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PHASIC TEMPERATURE AND PHOTOPERIOD CONTROL FOR SOYBEAN USING A MODIFIED CROPGRO MODEL

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A modified CROPGRO model is applied to phasic temperature and photoperiod control in order to optimize soybean production for NASA's program in Advanced Life Support. Baseline model simulations were established using data from soybean temperature experiments conducted at elevated CO_2 levels (1100 μmol mol^{-1}) at Utah State University (USU). The model simulations show little advantage in using phasic temperature control alone to increase average seed yield rate over the USU experimental values. However, simulations that combine phasic control of temperature (two phases) and photoperiod (two phases) do indicate the potential to improve seed yield (in g m^{-2} day^{-1}) by approximately 15% over those currently obtained experimentally at USU for soybean cultivar Hoyt. This temperature and photoperiod phasing is experimentally practical. The simulations suggest extending photoperiods over those typically used experimentally during later phases of the crop life cycle, which would lengthen grain fill duration and thereby increase mass per seed. The model simulations indicate that the timing and duration of extended photoperiods would be very important due to possible reductions in seed number m^{-2}. Besides affecting seed yield directly, the model simulations suggest that such reductions may also cause feedback inhibition of photosynthesis due to low seed sink strength at elevated CO_2 levels.

Phasic control Advanced life support Soybean modeling CROPGRO

INTRODUCTION

CROPGRO is a dynamic model that integrates plant processes to calculate daily plant growth and development for field conditions (2,6,8). It was previously modified for controlled, hydroponic environments to be a tool in the analysis and optimization of soybean production for NASA's program in Advanced Life Support (3). In this article, the model is applied to phasic control: the specification of a series of different environmental conditions during a crop's life cycle, with the goal of optimizing some aspect of productivity (11). Here, the focus is on maximizing seed yield averaged over the duration of the crop life cycle (i.e., maximizing g seed m^{-2} day^{-1}). These units are useful for advanced life support, where crops can be successively planted and harvested. The objective is that model simulations will guide the design of specific phasic control experiments.

Soybean phenology is dependent on both temperature and photoperiod (5). As modeled in the phenology

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subroutines of CROPGRO, soybean becomes more photoperiod sensitive and less temperature sensitive during development (9). Thus, both phasic temperature and photoperiod control are assessed here. As CROPGRO was previously modified for a single light/dark cycle temperature regime (26–22°C) (3), data from soybean temperature experiments are used for further model modification, as explained subsequently.

EXPERIMENTAL HYDROPONIC SOYBEAN DATA

Data came from hydroponic soybean [*Glycine max* (L.) Merr. cv. Hoyt] experiments conducted at Utah State University (USU) [(4); T. Dougher, unpublished data]. These experiments were conducted at elevated CO_2 levels (1100 µmol mol^{-1}), with a daily light integral of about 20 mol PAR m^{-2} day^{-1} (PAR, photosynthetically active radiation), using a 12-h photoperiod. Soybean cultivar (cv.) Hoyt (MG III, determinate growth habit) was grown due to its relatively high productivity and dwarf characteristics. The following light/dark cycle temperature regimes (°C) were used: 21/21 ($n = 2$), 23/19 ($n = 2$), 24/24 ($n = 2$), 26/22 ($n = 4$), 29/25 ($n = 4$), and 32/28 ($n = 2$), with root temperatures maintained at the average daily temperature of the shoot (n = number of experiments). Other environmental conditions and plant cultural techniques were described previously (4).

MODEL DEVELOPMENT FOR PHASIC TEMPERATURE CONTROL

For phasic temperature control analysis, seed yield, seed number m^{-2}, mass per seed, pod abortion, biomass, phenology, and daily gas exchange data from the USU temperature experiments were used to modify and calibrate CROPGRO. The evapotranspiration component of CROPGRO has not been adapted for growth chamber conditions, so air and canopy temperatures are assumed equivalent for the simulations in this article. Water and nutrients are simulated to be nonlimiting for the near optimal controlled, hydroponic environment at USU.

