Climate change and agroecosystems: the effect of elevated atmospheric CO_2 and temperature on crop growth, development, and yield.

Mudança climática e agroecossistemas: efeito do aumento de CO_2 atmosférico e temperatura sobre o crescimento, desenvolvimento e rendimento das culturas.

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- REVIEW -

ABSTRACT

The amount of carbon dioxide (CO_2) of the Earth´s atmosphere is increasing, which has the potential of increasing greenhouse effect and air temperature in the future. Plants respond to environment CO_2 and temperature. Therefore, climate change may affect agriculture. The purpose of this paper was to review the literature about the impact of a possible increase in atmospheric CO_2 concentration and temperature on crop growth, development, and yield. Increasing CO_2 concentration increases crop yield once the substrate for photosynthesis and the gradient of CO_2 concentration between atmosphere and leaf increase. C3 plants will benefit more than C4 plants at elevated CO_2. However, if global warming will take place, an increase in temperature may offset the benefits of increasing CO_2 on crop yield.

Key words: global warming, photosynthesis, agriculture, food supply.

RESUMO

A quantidade de dióxido de carbono (CO_2) na atmosfera terrestre está aumentando, o que poderá agravar o efeito estufa da atmosfera e o aquecimento do ar no futuro. As plantas respondem ao CO_2 e à temperatura do ambiente. Assim, a mudança climática projetada para o futuro poderá afetar a agricultura. O objetivo foi revisar a literatura sobre o impacto de possíveis aumentos da concentração de CO_2 atmosférico e da temperatura sobre o crescimento, desenvolvimento e rendimento das culturas agrícolas. O aumento da concentração de CO_2 aumenta o rendimento das culturas, uma vez que o substrato para fotossíntese e o gradiente de CO_2 entre a atmosfera e a folha aumentam. As plantas C3 terão maior benefício com o aumento de CO_2 do que as plantas C4. Se o aquecimento global acontecer, um aumento da temperatura do ar pode anular os benefícios do aumento do CO_2 sobre o rendimento das culturas.

Palavras-chave: aquecimento global, fotossíntese, agricultura, suprimento de alimento.

INTRODUCTION

Changes in Earth's climate have been projected by the end of this century because some atmospheric "greenhouse" gases, among them carbon dioxide (CO_2), are increasing (BACASTOW et al., 1985; IPCC, 2001). It is expected that atmospheric CO_2 concentration will double sometime during this century if fossil fuels burning continues and air temperature is predicted to rise 1.5 to 5ºC with more than 90% likelihood by 2100 (BAES et al., 1977; MAHLMAN, 1997). As a consequence of a possible increase in atmospheric CO_2 concentration and associated climate changes, several studies have been conducted in order to predict the effects of this climate change on crop growth, development, and yield.

Agroecosystems may be strongly influenced by the projected increase in atmospheric

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CO_2 concentration and associated climate change. The direct effect of increasing CO_2 concentration on plant growth is of particular interest because of the possibility of increasing crop yields in the future once the substrate for photosynthesis and the gradient of CO_2 concentration between atmosphere and leaf will increase. Current atmospheric CO_2 concentration (about $360\mu mol\ mol^{-1}$) is insufficient to saturate the ribulose 1.5-bisphosphate carboxylase (Rubisco), the enzyme responsible for primary carboxilation, the metabolic process that drives phostoynthesis, in C3 plants (BOWES, 1991; TAIZ & ZEIGER, 1991). Photosynthesis in C3 plants increases up to 800-1000 ppm (AMTHOR, 2001).

If the increase in atmospheric CO_2 concentration will be accompanied by an increase in air temperature, crops may shorten their growing cycle, which may offset the advantages of an increasing CO_2 concentration. Therefore, the interacting effects of CO_2 concentration and temperature on plant growth is complicated. How climate change will affect crop yield will be critical for agriculture as an enterprise and food supply activity worldwide.

The purpose of this paper is to review the literature about the impact of a possible increase in atmospheric CO_2 concentration and temperature on crop growth, development, and yield.

