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ABSTRACT

Changes in temperature, CO_2, and precipitation under the scenarios of climate change for the next 30 yr present a challenge to crop production. This review focuses on the impact of temperature, CO_2, and ozone on agronomic crops and the implications for crop production. Understanding these implications for agricultural crops is critical for developing cropping systems resilient to stresses induced by climate change. There is variation among crops in their response to CO_2, temperature, and precipitation changes and, with the regional differences in predicted climate, a situation is created in which the responses will be further complicated. For example, the temperature effects on soybean [*Glycine max* (L.) Merr.] could potentially cause yield reductions of 2.4% in the South but an increase of 1.7% in the Midwest. The frequency of years when temperatures exceed thresholds for damage during critical growth stages is likely to increase for some crops and regions. The increase in CO_2 contributes significantly to enhanced plant growth and improved water use efficiency (WUE); however, there may be a downscaling of these positive impacts due to higher temperatures plants will experience during their growth cycle. A challenge is to understand the interactions of the changing climatic parameters because of the interactions among temperature, CO_2, and precipitation on plant growth and development and also on the biotic stresses of weeds, insects, and diseases. Agronomists will have to consider the variations in temperature and precipitation as part of the production system if they are to ensure the food security required by an ever increasing population.

THERE IS MOUNTING evidence the current changes in climate across the Northern Hemisphere will continue into the future and affect temperature, precipitation, and atmospheric CO_2 concentration. Karl et al. (2009) presented an analysis of the recent changes in the climate of the United States and projected changes over the next century. Temperature and precipitation patterns across the United States for the next 30 yr show a warming trend of 1.5 to 2°C and a slight increase in precipitation over most of the country (e.g., Tebaldi et al., 2006; Karl et al., 2009). They projected an increase in the number of days when the temperature will be higher than the climatic normals by 5°C (heat-waves), which will impact agricultural systems. These authors also project an increase in warm nights, defined as occurring when the minimum temperature is above the 90th percentile of the climatological distribution for the day (Tebaldi et al., 2006; Karl et al., 2009). Coupled with these changes is the decrease in a number

of frost days by 10% in the eastern half of the United States and an increase in the length of the growing season by more than 10 d. Karl et al. (2009) showed that precipitation events would change in frequency and intensity with a projected increase in spring precipitation, particularly in the Northeast and Midwest United States, and a decline in the southwestern United States. The increase in extreme temperature events, warm nights, and more variable precipitation will impact agriculture and agricultural production. A trend for warmer winters will affect perennial crops and weeds, and also expand the potential habitable range of some insect and disease pests. Although there is uncertainty about the absolute magnitude of the changes over the next 50 yr, there is general agreement that CO_2 levels will increase to near 450 μmol mol^{-1} (ppm), temperatures will increase by 0.8 to 1.0°C, and precipitation will become more variable as defined in the IPCC AR4 analysis (IPCC, 2007). Changes in temperature have already caused longer growing seasons and begun to impact phenological phases (Schwartz et al., 2006; Wolfe et al., 2005, Xiao et al., 2008; Karl et al., 2009).

An example of the potential of climate change impacts on agriculture is illustrated in a recent study by Ortiz et al. (2008) in which they assessed the potential impact on India wheat (*Triticum aestivum* L.) production if air temperature increased 0.8°C over the next 50 yr. Their analysis showed that as much as 51% of the area in India currently classified as high potential, irrigated, low rainfall mega-environment would be reclassified to a heat-stressed, irrigated, short-season production mega-environment. This area currently accounts for 15% of the world's wheat production and would undergo significant reduction in yield unless cultivars and management practices adapted to the projected climate regime (e.g., higher levels of heat and water

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Abbreviations: ET, evapotranspiration ; FACE, free-air carbon dioxide enrichment; HI, harvest index; LAI, leaf area index; VPD, vapor pressure deficit; WUE, water use efficiency.

stress) were developed. Without adaptation, the impacts on the production potential would drastically alter the ability of India to produce a sufficient food supply for its population.

Projected increases in temperatures for the entire United States will increase soil water evaporation and crop transpiration. This could lead to an increase in soil water deficits and economic losses unless mitigated by other factors, such as: a corresponding increase in precipitation; an increase in crop WUE (associated with CO_2 effects on stomatal closure, see discussion below); reductions in leaf area or planting density; and farmer adaptations, for example, increasing use of supplemental irrigation. A recent climate analysis for the northeastern United States (Hayhoe et al., 2007) projected a significant increase in summer soil water deficits by mid-century even for this relatively humid region with little change in total annual precipitation. In the western United States, reduction in snow pack and earlier snow melt exacerbate the potential threat of drought for farmers because of the reduction in the reservoir of water available for irrigation (Lettenmaier et al., 2008). Similar results were reported by Wang (2005) after comparing 15 different models for the IPCC fourth assessment and concluded the increases in greenhouse gases will cause a worldwide increase in the occurrence of agricultural droughts. These models were consistent in their predictions of drier soil over the Southwest United States across all seasons. Across the Midwest, Mishra and Cherkauer (2010) found that droughts have actually decreased in the last half of the 20th century with the last significant widespread droughts in the 1930s. However, within this record, they found maize (*Zea mays* L.) and soybean yields to be correlated with meteorological drought and maximum daily temperature during the grain-filling period. Drought was found to be the major factor leading to yield variability of eight different crops over years for the Czech Republic (Hlavinka et al., 2009). Water availability will become a major determinant in crop yield (Rosenzweig et al., 2002) and the interaction with CO_2 and temperature will have to be understood better to adapt cropping systems to climate change.

The prediction of an increase in the frequency of high-precipitation events (e.g., >5 cm in 48 h) may be of great concern in many parts of the United States equally as drought because of the inability of the soil to maintain infiltration rates high enough to absorb high-intensity rainfall events (Hayhoe et al., 2007). This trend is projected to apply for many regions (Lettenmaier et al., 2008). Excessive rainfall during the spring planting season could cause delays creating a risk for both productivity and profitability for agronomic crops (Rosenzweig et al., 2002) as well as high value horticultural crops such as melon (*Cucumis melo*), sweet corn (*Zea mays* L. var. *rugosa*), and tomato (*Lycopersicon esculentum* L.) for which premiums are often paid for early season production. Crop losses associated with anoxia, increases to susceptibility to root diseases, increases in soil compaction (due to use of heavy farm equipment on wet soils), and more runoff and leaching of nutrients and agricultural chemicals into ground- and surface-waters may occur as the result of excess soil water and field flooding during the early growing season. The shift in the rainfall distribution because of high precipitation events could increase the likelihood of water deficiencies at other times because of the changes in rainfall frequency (Hatfield and Prueger, 2004). Increases in heavy rainfall due to more intense storms and associated turbulence and wind gusts, increase the potential for lodging of crops. Delayed harvest or excessive rainfall during harvest time increases the potential for decreasing quality of many crops and potential for disease infestation on grains.

Solar radiation is a driving variable in crop production and there is a belief that as water vapor and cloud cover increase there will be a decrease in incoming solar radiation. Stanhill and Cohen (2001) referred to this as "global dimming" and found for the past 50 yr a reduction of 2.7% per decade with the current totals now being reduced 20 W m^{-2}. These changes would impact crop water balance and evapotranspiration of crops with less effect on crop productivity because of the presence of other factors limiting productivity (e.g., water, temperature). Even though the assumption is for solar radiation changes to have a minimal impact on crop productivity, this review points out the need for better understanding of the impact of this variable as part of the climate change scenario. There must be efforts to develop adaptive management strategies to cope with climate change along with mitigation strategies to reduce the impact of agricultural practices on the environment. As agronomists we need to be engaged in helping develop both adaptative management and mitigation strategies to ensure the future food, feed, fuel, and fiber supply for the world's population. Adams et al. (1990) stated that agricultural productivity is sensitive to climate change and that there are positive effects from climate change (i.e., increased CO_2) and negative impacts (e.g., higher temperatures shortening grain-fill duration and increasing evapotranspiration rates). The uncertainty in the climate for the next decades and the potential impact on agricultural production were reviewed as part of the Climate Change Science Program (CCSP) under Synthesis and Assessment Product 4.3 (SAP4.3) and published as part of this report series (Hatfield et al., 2008). There is evidence that our climate is changing and that these changes in temperature, precipitation (both amount and frequency), CO_2, and O_3 will impact agriculture. The intent of this review is not to review the climate change literature but to evaluate the potential impacts of climate change on agricultural crops and to expand on some of the findings in the SAP4.3 report with focus on agronomic crops, to summarize the current state of knowledge, and to offer ideas as to where future efforts should be placed to reduce the potential negative impacts of climate change on agriculture and future food, feed, and fiber production.

CARBON DIOXIDE IMPACTS ON CROPS

Carbon dioxide levels in the atmosphere have increased steadily over the past 50 yr and the expectation is for a continued increase over the next 30 yr. By conservative estimates, the current levels of about 387 μmol mol^{-1} will increase to nearly 450 μmol mol^{-1} by 2050 and in fact are increasing faster than expected (Karl et al., 2009). To quantify the effect of changes in CO_2 concentrations, one must conduct plant growth and yield studies in systems where CO_2 concentration can be maintained above the ambient levels. These have been done in a combination of enclosed chambers and free-air carbon dioxide enrichment (FACE) studies. Kimball (1983) summarized early studies on the effects of increases from 330 to 660 μmol mol^{-1}. Subsequent implementation of FACE technology has enabled open-field studies and have increased the confidence in evaluating the effect of increasing CO_2 concentrations on plant response (e.g., Kimball and Mauney, 1993; Kimball et al., 1995, 2002; Ainsworth and Long., 2005; Kimball, 2010). However, Long et al. (2006) recently showed yield responses

Table 1. Response of plant physiological variables to a doubling of CO_2 concentrations from research studies.

Crop	Leaf photosynthesis	Total biomass	Grain yield	Leaf stomatal conductance	Canopy evapotranspiration
			— % change —		
Maize	3[†]	4[†,‡,§,¶]	4[†,‡]	−34[†]	
Sorghum	9[#,††]	3[‡‡]	0,8[#]	−37[††]	−13[§§]
Bean	50[¶¶]	30[¶¶]	27[¶¶]		
Cotton	33[##,†††]	36[##,†††]	44[##,†††]	−36[##,†††]	0[§§§§§§], −8[‡‡‡]
Peanut	27[¶¶]	36[¶¶]	30[¶¶]		
Rice	36[§§§]	30[§§§]	30[§§§,¶¶¶]		−10[###,††††]
Soybean	35[‡‡‡‡]	37[‡‡‡‡]	34[§§§§]−38[‡‡‡‡]	−40[‡‡‡‡]	−9[¶¶¶¶], −12[####,†††††]
Wheat	35[‡‡‡‡]	15−27[§§§§§]	31[¶¶¶¶¶]	−33 to −43[#####]	−8[††††††,‡‡‡‡‡,¶¶¶¶¶¶]

† Leakey et al. (2006).
‡ King and Greer (1986).
§ Ziska and Bunce (1997).
¶ Maroco et al. (1999).
# Prasad et al. (2006a).
†† Wall et al. (2001).
‡‡ Ottman et al. (2001).
§§ Triggs et al. (2004).
¶¶ Prasad et al. (2003).
Reddy et al. (1995a).

