Inferring Leaf Blade Development
from Examples

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Abstract. Morphogenesis is the process by which plant tissues are organized and differentiated to determine the morphological structure of their organs. Understanding leaf blade morphogenesis is a major unsolved challenge in plant sciences. Despite the advances, until now there is no a clear understanding of the physiological mechanisms underlying these morphological changes. In this work, we present a novel automatic approach to infer the geometrical structure of a leaf blade developmental model out of samples of sequences of the leaf development. The main idea is to infer the set of parameters of a non-linear ordinary differential equation model based on relative elementary rates of growth, which better adjusts an empirical leaf blade developmental sequence that was extracted from real images. From the resulting models leaf shape simulations were calculated. These simulations were compared against the 12 real sequences of leaf blade growing. The results show that the proposed method is able properly infer leaf blade parameters of leaf development for a variety of leaf shapes, both in simulated and real sequences.

Keywords: Computational ecology · Leaf morphogenesis modeling · Leaf morphology · Relative growth rate · Dynamic time warping

1 Introduction

Morphogenesis is the process by which plant tissues are organized and differentiated to determine the morphological structure of their organs [2]. The analysis and modeling of plant morphogenesis, and in particular leaf morphogenesis, is a paramount important problem in plant sciences, agriculture, industrial forestry and ecology [4]. A better comprehension of leaf morphology is fundamental to understand plant resilience capacity in response to adverse events, such as, global warming, reductions in the water supply and soil contamination [2,6].

Leaf morphogenesis critically depends on the plant genetic information and metabolic and hormonal regulation [3]. Nevertheless, this process can be severely altered by changes in the environmental conditions and in the supply of substrates and minerals [2]. In general, studies in leaf morphogenesis may require

large and complex experimental settings, spanning along extensive time periods [13]. The use of computational models can be a complementary tool suitable for the study to these dynamics in shorter times. In the recent years several models have been proposed to simulate leaf development [7]. These models have shown accurate visual results, however, they are highly dependent of parameters and may lack of biological interpretability. In this paper, we present a novel computational approach to model leaf growing dynamics out of real sample sequences of leaf development. The proposed approach automatically extracts parameters for a model of development, can be used to simulate accurately blade leaf development process and provides a set of biologically interpretable parameters.

2   Background and Related Work

Leaf Morphogenesis. The foliar morphogenesis refers to the set of processes that control the different aspects of the leaf growing [2]. Including, the regulation of the initial grow, the determination of the foliar symmetry, the shape and the definition of the leaf in subregions. The foliar shape is mainly determined by two morphogenetical processes: primary and secondary. The primary one includes the initiation of the lamina, the specification of their different domains (the mid vein, the petiole and the leaf base) and the formation of lamina structures, including, leaflets, lobes and serrations. In the secondary process leaf expansion occurs and specific tissues complete their differentiation [2].

Computational Description of Leaf Growth. Leaf shape may range from simple leaves with elliptical shapes to complex compound leaves with fractal shapes [7]. Because of this large morphological variability understanding of leaf development is still a major unsolved challenge in computational modeling and pattern recognition. Geometry of a biological form results from the growth. Foliar growing can be described in two ways: globally and locally. The first description is based on the idea that forms of related but different organisms can be obtained one from another by changing the coordinate system in which these shapes are expressed. This idea can be computationally implemented by using, for instance, shape deformation and morphing algorithms. These methods have been adapted to model blade leaf growth and development of leaf venation networks [9]. This approach provides consistent visual results, however, it is highly descriptive and it does not provide a biologically interpretable description of the leaf growing. Leaf development can also be described locally by considering how small regions are organized to form more complex objects. In this case, the size and dimensions of the regions can be characterized by using a single number, for example, a growing rate that describe in any moment in space-time the development properties of the unit [7]. This kind of description is commonly used by biologists to study plant development [6].

Geometric modeling of simple leaves was firstly explored by Scholten & Lindenmayer [11]. This model specifies the progression of the leaf shape over time. A similar model was subsequently employed to simulate development of leaf

venation patterns [9]. In this case, the complete surface of the leaf blade was propagated across the domain. Branching structures as the ones observed in compound leaves have been also modeled by using recursive structures, based for instance in the L-system formalism [7]. Alternative approaches based on physically based expansion models have been also explored in literature [8]. More recently, the dynamic of morphogens, which controls rate and direction of the organ growth, have been also considered to account for serration patterns commonly observed in leaf borders [3]. These models provide accurate visual results. However, their interpretability in biological terms can be limited.

