Simulating the development of *Fraxinus pennsylvanica* shoots using L-systems

Mark Hammel and Przemyslaw Prusinkiewicz
University of Calgary

William Remphrey
University of Manitoba

Campbell Davidson
Agriculture Canada

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> ...in that Empire, the Cartographer's art achieved such a degree of perfection that the Map of a single Province occupied an entire City, and the map of the Empire, an entire Province. In time, these vast Maps were no longer sufficient. The Guild of Cartographers created a Map of the Empire, which perfectly coincided with the Empire itself. But Succeeding Generations, with diminished interest in the Study of Cartography, believed that this immense Map was of no use...
>
> Viajes de Varones Prudentes, 1658
> (quoted by Umberto Eco [2, page 95])

1 Introduction

This paper presents a methodology for creating computer models that capture the development of plants using the formalism of L-systems and incorporating biological data. The modelling process is divided into the following steps:

- A qualitative model is constructed according to observations of plant growth and form.
- Measurements of key characteristics are gathered from actual plants.
- Statistical analysis is performed to convert the raw data into functions which describe growth.
- The quantitative model is formed from the qualitative model and growth functions, as well as approximated functions describing the growth of model elements for which data has not been obtained.

- A visualisation of the model is produced.
- An evaluation of the model is performed. The visualisation aids in exposing any flaws in the qualitative or quantitative models, and helps identify any incorrectly estimated functions.
- If a further iteration of this modelling process is required, this process is repeated. The choices and assumptions made in the construction of this model are then reconsidered and modifications are applied to improve the model's reflection of reality.

This paper makes use of a model of shoots of *Fraxinus pennsylvanica*, also called green ash, to illustrate the presented modelling methodology. It compliments research performed in 1994 as a collaboration between biologists and computer scientists, which resulted in a publication in the *Canadian Journal of Botany* [11]. In the following sections, a brief introduction to L-systems is given and then the methodology is described in greater detail.

2 L-systems

In Lindenmayer systems (L-systems) [7, 10], development is defined on the level of individual plant components — internodes (stem segments) elongate, buds initiate new lateral branches, leaves unfold, and so forth. To formally describe these processes, productions are used to capture each developmental event. They state how a component or module is replaced by a subsequent form. A string notation is employed to represent modules and productions [10].

For example, the following production defines an apex which is replaced by two new internodes, two lateral or branching apices, and another terminal apex (an apex is a generative centre for a plant, where new forms are initiated):

$$\mathtt{A} \rightarrow \mathtt{F[+A][-A]FA}$$

The symbol before the arrow is called the *predecessor* which is the module being replaced. The *word*, or sequence of symbols, after the arrow is called the *successor* and it indicates the modules replacing the predecessor. Apices are represented by the symbol `A` and internodes by `F`. Symbols which define geometric aspects of the model may also be included. In this example, the square brackets `[]` enclose the modules that compose a branch, and the `+` and `-` symbols indicate rotations. This production is illustrated in Figure 1.

3 Qualitative Model

The modelling process begins with the specification of the qualitative model. It captures aspects of the plant that can be obtained through observations and are deemed essential to its form and development. These include the arrangement (topology) and the sequence of activities of various plant modules. The main components of the plant are distinguished and their developmental stages are identified. The connections between these components are also defined.

The qualitative portion of the green ash model consists of three main parts: the bud, the shoot units, and the leaves.

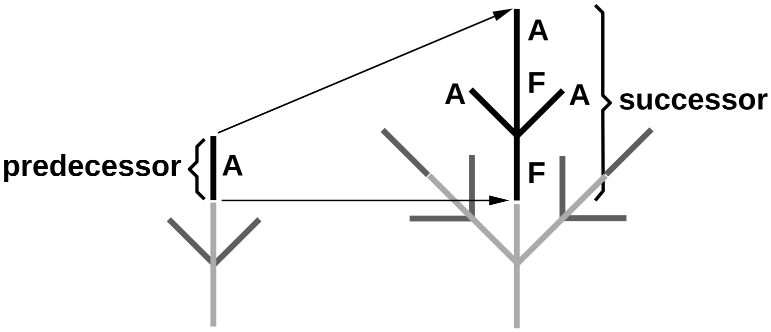

Figure 1: A production describing the development of a plant apex.

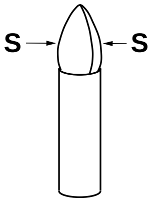

Figure 2: An initial green ash bud.