††† Reddy et al. (1997).
‡‡‡ Reddy et al. (2000).
§§§ Horie et al. (2000).
¶¶¶ Baker and Allen (1993a).
Baker et al. (1989).
†††† Yoshimoto et al. (2005).
‡‡‡‡ Ainsworth et al. (2002).
§§§§ Allen and Boote (2000).
¶¶¶¶ Allen et al. (2003).
Jones et al. (1985).

††††† Bernacchi et al. (2007).
‡‡‡‡‡ Long (1991).
§§§§§ Lawlor and Mitchell (2000).
¶¶¶¶¶ Amthor (2001).
Wall et al. (2006).
†††††† Andre and duCloux (1993).
‡‡‡‡‡‡ Kimball et al. (1999).
§§§§§§ Hunsaker et al. (1994).
¶¶¶¶¶¶ Hunsaker et al. (1996, 2000).

of cereal grains from the FACE experiments (about 15% with enrichment to 550 μmol mol^{-1} of CO_2) were less than those from some previous chamber-based studies (about 30% with enrichment to 660 μmol mol^{-1}), which raised concern. However, when the variability of results from a larger population of available chamber studies was considered it appears that results from the several types of experiments are not inconsistent.

The effects of increasing CO_2 concentrations on various crops are summarized in Table 1. Increases in plant growth vary among species. As expected the crops with the so-called C_4 photosynthetic pathway, maize, and sorghum [*Sorghum bicolor* (L.) Moench], have smaller responses than the C_3 crops. Cotton (*Gossypium hirsutum* L.) may be higher because it is a woody species. However, all show a positive response to CO_2 increases. In general, doubling CO_2 caused approximately a 30% increase in reproductive yield of C_3 species and <10% increase for C_4 species. Many C_3 weed species also show substantial growth benefits and resistance to herbicides at elevated CO_2 (Ziska, 2003b; Ziska et al., 1999), a topic which is further expanded in a later section on Projection for Weeds.

Concerns have been raised about the findings from small chambers and even of FACE approaches to studying the impact of increasing CO2 on plant response. The primary concerns are the experiment duration, small sample sizes for plant measurements, and lack of variation in other influencing factors, e.g., temperature or precipitation or N fertility affecting plant growth. Plant response to changes in CO2 concentration are complex and depend upon the species, interactions with temperature, soil moisture, nutrient management, and magnitude of acclimation to these factors (Long, 1991; Wolfe et al., 1998). The projections for increasing variability in precipitation and potential drought and increasing temperature as additional climatic factors, of course, may offset the positive impacts of rising CO2 on plant growth.

Crop Water Use Efficiency Interactions with Carbon Dioxide

Crop water use (i.e., transpiration, T) is determined by crop physiological and morphological characteristics (e.g., Kimball, 2007) and is often described by the Penman–Monteith equation

(Allen et al., 2005). The Penman–Monteith equation defines the mechanisms by which changes in temperature, CO_2, and O_3 directly affect water use (assuming O_3 as well as CO_2 affect stomatal resistance). Transpiration is affected through effects on crop growth and leaf area, changes in leaf stomatal aperture and conductance for water vapor loss, and vapor pressure gradient between the ambient air and substomatal cavity.

In the early stages of crop development, increases in leaf area are proportional to growth rate and transpiration increases as leaf area increases (Ritchie, 1972). As plants develop, there is an increase in mutual shading and interference among leaves within a plant canopy which causes plant transpiration to increase at a diminishing rate with increasing leaf area index (LAI) and asymptotically leveling at LAIs > 4 m^2 m^{-2}, progressively uncoupling transpiration from changes in LAI (Ritchie, 1972; Villalobos and Fereres, 1990; Sau et al., 2004). Doubling of atmospheric CO_2 from present-day levels will increase average C_3 species growth on the order of 30% under optimum conditions (e.g., Kimball, 1983, 2007, 2010; Kimball et al., 2002) with the expectation that an increase to 440 μmol mol^{-1} would increase C_3 plant growth on the order of 10%. Since T is most tightly coupled to changes in growth when plants are small and less after canopy closure, the overall impact of changes in CO_2 via LAI effect are expected to be small. Of greater importance is the duration of leaf area which will directly affect total seasonal crop water requirements. In determinate cereal crops that are adapted to today's temperature and growing-season length, increasing temperature will hasten plant maturity reducing leaf area duration with an overall reduction in total season water requirement. However, if alternative crops or perennial crops or varieties adapted to the higher temperatures and longer growing season are used, crop water requirements would likely increase. However, a direct effect of increasing atmospheric CO_2 is to cause partial stomatal closure. The result decreases conductance for water vapor loss from leaves to the atmosphere. A summary of the information available from chamber-based studies on the effects of elevated CO_2 on stomatal conductance have shown, on average, that doubling CO_2 reduces stomatal conductance by nearly 34% (e.g., Kimball and Idso, 1983). Morison (1987) found an average reduction of about 40% for both C_3

and C_4 species. Wand et al. (1999), after a meta-analysis on wild C_3 and C_4 grass species, grown with no stresses, concluded that elevated CO_2 reduced stomatal conductance by 39% in C_3 and 29% in C_4 species. In soybean, the reduction in conductance was about 40% for a doubling of CO_2 (Ainsworth et al., 2002; Ainsworth and Rogers, 2007). Ainsworth and Long (2005) did not observe significant differences in stomatal conductance of two C_3 and C_4 species when they summarized results from free-air CO_2 enrichment experiments where daytime CO_2 concentrations were increased from present to 550 to 600 $\mu mol\ mol^{-1}$. They found an average reduction in stomatal conductance of 20%. Thus, increases in atmospheric CO_2 concentration to nearly 450 $\mu mol\ mol^{-1}$ as estimated (IPCC, 2007) by 2040 likely will cause reductions of approximately 10% in stomatal conductance. Such a reduction in leaf-level stomatal conductance, when considered with energy balance in the whole canopy, should lead to decreases in transpiration and potential positive impacts on crop WUE.

The gradient of water vapor between a leaf and the atmosphere is considerably affected by the internal leaf water vapor pressure (e; kPa) which is tightly coupled to leaf temperature (T; °C) and can be calculated from Teten's equation, $e = 0.61078*exp\ [17.269*T/(T+237.3)]$. Consequently, any factor affecting the energy balance and leaf or canopy temperature will directly affect water vapor pressure inside the leaves and ultimately its water use. Increases in air temperature will directly increase crop canopy temperature, leaf water vapor pressure, and evapotranspiration (ET).

Although there is evidence increasing CO_2 increases water conservation at the leaf scale, these responses are tempered by competing processes at the whole-plant and/or ecosystem scale which in turn results in ET and soil water use being less affected by high CO_2 than is conductance (Field et al., 1995). Increased ET at elevated CO_2 has been reported by Hui et al. (2001). Compensatory effects between increased foliage temperature, derived from the changes in air temperature via the canopy energy balance, and increased LAI caused by CO_2 enrichment created negligible to small ET changes (Allen et al., 2003). Evidence from controlled environment chambers with soybean canopies showed a 12% reduction in seasonal transpiration and 51% increase in WUE when grown in ambient and doubled CO_2 (Jones et al., 1985). Observations of foliage temperatures in these chambers, measured by infrared thermometers, showed that foliage temperatures typically increased by 1 to 2°C (soybean), 1.5°C (dry bean), and 2°C (sorghum) to doubled CO_2 (Pan, 1996; Prasad et al., 2002, 2006a). In a different study Allen et al. (2003) reported similar findings that soybean foliage temperatures were 1.3°C warmer at mid-day when exposed to doubled CO_2. Comparable results between experiments in wheat (*Triticum aestivum* L.) have been found by Andre and du Cloux (1993) who reported 8% decrease in transpiration of wheat in response to doubled CO_2, and Hunsaker et al. (1996, 2000) who observed about a 4% reduction in ET with a 200 $\mu mol\ mol^{-1}$ CO_2 increase in a FACE studies when water and N were limiting. In contrast, cotton (*Gossipium hirsutum* L.) showed no change in ET in a similar FACE experiment (Hunsaker et al., 1994), but cotton's growth response was much greater than that of wheat (e.g., Kimball et al., 2002). Reddy et al. (2000) observed transpiration of cotton was reduced by 8% when exposed to doubled CO_2 and averaged over five temperature treatments in controlled–environment chambers,

and Kimball and Idso (1983) found a 4% reduction in seasonal water use at 650 $\mu mol\ mol^{-1}$ CO_2 vs. ambient in open-top chambers. FACE experiments in Illinois with soybean grown at 550 compared to 375 $\mu mol\ mol^{-1}$ showed a 9 to 16% decrease in ET with the range of differences caused by seasonal effects (Bernacchi et al., 2007). Analysis of their data reveals 12% reduction over 3 yr. There are impacts of temperature on the degree of CO_2 response. Soybean grown under a CO_2 doubling at 28/18°C treatment (about the same mean temperature as the Illinois site) showed a 9% reduction in ET, but there was no reduction in ET with CO_2 doubling at warm temperature treatment 40/30°C (Allen et al., 2003). Reduction in ET caused by changes in CO_2 will be mediated by temperature. This is confirmed in rice (*Oryza sativa* L.) where Horie et al. (2000) summarized that doubling CO_2 caused 15% reduction in ET at 26°C, but increased ET at higher temperatures (29.5°C). Exposure to higher temperatures reduces the impact of elevated CO_2 on stomatal conductance and observations have shown that at 24 to 26°C, WUE in rice increased by 50% with doubled CO_2, and declined as air temperature increased.
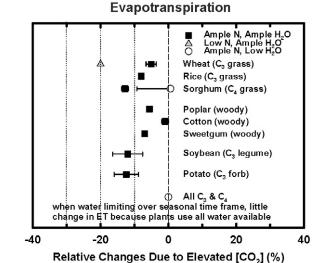
To evaluate the potential impacts of climate change on crop ET there is a need for detailed studies on the sensitivity of ET to a combination of weather and plant variables. An example of this type of approach using the Penman–Monteith equation for ET as described by Allen et al. (2005) with alfalfa (*Medicago sativa* L.) as the reference crop and hourly weather data for the year 2000 from the AZMET station (Brown, 1987) at Maricopa, AZ (33°2'60" N, 112° W, 358 m elevation) was reported by Kimball (2007). When all other variables were held constant and only temperature was changed, reference ET increased about 3.4%/C. Under climate change, relative humidity will remain constant more than absolute humidity (e.g., Dessler and Sherwood, 2009). Temperature increases with a constant relative humidity causes annual ET to change about 2.1%/°C. Changing absolute vapor pressure, due to result of changing precipitation patterns, would cause the ET to change −0.2% per percent increase in absolute humidity. Changes in solar radiation are not reported in the IPCC report (IPCC, 2001); however, expected increases in average global rainfall implies increases in cloudiness leading to decreases in solar radiation impinging on crops. When solar radiation changes, the sensitivity of reference ET is 0.6% per % change in radiation for a clear day and and 0.4% per % change in radiation for a whole year using the meteorological data from Maricopa, AZ. In a sensitivity analysis for wind speed ET would change about 0.3% per % change in wind speed for a clear day and 0.4% per % change in wind speed for a whole year. Changes in stomatal conductance and leaf area have the same relative effect on ET, and increase ET by 0.09 and 0.16% per % change in either variable for a clear summer days and whole year, respectively.

