Simulation of Apple Tree Development Using Mixed Statistical and Biomechanical Models

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1   Introduction

In the last twenty years, architectural studies in horticulture have led to a better understanding of fruit tree development and to improvements in tree and orchard management [7]. Tree architecture plays a key role in foliage distribution and consequently in light interception and carbon acquisition, which in turn strongly affect the reproductive growth of fruit trees. To integrate the acquired knowledge, we addressed the question of simulating the architecture of a developing tree over time. The objective of this project was to bring together the development of topology and geometry in a single simulation that characterises the architecture of an apple tree over time. As indicated previously [9, 3, 4], the simulation of shoot bending due to the weight of growing organs is particularly challenging because it is difficult to infer the mechanism of bending from direct measurements. To further the exploration of the bending dynamics in a developmental context, we have created an L-system simulation of a developing apple tree, called MAPPLET (*Markov **Apple Tree***), which is herein presented.

2   An Integrated Simulation

In MAPPLET, a tree's architecture is determined by two types of information: the tree topology (*i.e.*, the connections between plant entities, such as the sequence of the growth units and the placement of the organs) and the temporal co-ordination of developmental events, which includes both morphogenesis and organ growth. From this information, a tree's geometry is determined by a biomechanical simulation.

2.1   Development of Tree Topology

As current mechanistic models do not represent branch distribution with sufficient precision, the topology of the trees was modelled using two types of Markovian models [10]. The first model captures the branching structure of the shoot and the second model captures the sequence of annual shoot types along the axes. The Markovian models used in MAPPLET were originally devised to perform purely topological simulations of apple trees [16]. In these simulations, branching patterns were generated by hidden semi-Markov chains (HSMCs), with parameters depending on the shoot type (*i.e.*, long, medium, or short shoots). The elements of a sequence generated from one of these HSMCs describe the fate of the lateral buds in the following year. The type of the terminal shoot is determined between successive annual growth cycles using transition matrices of a simple Markov chain, which are selected according to the type of the current shoot and the age of the tree [8]. A distribution of shoot lengths, measured in the number of metamers, is attributed to each shoot type, whether in terminal or lateral position.

2.2   Chronological Control of Morphogenesis and Organ Dimensions

The parameters used in MAPPLET originate from a number of studies performed by the AFEF team. The values are mostly from several independent datasets collected on the Fuji cultivar. Where data were unavailable from Fuji, values from other apple cultivars were used (*e.g.*, for the plastochron, diameter growth and wood properties). In each shoot category, new metamers are produced with a plastochron of three days [6], and each

metamer elongates over ten days. The final length of internodes depends on their position in the shoot, such that the internodes at the beginning and end of each shoot are shorter than those of the middle. Thus the lengths of the internodes depend on the zone along the shoot to which they belong. These values were estimated from data measured on Fuji trees.

The widths of the internodes are controlled with the pipe model [17]. The inputs to this model are the radii of leaf petioles and the radii of terminal apices. Since observations showed that the diameter at the shoot base increases after the cessation of primary growth [5], we augmented the pipe model with an additional hypothesis, which postulates that the diameter of the terminal apices increases over the season proportionally to the length of the shoot.

In Fuji trees, a leaf grows sigmoidally over twelve days, at which time it reaches maturity [14]. If a metamer supports an inflorescence, the flowers last for ten days and, if it becomes a fruit, the fruit lasts until harvest (approximately one hundred and fifty days). We assumed that each inflorescence develops into, at most, one fruit. The mass of a fruit increases according to the expolinear model [13], here calibrated to the fruit of Fuji.

2.3 Determination of Plant Geometry Using Biomechanics

The bending of each internode is calculated according to its biomechanics. The model used in MAPPLET is derived from the work of Taylor-Hell [19], which, in turn, is based on Fournier's metaphor of bending beams applied to woody stems [9] and its initial implementation using L-systems [11]. Biomechanical simulations employ the fast information transfer construct in L-systems [12], and are divided into two phases [15]. First, bending moments acting on individual nodes are calculated in a backward scan of the L-system string (information is passed basipetally). Second, the shape of the branch is calculated in a forward (acropetal) scan of the string, taking these bending moments into account. As the modification of the branch shape changes the values of the bending moments, this computation of moments and shapes is carried out iteratively, until an equilibrium is found. The simulation takes into account negative geotropism, the elasticity of the wood, the amount of locally produced reaction wood, and the secondary branch growth, which results in a branch shape memory [2, 3].

