bender, Jager, and Weigel (1995) studied two wheat and two barley cultivars grown in pots under ambient and two elevated $[\text{CO}_2]$ in OTCs. They found overall decreases for most macronutrients and micronutrients under high $[\text{CO}_2]$, with nutrient concentrations more affected in straw than in grains, although the responses to elevated $[\text{CO}_2]$ were species- and cultivar-dependent. Idso and Idso (2001), in a qualitative narrative of several papers, suggested that more often than not high CO_2 caused decreases in leaf concentrations of essential mineral elements. Loladze (2002) performed a meta-analysis based on 25 studies covering 19 herbaceous and 11 woody species and concluded that leaf concentrations of macronutrients and micronutrients such as Fe, Zn, Mn and Cu all decreased under elevated CO_2 as compared to controls grown at ambient CO_2 .

Intriguingly, relatively more data concerning mineral composition exist on nonstaple crops than on crop species, particularly in their foliar content (Loladze, 2002). For the two major staple crops, rice and wheat, most studies suggest that, overall, decreased concentrations of nutrients, with the exception of a few minerals (see below), will be the norm in a high- CO_2 world. In rice, Senewera and Conroy (1997) found lower concentrations of four out of five measured elements: N (14%), P (5%), Fe (17%) and Zn (28%), but Ca increased (32%) under elevated CO_2 . In wheat, Loladze analyzed five published studies and noted slight decreases (ranging from ca. 3% to 10%, though significant) in P, Mg and Zn, and decreases superior to 10% in the concentrations of N, Ca, S, Fe, and Zn, whereas K concentration increased slightly. More recently, Högy and Fangmeier (2008) compiled existing data for mineral composition of wheat grains obtained with different CO_2 enrichment technologies and rooting volumes. They concluded that reductions in macronutrients such as N, Ca, Mg, and S were consistent for all wheat cultivars, whereas P and K responded differently to CO_2 enrichment, depending on the CO_2 exposure system and rooting volume. Högy and Fangmeier (2008) also noted high- CO_2 -induced decreases in the concentrations of all micronutrients by 3.7–18.3% over a range of CO_2 enrichment technologies, with the exception of Fe, which increased by 1.2% (but not significantly) in closed field chambers. From the above, although detailed information regarding mineral composition of major crops is scanty, the preponderance of evidence suggests that decreases in essential elements in grains of major crops such as wheat and rice are to be expected, which, ultimately, will aggravate the already acute

malnutrition in the world, putting millions at risk of the “hidden hunger” of micronutrient malnutrition (Stafford, 2008).

Idso and Idso (2001) suggested that plant mineral deficiencies associated with CO₂ enrichment might be relieved by larger fertilizer inputs in intensive agricultural settings. This statement must be cautiously envisaged, however, especially because high inputs of micronutrients beyond a certain critical level (that is too narrow for most micronutrients) can easily lead to toxicity and losses in both quality and quantity of grain yield, as shown for zinc (Rengel, Batten, & Crowley, 1999). In addition, high-micronutrient applications have been associated with nutrient disorders and environmental pollution.

5.3. Lipids

In soybean, oil content was positively correlated with increasing temperature from 25 °C to 36 °C (Wolf et al., 1982). Thomas et al. (2003) studied the combined effects of temperature and [CO₂] on the composition of soybean seeds and found that oil yield was highest at 32/22 °C (day/night) and decreased with further increase in temperature. Oleic acid concentration increased with increasing temperature, whereas linolenic acid decreased. Similar results were also obtained in sunflower by Izquierdo, Aguirrezábal, Andrade, and Pereyra (2002). Changes in fatty acid composition, such as the concentration of oleic acid, are associated with nutritional aspects as well as storage longevity (oleic acid is less susceptible to oxidation than linolenic acid). In any case, minimal concern for the effects of rising [CO₂] on composition and edible quality, as found in maize grains and soybean seeds, has been suggested (e.g., Rogers, Bingham, Cure, Smith, & Surano, 1983; Rogers, Cure, & Smith, 1986; Thomas et al., 2003).

In wheat, quantitative changes in oil composition observed in both non-starch and starch lipid fractions were also much more dependent on elevated temperature (+4 °C above ambient temperature) than on elevated [CO₂] (twice above ambient [CO₂]). Increased temperatures had the general effect of reducing the amounts of accumulated lipids, particularly non-polar lipids (13.22 g fatty acids kg⁻¹ fresh weight at ambient temperatures as opposed to 7.77 g fatty acids kg⁻¹ fresh weight). In addition, unexpected qualitative changes (e.g., increased apparent conversion of oleate to linoleate) were found at higher temperatures (Williams et al., 1995). Such alterations may remarkably influence the milling properties of wheat and the baking qualities of flour.

