Life Support & Biosphere Science, Vol. 4 pp. 77–85, 1997
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1069-9422/97 $10.00 + .00

DIFFUSE LIGHT AND WHEAT RADIATION-USE EFFICIENCY IN A CONTROLLED ENVIRONMENT

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Radiation-use efficiency (dry matter produced per unit absorbed radiation) of a spring wheat (*Triticum aestivum* L., cv. Veery-10) was 40% higher in controlled growth chamber experiments than under optimal field conditions. Simulations with CERES-Wheat, a field model modified to account for growth chamber conditions, suggest that the observed increase in radiation-use efficiency was due to the large fraction of diffuse light in the experimental chamber. Under optimal conditions in the field, the highest crop growth rates occur when the daily photosynthetic photon flux (PPF) is at its highest levels (50–60 mol m^{-2} d^{-1}). However, these high growth rates do not appear to be associated with the highest radiation-use efficiency. High PPF levels in the field occur on clear days when the fraction of direct radiation is high and the diffuse fraction is low. In controlled environments with reflective walls, high PPF levels with a large fraction of diffuse radiation can be obtained. Diffuse radiation penetrates to the lower leaves of a canopy better than direct radiation, with the result that the upper leaves are less light saturated and the lower leaves receive more light, increasing radiation-use efficiency, and thus growth rates. The data and model simulations presented here suggest that when diffuse light is a high fraction of the total PPF crop productivity can exceed the highest values attainable in the field under optimal conditions.

Controlled ecological life support systems   Radiation-use efficiency   Diffuse light   Wheat
Modeling   CERES-Wheat

INTRODUCTION

Experiments with wheat grown in hydroponics under controlled environmental conditions have produced high crop growth rates compared to field data (4,6). The best crop growth rates obtained under ambient CO_2 concentration (330–350 ppmv) and high daily light integrals (70–150 mol m^{-2} d^{-1} of photosynthetically active radiation, compared to 10–60 mol m^{-2} d^{-1} in the field) are about 60 g dry matter m^{-2} d^{-1}. By contrast, long-term field growth rates for several C_3 crops have not exceeded 15 g dry matter m^{-2} d^{-1} (4).

Crop radiation-use efficiency (RUE), defined herein as the ratio of total dry matter production to absorbed photosynthetically active radiation (APAR), can be used to investigate whether intrinsic differences in crop performance between field and growth chamber exist, helping to better understand the factors that boost productivity in controlled ecological life support systems (CELSS).

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The light incident upon a crop canopy can be divided into direct and diffuse fractions. We hypothesize in this work that the amount of diffuse light inside a growth chamber enhances crop RUE relative to field conditions, and thus contributes to the observed high growth rates. This hypothesis is consistent with several measurements and theoretical models indicating that crop RUE, although roughly constant in the field, increases with diffuse light (8,13). Previous modeling studies of crop RUE and diffuse light, however, have focused on field conditions where typically high diffuse fractions of light are correlated with low light intensities, for example, whenever cloud-cover is present (12). We consider here conditions characterized by both high light intensity and a large diffuse fraction, using a modified CERES-Wheat model (10) to analyze data covering the entire life cycle of a spring wheat crop grown in hydroponics under controlled environmental conditions. Crop RUE was calculated as total (shoots and roots) dry matter (DM) production per unit APAR in a given time interval, and expressed in units of g DM MJ^{-1} APAR. Both daily and life cycle values of crop RUE were considered.

MATERIALS AND METHODS

Experimental Data

Spring wheat (*Triticum aestivum* L., cv. Veery-10) was grown in hydroponics in a sealed, controlled environment chamber (Environmental Growth Chambers, Model EGC-13, Chagrin Falls, OH) with a constant CO_2 concentration (3) (Table 1). Experimental methods have been described previously (2). Canopy daytime net photosynthesis and nighttime dark respiration were measured and averaged over 3-min intervals via gas exchange monitoring throughout the life cycle. Canopy photosynthesis was calculated from the difference between CO_2 concentrations in prechamber and postchamber air as described elsewhere (2).