Based on the sensitivity calculations of Kimball (2007) for "standard" alfalfa using weather from Maricopa, AZ, the combined effect of increases in average global temperature by 0.8°C (assuming constant relative humidity) and atmospheric CO_2 concentration to nearly 450 $\mu mol\ mol^{-1}$ by 2040 are expected to increase ET about 1.9% for a clear summer day. Conversely, decrease in stomatal conductance of 10% caused by elevated CO_2 concentrations to 450 $\mu mol\ mol^{-1}$ with no change in temperature will decrease ET by about 0.9%.

Increasing temperature and CO_2 are of the same magnitude but act in opposite directions causing the net changes on ET to be minimal.

Observations of water use in FACE experiments where 550 μmol mol^{-1} CO_2 concentrations have been used have shown a reduction in water use by about 2 to 13% depending on species (Fig. 1). Interpolating linearly to CO_2 concentrations of 450 μmol mol^{-1} the corresponding reductions would be about one-third those observed in the FACE experiments (i.e., 1–4%). Furthermore, the limitations in extrapolating FACE plot data to larger areas (e.g., discussion in Triggs et al., 2004), shows that crop water requirements under elevated CO_2 are reduced only to a small extent.

Crop water use patterns and the timing of rain/irrigation events will affect the response to elevated CO_2 under rainfed conditions. Bernacchi et al. (2007) observed that the loss of latent heat energy (LE, i.e., water vapor) from soybean at ambient CO_2 levels in the FACE plots with adequate soil water was 10 to 60 W m^{-2} less compared to control plots. They observed when the control plots had exhausted their water supply water use declined. However, in the elevated CO_2 plots the stomata remained open and the plants continued to transpire because of the water conservation compared to control plots. This allowed the FACE plots to continue to photosynthesize and grow for a few days longer while the control plants ceased growth. Under rain-fed agriculture, which often experiences periods of drought, the net impact of elevated concentrations of CO_2 would be to enable conservation of soil water, thus sustaining crop productivity for more days than at today's CO_2 levels.

Assessment of the change in irrigation requirement under scenarios of climate change is critical to long-range planning for water resource allocation since agriculture is one of the primary water users. There have been few attempts to estimate future changes in irrigation water requirements, defined as the difference between seasonal ET for a well-watered crop and the amounts of precipitation and soil water storage available during a growing season. Projected climate changes obtained from general circulation models (GCMs) were coupled with crop water use impacts resulting from decreased stomatal conductance caused by elevated CO_2 in a simulation study (e.g., Allen et al., 1991; Izaurralde et al., 2003). Izaurralde et al. (2003) conducted a comprehensive assessment of climate change impacts on agricultural production and water resources of the conterminous United States using the EPIC crop growth model (Williams, 1995) to simulate growth and yield and future irrigation requirements of corn and alfalfa. Using the approach developed by Stockle et al. (1992a, 1992b), EPIC was modified to allow stomatal conductance to be reduced with increased CO_2 concentration (28% reduction corresponding to 560 μmol mol^{-1} CO_2) along with increasing photosynthesis through improved radiation use efficiency. They used the climate change projections generated for 2030 by the Hadley Centre (HadCM2) GCM because its climate sensitivity and projections are in the midrange of most of the GCMs. For maize, they calculated irrigation requirements in 2030 would decrease in the Lower Colorado Basin by –1% and increase in the Lower Mississippi Basin by 451% because of the change in temperature and humidity (Izaurralde et al., 2003). Even though there is variation in the sizes and baseline irrigation requirements among irrigation

Fig. 1. Relative changes in evapotranspiration due to elevated CO_2 concentrations in FACE experiments at about 550 μmol mol^{-1}. Wheat and cotton data from Table 2 of Kimball et al. (2002); rice datum from Yoshimoto et al. (2005); sorghum datum from Triggs et al. (2004); poplar datum from Tommasi et al. (2002); sweetgum from Wullschleger and Norby (2001); soybean datum from Bernacchi et al. (2007); and potato datum from Magliulo et al. (2003).

basins they reported for the United States an increase of 64% if stomatal effects were ignored or 35% if included. Similar calculations for alfalfa showed overall irrigation requirements to increase 50% when stomatal effects were not considered in the model and 29% with stomatal effects included.

Using observed sensitivity of soybean stomatal conductance to CO_2 in a crop climate model, Allen (1990) used a crop simulation model and the accompanying sensitivity analysis of stomatal conductance to CO_2 to demonstrate changes in CO_2 from 330 to 800 μmol mol^{-1} resulted in foliage temperature increases of about 1°C with low air vapor pressure deficit (VPD), but an increase of 2.5 to 4°C with air VPD in the range of 1.5 and 3 kPa, respectively. As VPD values increased above these levels, simulated foliage temperatures exceeded values observed at large VPD in the sunlit controlled-environment chambers (Allen, 1990; Prasad et al., 2002, 2006a; Allen et al., 2003). Experimental observation on soybean canopies showed that soybean canopies increased their conductance when exposed to progressively larger VPD (associated with higher temperature) so that observed canopy temperatures did not increase as much as predicted by the crop-climate model (Allen et al., 2003). The interaction of the positive impact of a doubling of CO_2 to reduce ET about 9% at cool temperatures (28/18°C) diminished and become negligible with temperature increased to 40/30°C and 44/34°C. Exposure to higher temperatures from both experimental evidence and simulation models shows the CO_2–induced benefit to conductance diminishes as temperatures increase.

Boote et al. (1997), using CROPGRO-Soybean model with hourly energy balance and stomatal conductance feedback to transpiration and leaf temperature (Pickering et al., 1995), studied the effects of 350 vs. 700 μmol mol^{-1} CO_2 with weather data from Ohio and Florida. Simulated transpiration was reduced 11 to 16% for irrigated sites and 7% for a rainfed site, while ET was reduced 6 to 8% for irrigated sites and 4% for the rainfed site. Combining the information to simulate WUE

showed an increase of 53 to 61%, which closely matches the 50 to 60% increase for soybean WUE reported by Allen et al. (2003). Model simulations produced at mid-day a 1°C higher foliage temperature under doubled CO_2, consistent with other studies. Smaller reductions in T and ET from the rainfed site were due to more effective and prolonged use of soil water and produced a larger yield response (44%) for rainfed crop than for irrigated (32%). Simulated reductions in transpiration were similar (11–16%) as those measured (12%) by Jones et al. (1985).

Water deficit conditions likely to occur under increasing variation of precipitation will increase the importance of understanding the interactions of CO_2 enrichment with climatic factors of water supply and evaporative demand. An advantage of elevated CO_2 will be evident first on reduced stomatal conductance which in turn leads to enhanced soil water conservation and less water stress detectable when crops are grown under conditions with periodic soil water deficit or under high evaporative demand. Reducing water stress has a positive impact on photosynthesis, growth, and yield and that has been documented for wheat (Wall et al., 2006) and sorghum (Ottman et al., 2001; Wall et al., 2001; Triggs et al., 2004). Sorghum showed significant CO_2–induced enhancement of biomass and grain yield for water deficit treatments; however, exhibited no significant enhancement when grown with full-irrigation at the Arizona FACE project (Ottman et al., 2001). In these studies, stomatal conductance was reduced by 32 to 37% (Wall et al., 2001), while ET was reduced 13% (Triggs et al., 2004). The potential of increasing water deficits caused by more variable precipitation patterns coupled with increasing CO_2 and temperatures suggests we need to be addressing how cropping systems respond to the interactions of soil water, CO_2, and temperature as part of adaptive management strategies.

OZONE IMPACTS ON CROPS

Although attention has been directed toward CO_2 increases as part of the climate change process less attention has been given to tropospheric O_3 even though these concentrations have increased in rural areas of the United States over the past 50 yr, and are forecast to continue to increase during the next 50 yr. Currently, the Midwest and eastern United States regions exhibit some of the highest rural O_3 levels worldwide. Ozone concentrations increase toward the east and south, showing levels in Illinois exceed those in Nebraska, Minnesota, and Iowa. Only western Europe and eastern China have similar (high) levels. Argentina and Brazil and most of the Southern Hemisphere have much lower levels of ozone, and they are expected to see little increase in O_3 over the next 50 yr. These increasing O_3 levels will impact crop production and efforts to increase ozone tolerance will be important to maintain the competitiveness of U.S. growers. Future trends in global O_3 concentrations are linked to IPCC scenarios, so that agricultural impacts from O_3 can be considered along with the other components in climate change. Modeled predictions for O_3 based on expected economic development and planned emission controls in individual countries estimate significant increases in annual mean surface O_3 concentrations in the major agricultural areas of the Northern Hemisphere (Dentener et al., 2005).

Daytime ozone levels in the Midwest have steadily increased over the last 100 yr and have climbed from <10 nmol mol^{-1} to

the present average of 60 nmol mol^{-1}. Implementation of control measures on NOx and VOCs emissions in North America and Western Europe are reducing peak ozone levels; however, global background tropospheric ozone concentrations continue to rise (Ashmore, 2005). Many plants suffer from ozone toxicity and greenhouse and small chamber studies have shown that the major agronomic crops, soybean, wheat, peanut (*Arachis hypogaea* L.), and cotton are the most sensitive (Ashmore, 2002).

Soybean has been the most extensively studied crop for O_3 effects. Its response varies greatly among cultivars, and is influenced by the O_3 profile and dynamics, nutrient and moisture conditions, and atmospheric CO_2 concentrations. The large volume of information on soybean response has been summarized in a meta-analysis of more than 50 studies on soybean, grown in controlled environment chambers at chronic levels of O_3, and they reveal exposure to high levels (>75 nmol mol^{-1}) of O_3 decreases photosynthesis, dry matter, and yield (Morgan et al., 2003; Morgan et al., 2004). Exposure to mild chronic levels (40–60 nmol mol^{-1}) produces similar responses, with dry matter and yield decreasing linearly with O_3 concentration (Morgan et al., 2003). Mills et al. (2000) developed an exposure/response relationship that serves as the basis for these relationships. The meta-analysis shows that chronic O_3 lowers the carbon uptake capacity in soybean through a reduction of photosynthetic capacity and leaf area. Exposure of soybean to chronic O_3 levels led to shorter plants with reduced dry mass and fewer pods containing fewer and smaller seeds. It has been observed that O_3 damage increases with the age of the soybean which is consistent with the hypothesis O_3 effects are cumulative over time (Adams et al., 1996; Miller et al., 1998). This additive effect through the season may indicate a greater sensitivity during seed filling (Tingey et al., 2002). Across these studies there was no indication of interactions with other stresses, even those expected to lower stomatal conductance and the pathway for O_3 entry into the leaf (Medlyn et al., 2001). A positive impact from elevated CO_2 and the resultant effect on stomatal conductance was to reduce the impacts from increasing O_3 (Heagle, 1989).

