

## Climate change and agroecosystems: the effect of elevated atmospheric CO<sub>2</sub> and temperature on crop growth, development, and yield.

**Mudança climática e agroecossistemas: efeito do aumento de CO<sub>2</sub> atmosférico e temperatura sobre o crescimento, desenvolvimento e rendimento das culturas.**

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### - REVIEW -

#### ABSTRACT

*The amount of carbon dioxide (CO<sub>2</sub>) 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<sub>2</sub> 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<sub>2</sub> concentration and temperature on crop growth, development, and yield. Increasing CO<sub>2</sub> concentration increases crop yield once the substrate for photosynthesis and the gradient of CO<sub>2</sub> concentration between atmosphere and leaf increase. C<sub>3</sub> plants will benefit more than C<sub>4</sub> plants at elevated CO<sub>2</sub>. However, if global warming will take place, an increase in temperature may offset the benefits of increasing CO<sub>2</sub> on crop yield.*

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

#### RESUMO

*A quantidade de dióxido de carbono (CO<sub>2</sub>) 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<sub>2</sub> 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<sub>2</sub> atmosférico e da temperatura sobre o crescimento, desenvolvimento e rendimento das culturas agrícolas. O aumento da concentração de CO<sub>2</sub> aumenta o rendimento das*

*culturas, uma vez que o substrato para fotossíntese e o gradiente de CO<sub>2</sub> entre a atmosfera e a folha aumentam. As plantas C<sub>3</sub> terão maior benefício com o aumento de CO<sub>2</sub> do que as plantas C<sub>4</sub>. Se o aquecimento global acontecer, um aumento da temperatura do ar pode anular os benefícios do aumento do CO<sub>2</sub> 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<sub>2</sub>), are increasing (BACASTOW et al., 1985; IPCC, 2001). It is expected that atmospheric CO<sub>2</sub> concentration will double sometime during this century if fossil fuels burning continues and air temperature is predicted to rise 1.5 to 5°C with more than 90% likelihood by 2100 (BAES et al., 1977; MAHLMAN, 1997). As a consequence of a possible increase in atmospheric CO<sub>2</sub> 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<sub>2</sub> concentration and associated climate change. The direct effect of increasing CO<sub>2</sub> 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<sub>2</sub> concentration between atmosphere and leaf will increase. Current atmospheric CO<sub>2</sub> concentration (about 360 μmol mol<sup>-1</sup>) is insufficient to saturate the ribulose 1.5-bisphosphate carboxylase (Rubisco), the enzyme responsible for primary carboxylation, the metabolic process that drives photosynthesis, 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<sub>2</sub> 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<sub>2</sub> concentration. Therefore, the interacting effects of CO<sub>2</sub> 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<sub>2</sub> concentration and temperature on crop growth, development, and yield.

#### Atmospheric CO<sub>2</sub> concentration and global warming

The CO<sub>2</sub> concentration of the Earth's atmosphere during the last ice aging may have been as low as 160-200 μmol mol<sup>-1</sup> (DELMAS et al., 1980). After industrial revolution, atmospheric CO<sub>2</sub> concentration has increased significantly, specially during the second half of the last century. Atmospheric CO<sub>2</sub> concentration is believed to be increasing at a rate of 0,4-0,5% year<sup>-1</sup> (IPCC, 1995; SOMBROEK & GOMMES, 1996) or 1-1,8 μmol mol<sup>-1</sup> per year (ROSENBERG et al., 1983; IPCC, 1995; UNSWORTH & HOGSETT, 1996). Atmospheric CO<sub>2</sub> concentration increased from about 315 μmol mol<sup>-1</sup> in 1958 to over 345 μmol mol<sup>-1</sup> in 1985 (BACASTOW et al., 1985). Consequently, the current 360 μmol mol<sup>-1</sup> 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). MITCHELL et al. (1995) suggested an increase of global temperature by 0.3°C decade<sup>-1</sup> considering greenhouse gases alone, and a 0.2°C decade<sup>-1</sup> 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<sup>-1</sup> (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<sub>2</sub> concentration

Characterizing the response of stomata to elevated CO<sub>2</sub> is important for understanding the effect of elevated CO<sub>2</sub> on crop response. Stomata close in response to elevated CO<sub>2</sub> (UNSWORTH & HOGSETT, 1996). A doubling CO<sub>2</sub> 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<sub>2</sub> concentration is not clear yet (MORISON, 1987; MOTT, 1990; VAN DE GEIJN & GOUDRIAAN, 1996). Stomata apparently do not respond directly to the CO<sub>2</sub> concentration around the leaf (MORISON, 1987). The CO<sub>2</sub> 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<sub>2</sub> (MEIDNER & MANSFIELD, 1965). Plants tend to regulate CO<sub>2</sub> concentration in the stomatal cavity (C<sub>i</sub>), so that for a given vapor pressure deficit there is a constant ratio C<sub>i</sub> with the atmospheric concentration, C<sub>i</sub>/C<sub>a</sub> (MORISON, 1987; MOTT, 1990). The ratio C<sub>i</sub>/C<sub>a</sub> 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 C<sub>i</sub>/C<sub>a</sub> regulation would lead to the partial closure at elevated CO<sub>2</sub> concentration. Photosynthesis and water-relations of native grassland species and C<sub>i</sub>/C<sub>a</sub> for C3 and C4 plants measured by JACKSON et al. (1994) confirm the conservation of the C<sub>i</sub>/C<sub>a</sub> value, with only a small tendency to rise with increasing CO<sub>2</sub> concentration.

