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 \((\text{CO}_2)\) is an essential plant resource that has increased globally by approximately 25 per cent since 1959, efforts to increase the biological conversion of atmospheric \(\text{CO}_2\) 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 \(\text{CO}_2\) 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 \(\text{CO}_2\) 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).

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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.

1. 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

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.


Figure 2. Average seed yield per plant (± s.e.) for 17 different rice lines from diverse geographical locations at either ambient (373 µmol mol−1) or elevated (664 µmol mol−1) atmospheric CO2. Data were obtained from the 1990s from field experiments conducted at the International Rice Research Institute and are reported in Ziska et al. [6].
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 high 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 CO₂, 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 methodical, 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 photorespiration and photosynthesis. 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 genetic 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].

Genotype sold in 2010) [13]. 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].

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Overall, these examples are strong arguments in favour of active intervention in breeding for higher CO2 concentrations to improve yield responses, and suggest that 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 CO$_2$ and/or climatic conditions for a large number of cultivars in order to begin the screening process. From a methodological viewpoint, maintaining control of CO$_2$ (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 m$^2$) evaluations of elevated CO$_2$ have been achieved using open-air CO$_2$ fumigation, or free-air CO$_2$ enrichment (FACE) technology [32]. However, rapidly fluctuating CO$_2$ concentrations within elevated FACE rings, or lack of night-time exposure to elevated CO$_2$ concentrations, may underestimate the fertilization effect of enriched CO$_2$ on plant growth [33,34]. Conversely, other studies using smaller enclosures (e.g. greenhouses) to enrich CO$_2$ have consistent CO$_2$ 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 CO$_2$, 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 CO$_2$, 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 CO$_2$. There have been a number of suggestions at different organismal levels that could mediate the CO$_2$ 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 CO$_2$ 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 CO$_2$; i.e. how to develop higher seed yields in the field based on CO$_2$ 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 CO$_2$ on yield [45]. However, it is now clear that such positive interactions do not always translate into additional seed yield with simultaneous increases in CO$_2$ and temperature as opposed to elevated CO$_2$ per se [46–48]. In contrast to CO$_2$ and temperature interactions, there are a number of studies indicating that under water-limited conditions the indirect effect of CO$_2$ on stomatal aperture (and potential reductions in transpirational water use) may enhance the relative effect of CO$_2$ 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 CO$_2$ 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 CO$_2$-response studies for a wide range of agronomic crops [52]. A significant challenge for CO$_2$ responsiveness will be to impose selection pressure or co-develop suitable management practices that will maintain desired quality and nutritional parameters.

6. CO$_2$ SELECTION: MEETING THE CHALLENGES
Screenings for yield response to elevated CO$_2$ 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 CO$_2$ fumigation, average plot size within FACE systems can be small from 1 to 5 m$^2$ [53,54], in part, because of edge effects near the ring. In addition, CO$_2$ supply costs would be considerable because continuous selection over several years would be required to develop lines sensitive to high CO$_2$. It is possible that new FACE prototypes [55,56] could increase CO$_2$ 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 CO$_2$.

There may, in fact, be a number of straightforward approaches in this regard, from initial screening of yield
higher yields associated with increased CO2 and other traits with marker comparisons for detecting elevated CO2-responsive quantitative trait loci. Such tools have made progress in the field of bioinformatics [63]. Such tools have made progress in the field of bioinformatics [63].

For example, there is considerable variability among rice cultivars in their responses to temperature and 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 yield 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 conditions.

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, Betrand 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 caloric 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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