How Do We Improve Crop Production in a Warming World?

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Future agricultural production will encounter multifaceted challenges from global climate change. Carbon dioxide (CO_2) and other greenhouse gases are accumulating in the atmosphere at unprecedented rates, causing increased radiative forcing (Le Quéré et al., 2009; Shindell et al., 2009). Continued emissions of greenhouse gases will increase annual temperatures by 2.5°C to 4.3°C in important crop-growing regions of the world by 2080 to 2099, according to the Intergovernmental Panel on Climate Change (IPCC) A1B scenario (Christensen et al., 2007). Growing season temperatures are expected to warm more than the annual averages, with reduced precipitation expected to accompany higher temperatures in some regions. Additionally, heat waves are expected to increase in frequency, intensity, and duration (Tebaldi et al., 2006; Christensen et al., 2007), and end-of-century growing season temperatures in the tropics and subtropics may exceed even the most extreme seasonal temperatures measured to date (Battisti and Naylor, 2009).

Despite these dramatic predictions for rising global temperatures and extreme temperature events, the latest IPCC assessment report predicts that adaptation of agriculture will result in increased yields of cereal crops (maize [*Zea mays*], wheat [*Triticum* spp.], and rice [*Oryza sativa*]) in mid- to high-latitude regions with modest increases in temperature across a range of CO_2 concentrations and precipitation changes (Easterling et al., 2007). With warming temperatures of 1°C to 3°C, yields at lower latitudes are predicted to decrease, although global food production is predicted to increase (Easterling et al., 2007). The IPCC projections assume that yield improvements from the latter half of the 20th century will continue into the future; however, based on historical temperature-crop yield relationships, potential ceilings to crop yields, and limitations to expansion of agricultural lands, that assumption may not be sound (Long and Ort, 2010). In fact, the relative rates of yield increase for all of the major cereal crops are already declining (Fischer and Edmeades, 2010).

In a global analysis of crop yields from 1981 to 2002, there was a negative response of wheat, maize, and barley (*Hordeum vulgare*) yields to rising temperature, costing an estimated $5 billion per year (Lobell and Field, 2007). An analysis of maize and soybean (*Glycine max*) production in the northern Corn Belt region of the United States found that productivity was adversely affected by rising growing season temperatures from 1976 to 2006 (Kucharik and Serbin, 2008). The response of maize and soybean to temperature is also nonlinear, and the decline in yields above the temperature optimum is significantly steeper than the incline below it (Schlenker and Roberts, 2009). Based on the nonlinearity of the temperature response, U.S. maize and soybean yields were predicted to decrease by 30% to 46% before the end of the century under the IPCC scenario with the slowest warming trend (Schlenker and Roberts, 2009). In addition to these historical trends, record crop yield losses were reported in 2003, when Europe experienced a heat wave with July temperatures up to 6°C above average and annual precipitation 50% below average (Ciais et al., 2005). Such extreme events are not well characterized in the IPCC assessment simulations (Easterling et al., 2007). Therefore, increased global temperatures and more frequent temperature extremes will greatly challenge agriculture in this century. Here, we identify regional priorities and biological targets for adaptation of agriculture to rising temperature.

IDENTIFYING PRIORITIES FOR ADAPTATION

Adaptation of agriculture to climate change is broadly defined as any response that improves an outcome (Reilly and Schimmelpfennig, 2000). The IPCC defined adaptation as the adjustment of agronomic practices, agricultural processes, and capital investments in response to climate change threats (Easterling et al., 2007). Examples of adaptations to climate change include adjustment of planting and harvest times, expansion of croplands to more permissive areas, changing genotypes or species to those with more appropriate thermal time or heat stress tolerance, developing new germplasm with improved traits, altering fertilization rates and irrigation practices, and using climate forecasting to reduce production risks (Howden et al., 2007). While the IPCC concluded that adaptations have substantial potential to take advantage of positive aspects of climate change and thereby offset negative impacts (Easterling et al.,

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2007), there are actually few existing quantitative data on the ability of adaptation to improve food security (Burke and Lobell, 2010), and there are several caveats to consider. Potential impacts of climate change on pests, diseases, air pollution, the magnitude of the CO_2 response, variability in climate, and climate extremes are not always adequately addressed in simulation models because they are not well understood. For example, the actual CO_2 fertilization response of crops is only half that expected (Long et al., 2006) and currently used in simulation models (Ainsworth et al., 2008). Perhaps even more important is the model assumption that a full range of adaptation strategies is available in different regions (Howden et al., 2007). While there remain uncertainties about the effectiveness of adaptation strategies, global food production and food security will almost certainly decline without significant financial and research investments in adapting agriculture to climate change.

