Tomato Growth Modeling Based on Interaction of its Structure-Function*

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Abstract

A new approach to model tomato’s growth in view of the interaction between its physiological function and morphological structure was discussed. The finite state automaton called reference axis based on physiological age scale (i.e. structure model) was well applied to build tomato’s topological structure and 3D geometrical structure including its leaf shape, leaf orientation and leaf insertion angle; while the tomato organ’s size was simulated using the hydraulic model which was based on plant’s transpiration law. We gave a detailed conceptual description of tomato growth axis and the spatial arrangement of its organs (internode, petiole, leaf, truss, fruit and etc) according to reference axis model. With the correct computation of its topological structure, the organ’s volume, surface, diameter and length were computed according to matter production and matter allocation mechanism at each developmental phase. The beta law was applied to simulate the sink variation. The parameters of the model were estimated from the data of given tomato (2001.5~7) using least square method. Good validation was obtained and the architecture of tomato at different stages was reproduced.

Keywords: tomato, structure-function model, reference axis, hydraulic function model, allocation and production of matter, topological structure

1 Introduction

Tomato modeling approaches could be concluded into three categories: morphogenesis model or structure model; function driven model; structure-function model.

Structure model would be the interest of producing beautiful and realistic 3D shape from the point of view of computer graphics. The finite automaton based on reference axis[1],

* This study is supported by Sino-French Laboratory for Computer Science, Automation and Applied Mathematics (LIAMA), Institute of Automation, Chinese Academy of Sciences. It is also supported by “863” project “study on the tomato growth model and intelligent management in greenhouse and its software development”(project code: 2002AA241221)
introduced in the following pages, belongs to this. It is made up of topological and geometrical structure. And it not only produces nice 3D shape including the spatial angular arrangement of leaf, but also can simulate the kinetic process such as its growth, ramification and death. The size of organs was got according to the field optic observation and stochastic analysis. However such model mainly stresses on shape generation while not caring about tomato’s volume or accurate size. It is not relevant to tomato’s ecophysiological function, so it cannot predict the possible influence of external environment on tomato growth and on organ change.

Most tomato growth models, in agronomy area, are function oriented. These models, from different points, describe the tomato physiological behavior. The famous crop models are TOMSIM and TOMGRO. TOMSIM developed by Heuvelink E[2], is a photosynthesis driven model, which computes the dry matter production according to leaf assimilation rates. It provides a good tool to expose the photosynthesis and respiration process of tomato. TOMGRO[3, 4, 5], a dynamic simulation system, describes the relationship between the environmental variation and dry matter production and distribution including temperature influence, solar radiation and CO2 enrichment. So for agricultural application and service, tomato function models no doubt have an instructive meaning for optimal growth condition in greenhouses.

Here we present a tomato structure-function model that is dynamic to link the tomato structure and function in that they are in fact interacted and influenced by each other[6, 7, 8]. As we know, for a crop to produce dry matter, its leaves must intercept radiation. However the amount of light energy received by leaves not only depends on the LAI (Leaf Area Index), but on the angular arrangement of individual leaves [9]. Similarly, when we study the influence of water and nutrition in the soil on the plant growth, the root architecture should not be overlooked. Just based on the above idea, the model was put forward expecting to obtain a more realistic simulation results.

In this paper, the tomato structure-function model first explores the finite automaton to get the tomato’s topological information, then based on the topological structure, the hydraulic model [7, 8] which represents the feature of physiological behavior, was used to compute the volume and size of organs. Matter was allocated among different items according to the source-sink relationship. At the end of growth cycles, the 3D geometrical structure with the information of organ shape, leaf insertion angle, leaf orientation and organ size was dressed up.

This paper is divided into five parts:
(1) The topological analysis of tomato based on reference axis technology;
(2) Description of tomato hydraulic model according to topological correct computation;
(3) The result presentation;
(4) Conclusion and further work;
(5) Acknowledgements.

2 The Analysis of Tomato Topological Structure

We define and produce the tomato topological structure using the finite automaton based on reference axis (in the following it is called “only structure model” of tomato). The parameters value of reference axis and their variation along the developmental stages are gotten according to long-term observation and statistical analysis. So we ensure that before simulation, these parameters have been fixed for some species of plants. They describe a
general growth rule about plant architecture (i.e. number of nodes and shoots along branches, ramification process, death process of buds, self pruning of organs, branching orientation...). One of merits is that the parameters referred to in the model are all directly obtained by experiments and no hidden parameters need to be calibrated by some estimation tool. Dressed by geometrical structure, this model can also generate realistic 3D plant shape.

