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Implications of Atmospheric and Climatic Change for Crop Yield and Water Use Efficiency

H. Wayne Polley*

ABSTRACT

Yield of water-limited crops is determined by crop water use and by plant water use efficiency, each of which will be affected by the anticipated rise in atmospheric carbon dioxide (CO_2) concentration and concomitant increase in temperature. At the leaf level, a given proportional increase in CO_2 concentration generally elicits a similar relative increase in transpiration efficiency (ratio of net photosynthesis to transpiration). The increase in transpiration efficiency may result both from an increase in photosynthetic rate and a decrease in stomatal conductance. Feedbacks involved in scaling from leaf to crop constrain the increase in net carbon gain and reduce the anti-transpiration effect of CO_2 enrichment. As a result, the increase in crop water use efficiency at high CO_2 typically is less than 75% of that measured at the leaf level. By accelerating crop development and reducing harvest index, higher temperatures often erode yield benefits of improved water use efficiency at high CO_2. The fraction of available water that is used by crops could increase with CO_2 concentration because of greater root growth and faster canopy closure, but these effects have received scant study. Field experiments indicate that CO_2 enrichment will increase crop water use efficiency mainly by increasing photosynthesis and growth. Yield should be most responsive to CO_2 when temperatures approximate the optimum for crop growth. Elevating CO_2 can ameliorate negative effects of above-optimal temperatures, but temperatures near the upper limit for crops will depress yields irrespective of CO_2 concentration.

CROP LOSSES TO WATER SHORTAGE may exceed those from all other causes combined (Kramer, 1980). If agriculture is to feed the world's burgeoning population, yields of water-limited crops must be improved substantially. Efforts to accomplish this have concentrated on increasing the fraction of available water that crops transpire and increasing plant water use efficiency (biomass produced per unit of transpiration). These and other components of crop water economy will be affected by anticipated global changes, changes that include correlated increases in both atmospheric carbon dioxide (CO_2) concentration and mean temperature.

Atmospheric CO_2 concentration has risen by about 37% during the last two centuries to the present level near 370 μmol mol^{-1} (Keeling and Whorf, 2000). The CO_2 concentration is projected to double again during the next century (Alcamo et al., 1996), and to contribute to a warmer climate. Also increasing are atmospheric concentrations of other trace gases (CH_4, N_2O, NO_x, CO) that could intensify global warming. The increase in CO_2 concentration alone is expected to warm Earth by 2 to 4.5°C by the middle of next century, with associated changes in precipitation (Giorgi et al., 1998). Warming is predicted to be greatest at high northern latitudes during autumn and winter.

That atmospheric CO_2 concentration is increasing is undeniable. Projections of future climate are more uncertain. Inclusion of aerosols in climatic models, for example, reduces anticipated changes in temperature and precipitation, and can yield regional estimates that differ from those obtained by simulating effects of CO_2 enrichment alone (Giorgi et al., 1998).

Global changes pose significant challenges to agriculture, but also provide opportunities to boost crop yields in water-limited environments. Here, I summarize some of the challenges and opportunities of a warmer and CO_2-rich world for crop water economy and production. Yield of water-limited crops is determined by water

USDA-ARS, Grassland, Soil and Water Research Laboratory, 808 E. Blackland Road, Temple, TX 76502; All programs and services of the U.S. Department of Agriculture are offered on a nondiscriminatory basis without regard to race, color, national origin, religion, sex, age, marital status, or handicap. Presented at the 1999 CSSA Symposium on Water Use Efficiency, organized by Div. C-2 chair, Dr. Tom Gerik. Received 19 Sept. 2000. *Corresponding author (polley@brc.tamus.edu).

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capture, water use efficiency, and harvest index. Effects of anticipated changes on each of these components of crop water economy will be reviewed, but emphasis will be given global change effects on crop water use efficiency as these have been researched most extensively.

Leaf Transpiration Efficiency

At the leaf level, instantaneous water use efficiency or transpiration efficiency (TE) may be defined as the ratio of the rate of net photosynthesis or assimilation rate (A) to transpiration (E), and approximated by

$$TE = \frac{A}{E} = \frac{1}{\Delta w} \times \frac{A}{g} = \frac{1}{\Delta w} \times \frac{(c_a - c_i)g_c}{1.6g_c} = \frac{1}{\Delta w} \times \frac{c_a\left(1 - \frac{c_i}{c_a}\right)}{1.6} \quad [1]$$

where c_a and c_i are external or ambient and leaf intercellular CO_2 concentrations, respectively, 1.6 is the ratio of diffusivities of water vapor and CO_2 in air, Δw is the mole fraction water vapor gradient from leaves to bulk air [leaf-to-air vapor pressure difference (vpd) divided by atmospheric pressure], and g and g_c are stomatal conductances to water vapor and CO_2, respectively. It is evident from Eq. [1] that TE is positively correlated with A and negatively correlated with both g and Δw. An increase in CO_2 concentration typically increases TE by stimulating A, by decreasing g, or by some combination of changes in both A and g.