Plant growth responses from chamber studies can be different compared to the open field studies (Long et al., 2006), and the results from chamber experiments have been questioned as the basis for estimating yield losses caused by O_3 damage (Elagoz and Manning, 2005). Exposure of soybean in FACE experiments to a 20% increase above ambient O_3 levels shows O_3-induced yield losses were nearly as large as those found with open air treatment. It was observed in 2003 in central Illinois that the background O_3 level was substantially lower throughout the growing season, averaging 45 nmol mol^{-1}, and increasing O_3 levels by 20% raised the concentration to the previous 10 yr average. Yields from plots exposed to elevated O_3 in 2003, were reduced approximately 25% (Morgan et al., 2006). Evaluation of the growth components in the soybean FACE showed a significant decrease in leaf area (Dermody et al., 2006), loss of photosynthetic capacity during grain filling, and earlier onset of leaf senescence (Morgan et al., 2004). These observations help explain why yield loss may be more closely linked to decreased seed size than decreased seed number (Morgan et al., 2006). Yield losses observed from the Illinois soybean FACE experiment between 2002 and 2005 averaged 0.5% per nmol mol^{-1} increase above the 30 nmol mol^{-1} threshold and is twice the sensitivity to O_3 exposure measured

Table 2. Cardinal base and optimum temperatures (°C) for vegetative development and reproductive development, optimum temperature for vegetative biomass, optimum temperature for maximum grain yield, and failure (ceiling) temperature at which grain yield fails to zero yield, for economically important crops. The optimum temperatures for vegetative production, reproductive (grain) yield, and failure point temperatures represent mean temperatures from studies where diurnal temperature range was up to 10°C.

Crop	Base temp. veg.	Opt. temp. veg.	Base temp. repro.	Opt. temp. repro.	Opt. temp. range veg. prod.	Opt. temp. range reprod. yield	Failure temp. reprod. yield
Maize	8[†]	34[†]	8[†]	34[†]		18-25[‡]	35[§]
Sorghum	8[††††]	34[††††]	8[††††]	31[‡‡‡‡]	26–34[§§§§]	25[‡‡‡‡,¶¶¶¶]	35[‡‡‡]
Bean					23[#####]	23–24[#####,††††††]	32[#####]
Cotton	14[####]	37[####]	14[####]	28–30[####]	34[†††††]	25–26[‡‡‡‡‡]	35[§§§§]
Peanut	10[¶¶¶¶¶]						
Rice	8[‡‡‡]	36[§§§]	8[‡‡‡]	33[‡‡‡]	33[¶¶¶]	23–26[§§§,###]	35–36[§§§]
Soybean	7[¶]	30[¶]	6[#]	26[#]	25–37[††]	22–24[††]	39[‡‡]
Wheat	0[§§]	26[§§]	1[§§]	26[§§]	20–30[¶¶]	15[##]	34[†††]

[†] Kiniry and Bonhomme (1991), Badu-Apraku et al. (1983).
[‡] Muchow et al. (1990).
[§] Herrero and Johnson (1980).
[¶] Hesketh et al. (1973).
[#] Boote et al. (1998).
[††] Boote et al. (1997).
[‡‡] Boote et al. (2005).
[§§] Hodges and Ritchie (1991).
[¶¶] Kobza and Edwards (1987).
[##] Chowdhury and Wardlaw (1978).

[†††] Tashiro and Wardlaw (1990).
[‡‡‡] Alocilja and Ritchie (1991).
[§§§] Baker et al. (1995).
[¶¶¶] Matsushima et al. (1964).
[###] Horie et al. (2000).
[††††] Alagarswamy and Ritchie (1991).
[‡‡‡‡] Prasad et al. (2006a).
[§§§§] Maiti (1996).
[¶¶¶¶] Downs (1972).
[####] K. R. Reddy et al. (1999, 2005).

[†††††] V. R. Reddy et al. (1995a).
[‡‡‡‡‡] K. R. Reddy et al. (2005).
[§§§§§] K. R. Reddy et al. (1992a, 1992b).
[¶¶¶¶¶] Ong (1986).
[#####] Prasad et al. (2002).
[††††††] Laing et al. (1984).

in growth chamber studies (Ashmore, 2002). Ozone damage in an average year may cause soybean yield losses of 10 to 25% in the Midwest, with increased yield losses in some years. Another meta-analysis for rice (*Oryza sativa* L.) was conducted by Ainsworth (2008) found the response to be similar to soybean with significant decreases in net photosynthesis, biomass, grain number and mass, and yield. This summary contradicts the previous observation that rice is less sensitive to O_3 than other crops (Wang and Mauzerall, 2004). A summary of O_3 exposure on yield and yield parameters from studies before 2000 are presented in Black et al. (2000) showing that, in addition to soybean, yield of C_3 crops, for example, wheat, oat (*Avena sativa* L.), French and snap bean (*Phaseolus vulgaris* L.), pepper (*Capsicum annuum* L.), rape (*Brassica napus* L.), and various cucurbits are highly sensitive to chronic O_3 exposure. Cotton yields are also highly sensitive to O_3 (Temple, 1990). There have been a few reports showing maize yield is reduced by O_3 (e.g., Rudorff et al., 1996); however, C_4 crops are generally considered less sensitive. In spite of these few reports the current annual economic losses in corn caused by exposure to O_3 in the United States and China is estimated to be in excess of one billion dollars (Van Dingenen et al., 2008).

While the research on elevated CO_2 on stomatal conductance has been extensive there has been less conducted on the effects of elevated O_3, but some research has provided some insights into these O_3 impacts. Barnes et al. (1995) and Balaguer et al. (1995) studied stomatal conductance response of wheat exposed to 700 μmol mol^{-1} CO_2, 75 nmol mol^{-1} O_3, and increased CO_2+O_3 in controlled environment chambers. Exposure to higher O_3 reduced conductance by about 20%, while both CO_2 and CO_2+O_3 reduced conductance by 40%. Wheat was exposed to 680 μmol mol^{-1} CO_2, 50 or 90 nmol mol^{-1} O_3, and the combined effect of CO_2+O_3 using open-top chambers revealed that these treatments caused reductions in stomatal conductance of nearly 50% with year and time after sowing causing a variation in the response (Donnelly et al., 2000). Observations of stomatal conductance in potato (*Solanum turberosum* L.) showed a reduction of about 50% by 680 μmol mol^{-1} CO_2 with similar

reductions with elevated CO_2 combined with elevated O_3; however, their results were variable and inconsistent among treatments (Lawson et al., 2002; Finnan et al., 2002). Noormets et al. (2001) measured stomatal conductance of aspen (*Populus tremuloides* Michx.) leaves using a FACE chamber combining CO_2 and O_3 treatments. The effect on stomatal conductance varied with leaf age and aspen clone and revealed the following responses: Control > O_3 > CO_2+O_3 > CO_2. These results are not consistent and recent results from a soybean FACE experiment where O_3 was elevated by 50% above ambient conditions showed no significant effect of O_3 on stomatal conductance (Bernacchi et al., 2006). Observations from chamber studies comparing elevated O_3 vs. zero O_3 on stomatal conductance have shown that reductions can occur. However, observations of field-grown plants exposed to present-day ambient levels of O_3 (considerably higher than zero) would suggest that changes in stomatal conductance resulting from O_3 levels expected by 2030 would be rather small.

Ozone is changing throughout the United States and understanding these impacts and interactions with other climate variables will help develop adaptive strategies to reduce potential yield loss. It is critical in these studies that the interaction with other variables (CO_2, temperature, and soil water availability) be part of the analysis.

Temperature Effects on Crop Plants

Crop species respond differently to temperature throughout their life cycles. Each species has a defined range of maximum and minimum temperatures within which growth occurs and an optimum temperature at which plant growth progresses at its fastest rate (Table 2). Growth rates slow as temperature increases above the optimum and cease when plants are exposed to their maximum (ceiling) temperature. Vegetative development (node and leaf appearance rate) hastens as temperatures increase up to the species optimum temperature. Vegetative development usually has a higher optimum temperature than reproductive development. Progression of a crop through phenological phases is accelerated by increasing temperatures up to the species-dependent optimum

Table 3. Percent grain yield response to increased temperature (0.8°C), increased CO$_2$ (380–440 µmol mol^{-1}), net effect of temperature and increased CO$_2$ on irrigated yield assuming additivity, and change in evapotranspiration (ET) of rainfed crops with temperature and CO$_2$. Current mean air temperature during reproductive growth is shown in parentheses for each crop/region to give starting reference, although yield of all the cereal crops declines with a temperature slope that originates below current mean air temperatures during grain filling. Data are from Hatfield et al. (2008).

Crop	Temperature (0.8°C)	CO$_2$ (380–440 µmol mol^{-1})[†]	Temp/CO$_2$ combined irrigated	Temp on ET[‡]	CO$_2$ on ET§
		–% change–			
Maize–Midwest (22.5°C)	−2.5	+1.0	−1.5	+1.2[2]	
Maize–South (26.7°C)	−2.5	+1.0	−1.5	+1.2[2]	
Soybean–Midwest (22.5°C)	+1.7	+7.4	+9.1	+1.2[2]	−2.1
Soybean–South (26.7°C)	−2.4	+7.4	+5.0	+1.2[2]	−2.1
Wheat–Plains (19.5°C)	−4.4	+6.8	+2.4	+1.2[2]	−1.4
Rice–South (26.7°C)	−8.0	+6.4	−1.6	+1.2[2]	−1.7
Sorghum (full range)	−6.2	+1.0	−5.2	+1.2[2]	−3.9
Cotton–South (26.7°C)	−3.5	+9.2	+5.7	+1.2[2]	−1.4
Peanut–South (26.7°C)	−3.3	+6.7	+3.4	+1.2[2]	
Bean–relative to 23°C	−5.8	+6.1	+0.3	+1.2[2]	

† Response to CO$_2$ increment, with Michaelis–Menten rectangular hyperbola interpolation.

‡ Response of ET to temperature increment 1.489 × 0.8°C from sensitivity of ASCE "standard" ET equation for nonwater-stressed alfalfa (Kimball, 2007).

§ Adapted from Table 2.7 of Hatfield et al. (2008) for mostly nonwater-stressed conditions.

temperature. There are differences among annual (nonperennial) crop species in their cardinal temperature values as shown in Table 2. Values reported in Table 2 represent conditions in which temperature is the only limiting variable. It is important to realize that plant temperatures can be quite different than air temperatures and can be warmer than air under water stressed conditions or cooler than air under adequate soil water conditions. A recent review by Hatfield et al. (2004) provides a summary of the current use of plant temperatures to quantify water stress in plants. Plant temperatures are measured with either attached thermometers to the leaf that are difficult to maintain or with relatively expensive infrared thermometers, and therefore plant temperatures have been observed much less often than air temperatures. Consequently, evaluations of plant responses to changes in temperature have been focused on air temperature rather than plant or canopy temperatures, including the values given in Table 2.