5.4. Proteins and their fractions

Taub et al. (2008) performed a meta-analysis (228 studies) to examine the effect of elevated atmospheric [CO₂] (540–958 ppm) on the protein concentration of major food crops. For wheat, barley and rice, the reduction in grain protein ranged from 10% to 15% of the value of ambient [CO₂] (315–400 ppm). For potato, the high-[CO₂]-induced reduction in tuber protein concentration was 14% and, for soybean, there was a much smaller, although statistically significant, decrease in protein concentration of 1.4% (see Section 3.3). It should be emphasized that nearly identical ranges in protein reduction were found using several CO₂ enrichment technologies, as shown in wheat by Högy and Fangmeier (2008). These results are particularly important because the major biotechnology companies are attempting to increase protein content in grain crops and will have to work against the effects of rising [CO₂] to achieve this goal (Ainsworth et al., 2008).

Higher N fertilization – sometimes several times current levels – can minimize (Bloom, 2006; Stafford, 2008), but not eliminate, the reduced protein concentration associated with increased atmospheric [CO₂] (Taub et al., 2008). It should be emphasized that fertilization at such rates would be unfeasible in terms of costs and

unacceptable in terms of environmental consequences (Stafford, 2008). In addition, excessive N supply may affect physical quality attributes, as demonstrated in rice grains (higher chalkiness and worse eating/cooking quality at high-N compared with mid- and low-N applications; Yang et al., 2007). Furthermore, at least for wheat, increases in N fertilization may be translated into higher biomass and yield production rather than enhanced redistribution of N from leaves and stems to the grains, resulting in lower grain protein concentration (Högy & Fangmeier, 2008). More importantly, not only the amounts of grain proteins, but also the type of proteins may be altered due to elevated CO₂, as shown for rice (Terao et al., 2005) and wheat (Högy & Fangmeier, 2008).

In wheat, the proportions and properties of the two main classes of gluten storage proteins (glutenin and gliadin), each of which comprises between 35% and 45% of the total grain proteins, are primarily responsible for dough and bread-making quality. In OTC experiments with potted plants, concentrations of these proteins have been shown to decrease at elevated [CO₂], but this response seems to be cultivar-dependent (Högy & Fangmeier, 2008). Although data on the effects of high [CO₂] on protein quality are currently limited, changes in dough properties and bread-making rheological properties in wheat are to be expected at elevated [CO₂].

In a comprehensive compilation of existing data on wheat, Högy and Fangmeier (2008) concluded that, in addition to the reduced protein concentration and possible changes in protein composition in grains, the concentrations of amino acids were significantly reduced by between 7.7% and 23.9% due to CO₂ enrichment in OTCs, except for proline, glycine, tyrosine, histidine, and lysine. Noteworthy, the proportion of the essential amino acids has been shown to increase at elevated [CO₂], as demonstrated for barley (Manderscheid et al., 1995); these relative changes were due mainly to the greater decrease in the amino acid glutamate, which compensated for the [CO₂]-induced decrease in the concentrations of the essential amino acids lysine and arginine. However, most information on [CO₂]-induced changes in amino acid composition has been restricted to enclosure studies with potted plants; more investigations are necessary, especially under real field conditions, to draw firmer conclusions.

5.5. Other food components

Elevated temperatures (especially if coupled with drought stress) are often associated with production of smaller, more fibrous leaves, which usually exhibit changes in nutritional quality – for example, decreasing N and increasing tannins and phenols (Morison & Lawlor, 1999). At elevated [CO₂], tannin and terpene contents also usually increase, especially under ample N supply (Idso & Idso, 2001). Despite these negative impacts on food quality, [CO₂] enrichment may have positive effects; e.g., vitamin C increased by 5% in orange juice harvested from optimally fertilized trees grown under twice-ambient [CO₂]. Elevated [CO₂] has also been demonstrated to increase the production of heart-helping digoxin in the woolly foxglove (*Digitalis lanata*) and a suite of cancer-fighting substances found in the common spider lily (*Hymenocallis littoralis*) (Idso & Idso, 2001).

5.6. Quality of animal forage

The combination of increased [CO₂], in conjunction with changes in rainfall and temperature, are likely to have significant impacts on grasslands and rangelands, e.g., increased biomass production in humid temperate grasslands (Easterling et al., 2007). However, these positive effects of elevated [CO₂] on forage quantity are likely to be lesser than the negative effects on forage quality (Milchunas et al., 2005; Pal et al., 2004).