Leaf A typically exhibits a curvilinear increase with CO_2 enrichment that continues to higher CO_2 concentrations in C_3 than in C_4 species (Pearcy and Ehleringer, 1984). The C_4 metabolism concentrates CO_2 at sites of fixation by the carboxylating enzyme, ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco), rendering C_4 photosynthesis relatively insensitive to increases in CO_2 above the current concentration. Higher temperature, by contrast, reduces net photosynthesis in C_3 plants by increasing the portion of fixed carbon that is lost in the process of photorespiration. By reducing photorespiration in C_3 plants, CO_2 enrichment increases A, the temperature optimum for CO_2 uptake, and the maximum temperature at which positive assimilation can occur (Long, 1991). Indeed, C_3 photosynthesis often responds relatively more to CO_2 when temperatures are high because the relative inhibitory effect of CO_2 on photorespiration rises as temperature and potential photorespiration increase. This is not always the case, however. Effects of temperature on photosynthetic response to CO_2 vary among species (Bunce, 1998). Exposure to low temperatures can improve photosynthetic response to CO_2, possibly by changing kinetic properties of Rubisco (Bunce, 1998).

Most herbaceous species studied respond to CO_2 enrichment by partially closing stomata (Morison, 1987; Field et al., 1995; Polley et al., 1997). In the absence of changes in Δw, partial stomatal closure slows transpiration and increases TE (Eq. 1). The magnitude of stomatal closure is correlated with stomatal opening at the current CO_2 concentration. Morison (1985) showed that g declined more per unit increase in CO_2 when g was high than low. Stomatal sensitivity to CO_2 was linearly related to g in both C_3 and C_4 species.

Variation in g is also linearly correlated with A, with the result that c_i/c_a remains relatively constant (is conservative) across CO_2 concentrations (Morison, 1993). Maintenance of a near-constant c_i/c_a implies that TE will increase linearly with c_a, Eq. [1]. Indeed if Δw (or vpd) remains constant, TE will increase by the same relative amount as does c_a in both C_3 and C_4 species (Fig. 1). Significantly, these trends have also been observed over lower-than-present CO_2 concentrations (Polley et al., 1993a), indicating that CO_2 enrichment may already have increased TE by about 37% since industrialization (Polley et al., 1993b). It also is worth noting that although CO_2 enrichment does not affect the *relative* advantage of C_4 over C_3 species in TE, the *absolute* difference in TE between C_4 and C_3 plants increases with CO_2 concentration if c_i/c_a and Δw (vpd) do not change (Fig. 1). Whether this potential advantage in TE of C_4 over C_3 species will be realized in the field is not clear. Much of the increase in C_4 TE at high CO_2 derives from reduced g, particularly when plants are well watered (Polley et al., 1996; Samarakoon and Gifford, 1996). Because g already is low in most C_4 species, the magnitude of any decline in g at high CO_2 will be small.

Higher temperatures usually are associated with higher vpd, so it often is difficult to ascertain direct effects of temperature on g (Morison, 1987). When vpd increases, however, stomata usually close partially and c_i declines (Bunce, 1993). Both the absolute and relative decline in g at elevated CO_2 may be smaller when vpd is high than when it is low (Bunce, 1993), although other patterns of stomatal response have been measured (Morison and Gifford, 1983).

Higher temperatures directly increase transpiration rates by increasing the leaf-to-air vapor pressure gradient (Δw) via two mechanisms (Nobel, 1974). 1. Air temperature influences evaporative demand of the atmosphere. The saturation vapor pressure of air increases as temperature rises. In the absence of changes in water vapor density, vapor pressure deficit of air and Δw will increase. 2. Air temperature affects leaf energy balance. Conduction of heat across the leaf boundary layer depends on the difference in temperature between the leaf and air. As air temperature rises, leaf temperature and vapor pressure inside the leaf also increase causing an increase in Δw and transpiration.

Crop Yield

CO_2 Concentration

Much is known of the response of A and g to CO_2 concentration and temperature. Greatest uncertainties arise in scaling these primary effects of global changes to crop yield and transpiration.

Effects of global changes on crop carbon (C) gain typically decline as spatial and temporal scales are expanded beyond short-term measurements of potential A at the leaf level. Several processes are involved. One