Exposure to higher temperatures causes faster development in nonperennial crops, which does not translate into an optimum for maximum production because the shorter life cycle means smaller plants, a shortened reproductive phase duration, and reduced yield potential because of reduced cumulative light interception during the growing season. Observations across species have shown optimum temperatures for yield are generally lower than the optimum temperature for leaf appearance rate, vegetative growth, or reproductive progression (Table 2). Yield may be impacted when temperatures fall below or above specific thresholds at critical times during development. The duration of the crop life cycle is determined by temperature and the location of specific cultivars to given production zones is a reflection of their specific temperature response. Another factor that has a major role in life cycle progression in many crops, especially for soybean, is the daylength sensitivity.

One of the critical phenological stages for high temperature impacts is the reproductive stage because of the effect on pollen viability, fertilization, and grain or fruit formation. Yield potential will be affected by chronic exposures to high temperatures during the pollination stage of initial grain or fruit set. Temperature extremes during the reproductive stage of development can produce some of the largest impacts on crop production. Schlenker and Roberts (2009) have emphasized

the importance of considering the nonlinearity of temperature effects on yield (the slope of the decline in yields above the optimum temperature is often steeper than the incline below it) in projecting climate change impacts. Temperature effects on individual species are discussed in the following section.

Temperature Effects on Individual Species

Exposure to temperature changes will affect all plants differently because of their unique temperature response. Climate change scenarios reveal temperatures will increase and the chance of plants being exposed to higher temperature extremes will be more likely. We have summarized the effects of temperature on different species important to world food, feed, and fiber production.

Maize

One of the most studied crops in terms of temperature response is maize and increasing temperature shortens the life cycle and duration of the reproductive phase causing a reduction in grain yield (Badu-Apraku et al., 1983; Muchow et al., 1990). Using both observed and simulated maize yields, Muchow et al. (1990) reported highest grain yields were from locations with relatively cool growing season mean temperatures (18.0–19.8°C at Grand Junction, CO), compared to warmer sites, for example, Champaign, IL (21.5–24.0°C), or warm tropical sites (26.3–28.9°C). This causes the simulated yields in the central Corn Belt to decrease 5 to 8% per 2°C temperature increase which leads to the prediction that a temperature rise of 0.8°C over the next 30 yr in the Midwest could decrease grain yields by 2 to 3% (2.5%, Table 3) assuming no complicating effect from soil water limitations. Their results may have underestimated the potential yield reduction with rising temperature because they did not incorporate temperature modifications to assimilation rate or respiration nor did they account for failures in grain-set due to rising temperature (Muchow et al., 1990). Lobell and Field (2007) separated the effects of temperature and rainfall using records from 1961 to 2002 and found an 8.3% yield reduction per 1°C rise in temperature. Runge (1968) observed maize yields were responsive to interactions of daily maximum temperature and rainfall 25 d prior and 15 d after anthesis. These interactions revealed when rainfall

was low (zero to 44 mm per 8 d), yield was reduced by 1.2 to 3.2% per 1°C rise. Conversely, when temperatures were warm (T_{max} of 35°C), yield was reduced 9% per 25.4 mm decline in rainfall.

Temperature effects on pollination and kernel set may be one of the critical responses related to climate change. Pollen viability decreases when exposure to temperatures above 35°C occurs (Herrero and Johnson, 1980; Schoper et al., 1987; Dupuis and Dumas, 1990).The critical duration of pollen viability (before silk reception) is a function of pollen moisture content and is strongly dependent on vapor pressure deficit (Fonseca and Westgate, 2005). Although there is limited data on sensitivity of kernel set in maize to elevated temperature, the in vitro evidence suggests that the thermal environment during endosperm cell division phase (8–10 d postanthesis) is critical (Jones et al., 1984). Temperatures of 35°C compared to 30°C during the endosperm division phase reduced subsequent kernel growth rate (potential) and final kernel size, even after the plants were returned to 30°C (Jones et al., 1984). Exposure to temperatures above 30°C damaged cell division and amyloplast replication in maize kernels which reduced the strength of the grain sink and ultimately yield (Commuri and Jones, 2001). In maize, leaf photosynthesis rate has a high temperature optimum of 33 to 38°C with no sensitivity of quantum efficiency to elevated temperature (Oberhuber and Edwards, 1993; Edwards and Baker, 1993), and photosynthesis rate is reduced above 38°C (Crafts-Brandner and Salvucci, 2002). Ben-Asher et al. (2008) evaluated high temperature effects on sweet corn in controlled environment chambers and found highest photosynthetic rates occurred at temperatures of 25/20 while at 40/35°C (light/dark) photosynthetic rates were 50 to 60% lower. They also observed that photosynthetic rate declined for each 1°C increase in temperature above 30°C.

Soybean

Optimium temperatures for the postanthesis phase of soybean has a low optimum temperature of about 23°C which results in the life cycle being slower and longer when mean daily temperatures exceed 23°C (Pan, 1996; Grimm et al., 1994). Optimum cardinal temperature of 23°C for the postanthesis period is close to the single seed growth rate (23.5°C) optimum temperature reported by Egli and Wardlaw (1980), and the same as the 23°C optimum temperature for seed size (Egli and Wardlaw, 1980; Baker et al., 1989; Pan, 1996; Thomas, 2001; Boote et al., 2005). Increasing the mean temperature above 23°C causes seed growth rate, seed size, and intensity of partitioning to grain (seed HI) to decrease until all of the parameters fall to zero at a mean temperature of 39°C (Pan, 1996; Thomas, 2001).

The cardinal temperature values for soybean are lower than those of maize and the values used for preanthesis reproductive development (time to anthesis) have a base of 6 and 26°C optimum as currently used in CROPGRO–soybean model (Boote et al., 1998). These are similar to the values of 2.5 and 25.3°C reported by Grimm et al. (1993). Using these temperature relationships for grain development as reported by Egli and Wardlaw (1980) for temperature effect on seed growth sink strength and the Grimm et al. (1993, 1994) derivation of temperature effects on reproductive development, the CROP-GRO model predicts the highest grain yield of soybean at 23 to 24°C, with progressive decline in yield, seed size, and harvest index (HI) with temperature increases above this optimum

range and finally showing no yield at 39°C (Boote et al., 1997, 1998). An analysis of 829 sites across the United States extracted from regional soybean yield trials (Piper et al., 1998) revealed that yield produced per day of season relative to mean air temperature showed the highest productivity at 22°C.

Exposure to high temperatures during the pollination stage has deleterious effects on pollen growth and survival. Viability of soybean pollen is reduced by exposure to instantaneous temperatures above 30°C (T_{opt}), but show a long gradual decline until failure at 47°C (Salem et al., 2007). Averages among many cultivars show cardinal temperatures (T_b, T_{opt}, T_{max}) of 13.2, 30.2, and 47.2°C, respectively, for pollen germination and for pollen tube growth of 12.1, 36.1, and 47.0°C, respectively. Differences in cardinal temperatures and tolerance of elevated temperature among cultivars were not significant. When soybean growth was compared at 38/30 vs. 30/22°C (day/night) temperatures, exposure to elevated temperatures reduced pollen production by 34%, pollen germination by 56%, and pollen tube elongation by 33% (Salem et al., 2007). Temperatures above 23°C show a progressive reduction in seed size (single seed growth rate) with a reduction in fertility above 30°C leading to a reduced seed HI at temperatures above 23°C (Baker et al., 1989).

Potential impacts of climate change through temperature on soybean are strongly related to mean temperatures during the postanthesis phase of soybean. In the upper Midwest, where mean soybean growing season temperatures are currently around 22.5°C, soybean yield may increase. However, for the southern United States with current growing season temperatures of 25 to 27°C, soybean yields are expected to decline with increased warming, 2.4% for 0.8°C increase from 26.7°C current mean. This is similar to the observations from Lobell and Field (2007) who reported a 1.3% decline in soybean yield per 1°C increase in temperature. Temperature impacts on soybean production cannot be ignored and changes in management systems to limit exposure to high temperatures during pollination would benefit yield.

Wheat

Rising temperatures will decrease the length of grain-filling period of wheat and other small grains (Sofield et al., 1974, 1977; Chowdhury and Wardlaw, 1978; Goudriaan and Unsworth, 1990). Shortened grain filling duration was attributed to factors other than assimilate limitation (Sofield et al., 1974; 1977). If we assume that daily photosynthesis is unchanged, then yield will decrease in direct proportion to the shortening of grain filling period. Evidence for the temperature effect is already seen in higher wheat yield potential in northern Europe than in the midwestern United States. Rising temperature effects on photosynthesis are an additional reduction factor on wheat yield, because of the linkage with water deficit effects (Paulsen, 1994).

Optimum temperature ranges for photosynthetic rate in wheat is 20 to 30°C (Kobza and Edwards, 1987) and is 10°C higher than the optimum temperature (15°C) for grain yield and single grain growth rate (Chowdhury and Wardlaw, 1978). Pushpalatha et al. (2008) observed that rubisco activity decreased in wheat plants with a reduction in the photosynthetic rate when wheat plants were exposed to high temperatures. Increases of temperature above 25 to 35°C, common during grain filling of wheat, will shorten the grain filling period and reduce wheat yields. Chowdhury and Wardlaw (1978) observed a nonlinear slope of

reduction in grain filling period to the mean temperatures and when this was applied to the wheat growing regions of the Great Plains, the projected reduction in yield is 7% per 1°C increase in air temperature between 18 and 21°C and 4% per 1°C when air temperatures increase above 21°C. These projections do not consider any additional reduction caused by temperature effects on photosynthesis or grain-set. A similar set of responses were found by Lawlor and Mitchell (2000) who observed temperature increases of 1°C rise would shorten reproductive phase by 6% and grain filling duration by 5% causing a proportion reduction in grain yield and HI. Observations from nine sites in Europe for spring wheat revealed a 6% decrease in yield per 1°C temperature rise (Bender et al., 1999). When these temperature increases are extrapolated to the global scale a 5.4% decrease in wheat yield per 1°C increase in temperature is expected (Lobell and Field, 2007). Exposure to 36/31°C temperatures for only 2 to 3 d before anthesis created small unfertilized kernels with symptoms of parthenocarpy, small shrunken kernels with notching, and chalking of kernels (Tashiro and Wardlaw, 1990). A recent summary by Wheeler et al. (2000) on temperature effects during the grain-filling period of wheat found a linear decrease in grain yield with increasing mean temperature.

One of the observed changes in temperature is an increase in nighttime temperatures. When temperatures increased above 14°C there was a decreased photosynthesis after 14 d of stress causing grain yields to decrease linearly with increasing nighttime temperatures from 14 to 23°C which in turn leads to lower HI's (Prasad et al., 2008). In their studies, when nighttime temperatures increased above 20°C there was a decrease in spikelet fertility, grains per spike, and grain size.

