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Modeling complex perennial plant patterns

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Introduction

The main assumption of plant architecture analysis is that plant is a highly structured organism in terms of development over time, topological organization and space occupancy. The objective of plant architecture analysis is thus to identify levels of organization, rules of development and gradients within plant structure. For perennial plants, most of the studies rely on retrospective measurements where plant structures are often described at macroscopic scales such as growth unit or annual shoot scales. The development of expertise in plant morphology and architecture has enabled such measurements on relatively old parts of perennial plants. This has opened new avenues particularly for studying forest trees which develop over long periods (Guédon et al., 2007; Chaubert-Pereira et al., 2009, 2010). Measurements take the form of a tree-graph (or sequences extracted from it) with descriptors of different natures (morphological, geometrical or physical) attached to each growth unit or annual shoot.

Because of this macroscopic scale of interest, models for analyzing complex patterns often found in perennial plants should combine structure with probabilities. Probabilities enable to represent fluctuations due to unobservable biological functions and their interactions acting at more microscopic scales than the scale of measurement. Generally, the objective of this type of analysis is to identify and characterize complex patterns which cannot be grasped directly from the data rather than to quantify well-known behaviors. In this respect, the analysis of complex perennial plant patterns fits into the general framework of pattern theory (Grenander and Miller, 2006).

Modeling approaches

The plant growing structure is affected by different types of time-varying environmental factors (e.g. climatic factors, individual light environment) and the plant response is most often delayed and “smoothed” due to the inertia of such large-scale organism. In the measured plant, the effects of ontogeny and environmental factors are mixed. A decomposition approach should thus be applied to separate in the measured plant development these two growth components. The mixed probabilistic/structural models for analyzing complex patterns in perennial plants generally incorporate the following building blocks:

- a supporting structure in the form of a sequence or a tree-graph,
- embedded patterns e.g. (i) alternating motifs corresponding to the alternation between flowering and vegetative growth units in the case of fruits trees (Costes and Guédon, submitted), (ii) roughly stationary growth phases in the case of forest trees (Guédon et al., 2007),
- three categories of variables: (i) “state” variable often for representing a non directly observable pattern (e.g. a growth phase), (ii) plant response variable, (iii) explanatory environmental variable.

The distinction between non-observable state variable and observed response variable is particularly useful for modeling multi-scale plant structuring. For instance, a growth phase can be represented by a state variable while observed response variables can represent the characteristics of growth units or annual shoots within this phase.
Dedicated models are available for analyzing patterns corresponding to long-range dependencies (e.g. growth phases) in sequences. These models cannot be generalized to tree-graphs and models incorporating a probabilistic component for analyzing such data always rely on first-order dependencies between “parent” and “child” entities - e.g. hidden Markov tree models (Durand et al., 2005) or multitype branching processes - and could only be extended to short-range dependencies. In sequence description, the variables qualify either the parent entities belonging to the sequence (e.g. annual shoot length) or the offspring entities (e.g. number of branches); see illustrations in Guédon et al. (2007). This latter case can be further extended by qualifying not only the first-order borne entities but more generally the entire borne branched systems. Such multivariate descriptions tend to reinforce the impact of sequence analysis for analyzing perennial plant patterns. Hence, models for analyzing sequences and models for analyzing tree-graphs should be considered as complementary. Moreover, sequences are far less constraining than tree-graphs in terms of measurement protocol. This point is illustrated by self-pruning which makes that only the trunk can be measured retrospectively among the oldest part of adult forest trees.

![Sequence diagram](image)

Figure 1. Apple tree GU succession along axes: (a) Non-observable mixed first/second-order Markov chain. Each vertex represents a possible memory i.e. a succession of GU types. L, M, S, F, stand for long, medium, short and flowering, respectively. Transitions are represented by arcs (the dashed arc corresponds to a less frequent transition). (b) Example of sequence of GU types.

The application of mixed probabilistic/structural models led us to identity unexpected patterns in perennial plants:

- The development of Corsican pine trunks takes the form of long stationary phases separated by breakpoints of high magnitude when growth globally decreases (instead of a smoothly decreasing trend) (Guédon et al., 2007).
- For different forest tree species, Chaubert-Pereira et al. (2009) showed that growth phases are not only defined by average growth level but also by growth fluctuation amplitudes in response to climatic factors and inter-individual heterogeneity, and that the individual tree status within a population may change between phases.
- In apple tree, two successive phases corresponding to different patterns of alternations between flowering and vegetative growth units (GUs) were identified (Costes and Guédon, submitted). In this study, instead of first classifying GUs in categories then characterizing the succession of GU types along the axes, we rather chose to merge these two steps and build a single integrative statistical model which is a hidden Markov model based on a variable-order Markov chain. The non-observable variable-order Markov chain represents the succession of GU types along the axes (Figure 1). The GU types are not observable directly but only indirectly through the two observed variables, namely the number of nodes and the non-flowering/flowering character of the GU. The application of this integrative model led to an unexpected characterization of the vegetative GUs in the two phases combining a morphological criterion (number of nodes) with structural criteria (occurrence of polycyclism, constraints on the succession of GUs).
Therefore, well-defined phases separated by breakpoints appeared as a key pattern organizing perennial plant ontogeny even if the modalities of phase succession and phase characteristics are diverse.

Perspectives

The models studied in Chaubert-Pereira et al. (2009, 2010) required long climate records from which yearly climatic explanatory variables were extracted (e.g. cumulative rainfall). Many long climate records are affected by artificial shifts due to changes in the conditions of measurement and incorporate various kinds of spurious data; see Caussinus and Mestre (2004). Moreover, few climate records are available for periods extending before the Second World War which may be a definitive drawback for studying old forest trees over their entire lifespan. In the case where climatic data are not available, a possibility would be to introduce a year random effect common to all the trees to model the synchronous part of the growth fluctuations. We are currently developing such “implicit” modeling of the climate influence.

One field of intense research in statistical modeling for structured data concerns the combination of different latent structures. This research direction is in particular illustrated by the model proposed by Chaubert-Pereira et al. (2009, 2010) which combines two latent structures: (i) a non-observable semi-Markov chain that represents successive growth phases and (ii) random effects that represent the growth level deviation in each phase of a tree with reference to the “average” tree. One limitation of this type of model is the fact that they can only incorporate Gaussian plant response variables. The next step will consist in incorporating categorical or count response variables (e.g. apex death/life, non-flowering/flowering character, number of growth units) in such models.

Incorporating individual random effects in latent structure models open new perspectives for statistical genetics. In this context, the plant structure is usually summarized by a set of global variables (e.g. main stem height, crown volume). Segura et al. (2008) proposed a first approach based on linear mixed models for analyzing the influence of genetic factors on apple tree structure development over a few years. We expect that the capability to explicitly represent complex plant structures will enable to better take into account plant ontogeny in such context.

References


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