The possibility of acclimation of the stomata movement to long-term exposure to elevated CO<sub>2</sub> concentration has been pointed out, but this is a controversial issue. Some studies suggest that the lower stomatal conductance (g<sub>s</sub>) does not only persist over extended exposure periods to elevated CO<sub>2</sub> concentration, but it is also kept after subsequent lowering of the CO<sub>2</sub> concentration (VAN DE GEIJN & GOUDRIAAN, 1996). STANGHELLINI & BUNCE (1994) reported that g<sub>s</sub> of tomato plants cultivated at high CO<sub>2</sub> concentration was less sensitive to short-term CO<sub>2</sub> concentration fluctuations and higher than that of plants grown at ambient CO<sub>2</sub> concentration and measured at double current CO<sub>2</sub> concentration. This may indicate that the sensitivity of g<sub>s</sub> of high CO<sub>2</sub> concentration plants to change in CO<sub>2</sub> concentration is reduced, but still a lower g<sub>s</sub> exists when compared to leaves growing and measured in present CO<sub>2</sub> concentration conditions (VAN DE GEIJN & GOUDRIAAN, 1996).

Studies have shown that short-term gain of elevated CO<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub>.

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<sub>2</sub> 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<sub>2</sub> concentration and the root:shoot ratio increased about 10% at elevated CO<sub>2</sub> concentration (USUDA & SHINOGAWARA, 1998).

Plant growth and development response to elevated CO<sub>2</sub> concentration and temperature

Since long time ago, the effect of CO<sub>2</sub> concentration on crop yield has been studied. According to KIMBALL (1983a), de Saussure, in 1804, first demonstrated that peas exposed to high CO<sub>2</sub> concentration "grew better" than control plants in ambient air. Fertilization or enrichment of air with CO<sub>2</sub> 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<sub>2</sub> concentration and plant response. Very few studies indicate a yield depression at elevated CO<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub> 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	-	WHEELER 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 <sup>1</sup>	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)

<sup>1</sup>37% increase in annual yield (fresh weight) and 105% in dry weight of roots.

ns=not significant

CO<sub>2</sub> mol<sup>-1</sup> would be about 30 to 40% and 9%, greater than present yields, respectively. Below-ground growth is also increased at elevated CO<sub>2</sub> 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<sub>2</sub> concentration. AOKI & YABUKI (1977) found that dry matter production and photosynthetic rate of cucumber increased in plants exposed to CO<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub> metabolism: C3, C4 and CAM, and each responds to elevated CO<sub>2</sub> 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<sub>2</sub> 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<sub>a</sub> and C<sub>chl</sub> are the CO<sub>2</sub> concentrations in the atmosphere and at the chloroplast level (available to the photosynthetic biochemistry), and r<sub>a</sub>, r<sub>s</sub> and r<sub>m</sub> are the air, stomatal and mesophyll resistances to the diffusion of CO<sub>2</sub>.

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<sub>tc</sub> is the stomatal + leaf boundary layer conductance to CO<sub>2</sub> and C<sub>a</sub> and C<sub>i</sub> are the mole fractions of ambient and leaf intercellular spaces CO<sub>2</sub>. If atmospheric CO<sub>2</sub> concentration increases, the gradient or "driving force" for photosynthesis (C<sub>a</sub>-C<sub>chl</sub>) or (C<sub>a</sub>-C<sub>i</sub>) is increased, an effect of relatively greater significance in C3 plants (because C<sub>i</sub> is higher in plants having photorespiration) than in C4 plants, where the CO<sub>2</sub> concentration difference (C<sub>a</sub>-C<sub>i</sub>) is usually greater (ROSENBERG et al., 1983).

