Life Support & Biosphere Science, Vol. 4 pp. 49–54, 1997
1069-9422/97 $10.00 + .00

PHASIC TEMPERATURE CONTROL APPRAISED WITH THE CERES-WHEAT MODEL

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Phasic control refers to the specification of a series of different environmental conditions during a crop's life cycle, with the goal of optimizing some aspect of productivity. Because of the enormous number of possible scenarios, phasic control is an ideal situation for modeling to provide guidance prior to experiments. Here we use the Ceres-Wheat model, modified for hydroponic growth chambers, to examine temperature effects. We first establish a baseline by running the model at constant temperatures from 10°C to 30°C. Grain yield per day peaks at 15°C at a value that is 25% higher than the yield at the commonly used 23°C. We then show results for phasic control limited to a single shift in temperature and, finally, we examine scenarios that allow each of the five phases of the life cycle to have a different temperature. Results indicate that grain yield might be increased by 15–20% over the best yield at constant temperature, primarily from a boosted harvest index, which has the additional advantage of less waste biomass. Such gains, if achievable, would help optimize food production for life support systems. Experimental work should first verify the relationship between yield and temperature, and then move to selected scenarios of phasic control, based on model predictions.

Phasic control Ceres-Wheat Crop modeling Bioregenerative life support Temperature effects

INTRODUCTION

An ongoing goal of NASA's program in Advanced Life Support is to provide food from crops as efficiently as possible in terms of energy, using as little area and volume as possible. Unlike agriculture on Earth, in which farmers watch the skies and hope that the weather will bring favors, space crops will be coddled with a full suite of ideal environmental conditions in their growth chambers (3). The overall research goal, therefore, focuses upon a key question: Exactly what are the ideal conditions for optimized production?

A higher level of CO_2 has been one definitive answer. Experiments in growth chambers routinely obtain yields for wheat that are about 25% higher using a CO_2 level about three to four times that of our current atmosphere (2). Another important environmental factor is temperature. It strongly affects the duration of the life cycle and has some effect on the photosynthetic rate; thus, temperature influences, in a highly complex manner, the overall growth and development of the crop.

In particular, it should be possible to increase yields by manipulating temperatures during a crop's life cycle by a strategy called *phasic control* (1,7). Rather than

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maintaining a constant temperature throughout the life cycle, a scenario using phasic control would shift temperatures at one or more of the transitions between particular phases of a crop's development. The timing and magnitude of these shifts would be planned to maximize the harvested yield. One might, for example, want to apply warmer temperatures early in the life cycle to speed up vegetative growth and then use cooler temperatures later to lengthen the period of grain filling (1).

What temperature settings for the various phases should be used? The number of possibilities are huge—a situation that is thus ideal for modeling studies to explore potentials, narrow down possibilities, and thus assess the most promising temperature scenarios prior to experimentation. In this article we will use the Ceres-Wheat model, a field-crop simulator that has already been modified for the high yields of hydroponic growth chambers (5,6). The model is first used to establish a baseline of crop yields as a function of constant temperature. Finally, we explore what gains in yield can be expected from phasing the temperature during the crop's life cycle.

TEMPERATURE, LIFE CYCLE, AND PRODUCTIVITY

A key concern in the development of the Ceres-Wheat model has been the prediction of the duration of the life cycle (4). For our concerns, temperature is a main controlling factor. Temperature presents the best first possibility for phasic control, because it is easily controlled within a broad range in the chambers and it is known to produce large variations in the developmental rate of the crop.

High temperatures speed up the developmental rate; cool temperatures slow it down. Ceres-Wheat follows five sequential phases that affect a host of crop dynamics, such as biomass partitioning to plant organs and grain number. The five phases are designated P1 to P5. As initially established (4), each phase has a duration set by an accumulation of degree-days above a base temperature (0°C for P1 to P4, 1°C for P5). The definitions of the five phases are as follows, with their durations in thermal time shown in parentheses:

P1. Emergence of plant to end of terminal spiklet formation (347 degree-days).
P2. From terminal spiklet formation to end of leaf growth and beginning of ear growth (247 degree-days).
P3. Beginning to end of ear growth and anthesis (165 degree-days).
P4. Exponential grain filling (200 degree-days).
P5. Linear grain filling (450 degree-days).