The negative effects of elevated $[\text{CO}_2]$ on forage N and crude protein concentrations are usually greater than for fiber (e.g., celluloses, lignin) fractions, which can result in lower digestibility under high $[\text{CO}_2]$ (Idso & Idso, 2001; Milchunas et al., 2005). This supports the hypothesis that N rather than carbon soluble and fiber fractions would mediate forage quality responses to elevated $[\text{CO}_2]$ (Milchunas et al., 2005). Nonetheless, in high-quality grass species for ruminants, elevated $[\text{CO}_2]$ and temperature increase may have only minor impacts on the digestibility and fiber composition (Porter & Semenov, 2005). In contrast, livestock that graze rangelands with low protein-containing forage may be more affected by increased C:N ratios than energy-limited livestock that graze protein rich pastures (Milchunas et al., 2005; Porter & Semenov, 2005). Lowering the protein-to-gross energy ratio in forage could reduce the incorporation of protein into the muscle of pigs, leading to less efficient utilization of feed and more waste, including emissions of methane (Porteous et al., 2009; Porter & Semenov, 2005), further aggravating the problems of ongoing climatic changes.

The reduction in N and crude protein content in forage crops may reflect an interaction between elevated $[\text{CO}_2]$ and low-N fertilizer inputs and may have implications for protein quality (i.e., digestibility and amino acid composition) for non-ruminant animals (Porteous et al., 2009). The magnitude of decreases in both N and crude protein differs among forage species, cultivars, N applications and CO_2 exposure conditions, as found in cereals and grass monocultures (Weigel & Manderscheid, 2005). Despite Porteous et al. (2009) pointed out that decreases in both N and crude protein under high $[\text{CO}_2]$ could to some extent be reverted by high-N applications, Weigel and Manderscheid (2005) concluded that there is no unambiguous evidence whether current application rates of N fertilizers could contribute to meet the quality requirements for forage crops with respect to plant N concentrations in a future high- CO_2 world.

6. Concluding remarks

Despite there being a growing body of evidence suggesting that C_3 crops are likely to produce more harvestable products and that both C_3 and C_4 crops are likely to use less water with rising atmospheric $[\text{CO}_2]$ in the absence of stressful conditions, large uncertainties remain about food production in a future scenario with global warming and altered regional patterns of precipitation. In addition, there is currently a limited ability to include realistic impacts of pests and diseases in a changing climate, which otherwise would be an essential aspect for future food security (Gregory, Johnson, Newton, & Ingram, 2009). In fact, both chemical and microbiological risks are foreseen to impair food and feed safety as a consequence of climate change: in particular, mycotoxins, pesticide residues, trace metals and other chemicals could affect food and feed safety (Miraglia et al., 2009). There is, therefore, an urgent need for scientific research that can improve our understanding of the interactions of rising atmospheric $[\text{CO}_2]$ with other environmental variables, such as temperature, water supply and ozone concentration, as well as with biotic factors such as pests and diseases, under real field conditions. In doing so, it is necessary not only to quantify the effects of climatic changes on crop production but also on food quality. It is also necessary to assess responses of crops other than the key cereal grains, and in climate regions other than temperate ones, notably those of importance to developing countries in the tropics and subtropics (Tubiello et al., 2007). Furthermore, since distinct varieties seem to respond differently to elevated CO_2 and temperature in terms of harvestable yield, future research should be also directed towards selecting promising genotypes for a changing global climate.

For obvious reasons, the above-mentioned challenges constitute difficult and daunting tasks, and will certainly require unprecedented transdisciplinary research teams with collaborative research spanning from genomics to agro-ecosystem levels in order to reduce our uncertainties about future food production and security. Alternatively, less uncertainty seems to exist about the expected changes in food quality, which is likely to be impaired with elevated $[\text{CO}_2]$ and particularly with warmer temperatures. For example, protein concentration has been shown to consistently decrease due to CO_2 enrichment for most crops (Taub et al., 2008). Although some increased yield may compensate, to some extent, for slightly lower food quality (in terms of proteins but not lipids and carbohydrates) in a globally altered environment, agronomic and physiological strategies for mitigating changes in food quality should be a priority area for further studies, particularly because they will be increasingly associated with food security.