3   Materials and Methods

The proposed approach is illustrated in figure 1. Firstly, an empirical sequence of the leaf lamina border is extracted out of real samples of the leaf development. Following, a local model of the leaf lamina growing is used to simulate an instance of the leaf growing dynamic, this model is dependent on a set of parameters θ. A cost function $J(\theta)$ that measures the similarity between the empirical sequence and the simulated sequence is computed. Finally, a Monte Carlo based optimization algorithm is used to find the optimal set of parameters θ^* that minimize the cost function.
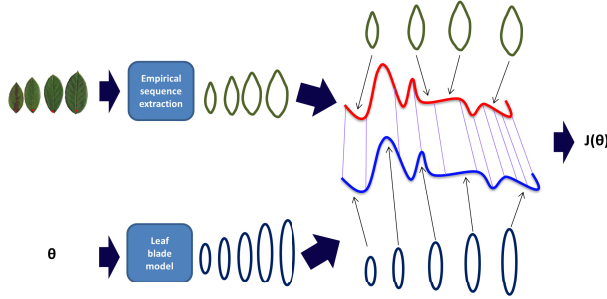
Fig. 1. Proposed approach. An empirical sequence of the leaf lamina border is extracted out of real samples of the leaf development. Following, a local model of the leaf lamina growing is used to simulate an instance of the leaf growing dynamic depending on a set of parameters θ. Finally, a cost function $J(\theta)$ that measures the similarity between the empirical sequence and the simulated sequence is computed.

3.1   Leaves Data and Empirical Sequence Extraction

The sequence of leaf development was sampled for 12 plant species. Each sequence contained 15 different leaf samples organized in an incremental way according to their developmental stage. For each sample in the sequence, foliar lamina was acquired at 300 *ppp* by using desktop scanner (MP250-Canon) [5]. Images were stored in RGB format. Figure 2 shows a sequence of example.
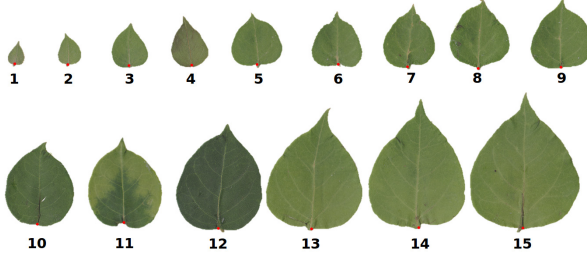
Fig. 2. Example of a leaf development sequence.

The leaf borders were extracted by using binary thresholding and contour tracing algorithms [12]. Spurious regions were removed by using morphological operators. Leaf base for each contour was manually selected. The leaf contours inside a sequence were reoriented to coincide in their basis by using principal component analysis (PCA) and rigid transforms [12].

3.2   Leaf Blade Development Model

To simulate the leaf blade development a relative growth rate (RGR) model was used. RGR is a standardized measurement of growth with the benefit of avoiding, as far as possible, the inherent differences in scale when comparing contrasting organisms. In plant studies RGR is an indicator of the plant productivity as related to environmental stress and disturbance regimes. Applications of RGR include the study of dry weight, biomass, leaf area, stem volume, basal area and stem diameter. Relative growth rates are also pre-requisites for quantifying and modeling allometric relationships in plants [6].

To define RGR we can start with a quantity of interest, for instance, the leaf width $w(t)$. Given two measures of leaf width in two different times t_i and t_{i+1}, the absolute growth can be defined as $\Delta w = w(t_{i+1}) - w(t_i)$, this quantity is dependent on both the time difference $t_{i+1} - t_i$ and the initial size $w(t_{i+1})$. In order to have a growth description independent of these two quantities, the absolute growth can be normalized, i.e., $\frac{\Delta w}{(t_{i+1}-t_i)w(t_i)}$. For instantaneous times, this quantity is called RGR and can be defined at time t as $RGR = \frac{w'(t)}{w(t)}$. RGR is the increase in size of some quantify relative to the size of the quantity present at the start of a given time interval. Different RGR can be specified depending on the growing direction. By using RGR, growth rates can be compared among species and individuals that differ widely in size.