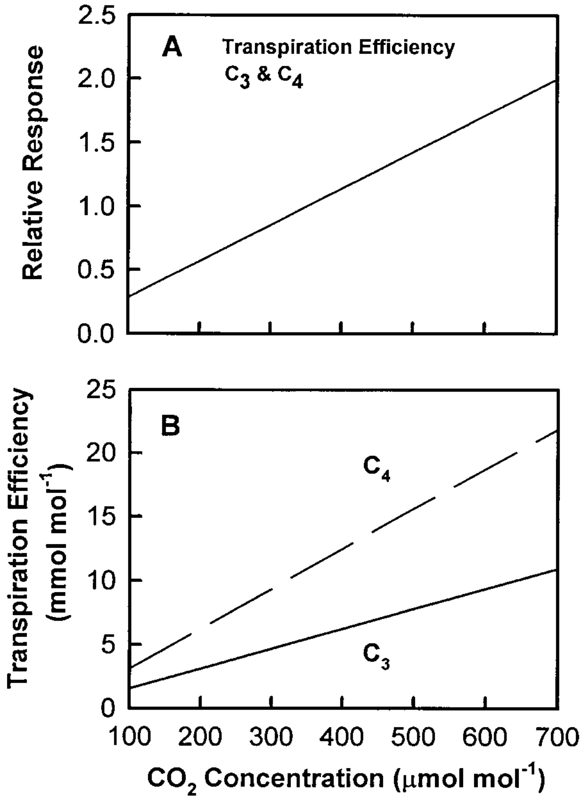

Fig. 1. Responses of transpiration efficiency (TE) to CO_2 concentration in C_3 and C_4 plants: (A) relative increases in TE with increasing CO_2 concentration (normalized to 350 µmol mol^{-1} CO_2), and (B) possible absolute responses of TE to CO_2. Transpiration efficiency was calculated assuming a ratio of intercellular to atmospheric CO_2 concentration of 0.7 for C_3 plants and 0.4 for C_4 species and a mole fraction water vapor gradient from the leaf to bulk air of 12×10^{-3} mole $mole^{-1}$ across CO_2 concentrations.

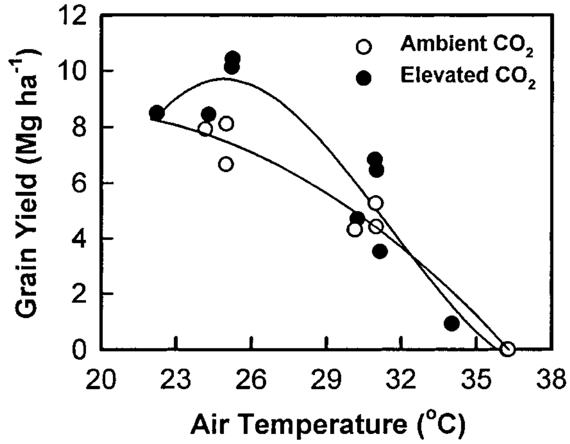

Fig. 2. Grain yield of rice grown to maturity at ambient (330 µmol mol^{-1}) and elevated CO_2 concentrations (660 µmol mol^{-1}) and different mean temperatures. Data are from five experiments. Lines are regression fits describing relationships between grain yield and mean temperature at the two CO_2 concentrations. The figure was adapted from Baker and Allen (1993).

of these may be loss of photosynthetic capacity following prolonged exposure to elevated CO_2 (Sage, 1994). Downward regulation of photosynthesis usually is linked to a decrease in photosynthetic enzymes, feedback inhibition of photosynthesis following accumulation of carbohydrates in leaves because of insufficient sink demand, or reallocation of N away from the photosynthetic apparatus to meet other demands within the plant (Bowes, 1991). While common in studies that employ a restricted rooting volume or nutrient deficiency, evidence for downward adjustment of photosynthetic capacity is more limited in field studies (Sage, 1994). Photosynthetic capacity of rice (*Oryza sativa* L.) canopies declined with increasing growth CO_2 concentration (Baker et al., 1990c), but CO_2 had no effect on photosynthetic potential of field-grown soybean (*Glycine max* (L.) Merr.; Campbell et al., 1990), wheat (*Triticum aestivum* L.; Kimball et al., 1995), or rice in another study (Baker et al., 1997b). Available evidence indicates that changes in temperature of the magnitude predicted during the next century usually have little influence on the extent to which photosynthetic capacity adjusts to CO_2 (Bunce, 1992; Stirling et al., 1997). A slight increase in temperature could contribute to downward regulation, however, if photosynthetic response to CO_2 is more sensitive than is growth to the rise in temperature (Dijkstra et al., 1999) or if the rise in temperature reduces growth of a carbon sink, like seeds (Lin et al., 1997). In both situations, limitations on plant capacity to utilize photosynthate can lead to loss of photosynthetic capacity.

Even in the absence of photosynthetic acclimation, yield will not necessarily increase as much as expected from the response of A of sunlit leaves to CO_2. Processes at the crop level place additional constraints on both C gain and retention. Shading of lower leaves following canopy closure, respiration by non-photosynthetic tissues during daylight and by all tissues at night, and feedback control of photosynthesis by C sinks all may reduce crop response to CO_2. It has been speculated that higher temperatures will reduce net C gain by increasing respiration more than photosynthesis. This prediction has not been supported by temperature experiments, however (Gifford, 1995; Ziska and Bunce, 1998). Indeed, CO_2 enrichment may have just the opposite effect, and reduce leaf or whole-plant respiration rates and the ratio of dark respiration to net photosynthesis (Polley et al., 1993b; Wullschleger et al., 1994; Ziska and Bunce, 1998).