The simulation begins with a single bud (Figure 2). This is captured by the L-system *axiom*, or the initial sequence of modules:

$$\omega : \{\,\texttt{[S]}\ \texttt{[S]}\,\}^K \texttt{A}$$

The axiom represents the bud as a sequence of bud scale pairs, each pair enclosing the next. Each scale `S` is represented as a branch. The "exponent" K is used to specify the K-fold repetition of bud scale pairs. The apex `A` is initially contained within the bud. The label ω identifies this statement as the axiom.

After some amount of time has passed, the bud scales fall from the tree. This event is captured by production p_1:

$$p_1 : \texttt{S} \rightarrow \lambda$$

The symbol λ represents the *empty* word. As a result, each bud scale `S` is removed from the model.

The basic function of the apex is to produce *shoot units*, as shown by production p_2:

$$p_2 : \texttt{A} \rightarrow \texttt{I}\,\texttt{[L]}\ \texttt{[B]}\ \texttt{[L]}\ \texttt{[B]}\,\texttt{A}$$

Each shoot unit consists of an internode `I`, a pair of leaves `L`, a pair of lateral buds `B`, and another apex `A`. The appearance of the apex in the successor provides for the repeated application of this production (Figure 3).

After a predefined number of shoot units have been initiated, production stops with the apex forming a terminal bud `T`:

$$p_3 : \texttt{A} \rightarrow \texttt{T}$$

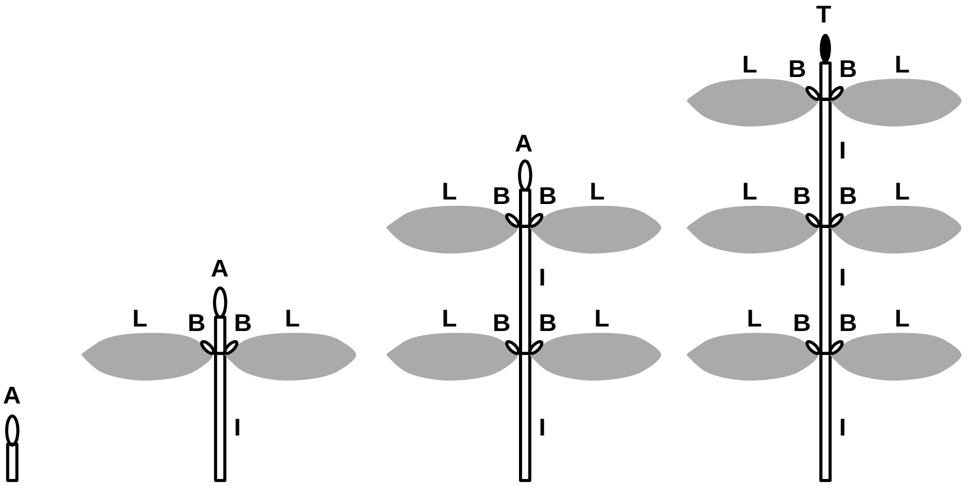

Figure 3: The development of a green ash shoot unit.

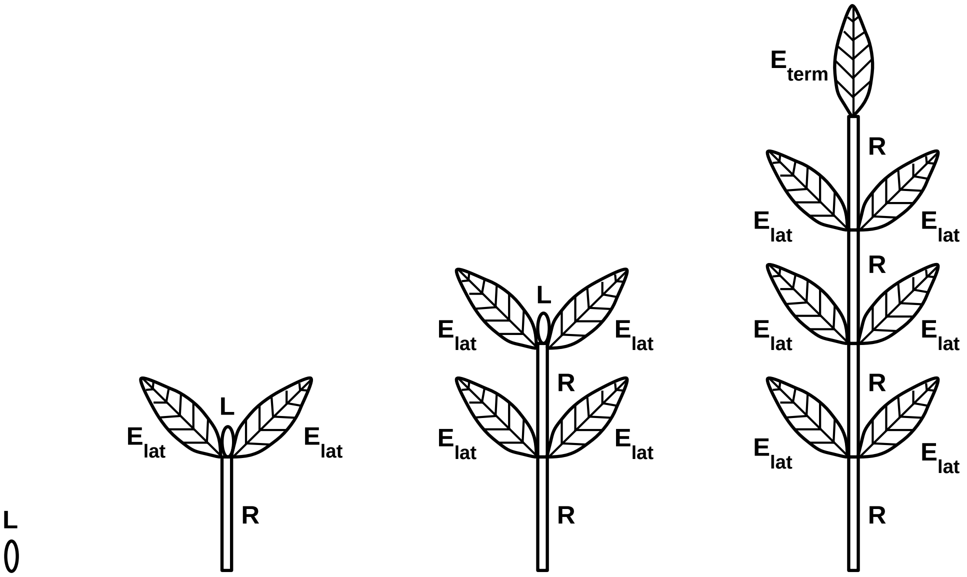

Figure 4: Development of a green ash leaf.

