Life Supp & Biosph Sci, Vol. 1, pp. 119–127 © Cognizant Comm. Corp. 1995, Printed in the USA 1069-9422/95 $5.00 + .00

AN APPROACH TO CROP MODELING WITH THE ENERGY CASCADE

TYLER VOLK, Ph.D.,[1]* BRUCE BUGBEE, Ph.D.,[2] and RAYMOND M. WHEELER, Ph.D.[3]

[1]Department of Biology, 34 Stuyvesant St., New York University,
New York, NY 10003-7599
[2]Plants, Soils, and Biometeorology Department, Utah State University, Logan, UT 84322-4820
[3]NASA Biological Operations and Life Support, Mail Code MD-RES, Kennedy Space Center, FL 32899

Use of plants in advanced life support requires models of crop growth to analyze data, to evaluate areas for improvement, and, for design and engineering, to predict the gas exchanges of crops. We used data from experiments at Utah State University and the Kennedy Space Center for wheat (*Triticum aestivum* L.) and examined it for time dependence of the major three components in the energy cascade: photosynthetic photon absorption, canopy quantum yield, and carbon use efficiency. From the Utah State data, we developed a model with a total of five trends: absorption increasing until canopy closure, then constant; quantum yield as constant, then decreasing during senescence; carbon use as constant. This system probably is the lower limit of simplicity to which a model can be reduced and yet provide substantial utility. We demonstrated this utility by using the model to predict photosynthesis and respiration for experiments at Kennedy Space Center. The most uncertainty arose in predicting a start time for the senescent decrease of canopy quantum yield. The model should be generally applicable to other crops grown in controlled environments, as a generic tool for the design of life support systems.

Crop model *Triticum aestivum* L. Wheat Wheat modeling Energy use efficiency
Light utilization efficiency Carbon use efficiency

INTRODUCTION

To establish a role for plants in advanced life support it is crucial to explore the potential limits of crop productivity. This includes examining the efficiencies of growth and, for engineering analysis, characterizing the rates of gas exchange of carbon dioxide and oxygen, and the production of water vapor and organic volatiles. Much research so far has focused on CO_2, because carbon is a keystone element in organic systems, because CO_2 controls growth, and because CO_2 is valuable for monitoring and understanding photosynthesis at the canopy level.

Here we adopt an analysis that distinguishes three major components in productivity during plant growth and development. These are: 1) absorption of photosynthetic photon flux (PPF); 2) conversion of the energy of absorbed photons into nonstructural carbohydrate (sucrose) during photosynthesis, herein called canopy quantum yield; and 3) conversion of the carbohydrate into structural and enzyme portions of plant biomass, herein called carbon use efficiency.

---

*Address correspondence to Tyler Volk.

Details of these components and estimates of both their theoretical and potentially achievable maxima have been previously described (Bugbee, 1992a; Bugbee and Monje, 1992).

We call this sequence the energy cascade, a series of primary steps in the conversion of the energy of photons to that of biomass. Our goal is to use the energy cascade as a modeling strategy for crops being studied as candidates in the NASA program in Controlled Ecological Life Support Systems (CELSS). This approach is significantly different from previous CELSS crop models (Volk and Cullingford, 1992; Miller, Edeen, and Sirko, 1992; Volk and Rummel, 1989), which did not consider the more fundamental components used here.

We emphasize the word "approach." The model is not finished in the sense of being applicable over all environmental conditions for all times scales. The limitations discussed were expected and anticipated. We believe, however, that the energy cascade has great potential as a basic skeleton that can be fleshed out as needs arise. We have developed this first version of the model using data from Utah State University, and then have applied it to predict data at the Kennedy Space Center.

DATA AND FUNDAMENTAL EQUATIONS

The data used are from experiments at Utah State University (USU) and the Kennedy Space Center (KSC).

The USU experiments collected data from a hydroponics growth chamber with continuous monitoring of net canopy CO_2 uptake during the light hours, canopy respiration during the hours of darkness, and root respiration at all times. Technical details of the system have been described previously (Bugbee, 1992b). The data used in this study came from two recent trials (Monje, 1993).