Atmospheric CO_2 concentration and global warming

The CO_2 concentration of the Earth's atmosphere during the last ice aging may have been as low as 160-200 µmol mol-1 (DELMAS et al., 1980). After industrial revolution, atmospheric CO_2 concentration has increased significantly, specially during the second half of the last century. Atmospheric CO_2 concentration is believed to be increasing at a rate of 0,4-0,5% year-1 (IPCC, 1995; SOMBROEK & GOMMES, 1996) or $1-1,8\mu mol\ mol^{-1}$ per year (ROSENBERG et al., 1983; IPCC, 1995; UNSWORTH & HOGSETT, 1996). Atmospheric CO_2 concentration increased from about $315\mu mol\ mol^{-1}$ in 1958 to over $345\mu mol\ mol^{-1}$ in 1985 (BACASTOW et al., 1985). Consequently, the current $360\mu mol\ mol^{-1}$ concentration is expected to double by the end of this century.

Carbon dioxide is considered a greenhouse gas due to its high absorptance in several wavelengths of the thermal infrared radiation emitted by Earth's surface. The greater the content of gases in the atmosphere that absorb thermal infrared radiation emitted from the Earth surface the greater the thermal infrared radiation emitted by the atmosphere towards the Earth surface (ROSENBERG et al., 1983; MAHLMAN, 1997). Consequently, the long wave

balance of the surface will be less negative and more energy will be available for latent and sensible heat fluxes at the Earth's surface. As more energy is available for sensible heat flux, air temperature is expected to rise.

The rate that air temperature will increase is still a controversial issue. Observed decreases in lower stratosphere ozone may have a cooling effect (IPCC, 1995; MAHLMAN, 1997). Other human-produced aerosols like sulfates are estimated to have also a cooling effect (MITCHELL et al., 1995; MAHLMAN, 1997). However, the cooling effect of sulfate particles remains insufficiently quantified (MAHLMAN, 1997). MITCHEL et al. (1995) suggested an increase of global temperature by 0.3°C decade^{-1} considering greenhouse gases alone, and a 0.2°C decade^{-1} increase when sulfate aerosols were included in the model. The Intergovernmental Panel on Climate Change – 1995 projected a globally-averaged annual mean warming rate of 0.23°C decade^{-1} (IPCC, 1995). Overall, air temperature may increase from 1°C up to 6°C by the end of this century (WILSON & MITCHELL, 1987; IPCC, 1990; 1995; 2001; MAHLMAN, 1997; MITCHELL et al. 1995). There is evidence that global mean air temperatures have increased by about 0.5°C in the past century (JONES & FARHER, 1991) and observations over a large portion of the Earth's land suggest that minimum temperatures have increased about three times more than the corresponding maximum temperatures (KARL et al., 1991). While the magnitude of increase remains controversial, there is widespread agreement that air temperature will continue to increase in this century. This increase will have an effect on regional climate, which will subsequently influence crop growth, development, and yield. Therefore, our challenge is to evaluate the effects of all possible climate change scenarios on these processes. Moreover, sudden cooling of the atmosphere due to several non anthropogenic factors (i.e. volcanic eruptions, comet/asteroid impact, change in sun spots, and ocean currents) responsible for events of 0.5 – 1°C dropping in mean temperature worldwide, with a frequency of about one event per century, may also affect negatively agricultural production globally, with crop failures (ENGVILD, 2003).

Stomata and elevated CO_2 concentration

Characterizing the response of stomata to elevated CO_2 is important for understanding the effect of elevated CO_2 on crop response. Stomata close in response to elevated CO_2 (UNSWORTH & HOGSETT, 1996). A doubling CO_2 concentration may reduce the

conductance at the leaf level by 30-40%, although large differences among species exist (MORISON & GIFFORD, 1983; CURE, 1985; UNSWORTH & HOGSETT, 1996) and values as high as 50-70% decrease can be found in the literature (ROSENBERG et al., 1990), with similar response between C3 and C4 species (KIMBALL & IDSO, 1983; CURE, 1985; MORISON, 1987).