Green ash leaves have a compound structure. Each compound leaf consists of several leaflets $\mathtt{E}_{\mathrm{lat}}$ extending from a stem called a *rachis*. The rachis is divided up into a number of rachis segments $\mathtt{R}$ which connect adjacent pairs of leaflets (Figure 4). The leaf ends with a terminal leaflet $\mathtt{E}_{\mathrm{term}}$. The development of this structure is captured in a manner similar to that of the apex:

$$\begin{aligned} p_4 : \quad & \mathtt{L} \rightarrow \mathtt{R[E_{lat}][E_{lat}]L} \\ p_5 : \quad & \mathtt{L} \rightarrow \mathtt{RE_{term}} \end{aligned}$$

Production p_4 describes the repeated production of the rachis/leaflet combination. When a predefined number of these combinations has been initiated, production p_5 introduces the final rachis segment and terminal leaflet.

4 Data Collection

Section 3 describes the modules that form the green ash model, and the events which define their development. For example, production p_4 indicates that a leaf is composed of a sequence of leaflet pairs and rachis segments ending with a terminal leaflet, but there are a number of questions remaining. What is the length of the rachis segment? What is the orientation of the leaflets? What is the size and shape of the leaflets? To answers these questions, one must collect field measurements of actual plants.

The collection of data over a long period of time across a large number of plants can be a difficult and time-consuming process. One cannot reduce the duration of the collection period since it is the development within this time frame that is being modelled. In addition, enough plants must be considered to ensure that measurements are not biased by deviations in the development of a few plants. Therefore, only those features which are perceived to be essential to the model are measured while others are estimated based on visual inspection (Section 6). In the case of green ash, data was collected from trees at two sites in Manitoba — the Agriculture Research Station in Morden and the University of Manitoba in Winnipeg [1, 12, 13, 14]. Internode length, rachis segment length, and leaflet length and width were identified as the key features of green ash shoots. Measurements of these characteristics were collected every two days during the growing season.

5 Statistical Analysis of Experimental Data

It has been observed that many biological growth processes follow a sigmoidal curve (Figure 5): the rate of growth begins slowly, speeds up, and then decelerates before completing. The logistic form of this function is commonly used in biology to describe this behaviour, and is used in the green ash model:

$$x = \frac{a}{1 + be^{-ct}}$$

The variable x is the particular characteristic (internode length, rachis segment length, leaflet length and width) for which the growth function is defined and t is time. Nonlinear regression was applied to estimate the values of coefficients a, b, and c as functions of the measured data and such features

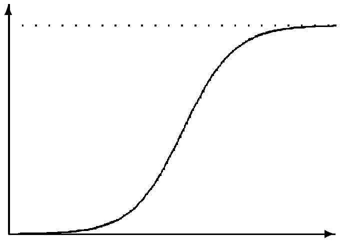

Figure 5: A sigmoidal growth function.

as the particular internode or rachis number, the total number of internodes in the shoot, or the number of leaflet pairs in a leaf.

For example, after retaining those parameters found to be statistically significant, the values of the coefficients for the growth of internode length were estimated by:

$$\begin{aligned} a &= k_1 + k_2 o + k_3 M + k_4 m + k_5 m^2 \\ b &= 11.5 \times 10^6 \\ c &= 0.58 + 0.0144a - 0.0244m \end{aligned}$$

where $k_1, \ldots, k_5$ are constants, o is the parent shoot order, M is the number of shoot units in the shoot, and m is the internode number within that shoot. Notice that c is also a function of the final internode length a.

6 Estimation of Remaining Data

The logistic functions described in the previous section constitute a part of the quantitative model, but as mentioned in Section 4, not all plant features are measured. Therefore, additional data must be estimated to complete the quantitative model. With green ash, photographic and field observations were used to determine such characteristics as leaf growth and gradual changes of leaflet orientation.

The sigmoidal function used to capture these observations are interactively manipulated to achieve the proper behaviour of the model. Consequently, a cubic form was chosen in place of the logistic curve due to the straightforward role of its coefficients:

$$x = \frac{3a}{T^2}t^2 - \frac{2a}{T^3}t^3$$

In this function, the coefficients are a, the maximum value of the function, and T, the time taken to reach that maximum.