We also considered hydroponics data from NASA's Biomass Production Chamber at KSC. These experiments also used CO_2 monitoring to yield values of net photosynthesis and total dark respiration (without separating root and shoot respiration). The facility and its capabilities have been previously described (Wheeler, 1992), as have the data used here (Wheeler et al., 1993).

Table 1 summarizes the experimental conditions for four cases: low CO_2 and high CO_2 from USU (USU1 and USU2), and two different light treatments from KSC (KSC1 and KSC2).

The experimentally measured value for net canopy uptake of CO_2 during the hours of light is called net photosynthesis (P_n). During the dark the plants release CO_2, another experimentally measured value. Because the dark hours in these experiments were short (4 h per day), the rate of CO_2 release during the dark was probably approximately equal to the respiration (R) that occurred during the light. With this assumption, a third quantity, usually called gross photosynthesis (P_g), can be computed from the data of USU and KSC as $P_g = P_n + R$. (We take both the influx P_n and the efflux R to be positive values in our equations.)

Gross photosynthesis is the actual fixation of carbon into primary sugars by the Calvin cycle, which requires light. These sugars are then converted by the plant into all the other components, in processes generally called one of two terms: dark respiration or biosynthesis ("dark" in this context does not mean it occurs in the absence of light, only that light is not necessary). This dark respiration or biosynthesis requires not only the transfer of carbon into new molecules, but also the oxidation of a portion of the primary sugars as energy sources, which produces carbon dioxide as a respired efflux.

With this brief background, the numerical components of the energy cascade can be defined. First, a fraction of the PPF is absorbed, designated by A. Second, a fraction of this absorbed energy is converted into primary compounds in gross photosynthesis. A measure of the efficiency of this conversion is the quantum yield Q (moles carbon per mole of absorbed photosynthetic photons), here taken over the entire canopy during the experiments of USU and KSC. Finally, a fraction of the quantum yield becomes new biomass through dark respiration. Its measure is the so-called carbon use efficiency C (moles carbon per

Table 1. Crop Growth Parameters for Experiments From Utah State University (USU1, USU2) and Kennedy Space Center (KSC1, KSC2)

Condition	USU1	USU2	KSC1	KSC2
PPF*	1400	1400	550	690
CO_2 (μatm)	330	1200	1000	1000
T (day/night)†	23/23	23/23	20.2/16.8	20.1/16.4
Plants m^{-2}	700	700	1500	1500
Area (m^2)‡	1.0	1.0	20.0	20.0
Cultivar	Veery-10	Veery-10	Yecora Rojo	Yecora Rojo

*The PPF (μmol m^{-2} s^{-1}) at USU was 300 between days 0 and 1.5, 800 between days 1.5 and 8, and thereafter 1400. PPF averages for KSC are from Wheeler et al. (1993). The PPF for KSC1 was 660 until day 24 after emergence when the lamps were dimmed to about 500. All photoperiods were 20 hours light.

†Temperatures for KSC1 were 23°C for the first 20 days after planting, 20°C until day 33, then 20°C/16°C (light/dark) for the remainder. Temperatures for KSC2 were 23°C for the first 10 days after planting, then 20°C/16°C (light/dark) for the remainder.

‡Areas for USU1 and USU2 were measured during the life cycle, increasing from 0.7 to 1.1.

mole carbon), defined by the ratio $C = P_n/P_g$. (We compute C during the light; however, it is often defined on a 24-h basis.) Mathematically, we have arrived at the following set of equations.

$$P_g = Q\,A\,\mathrm{PPF} \qquad (1)$$

$$P_n = C\,Q\,A\,\mathrm{PPF} \qquad (2)$$

$$R = (1 - C)\,Q\,A\,\mathrm{PPF} \qquad (3)$$

Table 2 lists all symbols and their units. In data analysis or for a predictive model that uses equations (1)–(3), it is also desirable to compute the crop growth rate CGR (g biomass m^{-2} d^{-1}) and total accumulated biomass B (g m^{-2}), knowing the photoperiod H (hours of light per day) and a conversion constant K. Note that one must subtract the respiration that occurs during the dark hours to compute CGR.