Phases P1 to P3 require a cultivar-specific multiplier for the degree-days and the entire duration of P5 is set as a cultivar-specific parameter; these are included as previous modifications of Ceres-Wheat for the cultivar Veery-10 grown in controlled chambers at Utah State University and used in this study [(6); calibrations for other cultivars are easily achievable with our model]. At constant 23°C, using these degree-days values predicts durations in days of 15.1, 10.7, 7.2, 8.7, and 20.5 for P1 through P5, respectively. The total life cycle at 23°C would thus be 62 days, which is within 24 h of what is observed experimentally (2). The outputs of the model over a range of constant temperatures from 10 to 30°C serve as a baseline of results with which the later results of phased temperatures can be compared (Fig. 1).

The curve of duration of life cycle versus temperature in Figure 1c is hyperbolic. From about 145 days at 10°C it declines to less than 50 days at 30°C, a straightforward result from the durations of the phases noted above. Also in Figure 1c is the harvest index: the ratio of the grain yield to total harvested biomass at the end of the life cycle. Harvest index is also inversely related to temperature, but in an approximately linear manner. The model results indicate, for example, that a constant temperature of 10°C would increase harvest index from 40% to 44%, compared to a constant 23°C.

The predicted harvested dry masses of grain and total biomass, in g m^{-2}, are shown in Figure 1b. Both increase with cooler temperatures. The values at 10°C are nearly a factor of six (for total biomass) and seven (for grain yield) higher than those at 30°C. About half of these increases are accountable to the factor of three in the duration of the life cycle. But after accounting for that one can see that what is arguably the most crucial component to focus on, the average yield per day, must vary as well, being relatively low at 30°C.

In a fully operational food production system with controlled environments, the key factor for optimization is not simply the harvested grain, but rather the harvested grain averaged over the duration of the life cycle. At the end of the life cycle, the facility can be turned around and the crop replanted continuously (unlike the situation in field agriculture). Crop productiv-