3 Simulation Outputs

The architectural development of a typical tree produced by MAPPLET is shown in Figure 1. To assess the model, the simulated trees were compared to two digitised Fuji apple trees [8], using a common set of descriptors. These two trees do not constitute an enterely independent dataset, because they were also used to estimate HSMC models and the value of the pipe model exponent (while others parameters came from independent datasets). However, the geometry, and consequently the set of descriptors used to perform the comparisons were considered independent between the digitised and simulated trees. The comparisons were performed at different scales of observation and for different values of input parameters. At small scales, descriptors of the shoots' morphology included, for example, the basal diameter and shoot length. At larger scales, envelopes encompassing a tree's crown and fruiting branches were calculated.

Figure 2 shows that, visually, the simulated trees are qualitatively close to the observed Fuji trees. An examination of the envelopes around the trees' crowns and branches revealed that the bending of the branches was slightly underestimated. A sensitivity analysis of the graphical and numerical outputs, as they vary over a range of parameters, led us to identify which parameters have large effects on a tree's form and which ones require further experimental data to improve the model. For example, the shoots' basal diameters were underestimated in the first and second order branches within the explored range of values of the pipe model exponent, while the same exponent value produces basal diameters close to those observed in higher-order branches (Figure 3). The simulated secondary growth dynamics, resulting from the augmented pipe model, is similar in character to those of observed axes: there is an initial rapid growth followed by a slower growth that continues after primary growth has ceased (Figure 4).

By integrating physical and architectural parameters calibrated to observed trees, MAPPLET produces simulated trees that are subject to gravity and account for known growth dynamics. Presently, MAPPLET still has a number of limitations that may be addressed in further research. Of particular note is the absence of gravimorphic responses to branch bending (*e.g.*, the preference of long shoots to grow from buds in dorsal positions). Nevertheless, the data obtained from the simulated trees produced by MAPPLET complement those obtained with digitisation methods [18]. Simulated trees can be sampled continually, while digitisation is a time consuming process, typically done only once annually. Though MAPPLET is currently used for synthesising existing data, it is also a platform appropriate for future *in silico* explorations, such as examining light interception or the interaction of architecture and physiology, as initiated in L-PEACH [1].

4 Acknowledgements

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Figure 1: A simulated apple tree from the second through fifth year of growth

Figure 2: Fuji tree shapes in the fifth year of growth. From left to right, three trees simulated with different values of the pipe model exponent ($P = 2.0$, $P = 2.5$ & $P = 3.0$), and a digitised tree. The envelopes on the trees are calculated for branching systems originating in the second year of growth.
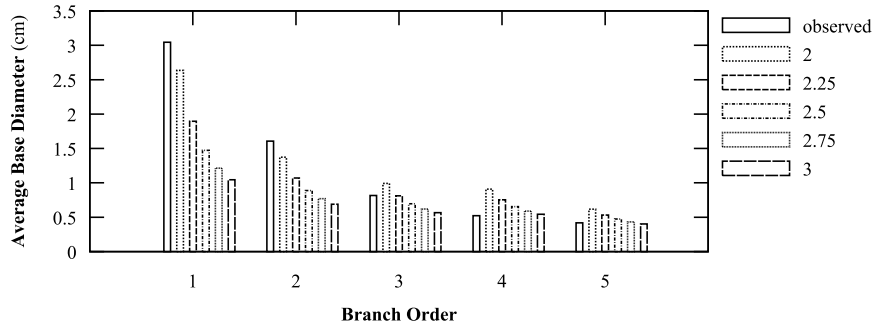

Figure 3: Variation of the average base diameter of the axes in different branching orders, with respect to P, the value of exponent in the pipe model
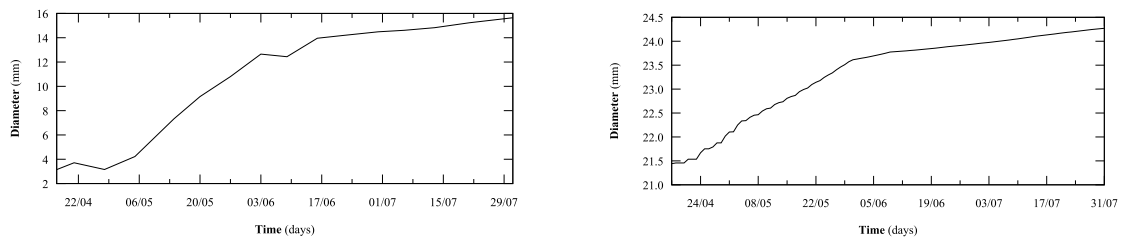

Figure 4: Comparison of the basal diameters of a first-order branch over a season from (Left) an observed tree and (Right) from a simulated tree