Temperature

Temperature effects on yield are complex. Crop responses to a change in temperature depend on the temperature optima of photosynthesis, growth, and yield, all of which may differ (Conroy et al., 1994). When temperature is below the optimum for photosynthesis, a small increase in temperature can greatly stimulate crop growth. The converse is true when temperature is near the maximum for yield. A small increase in temperature can dramatically reduce yield (Fig. 2; Baker and Allen, 1993). Crop responses to expected increases in temperature also depend on interactions with CO_2 enrichment. High temperatures reduce net C gain in C_3 species by increasing photorespiration. By reducing photorespiration, CO_2 enrichment is expected to increase pho-

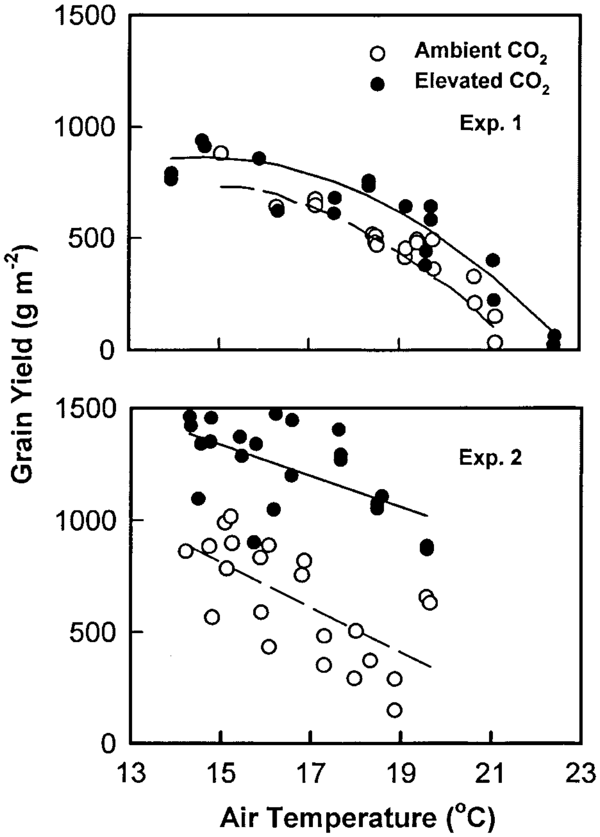

Fig. 3. Relationship between grain yield of wheat and mean temperature from anthesis to maturity from two experiments (Exp. 1, 2) in which plants were grown at ambient (380–390 μmol mol^{-1}) and elevated CO_2 concentrations (684–713 μmol mol^{-1}). The figure was redrawn from Wheeler et al. (1996).

tosynthesis more at high than low temperature (Long, 1991), and thereby at least partially to offset negative effects of above-optimal temperatures on yield.

The expectation that stimulatory effects of CO_2 enrichment on plant biomass or economic yield increase at higher temperature has been supported in some studies (Imai and Murata, 1979; Idso et al., 1987; Sionit et al., 1987; Baker et al., 1989; Idso and Kimball, 1989; Rawson, 1995; Van Oijen et al., 1999), but not in others (Rawson, 1992; Baker and Allen, 1993; Wheeler et al., 1994; Ziska and Bunce, 1994; Ziska et al., 1996, 1997). Wheeler et al. (1996) observed the former trend in wheat (Fig. 3). Temperature had little influence on the *absolute* response of grain yield to CO_2, but higher temperature increased the *relative* enhancement in yield at high CO_2. Increasing temperature increased the stimulatory effect of high CO_2 on aboveground biomass of soybean (Baker et al., 1989), but temperature did not affect responsiveness of rice to CO_2 (Baker and Allen, 1993). Possible causes for varied responses to CO_2 and temperature are several. 1. Responses to temperature depend on stage of crop development as well as on nutrition, light, and other aspects of the environment (Rawson, 1992; Dijkstra et al., 1999). 2. The temperature response of crop growth and yield must be considered to predict CO_2 effects (Fig. 2). A small increase in temperature at low temperatures will affect crop response to CO_2 less than will a similar increase near the plant's temperature optimum (Rawson, 1995). 3. Temperature effects on CO_2 response depend on the component of total biomass measured. Increasing temperature from 26/19 to 31/24°C (day/night) increased the stimulatory effect of CO_2 enrichment on aboveground biomass of soybean, but did not affect the response of economic yield to CO_2 (Baker et al., 1989). The opposite pattern was observed in cauliflower (*Brassica oleracea* L. *botrytis*). The CO_2 effect on total biomass was independent of temperature, but there was a positive interaction between temperature and CO_2 for yield (Wheeler et al., 1995). Partial explanation for these patterns may lie in the importance of temperature during formation of the harvestable organ. A change in mean temperature or the occurrence of temperature extremes during growth of harvestable tissue could confound attempts at simple correlations between yield and mean temperature over the crop cycle (Wheeler et al., 1996). 4. Higher temperatures may accelerate crop development and reduce the time during which C is gained (Rawson, 1992; Ziska et al., 1997). Elevating CO_2 would be expected to reduce negative effects of faster development on yield by increasing photosynthetic rates, but this does not always occur. In some crops, CO_2 enrichment exacerbates the decline in crop duration (Baker et al., 1989, 1990b; Kimball et al., 1995). Faster development at elevated CO_2 often is associated with a slight increase in leaf temperature (Kimball et al., 1995) that results because partial stomatal closure reduces evaporative cooling. Rawson (1992) noted, however, that increases in leaf temperature are too small to explain the acceleration in development observed. He speculated that faster development at high CO_2 is explained by an increase in supply of carbohydrates. No explanation apparently has been advanced to explain the slowing of development observed at elevated CO_2 in maize (*Zea mays* L.; Hesketh and Hellmers, 1973) and sorghum [*Sorghum bicolor* (L.) Moench; Chaudhuri et al., 1986].