Acknowledgments

F.M. DaMatta acknowledges research fellowships granted by the Minas Gerais State Research Foundation (Fapemig) and by the National Council for Scientific and Technological Development (CNPq, Brazil). M.S.B. acknowledges support by FAPESP (Grant Number 07/59708-1), CNPq and the Ministry of Science and Technology of Brazil for financial support to scientific activities on the responses of plants to the global climatic change. A.G. and B.C.A. acknowledge support from CNPq and Eletronorte (Pará State, Brazil).

References

- Ainsworth, E. A., Beier, C., Calfapietra, C., Ceulemans, R., Durand-Tardif, M., Farquhar, G. D., et al. (2008). Next generation of elevated $[\text{CO}_2]$ experiments with crops: A critical investment for feeding the future world. *Plant, Cell and Environment*, 31, 1317–1324.
- Ainsworth, E. A., Davey, P. A., Bernacchi, C. J., Dermody, O. C., Heaton, E. A., Moore, D. J., et al. (2002). A metaanalysis of elevated $[\text{CO}_2]$ effects on soybean (*Glycine max*) physiology, growth and yield. *Global Change Biology*, 8, 695–709.
- Ainsworth, E. A., Leakey, A. D. B., Ort, D. R., & Long, S. P. (2008). FACE-ing the facts: Inconsistencies and interdependence among field, chamber and modeling studies of elevated $[\text{CO}_2]$ impacts on crop yield and food supply. *New Phytologist*, 179, 5–9.
- Ainsworth, E. A., & Long, S. P. (2005). What have we learned from 15 years of free air CO_2 enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO_2 . *New Phytologist*, 165, 351–372.
- Ainsworth, E. A., & Rogers, A. (2007). The response of photosynthesis and stomatal conductance to rising $[\text{CO}_2]$: Mechanisms and environmental interactions. *Plant, Cell and Environment*, 30, 258–270.
- Ainsworth, E. A., Rogers, A., & Leakey, A. D. B. (2008). Targets for crop biotechnology in a future high- CO_2 and high- O_3 world. *Plant Physiology*, 147, 13–19.
- Arp, W. J. (1991). Effects of source-sink relations on photosynthetic acclimation to elevated CO_2 . *Plant, Cell and Environment*, 14, 869–875.
- Bannayan, M., Tojo Soler, C. M., Garcia y Garcia, A., Guerra, L. C., & Hoogenboom, G. (2009). Interactive effects of elevated $[\text{CO}_2]$ and temperature on growth and development of a short- and long-season peanut cultivar. *Climatic Change*, 93, 389–406.
- Barnabás, B., Järgen, K., & Fehér, A. (2008). The effect of drought and heat stress on reproductive processes in cereals. *Plant, Cell and Environment*, 31, 11–38.
- Behboudian, M. H., & Tod, C. (1995). Postharvest attributes of 'Virosa' tomato fruit produced in an enriched carbon dioxide environment. *HortScience*, 30, 490–491.
- Bengtsson, M., Shen, Y., & Oki, T. (2006). A SRES-based gridded global population dataset for 1990–2100. *Population and Environment*, 28, 113–131.
- Bloom, A. J. (2006). Rising carbon dioxide concentrations and the future of crop production. *Journal of the Science of Food and Agriculture*, 86, 1289–1291.
- Challinor, A. J., Ewert, F., Arnold, S., Simelton, E., & Fraser, E. (2009). Crops and climate change: Progress, trends, and challenges in simulating impacts and informing adaptation. *Journal of Experimental Botany*. doi:10.1093/jxb/erp062.
- Challinor, A. J., & Wheeler, T. R. (2008a). Use of a crop model ensemble to quantify CO_2 stimulation of water-stressed and well-watered crops. *Agricultural and Forest Meteorology*, 148, 1062–1077.
- Challinor, A. J., & Wheeler, T. R. (2008b). Crop yield reduction in the tropics under climate change: Processes and uncertainties. *Agricultural and Forest Meteorology*, 148, 343–356.
- Craufurd, P. Q., & Wheeler, T. R. (2009). Climate change and the flowering time of annual crops. *Journal of Experimental Botany*, 60, 2529–2539.