What should be the top priorities for these investments? Arguably, crops in food-insecure regions where the majority of the world's malnourished people live top the priority list. Recent funding in agricultural development from the Gates and Rockefeller Foundations have focused on these areas where human well-being and ecosystem function are closely tied (Millennium Ecosystem Assessment, 2005). The tropical location of many of these regions also limits available adaptation options and shortens the time frame for identifying solutions. Crop priorities for adaptation to climate change anticipated for 2030 in 12 major food-insecure regions, primarily in Africa and Asia, were recently identified (Lobell et al., 2008). Based on statistical crop models, wheat and rice in southeast Asia and maize in southern Africa were most likely to be negatively impacted by climate change in the absence of adaptation strategies. However, the most extreme predictions for negative outcomes of climate change identified millet, groundnut, and rapeseed (*Brassica napus*) in southern Asia, sorghum (*Sorghum bicolor*) in Sahel, and maize in southern Africa as priorities for adaptation (Lobell et al., 2008).

Strong cases can also be made to support adaptation of the world's most important crops in their primary production regions. Rice provides a staple food for more than half of the world's current population and is predominantly produced in south, southeast, and east Asia, from Pakistan to Japan, with China leading global production (IRRI, 2002). Rice production is sensitive to increasing temperature (Peng et al., 2004), which may limit the positive yield response to rising CO_2 concentration (Ainsworth, 2008). Current temperatures are already approaching critical levels during susceptible stages of rice development in many Asian countries, and drought stress will be exacerbated as temperatures rise (Wassmann et al., 2009). Wheat is the second most important source of calories for human consumption, and global yields declined by 1% from 1997 to 2007 (Long and Ort, 2010). China, India, and the United States are the top three producers of wheat (FAO, 2009). By 2050, anticipated climate changes will likely cause reclassification of the Indo-Gangetic Plains of India from a favorable, high-potential wheat production environment to a heat-stressed, short-season production environment (Ortiz et al., 2008). The Indo-Gangetic Plains produce approximately 15% of the world's wheat crop, and identifying and developing wheat varieties with improved high-temperature stress tolerance will be critical to maintaining food security for the approximately 200 million people who depend upon local food production in that region (Ortiz et al., 2008). The same climate change scenarios that will make land in India less suitable for wheat may cause an expansion of suitable wheat-growing areas in North America and Eurasia (Ortiz et al., 2008), and developing varieties to take maximum advantage of new growing areas could also help sustain global wheat production.

In addition to rice and wheat, maize and soybean are the other two most widely produced crops in the world (FAO, 2009). The United States produces approximately 40% of the world's maize and soybean and is a leading exporter of both crops and, therefore, an important determinant of the global market for both crops. Additionally, there has been significant investigation of impacts of climate change on U.S. production of maize and soybean; therefore, investing in adaptation efforts for maximizing the production of these crops in the United States may be more likely to achieve favorable outcomes. As discussed previously, the assumption that warming of temperate regions will increase crop production is in contrast to evidence of adverse effects of recent temperature changes on U.S. maize and soybean production (Lobell and Asner, 2003; Kucharik and Serbin, 2008). As a C_4 crop, maize is unlikely to directly benefit from rising atmospheric CO_2 concentration (Long et al., 2006). Moreover, maize is the most widely grown C_4 grain crop in both food-secure and food-insecure regions (Leakey, 2009), so adapting maize to higher temperatures would likely be a priority investment. Clearly, different countries and regions will have their own specific priorities for adaptation. In order to increase global food production and security in a warmer future, broad investment in many of these priorities is an urgent matter.

TARGETS FOR ADAPTATION

The effects of warmer temperature on photosynthesis will be one of the most important determinants of the impact of global warming on crop yield. The reactions catalyzed by Rubisco are directly affected by temperature. Even though Rubisco itself is quite thermal stable and the rate of carboxylation continues to increase beyond 50°C, decreased discrimination by Rubisco for its alternative substrate oxygen and increased solubility of oxygen relative to CO_2 with rising temperature conspire to inhibit net photosynthesis in C_3 plants due to increased photorespiration. It may

