Review

Food security and climate change: on the potential to adapt global crop production by active selection to rising atmospheric carbon dioxide

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Agricultural production is under increasing pressure by global anthropogenic changes, including rising population, diversion of cereals to biofuels, increased protein demands and climatic extremes. Because of the immediate and dynamic nature of these changes, adaptation measures are urgently needed to ensure both the stability and continued increase of the global food supply. Although potential adaptation options often consider regional or sectoral variations of existing risk management (e.g. earlier planting dates, choice of crop), there may be a global-centric strategy for increasing productivity. In spite of the recognition that atmospheric carbon dioxide (CO₂) is an essential plant resource that has increased globally by approximately 25 per cent since 1959, efforts to increase the biological conversion of atmospheric CO₂ to stimulate seed yield through crop selection is not generally recognized as an effective adaptation measure. In this review, we challenge that viewpoint through an assessment of existing studies on CO₂ and intraspecific variability to illustrate the potential biological basis for differential plant response among crop lines and demonstrate that while technical hurdles remain, active selection and breeding for CO₂ responsiveness among cereal varieties may provide one of the simplest and direct strategies for increasing global yields and maintaining food security with anthropogenic change.

Keywords: adaptation; breeding; climate change; carbon dioxide; food security

1. INTRODUCTION

The impact of the green revolution of the 1960s and 1970s in stimulating cereal productivity and ensuring near-global food security is well recognized. However, a current analysis of yield increases of eight key cereals relative to the increase in the human population since that period indicates that any green revolution-induced increases in cereal production, relative to population growth are now at an end (figure 1).

If the gains of the green revolution relative to population have been negated, challenges for the agricultural sector remain. There is necessity for more: more cereals for biofuel, more grain for meat, more food for the additional 2 billion people expected by 2050; and as these demands mount, available resources are becoming strained, with less arable land, less water for irrigation and less energy for fertilizer production. Additional emerging constraints include the need to reduce net greenhouse gas emissions, desires to foster biodiverse landscapes and regions, ongoing degradation of soil and other natural resources, and the rising cost of agricultural...
inputs [1]. This environmental uncertainty is paralleled by food insecurity with both food prices and volatility at record levels. As multi-factor pressures on food supply and distribution become more evident, the need for agricultural adaptation becomes immediate and germane.

Agricultural adaptation is multi-faceted, and should include a number of on-farm strategies related to planting times, irrigation, fertilizer, disease and pest management, shifting crop zones, etc., as well as off-farm strategies across the value chain dealing with non-production inputs [1]. This environmental uncertainty is paralleled by food insecurity with both food prices and volatility at record levels. As multi-factor pressures on food supply and distribution become more evident, the need for agricultural adaptation becomes immediate and germane.

Figure 1. Average change by decade (i.e. 1960s, 1970s, etc.) ± s.e., in per cent growth of eight basic cereals (barley, corn, millet, oat, rice, rye, sorghum, wheat) as directly consumed by the human population (i.e. not used for biofuels or animal feed) and the average change by decade in per cent population growth. Gains in cereal production over population represent the ‘green revolution’ of the 1960s. Around 2003, net per cent gains in cereals and those in population were roughly equivalent, and the green revolution ended. Data are from Food and Agriculture Organization statistics, available at http://faostat.fao.org/site/345/default.aspx.

2. THE RESPONSE OF CROPS TO RISING CO₂: ASSESSING POTENTIAL

At biologically relevant temperatures, it is recognized that there are four abiotic resources necessary for plant growth to occur: (i) light; (ii) nutrients; (iii) water; and (iv) CO₂. Because approximately 93 per cent of all plant species currently lack optimal levels of CO₂ for photosynthesis (i.e. those plants with the C₃ photosynthetic pathway), the anthropogenically driven increase in global atmospheric CO₂ represents an increase in an available growth resource. Since 1959, concentrations of atmospheric CO₂ have increased from 318 to 395 μmol mol⁻¹, and, depending on anthropogenic emission rates, may exceed 1000 μmol mol⁻¹ by the end of the century [1]. Increases in CO₂ concentration have been shown in numerous studies to increase carbon fixation with subsequent effects on plant growth, development, morphology and reproduction [5].