- Curtis, P. S., & Wang, X. (1998). A meta-analysis of elevated CO₂ effects on woody plant mass, form, and physiology. *Oecologia*, *113*, 299–313.
- De Souza, A. P., Gaspar, M., Silva, E. A., Ulian, E. C., Wacławowski, A. J., Nishiyama, M. Y., Jr., et al. (2008). Elevated CO₂ increases photosynthesis, biomass and productivity, and modifies gene expression in sugarcane. *Plant, Cell and Environment*, *31*, 1116–1127.
- Demmers-Derks, H. H., Mitchell, R. A. C., Mitchell, V. J., & Lawlor, D. W. (1998). Response of sugar beet (*Beta vulgaris* L.) yield and biochemical composition to elevated CO₂ and temperature at two nitrogen applications. *Plant, Cell and Environment*, *21*, 829–836.
- Drake, B. G., Azcon-Bieto, J., Berry, J., Bunce, J., Dijkstra, P., Farrar, J., et al. (1999). Does elevated atmospheric CO₂ concentration inhibit mitochondrial respiration in green plants? *Plant, Cell and Environment*, *22*, 649–657.
- Drake, B. G., Gonzalez-Meler, M. A., & Long, S. P. (1997). More efficient plants: A consequence of rising atmospheric CO₂? *Annual Review of Plant Physiology and Plant Molecular Biology*, *48*, 609–639.
- Easterling, W. E., Aggarwal, P. K., Batima, P., Brander, L. M., Erda, L., Howden, S. M., et al. (2007). Food, fibre and forest products. In M. L. Parry, O. F. Canziani, J. P. Palutikof, P. J. van der Linden, & C. E. Hanson (Eds.), *Climate change 2007: Impacts, adaptation and vulnerability. Contribution of Working Group II to the fourth assessment report of the intergovernmental panel on climate change* (pp. 273–313). Cambridge: Cambridge University Press.
- Ellsworth, D. S., Reich, P. B., Naumburg, E. S., Koch, G. W., Kubiske, M. E., & Smith, S. D. (2004). Photosynthesis, carboxylation and leaf nitrogen responses of 16 species to elevated pCO₂ across four free-air CO₂ enrichment experiments in forest, grassland and desert. *Global Change Biology*, *10*, 2121–2138.
- Erda, L., Wei, X., Hui, J., Yinlong, X., Yue, L., Liping, B., et al. (2005). Climate change impacts on crop yield and quality with CO₂ fertilization in China. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *360*, 2149–2154.
- Fangmeier, A., De Temmerman, L., Mortensen, L., Kemp, K., Burke, J., Mitchell, R., et al. (1999). Effects on nutrients and on grain quality in spring wheat crops grown under elevated CO₂ concentrations and stress conditions in the European, multiple-site experiment “ESPACE-wheat”. *European Journal of Agronomy*, *10*, 215–229.
- Fuhrer, J. (2003). Agroecosystem responses to combinations of elevated CO₂, ozone, and global climate change. *Agriculture, Ecosystems and Environment*, *97*, 1–20.
- Gifford, R. M. (2003). Plant respiration in productivity models: Conceptualisation, representation and issues for global terrestrial carbon-cycle research. *Functional Plant Biology*, *30*, 171–186.
- Gregory, P. J., Johnson, S. N., Newton, A. C., & Ingram, J. S. I. (2009). Integrating pests and pathogens into the climate change/food security debate. *Journal of Experimental Botany*. doi:10.1093/jxb/erp080.
- Hay, R., & Porter, J. (2006). *The physiology of crop yield* (2nd ed.). Oxford: Blackwell.
- Hesketh, J., & Hellmers, H. (1973). Floral initiation in four plant species growing in CO₂-enriched air. *Environmental Control in Biology*, *11*, 51–53.
- Högy, P., & Fangmeier, A. (2008). Effects of elevated atmospheric CO₂ on grain quality of wheat. *Journal of Cereal Science*, *48*, 580–591.
- Holtum, J. A. M., & Winter, K. (2003). Photosynthetic CO₂ uptake in seedlings of two tropical tree species exposed to oscillating elevated concentrations of CO₂. *Planta*, *218*, 152–158.
- Idso, S. B., & Idso, K. E. (2001). Effects of atmospheric CO₂ enrichment on plant constituents related to animal and human health. *Environmental and Experimental Botany*, *45*, 179–199.
- Ingram, J. S. I., Gregory, P. J., & Izac, A.-M. (2008). The role of agronomic research in climate change and food security policy. *Agriculture, Ecosystems and Environment*, *126*, 4–12.
