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A MODIFIED CROPGRO MODEL FOR SIMULATING SOYBEAN GROWTH IN CONTROLLED ENVIRONMENTS

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The CROPGRO crop growth model is adapted in order to analyze experimental data from a soybean (cv. Hoyt) experiment conducted at elevated CO_2 levels (1200 μmol mol^{-1}) at Kennedy Space Center, FL. The following adaptations to original CROPGRO produced model agreement with gas-exchange data: the input of square-wave temperature and photosynthetically active radiation (PAR) profiles; the input of the appropriate hydroponic substrate PAR albedo; modified biomass partitioning and developmental parameters; an increased leaf area expansion rate through the fifth vegetative node; a decreased specific leaf area after the fifth vegetative node; and an increased incident diffuse PAR fraction over typical field values. The model demonstrated here suggests that with continued development, modified CROPGRO will be a useful tool in the analysis and eventual optimization of legume production in bioregenerative life support systems.

Soybean modeling CROPGRO Diffuse light CELSS BLSS

INTRODUCTION

Through simulations, a developed crop model can explore many more environmental settings and plant responses than may be accomplished through actual experiments. The results of simulations may be used to identify and explore critical features of a data set, and guide the design of specific growth chamber experiments. Accurate simulations are especially valuable to integrated programs, such as for NASA's bioregenerative life support system (BLSS) program (formerly referred to as controlled ecological life support system, or CELSS).

Soybean is a BLSS candidate crop based on the high protein and oil content of the seeds, and growth chamber experiments with soybean have been conducted at Kennedy Space Center (KSC), FL, for NASA's BLSS program since 1989 (14,15). Growth chamber conditions can be simulated by modifying an existing soybean model, CROPGRO, developed for field conditions to aid farmers in decision making (7). In this article, we describe and demonstrate our modified CROPGRO model as applied to data obtained from soybean experiments in KSC's Biomass Production Chamber.

THE CROPGRO MODEL

CROPGRO is an elaborate, dynamic model that uses one common FORTRAN code to predict daily growth and development of soybean, peanut, and dry bean until crop harvest. It was derived from its predecessor models, SOYGRO, PNUTGRO, and BEANGRO (8). Crop development, photosynthesis, transpiration, respiration, leaf area growth, vegetative partitioning, pod addition,

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and seed growth are simulated in response to temperature, solar radiation, photoperiod, soil–water balance, and cultural practices such as row spacing, planting date, and cultivar choice (11,16). Genetic traits (which include duration of vegetative and reproductive growth, sensitivity to photoperiod, maximum leaf photosynthesis, and other processes) may be modified to represent controlled environment growth chamber conditions for specific cultivars.

The CROPGRO version modified here is integrated into the Decision Support System for Agrotechnology Transfer (DSSAT, version 3) (13). Crop parameters for soybean are contained in DSSATv3 input files to CROPGRO, and are readily edited. Genetic trait parameters and environmental variables (such as ambient CO_2, daily light integral, photoperiod, and maximum and minimum daily temperatures) may be entered interactively for each model simulation through the sensitivity analysis option of DSSATv3.

The CROPGRO module contains the evapotranspiration–leaf photosynthesis model ETPHOT (1–3,11). ETPHOT incorporates hedgerow light interception, C3-leaf biochemical photosynthesis, and a canopy evapotranspiration and temperature energy balance. The evapotranspiration component has not been adapted for growth chamber conditions, and is not used in the model simulations in this article.

In ETPHOT, the canopy is modeled as a single leaf area index (LAI) layer, with this layer divided into two leaf populations: "sunlit" and "shaded" leaves (using field terminology). Submodels calculate the absorption of direct and diffuse light, which are defined below for growth chamber conditions, and leaf gross photosynthesis for each leaf population. Canopy gross photosynthesis is obtained by summing over sunlit and shaded leaf areas (see Appendix for leaf and canopy photosynthesis equations). Daily canopy gross photosynthesis is reduced by daily maintenance and growth respiration to yield daily net CO_2 assimilation. The carbon contents of the biochemical components in different plant organs determine the daily biomass gain (4,5).

COMPARISON OF MODEL SIMULATIONS WITH KSC GAS-EXCHANGE DATA

In this section, a recent KSC soybean experiment (BSB951, harvested in January, 1996) is used to demonstrate the development of modified CROPGRO. The environmental conditions for this experiment are given in Table 1 footnote. Soybean cultivar (cv.) Hoyt was grown due to its relatively high productivity and dwarf characteristics, using high-pressure sodium lamps as light sources.

Modifications to CROPGRO are outlined in Figure 1, where simulations of daily net CO_2 assimilation (= net photosynthesis during light cycle minus respiration during dark cycle) are compared with KSC gas-exchange data for a cumulative sequence of model adaptations. In these simulations, water and nutrients are considered to be nonlimiting, which is consistent with the near optimal controlled, hydroponic, environment of the Biomass Production Chamber.