The mechanism behind stomata closure in response to elevated CO_2 concentration is not clear yet (MORISON, 1987; MOTT, 1990; VAN DE GEIJN & GOUDRIAAN, 1996). Stomata apparently do not respond directly to the CO_2 concentration around the leaf (MORISON, 1987). The CO_2 sensor for stomatal action is considered to be located in the epidermis and is presumably in the guard cells (MORAVIEFF, 1956; PALLAGHY, 1971), the inner lateral walls of which are permeable to CO_2 (MEIDNER & MANSFIELD, 1965). Plants tend to regulate CO_2 concentration in the stomatal cavity (Ci), so that for a given vapor pressure deficit there is a constant ratio Ci with the atmospheric concentration, Ci/Ca (MORISON, 1987; MOTT, 1990). The ratio Ci/Ca in stationary conditions is about two-thirds for C3 and one-third for C4 plants (WONG et al., 1979; VAN DE GEIJN & GOUDRIAAN, 1996). Thus, a Ci/Ca regulation would lead to the partial closure at elevated CO_2 concentration. Photosynthesis and water-relations of native grassland species and Ci/Ca for C3 and C4 plants measured by JACKSON et al. (1994) confirm the conservation of the Ci/Ca value, with only a small tendency to rise with increasing CO_2 concentration.

The possibility of acclimation of the stomata movement to long-term exposure to elevated CO_2 concentration has been pointed out, but this is a controversial issue. Some studies suggest that the lower stomatal conductance (g_s) does not only persist over extended exposure periods to elevated CO_2 concentration, but it is also kept after subsequent lowering of the CO_2 concentration (VAN DE GEIJN & GOUDRIAAN, 1996). STANGHELLINI & BUNCE (1994) reported that g_s of tomato plants cultivated at high CO_2 concentration was less sensitive to shortterm CO_2 concentration fluctuations and higher than that of plants grown at ambient CO_2 concentration and measured at double current CO_2 concentration. This may indicate that the sensitivity of g_s of high CO_2 concentration plants to change in CO_2 concentration is reduced, but still a lower g_s exists when compared to leaves growing and measured in present CO_2 concentration conditions (VAN DE GEIJN & GOUDRIAAN, 1996).

Studies have shown that short-term gain of elevated CO_2 may be offset in the long-term by a negative acclimation of photosynthetic capacity (USUDA & SHINOGAWARA, 1998). One of the mechanisms of negative acclimation of photosynthetic capacity after long-term treatments with elevated CO_2 concentration is the decreased activity and content of Rubisco (STITT, 1991; ROWLAND-BAMFORD et al., 1991). Also, negative acclimation has been associated to an imbalance between source capacity and sink capacity (USUDA & SHINOGAWARA, 1998). The rate of photosynthesis at the source might exceed the capacity of the sinks at elevated CO_2.

Among agricultural crops, rice has showed marked acclimation (ROWLAND-BAMFORD et al., 1991; VU et al., 1997) and soybean appears less affected (CAMPBELL et al., 1988; VU et al., 1997). Wheat did not show evidence of any significant acclimation or down-regulation of photosynthesis at the biochemical level to elevated CO_2 when grown in field conditions (NIE et al., 1995a,b) in contrast with studies in pots (SAGE, 1994). Some other species have been reported do not respond negatively to acclimation including tuber plants. Radish sink strength and activity was greater in plants grown at elevated CO_2 concentration and the root:shoot ratio increased about 10% at elevated CO_2 concentration (USUDA & SHINOGAWARA, 1998).

Plant growth and development response to elevated CO_2 concentration and temperature

Since long time ago, the effect of CO_2 concentration on crop yield has been studied. According to KIMBALL (1983a), de Saussure, in 1804, first demonstrated that peas exposed to high CO_2 concentration "grew better" than control plants in ambient air. Fertilization or enrichment of air with CO_2 in commercial greenhouses has been practiced for a considerable time (ROSENBERG et al., 1983). WITTNER (1967) reviewed the history of this practice and showed that increased yield and improved quality has been achieved with a number of crops like lettuce, tomato, cucumber and a wide range of flower crops. ALLEN (1979) assembled data from a wide range of greenhouse and growth chamber experiments about atmospheric CO_2 concentration and plant response. Very few studies indicate a yield depression at elevated CO_2 concentration and those are primarily with flower crops (ROSENBERG et al., 1983).