A number of plant growth functions have been proposed in the literature. They are often combinations of power functions and exponential functions [6]. Most functions of relative growth rate have the advantage that they have fewer model parameters than the corresponding functions of absolute growth rate. In this work, we used RGRs proposed by Bilsborough et al [3], which were

previously used to model leaf blade growth of *Arabidopsis Thaliana*. In this case, two relative elementary rates of growth ($RERG$) depending on both directions x (lateral) and y (longitudinal) directions are defined as:

$$RERG_x(x,y) = \begin{cases} \alpha_x(1 - \frac{y}{Th_x}) & 0 \leq y < Th_x \\ 0 & otherwise \end{cases} \quad RERG_y(x,y) = \begin{cases} \alpha_y(1 - \frac{y}{Th_y}) & 0 \leq y < Th_y \\ 0 & otherwise \end{cases}$$

where α_x and α_y represent maximum lateral and longitudinal growths, respectively. Th_x and Th_y the longitudinal extents of lateral and longitudinal growth inhibition. $RERG_y(x,y)$ ($RERG_x(x,y)$) are functions that represents the increase in leaf lamina width (length) relative to the size of the width (length) present at the start of a given time interval. Note that these quantities can also be interpreted also as a vector field of RGR. This vector field provides information about the displacement of a wall (i,j) between cells i and j in the transversal direction. This displacement can be obtained from the integration of $RERG_X$ along the x-axis direction $\frac{dx}{dt} = \int_0^x RERG_x(s,y)ds$ with y is the ordinate of the center of the wall between cells i and j. A similar expression can be obtained for displacement for the longitudinal direction, $\frac{dy}{dt} = \int_0^y RERG_y(x,s)ds$. These two integrals can be solved analytically:

$$\frac{dx}{dt} = \begin{cases} \alpha_x(1 - \frac{y}{Th_x})x & 0 \leq y < Th_x \\ 0 & otherwise \end{cases} \quad \frac{dy}{dt} = \begin{cases} \alpha_y(y - \frac{y^2}{2Th_y}) & 0 \leq y < Th_y \\ \alpha_y \frac{Th_y}{2} & otherwise \end{cases}$$

These two equations describe the dynamic of the border displacement. By solving numerically this system a leaf growing instance can be simulated. Note that by choosing a different set of parameters $\theta = (\alpha_x, Th_x, \alpha_y, Th_y)$ a different leaf shape can be obtained. Note that other leaf development models do not account for the REGs parameters. Therefore, this work is focused on REGs based growing models.

3.3   Cost Function

Dynamic Time Warping. As cost function we used dynamic time warping (DTW). This is an algorithm for measuring similarity between two temporal sequences which may vary in time or speed [10]. Suppose we have two time series X and Y^θ not necessarily of the same length, as follows

$$X = x_1, x_2, \ldots, x_n \quad Y^\theta = y_1^\theta, y_2^\theta, \ldots, y_m^\theta$$

here X corresponds to the empirical sequence and Y_θ to the sequence of development obtained by using the blade development model described in section 3.2. To align both sequences first a local dissimilarity function $d(i,j)$ between the empirical blade border x_i and the simulated blade border y_j^θ is computed. Using these distances a matrix distance with $n \times m$ can be constructed. To find the best match between these two sequences a warping path can be defined. A warping path W is a set of elements that defines a mapping between X and Y^θ. The k-th element of W is defined as $w_k = (i,j)_k$, therefore W can be written as $W = w_1, w_2, \ldots, w_K$, $\max(m,n) \leq K < n+m+1$. The warping path is subject

to different constraints, namely, boundary conditions, continuity and monoticity. Boundary conditions refers to the fact that W should start and finish in the diagonally opposite corner cells of the distance matrix, i.e., $w_1 = (1,1)$ and $w_K = (n,m)$. Continuity restricts the allowable steps in the warping path to adjacent cells (including diagonally adjacent cells), i.e., given $w = (a,b)$ then $w_{k-1} = (a',b')$ where $(a-a') \le 1$ and $(b-b') \le 1$. Monoticity forces the points in W to be monotonically spaced in time, i.e., given $w_k = (a,b)$ then $w_{k-1} = (a',b')$ where $aa' \ge 0$ and $b - b' \ge 0$. Figure 3 illustrates a path W that satisfies the above conditions. Given these conditions, we are interested in the warping that minimizes the following warping costs:

$$DTW(X,Y^\theta) = \min\left\{\sqrt{\textstyle\sum_{k=1}^{K} w_k}/K\right\} \tag{1}$$

the K in the denominator compensate warping paths that may have different lengths. An efficient solution to problem 1 can be found by computing the cumulative distance $\gamma(i,j)$ between cells i and j. This distance can be defined recursively as the distance $d(i,j)$ found in the current cell and the minimum of the cumulative distances of the adjacent elements $\gamma(i,j) = d(x_i, y_j^\theta) + \min\{\gamma(i-1,j-1), \gamma(i-1,j), \gamma(i,j-1)\}$. This problem can be solved by using dynamic programming [10], the path W can be reconstructed by using a backtracking algorithm.

