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A DYNAMIC TOMATO GROWTH AND YIELD MODEL (TOMGRO)

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ABSTRACT

Models of the greenhouse environment and of crops are needed to determine optimal strategies for environment control in regions where new greenhouse industries are developing. In this research, a physiological model of tomato crop development and yield was developed. A series of differential equations represent the changes in numbers and weights of leaves, fruit, and stem segments and in the areas of leaves, as new organs are initiated, age, and senesce or are picked. The model uses a source-sink approach for partitioning carbohydrate into growth of different organs. An experiment was conducted in six outdoor, controlled environment, growth chambers to quantify the effects of temperature, CO₂, and light on tomato growth processes for calibrating the model. The model accurately described the differences in growth and yield of tomatoes that were observed in the experiment. With additional testing, the model can be used to help determine strategic and tactical decisions concerning greenhouse environment control over practical ranges of CO₂ and temperature. **KEYWORDS.** Environment control, Greenhouses, Modeling.

INTRODUCTION

In recent years, greenhouse production of tomatoes has steadily increased in the southern U.S. and Israel where sunlight is abundant, temperatures are high, and primary harvest occurs in the winter months. Greenhouse control strategies developed under more northerly climates may not be optimal for greenhouse tomatoes in these regions. Growth and yield of tomatoes are controlled to a large extent by light, temperature, and carbon dioxide (CO₂) concentration that the plants are exposed to when nutrient and pest management practices are adequate. Previous research has suggested that an optimization

approach be used to determine how to control these variables in greenhouses for maximum profit, taking into account the costs of operation and increased crop value under the modified environment (Udink ten Cate et al., 1978; Challa and van de Vooren, 1980; Seginer and Raviv, 1984). This approach requires physical models of the greenhouse environment and control devices, biological models of crop growth and yield as affected by environment, economic information on the crop and operation of the greenhouse devices, and a method to integrate these models and determine the most profitable combination of control variables.

The objectives of this research were (a) to develop a dynamic tomato growth and yield model that responds to temperature, CO₂, and PPFD (photosynthetic photon flux density) for integration with a model of the greenhouse environment for studying temperature and CO₂ control, and (b) to conduct controlled environment experiments with different temperature and CO₂ treatments for calibrating the model.

MODEL DESCRIPTION

Few previous tomato modeling efforts have included fruit yield. Wolf et al. (1986) developed a model to predict the phenological development of the tomato plant from planting through flowering to maturity of the fruit. Temperature was the major environmental variable in their model. Acock et al. (1978) developed a canopy photosynthesis model dependent on light and CO₂. Gent and Enoch (1983) developed a model of vegetative growth for tomato in which photosynthesis and dry matter growth depended on light, CO₂, and temperature. Hoogenboom (1980) described a season-long tomato model based on daily time steps. Kano and van Bavel (1988) briefly described a deterministic model for greenhouse tomatoes in which light, CO₂, and temperature affected photosynthesis, respiration, development of fruit clusters, and other processes. The ultimate goal of this latter model was for use in studying greenhouse environment control. Simulation of dry matter partitioning based on source/sink relationships has been used successfully in models of various crops (Hesketh and Jones, 1976). A review of this previous research led us to the conclusion that modeling tomato growth and yield under greenhouse conditions is feasible, that source/sink relationships and age structure of state variables should be included, and that short time steps (on the order of minutes) were needed to address control needs within a day's time period.

The model developed in this research (TOMGRO) was designed to respond to dynamically changing temperature,

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solar radiation, and CO₂ concentration inside the greenhouse. The tomato plant in the model is represented by seven state variable vectors consisting of physiological age classes of plant components: numbers of leaves, numbers of main stem segments, numbers of fruits, dry weights of leaves plus petioles, dry weights of main stem segments, dry weights of fruits, and areas of leaves. Plant growth occurs through changes in these numbers, weights, and areas in each age class of each component. Other variables, such as total plant weight, leaf area index, etc., are computed from these seven state variable vectors. Only the main vegetative stem is considered, assuming that all vegetative branches are removed as soon as formed (a common practice in greenhouse production systems). The plants are assumed to be well watered and fertilized. Figure 1 shows the relationships between variables and processes in the model.

Time in the model is updated by two loops. The main loop increments time daily and a "fast" loop increments time hourly or more frequently if desired within each day. Within the fast loop, temperature, CO₂, and light (photosynthetic photon flux density, PPFD) are computed for that instant in time and development, photosynthesis, and respiration rates are computed and accumulated. Growth of the plant occurs in the daily loop where, at the end of the day, state variable vectors are updated.

ORGANOGENESIS/DEVELOPMENT

Changes in the numbers of plant organs occur through initiation of new leaves, stem segments and fruit, abortion of leaves and fruit, and physiological development of numbers from one age class to the next. The rate of initiation of new nodes (leaf or fruiting truss) is determined by temperature and adjusted slightly for elevated CO₂ levels. The rate of new leaf appearance is equal to the rate of node initiation until the first fruiting truss is formed, then it is reduced by the ratio 1/(1+TPL), where TPL is the number of fruiting trusses per leaf initiated on the main stem. After the first fruiting truss is formed at node FTRSN, the first flower completes its development FRLG nodes later, and the first fruit with diameter greater than 5 mm appears. Then, the new fruit initiation rate is equal to the rate of node formation multiplied by the ratio of new fruit to new nodes and by the ratio of carbohydrate supply

to demand (R_c). When new plant organs are initiated, their numbers (no./m²), initial masses (g/m²) and area (m² leaf/m² ground) are added to the first (youngest) age class for that component.