While differences between plant species in response to global increases in CO₂ are to be expected [5], a more pertinent adaptation question is: what is the extent of CO₂ stimulation among genotypes of a crop species? Is there sufficient genetic variation for breeders to begin selections for CO₂ responsiveness with respect to reproduction and seed yield?

An evaluation of 17 cultivated rice lines at ambient and 660 μmol mol⁻¹ CO₂ [6], the largest intraspecific crop comparison made to date, indicated that there was considerable genetic variation among yield in response to projected increases in atmospheric CO₂ (figure 2). That is, there was evidence suggesting that not all cultivars of rice were currently adapted to the present CO₂ concentration or equally responsive to elevated CO₂. Additional studies have confirmed that there is significant intraspecific variation in the yield response to elevated CO₂ among cowpea (Vigna unguiculata, L., Walp.) [7], common bean (Phaseolus vulgaris L.) [8], rice (Oryza sativa L.) [9,10], wheat (Triticum aestivum L.) [11] and soybean (Glycine max L. Merr.) [12], such that breeders could begin to select for CO₂ responsiveness among currently available germplasm.

However, as noted by Newton & Edwards [13], these data do not necessarily reflect any long-term benefit of CO₂ selection because it is unclear whether the plant germplasm being evaluated was necessarily adapted to the higher CO₂ concentration. A better test of adaptation would be to evaluate genotypes or populations at high CO₂ over multiple seasons as a means to simulate the...
benefits of plant breeding in the resulting progeny. Unfortunately, there are few multi-generational evaluations of any agronomic crop to projected CO2 levels [14].

An additional line of research that may be indicative of CO2 adaptation is the long-term temporal selection of plant populations around natural CO2 springs [15]. Because these populations have been grown at supra-ambient CO2 concentrations over evolutionarily relevant time spans, they should provide a source of CO2 adapted material. Newton et al. [16] examined populations of Dactylis glomerata isolated from ambient and elevated CO2 environments and determined that the main selection pressure was from atmospheric CO2 [17]. Furthermore, when these populations were tested in the short-term under elevated CO2 conditions, the high-CO2 adapted population produced 30 per cent more biomass relative to the ambient CO2 population [18]. Recent data for a perennial herb (Plantago asiatica) grown for multi-generations across a natural CO2 gradient also show greater evolutionary fitness, including higher relative growth rates, at elevated compared with ambient CO2 concentrations [19].

The data for D. glomerata [13,18] indicate that this species increased its biomass by 0.28 per cent for every μmol mol\(^{-1}\) increase in CO2. From 2000 to 2009, the mean CO2 growth rate was 2 μmol mol\(^{-1}\) CO2 per year, or a potential increase in biomass of 5.6 per cent per decade. This agrees well with the average decadal increase in forage yield that has already occurred from US breeding programmes for this species (approx. 4.5%) [20].

In summary, there appears to be sufficient evidence to suggest that (i) intraspecific variability exists among crop genotypes to begin selection for yield responses to increasing CO2s and (ii) breeding efforts could be a means to increase plant yields in the long-term as has been observed for multi-generational plants growing proximate to CO2 springs.

3. ARE NOT BREEDERS ALREADY SELECTING FOR CO2 RESPONSIVENESS?

There are, at present, no published records of any methodological, long-term attempts for the selection of crop lines with greater yield responsiveness to anthropogenic increases in atmospheric CO2. The reasons for the paucity of data on this issue are unclear. It may reflect, in part, the gradual increase in atmospheric CO2 and the assumption that empirical selection for increasing crop yield will, in a managed environment, choose the most CO2-responsive plants over time [21]. Alternatively, it may reflect the difficulty in quantifying CO2 impacts because any stimulation effects on growth or yield would be difficult to separate from the rapid genetic, technological and management progress that has coincided with the green revolution [22].