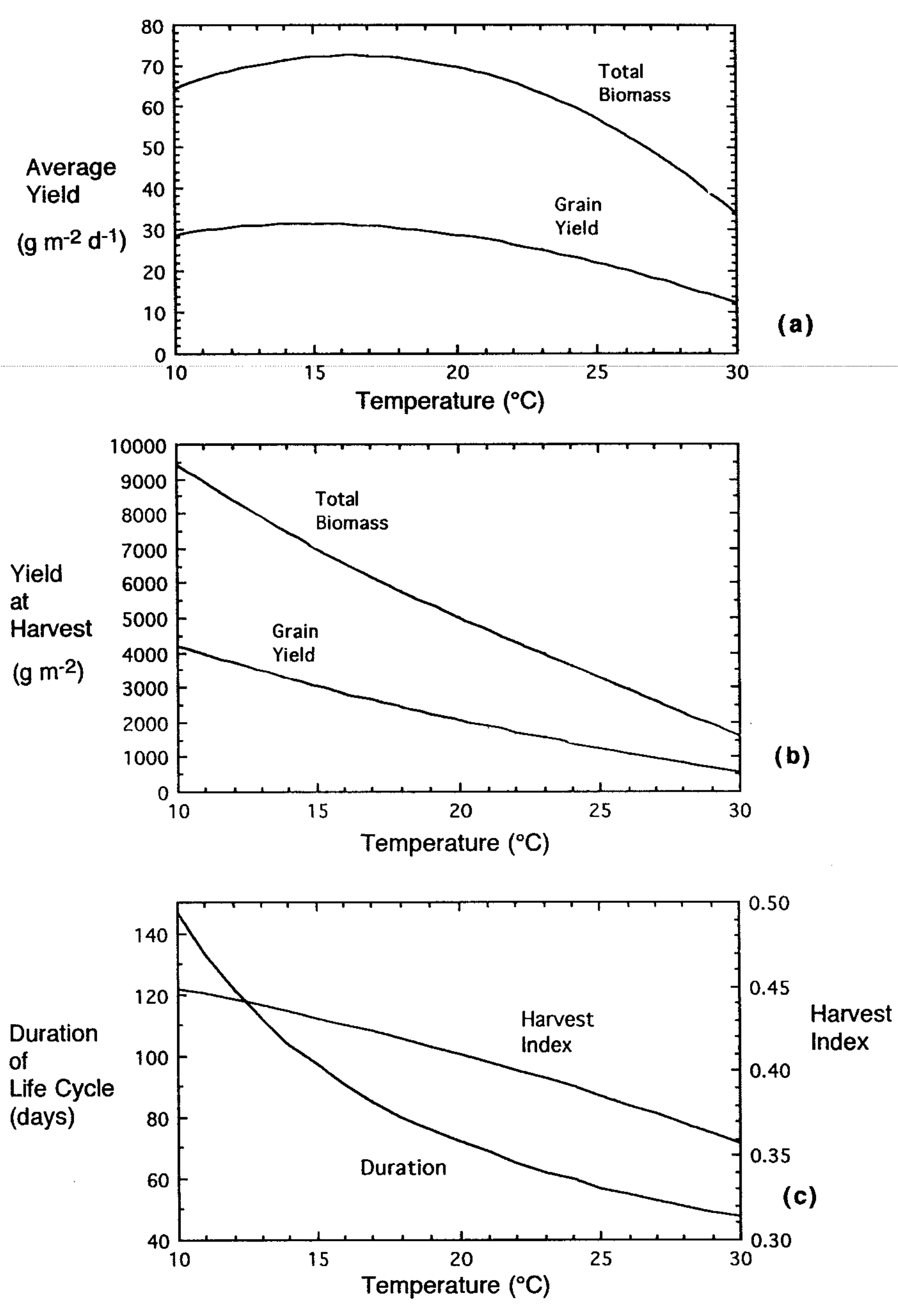

Figure 1. Key outputs from the modified Ceres-Wheat model, as functions of constant temperature: yields of total biomass and harvested grain [(a) average g m^{-2} d^{-1} and (b) life cycle totals in g m^{-2}], harvest index (harvested ratio of grain to biomass), and duration of life cycle. Model parameters were pCO_2 = 1200 ppm; 20 h daily of photosynthetically active radiation that following emergence gradually increased to 1400 μmol m^{-2} s^{-1} at day 8 and thereafter; planting density 720 plants m^{-2}; unlimited nutrients and water.

ity in controlled environments is best measured by a running average output of food and should focus on the units of g m^{-2} d^{-1}.

In Figure 1a, predicted grain yield has a broad peak occurring between 10°C and 20°C. The maximum at 15°C has a grain yield of 31.8 g m^{-2} d^{-1}. This is 26% higher than the yield at 23°C of 25.2 g m^{-2} d^{-1}, which matches the experimental results at that temperature (2). The peak shows the complex interactions between life cycle duration, total biomass, and harvest index, which are monotonic functions of temperature. Without a rather sophisticated model like Ceres-Wheat, such a result could not even be anticipated. It is interesting to note, also from Figure 1a, that the average total biomass in g m^{-2} d^{-1} broadly peaks at around 17°C, which is 2° warmer than the peak of average grain yield. Average total biomass could be important because some of this could enter secondary processing and be converted into edible additives to the diet. However, because of the substantial costs of this processing in terms of extra equipment, volume, mass, and system complexity (8), not to mention the costs of waste processing inedible biomass, the aim should be to elevate the harvest index as much as possible.

Overall, these results with constant temperature suggest that the average total biomass and average grain yield will both be larger at cool temperatures. Furthermore, this study puts a target value that phasic control must attempt to beat: namely, the 31.8 g m^{-2} d^{-1} of grain yield at 15°C. Can the best result offered by constant temperature be surpassed by phasic control, and if so, by how much?

