



Interactions of CO₂, Temperature and Management Practices: Simulations with a Modified Version of CERES-Wheat

Francesco N. Tubiello

Columbia University-Goddard Institute for Space Studies, 2880 Broadway,
New York, NY 10025, USA

Earth Systems Science Department, New York University, 34 Stuyvesant St,
New York, NY 10003, USA

Cynthia Rosenzweig

Columbia University-Goddard Institute for Space Studies, 2880 Broadway,
New York, NY 10025, USA

&

Tyler Volk

Earth Systems Science Department, New York University, 34 Stuyvesant St,
New York, NY 10003, USA

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ABSTRACT

*A new growth subroutine was developed for CERES-Wheat, a computer model of wheat (*Triticum aestivum*) growth and development. The new subroutine simulates canopy photosynthetic response to CO₂ concentrations and light levels, and includes the effects of temperature on canopy light-use efficiency. Its performance was compared to the original CERES-Wheat V-2.10 in 30 different cases. Biomass and yield predictions of the two models were well correlated (correlation coefficient $r > 0.95$). As an application, summer growth of spring wheat was simulated at one site. Modeled crop responses to higher mean temperatures, different amounts of minimum and maximum warming, and doubled CO₂ concentrations were compared to observations. The importance of irrigation and nitrogen fertilization in modulating the wheat crop climatic responses were also analyzed. Specifically, in agreement with observations, rainfed crops were found to be more sensitive to CO₂ increases than irrigated ones. On the other hand, low nitrogen applications depressed the ability of the wheat crop to respond positively to CO₂ increases. In general, the positive effects of high CO₂ on*

grain yield were found to be almost completely counterbalanced by the negative effects of high temperatures. Depending on how temperature minima and maxima were increased, yield changes averaged across management practices ranged from -4% to 8%.

INTRODUCTION

Atmospheric CO₂ levels have been steadily rising during the past century, as a result of fossil-fuel burning and land clearing (Siegenthaler & Sarmiento, 1993). Current levels are about 355 ppm, or 25% higher than the pre-industrial value of 280 ppm (Keeling, 1991). Other greenhouse gases (CH₄, CFCs, NO₂) are also on the rise in the atmosphere. If the current rate of emissions continues, global mean temperatures are predicted to increase 1.5–4.5°C by the middle of the next century (Hansen *et al.*, 1988; Houghton *et al.*, 1990). Precipitation patterns are also expected to change. Many studies indicate that high CO₂ levels and rising mean temperatures will affect crop yields (Kimball, 1983; Acock & Allen, 1985; Acock, 1991). While CO₂ alone would most probably increase yields, interactions with factors like temperature, precipitation and management practices make predictions less certain. Computer simulations, although no substitute for field experiments, can help estimate the net effects of such changes, particularly when many feedback mechanisms are at work. For these reasons, the authors modified CERES-Wheat V-2.10 (Otter-Nacke *et al.*, 1986; Ritchie & Otter-Nacke, 1985), a computer model simulating development and growth of wheat under a variety of climatological and management conditions. The new version was used to investigate the effects of CO₂ and temperature on wheat biomass and yield.

A number of changes had already been introduced to CERES-Wheat. Peart *et al.* (1989) and Rosenzweig (1989) used a multiplicative parameter to modify daily carbon assimilation as a function of CO₂ concentration. They also included a subroutine to calculate the effects of higher CO₂ levels on stomatal closure of wheat leaves. The present authors further modified CERES-Wheat by substituting its original calculations of daily biomass accumulation with more mechanistic equations for instantaneous photosynthesis.

A NEW PHOTOSYNTHETIC MODULE FOR CERES-WHEAT

CERES-Wheat V-2.10 simulates canopy photosynthesis with the following equation:

$$P_C = A(1 - e^{-kLAI})PAR^a \quad (1)$$

where P_C , in units of g biomass m⁻² day⁻¹, is the daily potential photosynthate; LAI is the canopy leaf area index; $k=0.85$ is the wheat canopy light-extinction coefficient; PAR is the daily incident photosynthetic active radiation, in units of MJ day⁻¹; $a=0.6$ is a dimensionless exponent; and $A=7.5$ is conversion factor. The potential photosynthate P_C is then further reduced by factors related to temperature, soil water deficit and nutrient stress, each of which is calculated in separate routines. There are three assumptions in the above CERES-Wheat equation for photosynthesis:

- (1) Respiration rates are proportional to gross photosynthesis, and are accounted for in P_C (the proportionality ratio is temperature-dependent, peaking at $T=18^\circ\text{C}$).
- (2) Daily biomass accumulation is directly proportional to daily intercepted light (Monteith, 1977).
- (3) Whole canopy leaf area behaves as a single leaf, i.e. light interception is simulated with a modified big-leaf model (Boote & Loomis, 1991).