Table 1. Experimental Conditions in the Growth Chamber

Experimental Parameter	Value
Planting density	720 plants m^{-2}
Photoperiod	20 h d^{-1}
Light intensity	1400 μmol m^{-2} s^{-1} PPF*
Air temperature	23°C day/night
Temperature of hydroponic solution and root environment	23°C day/night
Fraction diffuse light	~ 60%
CO_2 concentration	330 ppm

*300 μmol m^{-2} s^{-1} PPF from emergence to day 2, 800 μmol m^{-2} s^{-1} PPF from day 2 to day 7, and 1400 μmol m^{-2} s^{-1} PPF from day 8 to maturity.

Canopy light absorption, I_{abs}, was calculated as the difference between downward and upward PPF above the canopy (I_0 and I_{r0}, respectively), diminished by the amount of light absorbed at the soil surface, calculated as the difference between downward and upward PPF below the canopy (I_t and I_{rt}, respectively): $I_{abs} = (I_0 - I_{r0}) - (I_t - I_{rt})$. The four-component PPF fluxes were measured daily using a LICOR quantum sensor and a set of gallium arsenide photodiodes.

Daily total carbon gain by the canopy was calculated by combining measurements of daytime photosynthesis minus nighttime dark respiration rates. Total dry matter production was determined using an average value of 43% C in dry matter, based on measurements at harvest. Total dry matter was also directly measured at harvest after drying to a constant mass at 80°C.

The experimental conditions were characterized by both high radiation and a large fraction of diffuse light (Table 1). Four 1000-W high-pressure sodium lamps were evenly spaced above the planting area (1.0 m^2), their light filtered though a 40-mm film of recirculating water to reduce the heat load on the plants (4). The reflective, aluminum-coated side walls of the chamber further contributed to the amount of diffuse light reaching the plant canopy. The large fraction of diffuse light caused the virtual absence of shadows cast by solid objects placed in the chamber. Empirical estimates of the fraction of diffuse light in the growth chamber were made by blocking the direct radiation flux from the four lamp filaments with a 4 × 15-cm piece of black metal placed below each lamp. Measurements of light intensity at the top of the canopy indicated a diffuse fraction of at least 60%.

Modeling Experimental Data

We recently modified CERES-Wheat, a well-tested field model used in the prediction of wheat growth and yield worldwide (10). The new model calculates daily crop growth rate by scaling equations for photosynthesis from leaf to canopy. Its field predictions under current CO_2 levels are comparable to those made with the original CERES-Wheat and close to observed data (15). Model performance was tested against data from a controlled environment chamber. Some of the field-derived parameters in CERES-Wheat needed to be further modified to account for differences between field and hydroponic growth. These changes include: higher root respiration rates with respect to field parameterization; modification of model equations for leaf growth to include dependence on carbon uptake in addition to air temperature; and modifications to root partitioning functions during early vegetative growth and grain filling [see Appendix; (16)]. These modifications have allowed CERES-Wheat to reproduce additional, independent data sets from crops grown in environments other than the growth chamber used in the current work (17,18).

Growth Model Equations. Simple agronomic and terrestrial ecosystem models calculate total dry matter production, or net primary productivity (NPP), by multiplying an externally specified crop RUE parameter by absorbed light (9). We used the same approach to calculate NPP, but derived crop RUE by scaling equations for leaf photosynthesis. We wrote:

$$\mathrm{NPP} = (\alpha_{\mathrm{sun}}\,\varepsilon_{\mathrm{sun}} + \alpha_{\mathrm{sh}}\,\varepsilon_{\mathrm{sh}})\, f_W f_N f_T f_D\, \mathrm{APAR}. \quad (1)$$

The four factors ($f_W f_N f_T f_D$) have values in the range 0–1 and were calculated using original CERES-Wheat equations. Specifically, f_W and f_N represent water and nitrogen stress (no stress was assumed in hydroponics); f_T is a temperature stress factor that is lower than unity when temperatures differ from a crop photosynthetic optimum, set at $T_{\mathrm{opt}} = 18°\mathrm{C}$ ($f_T = 0.875$ for $T = 23°\mathrm{C}$); f_D is a phenological stress factor due to plant age, which decreases linearly during grain filling, simulating the effects of grain demand for leaf N on photosynthesis (7).