Model calibration resulted in simulated seed yield, seed number m^{-2}, mass per seed, and average seed yield rate to be within 10% of the USU data for all temperature experiments (Table 1). In order to achieve this agreement, it was necessary to increase the sensitivity of pod addition rate to cooler temperatures in CROPGRO for the USU experiments at 21/21°C and 23/19°C. Similarly, an increased sensitivity of seed growth rate to higher temperatures was necessary to better simulate mass per seed for the 32/28°C experiment (see Table 1). Thus, the available data and present model suggest a greater sensitivity to temperature extremes for cv. Hoyt than calibrated for soybean in original CROPGRO.

A modification to the model was found to be necessary, because it originally overpredicted total biomass by approximately 20–30% for these same low and high temperature regimes (i.e., 21/21, 23/19, 32/28°C). This was even though seed yield, seed number m^{-2}, and mass per seed were all predicted within about 5%. By comparison, biomass was simulated within 10% for the other temperature experiments. As developed for field conditions, CROPGRO uses all the assimilate produced by photosynthesis each day for either vegetative or repro-

Table 1. Comparison of Modified CROPGRO Simulations With USU Data for Soybean cv. Hoyt*

	Temperature (Light/Dark Cycle)											
	21/21°C ($n = 2$)		23/19°C ($n = 2$)		24/24°C ($n = 2$)		26/22°C ($n = 4$)		29/25°C ($n = 4$)		32/28°C ($n = 2$)	
	Data	Model	Data	Model	Data	Model	Data	Model	Data	Model	Data	Model
Seed yield (g m^{-2})	352	367	369	372	450	453	442	472	444	445	380	379
Harvest index (%)	33	30	33	30	39	41	39	40	38	40	37	32
Seed No. m^{-2}	2044	2175	2206	2220	2809	2809	2805	2919	2771	2926	2812	2790
Mass per seed (mg)	169	169	167	168	160	161	158	162	161	152	136	136
Crop life cycle duration†	97	103	97	103	97	92	91	92	89	87	87	88
Average seed yield rate (g m^{-2} day^{-1})	3.63	3.56	3.80	3.61	4.64	4.92	4.86	5.14	4.99	5.12	4.37	4.31

*Modified model with feedback inhibition of photosynthesis (see text). Data are averaged over n experiments. See text for experimental conditions.
†Days after planting.

ductive growth when nitrogen availability is simulated to be nonlimiting (i.e., the model is source driven). This resulted in considerable simulated vegetative growth during seed fill for the determinate soybean cultivar Hoyt, when seed demand, thus sink strength, for photosynthate was low compared to supply. The low-temperature USU experiments produced low seed numbers, while the higher temperature experiments produced low mass per seed, which resulted in relatively low yields in both cases (Table 1).

A feedback inhibition of photosynthesis due to low sink strength was therefore incorporated into CROPGRO, in order to prevent excessive vegetative growth during seed fill for determinate soybean cultivars (1). The mechanism used was to simulate an accumulation of starch in the leaves after the cessation of leaf expansion, producing a decline in the maximum leaf photosynthetic rate when starch levels exceed approximately 30% of total leaf mass (7). The inclusion of this feedback inhibition in modified CROPGRO successfully reduces the overprediction in biomass to between 10% and 15% for the 21/21, 23/19, and 32/28°C experiments, with a less than 1% change in simulated yields and other biomass values.

RESULTS USING PHASIC CONTROL

Incorporating the modifications described above, we next established baseline simulations, where light/dark cycle temperatures were kept constant throughout the crop life cycle. Photoperiod was set at 12 h as in the USU experiments. A default parameter setting developed for field conditions (9) was used for the photoperiod sensitivity of cv. Hoyt (MG III). For our simulations, soybean development was insensitive to photoperiods less than a critical value of 13.2 h (i.e., plant developmental rate as a function of photoperiod is maximal for photoperiods up to 13.2 h, and decreases for photoperiods greater than 13.2 h).