No physiological effects of CO₂ are simulated. The authors modified CERES-Wheat equations for photosynthesis by modifying assumptions (2) and (3). Assumption (1) was left unchanged.

Light interception

The single-leaf model of CERES-Wheat was replaced with a simplified version of the two-box 'sun + shade' model of Boote and Loomis (1991). The wheat canopy was divided into two light areas, one exposed to direct sunlight, the other shaded, but day-time variations in the angular distribution of light entering the canopy were not considered. Likewise, diffuse light transmitted to the shaded area was considered to be a fixed fraction of total radiation. The equations for light interception were thus written as:

$$\text{LAI}_{\text{Sun}} = (1 - e^{-k\text{LAI}})/k; \quad \text{LAI}_{\text{Shade}} = \text{LAI} - \text{LAI}_{\text{Sun}} \quad (2)$$

$$I_{\text{Sun}} = (1 - e^{-k\text{LAI}})(1 - \sigma)I \quad (3)$$

$$I_{\text{Shade}} = (1 - e^{-k\text{LAI}_{\text{Shade}}})\sigma I \quad (4)$$

where I is the photosynthetically active radiation above the canopy; σ is the fraction of light either reflected or transmitted by the leaves; k is a constant canopy light-extinction coefficient; and LAI is the canopy leaf area index, divided into a sunlit and a shaded part, LAI_{Sun} and $\text{LAI}_{\text{Shade}}$.

Photosynthesis

Boote's model for light interception was coupled with the equations for canopy photosynthesis of Charles-Edwards (1981) and Acock (1991). Because assumption (1) was not changed, equations were used to directly calculate potential *net* photosynthetic rates, rather than gross photosynthesis, in analogy to the original calculations in CERES-Wheat. No independent respiration term was included. Photosynthetic uptake was converted to biomass accumulation by a multiplying constant, A . Potential net photosynthesis was first calculated on a per leaf area basis in each of the two light areas:

$$P_{C,i} = \frac{\alpha I \phi C}{\alpha I + \phi C}, \quad i = \text{sun, shade} \quad (5)$$

in units of $\text{mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. The parameter α is the leaf light-use efficiency; I is the light absorbed per unit leaf area; C is the CO_2 ambient concentration; and ϕ is the overall conductance to CO_2 . Figure 1(a) shows the modeled photosynthetic response to light, as a function of leaf area index.

In eqn (5) for leaf photosynthesis, the overall conductance to CO_2 , ϕ , was modeled as a function of the CO_2 concentration and the leaf carboxylation conductance, τ (Charles-Edwards, 1981) (see Fig. 1b):

$$\phi(C) = \frac{\tau}{1 + \delta \tau C}. \quad (6)$$

The rate of light-saturated photosynthesis, $P_{C,\text{MAX}}$, was found by substituting eqn (6) into eqn (5), and calculating the limit for $I \rightarrow \infty$:

$$P_{C,\text{MAX}} = \frac{\tau C}{1 + \delta \tau C}. \quad (7)$$

The parameter $1/\delta$ in eqns (6) and (7) is thus the maximum rate of photosynthesis when both light and CO_2 are non-limiting (see Fig. 1c). The two parameters δ and τ were then calculated by specifying $P_{C,\text{MAX}}$ at two CO_2 levels in eqn (7). Finally, the effects of photorespiration on leaf light-use efficiency were included in the model by writing (Acock, 1991):

$$\alpha = \alpha_m (1 - \beta O / \tau C) \quad (8)$$

where O is the ambient oxygen concentration; α_m is the maximum leaf light-use efficiency, and β and τ are leaf carboxylation coefficients for O_2