The terms in parentheses in eq. (1) represent crop RUE under no water, nitrogen, temperature, or phenological stress. These terms were calculated by dividing the wheat canopy into two populations of leaves: sunlit (sun) and shaded (sh), such that α_i (i = sun, sh) was the fraction of total APAR absorbed by either sunlit or shaded leaves; and ε_i was the daily radiation-use efficiency of either population of leaves. The latter quantity was expressed as a fraction of a leaf parameter, q, representing maximum RUE under low light:

$$\varepsilon_i = q, \ (i = \mathrm{sun, sh})$$

where apar_i was the absorbed light per unit leaf area of either sunlit or shaded leaves; and $P_{\max}$ was the light-saturated leaf assimilation rate. Both q and $P_{\max}$ were chosen from published data (Table 2).

Light gradients within the canopy were modeled via a "light + shade" canopy light-interception scheme, with a fixed light source, using standard equations to calculate sunlit and shaded leaf area indices (LAI) as shown below. Such a simple approach provides a good approximation to more exact, but far more complex, calculations of canopy light interception (1,14).

Modification of Growth Equations for Closed Chamber Radiaton Regimes. The high fraction of diffuse light inside the growth chamber required modification of modeling approaches developed for the field. As mentioned earlier, the growth chamber had four lamps placed directly overhead, a water filter, and reflective walls. The "direct" component of total radiation was defined the intensity of incident light perpendicular to the chamber floor. A measure of diffuse light above the canopy was included by introducing a single parameter, σ, with values between zero and unity, defined as the fraction of total photosynthetically active radiation (PAR) (scattered direct and diffuse component) incident on the "shaded" leaves. We assumed a simple dependence of the parameter σ on LAI, because the fraction of total radiation above the canopy falling on the shaded leaves must be small when LAI is small and increasing as LAI increases. At canopy closure, light falling on the shaded leaves reaches a maximum value, σ_0:

$$\mathrm{LAI}_{\mathrm{sun}} = (1 - e^{-k\,\mathrm{LAI}})/k;\ \mathrm{LAI}_{\mathrm{sh}} = \mathrm{LAI} - \mathrm{LAI}_{\mathrm{sun}}; \quad (2a)$$

$$\mathrm{apar}_{\mathrm{sun}} = k(1 - r)\,(1 - \sigma)\,\mathrm{PAR};$$
$$\text{and } \sigma = \sigma_0\,\mathrm{LAI}_{\mathrm{sh}}/\mathrm{LAI}; \quad (2b)$$

$$\mathrm{apar}_{\mathrm{sh}} = (1 - r)\,(1 - e^{-k\,\mathrm{LAIsh}})\,\sigma\,\mathrm{PAR}/\mathrm{LAI}_{\mathrm{sh}}. \quad (2c)$$

Here $\mathrm{LAI}_{\mathrm{sun,sh}}$ represents leaf area indices for either sunlit or shaded leaves; k is the effective canopy light extinc-

Table 2. Model Parameters Used in CERES-Wheat for Simulating Growth Chamber Conditions

Symbol	Parameter	Value	Units
r	canopy PAR reflectance	5%	—
k	effective light absorption coefficient	0.85	—
q	leaf maximum RUE	7.7	g DM MJ^{-1} APAR
$P_{\max}$	light-saturated leaf net photosynthetic rate	1.0	mg CO$_2$ m^{-2} s^{-1}
σ_0	total light to shaded leaves	0.62	—