Compiling and analyzing the results of more than 770 reports about the CO_2 enrichment on the economic yield of 24 agricultural crops and 14 other species, KIMBALL (1983b) showed that only 39 out of 437 separate observations (i.e. 9%) yielded less than

their respective controls and the average relative increase was 28% considering all of the crops or 36% excluding flowers (Table 1). The effect of CO_2 enrichment on flower yield was generally lower than on food crops. Mean yield increases were 23%, 32%, 42%, 54% and 52% for fruit, cereal C3, leaf, legume and root crops, respectively. KIMBALL (1983a, b,

1986) estimated that a doubling CO_2 concentration, holding other factors constant, could lead to a 34 ± 6% increase in agricultural yields of C3 plants and a 14 ± 11% in C4 plants with a 95% confidence interval. Later, LAWLOR & MITCHELL (1991) concluded that provided adequate water, nutrients and pest control, yields of C3 and C4 crops growing in about 700 µmol

Table 1 - Experimental results of increasing in dry biomass and marketable yield of some crops in response to doubling CO_2 concentration.

Crop	% increase		Source
	Dry Biomass	Marketable yield	
Cereals C4			
Corn	9	29	CURE & ACOCK (1986)
	3.7(ns)	3.7(ns)	RUDORFF et al. (1996)
Sorghum	9	-	CURE & ACOCK (1986)
	-	6	UNSWORTH & HOGSETT (1996)
Cereals C3			
Wheat	31	35	CURE & ACOCK (1986)
	49	-	WHELER et al. (1995)
	17	8	KIMBALL et al. (1995)
Barley	30	70	CURE & ACOCK (1986)
Rice	-	25	KIMBALL (1983a)
Legumes			
Soybean	39	29	CURE & ACOCK (1986)
	-	45	BAKER et al. (1989)
	32	22	FUHRER (2003)
Bean	-	82	KIMBALL (1983a)
Green peas	-	89	KIMBALL (1983a)
Groundnut	-	31	CLIFFORD et al. (1993)
Vegetable crops			
Tomato	-	20	KIMBALL (1983a)
	-	2-26	ALLEN (1979)
Cucumber	-	30	KIMBALL (1983a)
Lettuce	-	35	KIMBALL (1983a)
	-	44	ALLEN (1979)
Special crops			
Tobacco	-	42	KIMBALL (1983a)
Cotton	84	-	IDSO et al. (1987a)
Sunflower	-	144	ALLEN (1979)
Tuber crops			
Potato	-	51	KIMBALL (1983a)
	-	43-75	ALLEN (1979)
Radish	-	28	KIMBALL (1983a)
	111	37/105[1]	USUDA & SHIMOGAWARA (1998)
Sweet potato	59	83	CURE & ACOCK (1986)
Flowers			
Carnation	-	9	KIMBALL (1983a)
	-	-0.5 - 11	ALLEN (1979)
Chrysanthemum	-	6	KIMBALL (1983a)
Cyclamen	-	35	KIMBALL (1983a)
Nasturtium	-	86	KIMBALL (1983a)
Rose	-	22	KIMBALL (1983a)
	-	8-27	ALLEN (1979)

[1]37% increase in annual yield (fresh weight) and 105% in dry weight of roots.
ns=not significant

CO2 mol-1 would be about 30 to 40% and 9%, greater than present yields, respectively. Below-ground growth is also increased at elevated CO_2 concentration (VAN DE GEIJN & VAN VEEN, 1993; ROGERS et al., 1994). Only at very extreme concentrations there is evidence of deleterious effects due to CO_2 concentration. AOKI & YABUKI (1977) found that dry matter production and photosynthetic rate of cucumber increased in plants exposed to CO_2 concentration up to 2400 ppm and, when the exposure was at 5000 ppm, the dry weight gain was below those achieved at lower concentrations. These high and deleterious CO_2 concentration are not expected in the atmosphere in the time scale analyzed in this review (one century ahead).

Crop yield increases in response to an increase in CO_2 concentration is explained by some physiological and biochemical processes. Two of the most crucial metabolic functions in determining the magnitude of plant growth are carbon assimilation and water use. There are three major categories of CO_2 metabolism: C3, C4 and CAM, and each responds to elevated CO_2 in a different way. The C3 photosynthetic pathway is less efficient than the C4 and considerable primary photosynthate is lost through photorespiration (ROSENBERG et al., 1990; TAIZ & ZEIGER, 1991). Response of plants to CO_2 concentration can be illustrated using a Flux Gradient approach that describes photosynthesis as a process analogous to electrical current flow and governed by Ohm's Law (ROSENBERG et al. 1983): $PS = (C_a - C_{chl})/(r_a + r_s + r_m)$, where PS is the rate of photosynthesis, C_a and C_{chl} are the CO_2 concentrations in the atmosphere and at the chloroplast level (available to the photosynthetic biochemistry), and r_a, r_s and r_m are the air, stomatal and mesophyl resistances to the diffusion of CO_2.