The simulations in Figure 1 correspond to the following adaptations to original CROPGRO: (A) input of square-wave temperature and PAR profiles; (B) simu-

Table 1. Modified CROPGRO Comparisons With KSC Soybean Data

	Leaf (% Dry Mass)	Seed (% Dry Mass)	Seed Yield ($g\ m^{-2}$)	Total Biomass ($g\ m^{2}$)	Crop Life Cycle (DAP)	Crop Life Cycle Absorbed PAR (% of Incident PAR)	Crop Life Cycle RUE	
							$g\ MJ^{-1}$	$kJ\ MJ^{-1}$
KSC data	24	38	513	1,351	89	76	2.57	47.3
Model simulations								
A	9	52	279	536	87	35	2.21	43.4
B	9	53	422	802	87	55	2.14	41.4
C	24	40	463	1,155	89	68	2.44	45.0
D	26	38	467	1,227	89	71	2.45	45.5
E	26	38	542	1,412	89	74	2.72	50.2

The following environmental conditions were used in KSC soybean experiment BSB951: CO_2 concentration = 1,200 $\mu mol\ mol^{-1}$; temperature (light/dark) = 26/22°C; photoperiod (light/dark) = 12/12 h. Average PAR = 38 mol $m^{-2}\ day^{-1}$. Planting density = 19.2 plants m^{-2}. DAP, days after planting. RUE (radiation-use efficiency), total biomass (or energy content of biomass) at harvest divided by cumulative absorbed PAR, at 0.217 MJ mol^{-1} PAR. The biomass energy content is calculated using heat of combustion values of 22.6 kJ g^{-1} for seed, and an average of 15.9 kJ g^{-1} for all other biomass. See the text and Figure 1 for details on the model simulations.

lation A, plus the input of the hydroponic substrate PAR albedo at KSC; (C) simulation B, plus the calibration of vegetative and reproductive partitioning, and developmental parameters; (D) simulation C, plus the calibration of leaf area parameters; and (E) simulation D, plus the parameterization of the incident diffuse PAR fraction. These adaptations are discussed in the following subsections. For comparison, a simulation using the original CROPGRO code and parameter setting is also shown in Figure 1.

A. Light and Temperature Profiles

In controlled environment growth chambers, incident PAR levels are maintained during the light cycle, or photoperiod, and air temperatures are maintained at their set values during the light and dark cycles. Thus, square-wave PAR and temperature profiles are used in modified CROPGRO.

Curve A of Figure 1 shows the daily net CO_2 assimilation that results when using these square-wave profiles, with both the incident diffuse PAR fraction and the substrate PAR albedo set equal to zero. This simulation is far below the KSC data (as is the original CROPGRO simulation). Experimental yield and biomass are underpredicted by 46% and 60%, respectively, and the integrated light absorption over the crop life cycle is only 35% of incident PAR (Table 1).

B. Substrate PAR Albedo

Incident PAR not intercepted by the canopy is reflected from the hydroponic substrate used in growth chambers. The amount of this reflection is determined by the particular substrate's PAR albedo. In CROPGRO, ETPHOT's submodels calculate this reflected PAR for sunlit and shaded leaves, which become additional terms in the absorbed PAR per unit leaf area for each leaf population.

In the Biomass Production Chamber at KSC, the hydroponic tray covers are made of white plastic, and the average PAR albedo for these covers is approximately 0.65. This value may be contrasted with typical soil values, which are on the order of 0.1. The change in daily net CO_2 assimilation that results when the KSC albedo is input to CROPGRO is shown in curve B of