Transpiration

Transpiration of crops, like growth, will not respond as much to CO_2 enrichment as predicted from leaf level measurements. At the leaf level and in chambers with well mixed air, transpiration is nearly linearly correlated with g. In scaling to the canopy level, several feedbacks reduce stomatal effects on transpiration. One of these feedbacks involves aerodynamics conductances to water vapor. Stomatal conductance is but one in a series of conductances, including leaf and canopy boundary layer conductances, that regulate transpiration. Stomatal control of transpiration depends partly on the ratio of canopy conductance (conductances integrated across leaves) to conductance of the canopy boundary layer (aerodynamic conductance within and immediately above the vegetative canopy). When canopy conductances are high and this ratio is large, as for well-water crops with high rates of g, transpiration is relatively insensitive to changes in stomatal aperture (McNaughton and Jarvis, 1991). A second feedback involves stomatal effects on leaf temperature. Partial stomatal closure reduces transpiration rate and latent heat flux, leading to a rise in leaf temperature (Idso et al., 1993; Kimball et al., 1995) and a consequent increase in vpd between air and the plant canopy. This results is an increase in the driving gradient for water loss, which tends to offset effects of stomatal closure on transpiration. Higher canopy temperatures and reduced transpiration contribute to a third feedback on stomatal control of transpiration. The vapor pressure deficit of air within and immediately above vegetation depends partially on transpiration. Slower transpiration tends to dry air in the canopy boundary layer and to increase the vapor pressure gradient for transpiration. Bunce et al. (1997) parameterized a soil-vegetation-atmosphere simulation model with field measurements on alfalfa (*Medicago sativa* L.) and orchardgrass (*Dactylis glomerata* L.) crops grown at ambient and twice ambient CO_2 concentrations to study these feedbacks. Simulations indicated that aerodynamic conductances to water vapor were smaller than canopy conductances, and that leaf temperature and leaf to air vpd were higher at elevated than at ambient CO_2. Together, these feedbacks almost completely offset effects of 20 to 60% reductions in canopy conductance on water loss. Field et al. (1995) and Monteith (1995) discuss other processes operative at regional scales, including interactions between plants and the mixed layer of air above vegetation (the convective boundary layer), that may further suppress stomatal control of transpiration.

No CO_2 experiment fully accommodates these regional controls on transpiration, but available field measurements of crop transpiration indicate a pattern of little CO_2 effect on total water use (Jones et al., 1984; Chaudhuri et al., 1986; Kimball et al., 1994, 1995; Baker et al., 1997a). Total transpiration is the product of leaf area and water loss per unit of leaf area. The relevant question in assessing the contribution of lower transpiration to CO_2 effects on water use efficiency is whether CO_2 enrichment reduces transpiration per unit of leaf area. Unfortunately, this question is more difficult to address than may be expected. There are several reasons. 1. Elevating CO_2 often increases leaf area. Without information on the time course of canopy development, it is impossible to determine whether changes in leaf transpiration rates affect water use efficiency (Jones et al., 1984; Kimball et al., 1994). 2. Temporal changes in soil water content can further complicate interpretation. As soil water varies, the contribution of leaf level processes to changes in water use efficiency may also vary (Samarakoon and Gifford, 1995). 3. Water losses to transpiration and evaporation are rarely separated, so calculations of plant water loss usually contain uncertainty. Studies in which canopy gas exchange rates were expressed on a leaf area basis or in which CO_2 did not affect leaf area provide our best clues as to whether CO_2 enrichment will improve crop water use efficiency significantly by reducing transpiration rates. The few field studies of this type indicate that slower transpiration plays a secondary role to increased photosynthesis and growth in improving in crop water use efficiency at high CO_2 (e.g., Baker and Allen, 1993; Kimball et al., 1995; Baker et al., 1997b).

Crop Water Use Efficiency

For a number of reasons, therefore, CO_2 enrichment does not increase water use efficiency of field grown crops as much as inferred from leaf gas exchange studies or measurements on individually grown plants. No field study fully accommodates feedbacks that could lessen stomatal control of transpiration and reduce water savings and water use efficiency at high CO_2. Water loss in most studies also includes evaporation, over which plants exert only indirect control. Nevertheless, field experiments indicate that the increase in crop water use efficiency will be proportionally less than that in CO_2 concentration (Table 1). Rarely, it appears, does the relative increase in water use efficiency exceed 75% of that in CO_2 concentration. The response of water use efficiency to CO_2 frequently is much smaller.

Field studies of interactive effects of CO_2 concentration and soil water availability on crop yield are few (Rogers et al., 1986; Chaudhuri et al., 1990a; Kimball et al., 1995; Baker et al., 1997b), but these experiments and studies in controlled environments (Gifford, 1979; Sionit et al., 1980) usually indicate no loss of relative enhancement in biomass or economic yield at high CO_2 when water is limiting. Indeed, the opposite generally

Table 1. Relative increase in water use efficiency (WUE) of field-grown crops with CO_2 enrichment above the ambient CO_2 concentration. Crops were well-watered unless noted. Water use efficiency was calculated from canopy gas exchange measurements or as the ratio of total or grain mass to water loss.