Mathematically, the net rate of change of numbers of stem segments, leaves, and fruit in the youngest age classes are given by the rate of initiation of new organs of each type minus those that age and move into the next age class, or:

$$\frac{dN_s(1)}{dt} = \text{GENR} \cdot \text{PLM2} - r_L(T) \cdot F(C) \cdot n_L \cdot N_s(1) \quad (1)$$

$$\frac{dN_L(1)}{dt} = \text{GENR} \cdot \text{PLM2} / (1 + \text{TPL}) - r_L(T) \cdot F(C) \cdot n_L \cdot N_L(1) - P_L(1) \quad (2)$$

$$\frac{dN_F(1)}{dt} = \text{GENR} \cdot \text{PLM2} \cdot \text{FPN}(\text{PLSTN}) \cdot R_c - r_F(T) \cdot F(C) \cdot n_F \cdot N_F(1) - P_F(1) \quad (3)$$

where

- N_s(i), N_L(i), N_F(i) = the numbers of stems, leaves, and fruit/m², respectively, for age class i,
- GENR = rate of new node appearance, no./plant-d,
- PLM2 = plant density (no./m²),
- FPN = fruit initiated per new node depending on PLSTN,
- PLSTN = total number of nodes on the plant on a given day,
- TPL = ratio of new fruiting trusses to new leaves,
- R_c = ratio of carbon supply to demand for the crop,
- r_L(T) = overall rate of development of leaves at temperature (T) and 350 ppm carbon dioxide concentration, (1/d),
- F(C) = scalar function of CO₂ concentration (C) that modifies the rate of development for CO₂ levels above or below 350 ppm,
- n_L = number of leaf age classes, 20 in the present model,
- r_F(T) = rate of development of fruit at temperature T and 350 ppm CO₂ concentration (1/d), and
- n_F = number of fruit age classes, 20 in the present model.

The last term in equation 2, P_L(i), accounts for leaf losses caused by shading, insect damage or diseases. The product r_L(T)·F(C)·n_L represents the proportion of the number of leaves in each class (i) that moves to the next class (i+1) in one day. The last term in equation 3, P_F(i), accounts for fruit losses.

Functions were added in the model to reduce fruit initiation rate if temperatures were too high (above THIGH) or too low (below TLOW). The magnitude and duration of temperatures going above THIGH or below TLOW were expressed in degree days above or below these thresholds each day and fruit initiation rate was reduced in proportion to these accumulated values. Since our experiments were maintained below 28° and above 12° C at all times, our data could not be used to quantify

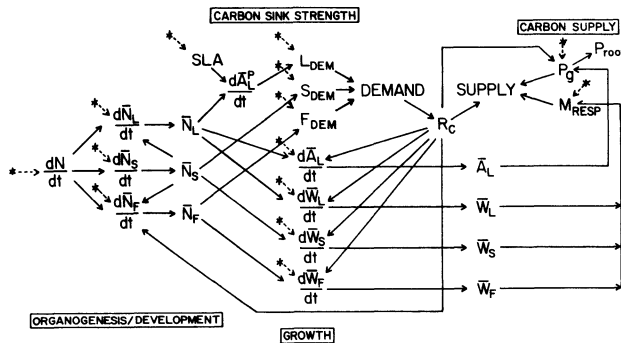


Figure 1—Schematic of the overall development, sink strength, carbon supply, and the actual growth of tomato plant state variables in TOMGRO. The direction of the arrows indicates causal effects, and the * indicates an effect of one or more environmental variables on the process rates. Variables with bars over them represent vectors of state variables with age classes.

these functions, and they will not be further discussed in this article.

GENR is the rate of node initiation per plant under current temperature and CO₂ conditions computed by:

$$\text{GENR} = \text{GENRAT} * F_n(T) * F(C) \quad (4)$$

A maximum rate of node initiation (GENRAT) is multiplied by a temperature function [$F_n(T)$, Table 3] which reduces the rate if temperature is outside the optimum range for vegetative development. Based on our experiments (see below), there appeared to be a small effect of CO₂ on rate of node appearance. A function ($F(C)$) was defined to adjust up or down the rate for CO₂ levels above or below 350 ppm, respectively. $F(C)$ was assumed to be a linear function of CO₂:

$$F(C) = 1 + S_{\text{CO}_2} * (\text{CO}_2 - 350) \quad (5)$$

After entering the first age class, numbers of leaves, stem segments, and fruit move through successive age classes based on development rates for each component that depend on temperature and CO₂. Weights and areas also move through the age classes, and within any day, new weight and area can be added to each class by new growth. Abortion of leaves occurs as they reach maturity (the oldest age class) and as they become heavily shaded (when Leaf Area Index (LAI) exceeds XLAIM).

The net rate of change of the number of leaves in a particular age class, $N_L(i)$, is given by the following equation, for $i > 1$:

$$\frac{dN_L(i)}{dt} = r_L(T) * F(C) * n_L * N_L(i-1) - r_L(T) * F(C) * n_L * N_L(i) - P_L(i) \quad (6)$$

The equations for stem segment and fruit development through the age classes are the same as for leaves, with subscripts on the variables designating stem segments and fruit instead of leaves. For the last age classes, equation 6 and the corresponding stem segment and fruit equations contain only the first and last terms.

CARBON SINK STRENGTH

Sink strength is computed by calculating the potential rate of dry weight increase by each age class of each plant component. For leaves, it is assumed that potential leaf area expansion rate controls leaf sink strength and depends only on physiological age of the leaf, temperature, and CO₂. This rate is divided by specific leaf area (SLA, m²/g leaf), which depends on light, CO₂, and temperature, to obtain a demand for each age class ($L_{\text{dem}}(i)$), taking into account petiole growth as well.