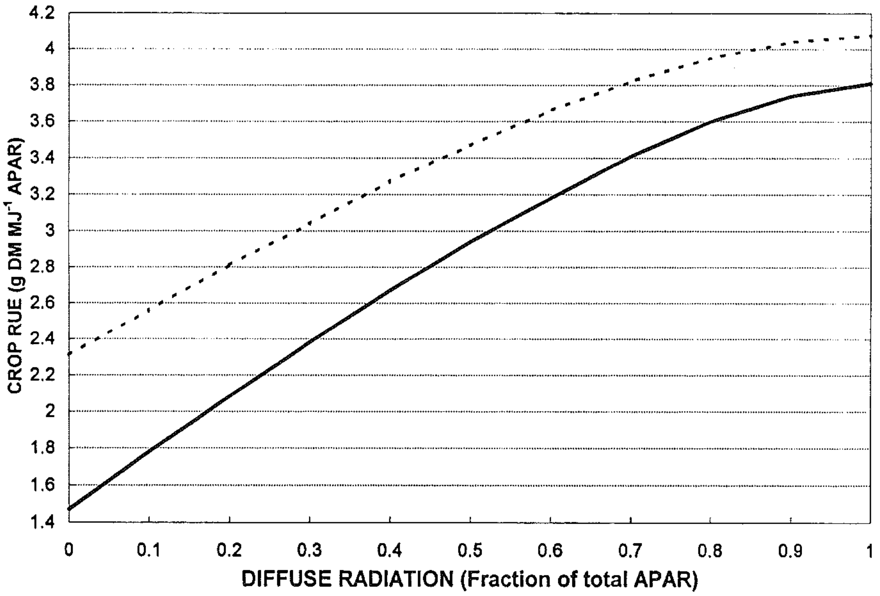

Figure 1. Simulated crop RUE as a function of the fraction of diffuse light above the canopy. Two average light levels: high, 1400 μmol m^{-2} s^{-1} (solid line), corresponding to light levels used in this experiment; and low, 700 μmol m^{-2} s^{-1} (dotted line). RUE was averaged over the crop life cycle.

tion coefficient, used for scattering of both direct and diffuse light; and r is the canopy reflectance (see Table 2). By comparing eqs. (2a)–(2c) to those developed by Sinclair et al. (12), which explicitly include the direct (f_{dir}) and diffuse (f_{diff}) fraction of incoming radiation for a "light + shade" scheme, it can be shown that the parameter σ_0 defined in eq. (2b) may be expressed as: $\sigma_0 = \tau f_{dir} + f_{diff}$, with τ being the leaf transmittance of light. As a consequence, $\tau \leq \sigma_0 \leq 1$. Our equations differ from those developed by Sinclair et al. (12) in that they include a canopy reflectance term, r, and a term, eq. (2c), for scattering of diffuse light by shaded leaves (3).

Our modified photosynthetic model has been used to successfully reproduce wheat dry matter production and yield under a variety of field and management conditions. By choosing σ_0 in the range 0–20%, this model performs similarly to previous field-specific models of wheat (10,20). In particular, the model-predicted crop RUE in the field was found to be in agreement (data not shown) with the published field measurements previously discussed.

RESULTS AND DISCUSSION

Experimental Results

Three replicate experiments were performed at the Crop Physiology Laboratories of Utah State Univer-

Table 3. Observed Data and Simulation Results

Experimental Parameter	Observed	Simulated
Days to anthesis	33 ± 0.5	33
Days to maturity	63	63
Total dry matter production (g m^{-2})	3530 ± 140*	3449
Percent total light absorption	83%	80%
Crop RUE (g DM MJ^{-1} APAR)	3.2	3.3
Max canopy photosynthesis (mg CO_2 m^{-2} s^{-1})	2.0, on day 28	2.1, on day 29
Max LAI	30	17.3
Max total respiration rate (mg CO_2 m^{-2} s^{-1})	1.0, on day 30	1.1, on day 30
Carbon partitioning to organs:		
Shoots	55.0 ± 1.0%	53.6%
Roots	5.5 ± 0.4%	6.4%
Seed (harvest index)	39.6 ± 0.9 %	40.0%
Mass seed^{-1} (mg)	29.0 ± 1.9	29.3
Kernel number plant^{-1}	66.7 ± 2.0	65.3

*Measured at harvest.