Tomato can be looked as single stemmed (i.e. corner-model plant). But considering its complex leaf structure, we give a more detailed definition about its topological structure than other corner-model crop like sunflower, maize, or wheat [10]. About the structure model, physiological age is the state variable of reference axis automaton, which indicates the growing capability of buds and organs along their life. However, the structure of the reference axis to represent the global plant may vary depending on the view of the agronomists. In this paper, according to observation, we consider the tomato as a main stem bearing complex organs that are leaves and trusses. A leaf consists of a branching petiole on which blades are borne, blades can belong two different categories (small or big). A truss consists of a branching petiole and fruits on it.

![Diagram of growth axis and branching depth inside tomato plant](image)

Fig.1 Description of growth axis and branching depth inside tomato plant

Different growth axis correspond to different range of physiological age like the following:
- Main stem: it consists of growth units, and each growth unit has one node.
- Leaf-main petiole: this lateral axis is borne on each node in the main axis. At the beginning of simulation, the maximum number of nodes will be set that means the limit of length of petiole.
- Truss-main petiole: this lateral axis is borne on every three nodes in the main axis, similarly the maximum number of that parameter can represents maximum number of fruits in this truss. Truss_main petiole follows the statistical law.
- Petiole axis: it can be either petiole axis in the leaf(leaf-petiole) or the one in the truss (truss-petiole). The leaf-petiole(or truss-petiole) is borne stochastically on the leaf-main petiole(or truss-petiole) and bears a terminal blade(fruit). The occurrence of leaf_petiole borne on the leaf_main petiole is determined by Markov state transition law.
- Petiole-terminal axis: same to above petiole, it can also refer to either the petiole-terminal axis in the leaf or the one in the truss. This axis is borne at the end of the leaf-main petiole or truss-main petiole.
- Blade (fruit) axis: The axis that will be no longer ramified.
The relationship of different axis also called hierarchical structure can be well illustrated just as representation in Fig. 2.

During the simulation, the exact value of each parameter needed by model is given related to reference axis (or physiological age).

Fig. 2 Hierarchical relationship among growth axis with different physiological age. (a) Main stem; (b) main stem and its ramification; (c) leaf structure; (d) truss structure

The growth engine of tomato

We simulate the output of tomato topological structure based on growth engine. Growth engine is made up of growth rule, ramification rule, death rule and event control. Event is used to control bud growth, branch ramification and bud death process of tomato. The event with earliest time will happen the earliest. On main axis, supposing that the time length for a test (growth unit) is 1, so the occurrence time for growth units along the main axis will be 1, 2, 3... Since we need to set up the complete leaves (trusses) in a single time step, we will give a growth rhythm some times faster for each leaf (truss) part (it is determined by experiment or observation). So the ordinal occurrence time for the ten tests will be individually 1.01, 1.02, 1.03... 1.10. Thus simulating global immediate setup of leaves and truss.

In the growth engine, we introduced the concepts of "test" node and "real" node. Whether the happening of a real internode or not follows binominal law according to the occurrence probability of test nodes. In tomato model, the growth of truss-branch axis exhibits the nature of stochastic as shown in Fig. 3., and the number of nodes determines the number of fruits in a truss, which can well simulate the statistical phenomena in reality.
Branch ramification rule with Markov state transition law can simulate the stochastic variation such as the diversity of blades in one leaf. The way to ramify for a lateral bud is determined together by the physiological age of current growth unit, the position of current node, branching probability and ramification type (immediate branching or unit delayed branching for tomato). The number of blades is determined by the random number of nodes along the main petiole. The balance between big and small blades is determined by Markov process.

The structure model of tomato also contains how to compute its geometrical structure. In the model based on only structure description, the geometrical size of organs, say length or diameter, is related to its physiological age, its chronological age and its current position along the axis. And the computed size has nothing to do with the physiological or ecological function of tomato. It is only mapped values according to measurements. With geometrical size and orientation, combined with some symbol files (describing the shape of the organ), we can construct the 3D geometrical shape for tomato.

3 Structure-Function Model of Tomato

We have discussed the computation of the topological structure of tomato. Now we will introduce the hydraulic model to simulate production and allocation of fresh matter.