Rice

Temperature response of rice has been well documented (Baker and Allen, 1993a, 1993b; Baker et al., 1995; Horie et al., 2000). When temperature increases from a base of 8°C to 36–40°C (the thermal threshold of survival) there is an increase in leaf appearance rate (Alocilja and Ritchie, 1991; Baker et al., 1995), biomass increases until temperatures reach 33°C (Matsushima et al., 1964); however, grain formation and yield is maximum at the optimum temperature of 25°C (Baker et al., 1995). Baker et al. (1995) concluded from their sunlit controlled-environment chambers experiments that the optimum mean temperature for grain formation and grain yield of rice is 25°C and grain yield is reduced 10% per 1°C temperature increase above 25°C until 35 to 36°C mean temperature when no yield is obtained. In their experiments they used a 7°C day/night temperature differential (Baker and Allen, 1993a; Peng et al., 2004). Exposure to temperatures above 25°C causes a yield decline due to shorter grain filling duration (Chowdhury and Wardlaw, 1978; Snyder, 2000). Further increase in temperature above 25°C causes progressive failure to produce filled grains caused by reduced pollen viability and pollen production (Kim et al., 1996; Matsui et al., 1997; Prasad et al., 2006b). Viability of pollen and production declines as daytime maximum temperature (T_{max}) exceeds 33°C and is zero at T_{max} of 40°C (Kim et al., 1996). Flowering of rice occurs near mid-day which makes T_{max} a good indicator of heat-stress on spikelet sterility. Exposure to temperatures above 33°C in rice within 1 to 3 h after anthesis (dehiscence of the anther, shedding of pollen, germination of pollen grains on stigma, and elongation of pollen tubes) can have negative impacts on reproduction (Satake and Yoshida, 1978). Current observations in rice reveal that anthesis occurs between about 0900 to 1100 h in rice (Prasad et al., 2006b).

Grain size of rice remains relatively constant and declines slowly with increasing temperatures, until the pollination failure point (Baker and Allen, 1993a). There is no difference in the rice ecotypes, *japonica* and *indica,* in their upper temperature threshold (Snyder, 2000; Prasad et al., 2006b); however, the *indica* types are more sensitive to night temperatures <19°C (Snyder, 2000). There are significant genotypic variations in heat tolerance for percent filled grains, pollen production, pollen shed, and pollen viability based on screening of rice genotypes and ecotypes for heat tolerance (33.1/27.3°C vs. 28.3/21.3°C mean day/night temperatures) (Prasad et al.,2006b). Exposure to this increase in temperature for 14 cultivars caused a 9 to 86% reduction in spikelet fertility, 0 to 93% reduction in grain weight per panicle, and 16 to 86% reduction in HI. As expected the most tolerant cultivar showed the smallest decreases in spikelet fertility, grain yield, and HI to elevated temperature. Cheng et al. (2010) combined increased CO_2 (360 or 680 μmol mol^{-1}) and high night temperatures (22 or 32°C with a daytime temperature of 32°C) and found that (i) high night temperatures increased living leaf N concentration and leaf area and caused higher photosynthetic capacity during the last stage of growth; (ii) carbon assimilation increased with higher night temperatures despite the increased carbon loss to respiration; (iii) elevated CO_2 did not affect the allocations of C or N between the ear and stem during reproductive growth; and (iv) higher nighttime temperatures caused a significant decrease in the C and N allocation to the ears. They concluded that effect of the higher nighttime temperatures on the translocation of C and N to the ears will reduce the positive impact of increased CO_2. The current mean air temperatures for the southern United States and many tropical regions during the rice grain filling phase in summer are nearly 26 to 27°C which are above the 25°C optimum and leads to the conclusion that further increases in air temperatures above current levels will reduce rice yield, by about 10% per 1°C rise. This is confirmed by an earlier study from Peng et al. (2004) who found that minimum temperatures were the most significant variable affecting rice yield.

There is evidence that exposure to cold temperatures are also detrimental in the pollination stage. Imin et al. (2004) observed that cold temperatures reduced the viability of the anthers and this has been significant enough to begin a screening program for tolerance to low temperatures (Sayfa et al., 2010). An analysis of the interactions of maximum and minimum temperatures with solar radiation was conducted using farmer-managed fields across 227 locations in tropical and subtropical Asia by Welch et al. (2010). Their observations revealed both temperature and solar radiation significantly impacted rice yields and increased minimum temperatures decreased yield while higher maximum temperatures increased yields because the maximum temperatures were not above the optimal threshold. They suggested moderate warming in the future would decrease yields and would increase in magnitude with increased warming because the effect of higher maximum temperatures would become negative (Welch et al., 2010).

Sorghum

In sorghum, the observed vegetative development has a base temperature 8°C with an optimum of 34°C (Alagarswamy and Ritchie, 1991), with an optimum temperature for preanthesis reproductive development of 31°C (Prasad et al., 2006a). The optimum temperature range for sorghum vegetative growth is between 26 and 34°C and for reproductive growth is 25 to 28°C (Maiti, 1996). Maximum dry matter production and grain yield has been observed at 27/22°C when compared to temperatures 3 or 6°C lower or 3 or 6°C warmer (Downs, 1972). Duration of grain filling reduces as temperature increases (Chowdhury and Wardlaw, 1978; Prasad et al., 2006a). Temperature increases above 36/26°C to 40/30°C (diurnal max/min) causes panicle emergence to be delayed by 20 d with no panicles formed at 44/34°C (Prasad et al., 2006a). Grain yield, HI, pollen viability, and percent seed-set were highest at 32/22°C and progressively reduced as temperature increased, falling to zero at 40/30°C (Prasad et al., 2006a). The highest vegetative biomass was observed at 40/30°C and photosynthetic rates were highest until temperatures reached 44/34°C. Exposure to temperatures above 36/26°C caused a reduction in seed size. There are compensating effects when the temperatures are cooler than optimum for biomass/photosynthesis (27/22°C) because yield loss from shorter filling period would be offset by increases in photosynthesis. Relating the yield response of sorghum to a shortening of filling period would cause a yield decline of 7.8% per 1°C temperature rise from 18.5 to 27.5°C (Chowdhury and Wardlaw, 1978). The temperature responses assembled by Chowdhury and Wardlaw (1978) are confirmed by estimates of an 8.4% decrease in global mean sorghum yield per 1°C increase in temperature as reported by Lobell and Field (2007).

Cotton

Cotton is considered to be adapted to high temperature environments; however, reproductive processes are adversely affected by elevated temperature (Reddy et al., 1991, 1995b, 2000, 2005). Since cotton is a tropical crop, leaf appearance rate has a relatively high base temperature of 14°C and a relatively high optimum temperature of 37°C, with both leaf and vegetative growth tolerant of elevated temperatures (Reddy et al., 1999, 2005). In contrast, the reproductive progression (emergence to square, square to first flower) has a temperature optimum of 28 to 30°C, along with a relatively high base temperature of 14°C (Reddy et al., 1997, 1999). Maximum growth rate per boll occurs at 25 to 26°C, and then declines at higher temperatures. Boll harvest index was highest at 28°C with further declines with increasing temperatures until zero boll harvest index occurs at 33 to 34°C (Reddy et al., 2005). Temperatures <20°C caused the largest boll size and boll size declines progressively with temperature increases. As temperatures increase up to 35/27°C day/night temperature there was an initial compensation with increased boll number set; however, exposure to mean temperatures above 30°C caused percent boll set, boll number, boll filling period, rate of boll growth, boll size, and yield to decrease (Reddy et al., 2005). Exposure to short-term air temperatures above 32°C decreases pollen viability and temperatures above 29°C reduces pollen tube elongation (Kakani et al., 2005) and progressively reduces successful boll formation to zero boll yield at 40/32°C day/night (35°C mean) temperature (Reddy et al., 1992a, 1992b). Failure point temperatures of cotton are below those of soybean and peanut and similar to rice and sorghum. A well-defined cotton yield response to temperature

does not exist and development of a quadratic (parabolic) yield response to temperature from the optimum of 25°C to the failure temperature of 35°C showed a 0.8°C increase from 26.7 to 27.5°C decreased yield by 3.5%. A 1°C temperature increase on cotton yield was evaluated by Pettigrew (2008) who observed lint yield in two cultivars was reduced by 10% due to a reduction in boll mass and less seed in the bolls.

Peanut

Peanut is an important crop in the southern United States with a base temperature for peanut leaf appearance rate and onset of anthesis of 10 and 11°C, respectively (Ong, 1986). Optimum temperatures for leaf appearance rate are above 30°C, while the optimum for rate for vegetative development to anthesis is 29 to 33°C (Bolhuis and deGroot, 1959). Photosynthesis has a high temperature optimum of 36°C. Cox (1979) found the optimum temperature for single pod growth rate and pod size was 24°C, with slower growth rate and smaller pod size at higher temperatures. Williams et al. (1975) conducted a study across varying elevations to evaluate temperature effects on peanut, in which the observed peanut yield was highest at a mean temperature of 20°C (27/15°C max/min) because these temperatures contributed to the longest life cycle and reproductive period. From sunlit, controlled-environment chambers, Prasad et al. (2003) concluded the optimum mean temperature for pod yield, seed yield, pod harvest index, and seed size was lower than 26°C. Using quadratic projections to peak and minimum showed the optimum temperature was 23 to 24°C, along with a failure point temperature of 40°C for zero yield and zero HI. Prasad et al. (2003) observed that pollen viability and percent seed-set began to fail at about 31°C, reaching zero at about 39 to 40°C (44/34°C treatment). An analysis of individual flowers showed the sensitive period to elevated temperature begins 6 d before opening of the flower and ends 1 d after, with greatest sensitivity on the day of flower opening (Prasad et al., 2001; Prasad et al., 2001). When exposed to bud temperature of 33°C there was a reduction in percent fruit-set with a linear decline to zero fruit-set at 43°C bud temperature (Prasad et al., 2001). Observations of genotypic differences to heat tolerance of peanut through pollen viability have been found (Craufurd et al., 2003). Since air temperature in the southern United States for the peanut growing season already averages 26.7°C, temperature increases will further reduce seed yields (4.1% per 1°C, or 3.3% for a 0.8°C rise in range of 26–27°C) based on the relationship from Prasad et al. (2003).

Dry Bean and Cowpea

Red kidney bean is typical of many vegetable crops grown in cool regions of the United States. Red kidney bean was found to be quite sensitive to elevated temperature with highest seed yield at 28/18°C (23°C mean) or lower (lower temperatures were not tested), and a linear decline to zero yield with temperature increases to 37/27°C (32°C mean) (Prasad et al., 2002). In their study, pollen production per flower was reduced above 31/21°C, pollen viability above 34/24°C, and seed size above 31/21°C. Laing et al. (1984) observed the highest bean yield occurred at 24°C and declined with higher temperatures. Gross and Kigel (1994) reported reduced fruit-set when flower buds were exposed to 32/27°C during the 6 to 12 d before anthesis and at anthesis due to nonviable pollen, failure of anther dehiscence, and reduced pollen tube growth. Jifon and Wolfe (2005) examined the

interaction of heat stress and elevated CO_2 on growth and yield of red kidney bean and found no CO_2 benefit to pod yield at high temperatures when reproductive development was reduced.