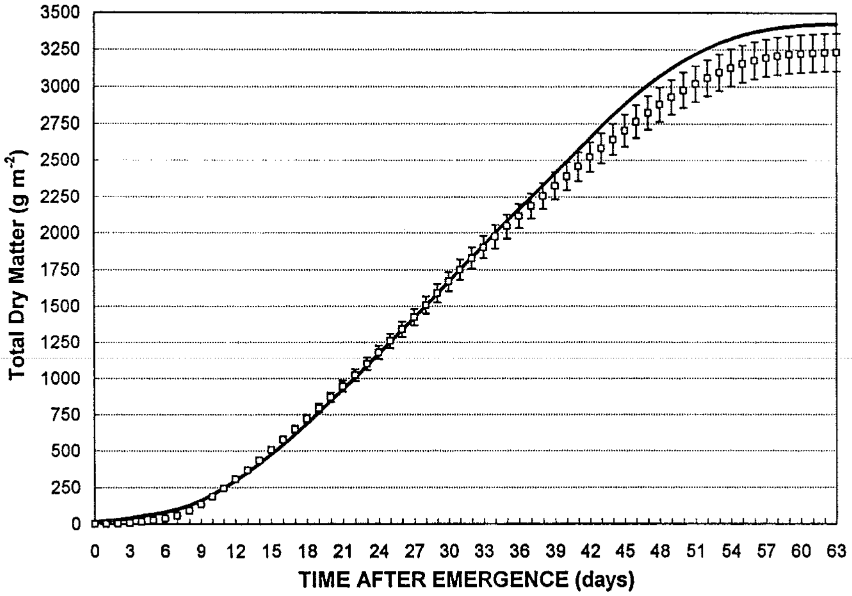

Figure 2. Simulated (solid line) and observed (symbols) dry matter production. Total dry matter (squares) was calculated from observed gas exchange parameters. Final dry matter calculated from gas exchange (3210 g m^{-2}) was 9% lower than actually measured at harvest (3530 g m^{-2}). Vertical bars in the graph indicate 4% SEM from three replicates.

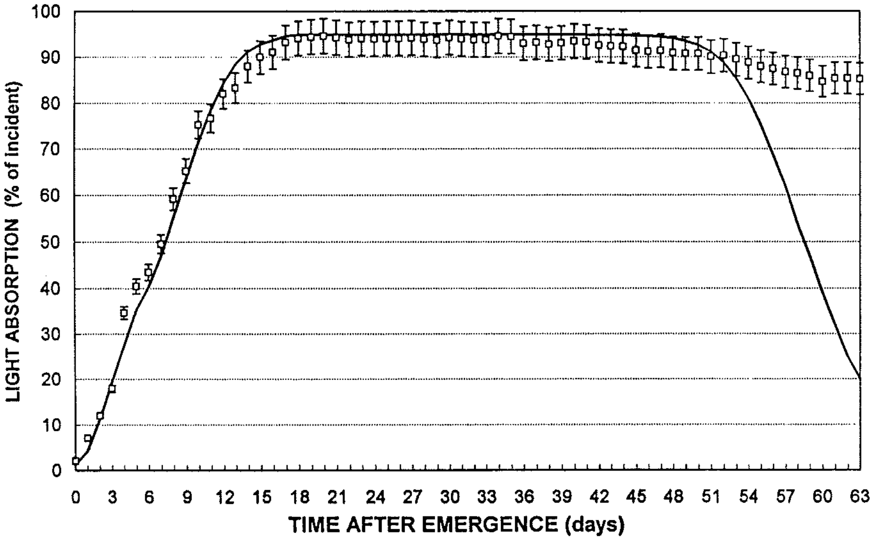

Figure 3. Simulated (solid line) versus observed canopy light absorption. The model calculated absorption from green leaf area only. Vertical bars in the graph indicate 4% SEM from three replicates. The discrepancy between model and observation during the last 10 days of the life cycle was possibly due to additional light absorption by senesced leaves in the canopy.

sity, Logan, UT, with a standard error of the mean below 5%.

The wheat crop reached anthesis 33 days after emergence (DAE) and physiological maturity at 63 DAE. The harvested total dry matter was about 3500 g DM m^{-2}, corresponding to a life cycle mean growth rate of 56 g DM m^{-2} d^{-1}, about four times greater than the highest values reported for C_3 crops in the field. Such a large increase in crop productivity was only in part attributable to the 20-h photoperiod used in our experiments. In fact, the calculated radiation-use efficiency in the growth chamber was consistently higher than under optimal field conditions: the life cycle mean crop RUE was 3.2 g DM MJ^{-1} APAR, more than 40% higher than field measurements for unstressed wheat crops, 2.2 g DM MJ^{-1} APAR (8).