Mathematically, potential leaf area expansion rate is computed for each age class ($dA_{LP}(i)/dt$, m²(leaf)/m²(ground)-d):

$$\frac{dA_{LP}(i)}{dt} = N_L(i) * \text{POL}(i) * F_n(T) * F(C) \quad (7)$$

where $\text{POL}(i)$ is the rate of expansion at optimal temperature and 350 ppm CO₂ concentration, m²/leaf-d,

for a leaf in age class i .

It is assumed by this equation that the leaf expansion rates are controlled by the same temperature and CO₂ functions that control node initiation rate. Sink strength or demand for dry matter growth for leaves is computed by:

$$L_{\text{dem}} = (1 + \text{FRPET}) * \sum_{i=1}^{n_L} \frac{dA_{LP}(i)}{dt} / \text{SLA}(T, C, \text{PAR}) \quad (8)$$

where $\text{SLA}(T, C, \text{PAR})$ is the average specific leaf area of leaves that grow on a given day depending on T , CO₂, and PPFD for the day; and FRPET is the ratio of petiole weight to leaf blade weight. Units of L_{dem} are g dry weight/m²-d.

It was determined from the experiments in Gainesville that SLA varied considerably depending on temperature and CO₂ treatment. In earlier work on peanut and soybean models, Boote et al. (1986) developed a function describing the dependence of SLA on each day's environment, specifically daily temperature and total incoming radiation. With this function SLA is scaled between its maximum (thin leaf) and its minimum. In general, SLA is low under low temperatures, high sunlight conditions, and high CO₂. We adapted the relationship used by Boote et al. and added an effect of CO₂ level. Light effects on SLA are described by S_p :

$$S_p = S_{mn} + (S_{mx} - S_{mn}) * \text{EXP}(-0.471 * \text{PAR}) \quad (9)$$

where

S_{mn} = minimum SLA (i.e., under high light, low temperature), m²/g,

S_{mx} = maximum SLA (i.e., under high temperature, low light), m²/g,

PAR = daily total PPFD, mol(photon)/m².

When PAR approaches zero, S_p approaches S_{mn} , and as PAR becomes very large, S_p approaches S_{mx} .

A function (S_T) describing the relative change in specific leaf weight (SLW=l/SLA) due to temperature (T) was developed as:

$$S_T = 1 + \beta_T (24 - T) \quad (10)$$

where β_T is the change in SLW per °C. This equation is normalized to a temperature of 24° C, which is an arbitrary reference based on results from our temperature treatments. As temperature increases, S_T gets smaller. For CO₂, we added a third function, S_c , the relative increase in SLW due to carbon dioxide concentration:

$$S_c = 1 + \beta_c (\text{CO}_2 - 350) \quad (11)$$

where β_c is the the change in SLW per ppm CO₂.

Finally, SLA for all leaves that grow during a day is:

$$\text{SLA}(T, C, \text{PAR}) = S_p / (S_T * S_c) \quad (12)$$

Under constant temperature and CO₂ conditions, this equation worked fairly well. Under varying temperatures and CO₂ levels, weighted averages of S_T and S_c are

computed first before computing SLA at the end of each day. In applying these equations, SLA was restricted to be between S_{mn} and S_{mx} regardless of the range of T and CO_2 . Ideally, SLA for new growth would be computed by considering the interacting processes of photosynthesis, leaf expansion, tissue synthesis, and transport from the leaf. Further research is needed to adequately pursue this approach.

We assumed that stem segment demand (S_{dem}) is proportional to leaf growth rate for each age class, thus total stem demand is:

$$S_{dem} = \sum_{i=1}^{n_L} L_{dem}(i) * FRSTM * N_s(i) / N_L(i) \quad (13)$$

where $FRSTM$ is the ratio of stem segment to leaf growth rates, assumed constant over all age classes.

Total fruit growth demand (F_{dem}) depends on physiological age, temperature, and CO_2 and is computed as:

$$F_{dem} = \sum_{i=1}^{n_F} N_F(i) * POF(i) * F_n(T) * F(C) \quad (14)$$

where $POF(i)$ = potential growth rate of a fruit in age class i at optimal temperature and 350 ppm CO_2 concentration.

$F_n(T)$ and $F(C)$ are functions to modify the $POF(i)$ rates when temperature is not optimal and CO_2 differs from 350 ppm. The 350 ppm CO_2 concentration was selected as an arbitrary reference near current ambient levels for convenience.

Total above ground dry weight growth demand ($DEMAND$), g tissue/m²-d of the tomato crop is thus:

$$DEMAND = L_{dem} + S_{dem} + F_{dem} \quad (15)$$

CARBON SUPPLY

Carbohydrate availability for growth is based on photosynthesis and respiration calculations. Photosynthetic rate, P_g , is computed at each time step within a day for the whole canopy using the model of Acock et al. (1978):

$$P_g = \frac{D * LF_{max} * PGRED(T)}{K} \quad (16)$$

$$\ln \left[\frac{(1-m) * LF_{max} + Q_e * K * PPFD}{(1-m) * LF_{max} + Q_e * K * PPFD * EXP(-K * LAI)} \right]$$

where

- D = coefficient to convert P_g from $\mu\text{mol}(CO_2)/m^2\text{-s}$ to $g(CH_2O)/m^2\text{-d}$,
- K = light extinction coefficient,
- m = leaf light transmission coefficient,
- LF_{max} = maximum leaf photosynthetic rate, $\mu\text{mol}/m^2\text{-s}$,
- Q_e = leaf quantum efficiency, $\mu\text{mol}(CO_2)$ fixed) / $\mu\text{mol}(\text{photon})$,
- $PPFD$ = photosynthetic photon flux density $\mu\text{mol}/m^2\text{-s}$,
- LAI = canopy leaf area index,

$PGRED(T)$ = function to modify P_g under suboptimal daytime temperatures.