Species	Measurement type	% increase in WUE	% increase in CO_2	Ambient CO_2 (μmol mol^{-1})	Reference
Soybean	Gas exchange	102	142	330	Jones et al. (1985)
Cotton	Total biomass				Mauney et al. (1994)
wet		28–39	49	370	
dry		19–37	49	370	
Rice	Gas exchange	13–53	100	330	Baker et al. (1990c)
Rice	Gas exchange				Baker et al. (1997b)
wet		34–53	100	350	
dry		125	100	350	
Wheat	Grain mass				Chaudhuri et al. (1990a)
wet		40	143	340	
dry		46	143	340	
Wheat	Grain mass				Kimball et al. (1995)
wet		17	49	370	
dry		32	49	370	
Sorghum	Total biomass	34	100	330	Chaudhuri et al. (1986)

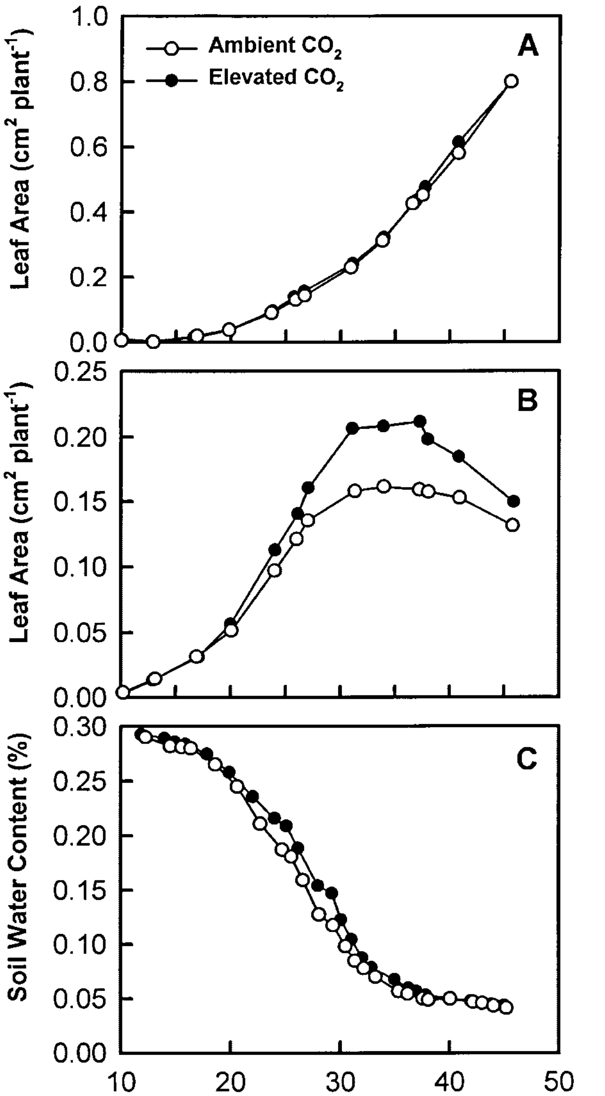

Fig. 4. Leaf area per plant of maize grown at ambient and elevated CO_2 concentrations in (A) continuously wet and (B) drying soil, and (C) the water content of drying soil. Note the difference in scale of the y-axis between A and B. Figures were adapted from Samarakoon and Gifford (1996).

is true. The absolute response of yield to CO_2 may decline, but the relative enhancement in yield at high CO_2 usually is greater when water is limiting than when it is ample (Idso and Idso, 1994). Enhancement in grain yield of wheat at 550 μmol mol^{-1} CO_2, for example, rose from 8% to 21% when water became limiting, apparently with little change in harvest index (Kimball et al., 1995). This resulted in an increase in grain produced per unit of water lost to evapotranspiration at high CO_2 of 17% under well-water conditions and 32% at limited water.

This enhancement in CO_2 effect on growth and water use efficiency when soils dry results partly from slower transpiration and a delay in the onset of drought (Rogers et al., 1984; Baker et al., 1997a; Allen et al., 1998). This is especially true of C_4 species, many of which exhibit little photosynthetic response to CO_2 until soil begins to dry (Gifford and Morison, 1985). Leaf area of maize did not respond to CO_2 when well-watered, but increased by up to 35% at elevated CO_2 as soil dried (Fig. 4; Samarakoon and Gifford, 1996). Plant biomass responded similarly. There are at least three mechanisms by which CO_2 enrichment could stimulate C_4 photosynthesis and growth in drying soil. 1. By reducing transpiration rates and slowing soil water depletion (Fig. 4), CO_2 enrichment should delay negative effects of water deficit on photosynthetic metabolism, and 2. promote higher leaf turgors, which in turn increase leaf expansion and stem growth. 3. Partial stomatal closure under water stress may reduce c_i to levels over which C_4 photosynthesis is sensitive to CO_2 concentration. There is another benefit of CO_2 enrichment to droughted plants that does not require differences in soil water depletion between CO_2 treatments. It is mediated through stomatal sensitivity to plant water status. Grant et al. (1995) discuss this benefit in a study of wheat response to CO_2 as soil dried. By about 2 wk into a drying cycle, soil water had decreased to similar levels at ambient and elevated CO_2 concentrations. Plant water potentials declined as soil dried, causing partial stomatal closure. The decline in stomatal and canopy conductance, however, was greater at the current than elevated CO_2 concentration. Larger carbohydrate pools and greater rooting density at high CO_2 apparently slowed the decrease in plant turgor and in g. This increased the difference in c_i and, consequently, in canopy photosynthetic rates between CO_2 concentrations. The measured increase in canopy photosynthetic rate from 370 to 550 μmol mol^{-1} CO_2 rose from 14% under well-watered conditions to 112% when soils dried.