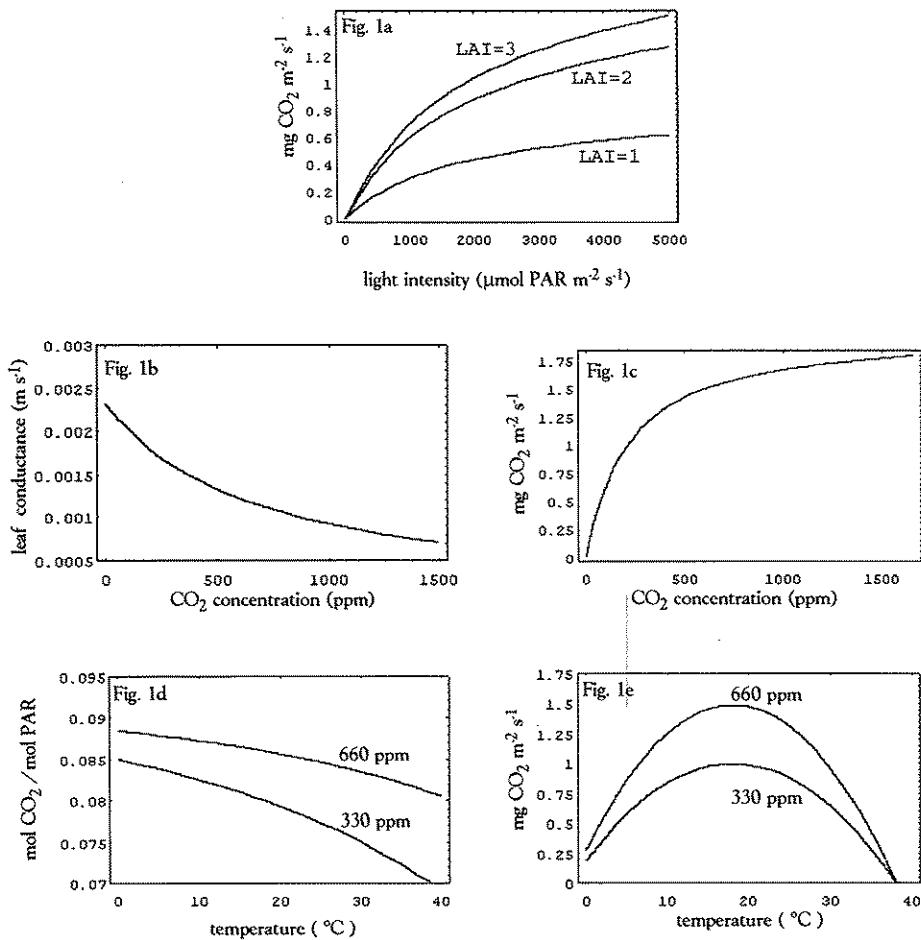


Fig. 1. Modeled photosynthetic responses to light, CO₂ and temperature: (a) canopy response to light as a function of leaf area index, at 330 ppm CO₂; (b) leaf conductance to CO₂ as a function of CO₂ concentration itself; (c) light-saturated rates of leaf photosynthesis as a function of CO₂ concentration; (d) temperature effects on light-use efficiency due to photorespiration, calculated at both ambient (330 ppm) and double CO₂ concentration; (e) effects of temperature on canopy photosynthetic rates due to plant respiration, at both ambient and double CO₂ concentration (same model as in CERES-Wheat V-2.10).

and CO₂, respectively. The ratio β/τ is temperature dependent (see Fig. 1d), but it is found to be approximately species-independent in C₃ plants (Charles-Edwards, 1981).

Since the model is divided into two light area, integration of eqn (5) throughout the canopy, as done by Acock *et al.* (1978), was not necessary.

Canopy total potential assimilation was instead expressed as:

$$P_C = A (P_{C,\text{sun}} \text{LAI}_{\text{sun}} + P_{C,\text{sh}} \text{LAI}_{\text{sh}}) \quad (9)$$

where A is a conversion factor into units of $\text{g biomass m}^{-2} \text{s}^{-1}$. Equation (9) was integrated in time-steps of one hour, using a full sine wave to account for variation of light intensity throughout the day. Following CERES-Wheat V-2-10, potential assimilation was then reduced as a function of temperature (see Fig. 1c).

Choice of coefficients and determination of parameters

Since quantities were expressed on a per leaf area basis, measurements of leaf photosynthesis were used directly to specify most of the coefficients in the equations. The following values were chosen from the literature: $\sigma = 0.20$ (Boote & Loomis, 1991); $k = 0.85$ (Ritchie & Otter-Nacke, 1985; Otter-Nacke *et al.*, 1986); $\beta/\tau = 1.2 \times 10^{-4} e^{0.0295T}$ (Acock, 1991); $P_{C,\text{MAX}} = 1 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ at 330 ppm (Teramura *et al.*, 1990; Boote & Loomis, 1991). The maximum light-use efficiency, α_m , and the conversion constant, A , were obtained by least-squares fit in order to maximize agreement between the original CERES-Wheat and the authors' modified version. Thirty base cases were used for the fit, comparing simulations of wheat grown in four locations: Manhattan, Kansas, USA; Swift Current, Canada; Rothamsted,

TABLE 1
Parameters for Leaf Photosynthesis used in the Model^a

Parameter	Symbol	Units	330 ppm	660 ppm	Maximum
Leaf reflectance and transmittance	σ	nondimensional	20%	20%	20%
Light-extinction coefficient	k	nondimensional	0.85	0.85	0.85
Light-use efficiency	α	$\text{mol CO}_2/\text{mol PAR}$	0.080	0.086	0.090*
Leaf conductance	ϕ	m s^{-1}	1.5×10^{-3}	0.8×10^{-3}	2.3×10^{-3} **
Light-saturated photosynthesis	$P_{C,\text{MAX}}$	$\text{mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$	1	1.5	1.8***

Notes:

* α_m .