- IPCC (2007). *Climate change 2007: The physical science basis. Summary for policymakers*. Paris: WMO/UNEP.
- Izquierdo, N., Aguirrezábal, L., Andrade, F., & Pereyra, V. (2002). Night temperature affects fatty acid composition in sunflower oil depending on the hybrid and the phenological stage. *Field Crops Research*, *77*, 115–126.
- Jablonski, L. M., Xianzhong, W., & Curtis, P. S. (2002). Plant reproduction under elevated CO₂ conditions: A meta-analysis of reports on 79 crop and wild species. *New Phytologist*, *156*, 9–26.
- Kimball, B. A., & Bernacchi, C. J. (2006). Evapotranspiration, canopy temperature, and plant water relations. In J. Nösberger, S. P. Long, R. J. Norby, M. Stitt, G. R. Hendrey, & H. Blum (Eds.), *Managed ecosystems and CO₂* (pp. 311–324). Berlin: Springer-Verlag.
- Kimball, B. A., Idso, S. B., Johnson, S., & Rillig, M. T. (2007). Seventeen years of carbon dioxide enrichment of sour orange trees: Final results. *Global Change Biology*, *13*, 2171–2183.
- Leakey, A. D. B., Ainsworth, E. A., Bernacchi, C. J., Rogers, A., Long, S. P., & Ort, D. R. (2009). Elevated CO₂ effects on plant carbon, nitrogen, and water relations: Six important lessons from FACE. *Journal of Experimental Botany*. doi:10.1093/jxb/erp096.
- Leakey, A. D. B., Uribelarrea, M., Ainsworth, E. A., Naidu, S. L., Rogers, A., Ort, D. R., et al. (2006). Photosynthesis, productivity, and yield of maize are not affected by open-air elevation of CO₂ concentration in the absence of drought. *Plant Physiology*, *140*, 779–790.
- Leakey, A. D. B., Xu, F., Gillespie, K. M., McGrath, J. M., Ainsworth, E. A., & Ort, D. R. (2009). The genomic basis for stimulated respiratory carbon loss to the atmosphere by plants growing under elevated [CO₂]. *Proceedings of the National Academy of Sciences, USA*, *106*, 3597–3602.
- Loladze, I. (2002). Rising atmospheric CO₂ and human nutrition: Toward globally imbalanced plant stoichiometry? *Trends in Ecology & Evolution*, *17*, 457–461.
- Long, S. P. (1991). Modification of the response of photosynthetic productivity to rising temperature by atmospheric CO₂ concentrations: Has its importance been underestimated? *Plant, Cell and Environment*, *14*, 729–739.
- Long, S. P., Ainsworth, E. A., Leakey, A. D. B., & Ort, D. R. (2006). Food for thought: Lower-than-expected crop yield stimulation with rising CO₂ conditions. *Science*, *312*, 1918–1921.
- Long, S. P., Ainsworth, E. A., Rogers, A., & Ort, D. R. (2004). Rising atmospheric carbon dioxide: Plants FACE the future. *Annual Review of Plant Biology*, *55*, 591–628.
- Manderscheid, R., Bender, J., Jäger, H.-J., & Weigel, H. J. (1995). Effects of season long CO₂ enrichment on cereals. II. Nutrient concentrations and grain quality. *Agriculture, Ecosystems and Environment*, *54*, 175–185.
- Maroco, J. P., Edwards, G. E., & Ku, M. S. B. (1999). Photosynthetic acclimation of maize to growth under elevated levels of carbon dioxide. *Planta*, *210*, 115–125.
- Matsui, T., Namuco, O. S., Ziska, L. H., & Horie, T. (1997). Effects of high temperature and CO₂ concentration on spikelet sterility in indica rice. *Field Crops Research*, *51*, 213–219.
- McLeod, A., & Long, S. P. (1999). Free air carbon dioxide enrichment (FACE) in global change research: A review. *Advances in Ecological Research*, *28*, 1–55.
- Miglietta, F., Magliulo, V., Bindi, M., Cerio, L., Vaccari, F. P., Loduca, V., et al. (1998). Free air CO₂ enrichment of potato (*Solanum tuberosum* L.): Development, growth and yield. *Global Change Biology*, *4*, 163–172.
- Miglietta, F., & Raschi, A. (1993). Studying the effect of elevated CO₂ in the open in a naturally enriched environment in central Italy. *Vegetatio*, *104*, 391–400.
- Milchunas, D. G., Mosier, A. R., Morgan, J. A., LeCain, D. R., King, J. Y., & Nelson, J. A. (2005). Elevated CO₂ and defoliation effects on a shortgrass steppe: Forage quality versus quantity for ruminants. *Agriculture, Ecosystems and Environment*, *111*, 166–184.
