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Integrative models for analyzing jointly shoot growth and branching patterns

Jean Peyhardi[1,2], **Evelyne Costes**[3], **Yves Caraglio**[4], **Pierre-Éric Lauri**[3], **Catherine Trottier**[2] and **Yann Guédon**[1]

[1]*CIRAD, UMR AGAP and Inria, Virtual Plants, F-34095 Montpellier, France,* [2]*Université Montpellier 2, Institut de Mathématiques et de Modélisation de Montpellier, F-34095 Montpellier, France,* [3]*INRA, UMR AGAP, F-34398 Montpellier, France,* [4]*CIRAD, UMR AMAP, F-34398 Montpellier, France*

**correspondence:* guedon@cirad.fr

Highlights: The branching pattern of a shoot may be influenced by numerous factors varying along the shoot such as the internode length, the leaf surface or the local curvature. We introduce a generalization of hidden semi-Markov chains for categorical response variables that incorporates explanatory variables varying with the index parameter. Using this model, we demonstrate the influence of the growth pattern of a shoot on its immediate branching.

Keywords: branching pattern; generalized linear model; growth pattern; semi-Markov switching regression model.

INTRODUCTION

Branching patterns of a shoot often take the form of a succession of well-differentiated homogeneous branching zones where the composition properties, in terms of axillary productions, do not change substantially within each zone, but change markedly between zones. These branching patterns have been analysed using segmentation models and in particular hidden semi-Markov chains (Guédon et al. 2001). Branching patterns are modulated by both factors that have a global effect on the pattern and factors varying along the shoot that have differentiated effects on the successive axillary productions. We previously investigated the influence of the architectural position of a shoot, which can be viewed as a factor having a global effect, on apple tree branching patterns (Renton et al. 2006).

Here, we focus on factors varying along the shoot that modulate its branching pattern. For example, it has been shown that shoot growth modulates the branching pattern, in particular the immediate (or sylleptic) branching; see Lauri and Térouanne (1998) for an illustration in the apple tree case. Other potential factors include the local curvature of the shoot (Han et al. 2007). To this end, we introduce a new family of integrative models for analysing jointly the succession and length of branching zones and the modulation of the axillary productions within each zone by factors varying along the shoot. These models generalize hidden semi-Markov chains for categorical variables (Guédon et al. 2001) by incorporating explanatory variables and are called semi-Markov switching generalized linear models (SMS-GLMs). It should be noted that another family of semi-Markov switching regression models has been previously introduced for analysing forest tree growth components. More precisely, semi-Markov switching linear mixed models were used to identify and characterize the ontogenetic, environmental and individual growth components on the basis of tree main stems described by annual shoot and climatic data (Chaubert-Pereira et al. 2009).

RESULTS

The proposed approach is illustrated by the analysis of the immediate branching pattern of apple tree, cv. Fuji. The data set comprised 22 shoots of cumulative length 1494 (length between 63 and 73 nodes). For each tree, the first annual shoot of the trunk was described by node from the base to the top where, for each node, the type of axillary production chosen among latent bud, immediate short shoot and immediate long shoot, and the internode length (in cm) was recorded.

A semi-Markov switching generalized linear model, which is a two-scale segmentation model, was built on the basis of this data set. In this framework, the succession and length of branching zones (coarse scale) are represented by a non-observable semi-Markov chain while the axillary productions within a branching zone modulated by factors varying along the shoot (fine scale) are represented by generalized linear models attached to each state of the semi-Markov chain. A SMS-GLM combines three categories of variables: (i) "state" variable representing the non-directly observable branching zones, (ii) plant response categorical variable (types of axillary production), (iii) explanatory variables varying with the node rank (e.g., the internode length).