Plant physiologists would rather use conductance instead of resistance, so the Flux Gradient approach can be written as (BALL, 1987): $A = g_{tc}(C_a - C_i)$, where A is the assimilation rate, g_{tc} is the stomatal + leaf boundary layer conductance to CO_2 and C_a and C_i are the mole fractions of ambient and leaf intercellular spaces CO_2. If atmospheric CO_2 concentration increases, the gradient or "driving force" for photosynthesis (C_a-C_{chl}) or(C_a-C_i) is increased, an effect of relatively greater significance in C3 plants (because C_i is higher in plants having photorespiration) than in C4 plants, where the CO_2 concentration difference (Ca-Ci) is usually greater (ROSENBERG et al., 1983).

Two responses to elevated CO_2 are an increase in the rate of photosynthesis and a decrease in stomata conductance (UNSWORTH & HOGSETT,

1996). In the Flux Gradient approach, r_a is not affected by ambient CO_2 concentration and r_m may be slightly responsive. The r_c is relatively small compared to the sum of r_a and r_m, so its influence on photosynthesis will also be relatively small, unless an almost complete stomatal closure is induced (ROSENBERG et al., 1983). Therefore, the increase of the "driving force" has a stronger effect than a decrease in g_s at elevated CO_2 concentration. Despite a stomatal conductance decrease is observed with CO_2 concentration increase, Ci is increased (LAWLOR & MITCHELL, 1991) which leads to a net photosynthesis increase, regardless the incident light is saturating or limiting (LONG, 1991; STITT, 1991).

The current CO_2 concentration in the atmosphere is limiting to photosynthesis of C3 plants because it is insufficient to saturate Rubisco (BOWES, 1991; TAIZ & ZEIGER, 1991;VU et al., 1997). In C3 plants, the increase in ambient CO_2 concentration suppresses photorespiration, because this process proceeds at a rate dependent upon competition between O_2 and CO_2 for enzymatic sites (EHLERINGER & BJORKMAN, 1977). An increase in the availability of CO_2 increases carboxilation and decreases the oxigenase activity of Rubisco, hence reducing CO_2 loss through photorespiration. Therefore, a net increase in photosynthesis occurs (BOWES, 1991; TAIZ & ZEIGER, 1991;VU et al., 1997). The C4 and CAM plants have Ci concentrating mechanisms, so their photosynthetic performance is not expected to increase greatly in response to atmospheric CO_2 concentration increase. The CO_2 concentrating mechanisms of these plants allows the leaf to maintain high photosynthetic rates at lower internal CO_2 concentration values, because they require lower rates of stomatal conductance for a given rate of photosynthesis (TAIZ & ZEIGER, 1991). Therefore, photosynthesis of C4 and CAM species is much less sensitive or even insensitive to increased CO_2 concentration compared to C3 species. This hypothesis has been confirmed by experimental results showing that crop yield was increased less in C4 compared to C3 plants (KIMBALL, 1983a, b, 1986; CURE & ACOCK, 1986; LAWLOR & MITCHELL, 1991) and is an assumption widely used in crop models to predict the response of crops to increasing CO_2 concentration (ADAMS et al., 1990; EL MAAYAR et al., 1997; SAVABI & STOKLE, 2001). An example is maize, reported not to be sensitive to CO_2 enrichment (SURANO & SHINN, 1984; HOCKING & MEYER, 1991; RUDORFF et al., 1996). The increase in net photosynthesis in C3 species has been reported as high as 50 – 100% when CO_2 concentration doubles

compared to 10% in C4 species (UNSWORTH & HOGSETT, 1996), and photosynthesis in C3 plants increases up to 800-1000 ppm (AMTHOR, 2001).

Probably the most important physical effect of transpiration in plants is the cooling that takes place at the transpiring surface (ROSENBERG et al., 1983). Because large quantities of energy are required in the phase change from liquid to vapor, evaporation provides a very efficient mechanism for heat dissipation. Reduced transpiration can easily result in an increase of 2-3°C in plant temperature increases as high as 10-12°C under extreme conditions (POLJACKOFF-MAYBER & GALE, 1972; BLAD et al., 1981).