Simulations of Crop RUE

When the modified CERES-Wheat model was run under closed chamber conditions, with modified equations for hydroponic growth and σ values typical of field simulations, it underestimated the observed total dry matter production and crop RUE by about 40%. The simulated life cycle average crop RUE was typical of field measurements (2.3 g DM MJ^{-1} APAR). It was necessary to increase the parameter σ_0 to 0.62 in order to reproduce the observed biomass production and crop RUE under controlled conditions. By assuming a leaf transmittance of 5–10% (1), this value corresponds to a diffuse fraction of 58–60%, consistent with our estimates.

Our calculations extend those by Sinclair et al. (12), who estimated that in the field an increase in the fraction of diffuse light from 10% to 50% enhances daily RUE by as much as 50% in C_3 crops. However, because of their interest in investigating field conditions, these authors covaried the fraction of diffuse light and the absolute amount of radiation above the canopy. In their calculations a high diffuse ratio corresponded to low absolute light intensity and vice versa. The effects of diffuse light on *life cycle* averages of crop RUE for a given total light intensity above the canopy and growth chamber conditions were calculated (Fig. 1). Life cycle crop RUE for wheat was calculated under two different light regimes: low (700 µmol m^{-2} s^{-1} photosynthetic photon flux, PPF) and high (1400 µmol m^{-2} s^{-1} PPF), with varying fractions of diffuse light (0–100%). The simulations show that increasing fractions of diffuse light up to 50% caused a roughly linear increase in crop RUE, the increases being larger under high light than under low light.

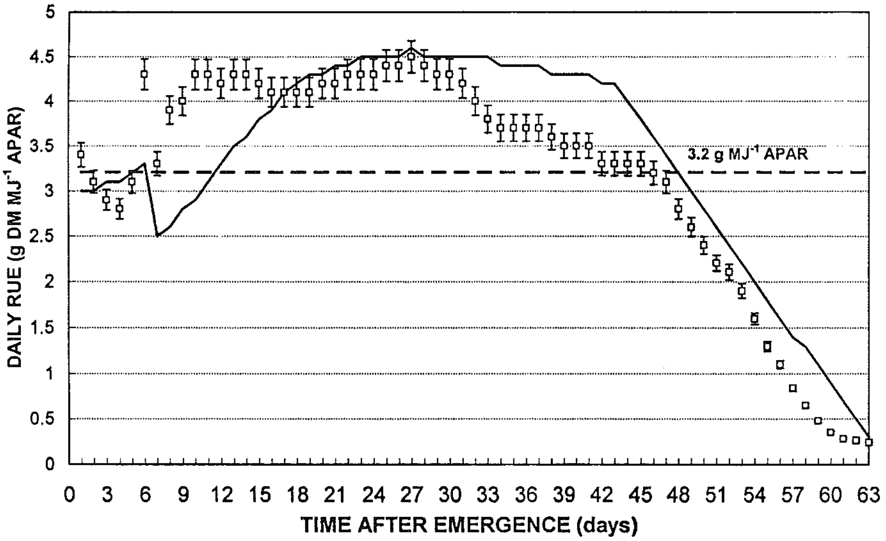

Figure 4. Simulated (solid line) and measured (symbols) daily crop RUE. Also indicated is the average crop RUE, calculated as the ratio of total dry matter produced to total light absorbed. Vertical bars in the graph indicate 4% SEM from three replicates.

Simulations of Dry Matter Production

Model simulations were compared with observed phenological events, whole-canopy instantaneous photosynthesis and respiration, and dry matter distribution among plant organs at harvest (Table 3). Comparisons between measured and simulated data for total dry matter production, canopy light absorption, and crop RUE are shown in Figures 2–4. The gradual redistribution of absorbed light from sunlit to shaded leaves as successive leaves emerged allowed the model to simulate daily RUE correctly. The sudden decrease in simulated RUE on day 7 after emergence was due to light saturation of canopy leaves, mostly sunlit (LAI ~ 1), as the light levels were increased from 800 to 1400 μmol m^{-2} s^{-1} PPF (Table 1). This effect was not observed in the experimental data, perhaps because the wheat canopy was already closed. The strong constraint imposed on daily NPP by the phenological stress factor, f_D, dominated the simulation of daily RUE after anthesis, showing a roughly constant decline until maturity, in close agreement with experimental observations.

