

REDUCED STATE–VARIABLE TOMATO GROWTH MODEL

J. W. Jones, A. Kenig, C. E. Vallejos

ABSTRACT. A number of physiologically based tomato crop models have been developed for use in studying greenhouse environment control. However, these models may have hundreds of state variables and thus cannot be used with optimal control methods to determine how to operate greenhouse environment control equipment over time to maximize profit. The objectives of this research were to develop a dynamic tomato growth model with a minimum number of state variables and to determine its applicability across different growing conditions. Our overall approach was to simplify an existing tomato growth model (TOMGRO) by reducing its number of state variables to five while retaining much of its physiological detail. The reduced model, with number of mainstem nodes, leaf area index, total plant weight, fruit weight, and mature fruit weight as state variables, contains the same process equations for photosynthesis, respiration, and development as the comprehensive model, but new leaf area and dry matter growth relationships were developed. Data from two experiments and a commercial greenhouse in Florida and an experiment in Avignon, France, were used to evaluate the model. The model was programmed in a spreadsheet, and parameters were estimated by minimizing RMSE for each experiment. Results showed that the reduced state variable model could accurately describe tomato growth and yield across the different locations and years. Parameters for vegetative growth in the model were consistent across locations, however, parameters for fruit growth and development varied with location. We attributed these results to differences in varieties and management. This model could be easily adapted for simulating other greenhouse crops.

Keywords. Greenhouse environment, Control systems, Crop model, Model simplification.

There has been an increasing interest during recent years in optimal control of greenhouse environments. Modern greenhouses have highly sophisticated measurement and control systems as well as computers that operate these systems and integrate other important information for greenhouse management. With such equipment, it is now feasible to implement control systems that optimize profits, taking into account the costs of control and value of the crop being produced. However, this is a difficult step to take. The main problem to overcome is understanding the complexities of the crop responses to its environment and management practices as well as the dynamics of the greenhouse environment in response to external conditions, greenhouse characteristics, and management. Because of such complexities, researchers have been developing models of greenhouse environments and crops for use in determining optimal greenhouse environment control practices (Bakker et al., 1995).

A number of vegetable crop models have been developed for such purposes (Gary et al., 1998). For example, a number of models have been developed for simulating the dynamic responses of tomato (*Lycopersicon esculentum*) to its environment (Jones et al., 1991; Dayan et al., 1993a,b; de Koning, 1994; Heuvelink, 1989; Marcelis et al., 1998). Some studies have used tomato crop models to determine near optimal greenhouse environmental control policies (Seginer and Sher, 1993; Seginer and McClendon, 1992; Marsh and Albright, 1991; Jones et al., 1994; Hwang and Jones, 1994). However, most crop models are too complex for use in rigorous optimal control studies due to the “curse of dimensionality”. These crop models typically have many state variables [e.g., TOMGRO ver. 1.0 has 69 state variables (Jones et al., 1991), and TOMGRO ver. 3.0 has 574 state variables (Kenig and Jones, 1997)]. Although techniques have been developed to use these models to approximate optimal control (Seginer and McClendon, 1992), one cannot know how close the solution is to the truly optimal one. If these complex crop models could be simplified by reducing the number of state variables to five or less, they would be far more useful in optimal control applications. The question is, however, whether this can be done without sacrificing the model’s ability to simulate growth and yield responses to environments under real greenhouse growing conditions.

Several approaches have been used to reduce the number of state variables of crop models. Tap and van Straten (1995) used scientific reasoning based on physiological understanding of the tomato crop to reduce the number of state variables in the complex model developed by de Koning (1994). Ioslovich and Seginer (1995) used principal component analysis to determine the

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The authors are **James W. Jones**, ASAE Fellow Engineer, Distinguished Prof., Agricultural and Biological Engineering Department, University of Florida, Gainesville, Fla.; **Arie Kenig**, Research Scientist, Agricultural Research Organization, Eilat, Israel; and **C. Eduardo Vallejos**, Associate Professor, Horticultural Sciences Department, University of Florida, Gainesville, Fla. **Corresponding author:** Dr. James W. Jones, University of Florida, Agricultural and Biological Engineering Department, PO Box 110570, Gainesville, FL 32611; voice: (352) 392-8694; fax: (352) 392-4092; e-mail: jjones@agen.ufl.edu.

best sets of transformed state variables (from 2 to 16) to describe simulated results from the TOMGRO ver. 1.0 model. They then used neural networks to model the dynamics of the transformed state variables. Although these efforts to simplify complex models by reducing the number of state variables have shown promise, none have demonstrated how well such models will perform under conditions different from those under which they were developed. Research is needed to determine if reduced models are generally applicable across growing conditions. Therefore, the objectives of this research were to develop a reduced state variable tomato crop model (based on the comprehensive TOMGRO ver. 3.0 model) and to evaluate its performance using crop growth data collected under different greenhouse environment conditions. Two hypotheses were proposed to help guide this study. First, it was hypothesized that a reduced state variable tomato model can be applied across growing locations and conditions. The second hypothesis was that the parameters for the reduced model, developed for one location, could be used to simulate tomato growth and yield at other locations where greenhouse environments and management differed, without additional parameter estimation.

THE TOMGRO MODELS

The original TOMGRO model (Jones et al., 1991; Dayan et al., 1993a,b) was composed of 69 state variables. The crop is divided into components of leaves, stems, fruit and roots. Leaves, stems, and fruit are divided into 10 age classes. The areas of leaves, masses of leaves, stems, and fruits, and numbers of leaves, stems, and fruits are predicted for each of 10 age classes in the model. The last class of fruit (number and mass) do not affect plant processes so the age classes created 68 state variables. In addition, physiological development is maintained as a state variable (number of main stem nodes per plant). Total plant mass is the sum of masses of leaves and stems in each of the 10 age classes plus fruit mass in the first 9 age classes.

Gary et al. (1995) modified the original TOMGRO model to more accurately describe leaf area expansion under varying environmental conditions, and to more explicitly account for fruit addition and growth on trusses (fruiting branches) on the tomato plants (TOMGRO ver. 2.0). Evaluations of the model, using sensitivity analyses and comparisons to experimental data, showed that it was not able to adequately simulate growth and yield under high temperatures. Thus, a new version was developed to improve predictions under high temperature conditions. The new model, TOMGRO ver. 3.0 (Kenig and Jones, 1997), used the original TOMGRO as the basis for many of its functions, incorporated the improvements made by Gary et al. (1993, 1995) to leaf area development and fruit truss dynamics, and included a new function to reduce fruit set and growth under high temperatures.

