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Growing wheat in Biosphere 2 under elevated CO_2: Observations and modeling

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Abstract

Spring wheat (*Triticum aestivum* L., cv. Yecora Rojo) was grown in the intensive agricultural biome (IAB) of Biosphere 2 during the 1995–1996 winter/spring season. Environmental conditions were characterized by a day/night temperature regime of 27/17°C, relative humidity (RH) levels around 45%, mean atmospheric CO_2 concentration of 450 ppmv, and natural light conditions with mean intensities about half of outside levels. Weekly samples of above-ground plant matter were collected throughout the growing season and phenological events recorded. A computer model, CERES-Wheat, previously tested under both field and controlled conditions, was used to simulate the observed crop growth and to help in data analysis. We found that CERES-Wheat simulated the data collected at Biosphere 2 to within 10% of observed, thus suggesting that wheat growth inside the IAB was comparable to that documented in other environments. The model predicts phenological stages and final dry matter (DM) production within 10% of the observed data. Measured DM production rates, normalized for light absorbed by the crop, suggested photosynthetic efficiencies intermediate between those observed under optimal field conditions and those recorded in NASA-Controlled Ecological Life-Support Systems (CELSS). We suggest that such a difference can be explained primarily in terms of low light levels inside the IAB, with

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additional effects due to elevated CO_2 concentrations and diffuse light fractions.

Keywords: Wheat; Biosphere 2; Controlled environments; Crop models; Elevated CO_2

1. Introduction

Increases in atmospheric CO_2 concentration and associated climate change may greatly affect wheat production in the next century, with important consequences for the world food supply (IPCC, 1996). Current knowledge on the interactions of CO_2 and key environmental and management factors are insufficient to draw definitive conclusions regarding the magnitude or even the direction of future changes in wheat yields. Elevated CO_2 alone will tend to increase photosynthetic rates, and therefore grain yields. Warmer temperatures will affect wheat growth and development negatively, counterbalancing to some extent the CO_2 effects. Recently it has been recognized that changes in climate variability may also have important effects on crop yield. Finally, management factors will certainly contribute to wheat yield responses under climate change. Crops with low nitrogen supplies are less likely to respond to elevated CO_2 (Sionit et al., 1981). Water stress, on the contrary, tends to enhance a plant's relative response to CO_2 due to increases in water-use efficiency (Chaudhuri et al., 1990).

In an attempt to reduce present uncertainties, dynamic crop-growth models originally developed to aid farmers optimize available resources have been used to assess the potential impacts of climate change on agricultural production (Rosenberg, 1993; Rosenzweig and Parry, 1994). The assumptions in these models, often based on empirical relations, need to be continuously improved and tested under both field and controlled-environment conditions (Rosenzweig and Tubiello, 1997). Collection of data for model-testing and further development should focus on long-term exposure to elevated CO_2, because crop growth is affected by several factors—plant acclimation, source-sink relationships, plant phenology, water and nutrient stresses, etc.,—during its entire life-cycle (Arp, 1991). There is a specific need to design experiments that improve our knowledge in the area of CO_2/temperature interactions, presently based only on a few studies (e.g. Baker and Allen, 1993; Rawson, 1995). Model equations that describe such processes are essentially untested (Mitchell et al., 1995).

Experiments designed to provide better links between field-level observations and model simulations are particularly important. For example, equations predicting canopy responses to CO_2 concentration are often based on leaf-level observations, but are virtually untested at the field scale. Only a few experiments that use CO_2-enriched open fields have been performed to date, most notably the Free-Air CO_2 Enrichment studies of Kimball et al. (1995). The intensive agricultural biome (IAB) of Biosphere 2 is an ideal site for experiments with agricultural crops under elevated CO_2, offering excellent environmental controls, and at the same time providing a growing environment that, because of the size of both its planting area and soil depth, is closer to mimicking field conditions than any other existing growth-chamber (Marino et al., 1999). We provide herein a first example illustrating the potential for integrating crop models and data from Biosphere 2. The results presented here describe a spring wheat experiment under elevated CO_2 that we performed during the 1995–1996 winter season. Model simulations were performed with CERES-Wheat, a well-tested field model for the predictions of wheat yields worldwide (Ritchie and Otter-Nacke, 1985). We used a new version of the model that can simulate growth under elevated CO_2 and includes effects of diffuse light on crop photosynthesis, which is important in growth-chamber conditions. In its latter version, CERES-Wheat has been used to reproduce wheat growth under ambient and elevated CO_2 in both field and growth-chamber environments (Tubiello et al., 1995; Volk et al., 1997).