Figure 6: Simulation of the expansion of a green ash shoot over the course of 35 days.

7 Quantitative Model

The quantitative model combines the qualitative model with the calculated and estimated growth functions. Differential L-systems [9] are used to associate the functions with geometric properties of individual models. The resulting model can simulate growth with continuous changes of form combined with instantaneous developmental events.

8 Visualisation

The visualisation of the green ash model is very straightforward. Cylinders are used to represent internodes and rachis segments. Cubic patches are used to represent leaflets and bud scales. The simulation of the growth of green ash is sampled at discrete time intervals to construct consecutive animation frames. Due to the use of differential L-systems, the sampling process is disassociated from the model. Figure 6 shows selected stages of the development of a green ash shoot that results from this simulation.

9 Evaluation and Re-iteration

The visualisation of the completed model is integral to the modelling process itself. It is difficult to mathematically evaluate shape and form alone, not to mention how they change over time. If there are any inaccuracies present in the model, the visualisation will often make them clearly evident. This is especially true when comparing the timing of concurrent processes. For example, in the green ash model, the data collection for internode length began only when the internodes were large enough to accurately measure and the bud had opened up enough to reveal them. The resulting logistic functions provided an extrapolation of the length to earlier ages. Visualisation revealed inaccuracies in this extrapolation. Bud burst, or the time at which the first internode is large enough to cause the bud to open, was occuring a week to ten days later in the model than in observed plants.

Similar problems were encountered during the modelling of leaflets. When leaflets are initiated, they are folded along the mid-rib. We found that the timing of the unfolding process was critical. Values that were perceived to be reasonable estimations of the duration of unfolding were shown to be clearly wrong by the visualisation.

Thus, visualisation can bring to light improvements that must be made to the model. This causes the model makers to return to the start of the modelling process to alter the qualitative model, collect new data, and so on, following the steps in sequence up to another evaluation, at which point further iterations may be required. Through this iterative process, a model meeting the needs of the developers can eventually be obtained.

10 Conclusions

This paper has presented a methodology for constructing developmental plant models, and illustrated it using a model of green ash. The proposed methodology consists of a sequence of steps:

- definition of a qualitative model expressed as a “skeletal” L-system,
- acquisition of field data, guided by the qualitative model,
- statistical analysis of the field data,
- estimation of growth parameters that were not measured in the field,
- definition of a quantitative model expressed as a differential L-system; this model results from the incorporation of growth functions into the initial L-system,
- visualisation of the model,
- evaluation of the results.

The shortcomings revealed during the evaluation form the basis for the next iteration of the same procedure, beginning with adjustments to the quantitative model and acquisition of additional data. The model is gradually refined through a sequence of such iterations until it approximates reality with the required accuracy.

According to the proposed methodology, measurements do not precede model construction, but are guided by a qualitative model that reflects our initial hypotheses regarding observed processes and structures. As it is impossible to measure all numerical parameters that describe the development of a complex branching structure in the finest detail, the process of measurement depends on a careful choice of parameters deemed to be important. In a more general setting of models of morphogenesis, this dependence was described by Sattler [15]: "Facts are low-level hypotheses that are theory-laden and reflect basic philosophical biases."

The measurement of plant structure is a time-consuming effort, especially when data is gathered repetitively to capture a developmental process. The data incorporated in the model of green ash was collected manually, using rulers, calipers, and protractors. The data collection process can be simplified using three-dimensional digitisers coupled with appropriate data-entry programs [4, 8]. The automatic transfer of data to the statistic programs and, eventually, to a comprehensive plant model, remains an open technical problem.

The iterative character of model construction, where reality is approximated with gradually increasing accuracy but the perfectly "true" model may never be obtained, is a manifestation of the cyclic process of theory construction in the scientific methodology [6, Chapter 5]. In the context of synthesis (inference) of L-systems, this cyclic process was described by Herman and Rozenberg [5, Page 263]. The observation that the construction of any plant model amounts to a small scientific discovery highlights the inherent difficulty of the modelling process, and explains why the ultimate goal of automatic (algorithmic) model construction may be difficult to achieve.

The accuracy with which a model reflects reality is only one of the model's characteristics and, by itself, does not determine the model's usefulness. Each model represents a tradeoff between accuracy and complexity [3], and the best model for a given application is usually the least complex model that is sufficiently precise. A quantitative analysis of this tradeoff requires introduction of proper measures of the accuracy and complexity of biological models. Both problems present interesting areas open for further research.

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