Equation 16 includes the effects of leaf area index, light, and temperature on instantaneous photosynthetic rate. The effect of CO_2 was added to this relationship through its effect on LF_{max} by the following equation:

$$LF_{max} = \tau * CO_2 \quad (17)$$

where τ is the carbon dioxide use efficiency, $\mu\text{mol}(CO_2)/m^2\text{-s}\text{-ppm}(CO_2)$.

Maintenance respiration is computed by:

$$M_{resp} = Q_{10}^{0.1*(T-2.0)} (R_L * (W_L + W_S) + R_F * W_F) \quad (18)$$

where

- M_{resp} = maintenance respiration, $g(CH_2O)/m^2\text{-d}$,
- Q_{10} = sensitivity to temperature,
- R_L, R_F = relative respiration requirement for vegetative tissue and fruit, respectively, $g(CH_2O)/g \text{ tissue-d}$, and
- W_L, W_S, W_F = total leaf, stem and fruit weight, respectively, g/m^2 .

An overall conversion efficiency, E , expressed in terms of dry weight, ($g \text{ tissue}/gCH_2O$), accounts for growth respiration losses and the difference in molecular weight, on a carbon basis, between plant tissue and CH_2O . Overall supply of photosynthate for tissue growth is, therefore, $E * (P_g - M_{resp})$ for root and shoot.

It is assumed that root growth is a phenology-dependent fraction (P_{root}) of the above ground growth potential. Thus, overall supply of carbon for aboveground growth is computed by:

$$SUPPLY = E * (P_g - M_{resp}) * (1 - P_{root}) \quad (19)$$

The ratio R_c is computed by dividing $SUPPLY$ by $DEMAND$ and restricting it to be between zero and 1.

GROWTH

Final growth rates by age class of each organ depend on the ratio of carbon supply to demand, R_c . If $R_c \geq 1.0$, supply is greater than demand and growth rates are $L_{dem}(i)$, $S_{dem}(i)$, and $F_{dem}(i)$ for all i , and in the model photosynthesis is reduced to exactly meet the sink strength on a daily basis in a feedback loop shown in figure 1. There is no dynamic carbon pool in the present model to allow for carrying excess supply to the next day. If $R_c < 1$, carbohydrate supply is limiting, and weight and area growth rates of each age class are computed by multiplying demand by R_c . For organs in age class i , actual dry matter growth rates ($g/m^2\text{-d}$) are computed by:

$$g_F(i) = F_{dem}(i) * R_c \quad (20)$$

$$g_L(i) = L_{dem}(i) * R_c \quad (21)$$

$$g_S(i) = S_{dem}(i) * R_c \quad (22)$$

Leaf area expansion rate is reduced similarly or:

$$\frac{dA_L(i)}{dt} = \frac{dA_{Lp}(i)}{dt} * R_c \quad (23)$$

When compared with equation 6, the equations for mass and area rates of growth contain an extra term each for the growth rate of mass or area on a given day. For example, the net rate of change in weight of fruit ($W_F(i)$) in the i th age class (g/m^2-d) is given by:

$$\frac{dW_F(i)}{dt} = g_F(i) + r_F(T) * F(C) * n_F * W_F(i-1) - r_F(T) * F(C) * n_F * W_F(i) \quad (24)$$

where

$g_F(i)$ = dry weight growth rate of fruit in the i th age class, (g/m^2-d),

$r_F(T)$ = overall rate of development of fruit under the current temperature, ($1/d$), and

n_F = number of fruit age classes.

Equations for mass growth of leaves and stem segments are similar to the one for fruit (eq. 24). These equations with coefficients and functions fully describe the tomato model TOMGRO.

MATERIALS AND METHODS

An experimental study was conducted in Gainesville, FL, to provide data over a range of temperatures, CO_2 levels, and light levels for estimating the parameters and functional relationships for calibrating the model. Ideally, model development would have preceded the experiments, and the list of information in Table 1 would have provided the basis for specific measurements. However, the experiments and model development in this study were concurrent, and some of the functions and constants in Table 1 were formulated as a result of observations during the experiment or during data analysis. Therefore, although presented separately, the experiments were part of the model development process.

The experiments were conducted in six outdoor environmentally controlled growth chambers exposed to natural sunlight. The chambers were 2 x 1 m in area and 1.5 m in height and were placed on 1 m deep steel lysimeters. Temperature, dew point temperature, and CO_2 concentration of the air in the closed chambers were controlled by a central computer as described by Jones et al. (1984). Light level in the chambers was about 85% of that outside the chambers.

On 4 February 1986, tomato seedlings of an indeterminate Israeli variety (K111), were transplanted into the chambers in rows 0.50 m apart, 0.08 m between plants, resulting in 44 plants in each chamber (22 plants/ m^2). At the end of February, a steel plate was placed in the chambers to separate the soil from the chamber top, and slits between plants and steel plates were sealed with closed-cell polyurethane strips. Every two or three weeks, one or more plants from each chamber was sampled such that at the end of the experiment (15 May), six plants remained in each chamber ($3/m^2$). Vegetative branches were pruned weekly so that plants had one stem. Twice per week, flowers were shaken with a hand-held vibrator to enhance pollination. Irrigation was applied about every two days to prevent water stress. Nutrients were supplied with

TABLE 1. Functions and constants required for simulating tomato growth and yield by TOMGRO*

Constants	Value†	Functions
D	2.593	<u>Age Class Functions</u>
E	0.70	POF(i)
FRLG	6	POL(i)
FRPET	0.49	
FRSTM	0.33	
FTRSN	12	
GENRAT	0.5	<u>Plant Age Functions</u>
K	0.58	FPN
m	0.1	P _{root}
Q ₁₀	1.4	
Q _e	0.0645	
R _L	0.015	
R _F	0.010	<u>Environmental Variable Functions</u>
SCO ₂	0.0003	$r_L(T)$
S _{mm}	0.024	$r_F(T)$
S _{mx}	0.075	$F_n(T)$
TPL	0.33	PGRED(T)
XLAIM	5.00	SLA(T,C,PPFD)‡
β_c	0.00085	F(C)
β_T	0.085	
τ	0.0693	

* Specific relationships for the functions used in TOMGRO for the K-111 variety are given in Tables 3-5.