Nevertheless, if breeders are already, in effect, passively selecting the most CO2-responsive cultivars, there is little need to initiate any active CO2 breeding programme. While this may be difficult to determine for future CO2 levels, it may be possible to assess for recent increases by comparing cultivated lines released in the early- and late twentieth century; i.e. when CO2 rose from approximately 290 to 370 μmol mol\(^{-1}\), an increase of 28 per cent. If breeders are selecting for CO2 sensitivity de facto, then as with the CO2 springs experiment; modern, adapted CO2 lines should show a greater CO2 response when grown at current CO2 levels relative to cultivars that were developed during the early twentieth century.

To test this hypothesis, oat cultivars released during the 1920s were compared with lines released during the 1990s from a given breeding site for seven different geographical locations [23]. Because the breeding settings were the same, edaphic and abiotic characteristics should be similar, and not a confounding factor. Because oat has a very low outcrossing rate, it can be reasonably assumed that these lines have not changed genetically since their release.

When compared at similar CO2 concentrations, 300 and 400 μmol mol\(^{-1}\), i.e. the approximate atmospheric CO2 concentration in the 1920 and the 1990s, respectively, there was no greater relative response observed for the 1990s cultivars relative to those released in the 1920s (figure 3). Indeed, the opposite outcome was observed, with lines released during the 1920s showing a greater relative and diverse response to the twentieth century increase in atmospheric CO2 for all measured parameters (figure 3). Although seed yield was not measured for oats, other data for wheat [11,24,25] indicate a greater relative increase in yield for older cultivars to both recent and projected increases in atmospheric CO2 concentration.

Overall, while additional data are needed, there is no indication that breeders have, in fact, maximized CO2 responsiveness among newer cereal cultivars, even though atmospheric CO2 has increased significantly in recent decades.

4. THE CASE FOR ACTIVE SELECTION

While breeding efforts have made significant increases in crop yields during the twentieth century, it is not clear that these efforts have increased CO2 sensitivity among modern cultivars. The underlying reasons have not been entirely elucidated.

At the physiological level, selection for CO2 sensitivity is not likely to happen passively. First, the form of rubisco in present day C3 plants is optimized for an atmospheric CO2 concentration of approximately 220 μmol mol\(^{-1}\), and not for the present concentration of 395 μmol mol\(^{-1}\) [26]. Rubisco is the enzyme that catalyzes both carboxylation and oxygenation of RuBP, and is critical in controlling the balance between photosynthesis and respiration. Zhu et al. [26] have suggested that optimizing rubisco for the current atmospheric CO2 concentration would increase carbon assimilation by 10 per cent per se.

Second, it is generally recognized that advances in plant breeding are associated with recurrent selection, usually in field environments. As a consequence, selection for say, pest resistance, should be occurring concurrently with rising CO2 and, as a result, reflect CO2 adaptation. However, plant breeding is a long-term process that can extend over decades, and indirect selection for yield under field conditions is likely to be inefficient because yield is related to a number of abiotic and biotic factors. Re-selection could offer the possibility of adjusting a cultivar to a new CO2 value, but often proprietary rights require that cultivars are maintained in their original genotypic condition; (i.e. a 1980 genotype remains the same...
Interestingly, a recent study examining 30 years of yield trials with IR 8, one of the original ‘green revolution’ rice cultivars, indicated a 15 per cent loss in yield relative to yields achieved in the 1960s, emphasizing the need for maintenance breeding as a means to adapt to changing climates (e.g. CO2) [27]. Last, it has been hypothesized that, with the onset of the green revolution, greater emphasis was placed on genetic uniformity as a means to maintain economic consistency in response to water and fertilizer, particularly among large-scale farms [28]. Such uniformity in management may, in turn, limit the extent of genetic variation in response to environmental changes, such as CO2 [29]. The comparison of early- and late twentieth century oat lines (figure 3) was consistent with this later hypothesis as the more recently released oat cultivars showed greater uniformity among vegetative and reproductive traits [23].

