

CLIMATE CHANGE IMPACTS ON CROP GROWTH IN THE CENTRAL HIGH PLAINS

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ABSTRACT

Historic annual increases in global carbon dioxide (CO₂) concentration are expected to continue; increased global temperatures are forecast as well. Crop productivity can benefit from increased ambient CO₂ as similar assimilation rates can be maintained with smaller canopy conductance, resulting in modestly reduced crop water requirement. Cool-season grass crops and broadleaf crops will likely gain photosynthetic efficiencies with elevated CO₂ levels. When elevated temperatures exceed optimal conditions for assimilation, stress responses can include damage to the light-harvesting complex of leaves, impaired carbon-fixing enzymes, thereby reducing components of yield including seed potential, seed set, grain fill rate, and grain fill duration. Field studies conducted under conditions of elevated CO₂ indicate that benefits of elevated CO₂ are reduced by heat-induced stress responses. Crop cultural practices can be adapted to avoid stress, genetic advances may yield germplasm capable of tolerating or resisting stress factors.

INTRODUCTION

Climate change forecasts for the central High Plains, pertinent to crop growth, indicate increases in ambient carbon dioxide (CO₂) concentration, average annual temperatures, and intensity of hydrologic events (e.g. storms and drought) (IPCC, 2007). Field and controlled environment studies document substantial effects of these expected climate changes on factors affecting crop yield formation. Briefly, transpiration efficiency tends to increase with elevated ambient CO₂; elevated temperatures can impair yield formation by damaging photosynthetic capacity, reducing enzyme activity, impairing seed-set and grain-fill rates, increasing respiratory losses of assimilates, and reducing radiation capture due to accelerated crop development. Climate change forecasts indicate greater temperature increases in the High Plains relative to eastern regions. Though the High Plains may encounter greater impacts, qualitatively similar effects may be expected in the eastern Great Plains. Opportunities to mitigate these effects may require discovery and utilization of genetic resources to

provide tolerant/resistant cultivars as well as revised crop cultural practices. A summary of critical processes is outlined below.

EXPECTED CLIMATE CHANGE FACTORS

Increased atmospheric CO₂ concentrations recorded at Mauna Loa are a matter of historic record (Howell, 2009). Forecasts for continued increases in ambient CO₂ depend on expected rates of fossil fuel combustion. Increased global temperatures are a more recent phenomenon (Figure 1) and are associated with greenhouse gas effects. Forecasts for continued global warming depend on the rate of greenhouse gas accumulation and modeled effects on global surface-atmosphere exchange processes. This review will focus on the expected impacts of increased atmospheric CO₂ and increased temperatures on crop productivity and yield formation, considering current knowledge of plant physiology.