† Based on analysis of data from the current study.

‡ This function is described in the text, equation (9)-(12).

irrigation, the amounts based on monthly soil analyses. Diseases and insects were controlled to minimal levels with preventive applications of pesticides. Treatments in the chambers consisted of combinations of three nighttime temperatures (20, 16, and 12° C) and two CO_2 levels (350 and 950 ppm). Daytime temperature was held constant at 28° C in all chambers for 13 h each day. Nighttime dewpoint temperature was 8° C in all chambers; whereas, it was 21° C in the day.

Canopy carbon dioxide exchange rates were recorded every 5 min and used with the chamber leakage rate (measured by N_2O depletion) to compute net canopy photosynthesis at hourly intervals. Photosynthetic photon flux density, above and below canopy, was measured every 20 s and accumulated to provide hourly values. Selected days during the season were used for estimating parameters for the photosynthesis model. These days were selected when all control and measurement operations were performing as expected; i.e., the chambers remained closed all day and no auxiliary experiments were being conducted. Twelve days, grouped into four groups of about the same age, were selected (29, 30, 31 March; 2, 9, 10, 11 April; 23, 24, 26, 27 April; and 2 May). A nonlinear regression procedure was used to estimate LF_{max} and Q_e for each chamber and each group of data. Light extinction coefficient, K, was computed for each chamber from the PPFD measurements above and below the canopies using Beer's law.

Plant samples were taken into the laboratory for measuring the area of each leaf, counting nodes, trusses, and fruit, and drying and weighing component parts (leaves, stem segments, fruit, and mature fruit) of the plants. These data were used as the basis for quantifying the effects of temperature and CO_2 on development rates of leaves and fruit, on initiation rate of new nodes, and on fruit, leaf, and

stem dry matter growth rates for table look-up functions in TOMGRO for the ranges of these variables in the experiment. Data were recorded on a per plant basis and used to compute LAI and values per m² based on the plant density on each sampling date.

RESULTS

PHOTOSYNTHESIS

Data from these experiments were used to estimate the parameters for the photosynthesis equation (16): light extinction coefficient (K), quantum efficiency (Q_e), and maximum leaf photosynthetic rate (LF_{max}).

A value of $m=0.1$ was assumed for fitting the other parameters in the model. LAI was interpolated for each chamber for the day of photosynthesis observations from successive sampling dates. When K values were computed as daily averages for each chamber, there was little difference among treatments. Using the data from all chambers and all selected days, an average K value of 0.58 was computed. Apparent gross photosynthesis was computed from the data by adding dark respiration, R , an unknown variable that was also estimated in the procedure along with LF_{max} and Q_e . A linear regression analysis of Q_e showed that neither canopy age nor treatment had a significant effect on its value, so an overall average Q_e of 0.0645 mmol(CO₂)/mmol photon was computed. Fixing K , Q_e , and m , and knowing LAI allowed the regression procedure to estimate only LF_{max} and respiration rate, R , Table 2. The value of τ (eq. 17) was found to be 0.0693 mmol(CO₂)/m²-s per ppm CO₂ concentration, or 1.55×10^{-3} m/s, which compares favorably with the value of $1.6 \pm 0.7 \times 10^{-3}$ m/s for tomato reported by Acock et al. (1978). There were no apparent differences in model parameters for different nighttime temperature treatments.

DEVELOPMENT AND GROWTH

A linear reduction in the rate of node initiation was assumed between 12° and 28° C, with the rate at 12° C estimated to be 55% of that at 28° C from our data (Table 3). Previous research (Wolf et al., 1986) showed that the

development rate of leaves (and fruit) was linearly related to temperature between 9° C and 28° C. At 28° C and 350 ppm CO₂ concentration, the rate of node formation was one node every two days. Table 4 gives the relationship between fruit addition rate (FPN) and development of the plant as expressed by node number.

Area expansion rates for leaves of different ages were based on data taken on 29 April for area per leaf vs. fruiting truss. Numbering the fruiting trusses from the top of the plant and grouping all (usually 3) leaves between trusses, the rate of expansion per truss could be determined (fig. 2). This process normalized the development to a physiological time scale. There was little difference in the timing of development or maximum area of leaves. With two physiological days between nodes and one fruiting truss out of four nodes, it was estimated that area expansion was completed after 56 physiological days (7 trusses) and that leaves started aborting after 72 physiological days (9 trusses). The area expansion rate per truss was computed directly from these data and normalized to 100% development to provide an input function of potential area expansion rate vs. age class, POL(i), (Table 5).

SLA varied from about 0.02 to 0.04 m²/g among the different treatments during the mid to late part of the season. The values of b_c and b_T were estimated to be 0.00085 and 0.085, respectively, from these data. Figure 3 shows observed and simulated development of LAI for three treatments. Very little difference existed between LAI for low and high CO₂, but LAI development for low night temperature lagged behind the 20° C treatment by about 10 days until a full canopy was reached.