** τ .

*** $1/\delta$.

^a Values shown are at ambient (330 ppm) and double (660 ppm) CO_2 concentration. Light-use efficiency is calculated at ambient oxygen concentration (21%) and temperature $T = 18^\circ\text{C}$. Maximum values (light and CO_2 non-limiting) are also given.

UK; and Tel Hadya, Syria. These cases cover a wide range of meteorological conditions and management practices, using weather, soil, and cultivar data provided in CERES-Wheat V-2.10. The following were found: $A = 2.94$ and $\alpha_m = 0.09$ mol CO₂/mol PAR. The parameter for maximum light-use efficiency gives $\alpha = 0.08$ mol CO₂/mol PAR (or 16.2×10^{-9} kg CO₂J⁻¹) at ambient CO₂ concentrations and $T = 18^\circ\text{C}$ (see Fig. 1d). This value is comparable to that of 17×10^{-9} kg CO₂J⁻¹ used by Goudriaan *et al.* (1984) in simulations of wheat growth. Table 1 summarizes the values of the model's key leaf parameters.

As shown in Fig. 2, values of biomass and yield simulated with our modified model were highly correlated with those predicted by CERES-Wheat ($r = 0.98$ and $r = 0.95$ for biomass and yield, respectively).

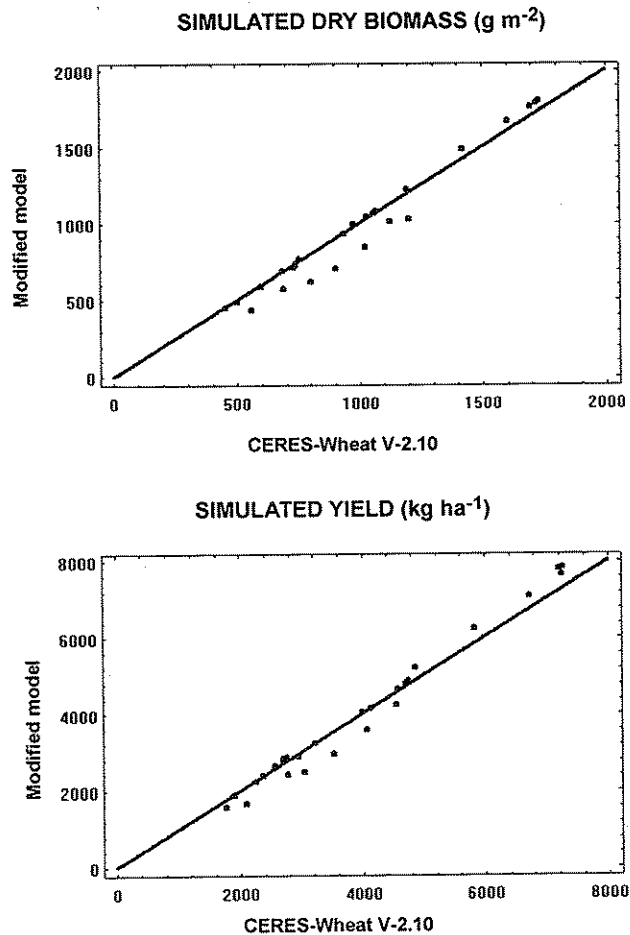


Fig. 2. Comparison of biomass and grain yield predictions between the modified model and CERES-Wheat V-2.10. Correlation coefficients are $r = 0.98$ and $r = 0.95$, respectively.

Validity of model simulations

The modified version of CERES-Wheat developed as described here is intended for use in investigations of CO₂ and temperature effects on wheat. Various limitations apply to its predictions. First, CERES-Wheat simulates wheat phenological and morphological development as observed in ambient CO₂ concentrations. As a result, changes in plant structure and growth stages caused by different CO₂ levels are not included in the simulations. Second, temperature effects on both instantaneous photosynthesis and canopy energy balance introduce large factors of uncertainty. Although direct temperature effects on light-use efficiency were included, the temperature-dependent interactions of gross photosynthesis and respiration, interpolated from field data in CERES-Wheat, were not modified. In addition, energy balance calculations were not used to simulate leaf temperature, a variable that plays an important role in determining the canopy transpirational demands.