The plant in TOMGRO ver. 3.0 consists of a single main stem composed of stem segments joined by nodes. All vegetative branches or "suckers" are assumed to be pruned from the plant. At each node there is either a leaf or a fruiting truss. The first few nodes on the plant produce only leaves. When the plant reaches a particular node, a truss is formed. Thereafter, every fourth node is a truss and all

other nodes form leaves (i.e., 3 leaves per truss). Nodes on the main stem are initiated at a rate controlled by temperature. The model simulates numbers of nodes, leaves, and trusses using the temperature-controlled node appearance rate and the morphological characteristics of the plants. Individual nodes and leaves initiated on the main vegetative stem are counted, but leaves and mainstem growth is maintained for all leaf and stem segments for a particular truss. In addition, fruit growth is maintained for each fruit position on each truss on the plant. Thus, the main dry weight state variables are leaf and stem weights for each of the initiated trusses, and fruit age and weight for each position on each truss on the plant.

Leaf area and leaf dry weight are modeled for these leaf units on each truss. Leaf area expansion depends on thermal time whereas leaf mass growth depends on photosynthesis and the allocation of CH_2O to leaves. Leaves compete with fruit and stems for carbohydrates. Stem growth is assumed to be directly proportional to leaf mass growth. A certain fraction of carbohydrate is allocated for root growth each day, and this fraction varies with plant development (characterized by node number). The structure outlined above results in a maximum of 574 state variables in TOMGRO ver. 3.0 (Kenig and Jones, 1997).

The basic process calculations (i.e., photosynthesis, respiration, node development) are the same for all versions of TOMGRO. These basic process rates, including their dependencies on temperature, light, and CO_2 , are used in the reduced model. We will refer to the TOMGRO ver. 3.0 as the "comprehensive model" hereafter because the reduced model incorporates the new functions on effects of high temperature on fruit growth and leaf area development reported by Vallejos et al. (1997).

DESCRIPTION OF THE REDUCED MODEL

Our overall approach was to simplify the TOMGRO model by reducing the number of state variables (to five) while retaining much of the physiological detail from the comprehensive model. A similar attempt was used by Tap and van Straten (1995) for simplifying the tomato model developed by de Koning (1994). However, our approach differs from theirs in the choice of state variables and in the relationships used to describe the various processes. Specifically, the state variables in the reduced model were selected by lumping fruit into two state variables (total fruit weight, W_F , and mature fruit weight, W_M) thereby eliminating age structure and position information. In addition, leaves and stems were lumped together as vegetative tissue, and total plant weight (W) is maintained in the reduced model. Finally, plant development (node number, N) and leaf area index (LAI) are modeled, resulting in the five state variables listed in table 1.

Calculations of vegetative node development, photosynthesis, and respiration rates in the reduced model were kept the same as for the comprehensive model (Kenig and Jones, 1997). Parameters were also kept the same for the equations that describe these processes. These rates are computed hourly and integrated to obtain daily totals which are then used to compute daily net growth and its partitioning to different components. New relationships were developed for daily calculations of leaf area

Table 1. Definition of variables

| Variable | Definition | Units |
|--|---|---|
| State Variables | | |
| N | Number of nodes on mainstem | no. node |
| LAI | Leaf Area Index | m ² [leaf] m ⁻² [ground] |
| W | Aboveground dry weight | g[d.w.] m ⁻² [ground] |
| W _F | Total fruit dry weight | g[d.w.] m ⁻² [ground] |
| W _M | Mature fruit dry weight | g[d.w.] m ⁻² [ground] |
| Other Variables | | |
| α _F | Maximum partitioning of new growth to fruit | [fraction] d ⁻¹ |
| β | Coefficient in expolinear equation | node ⁻¹ |
| δ | Maximum leaf area expansion per node, coefficient in expolinear equation | m ² [leaf] node ⁻¹ |
| κ _F | Development time from first fruit to first ripe fruit | node |
| λ(T _d) | Temperature function to reduce rate of leaf area expansion | unitless (0 to 1 function) |
| θ | Transition coefficient between vegetative and full fruit growth | node ⁻¹ |
| ρ | Plant density | no.[plants] m ⁻² [ground] |
| D _F (T _d) | Function for rate of development of fruit vs. average daily temperature, T _d | d ⁻¹ |
| E | Growth efficiency, ratio of biomass to photosynthate available for growth | g[d.w.] g ⁻¹ [CH ₂ O] |
| f _F (T _d) | Function to modify partitioning to fruit vs. Average daily temperature, T _d | unitless (0 to 1 function) |
| f _N (T) | Function to modify node development rate as a function of hourly temperature | unitless (0 to 1 function) |
| f _R (N) | Fraction partitioning of biomass to roots as a function of development (node) | unitless (0 to 1 function) |
| g _F (T _{daytime}) | Function to reduce growth due to high daytime temperature, T _{daytime} | unitless (0 to 1 function) |
| GR _{net} | Net aboveground growth rate | g[d.w.] m ⁻² [ground] d ⁻¹ |
| LAI _{max} | Maximum leaf area index | m ² [leaf] m ⁻² [ground] |
| N _b | Coefficient in expolinear equation, projection of linear segment of LAI vs N to horizontal axis | node |
| N _{FF} | Nodes per plant when first fruit appears | node |
| N _m | Maximum rate of node appearance (at optimal temperatures) | node d ⁻¹ |
| p _l | Loss of leaf d.w. per node after LAI _{MAX} is reached | g[leaf] node ⁻¹ |
| P _g | Gross photosynthesis, integrated over a day | g[CH ₂ O] m ⁻² [ground] d ⁻¹ |
| Q ₁₀ | Coefficient in maintenance respiration equation | unitless |
| r _m | Maintenance respiration coefficient | g[CH ₂ O] g ⁻¹ [d.w.] d ⁻¹ |
| R _m | Daily maintenance respiration | g[CH ₂ O] m ⁻² [ground] d ⁻¹ |
| t | time | d |
| T | Hourly temperature | °C |
| T _{CRIT} | Mean daytime temperature above which fruit abortion starts | °C |
| T _d | Average daily temperature | °C |
| T _{daytime} | Average temperature during daytime hours | °C |
| V _{max} | Maximum increase in vegetative tissue d.w. growth per node | g[d.w.] node ⁻¹ |

expansion, dry matter partitioning to fruit and vegetative tissue, and mature fruit development in the reduced model.

NUMBER OF NODES (N)

The rate of node development (dN/dt) was modeled as a maximum rate of node appearance rate per day (N_m) multiplied by a function that reduces vegetative development under non-optimal temperatures on an hourly basis during each day.

$$dN/dt = N_m \cdot f_N(T) \quad (1)$$

All variables are defined in table 1. In this equation, temperature, T, is assumed to depend on time, t, on an hourly basis. This development rate is computed hourly and integrated to provide daily development rate. This equation and its parameters are exactly the same as in all versions of TOMGRO. Thus, predictions of nodes on plants by the reduced model are the same as those made by the comprehensive model across all temperatures.