- Miraglia, M., Marvin, H. J. P., Kleter, G. A., Battilani, P., Brera, C., Coni, E., et al. (2009). Climate change and food safety: An emerging issue with special focus on Europe. *Food and Chemical Toxicology*, *47*, 1009–1021.
- Mitchell, R. A. C., Mitchell, V., Driscoll, S. P., Franklin, J., & Lawlor, D. W. (1993). Effects of increased CO₂ concentration and temperature on growth and yield of winter wheat at two levels of nitrogen application. *Plant, Cell and Environment*, *16*, 521–529.
- Morison, J. I. L., & Lawlor, D. W. (1999). Interactions between increasing CO₂ concentration and temperature on plant growth. *Plant, Cell and Environment*, *22*, 659–682.
- Pal, M., Karthikeyapandian, V., Jain, V., Srivastava, A. C., Raj, A., & Sengupta, U. K. (2004). Biomass production and nutritional levels of berseem (*Trifolium alexandrinum*) grown under elevated CO₂. *Agriculture, Ecosystems and Environment*, *101*, 31–38.
- Polley, H. W. (2002). Implications of atmospheric and climate change for crop yield. *Crop Science*, *42*, 131–140.
- Porteus, F., Hill, J., Ball, A. S., Pinter, P. J., Kimball, A., Wall, G. W., et al. (2009). Effect of free air carbon dioxide enrichment (FACE) on the chemical composition and nutritive value of wheat grain and straw. *Animal Feed Science and Technology*, *149*, 322–332.
- Porter, J. R., & Semenov, M. A. (2005). Crop responses to climatic variation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *360*, 2021–2035.
- Rengel, Z., Batten, G. D., & Crowley, D. E. (1999). Agronomic approaches for improving the micronutrient density in edible portions of field crops. *Field Crops Research*, *60*, 27–40.
- Rogers, H. H., Bingham, G. E., Cure, J. D., Smith, J. M., & Surano, K. A. (1983). Responses of selected plant species to elevated carbon dioxide in the field. *Journal of Environmental Quality*, *12*, 569.
- Rogers, H. H., Cure, J. D., & Smith, J. M. (1986). Soybean growth and yield response to elevated carbon dioxide. *Agriculture, Ecosystems and Environment*, *16*, 113–128.
- Ronchi, C. P., DaMatta, F. M., Batista, K. D., Moraes, G. A. B. K., Loureiro, M. E., & Ducatti, C. (2006). Growth and photosynthetic down-regulation in *Coffea arabica* in response to restricted root volume. *Functional Plant Biology*, *33*, 1013–1023.
- Sage, R. F., Way, D. A., & Kubien, D. S. (2008). Rubisco, Rubisco activase, and global climate change. *Journal of Experimental Botany*, *59*, 1581–1595.
- Sebastian, S. A., Kerr, P. S., Pearlstein, R. W., & Hitz, W. D. (2000). Soybean germplasm with novel genes for improved digestibility. In J. K. Drackley (Ed.), *Soy in animal nutrition* (pp. 56–74). Savory, IL: Federation of Animal Science Society.
- Seneweera, S. P., & Conroy, J. P. (1997). Growth, grain yield and quality of rice (*Oryza sativa* L.) in response to elevated CO₂ and phosphorus nutrition. *Soil Science and Plant Nutrition*, *43*, 1131–1136.
- Socias, F. X., Medrano, H., & Sharkey, T. D. (1993). Feedback limitation of photosynthesis of *Phaseolus vulgaris* L. grown in elevated CO₂. *Plant, Cell and Environment*, *16*, 81–86.
- Springer, C. J., & Ward, J. K. (2007). Flowering time and elevated atmospheric CO₂. *New Phytologist*, *176*, 243–255.
- Stafford, N. (2008). The other greenhouse effects. *Nature*, *448*, 526–528.
- Taiz, L., & Zeiger, E. (2006). *Plant physiology* (4th ed.). Sunderland: Sinauer Associates.
- Taub, D., Miller, B., & Allen, H. (2008). Effects of elevated CO₂ on the protein concentration of food crops: A meta-analysis. *Global Change Biology*, *14*, 565–575.
- Terao, T., Miura, S., Yanagihara, T., Hirose, T., Nagata, K., Tabuchi, H., et al. (2005). Influence of free-air CO₂ enrichment (FACE) on the eating quality of rice. *Journal of the Science of Food and Agriculture*, *85*, 1861–1868.