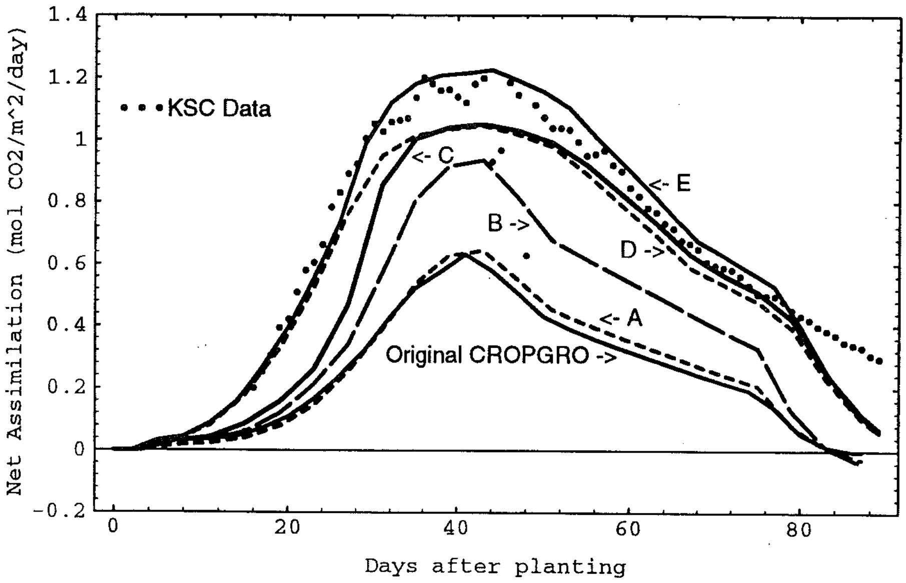

Figure 1. Comparison of daily net CO_2 assimilation between KSC soybean data (experiment BSB951) and modified CROPGRO simulations. Daily net CO_2 assimilation = net photosynthesis during light cycle minus respiration during dark cycle. Labels A through E denote model modifications as described in the text (see also Table 1). Dots denote KSC gas-exchange data, which have been adjusted so that net assimilation corresponds to the measured biomass given in Table 1. For comparison, a simulation of the KSC gas-exchange data using the original CROPGRO code and parameter settings is also shown.

Figure 1, and is substantial. The integrated PAR absorption in this simulation is increased from 35% in A to 55%, which helps boost the biomass by 50% compared to A. This biomass, however, is still far short of the KSC data (Table 1).

C. Biomass Partitioning and Development

Thus far, the simulated harvest index is too large, and leaf mass fraction too small compared with the KSC data (Table 1). To accurately simulate harvest index, as well as times for first flower, first pod, first seed, and crop life cycle, genetic parameters in CROPGRO were calibrated for cv. Hoyt based on KSC data. Although this calibration resulted in a close agreement with the measured harvest index, only 12% of total biomass was partitioned to the leaves (not shown), compared to 24% for the data.

Accurate simulation of leaf mass under growth chamber conditions is an important modeling consideration, as both leaf mass and specific leaf area are used in CROPGRO to calculate leaf area, which determines light absorption. In turn, light absorption determines both leaf and canopy gross photosynthesis (see Appendix). Therefore, the biomass partitioned to leaves was increased, and that to roots and stems decreased, to achieve better agreement between the simulated leaf fraction and the KSC data (Table 1). This change resulted in better simulation of root and stem partitioning as well (not shown).

The daily net CO_2 assimilation that results from incorporating these changes in biomass partitioning and development into CROPGRO is shown in curve C of Figure 1. Although biomass is increased by 44% over B (Table 1), it is seen that C still does not capture the early rise in daily net assimilation during the first 20 days exhibited by the data, even with the model's corrected leaf partitioning.

D. Leaf Area Growth

The next modification was to increase a single CROPGRO parameter that determines leaf area expansion from emergence through the fifth vegetative node. This change has the desired effect of capturing the early rise in daily net CO_2 assimilation exhibited by the data, as seen in curve D of Figure 1. It was also necessary to decrease the specific leaf area after the fifth vegetative node, to limit the maximum LAI in our final model run (E) to its estimated value of about 4.0 in the KSC experiment. As this specific leaf area modification also affects leaf area growth, it is incorporated into D.

In Table 1 we present the crop life cycle radiation-use efficiency (RUE) as simulated by modified CROPGRO. We present RUE as biomass at harvest divided by cumulative absorbed PAR (in g MJ^{-1}), and also in terms of biomass energy content at harvest (heat of combustion, in kJ MJ^{-1}). Of interest here is the response of soybean RUE to the various modifications made to original CROPGRO.

It is seen in Table 1 that biomass RUE (in g MJ^{-1}) for simulations C and D are similar, both being about 10–15% higher than those for simulations A and B, respectively. This difference in biomass RUE may be attributed to the different harvest indices in these simulations (Table 1). As the carbon (i.e., lipid and protein) content of soybean seed is higher than for vegetative tissue (10), the simulations with the higher harvest indices (A and B) may be expected to have lower biomass RUEs, owing to the greater carbon assimilation requirements per gram of biomass (4).

Even in energy units, however, RUEs for simulations C and D exceed those for A and B (Table 1). Although the heat of combustion values for lipids and proteins is greater than for carbohydrates, they do not compensate for the differences in growth respiration requirements used in CROPGRO (1.166 g glucose g^{-1} product for lipids, 1.224 g g^{-1} for protein from NO_3, and 0.112 g g^{-1} for carbohydrates).

It may also be seen in Table 1 that both biomass and energy RUEs are less for simulation B than for A, even though the harvest indices are similar. This arises from the nonlinear effects of absorbed PAR on photosynthesis (see Appendix), combined with the particular LAI values for these simulations (not shown). The result is that the relative increase in total biomass between simulations A and B is less than the relative increase in crop life cycle PAR absorption (Table 1).