Individual fruit (starting after flowers aborted and fruit were greater than 5 mm in diameter) developed toward maturity faster than leaves. The maximum rate of fruit development was estimated to be 0.032 per day resulting in a minimum time to develop of 32 days under constant 28° C temperatures. Through a sensitivity analysis, sink strength was estimated to reach a maximum value of 0.27 g/fruit per day (Table 5). It was assumed that this value was reached at 30% of the fruit development period and

TABLE 2. Estimates of maximum leaf photosynthetic rate (LF_{max}) and dark respiration (R) for the four sets of data with $K = 0.58$, $Q_e = 0.0645$ and $m = 0.1$

Group	Average Days from Planting	Treatment (CO ₂ Level / Night Temperature)					
		350/20	350/16	350/12	950/12	950/16	950/12
LF _{max}		----- μmol (photon)/m ² -2 -----					
1	55	26.91	25.56	25.53	58.63	55.09	69.55
2	65	21.02	23.77	21.66	52.92	56.92	48.95
3	80	17.62	18.07	16.77	40.30	38.55	45.18
4	87	20.84	23.29	18.17	49.46	62.04	51.00
Average		21.60	22.67	20.53	50.33	53.15	53.67
R							
1	55	7.36	8.11	7.41	7.91	8.72	8.48
2	65	5.79	6.88	5.61	10.44	9.86	8.72
3	80	6.41	6.37	5.80	6.34	7.08	5.23
5	87	6.74	8.18	7.24	7.05	8.71	8.67
Average		6.58	7.38	6.52	7.94	8.59	7.78

TABLE 3. Values used for the temperature functions in TOMGRO V1.0

Temperature	$r_L(T)^*$	$r_F(T)^\dagger$	$F_n(T)^\ddagger$	$PGRED(T)^\S$
°C	1/days	1/days	-	-
0.0	0.0	0.0	0.0	0.0
9.0	0.0	0.0	0.0	0.67
12.0	0.0048	0.0053	0.55	1.00
15.0	0.0063	0.0103		1.00
21.0	0.0095	0.0203		1.00
28.0	0.0130	0.032	1.0	1.00
35.0	0.0130	0.032		0.0
50.0	0.0	0.0	0.0	0.0

* $r_L(T)$ is the rate of development or aging of leaves at temperature T.

† $r_F(T)$ is the rate of development or aging of fruit at temperature T.

‡ $F_n(T)$ is the function to reduce rate of node initiation when T is outside the optimum range, and to reduce sink strength of growing organs.

§ $PGRED(T)$ is the function to reduce photosynthetic rate for temperatures outside the optimum range.

Note: The model linearly interpolates functional values between temperatures for which values are given.

maintained until the last 10% of fruit development. Sink strength was also assumed to depend on temperature in the same manner as leaf area expansion. More research is needed to define the effect of temperature on potential fruit growth rates.

The model developed in this study was shown to describe tomato growth and development reasonably well for the range of temperature and CO₂ concentrations tested. Figures 4 and 5 show number and weight of mature fruit for 20/350, 12/350, and 20/950 treatments, respectively. After determining model parameters using three of the treatments, results of the other combinations of temperature and CO₂ (16/350, 16/950, and 12/950) were predicted well by the model (results not shown).

SENSITIVITY ANALYSIS

A sensitivity analysis was performed to examine the behavior of model predictions under various constant temperature and PPFD combinations. Four daily total photosynthetically active radiation levels were selected (10, 20, 30, and 40 mol(photon)/m²-day) and held constant over 120-day simulations. For this analysis, CO₂ level was constant at 350 ppm and day/night temperatures were held at 28/20° C each day. Results are summarized in Table 6 and in

TABLE 4. Values for functions of node number in TOMGRO; FPN (fruit per node) and P_{ROOT} (fraction carbohydrate partitioned to roots)

Node Number	FPN*	P _{ROOT}
1	0.5	0.2
2	1.0	-
9	2.0	-
12	2.5	0.15
15	3.0	-
21	3.5	0.10
30	3.5	0.07
50	3.5	0.07
90	3.5	0.07

* Node No. for fruit per node (FPN) refers to the node number above the first truss.

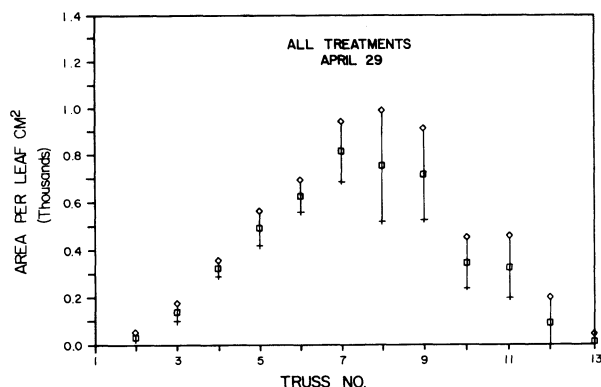


Figure 2—Area per leaf vs. truss number measured from the top of the plants. Average and standard deviation limits from all treatments, 29 April 1986, Gainesville, FL.

figure 6. Responses were not linear. LAI at 120 days varied only between 5.93 and 8.14, partly because leaves grown in the lower light were thinner which helped compensate for the large reductions in photosynthesis. Yield of mature fruit more than quadrupled as PPFD went from 10 to 40, due to higher number of fruit and about doubled fruit size.

Results from the temperature simulations with constant PPFD of 40 and constant CO₂ of 350 are summarized in Table 7 and figure 7. There were fewer nodes per plant for the 20/12 temperature, but LAI reached about 8.2 for all temperatures. The time of fruit development was delayed by the lower simulated temperature treatments in contrast to the simulated PPFD treatments (figs. 6 and 7). Mature fruit yield was an order of magnitude larger for the highest temperatures (28/20 and 30/24) than for the lowest temperature (20/12), but this was due to numbers of fruit increasing with increasing temperatures (Table 7). Mature fruit size decreased by 25% over the range of temperatures selected.