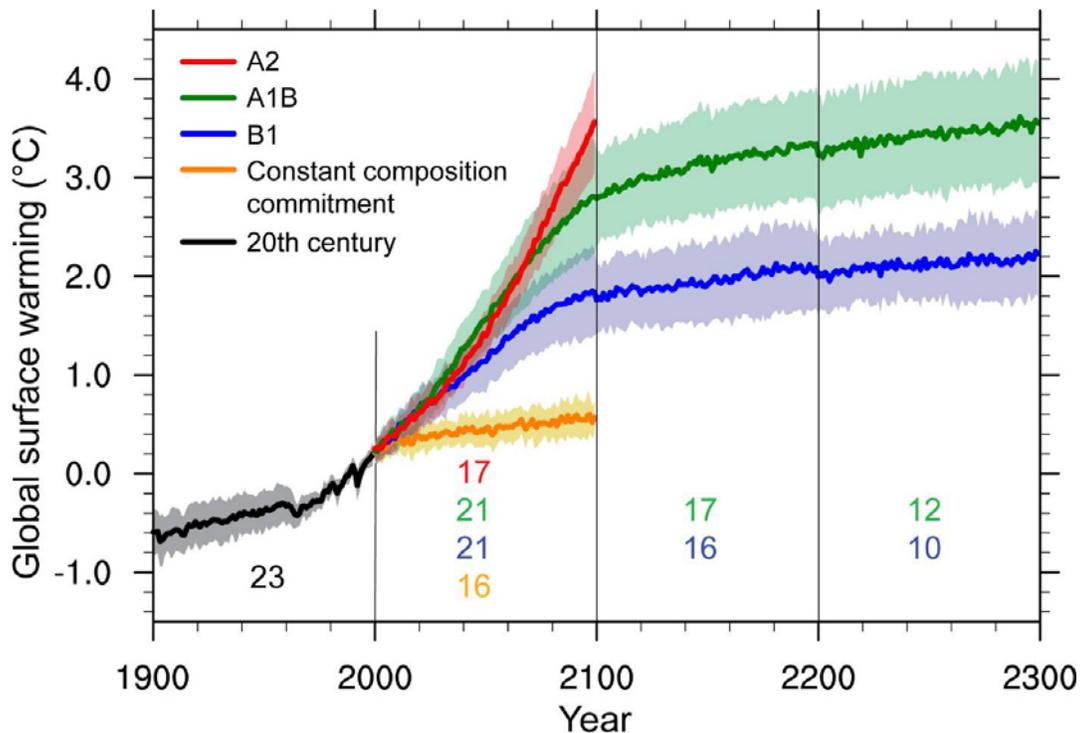


Figure 1. Global surface temperature forecast from climate change model experiments from 16 groups (11 countries) and 23 models collected at PCMDI (over 31 terabytes of model data). Committed warming averages 0.1°C per decade for the first two decades of the 21st century; across all scenarios, the average warming is 0.2°C per decade for that time period (recent observed trend 0.2°C per decade). Source: IPCC (2007) Ch. 10, Fig. 10.4, TS-32; after Feddema (2008).

CROP YIELD FORMATION

Crop yield (Y_T) can be related to water use (ET), considering the transpiration (T) component of ET, biomass productivity relative to T (TE, transpiration efficiency) and the grain fraction of biomass (HI, harvest index; Passioura 1977).

$$Y_T = TE \cdot \frac{T}{ET} \cdot ET \cdot HI \quad [1]$$

Each component of this relationship can be altered by genetic, environmental and/or crop management effects. Tanner and Sinclair (1983) provided evidence that transpiration efficiency approaches a constant value, k_d , when adjusted for daily vapor pressure deficit (VPD) effects. This intrinsic transpiration efficiency is greater for crops, such as corn, which utilize C4 physiology (CO₂ fixation results in oxaloacetic acid, a four-carbon compound, $k_d = 0.118$ mbar), relative to that of crops, such as soybean, with C3 physiology (CO₂ fixation results in phosphoglyceric acid, a three-carbon compound, $k_d = 0.041$ mbar).

An analogous relationship (Earl and Davis, 2003) can be developed between yield (Y_R) and biomass productivity relative to photosynthetic electron supply (RUE, radiation use efficiency), considering the fraction of absorbed radiation used to drive assimilatory processes (Φ_{PSII} , quantum yield of photosystem II), intercepted photosynthetically active radiation (IPAR), photosynthetically active radiation (PAR) and HI.

$$Y_R = RUE \cdot \Phi_{PSII} \cdot \frac{IPAR}{PAR} \cdot PAR \cdot HI \quad [2]$$

Krall and Edwards (1991) demonstrated a direct linear relationship between gross photosynthesis and absorbed photosynthetically active radiation, when corrected for quantum yield of photosystem II. Kiniry et al. (1998) reported a linear relationship between RUE and VPD, analogous to that observed for TE. Equations [1] and [2] indicate that crop yield can be related to either the transpiration component of water use or the interception component of solar radiation, considering conversion efficiencies to biomass and yield formation factors. Rochette et al. (1996) demonstrated a linear relationship between the ET and net photosynthesis flux for well-watered corn after canopy closure when ET was adjusted for VPD effects. This supports interpretation of equations [1] and [2] as analogous. Together, these equations provide a framework for evaluating expected climate change effects on crop productivity and grain yield.