Finally, crop models tested in the IAB can be used to help optimize agricultural yield as a function of given climate, soils, and management parameters, thus potentially helping in planning future missions of live crews inside Biosphere 2. More simply, they can be used as tools for data interpretation. We use herein, data and model simulations to investigate whether intrinsic differences exist between our observed IAB data and those collected in other experiments. Merely analyzing observed biomass growth rates is not sufficient for comparison purposes, because total light absorbed—the primary driver for biomass production—varies enormously among environments. It is instead necessary to calculate crop radiation-use efficiencies (RUE), or a plant's capacity to produce biomass per unit of absorbed photosynthetically-active radiation (PAR). The RUE parameter allows for the resolution of 'true' differences in crop performance. For example, wheat growth rates observed under ambient CO_2 in Controlled Ecological Life Support Systems (CELSS) are about four times better than the best growth rates achieved in the field under optimal conditions (Bugbee and Salisbury, 1988). Once growth rates are normalized by total light absorbed however, the resulting RUE under CELSS conditions is only about 40% higher than in the field (Tubiello et al., 1997).

2. Materials and methods

The IAB was designed to grow a variety of food crops to sustain humans and animals during extended periods of closure of Biosphere 2 (Marino et al., 1999). It consists of a large planting area—about 1500 m^2—divided into 18 separate plots with soil depths of about 1 m and a vertical atmospheric spread of more than 10 m. The IAB can be considered an enormous growth-chamber, with nine air-handler units that deliver tight environmental control of temperature and relative humidity (RH). An air ventilation system can be used to provide control of internal CO_2 levels as needed. A system of internal sensors, including a Licor 6262 allows for monitoring of atmospheric CO_2 and water vapor concentrations (Rosenthal et al., 1999). The glass and space-frame structure that envelopes the IAB reduces incoming visible radiation by roughly 55%, and may be responsible for large diffuse fractions of light compared to outside light conditions, as discussed below.

2.1. Experimental conditions

We conducted a growth experiment with wheat during the 1995–1996 winter/spring months (Table 1). Yecora Rojo, a spring wheat cultivar, was planted over the entire IAB area on December 7, 1995, with a density of about 150 plants m^{-2} (in rows 10 cm apart). Each plot had previously been well-irrigated to facilitate seed germination. Irrigation with a soaker-hose system was supplied after planting at regular intervals to replace water loss due to evapotranspiration and thus keep the wheat plants from experiencing water stress. The irrigation system was not automatic and actual water amounts supplied during the growing season were not monitored. Temperature and RH control was provided by means of the air-handler system, with set points of min/max temperature values kept at 17/27°C, and RH levels at 45%. Temperature variations between the specified minimum and maximum values tracked the daily variations of outside temperature.

Measurements with light pyranometers performed inside the IAB during the experiment gave mean solar radiation values of about 7 MJ m^{-2} d^{-1}, about half of typical light intensities outside. Unfortunately, light levels were not measured continuously during the experimental period. Solar radiation data from Tucson, AZ, located about 30 miles south of Biosphere 2, were used instead to drive computer simulations, as discussed below.

Control of internal CO$_2$ concentrations was attempted by devising an air circulation system consisting of forcing external air inside the IAB with a fan situated in the Biosphere 2 west lung area (see, for technical details, Zabel et al., 1999), and operating at a controlled rate (initially 5000 cfm). Air exited the IAB from the habitat airlock. During the entire experiment the IAB was thus operated in flow-through mode. As we discuss later in this paper, the air-ventilation system was able to maintain a constant CO$_2$ level inside the IAB of about 500 ppmv prior to planting and during the first few weeks after emergence. As photosynthetic rates increased, CO$_2$ levels inside the IAB started to fluctuate around a mean value of roughly 450 ppmv, with amplitudes increasing from emergence to anthesis. Leaf-level measurements indicated that photosynthetic characteristics of crops grown inside the IAB are typical of plants grown under more stable CO$_2$ environments (Marino et al., 1999).