3.1 Production of matter

The fresh matter production is set up based on the transpiration law of plant. Fresh matter is considered as a byproduct of sap circulation in the plant. During the time interval $t$, the amount of evaporation is influenced by the difference of hydraulic potential gradient between soil and air the plant is subjected to and by resistance inside both blade and petiole under a stable climate. However, if no hydric stress, we can consider that matter production will be only related to climate and resistance. So in the current model, we make an electric similarity and introduce a constant $E$ to represent the hydraulic potential gradient or climate and a variable $R$ to represent the hydraulic resistance of the plant, and then the general model for the production of fresh matter is as follows:

$$Q_m(t) = \frac{E}{R}$$

(1)
If we assume the major hydraulic resistance lies in the alive leaves of the whole plant, according to Darcy’s law, we use the following formula to compute the hydraulic resistance of a single leaf.

\[ R = \frac{\rho_1 e}{S} + \frac{\rho_2 l}{s}. \tag{2} \]

where the first term means the resistance of blade and the second one for the petiole. And \( S \) is the leaf surface and \( e \) is the thickness of leaf; \( \rho_1, \rho_2 \) is the resistivity of blade and petiole; for petiole, \( l \) is the length of petiole and \( s \) is the section area of petiole. According to allometry rule, the ratio \( l/s \) is usually constant. So the above formula can also written as

\[ R = \frac{r_1 e}{S} + r_2. \]

In our tomato model, \( r_1, r_2 \), the hidden parameters, are expressed as \( R_B(i), R_P(i) \) respectively representing the resistivities of the \( i \)th leaf. And they are the function of physiological age. Furthermore, from the topological structure, we defined that blade and petiole belong to different reference axis with different physiological age range, so we give the formula (3.1)

\[ R_i(k) = \frac{R_B(i) * e^2}{V_B(i)(k)} + R_P(i). \tag{3.1} \]

where \( V_B(i)(k) \) is the cumulative volume of blades on the \( i \)th leaf. To get the global resistance (at the cycle \( t=k \)), we assume that the leaves can be seen as a set of resistances put in parallel:

\[ \frac{1}{R(k)} = \sum_{j}^{N} \frac{1}{R_j(k)}. \tag{3} \]

where \( N \) is the number of leaves at age \( k \).

### 3.2 Allocation of matter

The other important issue is how to simulate the process of allocating the fresh matter into different organs inside the plant. In fact, it is up to the “demand” of organs for matter. Concretely, there are two factors, which determine their “demand”, one is the master sink and the other is the variation of sink along organs life. Master sink, in our model, is mainly related to physiological age, while the variation should be the function of chronological age and physiological age. We assume beta law is flexible enough model to fit the sink variation of organs during their life (see appendix for beta law definition). And it also has only two parameters \((n, p)\) to adjust its shape.

For a single growth unit which belongs to category \( o \), we define its master sink as \( P_o(age_{ut}) \), and variation of sink is \( f_o(age_{ut})(t) \), \( N_o(age_{ut}) \) is the number of nodes in the current growth unit, then we will get the demand for this current growth unit if its chronological age is \( t \):

\[ D_o(age_{ut})(t) = f_o(age_{ut})(t) * P_o(age_{ut}) * N_o(age_{ut}). \tag{4} \]

For tomato, the category of organs is defined as pith, petiole, blade and fruit. Main stem is formed because of the expansion of pith. When computing the demand of pith, the total demand of one growth unit is the sum of pith demand of all nodes in the current growth unit. However, from the computation of structure model, we have known that each growth unit on main stem only have one internode, and for other axis, the demand are computed considering a growth unit as a whole unit. So we can simplify the computation of the total
demand for all organs as follows:

\[
D(k) = D_e(k) + D_i(k) + D_b(k) + D_f(k)
\]

\[
= \sum_j f_e(\text{age}_{e,i,j})(k-t_{e,i,j}) \ast P_e(\text{age}_{e,i,j}) + \sum_j f_i(\text{age}_{e,i,j})(k-t_{e,i,j}) \ast P_e(\text{age}_{e,i,j})
\]

\[
+ \sum_j f_b(\text{age}_{b,j})(k-t_{b,j}) \ast P_b(\text{age}_{b,j}) + \sum_j f_f(\text{age}_{f,j})(k-t_{f,j}) \ast P_e(\text{age}_{f,j} - 1).
\]

(5)

where \(N_p\) is the number of growth units on main axis (\(\text{age}_{e UT,j}\) is the physiological age of the \(j\) growth unit), while \(N_E\), \(N_B\), \(N_F\) respectively refer to the total number of petiole axis (\(\text{age}_{e,i,j}\) is the physiological age of the \(j\) petiole axis), blade axis (\(\text{age}_{b,j}\) is the physiological age of the blade axis), fruit axis (\(\text{age}_{f,j}\) is the physiological age of fruit axis). \(t_{p,j}\) is the beginning time to grow for the \(j\) growth unit (or internode), and \(t_{E,j}, t_{B,j}, t_{F,j}\) is respectively occurring time for the \(j\) petiole, blade and fruit axis.