seem that a form of Rubisco better able to discriminate against oxygen would be advantageous in the face of rising temperatures. In fact, because there is an inverse relationship of specificity with catalytic rate, to maximize the daily integral of canopy photosynthesis it would be advantageous to trade off specificity for catalytic rate regardless of temperature (Zhu et al., 2010). Compared with Rubisco, the rate of regeneration of the CO_2 acceptor ribulose 1,5-bisphosphate (RuBP) is even more sensitive to temperature and more variable with growth conditions and among species (June et al., 2004). At current CO_2 levels, light-saturated photosynthesis operates at the transition between Rubisco-limited and RuBP-limited photosynthesis; thus, as [CO_2] increases, photosynthesis is increasingly limited by the capacity for RuBP regeneration. Additionally, RuBP regeneration limitation increases at higher temperature (Sage and Kubien, 2007) and RuBP-limited photosynthesis benefits from lower photorespiration at elevated CO_2, implying that increases in the RuBP regeneration rate should raise the temperature optimum of photosynthesis at elevated CO_2. Although there are 10 enzymes of the photosynthetic carbon reduction cycle along with the full suite of thylakoid electron transport reactions involved in RuBP regeneration, modeling and metabolic control analyses have consistently predicted that sedoheptulose-1,7-bisphosphatase, aldolase, and transketolase exert the greatest control (Harrison et al., 1998; Zhu et al., 2007). There are already proof-of-concept experiments showing that the overexpression of sedoheptulose-1,7-bisphosphatase, which was shown to stimulate photosynthesis, implying a RuBP regeneration limitation (Lefebvre et al., 2005), protects against the inhibition of photosynthesis by moderate heat stress (Feng et al., 2007). Thus, while attempts at manipulating Rubisco have so far yielded poor results, improving the temperature response of photosynthesis by manipulating RuBP regeneration appears much more promising.

In addition to stimulating photorespiratory activity, temperatures only slightly above the optimum for growth can have direct inhibitory effects on photosynthesis through impacts on components of the photosynthetic apparatus itself. Rubisco activase, which regulates the proportion of Rubisco that is catalytically active, is quite sensitive to moderate heat stress. The catalytic events that inactivate Rubisco increase with temperature, causing progressive inhibition of Rubisco-limited photosynthesis during mild heat stress (Crafts-Brandner and Salvucci, 2000). The recent discovery that Rubisco activase associates with the chloroplast GroEL homolog (cpn60β) suggests that this protein may be acting in the way of other hsp60s, in this case providing a mechanism to protect Rubisco activase and acclimate photosynthesis to heat stress (Salvucci, 2008). Kurek et al. (2007) showed that improvements to the thermal stability of Rubisco activase achieved by gene shuffling increased rates of photosynthesis and growth and enhanced yield in genetically transformed Arabidopsis exposed to moderate heat stress. In addition to the temperature sensitivity of Rubisco activase, at leaf temperatures as low as 36°C in cotton (*Gossypium hirsutum*), thylakoid membrane conductance to ions was compromised, which in turn led to lower photosynthesis even though PSI cyclic electron transport increased, compensating in part for the loss of proton motive force needed for ATP formation (Schrader et al., 2004).

What else might be done to adapt photosynthesis to the warming world? Lowering photorespiratory flux would reduce the inhibition of net photosynthesis of C_3 plants caused by rising temperature. A promising path to improved high-temperature tolerance is suggested by a "photorespiratory bypass" engineered in Arabidopsis chloroplasts by the introduction of the *Escherichia coli* glycolate catabolic pathway that substantially suppressed photorespiratory flux (Kebeish et al., 2007; Maurino and Peterhansel, 2010). This photorespiratory bypass in turn would be expected to increase the temperature optimum of net photosynthesis in transformed plants.

Although crop yield is frequently limited under agriculture conditions by carbon gain, the optimum temperature for photosynthesis, vegetative growth, and reproductive development is nearly always higher than the seasonal temperature optimum for yield. Thus, while any inhibition of photosynthesis caused by high-temperature excursions in the future should be expected to result in reduced yield, the temperature dependence of other physiological processes clearly will also play an important and in some cases more important role. The reproductive stage of development is determinant of yield in crops cultivated for seeds or fruits. In annual crops, higher temperatures can drive shorter life cycles, resulting in less seasonal photosynthesis, shorter reproductive phase, and thus lower yield. Vegetative development is accelerated in cereals with increasing temperature, but it is the dramatically shorter grain-filling period with rising temperature that portends major consequences for yield. Even assuming no differences in daily photosynthesis, yield of cereals decreases in proportion to the shortening of the grain-filling period as temperature increases. For example, temperatures as low as 25°C can reduce the grain-filling period in wheat, after which a 1°C temperature rise shortens the reproductive phase by 6%, shortens the grain-filling duration by 5%, and reduces grain yield and harvest index proportionally (Lawlor and Mitchell, 2000). This temperature effect on the duration of grain-filling period has already caused a lower yield potential for wheat in the midwestern United States than for northern Europe (Hatfield et al., 2008). A recent retrospective analysis of maize and soybean in the midwestern United States found for the period 1980 to 2007 yields that were more highly correlated with maximum daily temperature during the grain-filling and reproductive growth period than with drought (Mishra and Cherkauer, 2010). In photoperiod-responsive plants,