Table 1
IAB experimental conditions and model inputs. Duration of the experiment, 7 December 1995–29 March 1996. Cultivar: Yecora Rojo

Environmental Parameter	Value	Units
Planting density	150	Plants m^{-2}
Photoperiod	9.5–12.0	h
Monthly-mean light intensity	2.7–6.3	MJ PAR m^{-2} d^{-1}
Ambient temperature	27/17 day/night	°C
RH	45%	—
Atmospheric CO$_2$ concentration	330–550	ppmv

Weekly samples of above-ground plant matter were collected throughout the growing season, and phenological events recorded. Each sample consisted of 20 wheat plants, half of which were taken from the same plot (# 13), and the remaining half from random sampling of other plots. No significant difference was found among the two sample groups. The data discussed hereafter refer to samples from plot # 13 only. Each week we performed leaf area measurements using a Licor leaf-area meter. Weighing of above-ground biomass was performed after oven-drying the collected wheat plants for at least 3 days at 70°C.

2.2. Computer simulations

CERES-Wheat was developed to simulate plant phenology, growth and final grain yield of winter and spring wheat as a function of soil properties, cultivar type, daily weather, and management conditions (Ritchie and Otter-Nacke, 1985). It calculates in daily time-steps, plant phenological development as a function of accumulated heat units; water and nitrogen movement through the soil-plant continuum; dry matter (DM) production as a function of absorbed solar radiation, air temperature, water and nitrogen stress; and its subsequent partitioning to plant organs (leaf, stem, grain, root). Model parameters and equations needed to calculate crop phenology and biomass production are given in Table 2and Table 3. A more detailed discussion of model equations can be found in Tubiello et al. (1995).

Daily-mean temperature was calculated from the observed min/max range. A continuous time-series of solar radiation data for the IAB was not available to us. These data are needed to calculate PAR, the visible part of the solar spectrum used by the model to drive photosynthesis. A good estimate for PAR is about 50% of incoming solar radiation (Bugbee and Salisbury, 1988). In order to run the model, we collected monthly-means for the period December 1995–April 1996 for Tucson, AZ (30 miles south of Biosphere 2) from the Arizona Meteorological Service (AZMET), then reduced them by 50% to obtain PAR, and by 55% to account for the effects of the glass structure on incoming short-wave radiation. The resulting PAR monthly-mean estimates for the IAB were applied to each day of the corresponding simulation month (Table 4).

Because the plants were well-irrigated and the soil rich in organic matter and nitrogen (Marino et al., 1999), we ran simulations assuming no water and nitrogen stress. This simulation procedure allowed for easier comparisons of model results with optimal field and growth-chamber conditions, discussed later in this work. Phenological growth stages were calculated as a function of accumulated heat units, depending on three key model parameters (Table 2). Specifically, the phyllocron interval (*PHINT*), or leaf emergence rate, was used to determine the length of the first three growth stages, from emergence to terminal spikelet formation to end of ear growth and anthesis. Daylength affects the duration of the first stage in CERES-Wheat and depends on a second parameter, *DV*. We used an average daylength value of 9.5 h for the period December 1995–January 1996, when vegetative development took place. Finally, length of the grain filling stage depends