We introduce a proportional formula for allocation:

\[
\text{unitMatter} = \frac{Q_m(k-1)}{D_k}
\]

(6)

Then the matter allocated into some organ can be computed like this:

\[
\Delta V_o(\text{age}_{o})(k) = f_o(\text{age}_{o})(k-t_{age}_{o}) \ast P_o(\text{age}_{o}) \ast \text{unitMatter}
\]

\[
V_o(\text{age}_{o})(k) = V_o(\text{age}_{o})(k-1) + \Delta V_o(\text{age}_{o})(k)
\]

(7)

### 3.3 The computation of the sizes of organs

The geometrical sizes are computed according to the volume or matter allocated into organs. Here we only talk about the computation about the length and diameter. For different category of organs, the way to compute the length and diameter may be different. The length and diameter for leaf and fruit are calculated according to general plane or sphere geometrical rule. While for pith and petiole, they are computed according to an allometry rule.

For leaf and fruit, the length and diameter are considered as the same, i.e.

For leaf:

\[
l_B(\text{age}_{b})(k) = d_B(\text{age}_{b}) = \left( \frac{V_B(\text{age}_{b})(k)}{e} \right)^{\frac{1}{2}}
\]

(8)

While fruit is looked as sphere, so

\[
l_F(\text{age}_{f})(k) = d_F(\text{age}_{f}) = 2.0 \ast \left( \frac{3 \ast V_F(\text{age}_{f})(k)}{4 \pi} \right)^{\frac{1}{3}}
\]

(9)

For pith and petiole, they are looked as shape of cylinder, so their length and diameter are computed according to allometric rule such as:

Length of pith:

\[
l_p(\text{age}_{p})(k) = \left[ \frac{1+\text{shapeFactorB}(\text{age}_{p})}{(V_p(\text{age}_{p})(k))^\frac{1}{2}} \right]^{\frac{1}{2}} + \text{shapeFactorA}(\text{age}_{p})
\]

(10)
Diameter of pith:

\[ d_p(\text{age}_p)(k) = \left( 4 \times \frac{V_p(\text{age}_p)(k)}{l_p(\text{age}_p)(k) \pi} \right)^{\frac{1}{2}}. \]  

(11)

where shapeFactor \( A(\text{age}_p) \) and shapeFactor \( B(\text{age}_p) \) are respectively called as coefficient of proportion and shape.

The above computation is the same with petiole, and we will not list the formula for it here.

### 3.4 Main algorithm loop

The simulation of structure-function model of tomato is a looping process, into which function and structure will interact each other. For every event loop, five steps will be carried out as the following:

- Step 1: compute the topological structure using growth engine during the current time step.
- Step 2: compute the total demand of all existing organs based on computed topological stage at the function time.
- Step 3: allocate the fresh matter fabricated at the previous cycle into the different organs of current cycle (eventually adding the seed matter to the fresh matter).
- Step 4: compute the plant resistance and production of fresh matter at current cycle using above formula (1).
- Step 5: set the next time for function and return Step 1.

### 4 Calibration of function model

By the above analysis, we know that some parameters including directly measurable parameters and hidden parameters must have certain value before simulation. Through some experiments on tomato in greenhouse (2001.5~7), we get the following values for the directly measurable parameters:

Through the measurement of surface of leaf and its fresh weight and in view of its little variation along its developmental stage, we got a constant thickness: \( e = 0.035 \).

Pith and Petiole are considered as cylinder, and by measuring their surface of cross-section, length and volume and according to allometric rules, we can get approximately the coefficient shapeFactor \( A(\text{age}_p) \) and shapeFactor \( B(\text{age}_p) \)

\[ \text{shapeFactor } B(\text{age}_p) = 0 \]

The trend curve for shapeFactor \( A(\text{age}_p) \) is shown in Fig.4.

![ShapeFactor A](image)

**Fig.4** shapeFactor \( A \) varies with different organs
The maximum expanding cycle $T$ is observed as shown in Fig.5.

![Diagram](image)

Fig.5 Maximum expanding cycle of different organs. Functioning time for leaf $J T=15$

To calibrate the model, two steps were needed: firstly the external parameters could be measured directly or could be obtained by simply processing the experimental data as above; secondly we will use some special optimization algorithm to estimate the functional parameters that were hidden behind the measured data. Our structure-function model is in fact a nonlinear multivariable and multi-target function, so we adopt nonlinear least square for the estimation of hidden parameters. If the measured variables are used as target vector $y$, and $f(x, \beta)$ is the actual output of the model, and $\beta$ denotes the vector of m unknown parameters, the problem of nonlinear least square regression is to obtain the hidden parameters $\beta$ to produce the smallest residual sum of squares $b$, i.e.

$$b = \arg \min_{\beta} \left\{ \sum_{i=1}^{n} [y_i - f(x_i, \beta)]^2 \right\}$$

By using nonlinear least square method, the optimal values of hidden parameters are gotten for different developmental stage. (See Table 1, 2, 3).