Table 2. List of Symbols

Symbol	Name	Units
A	fraction PPF absorbed by canopy	nondimensional
A_{max}	fraction PPF absorbed after $t = t_a$	nondimensional
B	accumulated biomass	g m^{-2}
C	carbon use efficiency	mol carbon/mol carbon
CGR	crop growth rate	g m^{-2} d^{-1}
K	conversion constant = 0.098	see note*
H	photoperiod	h
P_g	gross photosynthesis	μmol CO_2 m^{-2} s^{-1}
P_n	net photosynthesis	μmol CO_2 m^{-2} s^{-1}
PPF	photosynthetic photon flux	μmol m^{-2} s^{-1}
R	respiration	μmol CO_2 m^{-2} s^{-1}
Q	canopy quantum yield	mol carbon/mol PPF
Q_{min}	canopy quantum yield at $t = t_m$	mol carbon/mol PPF
Q_{max}	canopy quantum yield until $t = t_q$	mol carbon/mol PPF
t	time	day
t_a	time of canopy closure	day
t_q	time of onset of senescence	day
t_m	time at crop maturity	day
T	growth chamber temperature	°C

*K is obtained by multiplying the following factors: 10^{-6} mol CO_2 per μmol CO_2, 12 g C per mol CO_2, 2.27 g biomass per g C, 3600 s per h.

$$\mathrm{CGR} = K\,[H P_n - (24 - H)R] \tag{4}$$

$$B = {}_0\!\int^t \mathrm{CGR}\; dt \tag{5}$$

MODEL DEVELOPMENT

From the fundamental set of equations (1)–(5), we now develop a model for the USU data for A, Q, and C shown in Figure 1. Figure 1a for the fractional absorption A of PPF shows two major trends. One is the nearly linear increase from an initial value near zero to a maximum at canopy closure. This rise is due to canopy fill and closure, basically a function of increasing leaf area index (Goudriaan and Monteith, 1990; Charles-Edwards, Doley, and Rimmington, 1986). The second trend is an approximately constant high value following canopy closure to the end of the life cycle. We thus model PPF absorption as a linear rise to a maximum at some time t_a, and then constant thereafter.

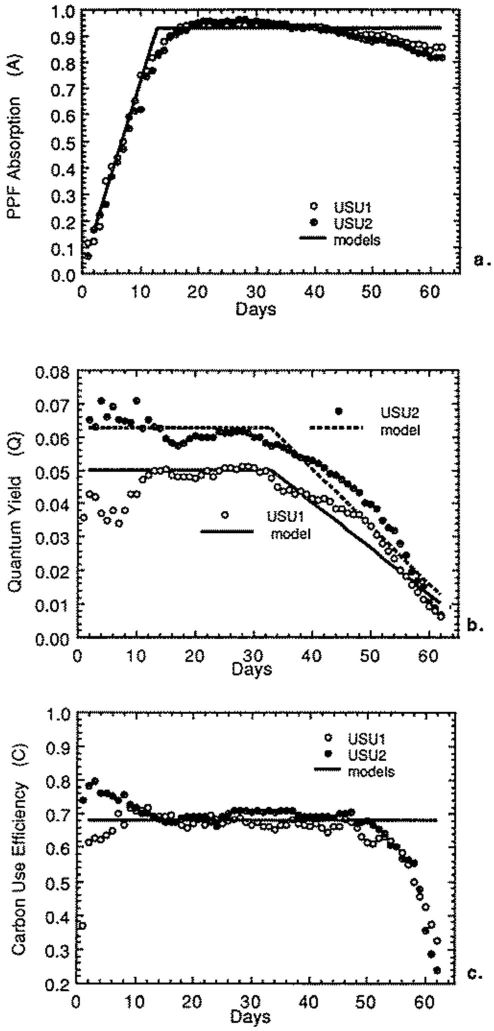

Figure 1. (a) PPF absorption A (nondimensional), (b) canopy quantum yield Q (mol carbon/mol absorbed PPF), and (c) carbon use efficiency C (mol carbon/mol carbon), for USU1 and USU2 data and models, plotted against days after emergence.