Thus, results of the simulations are valid to the extent that changes in canopy total assimilation and growth rates due to CO₂ effects on: leaf temperature; root and shoot respiration; plant phenology and morphology, are small compared to those due to: temperature effects on canopy life-cycle and vernalization; direct CO₂-fertilization; and water and nitrogen feedbacks.

EFFECTS OF HIGHER CO₂ CONCENTRATION

A recent review of crop responses to carbon dioxide indicates that wheat biomass might increase by about 30% under doubled CO₂ conditions (Lawlor & Mitchell, 1991). Earlier estimates are consistent with such values (Cure, 1985). However, many studies suggest that the range of wheat biomass and yield responses to high CO₂ levels is large, depending on factors such as water stress (Chaudhuri *et al.*, 1989), nutrients levels (Sionit *et al.*, 1981a), and light (Gifford, 1977). Developmental stage is an important factor as well (Fisher & Aguilar, 1976), with responses to CO₂ depending on such factors as availability of assimilates during grain filling (Sionit *et al.*, 1981b).

Gifford (1977) found that a 54% increase in leaf photosynthesis at doubled CO₂ resulted in about a 32% increase in biomass and a 43% increase in yield. A 50% increase in instantaneous photosynthesis at doubled CO₂ was also found in other studies (Akita & Moss, 1973; Chmora *et al.*, 1976; Havelka *et al.*, 1984; Teramura *et al.*, 1990). Sionit *et al.* (1981a) found that for a well-watered spring wheat the increase in dry biomass in

response to doubled CO₂ strongly depended on nutrients supplied to the canopy. Measured increases ranged from 8% to 36%, the larger response correlating with higher nutrient levels. Chaudhuri *et al.* (1989) found that the yield of wheat grown under higher CO₂ concentrations was dependent upon the degree of canopy water stress. Stomatal closure under high CO₂ lowers canopy transpiration, therefore reducing water stress relative to ambient CO₂ conditions. Yield increases for doubled CO₂ were about 35% under well-watered conditions, but over 50% for water-stressed wheat canopies.

In all experiments a roughly constant increase in instantaneous photosynthetic rates per unit leaf area of about 50% was observed at doubled CO₂ levels. In contrast, the wide range of observed biomass and yield responses appears to be mainly the result of a series of feedbacks, depending on water and nitrogen applications. The modified model was used to test this hypothesis. The ambient CO₂ level was set at 330 ppm, consistent with the CO₂ concentration used in many studies. The corresponding doubled CO₂ concentration was 660 ppm. Using eqn (7), the maximum photosynthetic rate $P_{C,MAX} = 1 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ was set at 330 ppm, and a 50% increase at 660 ppm was assumed. The solution to the resulting system of two equations yielded values for the two parameters δ and ϕ to be used in the simulations. It was found that $1/\delta = 1.8 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, and $\tau = 2.3 \times 10^{-3} \text{ m s}^{-1}$.

In addition, the evapotranspiration routine in CERES-Wheat was modified in order to include direct CO₂ effects on stomatal closure, as described by Allen *et al.* (1985). Such modifications were originally adapted for CERES-Wheat by Peart *et al.* (1989) and Rosenzweig (1989). The equations used by these authors, and introduced in the present model, reduce the transpirational demands of the wheat canopy as CO₂ concentration increases.

Simulation of indirect effects of CO₂ enrichment (positive and negative feedbacks due to higher leaf area, larger root masses, leaf senescence, etc.) on the wheat canopy were a result of the equations specified in the original CERES-Wheat model. In this respect, the comparison of the present simulation results with observations represented a further test of the predictive ability of CERES-Wheat.

APPLICATION: GROWTH SIMULATION OF SPRING WHEAT

Most of the experiments cited in the previous section involve spring wheat, which is easier to grow in experimental environments than winter wheat. In order to test the model results against such observations, simulations were run using a spring wheat variety, Manitou, grown in summer—May

to September—at the site of Swift Current, in the heart of the south-western Canadian wheat belt. The use of summer light in the runs might have minimized some of the possible errors related to the simulation of wheat morphology at doubled CO₂ concentrations. Comparing wheat growth at doubled CO₂ with that occurring in ambient levels, Gifford (1977) observed that in summer light both leaf specific weight and tillering did not change, while they increased when winter light levels were used.