Figure 3. The average relative stimulation (± s.e.) in vegetative characteristics of cultivated oat (Avena sativa) from seed released in the 1920s (old) and the 1990s (new) for seven geographical locations for an increase in approximately 100 μmol mol$^{-1}$ CO2 (i.e. the increase in atmospheric (CO2) from the 1920s (‘A’) to the 1990s (‘E’)). Relative stimulation was calculated as (E − A)/A for a given location; with a value of 1 (dashed line) indicating no difference. These data were taken from Ziska & Blumenthal [23].

 opportunities for increasing production will be missed if we assume that current selections will result in crop plants that are optimized to the current CO2 concentration.

5. INITIATING A CO2 SELECTION PROGRAMME: CHALLENGES

Presently, there is sufficient empirical evidence to advocate that substantial increases in crop production could be achieved by considering the most certain of anthropogenic climate changes—the rise in atmospheric CO2 concentration [30]. Although preliminary, the available data suggest that, at current and projected increases in atmospheric CO2, substantive increases in crop yields could be achieved by either active selection or development of plant material responsive to a higher CO2 environment.

Yet, in spite of the widely acknowledged need to increase agricultural productivity, systematic attempts to exploit CO2 as a means to increase crop yields are very limited. This seems surprising, particularly because atmospheric CO2 has increased rapidly in recent decades.
(e.g. 11% since 1990) [31]. Indeed, one could argue that if other abiotic resources had increased to a similar extent in so short a period (e.g. imagine an increase in global soil nitrogen by 11% since 1990), there would be a widespread agronomic impetus to begin an active breeding programme to optimize that resource.

(a) Methodology

One of the obvious technical challenges is to simulate future CO2 and/or climatic conditions for a large number of cultivars in order to begin the screening process. From a methodological viewpoint, maintaining control of CO2 (or any abiotic variable) becomes more difficult with increases in physical size, and hence the number of lines that can be screened at a given time may be limited. Although cultivar screening has not been specifically addressed, large-scale (300 m²) evaluations of elevated CO2 have been achieved using open-air CO2 fumigation, or free-air CO2 enrichment (FACE) technology [32]. However, rapidly fluctuating CO2 concentrations within elevated FACE rings, or lack of night-time exposure to elevated CO2 concentrations, may underestimate the fertilization effect of enriched CO2 on plant growth [33,34]. Conversely, other studies using smaller enclosures (e.g. greenhouses) to enrich CO2 have consistent CO2 delivery, but will differ significantly from in situ conditions [35].

In general, the cost and complexity of methodologies to accurately simulate future climatic conditions increases with spatial and temporal extremes [36]. As a consequence, most of what is currently known concerning rising CO2, and plant function is at the level of single leaves or whole plants. These levels of organization represent the most experimentally accessible data, while less is known for either very large (e.g. ecosystem) or very small (e.g. genetic regulation, proteomics) bioprocesses.

(b) Selection criteria

In spite of hundreds of studies that have documented the biological response of plant species to rising CO2, there is no clear consensus on what phenological, morphological and/or physiological characteristics are associated with cultivar selection for yield response as a function of atmospheric CO2. There have been a number of suggestions at different organismal levels that could mediate the CO2 response, including genetic (e.g. carbohydrate regulation of RNA) [37], biochemical (e.g. rubisco activase) [38], leaf (e.g. stomatal density [39] or photosynthesis [8]), whole plant (relative growth rate) [40], management (e.g. planting density) [41] and canopy (e.g. nitrogen applications) [42], but specific organismal characteristics consistently associated with CO2 responsiveness and crop yield have not been identified. Without a clear set of indices, breeders will have a difficult time selecting or developing promising crop archetypes.

(c) Scaling up of biological responses

Recent decades have seen many genomic and molecular innovations that have been widely viewed as increasing the precision of genetic transfer and hastening the release of new cultivars. However, as emphasized by Sinclair et al. [43], responses at the molecular level do not necessarily scale to greater yield in situ. This is particularly relevant for increases in atmospheric CO2; i.e. how to develop higher seed yields in the field based on CO2 induced increases in the photosynthetic rate of single leaves or whole plants in the laboratory. This is an obvious challenge for crop breeding efforts.