Table 2
Model symbols, parameters and values

Symbol	Description	Value	Units
CDD	Cumulative degree days		°C-days
PHINT	Phyllocron interval	82.4	°C-days
Ph	Phenological stages used in CERES-Wheat		
*Ph*1	Emergence to terminal spikelet (TS)	400**PHINT*/95	°C-days
*Ph*2	TS to beginning ear growth	3**PHINT*	°C-days
*Ph*3	Beginning to end ear growth	2**PHINT*	°C-days
*Ph*4	Anthesis and beginning grain growth	200	°C-days
*Ph*5	Linear grain filling to physiological maturity	590	°C-days
HRLT	Photoperiod	9.5–12.0	h
DV	Sensitivity to daylength	3.1 for *Ph*1 1.0 for *Ph*2–*Ph*5	—
AWR	Leaf area-to-width ratio	300	$cm^2 g^{-1}$
LAI	Canopy leaf area index		—
LAI_{sun}	Canopy sunlit leaf area index		—
LAI_{sh}	Canopy shaded leaf area index		—
r	Canopy PAR reflectance	5%	—
k	Effective light-interception coefficient	0.85	—
σ_0	Leaf light scattering coefficient	0.30	—
I_{sun}	Canopy-intercepted direct light		—
I_{sh}	Canopy-intercepted diffuse light		—
q	Leaf maximum quantum yield	0.00524	—
τ	Maximum leaf carboxylation conductance to CO_2	4.5×10^{-3}	$m s^{-1}$
δ	Rubisco-limited maximum rate of leaf net photosynthesis	2.12	mg CO_2 $m^{-2} s^{-1}$
P_{max}	Light-saturated leaf photosynthetic rate	1.0 at 330 ppmv	mg CO_2 $m^{-2} s^{-1}$
$P_{C,I}$	Canopy daily assimilate for leaf population *i*		mg CO_2 $m^{-2} s^{-1}$
P_C	Canopy daily assimilate		mg CO_2 $m^{-2} s^{-1}$
A	Carbon wt.% content in DM	43%	

on a third parameter, *Ph*5. Our model had been previously calibrated to reproduce all stages of development for Veery-10, a spring variety similar to the cultivar Yecora Rojo grown at Biosphere 2. Such a calibration has been previously tested with positive results in field experiments with Yecora Rojo (Tubiello et al., 1996), and was used here without modification. Parameters for leaf-level equations, used to predict canopy photosynthesis by scaling methods, were taken from previous studies, predicting a 50% increase of leaf photosynthetic rates for a CO_2 doubling from 330 to 660 ppmv. Measurements previously performed on wheat plants grown inside the IAB were in agreement with leaf-level model predictions. Only one free parameter was calibrated in this study to reproduce the observed data, σ, used to describe effects of diffuse light on canopy photosynthesis, and allowing the model to perform under a variety of experimental light settings. We found that the

Table 3
Model equations for plant phenology and canopy photosynthesis

Symbol	Equation
CDD	$\Sigma\, 0.5(T_{\max}+T_{\min})/DV$
LAI_{sun}	$(1-e^{-kLAI})/k$
LAI_{sh}	$LAI-LAI_{\text{sun}}$
I_{sun}	$k(1-r)(1-\sigma)\text{PAR};\ \sigma=\sigma_0 LAI_{\text{sh}}/LAI$
I_{sh}	$(1-r)(1-e^{-kLAI_{\text{shade}}})\sigma\text{PAR}/LAI_{\text{sh}}$
$P_{\max}$	$\tau C/1+\delta\tau C$
$P_{\text{C},i}$	$qI_i P_{\max}/qI_i+P_{\max}$
P_{c}	$A(P_{\text{C,sun}}LAI_{\text{sun}}+P_{\text{C,sh}}LAI_{\text{sh}})$

Table 4
Monthly-mean values of total solar radiation at Tucson, AZ, and estimates of PAR (400–700 nm wavelength) in the IAB

Month	Solar radiation (MJ m^{-2} d^{-1})	IAB PAR[a] (MJ PAR m^{-2} d^{-1})
December	11.9	2.7
January	14.3	3.2
February	14.5	3.3
March	22.5	5.1
April	27.5	6.3

[a] Phosynthetically active radiation.

observed data were best reproduced by setting $\sigma = 0.30$, indicating a fraction of diffuse light inside the IAB during the experimental period intermediate between typical field (10% on a clear day) and CELSS chamber environments (60%). Although it is likely that diffuse light inside the IAB is higher than outside, we do not have any measurement to date that could confirm it.