Two other simulations were run to determine the sensitivity of results to the function used to calculate fruit growth demand (eq. 14). We had assumed that fruit sink strength depended on temperature similar to node development rate. This may be a poor assumption since fruit sizes vary considerably under different temperature conditions. In other crops, it has been shown that temperature effects on reproductive processes are different

TABLE 5. Values for potential leaf area expansion (POL, cm²/leaf-day) and potential fruit growth rate (POF, g/fruit-day) as functions of percent development of these organs in TOMGRO V1.0

Percent of Development	Leaf Sink Strength (POL)	Fruit Sink Strength (POF)
	cm ² /leaf-d	g/fruit-d
10	6	0.03
20	15	0.07
30	26	0.10
40	29	0.13
50	29	0.27
60	29	0.27
70	29	0.27
80	25	0.27
90	0	0.10
100	0	0.00

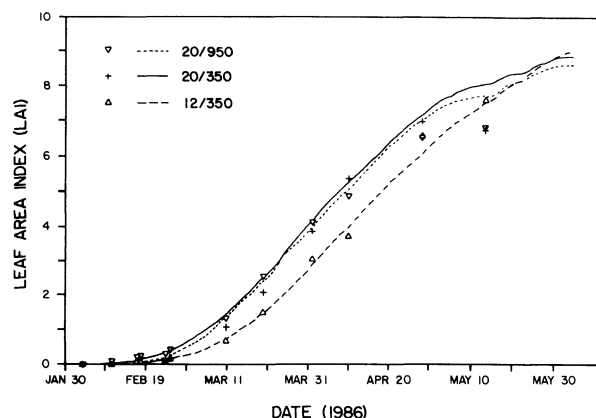


Figure 3—Simulated and observed tomato leaf area index for plants from three treatments in the 1986 experiment in Gainesville, FL.

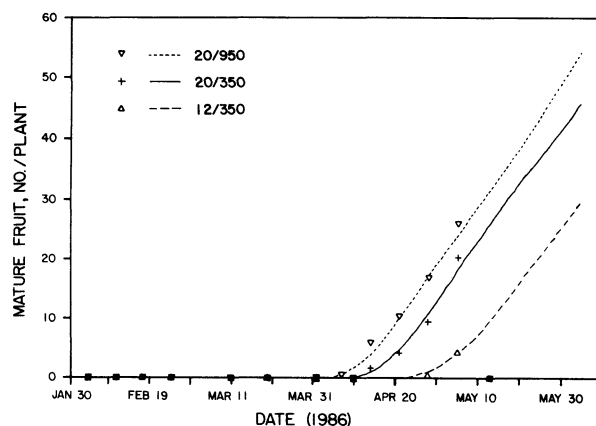


Figure 5—Simulated and observed number of mature tomato fruit per plant (cumulative) for three treatments from the 1986 experiment in Gainesville, FL.

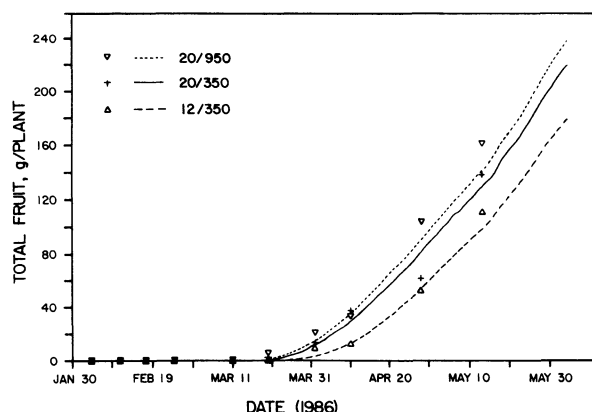


Figure 4—Simulated and observed dry weights of all tomato fruit (cumulative) per plant from the 1986 experiment in Gainesville, FL.

from vegetative processes (van Keulen and Seligman, 1987). We therefore removed the $F_n(T)$ function from equation 14 and re-ran simulations of our experimental treatments of 28/20, 350 ppm (treatment 1) and 28/12, 350 ppm (treatment 3).

Results from these simulations with no temperature effect on fruit demand also compared favorably with our experimental data. Figure 8 shows total fruit dry weight on the plants and mature fruit number for 28/20 and 28/12 treatments, each at 350 ppm. However, average fruit sizes were 3.69 and 4.27 g for 28/20 and 28/12, respectively. There was a larger difference in fruit size and slightly larger fruit for these simulations in contrast to the standard runs with temperature affecting fruit demand. These

simulations demonstrate that more experimental research is needed to determine temperature effects on fruit sink strength.

In other results, the model simulated reductions in fruit yield over a 200 day season of 30% when temperatures dropped from 28/16° C day/night to 20/12° C. An 18% increase in yield was simulated when CO₂ was increased from 350 to 950 ppm for 200 days, with temperatures of 28/16° C.

DISCUSSION

Tomato plants are highly responsive to changes in temperature, CO₂, and light levels. Not only is carbon fixation rate altered by changes in these variables, but dry matter partitioning into fruit vs. vegetative plant structures also changes. For our research on greenhouse environment control, we wanted a relatively simple model, but one that could realistically describe changes in tomato growth and yield under variable conditions. The model described in this article was a compromise between simplicity (one with three or four state variables) and robustness.

The mathematical structure is similar to existing crop models in many respects. It is based on a carbon balance in which photosynthesis and respiration rates are used to compute tissue synthesis. It uses source/sink concepts to compute partitioning, with both source and sink strengths of various organs depending on environmental conditions. It also has phenological development, under environmental control, as the basis for creation of new sinks. The resulting model has seven state variable vectors, each with 20 age classes. The model also has nine functional relationships

TABLE 6. Summary of simulated plant characteristics after 120 days at different daily total solar radiation levels

Daily PAR (mol(photon) /m ² -d)	No. Nodes Per Plant	LAI	No. Fruit / m ²	No. Mature Fruit / m ²	Mature Fruit Wt. g / m ²	Avg. Mature Fruit Size (g dry weight)
10	54	5.93	152	78	113	1.45
20	54	7.47	262	137	316	2.31
30	54	7.84	306	158	432	2.73
40	54	8.14	336	171	521	3.05

* Run at 28/20° C day/night temperatures and 350 ppm CO₂ concentrations.