To compute the local dissimilarity function $d(i,j)$ we reparametrized both curves x_i and y_j^θ to have 200 points equally spaced by using a linear interpolation. Following we defined the distance as the Frobenious norm between the corresponding reparametrized point sequences.
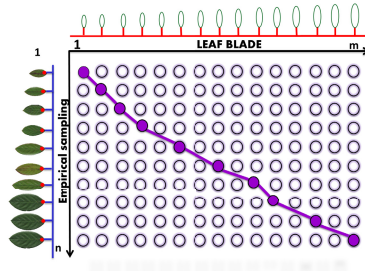

Fig. 3. Distance time warping.

Monte Carlo Optimization. In order to find the set of model parameters $\theta*$ associated to the data the following optimization problem $\theta^* = \underset{\theta}{\arg\min} J(\theta) = \underset{\theta}{\arg\min} DTW(X,Y^\theta)$. Because of the non-linear nature of the blade development model herein used a Monte Carlo optimization method was used to find the optimal set of parameters θ^* [1]. In particular, we used Simulated annealing
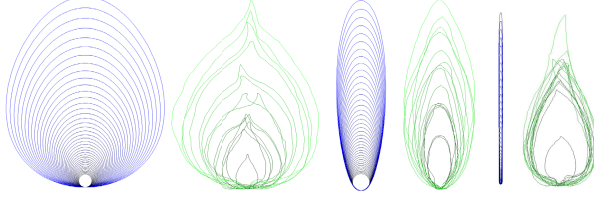
Fig. 4. Inferred sequences (blue) for an empirical sequences of leaf development (green).
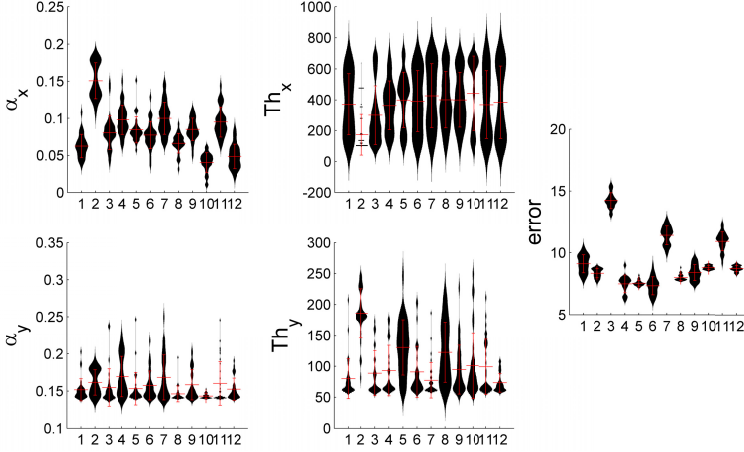
Fig. 5. Distribution plots of the inferred model parameters $(\alpha_x, Th_x, \alpha_y, Th_y)$ and the corresponding error (value of DTW) distribution for each leaf development sequence considered. Red lines indicate mean and standard deviations.

with 100 iterations. For the optimization, model parameters ranged uniformly between 0.01 and 0.18 for α_x, 100 and 700 for th_x, 0.14, 0.25 for α_y and 60 and 250 for th_y. To probe stability of the proposed method this experiment was repeated 30 times.

4 Results

Figure 4 shows three simulated sequences for three examples of the leaf development process. As observed, the method was able to properly infer the general developmental structure for the first two sequences. In the third sequence, the training sequence (green) does not reflect the leaf growing dynamic affecting the algorithm performance. Figure 5 shows the distribution of the model parameters estimated for the 12 development sequences (x-axis) for 30 runs. The proposed strategy provided different and stable parameter estimations for all the parameters. Interestingly, sequences 3 (last sequence of figure 4), 7 and 11 where the training samples do not reflect the leaf growing resulted in a higher approximation errors.

5   Conclusions

We have introduced a method to infer the geometrical structure of a leaf blade developmental model out of samples of sequences of the leaf development out of real leaf samples. The method is based on a non-linear ordinary differential equation model of relative elementary rates of growth. Experimental results indicate that the proposed method is able to extract stable parameters that may properly reconstruct the dynamic of the leaf growing.

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