3. Results and discussion

We present results from measurements and computer simulations relative to the entire growing cycle of Yecora Rojo inside the IAB. Table 5 lists the observed key phenological events, recorded when at least 50% of the plants had reached the specified growth phase. Wheat seedlings emerged on December 15, 1995, reached anthesis—that is, floral initiation,—on February 21, 1996, and physiological maturity on March 29, 1996. Plants were harvested 2 weeks later (see Fig. 1). Model simulations of phenological development were in excellent agreement with the observations (Fig. 2), with $R^2 = 0.996$, confirming our previous calibrations.

Above-ground DM production was about 830 g m^{-2}, resulting in average growth rates of 8 g DM m^{-2} d^{-1}. Mean grain yield was 315 g DM m^{-2}, with a

Table 5
Phenology, experiment and simulation results

Phenological event	Observed	Simulated
Terminal spikelet formation	52	49
Booting	58	60
Anthesis	67	68
Beginning of linear grain filling	76	77
Physiological maturity	103	105

harvest index (the ratio of grain to above-ground DM) of 38%. The variability in the observed data was large, with a coefficient of variation of about 30%. Important factors of variability inside the IAB might be within-plot soil heterogeneity, due to past management practice and crop use; non-uniform irrigation (a test performed after the experiment indicated 55% uniformity efficiency for the soaker-hose system); and differences in salinity levels throughout each plot.

Model simulations were in good agreement with the observed data (Table 6). Because CERES-Wheat can only simulate a crop response to daily-mean CO_2 concentration, we compared observed data to simulations at 330 and 550 ppmv, which predicted DM production of 700 g m^{-2} and 850 g m^{-2}, respectively, and had similar harvest indices of 32%. As shown in Fig. 3, the entire time-series of observed DM fell within the simulated range, providing an indirect test of the new CO_2 response functions built in CERES-Wheat. The slight disagreement between model and data towards the end of the growth cycle may be due to problems with our drying and weighing procedures for grain biomass, resulting in an overestimation of actual final grain DM and harvest index (see Table 6).

Most importantly, a comparison of the model-simulated range with the observed means and standard deviations indicated that experiments with wheat grown in the IAB under the specified daily-mean CO_2 levels (450 ppmv) may give inconclusive results in terms of characterizing crop response to CO_2 relative to ambient levels, because data variability may be larger than the observed signal. Additional simulations indicated that, if experimental variability is not reduced, future experiments in the IAB should be performed under CO_2 concentrations of at least 1000 ppmv in order to have statistically meaningful signal-to-noise ratios (above three standard deviations) in the results.

The observed mean growth rate, 8 g m^{-2}, was a remarkable 50% of record growth-rates obtained in the field for C3 crops (Bugbee and Salisbury, 1988). In addition, the IAB growth-rates were about 15% of those obtained in NASA-CELSS controlled chambers at comparable CO_2 levels (Bugbee and Monje, 1992). RUE was calculated with the help of the model (for lack of continuous data on light intensity and total absence of data on canopy light absorption), to investigate whether 'true' disparities in crop production between the IAB and other settings existed other than those related to different daily light integrals among environments. Observed data and model simulations suggested that the IAB wheat grew with a life-cycle mean efficiency of about 3 g DM MJ^{-1} APAR (Table 6), which is only 6% less than those obtained in NASA-CELSS chambers at ambient CO_2 levels