In the authors' simulations, spring wheat was grown in wood mountain loam soil, with a density of 250 plants m⁻², under fixed local meteorological conditions of light, temperature and precipitation (1975 summer season). Twelve different experiments were run, varying both irrigation and nitrogen applications. Two water regimes were simulated. A first group of six simulations was rain-fed. A second group of six simulations was irrigated. Irrigation was applied 15 times during the growing season, every two to three days on average. The total amount of irrigation water applied was 254 mm m⁻². Total precipitation was 161 mm m⁻². Within each set, nitrogen applications were varied, increasing from a minimum value of 20.5 kg ha⁻¹ to a maximum of 180 kg ha⁻¹. Average daily temperature over the growing season was about 19.5°C, while total accumulated degree-days were 1502°C day. In all cases, wheat was planted at the end of May and reached maturity after a period of about three months.

The simulation results refer to one growing season only. Some of the details in the trends found may therefore be a consequence of specific weather patterns.

Simulation results: biomass and yield response to doubled CO₂ levels

Effects of doubled CO₂ concentrations on both biomass and yield are shown in Figs 3 and 4. Qualitatively, the simulations reproduce some of the effects observed in the experiments previously described. First, within each water regime, biomass and yield increases relative to the base case were found to be correlated with nutrient levels. Biomass increased overall from 6% to about 37%, while yield increases were larger, from 7% to 46%, suggesting that at doubled CO₂ concentration a larger supply of assimilates was available at the time of grain filling. Second, relative responses to high CO₂ were larger in rain-fed canopies than in irrigated ones, showing that higher CO₂ compensated for water stress.

Simulated root-to-shoot ratios also increased in high CO₂. In both water regimes, increases were larger for nitrogen-stressed canopies than for well-fertilized ones. Various authors (Sionit *et al.*, 1981a; Goudriaan & de Reuter, 1983) have found similar results, although others have published opposite data (Morison & Gifford, 1984).

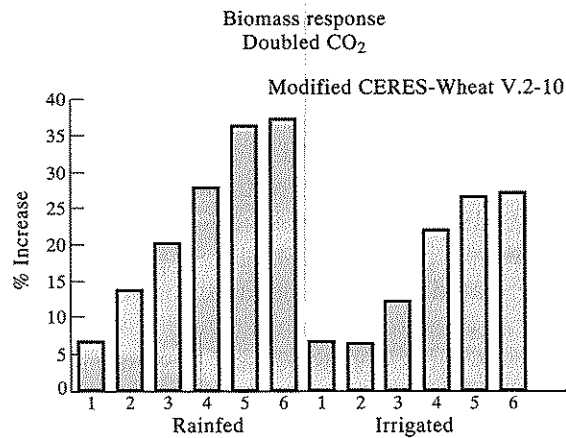


Fig. 3. Simulated biomass increases in response to doubled CO₂ concentrations. Increasing nitrogen applications are indicated as follows: 1 = 20 kg N ha⁻¹; 2 = 40 kg N ha⁻¹; 3 = 60 kg N ha⁻¹; 4 = 80 kg N ha⁻¹; 5 = 120 kg N ha⁻¹; 6 = 160 kg N ha⁻¹

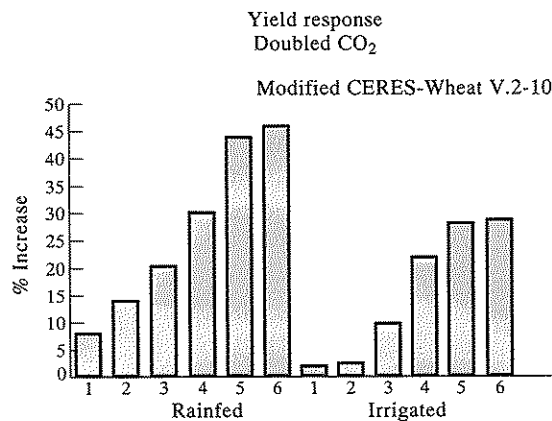


Fig. 4. Simulated yield increases in response to doubled CO₂ concentrations. Increasing nitrogen applications are indicated with numbers from 1 to 6, as specified in Fig. 3.