Heat-induced decreases in seed and fruit-set in cowpea (*Vigna unguiculata* L.) are linked to nonviable pollen (Hall, 1992). Hall (1992) reported differences among genetic cultivars for heat tolerance of cowpea lines. Screening for temperature tolerance within bean cultivars has not been done explicitly, but the Mesoamerican lines are more tolerant of warm tropical locations than are the Andean lines which include the red kidney bean type (Sexton et al., 1994). Using the decline slope for temperature response based on the data of Prasad et al. (2002), bean yield is projected to decrease 7.2% per 1°C temperature rise.

Synthesis of Temperature Effects

The pollination phase of development is one of the most sensitive to episodic temperature increases. The synchrony of anthesis in each crop will dictate the crop sensitivity and ability to compensate to exposure to high temperatures and then exposure to improved weather during the remainder of the growth cycle, for example, maize has a highly compressed phase of anthesis, while rice and sorghum spikelets may achieve anthesis over a period of a week or more. Soybean, peanut, and cotton produce pollen over several weeks and thereby increase the potential success of reproduction. The period of exposure to high temperatures may not be isolated to a narrow window during reproduction as was found for peanut (and presumably other legumes) where the sensitivity to elevated temperature for a given flower, extends from 6 d before opening (pollen cell division and formation) up through the day of anthesis (Prasad et al., 2001). Exposure to hot temperatures and the resultant affect on flower fertility may occur whether these flowers are in their formative 6-d phase or undergoing anthesis. Throughout the day, the first 6 h of the day appear to be more critical because pollen dehiscence, pollen tube growth, and fertilization are occurring during this period.

Observations have shown that rice and sorghum have a similar sensitivity of grain yield, seed HI, pollen viability, and success in grain formation in which pollen viability and percent fertility is reduced by exposure to instantaneous hourly air temperature above 33°C and reaches zero at 40°C (Kim et al., 1996; Prasad et al., 2006a, 2006b). Exposure to diurnal max/min day/night temperatures ranges of 40/30°C (35°C mean) produced no yield for rice and sorghum with the expectation of a similar response for maize. Higher temperatures will impact yields of all of the agronomic crops and exposure to episodic high temperatures will create stress on crop plants both in the vegetative and reproductive stages of development. Lobell (2007) evaluated the diurnal range of temperature on wheat, maize, and rice yields and observed yields to show a negative response to increased diurnal temperature ranges. He also observed a nonlinear response of yields to temperature because of the interaction of water and heat stress on hot days. Wassmann et al. (2009) reviewed the available literature on rice production and concluded that the reproductive period was the most sensitive to higher temperatures and we expect the same response in other cereal crops. The potential increase in the frequency of high temperature extremes during the growing season increases the likelihood for exposure of plants to high temperatures during the reproductive development stage. Two recent studies suggest that the increasing effect of temperature may have

larger impacts than reported in previous studies. Kucharik and Serbin (2008) and Schlenker and Roberts (2009) evaluated crop yields for maize, soybean, and cotton to changes in temperature. Kucharik and Serbin (2008) conducted their analysis for Wisconsin data from 1976 to 2008 and reported for each degree of warming in the future corn yields could decrease by 13% and soybean by 16% without a change in precipitation. In their analysis, they found that the temperature effect would be offset by increases in precipitation. Schlenker and Roberts (2009) used the warming scenarios from climate change models and the same temperature relationships for maize, soybean, and cotton that were used in our paper and concluded that the increasing temperatures would negatively impact yields. They estimated under the slowest warming scenarios crop yields would decline 30 to 46% by the end of the century and under the rapid warming scenario, yields would decline 63 to 82% (Schlenker and Roberts, 2009). These results suggest that increasing attention be given to understanding the role of temperature changes on crop productivity to develop effective adaptive management strategies.

Implications of Changes in Carbon Dioxide, Temperature, and Crop Water Use on Plant Productivity

Rising CO_2 from current concentrations to 380 to 450 μmol mol^{-1} coupled with a 0.8°C increase in temperature and regional variation in soil water deficits and heavy rainfall events for next 30 yr will have implications for the production of representative crops. The temperature responses detailed in the previous section show that our major agronomic crops could be expected to show signs of declining yields due to increased temperatures. When combined across temperature and CO_2 responses for the individual species then the impacts of climate change can be assessed. We are in an era of uncharted responses and while analysis of the current literature can provide an assessment of crop grain yield response to temperature, often we have to rely on interpolation of plant response between optimum and failure temperatures for grain yield (as extracted from Table 2). These responses are relative to current mean temperatures during the reproductive phase in different regions (e.g., soybean and maize in Midwestern and Southern regions, as well as cotton, sorghum, and peanut [*Arachis hypogaea* L.] in Southern regions). Crop responsiveness of grain yield to CO_2 is from Table 1, using Michaelis-Menten rectangular hyperbola interpolation with value of 1.0 at 350 μmol mol^{-1}, the enhancement ratio set at 700 μmol mol^{-1} and a compensation CO_2 concentration consistent with C_3 or C_4 species at 30°C. Using this generalized shape, the response for 380 to 440 μmol mol^{-1} CO_2 was 1.0% for C_4 and 6.1 to 9.4% for C_3 species, except for cotton which showed 9.4% response. With adequate water, maize in the Midwest had the net yield response of –1.5%, by combining the –2.5% from 0.8°C rise and +1.0% from CO_2 of 380 to 440 μmol mol^{-1} (Table 1). Yield response of maize in the South is likely more negative because of the temperature effect on growth and reproduction. Although maize is widely grown in the United States and produces the largest amount of grain, the certainty of temperature and CO_2 effects on maize yields is limited by minimal studies and contradictory reports on temperature and CO_2 responses. Soybean, assuming sufficient soil water availability in the Midwest, shows a net yield response of +9.1%, when we add the +1.7% from 0.8°C rise above current 22.5°C mean and

+7.4% from rising CO_2. A different picture emerges for soybean in the South, because the temperature increase will be detrimental, –2.4%, with 0.8°C temperature increment above the current 26.7°C, with the same CO_2 effect, gives a net yield response of +5.0%, even when water supplies are sufficient. Assuming no change in water availability, the net wheat yield response would be +2.4% derived from a projected –4.4% with 0.8°C rise and +6.8% increase from rising CO_2. Rice grown in the southern United States shows a net yield response of –1.6%, derived from the temperature effect of –8.0% projected from 0.8°C rise and +6.4% from CO_2 increases. Projected yield impacts for peanut show a net response of +3.4%, based on adding –3.3% from 0.8°C rise and +6.7% from CO_2 changes. Cotton yields are projected to have a net yield response of +5.7%, based on the additive effects from –3.5% from 0.8°C rise and +9.2% from increased CO_2. Sorghum yield response is less certain; however, yield reduction anticipated from shortened filling period provides a net yield decrease of 5.2%. Bean yield response is also less certain, with net yield effect of +0.3%, derived from combining a –5.8% response to 0.8°C rise and +6.1% from increased CO_2 (Table 3).

The increased potential for water deficits will also impact crop yields and to assess these impacts under climate change we can begin with the Table 3 responses to temperature and CO_2 for the water-sufficient cases. The underlying assumption is that yields will increase by the same extent caused by the increased CO_2 causing a reduction in ET. Estimates of future yields derived from simulations with CROPGRO–Soybean incorporating an energy balance option and stomatal feedback derived from CO_2 enrichment (350–700 μmol mol^{-1}, but with no temperature increase) produced a 44% yield increase for water-stressed crops compared to fully irrigated (32%). The yield increment was nearly proportional to the decrease in simulated transpiration (11–16%). Based on this assumption, the 380 to 440 μmol mol^{-1} CO_2 increment would further increase yield of C_3 crops (soybean, rice, wheat, and cotton) by an additional 1.4 to 2.1% (incremental reduction in ET from CO_2 in Table 1). However, the projected 0.8°C increases ET by 1.2%, nearly negating the effect of CO_2 on reducing ET. While it is difficult to predict the exact scenarios of precipitation changes under future climate change, the impact of both excess and deficit amounts of soil water on all crops will be substantial and cannot be ignored as part of the potential impacts on food security.

CLIMATE CHANGE ON GRAIN QUALITY

One of the emerging challenges will be to understand and quantify the impacts of changing climate on grain quality. Kimball et al. (2001) observed an interaction between N status in plants and grain quality in wheat and showed that low N reduced grain quality which was further exaggerated by high CO_2 concentrations. Conroy and Hocking (1993) showed a steady decline in grain protein from 1967 to 1990 in wheat grown in Australia. They suggested not all of this change can be specifically linked to rising CO_2, but CO_2 increases may be contributing to this decline. These observations suggest nutrient status in plants interacts with changing CO_2 concentrations although there is no specific statement on the impacts of rising CO_2 on N requirements in crops, other than the general concept that greater growth and yields require greater N supply. Erbs et al. (2010) completed a study on CO_2 enrichment and N management on grain quality in wheat and barley (*Hordeum vulgare* L.)

and found that increasing CO_2 to 550 μmol mol^{-1} with two rates of N, adequate and half of the N, affected crude protein, starch, total and soluble B-amylase, and single kernel hardiness. They observed that increasing CO_2 reduced crude protein by 4 to 13% in wheat and 11 to 13% in barley but increased starch by 4% when half-rate N was applied. They concluded that nutritional and processing quality of flour will be diminished for cereal grown under elevated CO_2 and low N fertilization. This study highlights the need to increase our understanding of these interactions because they are not well-defined and understanding these interactions would provide insights into the interactions of genetic by management interactions. In cultivated systems it is apparent that greater attention will have to be given to N management in cultivated crops with climate change to increase production efficiency and to maintain both yields and protein concentration in grains.

CLIMATE IMPACTS ON WEEDS
Carbon Dioxide

Among plant species, weeds, rather than crops, across several studies show the strongest relative response to rising CO_2 (Ziska, 2004). Even though individual plants of rice or wheat respond positively to rising CO_2, the increased response of weedy species to CO_2 create the potential for increased competition and increased crop production losses (Ziska, 2000, 2003a, 2003b; Ziska et al., 2005). Based on continuation of this phenomenon, rising CO_2 could lead to yield reductions in agricultural systems where weed control is not practiced or sufficient.

Climatic Factors

Although moisture is a recognized factor in weed seed establishment and final plant size, little is known about interactions between altered precipitation and weed biology. At the whole plant level, changes in precipitation and water availability are likely to affect weeds of agricultural importance in a number of ways. Several annual weeds, from cheatgrass (*Bromus tectorum*) to yellow star thistle (*Centaurea solstitialis*) depend on moisture for seed germination. More moisture is associated with overwintering and increased seed production for both species (Patterson, 1995a). However, both species are drought adapted, cheatgrass being able to complete its life-cycle quickly on available moisture, whereas star thistle can develop a deeper root system than many native plants. Timing of precipitation may also be critical. For example, greater spring-time moisture associated with El Niño events may expand cheatgrass habitat (Bradley and Mustard, 2005). Overall, changes in the timing and amount of precipitation are likely to alter several aspects of weeds including germination, plant size, seed production, and the distribution of water borne seeds. At the community level it is also probable that precipitation extremes will alter competition between invasive weeds and crops with subsequent effects on productivity (Patterson, 1995b).