Studies of combined effects of higher CO_2 concentration and temperature on crop water use efficiency are rare. Available results suggest that temperature, unlike CO_2, affects water use efficiency mainly by altering transpiration. Increasing temperature reduced photosynthetic water use efficiency of rice and soybean canopies by increasing water loss (Jones et al., 1985; Baker and Allen, 1993). Temperature over the range studied had little effect on canopy C gain or on canopy conductance to water vapor at a given CO_2 concentration. Water loss increased and water use efficiency declined at higher temperature because of the accompanying increase in evaporative demand of the atmosphere. Stronach et al. (1994) reported a similar trend for groundnut (*Arachis hypogaea* L.). Transpiration increased by about the same proportion as did atmospheric vapor pressure deficit at high temperature. When standardized for differences in vapor pressure deficit among treatments, water use efficiency showed no response to a 4°C increase in temperature.

Harvest Index

For crops, it is yield of the economically important product, rather than total biomass, that is of interest. The upper limit for CO_2 effects on economic yield is set by the increase in net C gain, but economic yield also depends on partitioning of carbon among plant organs. Most studies report little effect of CO_2 enrichment on carbon partitioning and harvest index (Chaudhuri et al., 1986; Baker et al., 1990a), but both increases (Kimball et al., 1995; Mayeux et al., 1997) and decreases in harvest index have been measured (Rogers et al., 1986; Baker et al., 1989; Ziska et al., 1996). Higher temperatures, by contrast, often reduce biomass distribution to economic yield. Harvest index of soybean declined at both the current and elevated CO_2 concentration as temperature increased (Baker et al., 1989). Economic yield and harvest index decline precipitously at temperatures that cause sterility or flower abortion (Baker and Allen, 1993; Conroy et al., 1994). In rice, CO_2 enrichment actually exacerbated the reduction in sterility at high temperature, possibly by increasing air temperature within the plant canopy (Matsui et al., 1997).

Crop Water Use

Ratio of Transpiration to Evaporation

We have considered global change effects on the efficiency with which crops convert transpired water to biomass and economic yield. Yield of water-limited crops also depends on water use, for biomass production is the product of transpiration and crop water use efficiency. The amount of water available for crops depends in turn on plant and environmental factors that affect plant access to and extraction of soil water and that regulate nonproductive losses of water to soil evaporation, deep drainage, and runoff. Direct and indirect effects of global changes on each of these aspects are likely, but have received little attention.

It is clear that crop yield can be improved considerably by reducing evaporation and other nonproductive losses of water, and thereby increasing the ratio of transpiration to evaporation (Turner, 1993). Evaporative losses have been estimated at between 10% and 50% of total water loss in cropped systems (Fischer and Turner, 1978). Evaporation depends on energy available at the soil surface and on water content of the upper soil. To reduce soil water loss, management has sought to reduce energy available at the soil surface. One way to accomplish this is by promoting faster canopy closure. Fertilization to increase crop growth rate (Turner, 1993), early and dense planting (Greenwood et al., 1992), and more narrow row spacing (Adams et al., 1976) all have been effective in speeding canopy closure and in increasing the fraction of available water that is used by plants. By increasing crop growth rates or maximum leaf area index (Jones et al., 1984; Kimball et al., 1995; Mayeux et al., 1997), CO_2 enrichment may provide a similar benefit. Greater leaf area at high CO_2 results from an increase in the size or number of leaves or some combination of the two (Morison and Gifford, 1984; Jones et al., 1984; Baker et al., 1990a). To the extent that growth increases with temperature, leaf area should also increase as temperature rises (Baker et al., 1989). Evaporation is seldom separated from transpiration when total water loss is measured in field experiments. Consequently, any increase in crop production that derived from lower evaporation at high CO_2 already is included in most calculations of water use efficiency.

It is interesting to note that tradeoffs exist within crop species between plant characteristics that increase transpiration efficiency and those that promote rapid crop growth (Turner, 1993). Consequently, genotypes with high transpiration efficiencies tend to intercept less radiation and to lose more water to evaporation than those with lower efficiencies. Benefits of more efficient water use are at least partially negated by greater water loss to evaporation. In contrast, CO_2 enrichment elicits correlated increases in transpiration efficiency and crop growth rate. As a result, CO_2 enrichment may increase both the ratio of transpiration to evaporation and the efficiency with which transpired water is converted to biomass.