Model Validity and Limitations

A number of limitations may affect the validity of these simulations. First, wheat plants grown in hydroponics may have a higher leaf N content than those grown under optimal field conditions (4). We implicitly assumed that leaf light-saturated photosynthetic rates under no nitrogen or water stress are similar in both field and hydroponic conditions. This is only true if the dependence of P_{max} on leaf N content is weak at optimal leaf N levels, as some authors have indicated (11). Second, the model phasic development and morphological calculations were developed from a field model, CERES-Wheat. Although the modifications of several empirical equations well described observed growth conditions in the controlled chamber, additional data from other controlled environment experiments should be used to further test the modified equations. Third, canopy respiration was not simulated independently, as the sum of growth and maintenance components. Rather, following CERES-Wheat, we calculated NPP directly, implicitly assuming that a fraction of gross daily production was respired by the crop (5). Although such an assumption may constitute only a rough approximation, some authors have used it successfully to reproduce photosynthesis and respiration data in controlled environments. For the data used here, the fraction of daily gross production respired was determined to be roughly constant until grain filling (19).

CONCLUSIONS

The result presented here suggest that crop RUE strongly depended on the fraction of diffuse light reaching the plant canopy. For a given amount of PPF, light that is diffuse may be better distributed within the canopy than is direct light, so that light sources that are high in the diffuse component should be advantageous to crop growth. Additionally, more leaves would operate below light saturation; thus, canopy photosynthesis is more efficient. When the diffuse light component above the canopy is high throughout the entire crop life cycle, as in the controlled environment of this work, dry matter production can exceed that attainable in the field under optimal growth conditions. Effects of diffuse light on crop RUE enhanced daily crop growth rates beyond the obvious increase due to the use of longer daily light integrals in the growth chamber.

The modified CERES-Wheat model was able to reproduce the observed data, including dry matter partitioning between shoots and roots. These results indicate that CERES-Wheat may be used to simulate wheat development and growth under controlled environments as well as under field conditions, provided specific modifications are made and that the diffuse fraction of light reaching the plant canopy is accounted for in model calculations.

APPENDIX: CHANGES TO CERES-WHEAT FOR GROWTH CHAMBER CONDITIONS

Feedback Between Carbon Assimilation and Leaf Growth

CERES-Wheat calculates leaf expansion and growth rates during the vegetative stage as a fixed function of accumulated temperature only, $f(\Sigma T)$. This method prevents the possibility for a positive feedback between high crop growth rates (like those in the growth chamber considered) and leaf area development. In fact, high crop growth rates promote leaf area growth, thus better canopy light interception, which further enhances growth rates (5). The original CERES-Wheat could not simulate correctly leaf growth before canopy closure (maximum light interception). In the original model, at least 35% of daily crop production (*CARBO*) is allocated to roots (*GRORT*) during the crop vegetative stage, as the remainder is partitioned to leaves (*GROLF*) as specified by the accumulated temperature: $GROLF = f(\Sigma T)$. CERES-Wheat was modified by requiring that exactly 35% of daily crop production be allocated to roots, whereas the remainder could be partitioned to leaves as a function of both temperature and carbon assimilation: $GROLF = \max(f(T), 65\% \ CARBO)$.

Root Partitioning Functions

The modifications to carbon partitioning to roots described above resulted in better simulations of root dry matter production during the crop vegetative stage. Further modifications were made during the simulated grain-filling stage, by setting the maximum allocation to roots to 10% rather than 20% of the daily assimilate.

Root Growth and Respiration Rates

The original CERES-Wheat calculates actual root growth rates with the following empirical function: $GRORT_{act} = \alpha GRORT - \beta ROOT$, where *GRORT* is the daily root growth, *ROOT* is the cumulative root dry matter; $\alpha = 0.60$ and $\beta = 0.05$ are parameters used to compute growth and maintenance respiration, respectively. In this work, maximum agreement between modeled and observed data was found by setting $\beta = 0.18$ and by leaving α unchanged.

ACKNOWLEDGMENTS

We thank Oscar Monje for his dedicated work at the Crop Physiology Lab of Utah State University. We also thank two anonymous reviewers whose suggestions and comments improved the quality of our presentation. This work was supported by NASA grants NAGW-4125 to New York University and NCC 2-139 to Utah State University.

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