E. Direct and Diffuse Light

In growth chambers, there are multiple lamps and reflective walls, rather than a single sun plus scattered sunlight from the sky's hemisphere in the field. Our simulations use the direct light extinction coefficient, which corresponds to the sun directly overhead for soybean canopies under field conditions (0.7). This effectively defines the direct beam radiation to be perpendicular to the horizontal. All the remaining, nonperpendicular light then becomes defined as diffuse. This component includes nonperpendicular beam radiation from the lamps, as well as light reflected from the growth chamber walls. In modified CROPGRO, this diffuse incident PAR component can be set to different values.

The diffuse incident light in the Biomass Production Chamber at KSC has been estimated to be approximately 0.6 by using a quantum sensor, which integrates PAR from all directions, with an opaque shield that blocks the nonperpendicular light component. Curve E of Figure 1 shows the change in net CO_2 assimilation that results from increasing the diffuse PAR fraction from zero (as in A through D) to 0.6. This curve captures the peak in daily net assimilation exhibited by the KSC data rather well. The result of this final addition is that yield and biomass are overpredicted by 6% and 5%, respectively, crop life cycle PAR absorption is underpredicted by 3%, and RUE is overpredicted by 6% (Table 1).

Previous work has shown the importance of accounting for the diffuse light fraction in modeling RUE under field conditions (9,12). In contrast to field conditions, however, both high diffuse light fractions and high incident PAR values may coexist in growth chambers, such as for the KSC experiment considered here. In Table 1 it is seen that modified CROPGRO's RUEs increase by about 10% as the diffuse light fraction is increased from 0 (as in D) to 0.6 (E) for the same incident PAR values (38 mol m^{-2} day^{-1} on average).

This increase in RUE with diffuse light arises from the increase in the PAR absorbed per unit leaf area by the shaded leaves with higher incident diffuse PAR fractions. The higher corresponding photosynthetic rates per unit leaf area for shaded leaves [eq. (1) in the Appendix] increases the contribution of these leaves in canopy photosynthesis [eq. (2) in the Appendix].

CONCLUSIONS

The soybean model demonstrated here suggests that with continued development, modified CROPGRO will be a useful tool for analyses of growth chamber experiments. The modifications made to original CROPGRO—the input of square-wave temperature and PAR profiles, the input of the appropriate hydroponic substrate PAR albedo, modified biomass partitioning and developmental parameters, an increased leaf area expansion rate through the fifth vegetative node, a decreased specific leaf area after the fifth vegetative node, and an increased incident diffuse PAR fraction over typical field values—have been shown to be necessary for model agreement with KSC gas-exchange data for soybean cv. Hoyt.

Additional growth chamber experiments will provide opportunities for further model development and testing, with the goal of using modified CROPGRO to predict harvest index, plant development, daily net CO_2 assimilation, and canopy light absorption under a range of growth chamber conditions. Other possible modifications of CROPGRO for analysis of growth chamber environments include: modeling the effective canopy height of soybean canopies under growth chamber conditions, an important consideration for a BLSS, where volume considerations are important (6,15); and adapting the evapotranspiration–energy balance submodel in CROPGRO for growth chamber conditions.

APPENDIX

In modified CROPGRO, the response of leaf gross photosynthesis (PG_{LF}) to the absorbed PAR per unit leaf area (PAR_{LF}) is calculated using a nonrectangular hyperbola, here with a curvature (Θ) equal to 0.7:

$$PG_{LF} = \{(Q_E\, PAR_{LF} + P_{max}) - [(Q_E\, PAR_{LF} + P_{max})^2 - (4\, \Theta\, Q_E\, PAR_{LF}\, P_{max})]^{1/2}\}/(2\, \Theta) \qquad (1)$$

where Q_E is quantum efficiency (mol CO_2 fixed mol^{-1} PAR), P_{max} is light-saturated leaf photosynthesis rate (μmol CO_2 m^{-2} s^{-1}), and PAR_{LF} is PAR absorbed per unit leaf area by sunlit (PAR_{sl}) or shaded (PAR_{sh}) leaves (μmol m^{-2} s^{-1}).

ETPHOT's submodels calculate direct and diffuse light absorption, and leaf photosynthesis for each leaf population, with canopy gross photosynthesis (PG_{CAN}) obtained by summing over sunlit and shaded leaf areas:

$$PG_{CAN} = PG_{sl}\, LAI_{sl} + PG_{sh}\, LAI_{sh} \qquad (2)$$

where LAI_{sl} and LAI_{sh} are sunlit and shaded leaf area indices, respectively, and PG_{sl} and PG_{sh} are PG_{LF} [from eq. (1)] for sunlit and shaded leaves, respectively.

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