which include most crop plants, the timing of the reproductive stages is determined by an interactive response to temperature and photoperiod. Whereas these relationships are reasonably well understood in the suboptimal through optimal temperature range, this understanding does not extend into the supra-optimal temperature range, but clearly, understanding how these higher temperatures will interact with photoperiod to determine flowering time will become increasingly important as climate change progresses (Craufurd and Wheeler, 2009).

Higher than optimal temperatures during reproductive stages have impacts beyond shortening the duration of grain filling. High-temperature stress that affects any of the reproductive processes, including pollen viability, female gametogenesis, pollen-pistil interaction, fertilization, and grain formation, can severely reduce yield even when the seasonal average temperature is within a favorable range, making it perhaps the most critical stage of growth in determining the response of crop yield to high temperatures. Whereas high-temperature stress has been shown to reduce the amount of pollen produced, given the vast amounts produced in most crop species it is not believed that decreased pollen production due to high temperature will cause significant reductions in reproductive output due to global warming. However, even small increases in temperature above the optimum can very negatively affect pollen viability via a range of mechanisms that will lead to yield penalties (Hedhly et al., 2008). It is even possible that high-temperature stress may cause altered genetic frequencies of the subsequent sporophytic generation (Hormaza and Herrero, 1994), thereby possibly forwarding consequences to future generations. Within a permissive range, warming temperatures accelerate both the rate of pollen tube growth as well as stigma and ovule development, thus maintaining the male-female synchrony necessary for successful seed set. However, under high-temperature stress, this synchrony can be lost, leading to lower fertility and yield reduction (Hedhly et al., 2008). Another type of loss of synchrony that can occur due to global change and have consequences for yield is in insect-pollinated crops, where alterations to the annual temperature cycle can uncouple insect life cycles with crop-flowering phenology (Memmott et al., 2007).

The remarkable increases in crop productivity of the "green revolution" achieved through conventional breeding were made largely without knowledge of the mechanisms underlying the genetic variability that was exploited for yield improvement. However, this approach may not be adequate to deliver improvements that will keep pace with the rapidly advancing elements of global change (Collins et al., 2008). The genetic basis for heat stress tolerance in crop plants is poorly understood. Identification of adaptive quantitative trait loci (QTLs) for high-temperature tolerance is one approach being taken to try to close these knowledge gaps. For example, multiple loci for heat tolerance have been identified in wheat (graining filling [Yang et al., 2002]) and maize (pollen heat tolerance [Frova and Sari-Gorla, 1994]), but to date, vastly more effort has been focused on tolerance to chilling and freezing than to heat stress. An important challenge of this adaptive QTL strategy for exploiting the segregation of natural alleles for improving crop abiotic stress tolerance is that QTLs often do not translate well across genetic backgrounds, frequently showing smaller adaptation effects or disappearing altogether in different backgrounds even under seemingly identical environmental conditions (Collins et al., 2008). To make the rapid progress that will be required to adapt crops ahead of the rapid advancement of global change, multiple approaches, including the targeted adaptation of specific reactions and processes for which there is a predictive basis for benefit, will be required.

CONCLUSION

There is now overwhelming evidence that "business as usual" crop development will be insufficient to adapt crops over the wide range of growing regions that will be required to meet expanding global agricultural demand. Moving crops pole-ward seems an inevitable element of the multifaceted adaptation to increasing global temperatures that must be implemented, but it would be misleading to believe that this alone can maintain yields. For example, migration of the North American Corn Belt into Canada vacates the high-quality prairie soils for the less productive soils farther north. And in many important agricultural areas of the world, pole-ward migration is not possible, such as the Wheat Belt of Australia, where an ocean lies to the south (Long and Ort, 2010). Even adapting crops in the highest priority regions will require broad investment, the integration of new technologies with conventional selection-based breeding, and the coordinated involvement of public and private sectors of the agricultural enterprise. Current and future increases in temperature portend perhaps the most significant and most urgent challenge for the adaptation of crops to global change.

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