CROP RESPONSES TO EXPECTED CLIMATE CHANGE FACTORS

Ambient CO₂

Crop productivity, with respect to water use, is expected to increase as ambient CO₂ increases. Elevated CO₂ increased productivity of plants with C3 physiology—with increased yield as well (Tubiello et al., 2007). As an example, Figure 2 shows effects of ambient CO₂ concentration (320, approximate 1965 condition and 390 ppm, approximate current condition, volume basis) on water vapor efflux and CO₂ influx across a leaf stoma. Calculations of leaf conductance assume identical assimilation rates (50 μmol m⁻² s⁻¹) and a constant ratio of CO₂ within the sub-stomatal cavity (C_i) to ambient (C_a): 0.5. In this example, stomatal conductance would be 16% smaller under current conditions of elevated ambient CO₂, relative to that around 1965. Associated with less stomatal conductance is reduced transpiration and a warmer canopy temperature. These results are expected for plants with both C3 and C4 physiology, though a greater relative increase in CO₂ fixation is expected for plants with C3 physiology due to inefficiencies associated with the carboxylating enzyme, Rubisco.

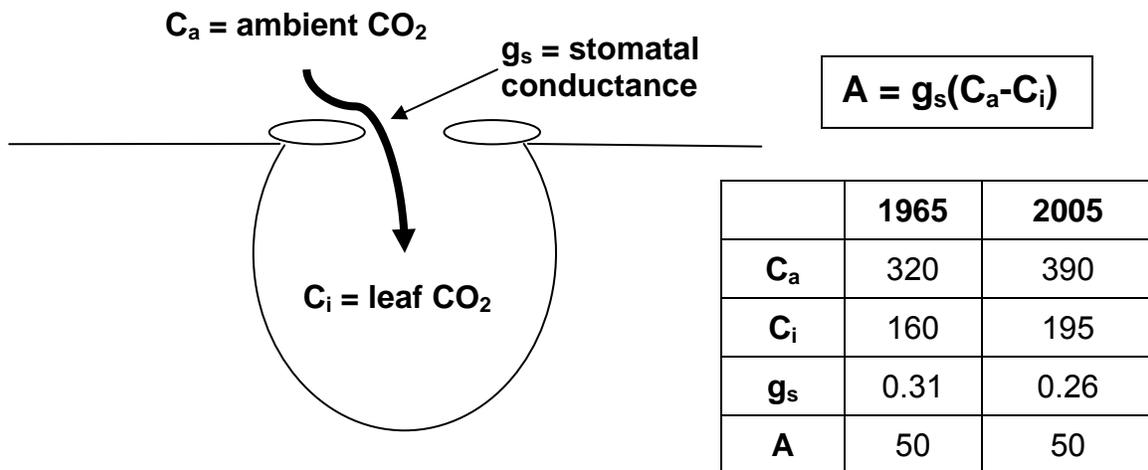


Figure 2. Schematic depicts CO₂ diffusion through stomatal aperture of a leaf, into the sub-stomatal cavity. Carbon fixation (**A**, assimilation) can be calculated as the product of stomatal conductance (**g_s**) and the gradient between ambient (**C_a**) and sub-stomatal (**C_i**) CO₂ concentrations. In this hypothetical example, the increase in atmospheric CO₂ concentrations, from 1965 to 2005, results in identical assimilation rates, with a smaller **g_s**. Smaller **g_s** tends to reduce evaporative loss of water, though canopy temperatures tend to increase.