MAXIMIZING DAILY YIELD

The possibilities for phasic control can become complex very quickly, so it is best to begin with the simplest possible scenario for phasic control, namely, one with a single shift in temperature. Because Ceres-Wheat has five phases, there are four ways that these five phases can be grouped into two clusters, requiring only two different temperatures during the life cycle (a single shift between P1 and P2, or P2 and P3, or P3 and P4, or P4 and P5). Yields for every temperature at 1°C intervals between 10°C and 30°C are computed, and the best results, for each of the four ways of clustering, are listed in Table 1.

Table 1. Best Results With Single-Shift Phasic Control

Temperatures (°C) P1 P2 P3 P4 P5	Grain Yield (g m^{-2} d^{-1})	Total Yield (g m^{-2} d^{-1})	Harvest Index (%)	Duration of Life Cycle (days)
28 14 ———>	35.5	70.4	50.4	90.7
19 —> 11 ———>	33.9	65.8	51.5	109.5
20 ———> 13 —>	34.4	66.2	52.0	91.0
15 ————> 12	32.2	69.5	46.3	104.3

The maximum yield for this single-shift phasic control is from the following: the single phase P1 at 28°C (duration of 12.4 days), followed by the cluster of P2 to P5 at 14°C (summed duration of 78.2 days). According to Ceres-Wheat, this temperature scenario will yield 35.5 g m^{-2} d^{-1} of grain, an amount nearly 12% more than the maximum for any run at constant temperature (31.8 g m^{-2} d^{-1} at 15°C). The harvest index for this best two-phase scenario is 50.3%, compared with 43.9% at the constant temperature of 15°C, a 15% increase. Interestingly, the total biomass per day is somewhat less, which means less total waste to process as well. The results in Table 1 suggest a number of scenarios that would be worth testing in the growth chambers, because two temperatures would be relatively easy to apply experimentally.

What about varying the temperature at all five phases (thus four shifts)? Here the advantages of phasic control would be maximized. Allowing each of the five stages to take on any temperature at 2°C intervals from 10°C to 30°C produces 10^5 possibilities. This enormous computation was approached with a Monte Carlo method in which each of five stages can take on, at random, any value at 2°C intervals. The results were then sorted and ranked. Findings from 200 random runs of the modified Ceres-Wheat are shown in Figure 2.

Some overall patterns are apparent. First, as also seen with the single-shift scenarios, increased yields occur with warm early temperatures and cool later ones. This is in keeping with the general concept of phasic control (1), in which vegetative growth should be sped up and grain filling slowed down, to maximize the time during which resources flow into the seed. The opposite scenario produces less productive crops, as seen in Figure 2, in which low yields are all characterized by extremely cool P1s and warm later phases, particularly P4 and P5. The best crop with a yield of 35.3 g m^{-2} d^{-1} in these randomized runs of 200, interestingly, is slightly less than the best yield of the two-phase runs (Table 1). Note that only 0.2% of the 10^5 possibilities were examined.