The partitioning of net radiation on the leaves under elevated CO_2 concentration is modified due to decrease in stomatal conductance, which causes a decrease in transpiration leading to an increase in leaf temperature (KIMBALL & IDSO, 1983; JONES et al., 1985). KIMBALL et al. (1995) reported an increase in sensible heat flux (H) up to 48% in spring wheat due to a 550μmol mol-1 during a clear day. During that day, the authors reported a decrease of up to 9% in latent heat flux (LE) in the plots with elevated CO2 concentration. During the crop season, the authors reported a decrease of 4% in net radiation (Rn), an increase of 0,6°C in canopy temperature and a decrease of 7,9% in evapotranspiration due to elevated CO_2. Evapotranspiration had a small decrease because there was an increase in vapor pressure deficit (VPD), the driving force to water vapor diffusion, due to an increase in leaf temperature, and there was also an increase in leaf area index (LAI) mainly during the early growing season. This reduction in evapotranspiration is similar to the reduction of 9% and 5% in the per-unit-leaf-area transpiration calculated and measured with lisimeters in cotton in summer conditions reported by IDSO et al. (1987a) but is not in agreement with some simulations made by ROSENBERG et al. (1990) who reported an increase in LE in wheat, grassland prairie and a deciduous forest at elevated CO_2 concentration. These contradictory results show that there are many uncertainties about the effect of increasing CO_2 concentration and that species may respond differently.

The temperature of the leaf surface may rise 0.5 - 1.7°C only due to doubling CO_2 concentration (IDSO et al., 1987a,b; KIMBALL et al., 1995; VAN DE GEIJN & GOUDRIAAN, 1996) or even up to 3°C, depending on the specie and the weather (ROSENBERG et al., 1990). Higher leaf temperatures may have important consequences on the longevity and photosynthetic capacity of the individual leaves and at the canopy level, as ageing may be accelerated and shortening the growing season (ELLIS et al., 1990; KIMBALL et al., 1995; VAN DE GEIJN & GOUDRIAAN, 1996). In the experiments reported in KIMBALL et al. (1995), elevated CO_2 with no change in air temperature accelerated spring wheat development by 2.3 days to mid-anthesis and shortened time to maturity by 6 days, which was attributed to higher plant canopy temperature. Such effects of elevated CO_2 are similar to the effects of moisture stress on canopy temperature, which explains the more rapid phenological development of droughtstressed plants (SHAYKEWICH, 1995).

Plant growth rate is related to temperature, increasing from a base value and decreasing beyond an optimum limit. Increase in temperature above the optimum reduces the activation state of Rubisco (HOLADAY et al., 1992; VU et al., 1997) and decreases both specificity for CO_2 and solubility of CO_2 relative to O_2 (JORDAN & OGREN, 1984; BROOKS & FARQUHAR, 1985). The latter two effects result in greater losses of CO_2 to photorespiration, which decreases net CO_2 assimilation. This effect occurs mainly in C3 plants, either at normal CO_2 concentration or at CO_2 concentration that saturates photosynthetic apparatus (TAIZ & ZEIGER, 1991). Therefore, there is an optimum temperature for maximum rate of photosynthesis, which in general is higher for C4 plants than C3 plants (ROSENBERG et al., 1983; TAIZ & ZEIGER, 1991). Dark respiration is also affected directly by temperature, increasing exponentially with increasing temperature, and so net photosynthesis becomes temperature-response sensitive (ROSENBERG et al., 1983; TAIZ & ZEIGER, 1991). VU et al. (1997) reported that the photosynthetic rate of rice and soybean grown at doubling CO_2 concentration was maximum at 35°C and 32°C, respectively, decreasing with further increases in temperature.