The data in Figure 1b for canopy quantum yield Q for USU1 and USU2 show values that are relatively high until flowering (anthesis, day 33). Afterwards Q declines steadily to the end of the crop's life cycle. Constant Q during at least the early part of the life cycle is consistent with other models (Maas, 1993; Goudriaan and Monteith, 1990; Charles-Edwards et al., 1986), whereas a senescence-related decrease during grain fill occurs in the Ceres wheat model (Ritchie, 1991). We thus assume constant Q until a particular point in the life cycle, t_q, and then a linearly decreasing Q to the end of the life cycle.

Values for the carbon use efficiency C, the third component of the energy cascade, are constant over much of the life cycle (Figure 1c). The main departures occur late in the life cycle. We ignore this late decrease as a second-order effect, because it operates upon a small and still declining Q. To maintain simplicity, we assume C to be constant over the life cycle.

This rationale leads to a conceptual system for A, Q, and C that consists of a total of five fundamental trends. Three represent periods when processes are constant. Two represent periods when rates of processes change: the increase in A during canopy fill and the decrease in Q during senescence. Formally, we have arrived at a system of equations (see Table 2 for terms):

$$A = \left(\frac{A_{\max}}{t_a}\right)t \qquad (\text{for } t \le t_a) \tag{6a}$$

$$A = A_{\max} \qquad (\text{for } t \ge t_a) \tag{6b}$$

$$Q = A_{\max} \qquad (\text{for } t \le t_q) \tag{7a}$$

$$Q = Q_{\max} - \left(\frac{Q_{\max} - Q_{\min}}{t_m - t_q}\right)(t - t_q) \qquad (\text{for } t \geq t_q) \qquad (7b)$$

$$C = \text{Constant} \qquad (8)$$

We next use the USU1 data to tune the model. Values for $A_{\max}$, t_a, $Q_{\max}$, and C are summarized in Table 3 and compared to the data in Figure 1. Time t_q, the onset of senescence of Q, appears to be approximately at anthesis (day 33). A value for Q at the end of the life cycle of $Q_{\min} = 0.2\ Q_{\max}$ yields a reasonable senescent decline.

With the tuned values for the parameters, as well as the PPF data as noted in Table 1, we place equations (6)–(8) into equations (2)–(4) to compute P_n, R, and CGR. The results are presented in Figure 2, and appear quite reasonable for USU1, capturing the rise and fall of the absolute values for P_n, R, and CGR. Despite the circularity in the modeling thus far, judgments were made regarding what to ignore and what to include in the three components, which, as Figure 2 shows, seem justified.

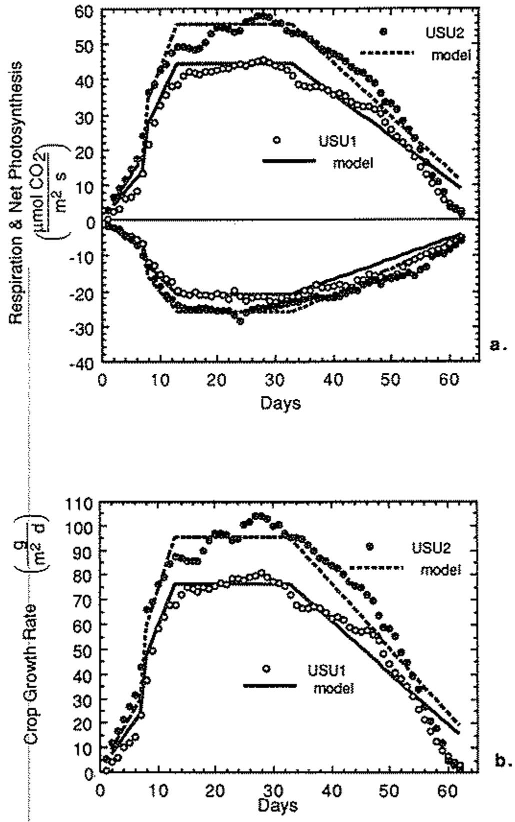

Figure 2. (a) Net photosynthesis P_n and respiration R, and (b) crop growth rate CGR, for USU1 and USU2 data and models, plotted against days after emergence. Although R is a positive value in the equations in the text, it is plotted here as negative, for clarity.