The photosynthetic efficacy of Rubisco, e.g. in fixing CO₂ into six-carbon sugars, is limited by the relative concentrations of CO₂ and O₂ at the reaction site (Ainsworth and Rogers, 2007). Typically, plants with C4 physiology sequester Rubisco in bundle sheath cells, where O₂ concentrations are small, hence the

superior productivity of plants with C4 physiology. Rubisco occurs in mesophyll cells of C3 plants, exposed to near-ambient O₂ concentrations, resulting in approximately one third of enzyme activity diverted from CO₂ fixation. Because of this difference, the increased assimilation response of plants with C3 physiology, to increased CO₂ concentration can generally be attributed to increased Rubisco efficacy in mesophyll cells, though plant acclimation to elevated CO₂ can introduce further complexities.

The relative impacts of elevated CO₂ on photosynthesis, growth and yield formation of plants with C3 and C4 physiology is somewhat controversial. Long et al. (2006) reported that Free-Air CO₂ Enrichment (FACE) technologies indicate ~ 50% less yield benefits from elevated CO₂ than earlier studies of crop responses to elevated CO₂, based on enclosure techniques. The FACE studies indicate plants with C4 physiology have little increase in assimilation with CO₂ enrichment (Rubisco tends to be CO₂-saturated at current ambient CO₂ levels) but stomatal conductance is reduced for these plants, thereby reducing water consumption. Wall et al. (2001) reported, for well-watered sorghum, that under FACE, stomatal conductance decreased 37% and assimilation increased 9%, and leaf water potential increased (reduced leaf water deficit) by 3%; however, no change in final shoot biomass was detected. Long et al. (2006) found increased productivity for plants with C3 physiology with CO₂ enrichment, but the yield increase was less than that projected from earlier enclosure studies. These studies show that, though assimilation capacity increased by 36%, the increase in canopy assimilation was 20%; biomass increase was 17% and yield increase was 13%. The limited yield response, relative to increased productivity potential, could result from plant acclimation to elevated CO₂ conditions. The FACE studies indicate that opportunities to realize the potential benefits of elevated CO₂ for C3 crops will require further development.

Table 1. Percentage increases in yield, biomass, and photosynthesis of crops grown at elevated CO₂ (550 ppm, volume basis) relative to ambient CO₂ in enclosure studies summarized by Cure and Acock (1986). Percentage increases for FACE studies were generated by meta-analysis of Long et al. (2006). Taken from Long et al. (2006).

Source	Wheat	Soybean	C4 Crops
	Yield		
Cure and Acock (1986)	19	22	27
FACE studies	13	14	0*
	Biomass		
Cure and Acock (1986)	24	30	8
FACE studies	10	25	0*
	Photosynthesis		
Cure and Acock (1986)	21	32	4
FACE studies	13	19	6

*Data from only one year in Leakey et al. (2006).

Evidence is emerging that plants adjust, or acclimate to elevated CO₂ conditions. Watling et al. (2000) reported changes in the carbon-fixing potential for sorghum grown at elevated CO₂, relative to the current condition. These changes included increased leakage of CO₂ from bundle sheath cells to mesophyll, requiring further metabolic processing, decreased activity of PEP carboxylase (the initial C₄ CO₂-fixing enzyme), resulting in reduced carboxylation efficiency and assimilation potential. Comparative analysis of gene expression in soybean (Ainsworth et al., 2006) under current and elevated CO₂ indicated that respiratory breakdown of starch, promoting cell expansion and leaf growth, was accelerated with elevated CO₂. Controlled environment and FACE studies confirm that increased ambient CO₂ can increase biomass productivity for C₃ crops, reduced crop water use, and elevated canopy temperatures for C₃ and C₄ crops. Realizing potential benefits of elevated CO₂ conditions will require discovery and utilization of adaptive traits as well as adaptive crop management.