Representative baseline simulations of average seed yield rate (g m^{-2} day^{-1}) versus temperature are presented in Figure 1 for the USU experimental conditions. These results were generated by simulating different light and dark cycle temperatures in 1°C increments over a range of 20–32°C. Peak production for these simulations occurs at light/dark cycle temperatures of 27/23°C (5.3 g m^{-2} day^{-1}). This yield rate is only about 3% greater than those simulated for the temperature regimes of 26/22 and 29/25°C used in the USU experiments (Table 1).

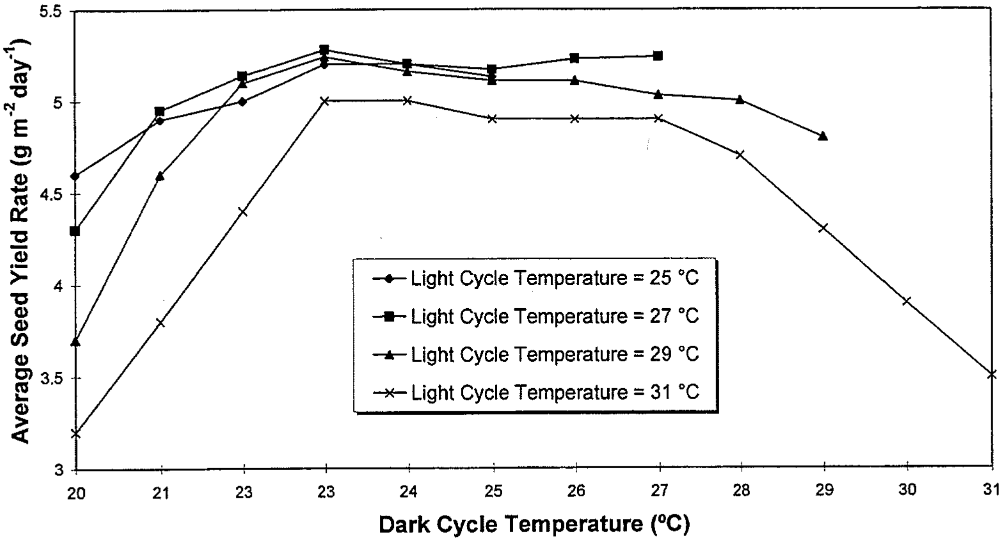

Figure 1. Baseline model simulations: average seed yield rate vs. temperature. Simulations are for constant light/dark cycle temperatures throughout the crop life cycle. Photoperiod = 12 h. Other environmental conditions are simulated as in the USU temperature experiments (see text). Peak production occurs for light/dark cycle temperatures of 27/23°C.

Phasic control, in general, is applied to improve seed yield rate by shortening the duration of vegetative growth, and lengthening that for seed fill. This was done here by simulating different light and dark cycle temperatures as for the baseline simulations, but for separate soybean developmental phases. The individual phases considered were plant emergence to first flower, first flower to first pod, first pod to first seed, first seed to end of pod set, and end of pod set to crop harvest. These individual phases were combined to produce two or three phases for the crop life cycle (e.g., emergence to first flower, first flower to harvest). A summary of the best simulations of seed yield rate for baseline, and for phasic temperature and photoperiod control scenarios is presented in Table 2.

As may be seen in Table 2, simulations of phasic temperature control with nonphasic photoperiod result in only modest improvements in seed yield rate for both two and three temperature phases (photoperiod = 12 h). Warmer temperatures through first flower (28/28°C) had the desired effect of decreasing the duration of vegetative growth by about 3 days over the best baseline simulation. However, soybean development in CROPGRO after first seed (R5) is fairly insensitive to temperature (9). Using cooler temperatures (~22°C) from R5 through harvest to increase the duration of grain fill adversely affected seed number, and lowered simulated seed yield rate (not shown).