(d) Interactions with other climatic variables

Carbon dioxide is not just the source of carbon for photosynthesis, but a longwave-radiation trapping gas, with consequences for surface temperatures and precipitation, climatic variables that will also affect crop productivity. Temperatures, particularly temperatures during anthesis, may be critical in maintaining crop productivity [44]. Initial assessments based on photosynthetic biochemistry suggested a positive interaction between projected increases in temperature and CO2 on yield [45]. However, it is now clear that such positive interactions do not always translate into additional seed yield with simultaneous increases in CO2 and temperature as opposed to elevated CO2 per se [46–48]. In contrast to CO2 and temperature interactions, there are a number of studies indicating that under water-limited conditions the indirect effect of CO2 on stomatal aperture (and potential reductions in transpirational water use) may enhance the relative effect of CO2 on crops [49,50], although this effect may be reduced at the canopy relative to the whole leaf level [51]. In any case, a fundamental challenge will be to consider CO2 selections for their performance in a range of temperature and moisture conditions to assess potential negative interactions with respect to yield. Such selections will, by necessity, include an evaluation of multiple-gene responses.

(e) Seed quality

Reductions in nitrogen and protein content have been observed in a number of CO2–response studies for a wide range of agronomic crops [52]. A significant challenge for CO2 responsiveness will be to impose selection pressure or co-develop suitable management practices that will maintain desired quality and nutritional parameters.

6. CO2 SELECTION: MEETING THE CHALLENGES

Screenings for yield response to elevated CO2 within a given crop species will necessitate evaluations of diverse germplasm and/or phenotypes, preferably under in situ climatic conditions and agronomic practices. Suitably located FACE facilities could provide for simultaneous screening of a large number of crop lines in this regard; however, in addition to concerns regarding temporal consistency of CO2 fumigation, average plot size within FACE systems can be small from 1 to 5 m² [53,54], in part, because of edge effects near the ring. In addition, CO2 supply costs would be considerable because continuous selection over several years would be required to develop lines sensitive to high CO2. It is possible that new FACE prototypes [55,56] could increase CO2 uniformity and reduce supply costs. However, at present, it will be necessary, particularly if screening is to occur in developing countries of crop origin (e.g. regions with poor infrastructure), to derive technologically simple and inexpensive screening methods that can identify promising crop genotypes that can respond strongly to CO2.

There may, in fact, be a number of straightforward approaches in this regard, from initial screening of yield
responses of plants in greenhouses or CO₂ concentration gradient tunnels prior to field testing [57], to using agronomic parameters as a guide to CO₂ responsiveness [41,58]. Alternatively, if a larger area is needed for a more traditional agronomic approach to screening, it may be possible to exploit urban to rural micro-climatic transects. Such a regional transect was used to study succession of plant communities, and showed constant increases in both CO₂ and temperature over a 5-year period for the urban (relative to the rural) area, consistent with short-term Intergovernmental Panel on Climate Change projections in global climate change [59,60]. While it can be argued that urban environments have other abiotic parameters that can affect crop growth (such as soil differences, controlled in the earlier-mentioned studies), the cumulative urban environment may also reflect many of the predicted abiotic parameters associated with anthropogenic climate change (e.g. nitrogen deposition, temperature, ozone). Other innovative approaches to simulate elevated CO₂ environments for screening, such as generating CO₂ from biogas, or exploiting existing CO₂ springs, should also be considered, particularly in developing countries where expensive and sophisticated facilities may not always be available.