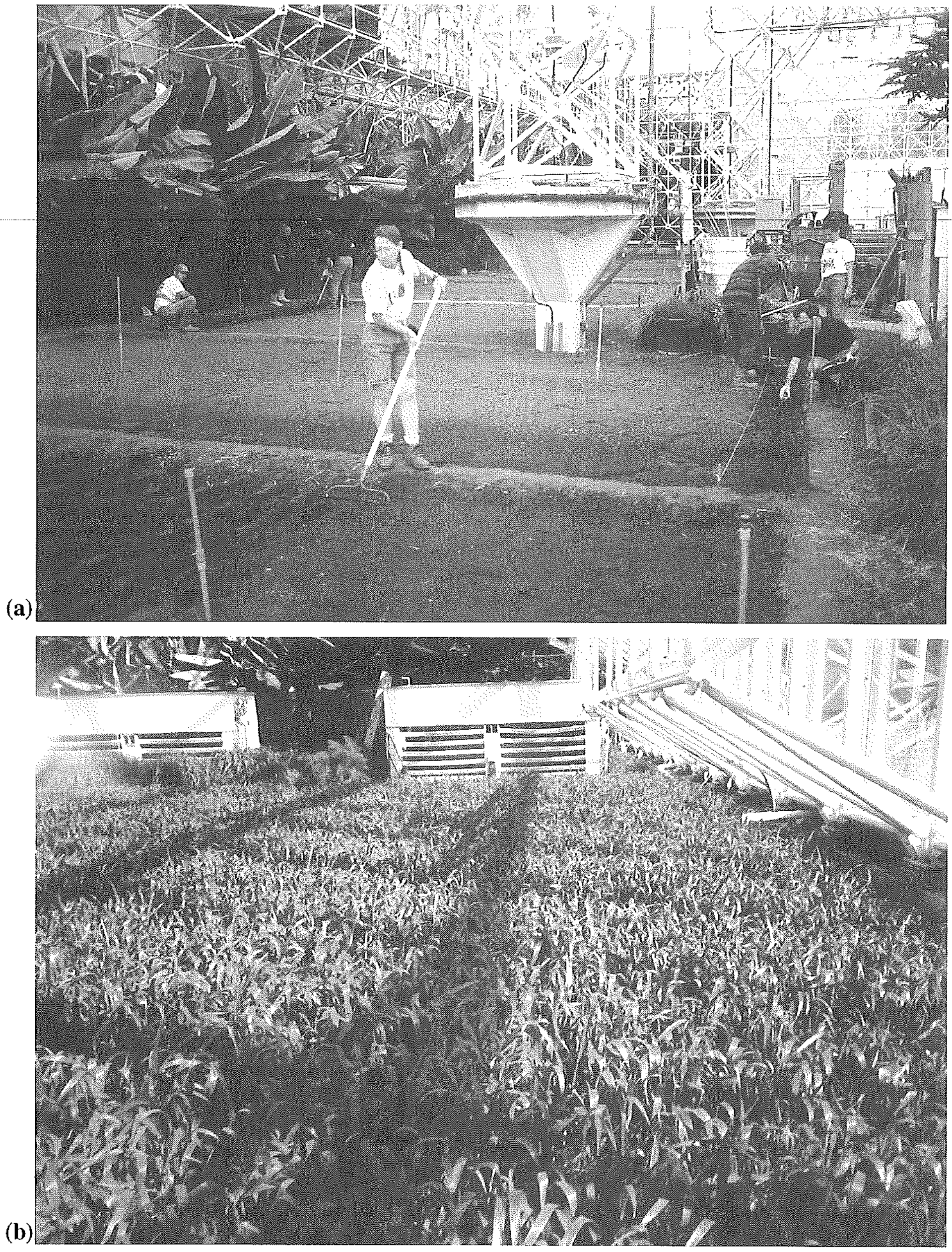

Fig. 1. Major experimental events, (a) planting; (b) vegetative stage; and (c) harvest maturity.