Water use efficiency at doubled CO₂ levels: stomatal closure versus root water uptake

The largest relative increases found for simulated wheat biomass and yield, 37% and 46% respectively, occurred in rain-fed conditions. Such relative increases were almost 50% larger than those occurring in irrigated canopies. This effect has been observed in the field (Chaudhuri *et al.*, 1990). Stomatal closure of wheat leaves in high CO₂ has usually been

proposed as an explanation (Gifford, 1979; Sionit *et al.*, 1981c), through reduction of transpiration per unit LAI and increase in canopy water-use efficiency (WUE, defined as the ratio of total dry biomass to total water transpired). Indeed, as Fig. 5 shows, simulated rain-fed canopies were found to exhibit larger increases in WUE than irrigated ones. Surprisingly, however, when all 12 simulations were run without the effects of stomatal closure (Peart *et al.*, 1989; Rosenzweig, 1989), relative increases in both biomass and yield were still found to be larger—about 30%—for rain-fed canopies than for irrigated ones. Further analysis of the model runs showed that root masses, in addition to stomatal closure, provided a strong feedback mechanism enhancing the CO₂ response of water-stressed canopies. In fact, larger root mass grown in doubled CO₂ allowed wheat canopies to uptake more water, therefore reducing water stress and further enhancing biomass accumulation. The larger water uptake was reflected in an increase in canopy total transpiration at doubled CO₂, along with WUE.

The same increases in root mass were found to characterize the growth of irrigated canopies in doubled CO₂. However, the positive feedback on biomass accumulation was not significant, since irrigated canopies were not water stressed.

Gifford (1979) speculated that larger roots might enhance the CO₂ response of water-stressed wheat canopies, in addition to stomatal closure. Larger root masses of canopies grown at higher CO₂ were observed in winter wheat (Chaudhuri *et al.*, 1990), while stomates of wheat leaves have been shown to respond weakly to increased CO₂ levels (Akita & Moss, 1973).

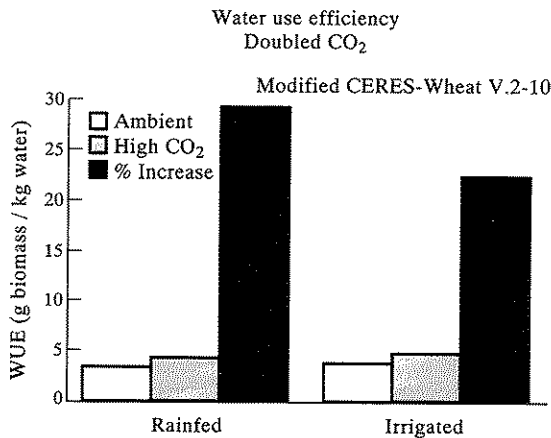


Fig. 5. Simulated water-use efficiency for wheat grown in ambient and doubled CO₂ concentrations. Values shown are for well fertilized (nitrogen application 6) canopies, corresponding to the largest relative increases in both biomass and yield.

Temperature effects

Temperature increases within the predicted range of global warming (Houghton *et al.*, 1990) were simulated to investigate possible effects on wheat yield. As a sensitivity analysis, the authors ran two simulations, scenarios A and B. In both the mean temperature of the previous runs was increased by 2°C. In scenario A, minimum and maximum temperatures were equally raised ($\Delta T_{\max} = \Delta T_{\min} = 2^\circ\text{C}$), while in scenario B, minima were raised three times as much as maxima ($\Delta T_{\max} = 1^\circ\text{C}$; $\Delta T_{\min} = 3^\circ\text{C}$). Recent studies suggest that global warming caused by accumulating greenhouse gases may bring larger increases in minimum night-time temperatures than in maximum daytime ones (Rind, 1991; Karl *et al.*, 1991). Indeed, temperature records of the last 50 years indicate that minimum temperatures have increased three times as much as maximum ones (Karl *et al.*, 1991). Figure 6 summarizes the results of the present study, showing the interactions of the temperature response with both water regimes. In both scenarios the overall effect of higher mean temperature on grain yield was negative. The average temperature for the simulations, about 19°C, was already above the CERES-Wheat photosynthetic optimum of 18°C. Temperature increases therefore diminished photosynthetic rates. Higher temperatures also raised transpirational demands and shortened the canopy life-cycle. As found with the simulations of doubled CO₂, the

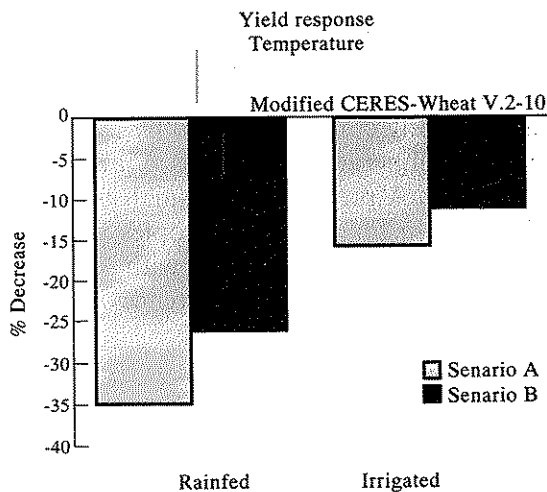


Fig. 6. Simulated yield decrease in response to a 2°C increase in mean ambient temperature. In scenario A, minimum and maximum temperatures were raised equally. In scenario B, minimum temperatures were raised three times as much as maximum temperatures. Values are averaged over nitrogen applications.

water regime influenced the canopy response to temperature. Rain-fed canopies were clearly more affected by temperature than irrigated ones. Larger transpirational demands, further increasing water stress, could perhaps explain such an effect (Butterfield & Morison, 1992). Indeed, grain yields decreased 50% more in the rain-fed water regime than in the irrigated one.