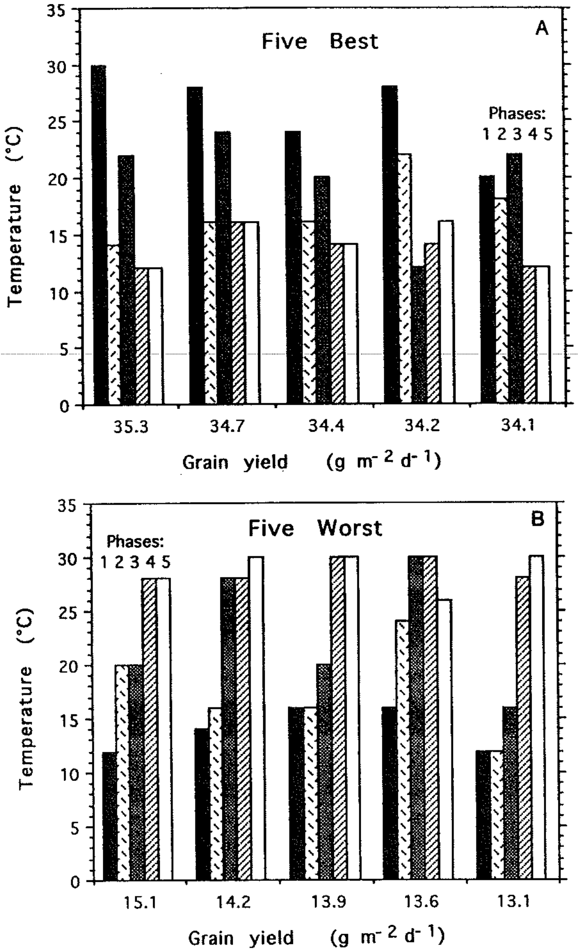

Figure 2. Results from 200 runs of the modified Ceres-Wheat model, in which temperatures for each of the five phases were randomly chosen at 2°C increments from 12° to 30°C. (A) The top five scenarios ranked by average grain yield, with temperatures for the phases of each scenario as a set of five bars. The average grain yield appears at the base of each set. (B) The five worst scenarios ranked by grain yield. The 200 runs represent 0.2% of the possible combinations ($200/10^5$). Another randomized set of runs would lead to different particular best and worst scenarios, but the same general pattern: increased yield with a warm first stage and cool final two; decreased yield with a cool early stage and warm later ones. The even widths of the bars do not, of course, imply equal durations for the stages, which are functions of the temperature (see definitions in text).

Averaging the temperatures of the five best scenarios gives the following scenario: P1 at 26°C, P2 at 17.2°C, P3 at 20°C, P4 at 13.6°C, and P5 at 14°C, with an average harvest index of 52%. This averaged scenario suggests that the temperature should be gradually decreased during the life cycle. Indeed, recent cultivar trials at Utah State University have begun to test these concepts. When the crop's temperature was started at 23°C and then gradually cooled to 17°C toward the end, harvest indexes above 50% have been achieved (B. Bugbee, unpublished data). Our modeling results indicate that the final temperature should be even somewhat cooler.

To see if the five-phase control could be optimized, the best scenario from Figure 2 was taken as a center point around which the temperatures for all five phases were varied systematically, the idea being that an even more productive scenario might lie in the vicinity of these temperature settings. Using such a systematic round following the Monte Carlo round, the best scenario was found with the impressive yield of 36.8 g m^{-2} d^{-1} of grain, about 4% higher than the best two-phase scenario and 16% higher than the best setting at constant temperature. It may be possible to find scenarios that give even higher yields, but likely only slightly higher. At this time, the best scenario is: P1 = 28°C for 12.4 days, P2 = 16°C for 15.3 days, P3 = 20°C for 8.3 days, P4 = 10°C for 20 days, P5 = 14°C for 34.6 days. The total life cycle is 90.6 days with a harvest index of 55.4%.

CONCLUSIONS

A modified Ceres-Wheat model has been applied to the following problem: What if temperature were allowed to be shifted at phase boundaries during the life cycle? It was suspected that warm conditions early in the life cycle (to speed up vegetative growth), followed by cool conditions later (to slow down grain filling) would enhance average grain yield. This has been dramatically confirmed with the model. It may be possible to increase average grain yield by about 12% with two-phase phasic control and perhaps 16% with full five-phase phasic control compared to the best single temperature setting.

Furthermore, the finding that the best single temperature setting (15°C) predicts a yield 26% greater than that obtained in experiments at 23°C is a matter of great potential importance. These results suggest that future experiments should test such low temperatures, to attempt to confirm the results indicated by the model. If these tests are positive, experiments with single-shift phasic control would then be justified. If those turn out successfully, full five-phase phasic control experiments could begin. Phasic control could possibly lead to smaller growing chambers because of increased production of grain and reduced equipment for waste processing because of increased harvest index.

We suspect that interactions in scenarios with phasic control will be found between planting density and temperature, and among density, temperature, and light intensity. Future efforts with the model will be directed toward such interactions, again with the aim of indicating the direction for future experiments toward the goal of optimized food production for advanced life support.

ACKNOWLEDGMENTS

This work was partially supported by NASA grants NAGW-4125 to New York University and NCC 2-139 to Utah State University. We thank the two reviewers and appreciate the detailed line editing provided by one.

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