- Thomas, J. M. G., Boote, K. J., Allen, L. H., Gallo-Meagher, M., & Davis, J. M. (2003). Elevated temperature and carbon dioxide effects on soybean seed composition and transcript abundance. *Crop Science*, *43*, 1548–1557.
- Thomas, J. M. G., Prasad, P. V. V., Boote, K. J., & Allen, L. H. (2009). Seed composition, seedling emergence and early seedling vigour of red kidney bean seed produced at elevated temperature and carbon dioxide. *Journal of Agronomy & Crop Science*, *195*, 148–156.
- Tubiello, F. N., Amthor, J. S., Boote, K. J., Donatelli, M., Easterling, W., Fischer, G., et al. (2007). Crop response to elevated CO₂ and world food supply. *European Journal of Agronomy*, *26*, 215–233.
- Tubiello, T. N., & Fischer, G. (2007). Reducing climate change impacts on agriculture: Global and regional effects of mitigation 2000–2080. *Technological Forecasting & Social Change*, *74*, 1030–1056.
- Tubiello, F. N., Soussana, J.-F., & Howden, S. M. (2007). Crop and pasture response to climate change. *Proceedings of the National Academy of Sciences, USA*, *104*, 19686–19690.
- Vara Prasad, P. V., Craufurd, P. Q., Summerfield, R. J., & Wheeler, T. R. (2000). Effects of short-episodes of heat stress on flower production and fruit-set of groundnut (*Arachis hypogaea* L.). *Journal of Experimental Botany*, *51*, 777–784.
- von Caemmerer, S., & Furbank, R. T. (2003). The C₄ pathway: An efficient CO₂ pump. *Photosynthesis Research*, *77*, 191–207.
- Vu, J. C. V., & Allen, L. H. (2009). Growth at elevated CO₂ delays the adverse effects of drought stress on leaf photosynthesis of the C₄ sugarcane. *Journal of Plant Physiology*, *166*, 107–116.
- Wallwork, M. A. B., Jenner, C. F., Logue, S. J., & Sedgley, M. (1998). Effect of high temperature during grain-filling on the structure of developing and malted barley grains. *Annals of Botany*, *82*, 587–599.
- Wand, S. J. E., Midgley, G. F., Jones, M. H., & Curtis, P. S. (1999). Responses of wild C₄ and C₃ grass (Poaceae) species to elevated atmospheric CO₂ concentration: A meta-analytic test of current theories and perceptions. *Global Change Biology*, *5*, 723–741.
- Weigel, H. J., & Manderscheid, R. (2005). CO₂ enrichment effects on forage and grain nitrogen content of pasture and cereal plants. *Journal of Crop Improvement*, *13*, 73–89.
- Williams, M., Shewry, P. R., Lawlor, D. W., & Harwood, J. L. (1995). The effects of elevated temperature and atmospheric carbon dioxide concentration on the quality of grain lipids in wheat (*Triticum aestivum* L.) grown at two levels of nitrogen application. *Plant, Cell and Environment*, *18*, 999–1009.
- Wolf, R. B., Cavins, J. F., Kleiman, R., & Black, L. T. (1982). Effect of temperature on soybean seed constituents: Oil, protein, moisture, fatty acids, amino acids and sugars. *Journal of the American Oil Chemists' Society*, *59*, 230–232.
- Yang, L., Wang, Y., Dong, G., Gu, H., Huang, J., Zhu, J., et al. (2007). The impact of free-air CO₂ enrichment (FACE) and nitrogen supply on grain quality of rice. *Field Crops Research*, *102*, 128–140.
- Yang, L., Wang, H., Liu, Y., Zhu, J., Huang, J., Liu, G., et al. (2009). Yield formation of CO₂-enriched inter-subspecific hybrid rice cultivar Liangyoupeijiu under fully open-air field condition in a warm sub-tropical climate. *Agriculture, Ecosystems and Environment*, *129*, 193–200.
- Ziska, L. H., & Bunce, J. A. (1997). Influence of increasing carbon dioxide concentration on the photosynthetic and growth stimulation of selected C₄ crops and weeds. *Photosynthesis Research*, *54*, 199–208.
- Ziska, L. H., & Bunce, J. A. (2006). Plant responses to rising atmospheric carbon dioxide. In J. I. L. Morison & M. D. Morecroft (Eds.), *Plant growth and climate change* (pp. 17–47). Oxford: Blackwell.
- Ziska, L. H., & Bunce, J. A. (2007). Predicting the impact of changing CO₂ on crop yields: Some thoughts on food. *New Phytologist*, *175*, 607–618.
- Ziska, L. H., Manalo, P. A., & Ordonez, R. (1996). Intraspecific variation in the response of rice (*Oryza sativa* L.) to increased CO₂: Evaluation of 17 cultivars. *Journal of Experimental Botany*, *47*, 1353–1359.
- Ziska, L. H., Namuco, O., Moya, T., & Quilang, J. (1997). Growth and yield response of field-grown tropical rice to increasing carbon dioxide and air temperature. *Agronomy Journal*, *89*, 45–53.