If the physical facilities for screening germplasm can be made accessible over the long-term, then trait selection for CO₂ sensitivity at different organismal levels can be elucidated. As is clear from the large number of published reports, it seems unlikely that there is one set of criteria associated with CO₂ responsiveness. Hence, it is worthwhile to use multiple strategies to discover specific CO₂ sensitive traits. Such strategies can range from the straightforward (such as comparative experiments involving isolines [61]; to biochemical approaches such as appropriate selection of carboxylases [62]) to sophisticated, state-of-the-art screening tools that use high-throughput genomics, quantitative genetics, molecular breeding and bioinformatics [63]. Such tools have made progress in detecting elevated CO₂-responsive quantitative trait loci associated with yield in rice [64]. Traditional breeding, especially for increased harvest index, could be of particular benefit as it would test the absolute, and not relative, yield response to increasing CO₂ [19]. Application of models that can identify phenotypic traits with marker-assisted selection may provide a useful tool to identify higher yields associated with increased CO₂ and other likely anthropogenic changes [65]. Another, under used approach with potential promise may simply be a direct comparison of genetic, morphological, physiological and phenological traits of plant species that have adapted evolutionarily to natural CO₂ springs compared with plants from ambient CO₂ at similar edaphic and abiotic comparisons.

Once identified, it will be necessary to test any CO₂ selections for interactions with other climatic parameters likely to change, particularly temperature and water availability. For example, there is considerable variability among rice cultivars in their responses to temperature and CO₂, leading to the possibility of selecting cultivars with increased yield and/or yield stability when produced under an elevated temperature and CO₂ environment [66]. Other interactions also need to be examined in greater detail, particularly soil characteristics that relate to nutrition and/or endophytic parameters that may be of adaptive benefit for atmospheric CO₂, or abiotic stresses (e.g. temperature) [67,68]. Plant environmental responses are often determined by their associations with microorganisms such as rhizobia and endophytes (e.g. the ‘extended phenotype’) [69]. This has also been observed for CO₂ responses [70]; for example, Bertrand et al. [71] found that CO₂ stimulated photosynthesis and nitrogenase activity increased the nutritive value of alfalfa (Medicago sativa), but these responses were associated with a specific plant-rhizobium complex. Additional studies with soybean have shown the benefits for co-selection of rhizobia and plants for CO₂ responsiveness [72], suggesting that selection for CO₂ responsiveness would benefit if done at the level of the extended phenotype.

Given economic resource constraints, which crop species should be a priority in CO₂ selection for food security? Corn, a C₄ species, is unlikely to respond significantly to rising CO₂ because the C₄ photosynthetic pathway is at near saturation at current CO₂ levels; and soybean, while important economically is only a minor caloric source globally. At present, rice and wheat are the dominant source of calories for the bulk of the human population (533 and 530 kcal capita⁻¹ day⁻¹, respectively) [73] and are obvious candidates for CO₂ selection. However, other C₃ crops that are important from a calorific standpoint would include potatoes, cassava and sweet potatoes. Unfortunately, relative to wheat and rice, fewer CO₂ studies have been conducted on these root crops.

When should a ‘high’ CO₂ cultivar be released? Selection of plants that perform better under elevated CO₂ may produce plant material that also does better at current CO₂ levels. However, it is also possible that greater CO₂ sensitivity lines will only outperform current cultivars at some future date (e.g. D. glomerata) [13]. Consequently, cultivar releases should be made in consideration with the appropriate future CO₂ concentration.

7. CONCLUSIONS: CLIMATE CHANGE, GLOBAL FOOD SECURITY AND CO₂ SELECTION: THE NEED IS NOW

To meet the challenge of maintaining food security, agriculture must adapt quickly. And while there are a myriad of strategies for doing so, one of the most opportune is to take advantage of the additional CO₂ that is being put into the Earth’s atmosphere.

However, developing and identifying new crop lines that are more responsive to CO₂ will take time (typically 7–14 years). It will also require a willingness to look beyond reductionist approaches; to initiate an intensive collaborative effort between molecular scientists and traditional breeders, between physiologists and agronomists, between bioinformatic specialists and modellers, between university and corporate interests, among farmers, industry, governments and civil society. These efforts, or course, will not be a complete solution to the issue of climate change and food security; however, adaptation to rising CO₂ remains one of the simplest research strategies to ensure that global food security can be maintained in lieu of the anthropogenic stresses likely to be experienced for the remainder of the twenty-first century.

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