The next phasic control scenario considered was to extend the duration of grain fill by increasing the photoperiod over the critical value of 13.2 h. The net effect of this on seed yield depends on the dynamics of seed growth rate and number, which in CROPGRO decline when photoperiods exceed critical values. The model was used to determine when in the crop life cycle to increase the photoperiod, and to what extent. Phasic temperature control was also used to maximize seed number, and so offset the negative effects of longer photoperiods. Extending the photoperiod at a constant daily light integral reduces PPF (photosynthetic photon flux, μmol m^{-2} s^{-1}), while maintaining a constant PPF requires a greater daily light integral. Both cases were examined for this study.

The results of the combined phasic temperature and photoperiod control scenarios suggest that it may be possible to improve seed yield rate over the best baseline and phasic temperature control simulations by extending the photoperiod from 12 to 14 h at the end of pod

Table 2. Baseline and Phasic Control Simulations for Soybean cv. Hoyt

					Phasic Temperature and Photoperiod Control			
			Phasic Temperature Control		Two *T* Phases Planting→R1: 28/28; 12 h R1→End of Pod Set: 23/23; 12 h End of Pod Set→Harvest: 23/23; 14 h		Three *T* Phases Planting→R1: 28/28; 12 h R1→End of Pod Set: 23/23; 12 h End of Pod Set→Harvest: 27/23; 14 h	
	Baseline		Two *T* Phases Planting→R1: 28/28; 12 h R1→Harvest: 27/23; 12 h	Three *T* Phases Planting→R1: 28/28; 12 h R1→R5: 24/24; 12 h R1→ Harvest: 27/23; 12 h				
	Life Cycle: 27/27; 12 h*	Life Cycle: 27/23; 12 h			Constant PPF	Constant Light Integral	Constant PPF	Constant Light Integral
Seed yield (g m^{-2})	451	475	468	475	582	552	586	550
Harvest index (%)	41	41	40	40	42	42	42	42
Seed No. m^{-2}	2881	3079	3048	3103	2955	2955	2955	2955
Mass per seed (mg)	157	154	153	153	197	187	198	186
Crop life cycle duration†	86	90	87	88	95	95	95	95
Photosynthetic efficiency (g seed mol^{-1})‡	0.266	0.271	0.273	0.274	0.290	0.294	0.292	0.293
Average seed yield rate (g m^{-2} day^{-1})	5.24	5.28	5.38	5.40	6.13	5.82	6.17	5.79

*Phase: light/dark cycle temperature (°C); photoperiod. R1 = first flower; R5 = first seed.
†Days after planting.
‡Photosynthetic efficiency = seed yield divided by incident PPF (from plant emergence through harvest).

set (see Table 2). For the parameter settings in CROPGRO, the minimum duration of the phase from R5 to the end of pod set is 35% of that from R5 to physiological maturity. While there is no reproductive stage that exactly corresponds to the end of pod set, there is an imprecise association with the cessation of blooming (12). As was the case for phasic temperature control with nonphasic photoperiod, the use of three temperature phases instead of two did not improve simulated seed yield rates (Table 2).

At constant PPF, the increased grain fill for the best phasic control simulation (two temperature phases and two photoperiod phases) resulted in a seed yield rate of about 6.1 g m^{-2} day^{-1}, roughly a 15% improvement over the best baseline simulation (Table 2), and nearly 20% greater than that simulated for the best USU experiments (about 5.1 g m^{-2} day^{-1}, Table 1). For this scenario, temperature was lowered to 23/23°C from first flower through harvest (Table 2).

Using a constant light integral rather than constant PPF lowered simulated seed yield rate by about 5% to 5.8 g m^{-2} day^{-1} (Table 2), indicating that the ratio of photosynthate supply to seed demand was inadequate at the lower PPF level for this simulation. As shown in Table 2, phasing the photoperiod improved the simulated photosynthetic efficiency (g seed per mol incident PPF) over baseline and phasic temperature control scenarios. There was only a slight loss in photosynthetic efficiency when phasing photoperiod under constant PPF compared to constant light integral. Additionally, harvest index was fairly constant across baseline and phasic control simulations.