The potential biomass yield of a crop is a product of the rate of biomass accumulation and the duration of growth. The rate of biomass accumulation is mainly influenced by the rate of photosynthesis of the canopy, as discussed above. The duration of growth for a particular cultivar is usually almost directly proportional to temperature. Highest potential yields of a particular annual crop are obtained in regions where the season duration is maximized because of relatively low temperature, assuming no water stress during the growing season. In regions such as the tropics where the temperature is usually relatively high, potential yield levels can reach those of cooler temperature regions only by combining yields from two or more crops in sequence, so that the duration of

the total growth periods is about the same in both species (RITCHIE &NESMITH, 1991). Therefore, in addition to an increase in respiration rate, low yields at high temperature should also be explained by the reduction in growth duration. Working with irrigated wheat in Australia, COOPER (1992) found that the greater the time between sowing and maturity, the higher was the yield. Similarly, RADDATZ et al. (1994) found that yields of wheat, barley, and canola on the Canadian Prairies increased as the estimated growth period (days from planting to maturity) increased.

Components of crop yield affected by temperature

Warm air temperatures accelerate grain growth rate, reduce the duration of grain filling, and may reduce grain weight (WIEGAND & CUELLAR, 1981; SIONIT et al., 1987; FREDERICK & CAMBERATO, 1995). BAKER et al. (1989) reported the response of soybean yield to elevated CO_2 concentration at three mean daily temperature regimes (22.8, 27.8 and 32.8°C). Seed yield decreased as a function of temperature either at normal or elevated CO_2 concentration. This decrease was related to a decrease in seed weight. In another study with soybean, a decrease in yield at elevated temperature (above 26/20°C daytime/nighttime) was associated with a decrease in pod number (SIONIT et al., 1987). The reduction of grain weight by heat stress in cereals is attributed to the effect of temperature on the rate and duration of grain growth period (ABROL & INGRAM, 1996; FUHRER, 2003). As temperature increased from 15/10°C to 21/16°C, duration of grain filling in wheat was reduced from 60 to 36 days and grain growth rate increased from 0.73 to 1.49 mg grain^{-1} day^{-1} with a result of minimal influence on grain weight at maturity. Further increase in temperature from 21/16°C to 30/25°C resulted in decline in grain filling duration from 36 to 22 days within a minimal increase in grain growth rate from 1.49 to 1.51mg grain^{-1} day^{-1}. Thus, grain weight was significantly reduced at the highest temperature due to an increase in the rate of development (ABROL & INGRAM, 1996).

For each degree C increase in mean air temperature during grain filling in wheat, the duration of grain filling was shortened by 3.1 days and final kernel weight was reduced by 2.8mg (WIEGAND & CUELLAR, 1981). Studies with wheat showed an average decrease of 2.8 days in grain filling period and a kernel weight decrease of 1,5mg for each degree C increase above the apparent optimum 15-20°C range for wheat (MARCELLOS & SINGLE, 1972; BAGGA & RAWSON, 1977; CHOWDHURY & WARLAW, 1978). High temperature reduction of grain yield results from:

(a) reduced number of grain formed; (b) shorter grain growth duration; and (c) inhibition of sucrose assimilation in grains (ABROL & INGRAN, 1996). BUTTERFIELD & MORISON (1992) in a simulation study showed that the period of grain filling in wheat was shortened by 14 days and 7 days at Edinburgh and Oxford (UK), respectively, with +2°C and 22 and 12 days with +4°C, i.e. a reduction of 21%, 14%, 33% and 24% in the length of this period, respectively.

As discussed, many authors have shown a deleterious effect of elevated temperature on grain yield. These results suggest that an increase in temperature may offset the benefits of increasing CO_2 concentration on crop yield. In a numerical study of wheat and rice growth, LAL et al. (1998) projected yield was 28% and 15% greater when CO_2 concentration was doubled but no changes in surface air temperature occurred. However, a 3°C and 2°C increase in average air temperature offset the yield increase due to double CO_2 concentration in wheat and rice, respectively. In an experimental study, WHELLER et al. (1996) presented evidence that an increase in mean seasonal temperature of only 1,0 – 1.8°C may offset the benefits to winter wheat grain yield from doubling CO_2 concentration. Similar results were reported by SAVABI & STOKLE (2001) that increase in yield of maize and soybean due to doubling CO_2 concentration may be offset by a 1.2 and 2.8°C increase in temperature. A recent study by MALL et al. (2004) showed that, in India, a decrease (10-20%) in soybean yield may be expected if air temperature increases at the time of doubling CO_2. MATTHEWS & WASSMANN (2003) projected decreases in rice production under climate change scenarios in several Asian countries. Other simulation studies have also provided results that support the hypothesis that increase in crop yields due to CO_2 increase can be offset by the negative effects of warmer temperatures (Table 2).