Now consider the case of USU2 with high CO_2. The average enhancement of Q over the life cycle with high CO_2 is about $1.25 \times Q$ at low CO_2 (Monje, 1993). This factor affects $Q_{\max}$ and $Q_{\min}$, as shown in Table 3. All other parameters of the model carry over from the calibrations of USU1.

Results for the USU2 case are also shown in Figures 1 and 2, and again, these results look encouraging. Our model is reasonable, simple, and consists of parts each related to a physiological process, which makes them conducive to more elaborate formulations, should such needs arise.

MODEL TESTING

We now turn to the data from the Kennedy Space Center, where wheat was grown under lower light conditions. The question is whether the energy cascade model tuned to the USU data can be applied to the KSC data with no or little additional tuning. For example, because the KSC experiments used relatively high levels of CO_2, one might expect that the quantum yield parameters from the USU2 data apply. We also have carried over values for $A_{\max}$ and C from the USU models. The cooler temperatures of the KSC experiments (see Table 1) resulted in a longer life cycle.

Predicting development is relatively straightforward if several cultivar-dependent parameters are known (Ritchie, 1991). We ended development at day 78 for the KSC models, having applied the results for the cultivar Yecora Rojo (Bugbee and Salisbury, 1988) to the simple equations for development given by Ritchie (1991). Anthesis, and thus the onset of senescence, was predicted at day 39. (Development over the life cycle is clearly an important topic for crops in life support, and although not particularly complex, is too lengthy to

Table 3. Model Parameters for Experiments From Utah State University (USU1, USU2) and Kennedy Space Center (KSC1, KSC2)

Parameter*	USU1	USU2	KSC1	KSC2
A_{max}	0.93	0.93	0.93	0.93
t_a	12	12	9	12
Q_{min}	0.01	0.0125	0.0125	0.0125
Q_{max}	0.05	0.0625	0.0625	0.0625
t_q	33	33	39	39
t_m	62	62	78	78
C	0.68	0.68	0.68	0.68

*See text or Table 2 for explanation.

be treated in more detail here.) The only remaining parameter is the time to canopy closure, t_a, which must be fit from the KSC data. The KSC planting density was about twice that in the USU experiments, and, not surprisingly, t_a is less, in this case about 9 days. All other parameters needed for the KSC models are the same as those developed for the USU models. Model parameters are summarized in Table 3.

Figures 3 and 4 show the model results for the two cases, KSC1 and KSC2, which differed in their PPF treatments (explained in the notes to Table 1).

The model is generally successful. The good representation for PPF absorption in Figure 3a was expected. Figure 3b shows only the model for Q, because of difficulties in computing this from the KSC data. Figure 3c shows that although the average KSC value for C is slightly higher than the USU value, the overall similarity is encouraging.

Turning to the crucial comparison for P_n, R, and CGR in Figure 4, we see that the models capture the general magnitudes of the data, getting to within about 10% of the average peak plateaus for P_n and CGR in both KSC1 and KSC2. The downward trend in Q due to senescence is also exhibited by the data. In KSC1, dimming the lamps at day 24 after emergence decreased P_n and CGR, and our model captures this change well, especially if one compares the difference between average peak values before and after the dimming to the model's predicted difference. Finally, although the time predicted for physiological maturity falls about 3–4 days short of the data, this is acceptable given the difficulties with predicting crop development for cultivars without a large data base. A more serious shortcoming is that the modeled onset of senescence comes too late; this is especially clear in KSC2, resulting in about a 20% overprediction for P_n and CGR between days 30 and 50. This may be caused by elevated ethylene levels in the nearly closed Biomass Production Chamber at KSC, which are not present in USU's steady-state open gas exchange system (Bugbee, 1992b).