LEAF AREA INDEX (LAI)

The expolinear equation developed by Goudriaan and Monteith (1990) was used as the basis for leaf area expansion. The equation:

$$LAI = \rho \cdot (\delta/\beta) \cdot \ln\{1 + \exp[\beta \cdot (N - N_b)]\} \quad (2)$$

expresses LAI as an explicit function of node position on the plant. Under constant temperature conditions, one can express LAI as a function of node number. Under cool temperatures, node appearance rate would be slow resulting in slow development of LAI. If temperature affects leaf area expansion rate the same as node development rate, we could compute LAI using equation 2. However, we found that high temperatures suppressed leaf expansion to a greater extent than node development (Vallejos et al., 1997). Thus, the derivative of equation 2 was computed with respect to node position (d(LAI)/dN). This derivative expresses the leaf area developed per node of plant development, and we assumed that this would vary with temperature. The equation for the time changes in LAI in the reduced model can be computed via the chain rule as:

$$d(LAI)/dt = d(LAI)/dN \cdot dN/dt \quad (3)$$

By substituting the expression for d(LAI)/dN and introducing a temperature function, the equation becomes:

$$\frac{d(LAI)}{dt} = \rho \cdot \delta \cdot \lambda(T_d) \frac{\exp[\beta \cdot (N - N_b)]}{1 + \exp[\beta \cdot (N - N_b)]} \cdot \frac{dN}{dt}$$

if $LAI \leq LAI_{max}$

$$\frac{d(LAI)}{dt} = 0.0 \quad \text{if } LAI > LAI_{max} \quad (4)$$

Just as in the comprehensive TOMGRO model, LAI is updated daily in the reduced model. When LAI reaches a maximum value (LAI_{max}), it is assumed that leaves will be pruned or senesced to maintain a constant maximum LAI thereafter. Thus, LAI_{max} is more dependent on management than on physiological factors for practical greenhouse conditions.

FRUIT DRY MATTER (W_F)

Fruit dry weight (W_F), was included in the reduced model by introducing a coefficient for the fraction of above- ground biomass growth partitioned daily to fruit after fruit development begins. Fruit development is assumed to begin at a specified developmental time or node position on the plant, N_{FF} . This parameter is not the node position of the truss where the first fruit appears; instead it is the number of nodes on the plant at the time when the first fruit on the plant is above 10 mm in diameter. To compute fruit growth, first, net aboveground biomass growth rate (GR_{net} , g m⁻² d⁻¹) in the reduced model is computed the same way as in the comprehensive model by:

$$GR_{net} = E \cdot (P_g - R_m) \cdot [1 - f_R(N)] \quad (5)$$

P_g is the daily integral of gross photosynthesis, computed hourly using exactly the same equation (Acock et al., 1978; Acock, 1991) and parameters as the comprehensive model (Jones et al., 1991; Kenig and Jones, 1997). R_m is the daily integral of maintenance respiration, computed hourly using the same Q_{10} relationship as the comprehensive model. The respiration coefficient is multiplied by the growing mass ($W - W_M$) and integrated over a day to compute R_m :

$$R_m = \int Q_{10}^{(T - 20) / 10} \cdot r_m \cdot (W - W_M) \cdot dt \quad (6)$$

The fraction of daily growth partitioned to roots, $f_R(N)$, varies with plant development using the same relationship as the comprehensive model. Partitioning of aboveground growth to fruit each day begins at node position N_{FF} and increases asymptotically to a maximum partitioning using the equation:

$$dW_F/dt = GR_{net} \cdot \alpha_F \cdot f_F(T_d) \cdot [1 - e^{-\theta(N - N_{FF})}]$$

$\times g(T_{daytime}) \quad \text{if } N > N_{FF} \quad (7)$

There are two temperature functions in equation 7; one accounts for cool average daily temperature effects on partitioning between vegetative and reproductive growth, $f_F(T_d)$, whereas the second function, $g(T_{daytime})$, modifies

partitioning to fruit under hot daytime conditions. Vallejos et al. (1997) found that fruit growth was reduced sharply as average daytime temperatures increased above 26°C, mostly due to abortion of fruit. A function, $g(T_{daytime})$, was included in TOMGRO ver. 3.0 to account for this effect. The equation for $g(T_{daytime})$ was taken from Kenig and Jones (1997), but modified to allow the critical temperature above which fruit growth is reduced (T_{CRIT}) to vary so that it could be estimated. The equation is:

$$g(T_{daytime}) = 1.0 - 0.154 \cdot (T_{daytime} - T_{CRIT})$$

if $T_{daytime} > T_{CRIT} \quad (8)$

where the 0.154 slope was based on the experiments of Vallejos et al. (1997).

ABOVEGROUND BIOMASS ACCUMULATION (W)

Biomass accumulation in the reduced model is the result of photosynthesis, respiration, and tissue conversion processes, just as it is in TOMGRO. The same equations are used in the reduced model to compute photosynthesis and respiration on an hourly basis as shown above. In addition, leaves can senesce in TOMGRO, which reduces total plant mass. In the reduced model, senescence and/or leaf pruning are assumed to occur after the plants reach their maximum LAI (LAI_{max}). Under most conditions, above ground biomass accumulation is computed by subtracting leaf removal or senescence from GR_{net} , or:

$$dW/dt = GR_{net} - p_1 \cdot \rho \cdot (dN/dt) \quad (9)$$

where p_1 is the dry matter of leaves removed per plant per node development after LAI_{max} is reached. It is assumed that p_1 is 0.0 before maximum LAI is reached, and a constant value thereafter.

Under some conditions, fruit dry matter growth may be very low due to high temperatures and there will be excess carbohydrate. Dry matter accumulation in the reduced model does not include explicit sink strength calculations. Therefore, we assume that there is a maximum rate of vegetative growth per node and that dW/dt may be restricted by this limit if fruit can not grow. This is expressed by the following equation:

$$(dW/dt)_{max} = dW_F/dt + (V_{max} - p_1) \cdot \rho \cdot dN/dt \quad (10)$$

and total above ground dry matter growth is the minimum of equations 9 and 10.

MATURE FRUIT BIOMASS ACCUMULATION (W_M)

In the TOMGRO model versions, mature fruit weight is simulated by computing development of each age class of fruit (TOMGRO ver. 1.0) or individual fruit (TOMGRO ver. 3.0). When each age class or individual fruit reaches full development, the group of fruit or individual fruit is mature. Thus, the models simulate the time lags between new fruit appearance and maturity. The effect of temperature on the amount of time required for a new fruit to mature was determined by Marcelis and Koning (1995). A temperature curve in TOMGRO ver. 3.0 expresses daily development of fruit as a function of temperature. In the reduced model, there are no compartments, thus we

introduced a lag (κ_F nodes) between the time of the first fruit and its maturity. After this time, an average development rate, which depends on daily average temperatures using the function derived from Marcelis and Koning (1995), is used to move fruit from green to mature stages. This is accomplished using the following equation:

$$dW_M/dt = D_F(T_d) \cdot (W_F - W_M) \quad \text{when } N > N_{FF} + \kappa_F \quad (11)$$

Equations 1 through 11 fully describe the reduced tomato growth and yield model with five state variables.