Future temperature change linked to global warming might be characterized by an asymmetry between daytime maxima and nighttime minima instead of a uniform increase (KARL et al., 1991). The increase in temperature would be more pronounced in the nighttime temperature leading to a decline in daily temperature range. ROSENZWEIG & TUBIELLO (1996) found that increasing temperature minima three times as much as maxima would lead to higher yields of wheat in the Central United States compared to increasing minima and maxima equally. An increase in nighttime respiration rates could depress biomass production. Higher minimum temperatures could extend the overwintering range of some insect pests

Table 2 - Impact on yield (% Y) and on crop growth period (R, days) due to elevated CO_2 and air temperature increase related to current yield and crop growth duration.

Crop	CO_2 (ppm)	Temperature increase (°C)										Site	Reference
		+1		+2		+3		+4		+5			
		%Y	R	%Y	R	%Y	R	%Y	R	%Y	R		
Wheat													
	660	25	-5	16	-10	2	-12	-	-	-32	-	India	LAL et al. (1998)
	555	-	-16	-8	-	-	-	-39	-15	-	-	Brazil	SIQUEIRA et al. (1994)[2]
	515	-	-	-	-	-	-	21	-	-	-	Canada	El MAAYAR et al. (1997)
	630	-	-	-	-	-	-	9 to-20	-	-	-	USA	ADAMS et al. (1990)[1]
	660	-	-	-	-	-	-	-	-	-32 to-50	-	USA	ADAMS et al. (1990)[1]
	550	5 to 25	-	to -35	-	-10 to-50	-	-15 to –70	-	-	-	USA	ROSENZWEIG & TUBIELO (1996)[3]
Soybean													
	555	-	-	-3	-3	-	-	-11	-1	-	-	Brazil	SIQUEIRA et al. (1994)[2]
	515	-	-	-	-	-	-	23	-	-	-	Canada	El MAAYAR et al. (1997)
	630	-	-	-	-	-	-	49 to -20	-	-	-	USA	ADAMS et al. (1990)[1]
	660	-	-	-	-	-	-	-	-	40 to -40	-	USA	ADAMS et al. (1990)[1]
Mayze													
	550	-	-	-9	-10	-	-	-20	-17	-	-	Brazil	SIQUEIRA et al. (1994)[2]
	515	-	-	-	-	-	-	6	-	-	-	Canada	El MAAYAR et al. (1997)
	630	-	-	-	-	-	-	49 to -20	-	-	-	USA	ADAMS et al. (1990)[1]
	660	-	-	-	-	-	-	-	-	40 to -20	-	USA	ADAMS et al. (1990)[1]
Rice													
	660	4	3	-5	-2	-	-	-	-	-25	-	India	LAL et al. (1998)

[1]Simulated range for the entire USA
[2]Average of several regions in Brazil
[3]Simulated range for Fargo (ND), North plate (NE), Dodge City (KA), and San Antonio (TX) - USA

and favor the growth of some weeds. These effects could further limit yields in the scenarios with higher minimum temperature increase (FUHRER, 2003). LAL et al. (1998) simulated that an increase of 1°C in minimum temperature in Northwest India would not affect the response of wheat to increase CO_2 concentration but an increase of 1°C in maximum temperature is enough to decrease the response of wheat to double CO_2 concentration. However, for rice the behavior was estimated to be the opposite.

CONCLUSIONS

While there may be differences in the projected impacts of climate change on agricultural production among regions and countries (MATTHEWS & WASSMANN, 2003), assuming no change in temperature, crop yield is expected to increase about 30% in C3 plants and 10% in C4 plants due to doubling CO_2 concentration. If temperature will change, an increase in air temperature as low as 1°C may offset the benefits of increasing CO_2 concentration on crop yield. Potential for adaptations of agriculture to climate change may be much more difficult in less-developed regions (FUHRER, 2003), and climate change-related problems are expected to take place sooner (a few months) after crop failure in developing countries than in developed countries (ENGVILD, 2003). Therefore, policymakers are encouraged to discuss strategies to minimize impacts of global warming on food supply whereas research should continue on search of alternatives to deal with climate change. Mitigatory actions have to be worked out involving plant breeders, agroclimatologists, extensionists, growers, and policymakers.

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