Overall, the KSC model appears successful. The magnitudes of the gas exchange measurements, which vary by about a factor of two between the USU and KSC experiments, are well simulated, as are the general trends.

DISCUSSION AND CONCLUSIONS

One final numerical evaluation of the model can be presented. For all four experiments, the crop growth rate has been integrated using equation (5) to show in Figure 5 the total biomass B for all four experiments. The figure shows the dramatic differences among the experiments in the magnitudes of B and in the duration of the life cycle, all of which are modeled reasonably well. Moreover, at physiological maturity all four models end with an error of about 6% or less.

One aim of a model is to incorporate terms that have physiological meaning (Volk and Bugbee, 1991). Such a model, when suitably simple, often prevails because it can serve as a solid base for additional development. More detail in our model

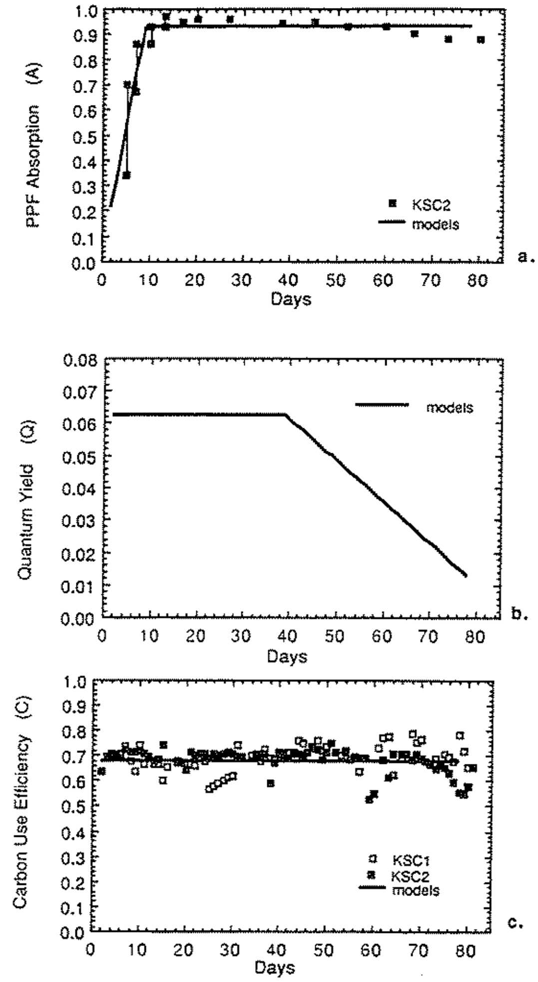

Figure 3. (a) PPF absorption A (nondimensional), (b) canopy quantum yield Q (mol carbon/mol absorbed PPF), and (c) carbon use efficiency C (mol carbon/mol carbon), for KSC1 and KSC2 data and models, plotted against days after emergence [shifted by 4 days from the data presented in Wheeler et al. (1993), to account for the difference between planting and emergence]. Data for Q were not computed due to uncertainties. The bars of uncertainty during canopy fill for absorption (only taken during KSC2) bracket data between a lower bound calculated by Corey (1989), without a measured reflected flux from the substrate back up into the canopy, and our computed upper bound, calculated by assuming an albedo for the substrate of 0.7, approximately that of the hydroponics growth trays at USU.