Increased atmospheric CO₂ can alter crop-pest interactions. Zavala et al. (2008) found that soybean could be more susceptible to coleopteran herbivores (e.g. invasive Japanese beetle and variant of western corn rootworm) under elevated CO₂ due to down-regulation of genes coding for production of cysteine proteinase inhibitors; these inhibitors are deterrents to coleopteran herbivores. Other unexpected consequences could involve enhanced growth of plant pests, with C₃ physiology, and reduced herbicide efficacy—further aggravating climate change impacts.

Temperature

Heat stress on crops can impair assimilation by damaging light-harvesting apparatus and by reducing carbon-fixing enzyme capacity. Yield formation processes, including seed set and grain fill rate, can be impaired at elevated temperatures. The duration of growing season—and subsequent radiation capture—can be reduced by increased temperatures, as indicated by the growing degree day concept. Muchow et al. (1990) found greatest grain yield potential of corn occurred in a cool, temperate environment, due to increased growth duration and increased radiation capture; under warmer sub-tropical conditions growth duration, light absorption, and grain yields were reduced. Factors affecting intensity of heat stress and crop responses to heat stress are briefly discussed.

Canopy temperatures are generally linked to ambient temperatures, but can increase with radiative loading and decrease with evaporative cooling. Canopy productivity can be damaged when temperatures exceed critical levels. Optimum temperatures for photosynthesis (light harvesting) and carbon-fixing enzymes are approximately 30 to 38 °C (86 – 100 °F) for corn (Oberhuber et al., 1993; Crafts-Brandner and Salvucci, 2002); 25 to 30 °C (77 – 86 °F) for winter wheat (Yamasaki et al., 2002) and 32 °C (90 °F) for soybean (Vu et al., 1997). Net

photosynthesis in corn was inhibited at leaf temperatures exceeding 38 °C (100 °F), though severity of inhibition decreased with acclimation (plant adjustment to greater temperature, Crafts-Brandner and Salvucci, 2002; Krall and Edwards, 1991).

The temperature acclimation process is thought to involve a protein known as Rubisco activase, which maintains the Rubisco enzyme in an active state when under heat stress. Rubisco activation in corn decreased for leaf temperatures greater than 32.5 °C (90 °F), with near-complete inactivation at 45 °C (113 °F, Crafts-Brandner and Salvucci, 2002). Acclimation of photosynthesis to temperature for winter wheat, in the range of 15 to 35 °C (59 – 95 °F), involved the light-harvesting apparatus (Yamasaki et al., 2002). Thermotolerance of C3 crops was increased by growth under elevated CO₂ conditions, but decreased for C4 crops (Wang et al., 2008). Ristic et al. (2008) reported a rapid, low-cost technique to detect heat tolerance of light-harvesting apparatus, indicated by chlorophyll content, in wheat, corn, and possibly other crops. Elevated temperatures can impair light-harvesting apparatus and inactivate critical carbon-fixing enzymes, thereby reducing assimilation rates and ultimate yield potential. The specific mechanisms affected by heat stress remain a subject of active investigation (Sage et al., 2008).

Seed number and seed weight are commonly critical components of grain yield formation. Heat stress can impair both aspects of yield potential. Potential seed number, commonly determined during ear, panicle, head, or pod formation, is influenced by assimilate supply at the end of juvenile development, which can be reduced by heat stress. Pollen viability and the pollination process can be impaired by heat stress, reducing seed set and yield potential (Lillemo et al., 2005; Schoper et al., 1986; Keigley and Mullen, 1986; Grote et al., 1994). Grain fill rate can be related to canopy productivity—particularly productivity of leaves in the upper canopy—during this developmental stage (Borras and Otegui, 2001). Thus effects of heat stress on radiation capture and carbon fixation (see above) may reduce the grain-fill/seed weight component of yield potential. Direct effects of heat stress on pollen viability, pollination and seed set can reduce seed number; indirect effects of heat stress on canopy productivity can reduce seed weight during grain fill. Muchow and Sinclair (1991) simulated effects of increased temperatures on corn yield; they reported a 10% yield decrease with 4 °C (7 °F) average temperature increase, despite an assumed 33% increase in normalized transpiration efficiency. These effects are expected for plants with either C3 or C4 physiology.