Two responses to elevated CO<sub>2</sub> are an increase in the rate of photosynthesis and a decrease in stomata conductance (UNSWORTH & HOGSETT,

1996). In the Flux Gradient approach, r<sub>a</sub> is not affected by ambient CO<sub>2</sub> concentration and r<sub>m</sub> may be slightly responsive. The r<sub>c</sub> is relatively small compared to the sum of r<sub>a</sub> and r<sub>m</sub>, 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<sub>s</sub> at elevated CO<sub>2</sub> concentration. Despite a stomatal conductance decrease is observed with CO<sub>2</sub> concentration increase, C<sub>i</sub> 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<sub>2</sub> 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<sub>2</sub> concentration suppresses photorespiration, because this process proceeds at a rate dependent upon competition between O<sub>2</sub> and CO<sub>2</sub> for enzymatic sites (EHLERINGER & BJORKMAN, 1977). An increase in the availability of CO<sub>2</sub> increases carboxylation and decreases the oxygenase activity of Rubisco, hence reducing CO<sub>2</sub> 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 C<sub>i</sub> concentrating mechanisms, so their photosynthetic performance is not expected to increase greatly in response to atmospheric CO<sub>2</sub> concentration increase. The CO<sub>2</sub> concentrating mechanisms of these plants allows the leaf to maintain high photosynthetic rates at lower internal CO<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub> concentration (ADAMS et al., 1990; EL MAAYAR et al., 1997; SAVABI & STOKLE, 2001). An example is maize, reported not to be sensitive to CO<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub> 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 550 μmol mol<sup>-1</sup> 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 CO<sub>2</sub> concentration. During the crop season, the authors reported a decrease of 4% in net radiation (R<sub>n</sub>), an increase of 0,6°C in canopy temperature and a decrease of 7,9% in evapotranspiration due to elevated CO<sub>2</sub>. 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<sub>2</sub> concentration. These contradictory results show that there are many uncertainties about the effect of increasing CO<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub> and solubility of CO<sub>2</sub> relative to O<sub>2</sub> (JORDAN & OGREN, 1984; BROOKS & FARQUHAR, 1985). The latter two effects result in greater losses of CO<sub>2</sub> to photorespiration, which decreases net CO<sub>2</sub> assimilation. This effect occurs mainly in C3 plants, either at normal CO<sub>2</sub> concentration or at CO<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub> 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<sup>-1</sup> day<sup>-1</sup> 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 1.51 mg grain<sup>-1</sup> day<sup>-1</sup>. 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 2.8 mg (WIEGAND & CUELLAR, 1981). Studies with wheat showed an average decrease of 2.8 days in grain filling period and a kernel weight decrease of 1.5 mg 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 & INGRAM, 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<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub> concentration. Similar results were reported by SAVABI & STOKLE (2001) that increase in yield of maize and soybean due to doubling CO<sub>2</sub> 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<sub>2</sub>. 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<sub>2</sub> 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<sub>2</sub> and air temperature increase related to current yield and crop growth duration.

Crop	CO <sub>2</sub> (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) <sup>2</sup>
	515	-	-	-	-	-	-	21	-	-	-	Canada	EI MAAAYAR et al. (1997)
	630	-	-	-	-	-	-	9 to-20	-	-	-	USA	ADAMS et al. (1990) <sup>1</sup>
	660	-	-	-	-	-	-	-	-	-32 to-50	-	USA	ADAMS et al. (1990) <sup>1</sup>
	550	5 to 25	-	to -35	-	-10 to-50	-	-15 to-70	-	-	-	USA	ROSENZWEIG & TUBIELO (1996) <sup>3</sup>
Soybean													
	555	-	-	-3	-3	-	-	-11	-1	-	-	Brazil	SIQUEIRA et al. (1994) <sup>2</sup>
	515	-	-	-	-	-	-	23	-	-	-	Canada	EI MAAAYAR et al. (1997)
	630	-	-	-	-	-	-	49 to-20	-	-	-	USA	ADAMS et al. (1990) <sup>1</sup>
	660	-	-	-	-	-	-	-	-	40 to -40	-	USA	ADAMS et al. (1990) <sup>1</sup>
Mayze													
	550	-	-	-9	-10	-	-	-20	-17	-	-	Brazil	SIQUEIRA et al. (1994) <sup>2</sup>
	515	-	-	-	-	-	-	6	-	-	-	Canada	EI MAAAYAR et al. (1997)
	630	-	-	-	-	-	-	49 to-20	-	-	-	USA	ADAMS et al. (1990) <sup>1</sup>
	660	-	-	-	-	-	-	-	-	40 to -20	-	USA	ADAMS et al. (1990) <sup>1</sup>
Rice													
	660	4	3	-5	-2	-	-	-	-	-25	-	India	LAL et al. (1998)

<sup>1</sup>Simulated range for the entire USA

<sup>2</sup>Average of several regions in Brazil

<sup>3</sup>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<sub>2</sub> concentration but an increase of 1°C in maximum temperature is enough to decrease the response of wheat to double CO<sub>2</sub> 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<sub>2</sub> concentration. If temperature will change, an increase in air temperature as low as 1°C

may offset the benefits of increasing CO<sub>2</sub> 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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