EXPERIMENTAL DATA

Data from greenhouse experiments in Gainesville, Florida, in 1993 and in 1994 were used to estimate parameters for the reduced model that were not in the comprehensive model. In addition, data from an Avignon, France, experiment in 1993 (Gary et al., 1995) and from a commercial tomato greenhouse in Lake City, Florida, (Hwang, 1993) were used to test the hypotheses concerning the applicability of the model at other locations.

1993 GAINESVILLE, FLORIDA, EXPERIMENT

Seeds of *Lycopersicon esculentum* (cv. Trust, F₁; DeRuiters Seeds, Bleiswijk, Holland) were sown into Rockwool seeding cubes on 8 June 1993. Seedlings in the cubes were placed in Rockwool growing blocks (7 × 7 × 7.5 cm) about one week after full cotyledon expansion. By July 1 (the transplanting date in 1993) seedlings had reached an average height of 10 cm and were transplanted, in the growing blocks, onto Rockwool slabs (92 cm × 10.2 cm). Plants were spaced 35 cm apart, resulting in a plant density of about 3.1 plants per square meter. All axillary shoots were removed as they appeared. An automatic drip irrigation system was used to deliver water and mineral nutrients to the tomato plants. All seedlings were raised in the same greenhouse location with an average day temperature of 26 to 30°C. At transplant the seedlings were split into the three different locations (cool, warm, and hot). Thirty tomato plants were grown at each location. On transplant day and 13, 22, and 40 days afterwards, six plants were harvested at each location for measurements of leaf areas and dry weights of different organs. Initial conditions for this and other experiments are in table 2.

A data logger (Campbell Scientific CR-10) was placed in the greenhouse near the plants in the cool location. Environmental conditions were monitored every minute, and hourly averages of temperature and light were recorded for each treatment location throughout the 40 days of

measurements. Average light level in the greenhouses was 13.84 MJ m⁻² d⁻¹ in 1993. Daily average temperatures were 26.3, 27.5, and 30.3 in 1993, whereas daytime averages were 27.9, 30.1, and 35.2, respectively for the cool, warm, and hot treatments. Additional details of this experiment are described by Vallejós et al. (1997).

1994 GAINESVILLE, FLORIDA, EXPERIMENT

Tomato seeds (*Lycopersicon esculentum* cv. Trust, F₁; DeRuiters Seeds, Bleiswijk, Holland) were sown in Rockwool 2.5 cm cubes on 13 May 1994. All seedlings were raised in the same greenhouse location with an average temperature of 26 to 30°C. Seedlings were transplanted into Rockwool slabs (7.5 × 15.2 × 92 cm) two and a half weeks after the planting day (1 June transplanting date in 1994). The slabs were placed in two parallel rows 92 cm apart, along 122-cm-wide benches; plants in a row were 5 cm apart. This resulted in an approximate plant density of 3.5 plants per square meter. At transplant, the seedlings were split into the three different locations in two different greenhouses (warm, cool, and hot locations, respectively). An automatic drip irrigation system was used to deliver water and mineral nutrients to the tomato plants. Plants in the second greenhouse, where the hot treatment was located, were exposed to much higher temperatures during the first weeks of the experiment. However, as the temperatures increased in the month of July, the doors of this greenhouse were opened to increase air circulation. Measurements of node numbers, leaf area index, and leaf, stem fruit, and ripe fruit dry weights were made at about 20-day intervals during this experiment. Additional details of this experiment are described by Vallejós et al. (1997).

Environmental conditions were monitored using the same instrumentation and procedures as in 1993, throughout the 79-day experiment. Average daily temperatures were 25.2, 26.1, and 28.1°C for the cool, warm, and hot treatments, respectively, and solar radiation averaged 10.60 MJ m⁻² d⁻¹ in the greenhouse, about 3.2 MJ m⁻² d⁻¹ lower than values in the 1993 experiment. Average daytime temperatures were 26.2, 27.5, and 31.1°C, respectively, for the cool, warm, and hot treatments.

AVIGNON, 1993

Data were obtained from an experiment conducted in Avignon, France, in 1993 for evaluation of the model over an extended season. Tomato plants were transplanted in a large research glasshouse. Details of this experiment are described by Gary et al. (1995). Hourly measurements of temperature and light were made inside the glasshouse during the 200-day experiment. At about two-week intervals, starting in early January 1993, plant measurements were made (number of mainstem nodes, leaf area index, total plant dry weight, and fruit dry weight). These data were obtained from C. Gary (personal communication) in computer format for use in testing the reduced model.

LAKE CITY, FLORIDA, 1988-1989 DATA

In the 1988-1989 tomato growing season in North Florida, Hwang (1993) monitored the greenhouse environment and tomato production inside a commercial greenhouse. Tomato plants (Variety Bigboy, a large fruit

Table 2. Plant density and initial conditions for each state variable for each experiment

| Variable | 1993 Gainesville | 1994 Gainesville | Avignon | Lake City |
|----------------|------------------|------------------|---------|-----------|
| ρ | 3.10 | 3.50 | 2.20 | 3.12 |
| N | 6.0 | 2.17 | 18.8 | 2.4 |
| LAI | 0.006 | 0.0028 | 0.220 | 0.0030 |
| W | 0.280 | 0.175 | 21.80 | 0.100 |
| W _F | 0.0 | 0.0 | 0.0 | 0.0 |
| W _M | 0.0 | 0.0 | 0.0 | 0.0 |

commercial variety adapted to North Florida greenhouse production) were transplanted on 15 September 1988, in a nutrient film production system at a plant density of 3.12 plants m⁻². The greenhouse had fans, heaters, and evaporative cooling pads which were operated by the grower throughout the season. A Campbell Scientific CR-10 data logger was placed in the commercial greenhouse to monitor environmental conditions every minute during the 250-day growing season as well as operation of fans, heaters, and evaporative cooling (Seginer et al., 1996). Hourly averages of solar radiation and temperatures were computed for use in evaluating greenhouse environment and tomato crop models. Hwang (1993) collected tomato growth and yield data as well as environmental data inside the commercial greenhouse. These data were also used for evaluation of the reduced model.

MODEL EVALUATION PROCEDURES

The reduced state variable model was programmed in Excel® spreadsheet for this study. In the first two columns of the spreadsheet, time is represented as day and hour of the day, respectively. Hourly temperature and light data, placed in the next two columns, are used to compute the different process rates on an hourly basis. Hourly rates of development, photosynthesis, and respiration are integrated (using rectangular integration) to create net daily rates of change in these variables. The five state variable equations are programmed to be integrated daily, using parameters placed in fixed locations in the spreadsheet, and using the daily net rates integrated over 24 h. This allows state variables to be represented as columns of numbers, computed from the dynamic equations described previously. In addition, all of the available observed data (number of mainstem nodes, leaf area index, total above ground dry weight, cumulative fruit dry weight, and mature fruit dry weight) were placed in the spreadsheet in rows corresponding to the dates the data were collected.