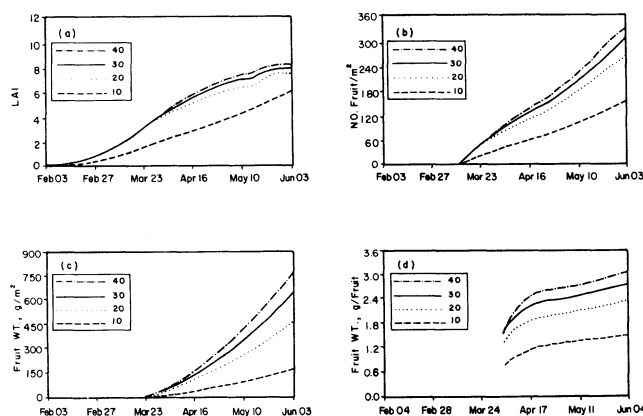


Figure 6—Simulated tomato growth responses to changes in daily, constant light levels (10 to 40 mol(photon)/m²-d) under constant day/night temperatures (28/20° C) and CO₂ level (350 ppm): (a) leaf area index, (b) number of fruit/m², (c) total fruit weight, and (d) average fruit size.

that must be determined empirically, and 21 coefficients that have to be quantified (Table 1). Experiments were conducted to estimate these coefficients and develop the functions required for the model. Ideally, the experiments would be done after the needed relationships were defined, and this was the case for many of the variables listed in Table 1. However, for some variables, the experiment resulted in revisions in the model. For example, POL(i), the sink strength term for leaves, represents the potential area expansion rate instead of potential dry matter sink strength. This was changed because highly variable SLA values were observed under the different conditions but areas of leaves were very consistent. Subsequently, a function was added to make SLA depend directly on T, P, and C for the day. For constant T and CO₂ conditions, this empirical approach worked well, but more work is needed to test this approach under variable conditions.

The model TOMGRO adequately described the important differences in tomato growth and yield observed in the controlled environment study. Validation of the model under independent experimental or commercial greenhouse conditions is needed and is currently in progress in the USA and in Israel (Jones et al., 1989). Undoubtedly, results of additional tests will lead to improvements in the model and its robustness. However, we concluded that the current model can be used now to study the possible effects of different environmental control strategies over practical ranges of CO₂, light, and temperature.

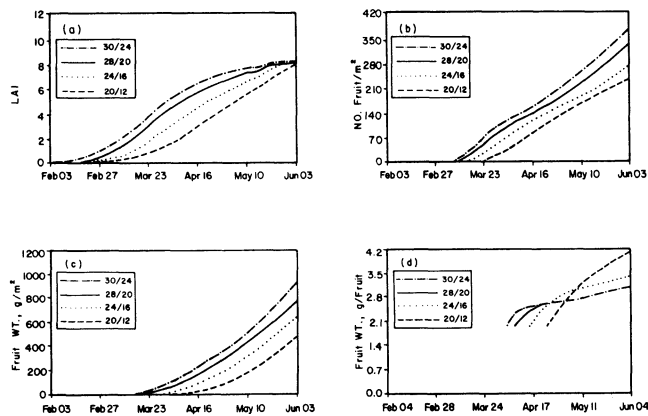


Figure 7—Simulated tomato growth responses to changes in day/night temperatures under constant daily light conditions (40 mol(photon)/m²-d) and CO₂ level (350 ppm): (a) leaf area index, (b) number of fruit/m², (c) total fruit weight, and (d) average fruit size.

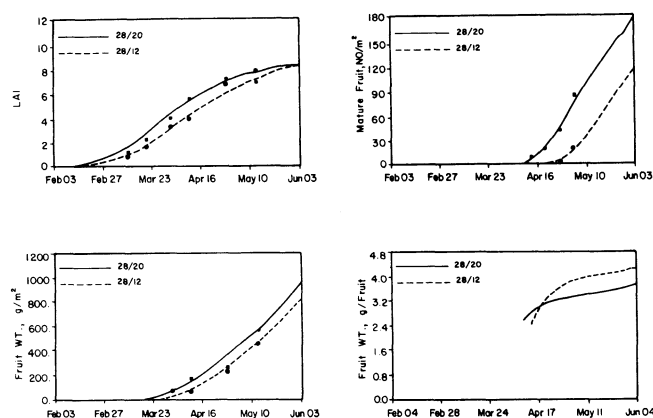


Figure 8—Simulated results for two experimental treatments (28/20 and 28/12 day/night temperatures, 350 ppm) with the assumption that fruit sink strength is not dependent on temperature between 12 and 28° C. Data points are from the experimental data for those two treatments in Gainesville; (a) leaf area index, (b) mature fruit number, (c) total fruit weight, and (d) average fruit size.

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TABLE 7. Summary of simulated plant characteristics after 120 days at different day/night temperatures*

Temperature	No. Nodes Per Plant	LAI	Fruit (No./m ²)	Mature Fruit (No./m ²)	Mature Fruit Wt. (g/m ²)	Avg. Mature Fruit Size (g dry weight)
20/12	42	8.11	235	13	52	4.00
24/16	48	8.30	272	106	357	3.37
38/20	54	8.14	336	171	521	3.05
30/24	58	8.28	380	214	651	3.04

* Run at 40 mol(photon)/m²-d solar radiation and 350 ppm CO₂.

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