Whether at constant light integral or PPF, the extended time period for grain fill resulting from longer photoperiods caused mass per seed to increase by approximately 15–20% over those attained in the USU experiments of Table 1 (Tables 1 and 2). The simulated mass per seed of ~197 mg in the best phasic control simulations is close to that attained for cv. Hoyt in other USU experiments (193 mg) (T. Dougher, unpublished data). Also, simulated seed number m^{-2} in the baseline and phasic control simulations (~3000) have been attained in some of the USU temperature experiments (4). Thus, our results are reasonable.

The sensitivity of soybean developmental rate to photoperiod in CROPGRO increases with maturity group (9). For cv. Hoyt (MG III), simulating a further increase in photoperiod at the end of pod set, from 12 to 15 h, decreased seed number and increased life cycle duration, reducing the simulated seed yield rate to 4.9 g m^{-2} day^{-1} (constant PPF). This result may be contrasted with the above simulated rate of 6.1 g m^{-2} day^{-1} obtained when increasing the photoperiod to 14 h at the end of pod set. Similarly, extending the photoperiod from 12 to 14 h before the end of pod set, at R5, reduced simulated seed yield rate to 5.2 g m^{-2} day^{-1} (constant PPF). Both these simulations resulted in a feedback inhibition of photosynthesis due to reduced sink strengths caused by lower seed numbers m^{-2}, whether at constant light integral or constant PPF (not shown).

The effect of the simulated feedback inhibition on seed yield in these two cases may be seen by removing this process from the model (i.e., by comparison with a source driven model). In the first case (a 15-h photoperiod at the end of pod set), the source driven model gives a seed yield rate of 5.0 g m^{-2} day^{-1} (vs. 4.9 g m^{-2} day^{-1} previously). In this case, the model with feedback inhibition reduced total biomass with only a small effect on seed yield (plant development is identical in both models). In the second case (extending the photoperiod at R5), the source driven model gives a seed yield rate of 5.8 g m^{-2} day^{-1} (vs. 5.2 g m^{-2} day^{-1} previously), so that the feedback inhibition reduced seed yield by about 10%.

DISCUSSION

Phasic temperature and photoperiod control simulations using a modified CROPGRO model indicate the potential to improve the average seed yield rate by approximately 15% over those presently obtained experimentally at Utah State University for soybean cultivar Hoyt. This potential improvement is pertinent, because system mass is a major consideration for advanced life support (10). A system level study, however, would also need to include power consumption and waste processing considerations, in addition to those involving increased crop productivity.

Model results suggest extending photoperiods over those used experimentally during later phases of the crop life cycle in order to lengthen the duration of grain fill, and thereby increase mass per seed. Our model simulations indicate the use of two temperature phases (emergence to first flower; first flower through harvest), and two photoperiod phases (emergence to the end of pod set; the end of pod set through harvest) (Table 2). This temperature and photoperiod phasing is experimentally practical. The model simulations also indicate little advantage in using phasic temperature control without phasing photoperiod.

Our results indicate that an important factor in achieving a higher average seed yield rate would be to minimize losses in seed number by appropriate timing and duration of extended photoperiods, and the use of phasic temperature control. This is not only because seed number affects yield directly, but also because the model simulations suggest the possibility of feedback inhibition of photosynthesis due to low seed sink strength, which may reduce yield as well as total biomass.

Only particular growth phases were incorporated into our model for this study. Also, default parameter settings developed for field conditions were used for the photoperiod sensitivity of cv. Hoyt, as well as for the occurrence of the end of pod set. The actual soybean response to phasic photoperiod control will depend on photoperiod sensitivity in controlled environments. This needs to be determined, as does the exact timing of the photoperiod extension for cv. Hoyt. Our results thus help focus opportunities for further experiments. Future modeling efforts should be expanded to include phasic irradiance control, so that the optimization of both crop productivity and energy efficiency may be analyzed.

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