Adaptive traits to increase transpiration efficiency could aggravate heat stress effects. Increasing canopy resistance under conditions of large evaporative demand can increase transpiration efficiency. Hall and Hoffman (1976) reported decreased leaf conductance of sunflower and pinto bean with increased VPD, independent of leaf water potential. Teare et al. (1973) compared canopy behavior of sorghum and soybean following a stress period. Canopy resistance

of sorghum canopy was nearly three times that of soybean; relative air temperature above the sorghum canopy was 3 °C greater than that above soybean, despite a larger root system and more water in the soil profile for the sorghum crop. Sloane et al. (1990) reported a slow-wilting soybean cultivar; this cultivar was later found to reduce water use, under conditions of large evaporative demand, by limiting maximum transpiration rates (Sinclair et al., 2008). Controlled environment studies demonstrated that leaf xylem conductivity limited water supply to evaporative surfaces, reducing transpiration rates when VPD exceeded 1.9 kPa. A simulation study (Sinclair et al., 2005) indicated that, under favorable conditions, grain sorghum yields were reduced for cultivars with the canopy trait of limited maximum transpiration but yields increased by 9-13% when yield potential was less than 450 kg ha⁻¹ (72 bu a⁻¹). The limited transpiration trait is expected to improve yield potential under water deficit conditions. However, this trait could increase likelihood of heat stress, as elevated VPD tends to correspond with radiative loading—particularly for irrigated crops in semi-arid regions.

Other consequences of elevated temperatures in crop production systems can include greater respiratory losses of photosynthate and shifts in crop-pest interactions. Warm night temperatures can result in increased loss of assimilates due to greater respiration rates, which can increase with temperature. Tropically adapted sorghum lines maintain productivity by restricting respiratory losses, while temperate-adapted sorghum lines fail to accumulate significant biomass under conditions of warm nights, due to accelerated respiratory losses (Kofoid, pers. comm.). Other production factors which could be affected by warmer global temperatures include increased survival of insect and disease pests (due to warmer winter conditions), increased productivity of weeds, and corresponding reduced efficacy of pesticides.

YIELD FORMATION FACTORS AFFECTED BY EXPECTED CLIMATE CHANGE

Productivity for crops with C3 physiology is expected to benefit from increased atmospheric CO₂; the corresponding yield formation factors would be TE for [1] and Φ_{PSII} for [2]. Secondary effects would include accelerated canopy formation, increasing the transpiration fraction of ET [1] and the intercepted fraction of PAR [2]. Though HI may have reached an upper limit by extensive breeding, for some crops, HI might be expected to increase, for other crops, to the extent that potential seed number, seed-set, and grain fill rate can be increased.

In contrast, warmer ambient temperatures and stress-augmented increases in canopy temperatures would likely reduce crop productivity and components of yield for crops with C3 or C4 physiology. Increased VPD would effectively reduce the TE factor of [1] while reduced efficacy of light-harvesting apparatus and carbon-fixation could combine to reduce the Φ_{PSII} factor of [2]. Reduced canopy formation would tend to decrease the transpiration fraction of ET [1] and the

interception fraction of PAR [2]; similarly, decreased harvest index could result from reduced potential seed number, seed-set, and grain fill rate.

Benefits of increased CO₂ could readily be offset by increased heat stress. Field studies comparing crop growth at ambient and elevated CO₂ levels indicate gains from elevated CO₂ levels were less than anticipated; the reduced level of benefits were attributed to stress responses to factors including elevated canopy temperature. Realizing full benefits of increased atmospheric CO₂ would require avoidance or tolerance of stress associated with rising global temperatures. Hubbert et al. (2007) found that photosynthesis in rice can be affected by breeding strategy; photosynthetic capacity and stability under heat stress could be a useful target when yield is limited by biomass accumulation rather than harvest index.

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