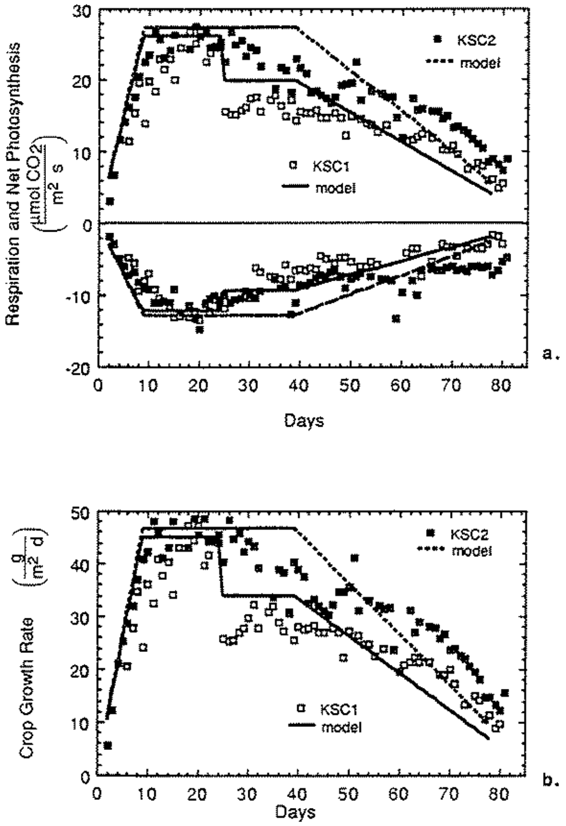

Figure 4. (a) Net photosynthesis P_n and respiration R, and (b) crop growth rate CGR, for KSC1 and KSC2 data and models, plotted against days after emergence. See note about R in caption to Figure 2.

may be warranted when a higher degree of replication is achieved in the crop growth data. For example, during the first 20 days the two KSC trials differ to a greater degree in the data than in the models, which, given their similar environmental conditions, we attribute to the uncontrolled variability common in crop experiments.

We believe our model will be valuable for the engineers of life support systems. It provides a useful approximation for gas exchange during the life cycle, as required by various design needs, for example, in the simulation and control of closed or semi-closed growth chambers (Blackwell et al., 1993). For crop physiologists, the model facilitates a comparison of components in the energy cascade between different data sets.

By predicting data, the assumptions about the underlying processes of the energy cascade can be tested and evaluated.

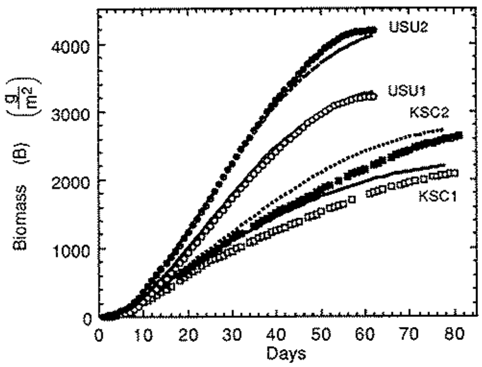

Figure 5. Biomass B for USU1, USU2, KSC1, and KSC2 data (points) and models (lines).

We expect that the energy cascade approach will lead to further model developments and guide experimental design by highlighting areas of uncertainty and periods during the life cycle that deserve special attention. The energy cascade serves as a framework to ask "what if" questions regarding how future advances in crop growth might affect system design and dynamics. Such design projections readily follow from our model, because light absorption, quantum yield, and carbon use efficiency can all be expressed as fractions of potentially achievable, maximum values (Bugbee, 1992a; Bugbee and Monje, 1992).

The model at this stage in its development clearly has specific limitations. It is restricted to the regime in which gross photosynthesis is an approximately linear function of PPF. We furthermore recommend that it only be used in a temperature range of 19–23 °C, with the cultivars and planting densities used at USU and KSC, and for 20-h photoperiods. Limiting the model to these conditions, though not ideal, is not unduly restrictive, because these are the conditions commonly used in the crop growth experiments for advanced life support. Given these limitations, our model can compute the net CO_2 uptake during the light, the respiration during the dark, the crop growth rate, and the accumulated biomass over a range of PPF values of interest to the engineers designing life support systems. Finally, the model is general enough to be easily extended to crops for which data on gas exchange is available, for example, lettuce, soybeans, white potatoes, and others.

ACKNOWLEDGEMENTS

We thank Oscar Monje and Kenneth Corey for their respective efforts at USU and KSC. Support was provided by NASA Cooperative Agreements NCC2-608 (for T.V.) and NCC2-139 (for B.B.). We are indebted to the two anonymous reviewers for their comprehensive and detailed comments.