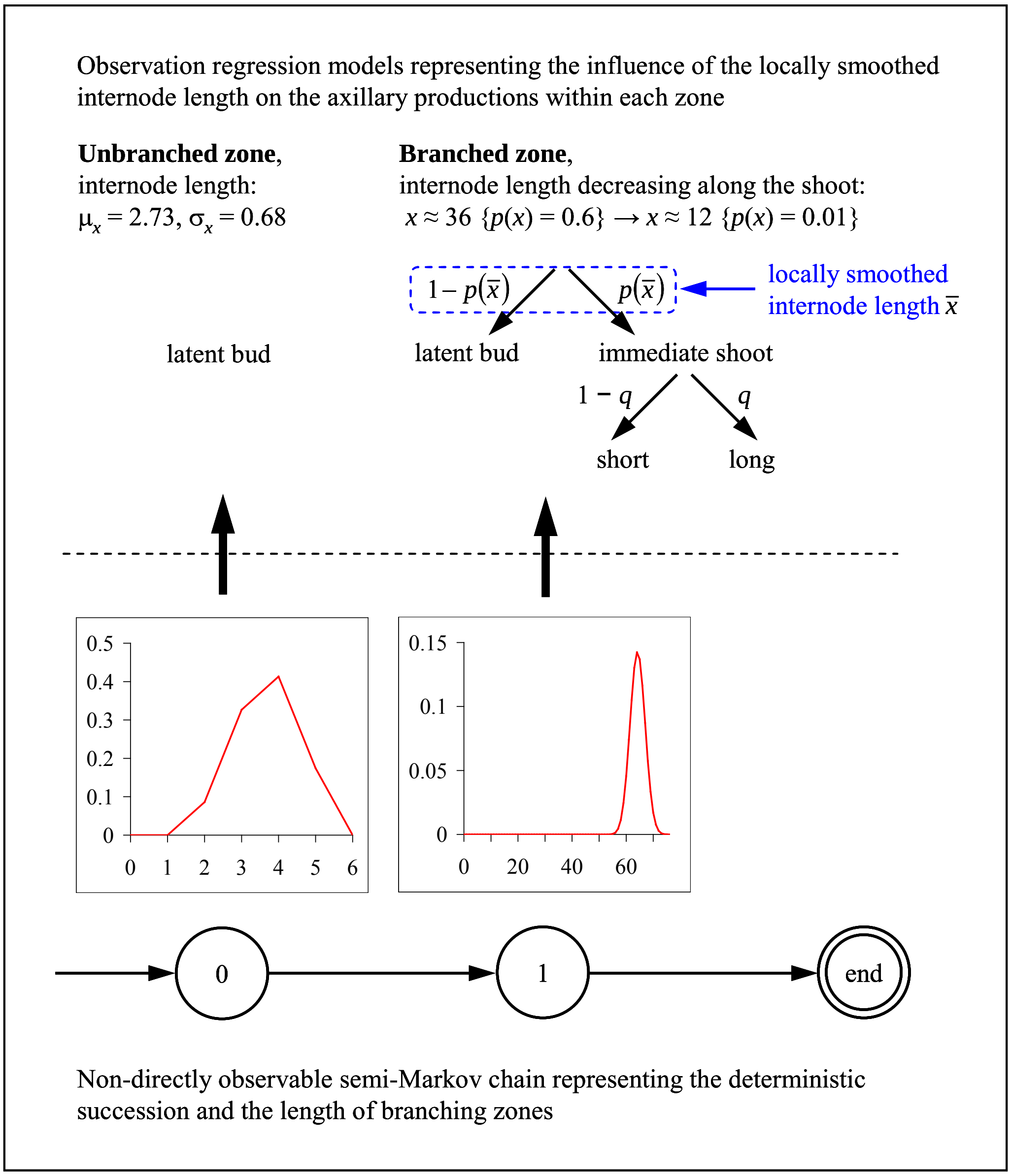

Figure 1. Semi-Markov switching generalized linear models. *Semi-Markov chain*: each state is represented by a vertex which is numbered. Vertices representing transient states are edged by a single line while the vertex representing the absorbing end state is edged by a double line. The possible transitions between states are represented by arcs (the attached probabilities are always 1). The arc entering in state 0 indicates that it is the only possible initial state. The occupancy distributions of the transient states are figured above the corresponding vertices. *Observation regression models*: for state 0 (unbranched zone), the observation model is degenerate since the only possible observation is latent bud. For state 1 (branched zone), the estimated branching probability p decreases with the internode length along the parent shoot. The locally smoothed internode length influences markedly the immediate shoot initiation but only slightly the subsequent growth of these immediate shoots (and the influence of the explanatory variable is only figured for the partition latent bud/immediate shoot).

The estimated SMS-GLM was composed of two transient states followed by a final absorbing end state modelling growth cessation (Renton et al. 2006); see Figure 1. The deterministic succession of states resulted from the iterative estimation procedure. We tested two types of transform of the measured internode length variable to build potential explanatory variables:

- shift of the variable, in particular backward shifts, since the internode elongation lasts about 12 days in apple tree and temporally overlaps the initiation of immediate shoots a few nodes below the apex.
- smoothing of the variable in order to remove the fluctuations and to extract the local internode length trend. This smoothing can be interpreted as an averaging over the internodes that elongate at a given time t.

The best model according to model selection criteria (Bayesian information criterion in this case) was obtained with no shift and a smoothing of the internode length obtained using a symmetric smoothing filter corresponding to the probability mass function of the binomial distribution of parameters 32 and 0.5 (95% of the mass concentrated on the 11 central values). This smoothing width appears to be consistent with the order of magnitude of the number of internodes that elongate at a given time *t*.

The unbranched zone of short internodes at the base of the shoot (state 0) corresponds to the preformed part of the shoot. The fact that the highest probability of branching and the longest internodes were found near the shoot base (around rank 10) likely resulted from the propagation mode of the observed young plants which issued from bud grafting on a one-year-old rootstock.

DISCUSSION

The example illustrates the fact that the definition of appropriate explanatory variables is a crucial step in the context of retrospective measurements. We are now investigating the extraction of explanatory variables on the basis of growth data follow up (e.g. leaf expansion). In this context, the extraction of explanatory variables requires two steps, (i) extraction of growth parameters using for instance nonlinear regression models (e.g. the maximum absolute growth rate deduced from the fit of a sigmoidal function), (ii) shifting and smoothing of growth parameters deduced from nonlinear regression models.

Concerning the observation regression models, a standard solution would have consisted of assuming that the categorical response variable was ordinal (with the following category order: latent bud, immediate short shoot and immediate long shoot) and to estimate an ordinal generalized linear model for the branched state. We chose to develop the more general framework of hierarchical models that enables to tackle not only the classical cases of nominal and ordinal categorical response variables but also the case of partially ordered categorical response variables. This framework relies on a recursive partitioning of categories into subsets. This hierarchical modelling is illustrated in the example where the categories are first partitioned into latent buds and immediate shoots, the immediate shoots being then partitioned into short and long shoots. Using this hierarchical modelling, it was possible to show applying model selection criteria that the locally smoothed internode length influences markedly the immediate shoot initiation but far less the subsequent growth of these immediate shoots which likely depended on environmental factors at this time.

Combining transform of explanatory variables and recursive partitioning of the axillary productions using hierarchical modelling, it was possible to test many assumptions concerning the influence of the growth pattern on the immediate branching pattern in our example.

This study together with the study of Chaubert-Pereira et al. (2009) illustrate the versatility of semi-Markov switching regression models where a semi-Markov chain can represent homogeneous branching zones at the node scale as well as growth phases at the annual shoot scale and where all the panoply of regression models can be incorporated depending on the type of the plant response variable (categorical variable for the type of axillary production and interval-scaled variable for the annual shoot length).

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