Water Extraction from Soil

Crop water use obviously depends on uptake from soil. In drying soils, water extraction is determined by the rate and pattern of root growth. Access to deeply-placed soil water is increased by rapid vertical penetration of roots and by greater maximum rooting depth (Sponchiado et al., 1989). Capture of water within the rooting zone is correlated with rooting density. The total amount of water removed and rate at which it was extracted from a given soil layer by barley (*Hordeum vulgare* L.) and chickpea (*Cicer arietinum* L.) were proportional to root length density (Gregory and Brown, 1989). Both the rate at which roots spread and root densities may rise with CO_2 concentration (Rogers et al., 1994). Increasing CO_2 concentration, for example, increased root length and dry weight densities of cotton (*Gossypium hirsutum* L.), especially as horizontal distance from row center increased (Prior et al., 1994). Wheat grown at elevated CO_2 achieved maximum rooting depth faster (Chaudhuri et al., 1990b) and showed greater horizontal root growth during early season (Wechsung et al., 1999). Carbon dioxide enrichment increased the number of sorghum roots at all depths over a 1.5 m profile (Chaudhuri et al., 1986), increased fine root biomass in sour orange trees (*Citrus aurantium* L.) (Idso and Kimball, 1992), and increased root branching (Del Castillo et al., 1989) and root volume in soybean (Rogers et al., 1992). These changes may increase water uptake by increasing the volume of soil explored by crop roots or by promoting a more thorough exploration of soil within the rooting zone. Carbon dioxide enrichment sometimes increases total evapotranspiration from crops (Chaudhuri et al., 1990a; Samarakoon and Gifford, 1995; Mayeux et al., 1997), but the extent to which this increase in water use reflects more thorough extraction of soil water by roots remains to be determined.

Summary

Feedbacks involved in scaling from leaf to canopy reduce positive effects of CO_2 enrichment on crop water use efficiency. When soils are wet, global change effects on production will largely mirror effects on photosynthesis. Rising CO_2 may increase yields substantially when plants are C limited or when photosynthate in excess of current requirements can be stored for later use (Allen et al., 1991; Lawlor and Mitchell, 1991). Indeed, it

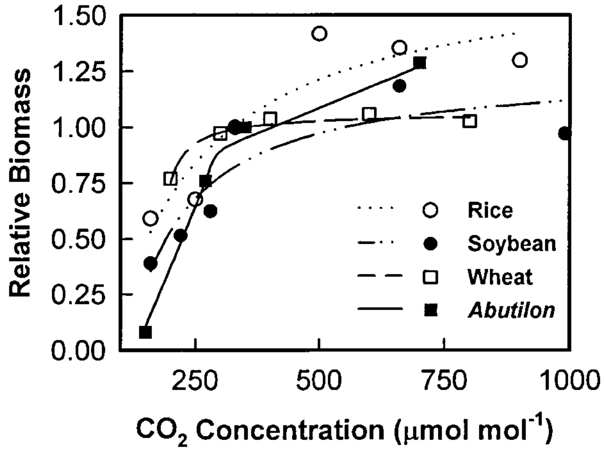

Fig. 5. Response of plant biomass to CO_2 concentration, normalized to 330 μmol mol^{-1} (rice, soybean, wheat) or 350 μmol mol^{-1} CO_2 (*Abutilon*). Data for rice, soybean, wheat, and *Abutilon* are from Baker et al. (1990a), Allen et al. (1991), Neales and Nicholls (1978), and Dippery et al. (1995), respectively.

is likely that crop yields already reflect benefits of the 37% increase in atmospheric CO_2 concentration since industrialization (Fig. 5; Allen et al., 1991; Mayeux et al., 1997). Yield increases at high CO_2 should occur most frequently in areas where temperatures approximate the optimum for crop growth. Further increases in temperature will reduce yields (Fig. 2) by decreasing C gain and accelerating crop development. Elevating CO_2 can ameliorate, but often will not offset, negative effects of above optimal temperatures. Data of Wheeler et al. (1996) indicate that a 1.0 to 1.8°C increase in mean temperature could negate beneficial effects of doubled CO_2 on yield of winter wheat. Results of Rawson (1995) for summer grown wheat support a similar conclusion (see also Ziska et al., 1997). In areas where high temperatures already are severely limiting, further increases in temperature will depress yields independently of changes in CO_2 concentration.

When soils begin to dry, production becomes sensitive to stomatal responses to both CO_2 concentration and plant water status. Rising CO_2 may increase crop growth if, by reducing g, it slows transpiration and delays the onset of drought (Rogers et al., 1984; Samarakoon and Gifford, 1996; Baker et al., 1997a; Allen et al., 1998). Higher temperatures, by contrast, offset water savings at high CO_2 by increasing evaporative demand.

It is clear that CO_2 enrichment alone will increase yields of water limited crops (Idso and Idso, 1994; Drake et al., 1997). It is not yet obvious how crops will respond to increases in both CO_2 concentration and temperature. Effects of higher temperature and CO_2 concentration on plants often are not additive, meaning that the combined influence of these changes cannot be predicted from knowledge of their individual effects (Idso et al., 1987; Long, 1991). In addition, it appears that the magnitude and even direction of crop responses to CO_2 enrichment and temperature change are species and even cultivar-specific (Baker and Allen, 1993; Conroy et al., 1994; Ziska et al., 1997). Understanding interactive effects of rising CO_2 concentration and temperature for crop yields and water economy is among the major challenges confronting research.

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