Along with precipitation, temperature is a primary abiotic variable that affects invasive weed biology. The probable impact of rising temperatures on the expansion of invasive weeds into higher latitudes is of particular concern. Many of the worst invasives for warm season crops in the southern United States originated in tropical or warm temperature areas; consequently, northward expansion of these invasives may accelerate with warming (Patterson, 1993). For example, itchgrass (*Rottboelliia cochinchinensis*), an invasive weed associated with significant yield reductions in

sugarcane for Louisiana (Lencse and Griffin, 1991), is also highly competitive in corn, cotton, soybean, grain sorghum, and rice systems (e.g., Lejeune et al., 1994). The response of this species to a 3°C increase in average temperature stimulated biomass by 88% and leaf area by 68% (Patterson et al., 1979), projecting increases in growth for the middle Atlantic states (Patterson et al., 1999). Northward migration of other invasive weeds, such as cogongrass (*Imperata cylindrica*) and witchweed (*Striga asiatica*), is also anticipated (Patterson, 1995a). Conversely, additional warming could also restrict the southern range of other invasive weeds, for example, wild proso millet (*Panicum miliaceum*) or Canada thistle (Ziska and Runion, 2007).

One of the most interesting forecasts regarding global warming and an invasive weed was made almost two decades ago in regard to Northward migration of kudzu (*Pueraria lobata*), an ubiquitous invasive of the southeastern United States. Sasek and Strain (1990) observed that the latitudinal distribution at that time was limited to southern regions by low winter temperatures of –15°C (Fig. 7 in Sasek and Strain, 1990). More recently, Wolfe et al. (2008) projected expansion of the habitable range of kudzu into the northeastern United States during the 21st century based on climate model projections of the northward migration of the –15°C isocline.

Mechanisms

Overall, the projected warming may be exceeding maximum rates of plant migration observed in postglacial periods (Malcolm et al., 2002), resulting in preferential selection for the most mobile plant species. Several characteristics associated with long-distance dispersal are commonly found among agronomic weeds (Rejmanek, 1996), suggesting that they will be among the fastest to migrate with increasing temperatures (Dukes and Mooney, 2000).

The basis for the enhanced response of weedy species within agroecosystems is not entirely evident. In some instances, the physiological characteristics of crop or a weed being a C_3 or C_4 plant will determine its response to CO_2 and its competitive abilities (Table 1 from Ziska and Runion, 2007). However, many of the problem weeds within a given crop are the wild (uncultivated) plants from the same genus or species (e.g., rice and wild rice, oat and wild oat, sorghum and shattercane) and will most likely exhibit the same photosynthetic pathway. An alternate suggestion is the greater range of responses observed for weeds with increasing atmospheric CO_2 is due to their greater genetic diversity compared to crops and with the greater gene pool there is a greater likelihood for a species to respond to a resource change (Treharne, 1989). Still, the degree of diversity may be of potential benefit at a time of climatic uncertainty. For example, identifying specific genetic, morphological, or phenotypic traits within wild lines, and the appropriate techniques for transferring these traits to cultivated lines, could, over time, be the focus of future work in any systematic effort to improve cultivated crop yields in response to rising atmospheric CO_2 or to climatic extremes (Ziska and McClung, 2008).

Management

An increasing number of studies demonstrate a decline in pesticide efficacy with rising CO_2 (reviewed by Archambault, 2007). The basis for this observed decline in efficacy is unclear; however, rising CO_2 could reduce pesticide absorption into leaves by decreasing the number or aperture of stomata or by changing leaf thickness or size. Changes in transpiration induced by CO_2 could limit uptake of soil-applied pesticides. To achieve effective weed control, timing of application may need to be adjusted if elevated CO_2 decreases the length of the weed seedling stage (i.e., the time of greatest chemical susceptibility). In spite of these climate effects on weeds, the overall assumption is that chemical control of weeds will be possible, either through additional sprayings, or increased herbicide concentrations; however, this would alter the environmental and economic costs of pesticide usage. Although there are other weed control methods (e.g., biological, mechanical, cultural), climatic and CO_2 changes and the overall effects of precipitation, temperature, wind, etc. may make nonchemical control less efficacious (Patterson, 1995a).

CLIMATE IMPACTS ON INSECTS AND PATHOGENS

Agroecosystems are complex mixtures of plants (economic and weeds) and insects and diseases. There are the direct impacts of climate change on the economic crop as well as weeds (previous section), insects, and diseases. A holistic understanding of the CO_2 and climate changes to beneficial and harmful insects, microbes, and other organisms in the environment is urgently needed to develop adaptive management of agroecosystems under climate change. Documented changes in spring arrival and/or geographic range of many insect and animal species due to climate change have been observed from studies in western Europe and other regions (Montaigne, 2004; Goho, 2004; Walther, 2002). Coakley et al. (1999) reported that temperature was the single most important factor affecting insect ecology, epidemiology, generations per growing season, and insect distribution, while plant pathogens are highly responsive to humidity and rainfall, along with temperature.

Greater insecticide use in warmer, more southern regions of the United States compared to cooler higher latitude regions has been observed. Comparing the frequency of pesticide sprays for control of lepidopteran insect pests in sweet corn currently ranges from 15 to 32 applications per year in Florida (Aerts et al., 1999), to four to eight applications in Delaware (Whalen et al., 2007), and zero to five applications per year in New York (Stivers, 1999) because of the temperature effects on insect populations. Populations of insect species, such as flea beetles (*Chaetocnema pulicaria*), are currently marginally overwintering in high latitude regions. This vector for bacterial Stewart's Wilt (*Erwinia sterwartii*), an economically important corn pathogen, will increase because of the warmer winters (Wolfe et al., 2008; Harrington et al., 2001).

Leaf and root pathogens will be favored by increases in humidity and frequency of heavy rainfall events projected for many parts of the United States (Coakley et al., 1999). Conversely, short- to medium-term droughts will decrease the duration of leaf wetness and reduce some forms of pathogen attack on leaves; however, such droughts will also negatively impact crop yields from lack of available soil water.

Plant–insect interactions may be affected by increasing CO_2 concentrations and this would have implications for insect management. Higher C/N ratio of leaves observed in plants grown at high CO_2 (Wolfe, 1994) will require increased insect feeding to meet N (protein) requirements (Coviella and Trumble, 1999).

Conversely, slower insect development on high CO_2–grown plants lengthens the insect life stages vulnerable to attack by parasitoids (Coviella and Trumble, 1999). An observation from a FACE study revealed early season soybeans grown at elevated CO_2 exhibited 57% more insect damage, presumably due to increases in simple sugars in leaves (Hamilton et al., 2005).

IMPLICATIONS

Climate change, either as increasing trends in temperature, CO_2, precipitation (decreasing as well as increasing), and/or O_3, will have impacts on agricultural systems. Production of annual and perennial crops will be affected by changes in the absolute values of these climatic variables and/or increased variation. Episodic temperature changes exceeding the thresholds during the pollination stage of development could be quite damaging to crop production because of the sensitivity of crop plants to temperature extremes during this growth stage. These changes coupled with variable precipitation that places the plant under conditions of water stress would exacerbate the temperature effects. Warmer temperatures during the night, especially during the reproductive period, will reduce fruit or grain size because the rapid rate of development and increased respiration rates. A recent analysis by Ko et al. (2010), using the CERES–Wheat 4.0 module in the RZWQM2 model, evaluated the interactions of increasing CO_2 obtained from a FACE experiment along with temperature, water, and N. They found the effects of water and N were greater than CO_2 effects on biomass and yield and that temperature effects offset the CO_2 effects. These results further confirm the concept that there are counterbalancing effects from different climate variables and that development of adaptation or mitigation strategies will have to account for the combined effects of climate variables on crop growth, development, and yield. In an effort to examine potential solutions to low yields in sub-Saharan Africa, Laux et al. (2010) evaluated planting dates under climate change scenarios to evaluate the effect of increasing CO_2 and higher temperature on groundnut (peanut) and maize. They found the positive effect of CO_2 would offset the temperature response in the next 10 to 20 yr but would be overcome by higher temperatures by 2080. Changing planting dates were beneficial for the driest locations because of the more effective use of precipitation and avoidance of high temperature stresses. Both of these types of analyses will have to be conducted to evaluate potential adaptation strategies for all cropping regions.

Increases in CO_2 concentrations offer positive impacts to plant growth and increased WUE. However, these positive impacts may not fully mitigate crop losses associated with heat stress, increases in evaporative demand, and/or decreases in water availability in some regions. The episodic variation in extremes may become the larger impact on plant growth and yield. To counteract these effects will require management systems that offer the largest degree of resilience to climatic stresses as possible. This will include the development of management systems for rainfed environments that can store the maximum amount of water in the soil profile and reduce water stress on the plant during critical growth periods.

CHALLENGES TO AGRONOMISTS

Increasing food security with the challenge of increasing climate change will require that the agricultural systems be viewed from a holistic perspective to understand the implications of the interactions of changing temperature, CO_2, and precipitation on the growth and development processes. The impacts of rising temperatures on reducing grain yield in crops can produce serious consequences in terms of stability of grain production, and the impacts of the high temperatures on grain set and pollination may not be offset by beneficial growth stimulations due to the direct effects of the rising CO_2 levels. These changes coupled with the increasing variability in precipitation offer a challenge to agronomists to begin to quantify how cropping systems can be made more resilient to stress. Coupling physiological responses with genetic traits provides an opportunity to create more robust cropping systems that can cope with the changing climate. These evaluations of the interaction of genetics with the environment, especially the potential climate change scenarios, will require an understanding of how these variables interact during the growth cycle of crops. The review by Wassmann et al. (2009) provides an overview of the possible adapation strategies for rice based on response to climate change. They concluded that germplasm improvement and natural resource management have proven to reduce susceptibilty of agricultural systems to stress and the maximum benefit will be realized when crop technology options are combined with advanced climatology tools. There will be changes in the distribution of crop plants with climate change and those changes require a lengthy treatise to discuss in detail and this review has only focused on the potential impacts to the current cropping systems.

Changes in the weed, insect, and disease dynamics under the changing climate will further exaggerate the stresses on plants. The expanded range of pests and potentially more favorable conditions creates a situation in which the resilience of cropping systems will have to account for the interactions of pest populations along with physiological changes. This also calls for more coordination among regional integrated pest management (IPM) programs to monitor pest range shifts and develop an early warning system for farmers. There is no lack of potential challenges to our crop production systems presented by the changes in climate. This creates an opportunity for agronomists to form partnerships to address these challenges and create a future for humankind that ensures an adequate food supply through increased food security.

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