To test the hypotheses, data from both experiments in Gainesville were used to estimate parameters for the reduced model. The model and parameters were then used to simulate tomato growth and yield for the Lake City and Avignon environmental conditions. Finally, parameters were estimated for Lake City and Avignon locations to compare with results using parameters from Gainesville. Parameters were estimated by searching over parameter space to minimize the error sum of squares between simulated and observed data.

Errors (Simulated – Observed) of each state variable were computed for each day when an observation was available for that state variable. The sums of squares of these errors were then computed for each state variable to provide measures of how well the model described observed data. The “Solver” procedure in the Excel

Table 3. List of parameters estimated using a least squares procedure and the variable used to estimate the parameters

| Parameters | Variable Used to fit the Parameters |
|---|-------------------------------------|
| δ, β, N_b | LAI |
| $\alpha_F, \vartheta, N_{FF}, T_{CRIT}$ | W_F |
| κ_F, D_{Fmax} | W_M |
| V_{max} | W |

software was used to estimate parameters using the criterion of minimum error sum of squares for each state variable. Table 3 shows the list of parameters estimated using this procedure as well as the state variable used to estimate each parameter. These parameters were chosen because they were not in the comprehensive model; they are parameters in the relationships developed to simulate LAI, fruit weight, and mature fruit weight without using the age classes of leaves and fruit. Other parameters, such as N_m, r_m , and the photosynthesis equation parameters, were kept the same as in the TOMGRO ver. 3.0 model (Kenig and Jones, 1997). This parameter estimation procedure was used for the Gainesville experiments, combining 1993 and 1994 data. First, the parameters that describe leaf area development (δ, β , and N_b) were estimated by selecting the combination of these parameters that minimized error sum of squares for LAI. Secondly, the parameters were estimated using cumulative fruit dry weight, followed by the two parameters that describe mature fruit production. Constraints were placed on certain parameters to make sure that they kept their physiological meaning. It was necessary to limit α_F to be less than 0.95, for example. Additionally, parameters for N_m (0.50 for Gainesville and Lake City and 0.55 for Avignon), p_1 (2.0), and r_m (0.016) were carried over from the TOMGRO model for all locations. LAI_{max} was not reached for the 1993 and 1994 data, and LAI_{max} for the Lake City and Avignon data depended on management of the crop more than on crop development. Leaves were pruned to maintain LAI between 2 and 4 in Lake City and between 1.5 and 3.0 in Avignon. Thus, LAI_{max} was set to 4.0 and 2.3 for these two locations, respectively.

The model was used to simulate tomato growth for Lake City and Avignon using parameters estimated from the Gainesville experiments. Root mean square errors (RMSE) were computed for characterizing the fit to LAI, W, W_F , and W_M for each location. Then, a similar procedure was used to estimate parameters for the Lake City and Avignon data sets, and a second set of RMSE values was computed. There were not enough data points for LAI in Lake City ($n = 4$), so no attempt was made to estimate leaf area development parameters for this location. Parameters estimated from the Gainesville data were used for Lake City. In addition, mature fruit dry weights were not recorded in Avignon, so it was not possible to estimate κ_F and D_{Fmax} for Avignon data.

Table 4. Parameters estimated for each set of experimental data

| Parameter | Gainesville, Florida | Lake City, Florida | Avignon, France |
|-------------|----------------------|--------------------|-----------------|
| δ | 0.038 | (0.038)* | 0.030 |
| β | 0.169 | (0.169)* | 0.169 |
| N_b | 16.0 | (16.0)* | 16.0 |
| α_F | 0.80 | 0.95 | 0.95 |
| ϑ | 0.135 | 0.200 | 0.200 |
| N_{FF} | 22.0 | 10.0 | 19.0 |
| T_{CRIT} | 24.4 | (24.4)* | 22.0 |
| κ_F | 5.0 | 5.0 | *‡ |
| D_{Fmax} | 0.08 | 0.04 | *‡ |
| V_{max} | *† | *† | 8.0 |

* Values based on parameters estimated from Gainesville.

† Not enough data were available to estimate V_{max} in Gainesville or Lake City.

‡ No mature fruit data were available to estimate these parameters for Avignon.