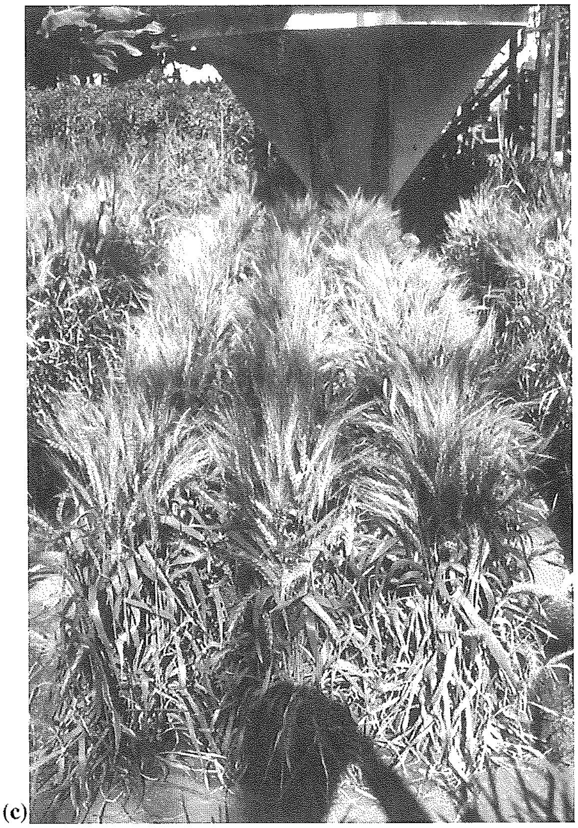

Fig. 1. (*Continued*)

(3.2 g MJ^{-1}, Tubiello et al., 1997), but about 40% higher than those reported for optimal field conditions under ambient CO_2 (2.0–2.2 g MJ^{-1} Gallagher and Biscoe, 1978). The IAB RUE might have been high partly because PAR intensity in the IAB was low during the experiment compared to typical field conditions. Under low light environments, canopy leaves are seldom light-saturated and thus can photosynthesize more efficiently (Norman and Arkebauer, 1991). In addition, previous studies suggest that a high ratio of diffuse-to-direct light enhances crop RUE (Sinclair et al., 1992). Thus, diffuse light inside the IAB—due to the space-frame structure, as well as elevated CO_2 levels—might also have contributed to increase crop RUE with respect to field values. In fact, additional model simulations indicated that low light levels in the IAB could alone explain more than half (about 55%) of the discussed 40% increase in RUE with respect to field conditions. In those simulations, elevated CO_2 contributed about 30% to such increase, while diffuse light was responsible for to the remaining 15%.

Finally, because CO_2 levels varied significantly during the day, by as much as 300 ppmv by the end of the growing season, it is difficult to interpret our data from a

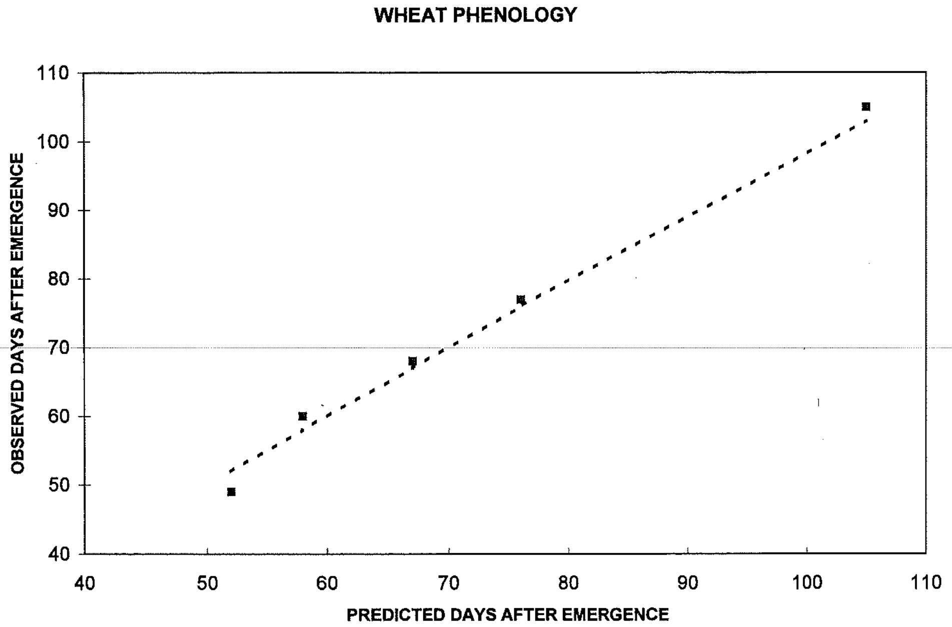

Fig. 2. Observed and simulated phenological stages. The dotted line represents the 1:1 correspondence.

physiological point of view. Large changes in CO_2 levels above a wheat canopy are not unusual, but are observed mostly at night—due to conditions of temperature inversion—when photosynthesis is not present (Loomis and Connor, 1992). A CO_2-control system would keep atmospheric CO_2 variations within acceptable limits and thus improve the quality of both data collection and model evaluation.