Differences caused by different minima and maxima temperature regimes were also pronounced. While average yield decreases in scenario A (both temperature minima and maxima raised by 2°C) were 35% for the rain-fed regime and 16% for the irrigated one, the corresponding decreases were only 26% and 11% in scenario B (minima raised three times as much as maxima). Raising minimum more than maximum temperatures resulted in a 27% reduction of the negative temperature effects at the simulation site.

Finally, the same temperature simulations were repeated using the original CERES-Wheat model, to investigate, by comparison of the two model results, temperature effects on light-use efficiency as they were modeled in the subroutine. Differences were found to be minor, on the order of a few percentage points. It is concluded that in the simulations, temperature effects on light-use efficiency over the entire life-cycle of the wheat canopy were small when compared to effects on carbon assimilation, potential transpiration and plant development.

Grain yield effects due to CO₂ and temperature

Simulations of grain yield were run by simultaneously doubling ambient CO₂ concentration and raising daily temperatures. Figure 7 shows the results, averaged over nitrogen applications. Decreases due to higher temperatures were generally counterbalanced by increases due to doubled CO₂ levels. However, temperature scenarios A and B gave significantly different results. Scenario A predicted very small overall changes in grain yield, with a 2% decrease for rain-fed canopies and a 4% increase for irrigated ones. On the contrary, simulations with scenario B showed yield increases of about 8%, with no marked differences between water regimes.

CONCLUSIONS

Modifications introduced in CERES-Wheat V-2.10 allow for simulations of wheat growth in both higher CO₂ and temperature. Model equations are written for instantaneous photosynthesis and are expressed on a per leaf area basis. As a result, they can be easily parameterized using measurements of leaf photosynthetic rates. Effects of CO₂/O₂ competition,

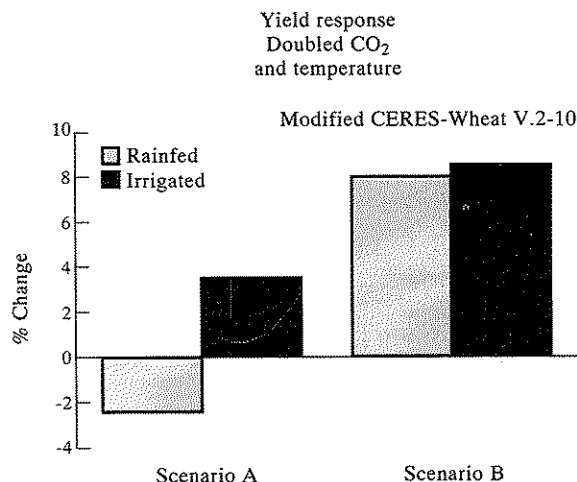


Fig. 7. Simulated yield variation in response to a 2°C increase in mean temperature and a doubling of CO₂. Scenarios A and B are the same as in Fig. 6. Values are averaged over nitrogen applications.

CO₂/light competition, and stomatal response to CO₂ were simulated. The new model version performed in ambient conditions comparably to CERES-Wheat V-2-10. In order to improve its simulation ability in different environmental conditions, however, modeling of canopy respiration and energy balance could be necessary.

Interactions between environmental variables and management practices were simulated at one site. A wide range of canopy responses to doubled CO₂ was reproduced, corresponding to the same increase in instantaneous photosynthetic rates modulated by different water and nitrogen applications. It was found that low fertility conditions depressed the ability of the wheat crop to respond positively to CO₂ increases, while water stress enhanced it. In addition to stomatal closure, increased root mass was found to strongly affect WUE of simulated water-stressed canopies, providing a positive feedback to CO₂ enhancement of biomass accumulation. On the contrary, higher temperatures had a negative effect on water-stressed canopies, depressing the CO₂ enhancement by further increasing transpirational demands.

Finally, the pattern of temperature change was important in determining the outcome of the results. At doubled CO₂ concentrations, equal increases in minimum and maximum temperatures caused small yield losses in rain-fed canopies, but gains in irrigated ones. When minimum temperatures were increased more than maximum ones, however, model simulations predicted yield gains in both water regimes.

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