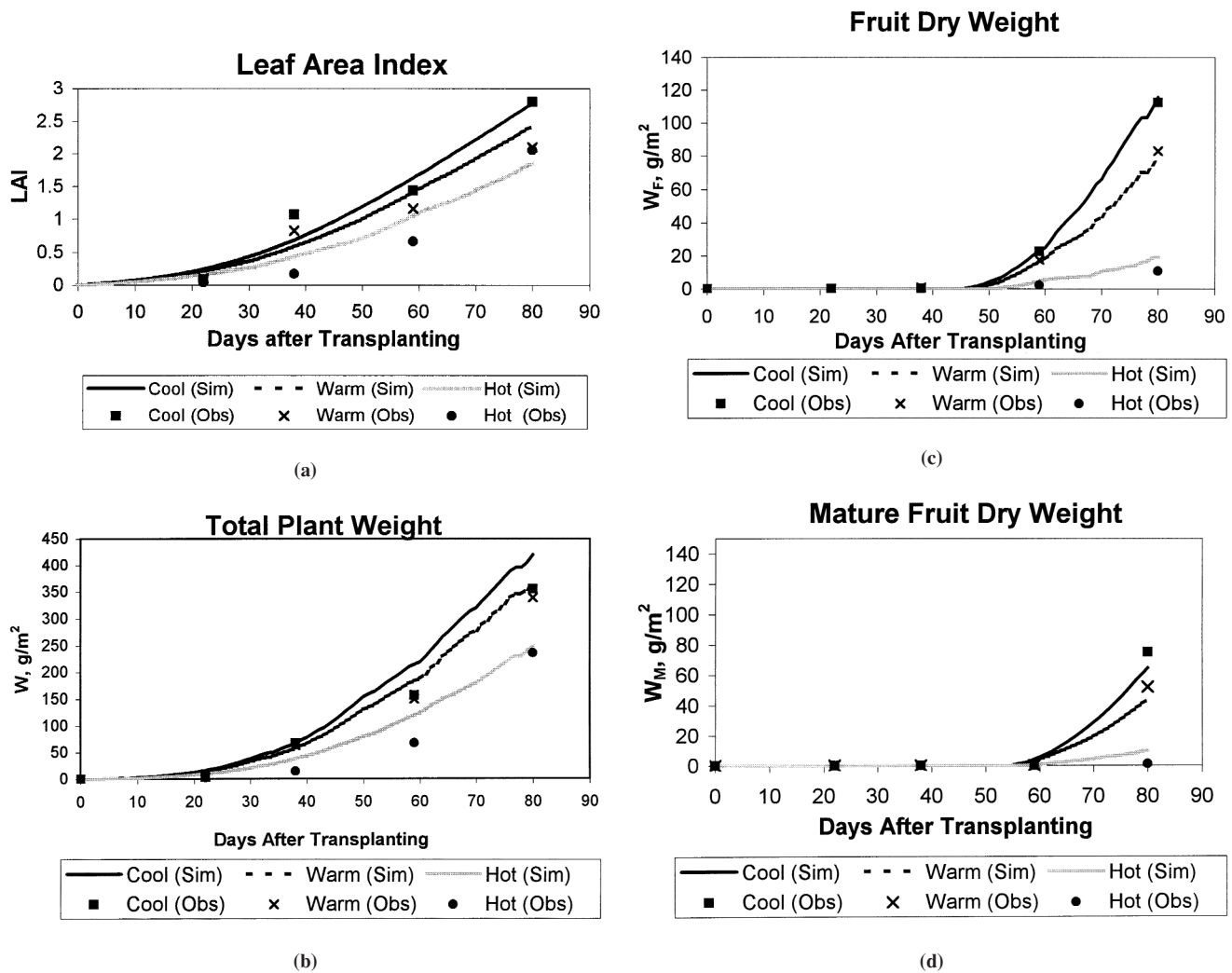


Figure 1—Simulated and observed tomato growth variables vs days after transplanting for the 1994 experiment in Gainesville, Florida; (a) leaf area index, (b) total aboveground plant weight, (c) total fruit dry weight, and (d) mature fruit dry weight.

Table 5. Root mean square errors (RMSE) and number of observations for each fitting procedure*

| Variable | Parameters | Gainesville | | | | Lake CityAvignon | | | |
|----------------|--------------------------------------|-------------|-------|----|-------------------|-------------------|---|-------------------|-------------------|
| | | n | RMSE | n | RMSE ₁ | RMSE ₂ | n | RMSE ₁ | RMSE ₂ |
| LAI | δ, β, N_b | 15 | 0.236 | 4 | 1.43 | 1.43 | 9 | 0.485 | 0.460 |
| W _F | $\alpha_F, \theta, N_{FF}, T_{CRIT}$ | 12 | 25.89 | 13 | 326.72 | 72.55 | 9 | 109.25 | 58.43 |
| W _M | κ_F, D_{Fmax} | 6 | 6.94 | 12 | 218.09 | 73.71 | - | - | - |
| W | V _{max} | 21 | 25.89 | 4 | 101.68 | 217.8 | 9 | 208.77 | 109.27 |

* Parameters were first fit to Gainesville data (1993 and 1994), then used to predict results for Lake City and Avignon; RMSE₁ summarizes the mean square error of prediction. A second set of RMSE values for Lake City and Avignon were obtained after fitting the model to data at these two locations

RESULTS

GAINESVILLE EXPERIMENTS

Values for the tomato model parameters estimated for the Gainesville, Florida, experiments are given in table 4. Graphical comparisons between simulated and measured values of LAI, total plant weight, fruit weight, and mature fruit weight are shown in figure 1a through d, respectively, for the 1994 experiment. Node numbers are not shown; the reduced model and comprehensive model have exactly the same equation to predict node development. Similar close comparison between observed and simulated values were observed for the 1993 data. Table 5 gives the RMSE values

computed using both 1993 and 1994 data sets from Gainesville. The critical daytime temperature (T_{CRIT}) was estimated to be 24.4°C, meaning that fruit growth was reduced when daytime temperature average exceeded this value. These results are similar to those reported by Peet et al. (1997) in which fruit growth decreased when average temperatures exceeded 25°C.

The graphs and RMSE values clearly demonstrate the ability of the reduced model to describe the differences among temperature treatments over the two years of experiments at this one location. Note that V_{max} was not estimated, so no parameters were varied specifically to fit the total above-ground biomass for this data set. Still, W was simulated very well for all treatments. This is not too surprising because LAI was simulated well in the reduced model, and we took the photosynthesis and respiration relationships and parameters in the reduced state variable model from the comprehensive model with no changes. The reduced model for fruit and mature fruit growth were new. A total of six parameters were estimated to fit these state variables. Results were good, as indicated by the RMSE values and graphs, which confirms that the methods of accounting for lags in fruit dynamics could be mimicked by this simplified model.

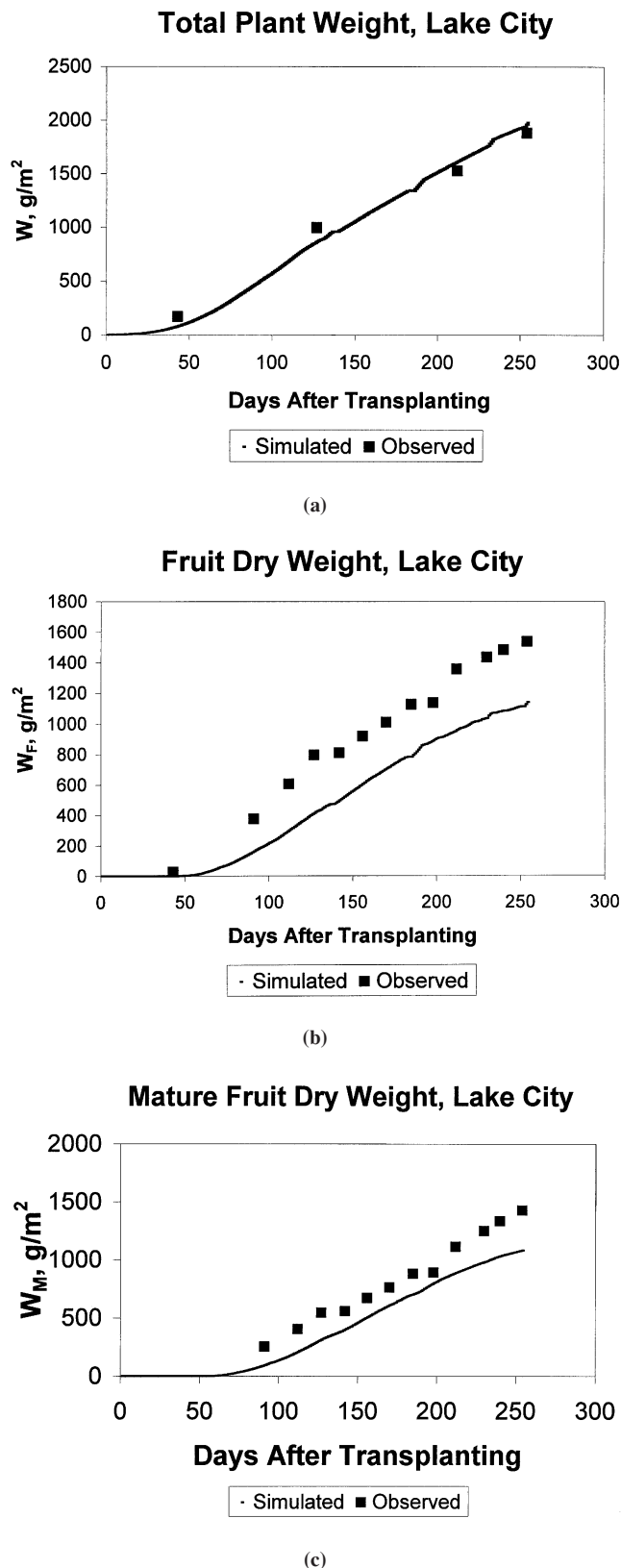


Figure 2—Simulated and observed tomato growth variables vs days after transplanting for the Lake City greenhouse; (a) total aboveground plant weight, (b) total fruit dry weight, and (c) mature fruit dry weight. Parameter values for the model were those estimated from the Gainesville experiments in 1993-1994.