4. Conclusions

We have used data from a spring-wheat experiment at Biosphere 2 under elevated CO_2 concentrations to test a computer model for wheat, CERES-Wheat, developed for the prediction of biomass production and yield under a variety of growth environments in both field and closed chamber conditions. By combining observed data and model analysis we were able to compare for the first time crop performance in Biosphere 2 to that of other environments. Although light is a limiting factor for biomass production inside Biosphere 2, our simulations suggest that the photosynthetic efficiency of crops grown in this facility is high, only slightly less than those obtained under record-producing NASA-CELSS chambers, due to a combination of low light levels, elevated CO_2 concentrations and diffuse light fractions.

Our work shows that a facility like the IAB of Biosphere 2 offers the possibility to investigate key research issues in crop production through a combination of

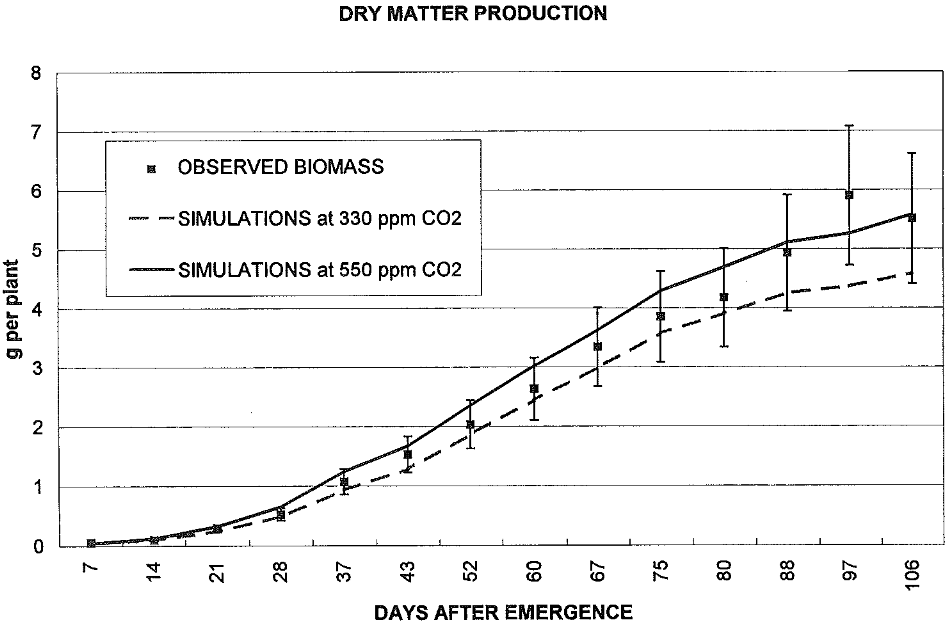

Fig. 3. Observed and simulated above-ground DM. Observed data are shown with error bars representing observed 30% standard deviations.

experiment and modeling techniques. Because of its large experimental area and tight environmental control, experiments performed in this facility can specifically help investigate effects of importance to future climate change and agriculture, under settings that resemble agricultural field conditions better than any other existing growth-chamber.

Table 6
Crop Production, experiment and simulation results

Parameter	Observed	Simulated	Simulated	Observed CELSS
Daily mean CO_2 concentration (ppmv)	Variable	330	550	330
Above-ground DM				
At anthesis (g m^{-2})	501 ± 150	437	537	
At harvest (g m^{-2})	827 ± 250	702	845	
Harvest yield (g m^{-2})	314 ± 94	222	275	
Harvest index	38 ± 11%	32%	33%	
Percent light absorption	N.A.	55%	59%	
DM capacity[a] (g m^{-2} d^{-1})	7.9	6.7	8.0	55.0
Yield capacity[a] (g m^{-2} d^{-1})	3.0	2.1	2.6	22.0
RUE (g DM MJ^{-1} APAR)	N.A.	2.9	3.2	3.2

[a] Total DM (or grain) production divided by number of days to maturity.

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