Tyler Volk, an Associate Professor in New York University's Department of Biology, specializes in modeling the role of life in biochemical cycles, including Earth and the miniaturized earths of advanced life support. During summers he escapes the Big Apple with computer and fax to New Mexico. With a Ph.D. from New York University, he has been active in the NASA CELSS Program for 8 years.

Bruce Bugbee, an Associate Professor in the Department of Plants, Soils, and Biometeorology at Utah State University, has worked in the CELSS Program for 12 years, exploring the limits of plant productivity. His interests include skiing and monitoring the CO_2 levels in his home during parties. His Ph.D is from Penn State University.

Raymond M. Wheeler, Senior Scientist at NASA's Kennedy Space Center, watches space shuttle launches while growing wheat, potatoes, and soybeans in closed chambers, prototypes of what someday may feed the astronauts. Following his Ph.D. from Utah State University, Ray worked for 5 years with Ted Tibbitts at The University of Wisconsin, conducting CELSS research.

REFERENCES

Blackwell, A. L., Maa, S., Kliss, M., and Blackwell, C. C. (1993). Generation of a modeling and simulation system for a semi-closed plant growth chamber. SAE Technical Paper #932128. Society of Automotive Engineers, Warrendale, PA.

Bugbee, B. (1992a). Determining the potential productivity of food crops in controlled environments. Adv. Space Res. 12(5): 85–95.

Bugbee, B. (1992b). Steady-state canopy gas exchange: System design and operation. HortScience 27: 770–776.

Bugbee, B. and Monje, O. (1992). The limits of crop productivity. BioScience 42: 494–502.

Bugbee, B. and Salisbury, F. B. (1988). Exploring the limits of crop productivity I. Photosynthetic efficiency of wheat in high irradiance environments. Plant Physiol. 88: 869–878.

Charles-Edwards, D. A., Doley, D., and Rimmington, G. M. (1986). Modeling plant growth and development. Sydney: Academic Press.

Corey, K. A. (1989). Dynamics of carbon dioxide exchange of a wheat community grown in a semi-closed environment. NASA/ASEE Summer Faculty Fellowship Program 1989 Research Reports, CR-166837. Editors Hosler, E. R. and Armstrong, D. W. NASA John F. Kennedy Space Center, pp. 58–84.

Goudriaan, J. and Monteith, J. L. (1990). A mathematical function for crop growth based on light interception and leaf area expansion. Ann. Bot. 66: 695–701.

Maas, S. J. (1993). Parameterized model of gramineous crop growth: I. Leaf area and dry mass simulation. Agron. J. 85: 348–353.

Miller, A. M., Edeen, M., and Sirko, R. J. (1992). Plant growth modeling at the JSC variable pressure growth chamber: An application of experimental design. SAE Technical Paper #921356. Society of Automotive Engineers, Warrendale, PA.

Monje, O. A. (1993). Effects of elevated CO_2 on crop growth rates, radiation absorption, canopy quantum yield, canopy carbon use efficiency, and root respiration of wheat. M.S. thesis, Utah State Univ., Logan.

Ritchie, J. T. (1991). Wheat phasic development. in Modeling plant and soil systems. Agronomy monograph No. 31. Editors Hanks, J. and Ritchie, J. T., pp. 31–54.

Volk, T. and Bugbee, B. (1991). Modeling light and temperature effects on leaf emergence in wheat and barley. Crop Sci. 31: 1218–1224.

Volk, T. and Cullingford, H. (1992). Crop growth and associated life support for a lunar farm. in The second conference on lunar bases and space activities of the 21st century. NASA Publication CP-3166. Editor Mendell, W. W., pp. 525–530.

Volk, T. and Rummel, J. D. (1989). Transpiration during life cycle in controlled wheat growth. Adv. Space Res. 9(8): 61–64.

Wheeler, R. M. (1992). Gas-exchange measurements using a large, closed plant growth chamber. HortScience 27: 777–780.

Wheeler, R. M., Corey, K. A., Sager, J. C., and Knott, W. M. (1993). Gas exchange characteristics of wheat stands grown in a closed, controlled environment. Crop Sci. 33: 161–168.