LAKE CITY EXPERIMENT

Figure 2 shows simulated W and W_F for the Lake City experiment using the coefficients estimated for the Gainesville location. Note that W was simulated remarkably well, especially taking into account that the tomato variety was different and the growing season was considerably longer in this commercial greenhouse experiment. This result provides strong evidence that the reduced model can simulate aboveground biomass across locations and conditions using the same parameters for N , LAI , photosynthesis, and respiration components of the reduced model. Root mean square errors are given in table 5 ($RMSE_1$). The $RMSE_1$ for W was 102 g m^{-2} , which is about 5% of the final observed value.

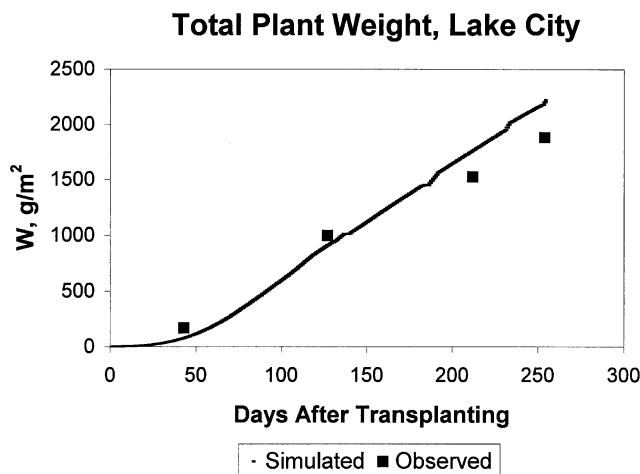
Results for W_F and W_M were not described very well by the reduced model as shown in figure 2 and as indicated by the $RMSE_1$ values in table 5. $RMSE_1$ values were about 20% of the final fruit weights. One major reason for this poor performance was that the lag in fruit production was not well simulated (fig. 2). One of the important parameters for fruit production is the stage of development at which time the first fruit starts growing (N_{FF}). The variety in Lake City had very large fruit compared with the variety grown in Gainesville and this trait could influence N_{FF} .

Figure 3 shows graphs comparing simulated and observed W , W_F , and W_M for Lake City obtained after fitting the parameters to this data set. Large differences were found in parameters estimated for Lake City when compared to those estimated from the Gainesville data for fruit growth (table 4). Note that we did not estimate parameters for LAI development because the early season LAI development was well simulated by the parameters from Gainesville, and there were only four data points for LAI in Lake City. The parameters N_{FF} , α_F , and ϑ were considerably different for Lake City; they contributed to earlier appearance of fruit, larger fraction of growth going to fruit, and more rapid growth after appearance, respectively. In contrast, mature fruit appeared to develop more slowly for this variety as indicated by D_{fmax} , the inverse of which is the minimum duration between fruit appearance and fruit maturity. $RMSE_2$ values (table 5) show considerable improvement for fruit and mature fruit. After fitting these data, the $RMSE_2$ values for fruit and mature fruit were about 5% of the final observed values, similar to the result for aboveground weight using parameters developed from Gainesville data. It is interesting to note that W was fit better using Gainesville parameters (fig. 3 and table 5), mostly because of late season measurements. This occurred because we did not modify any parameter to fit W when estimating the Lake City parameters, and there are interactions between vegetative and fruit growth that could modify total growth.

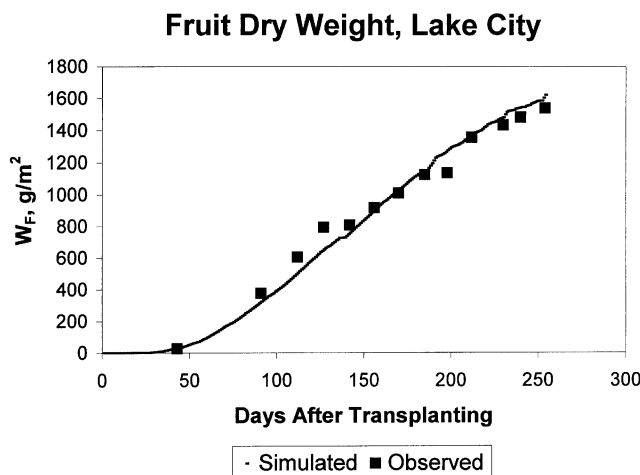
These results supported the first hypothesis that the model can be used across locations, but did not support the second one which stated that the same parameters could be used across locations also.

AVIGNON EXPERIMENT

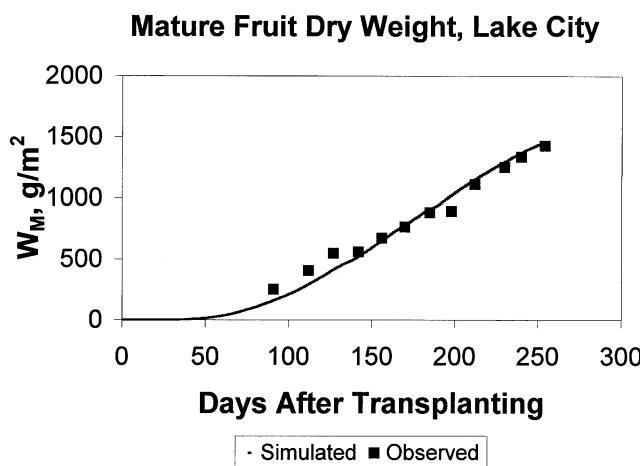
Figure 4 shows results comparing the reduced model simulations of W and W_F using Gainesville parameters to observed data. Table 5 gives the $RMSE_1$ values for the state variables. These results are similar to those from Lake City; W was simulated very well (especially early in the season



(a)

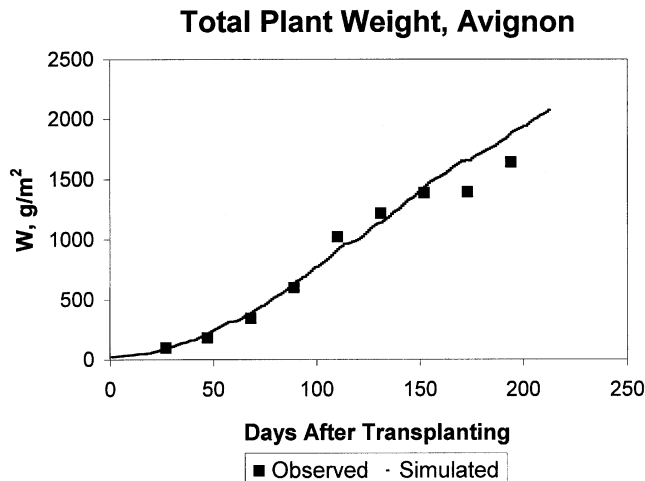


(b)