The following Fig.6 shows comparison between the original and the simulated data by tomato structure-function model. The 3D architectures of tomato were given in Fig.7 for these three stages.

<table>
<thead>
<tr>
<th>Table 1</th>
<th>Values of hidden parameters for the plant on 20, May</th>
</tr>
</thead>
<tbody>
<tr>
<td>$N$</td>
<td>5.0000</td>
</tr>
<tr>
<td>$P$</td>
<td>0.225643</td>
</tr>
<tr>
<td>Master Sink</td>
<td>0.3088</td>
</tr>
<tr>
<td>RB</td>
<td>28265</td>
</tr>
<tr>
<td>RP</td>
<td>140</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Table 2</th>
<th>Values of hidden parameters for the plant on 7, June</th>
</tr>
</thead>
<tbody>
<tr>
<td>$n$</td>
<td>5.0000</td>
</tr>
<tr>
<td>$p$</td>
<td>0.515103</td>
</tr>
<tr>
<td>Master Sink</td>
<td>0.32781</td>
</tr>
<tr>
<td>RB</td>
<td>24888.5</td>
</tr>
<tr>
<td>RP</td>
<td>130.4</td>
</tr>
</tbody>
</table>
Table 3  Values of hidden parameters for the plant on 20 June

<table>
<thead>
<tr>
<th></th>
<th>Pith</th>
<th>Petiole</th>
<th>Blade</th>
<th>Fruit</th>
</tr>
</thead>
<tbody>
<tr>
<td>$n$</td>
<td>5.0000</td>
<td>5.0000</td>
<td>5.0000</td>
<td>5.0000</td>
</tr>
<tr>
<td>$p$</td>
<td>0.43627</td>
<td>0.566389</td>
<td>0.599491</td>
<td>0.893179</td>
</tr>
<tr>
<td>Master Sink</td>
<td>0.365997</td>
<td>0.152587</td>
<td>1.0</td>
<td>3.1596</td>
</tr>
<tr>
<td>RB</td>
<td></td>
<td></td>
<td></td>
<td>23427</td>
</tr>
<tr>
<td>RP</td>
<td></td>
<td></td>
<td></td>
<td>134.4</td>
</tr>
</tbody>
</table>

20. May

- surface of blade
- diameter of internode

7 June

- surface of blade
- diameter of internode

20 June

- surface of internode
- diameter of internode

Fig. 6  Comparison between the original and the simulated data
5 Conclusion

The structure-function model for tomato discussed in this paper assumed that the climate is constant during the whole cycles of tomato growth, but in reality, it is not easy to always keep the ideal environment. When external environment has a big variation, for instance, temperature rises quickly or cloudy sky for some days at some stage of growth, you will find that the simulation results will produce a bigger error for some cycles. However, it provides a base to study the influence of environment on tomato growth. And this model was put forward just because it can not only simulate the physiological function, but can generate accurate geometrical information like the spatial arrangement of organs which will be an important factors to compute the amount of light interception at the leaf level [10]. Setting up a light influenced structure-function model will be main work next step. To implement that, we need to do further experiments to calibrate the numerical shape of tomato, to calibrate the radiation transmission model in the tomato canopy, to calibrate the hidden parameters of function model, and ultimately to calibrate light influenced model (or its photosynthesis driven model) for tomato. We expect to get better results than before when incorporating light interception, tomato’s structure and tomato’s physiological function.

Acknowledgements

This work is supported in part by LIAMA, NSFC (#60073007), and China 863 Program (#2002AA241221). Here, I wish to thank J.F Barczi and Philippe De Reffye (CIRAD, France) for their supervision.
Appendix

In our model, we use the following beta law formula to compute the variation of sink for organs.

\[
 f_o[i_o][j] = \frac{\left( \frac{j + 0.5}{T_o} \right)^{(n+1)*p} \left( 1 - \frac{j + 0.5}{T_o} \right)^{(n+1)*(1-p)-1}}{\sum_{j=0}^{T_o-1} f_o[i][j]}. 
\]

In Fig.8, you can find, for varying \( n, p \), that beta law can generate different shapes (\( T=20 \))

![Fig.8 Different shapes based on beta law for varying n and p](image)

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