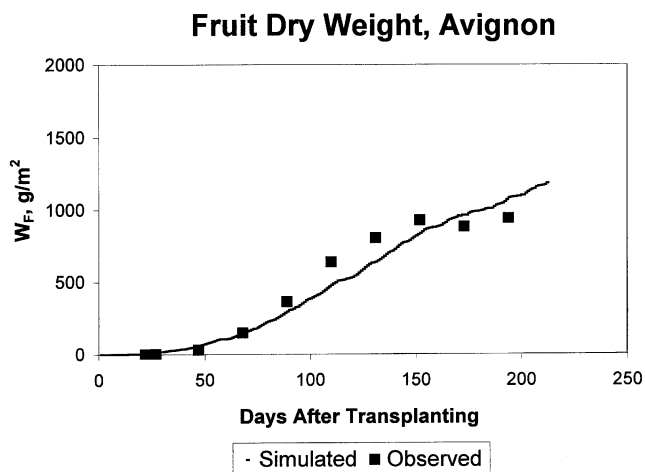


(c)

Figure 3—Simulated and observed tomato growth variables vs days after transplanting for the Lake City greenhouse; (a) total aboveground plant weight, (b) total fruit dry weight, and (c) mature fruit dry weight. These results were obtained using model parameters estimated from the Lake City data.



(a)



(b)

Figure 4—Simulated and observed tomato growth variables vs days after transplanting for the Avignon, France, study; (a) total aboveground plant weight, and (b) total fruit dry weight. Parameter values for the model were those estimated from the Gainesville experiments in 1993-1994.

before high temperatures reduced growth), but fruit were not simulated as well. There was a lag in simulated fruit production compared with observed data. Data were not available for mature fruit.

The fitting procedure was used to fit parameters related to LAI, W , W_F , W_M , and W state variables. Because simulated LAI development was slightly higher than observed, the fitting procedure reduced one of the LAI parameters (δ), but this parameter had little effect on overall results (data not shown). More importantly, the fruit development parameters changed considerably (table 4). Temperatures during the last month of this experiment were high, which likely caused reduced fruit growth seen in figure 5. The value of T_{CRIT} was reduced by the fitting procedure from 24.4 to 22.0, implying that the variety grown in Avignon was more sensitive to high temperatures than the varieties grown in Gainesville and Lake City. Previous research has shown that some varieties of tomatoes are more sensitive to heat stress than others.

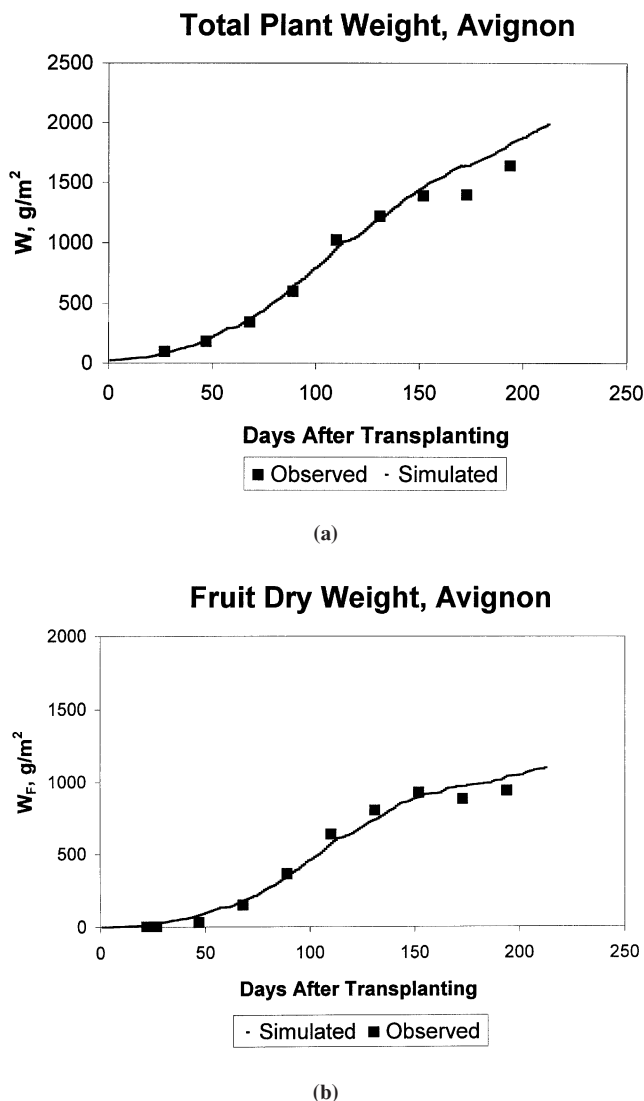


Figure 5—Simulated and observed tomato growth variables vs days after transplanting for the Avignon, France study; (a) total aboveground plant weight, and (b) total fruit dry weight. These results were obtained using model parameters estimated from the Avignon data.

Rainwater et al. (1996) found that yield of a heat-sensitive tomato variety was reduced by 79% when grown in hot conditions (average temperatures of 34°C) whereas yields of other varieties were reduced less (22 to 51%). RMSE values for W_F and W were both lower by more than a factor of two when parameters were estimated for Avignon compared with the use of Gainesville parameters. Mature fruit development parameters could not be estimated because mature fruit were not sampled in the Avignon experiment. Avignon results further supported the first but not the second hypothesis.

CONCLUSIONS

We concluded that it is possible to reduce comprehensive crop models with many state variables to a model with only five state variables to simulate growth and yield of greenhouse tomato using the physiological approach described in this article. The reduced tomato growth and yield model described growth and yield,

including the timing of yield, in three different locations with different weather conditions and varieties, supporting our first hypothesis. We concluded that it is also possible to use the same reduced model with parameters estimated at one location to simulate leaf area and above-ground weight of tomato growing in greenhouse conditions in other locations. However, our results did not support the second hypothesis for simulating tomato fruit and mature fruit growth variables. We attributed this failure to differences in varietal characteristics related to fruiting behavior, and also to management. For example, pruning of trusses (early as well as later in the season) could influence the timing of fruit growth and partitioning of biomass to fruit. This means that parameters may have to be estimated for specific management conditions as well as specific varieties if one wants to use this model to predict fruit growth at a different location or for a different variety. Because the reduced model is simple compared with the comprehensive model and there are fewer parameters to estimate, this is not an unreasonable task. Finally, we conclude that the reduced model can be used in its current form to simulate single stem, greenhouse tomato development (N), LAI, and W using the parameters in this article. It also is likely that this simple model can be used to simulate other greenhouse crops when water and nutrients are not limiting; additional work is needed to test this possibility.

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