Characterizing the balance between ontogeny and environmental constraints in forest tree development using growth phase duration distributions

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Highlights: We built segmentation models to identify tree growth phases on the basis of retrospective measurement of annual shoot characteristics along the main stem. Growth phase duration distributions estimated within these models characterize the balance between ontogeny and environmental constraints in tree development at the population scale. These distributions have very contrasted characteristics in terms of shape and relative dispersion between ontogeny-driven and environment-driven tree development.

Keywords: developmental plasticity; growth trajectory; hidden semi-Markov chain; segmentation model.

INTRODUCTION

Tree developmental plasticity is a key determinant of forest dynamics and composition. This study aimed to identify robust indicators that summarize the balance between ontogeny and environmental constraints in tree development using different species growing in contrasted conditions.

Observed apical growth, as given for instance by the length of successive annual shoots along a tree main stem, results mainly from an ontogenetic component and an environmental component. In this study, the ontogeny was viewed as a developmentally programmed growth trajectory preadjusted to the most likely environments (Yagi 2009). The ontogenetic component is assumed to be structured as a succession of roughly stationary growth phases that are asynchronous between individuals (Guédon et al. 2007). We applied segmentation models to identify growth phases on the basis of characteristics measured retrospectively on successive annual shoots along a tree main stem. When building segmentation models for different tree species growing in contrasted conditions (Guédon et al. 2007; Chaubert-Pereira et al. 2009; Taugourdeau et al. 2011), growth phase duration distribution emerged as a potential indicator that could summarize the balance between ontogeny and environmental constraints in tree development at the population scale. Growth phase duration distributions ranged from bell-shaped distributions with small relative dispersions for trees growing in open field conditions to right-skewed distributions with larger relative dispersions for trees growing in understorey. The objective here is thus to investigate systematically this indicator.

RESULTS

The analysis of the duration of growth phases is illustrated by both evergreen (Corsican pine and silver fir) and deciduous (sessile oak and Persian walnut) tree species growing in contrasted conditions ranging from managed forest stands (Corsican pine and sessile oak) to unmanaged understoreys (silver fir and Persian walnut). All these data sets include a large number of individuals (between 65 and 208) and correspond mostly to young trees before their maximum growth. For each data set, a hidden semi-Markov chain (HSMC), which is a two-scale segmentation model (Guédon et al. 2007), was built. In this framework, the succession and duration of growth phases (coarse scale) are represented by a non-observable semi-Markov chain while annual shoot characteristics (e.g. length, number of growth units) within a growth phase (fine scale) are represented by observation distributions attached to each state of the semi-Markov chain. Hidden semi-Markov chains were compared with simple hidden Markov chains (HMCs) which corresponds to the purely opportunistic development assumption driven by changing environmental constraints (Taugourdeau et al. 2011). In a HSMC, the duration of each growth phase is explicitly modelled by a dedicated parametric discrete distribution, while in a HMC, the duration of each growth phase is implicitly modelled by a geometric distribution, which is the unique "memoryless" discrete distribution. The assumption of geometric state occupancy distributions (the shorter the growth phase duration, the more probable it is) should here be viewed as a limiting case and a minimal duration > one year in a given growth

phase is a more realistic assumption. HSMCs and HMCs were estimated on the basis of bivariate sequences along the main stems with the annual shoot length as first variable (the index parameter of the sequence was thus the year) and as second variable:

- the number of branches per tier for Corsican pine and silver fir,
- the number of growth units for sessile oak,
- the absence/presence of branches for Persian walnut.

There were three states (i.e. two successive transient states followed by a final absorbing state) for Corsican pine, silver fir and Persian walnut and two for sessile oak. As the last year of measurement was arbitrary with regard to tree development, the duration of the last growth phase was assumed to be systematically truncated and could not be modelled.

As a result of the estimation procedure, the succession of states was deterministic for each estimated model. This deterministic succession of states supports the assumption of a succession of growth phases. The integrated completed likelihood criterion (a model selection criterion which takes account of the segmentation objective) clearly favoured the estimated HSMC in the Corsican pine and sessile oak cases while the estimated HSMC and HMC were quite close according to this criterion in the silver fir and Persian walnut cases. While the Corsican pine and sessile oak developments were far from an opportunistic development driven by changing environmental constraints, the silver fir and Persian walnut developments were close to an opportunistic development. Using different methods (Guédon et al. 2007), we checked that the estimated state occupancy distributions representing growth phase durations reflected mainly between-individual differences rather than within-individual differences (i.e. different possible segmentations of a given individual) and were readily interpretable as population parameters.

Table 1. State occupancy distributions estimated for each HSMC: parametric definition, mode and coefficient of skewness.

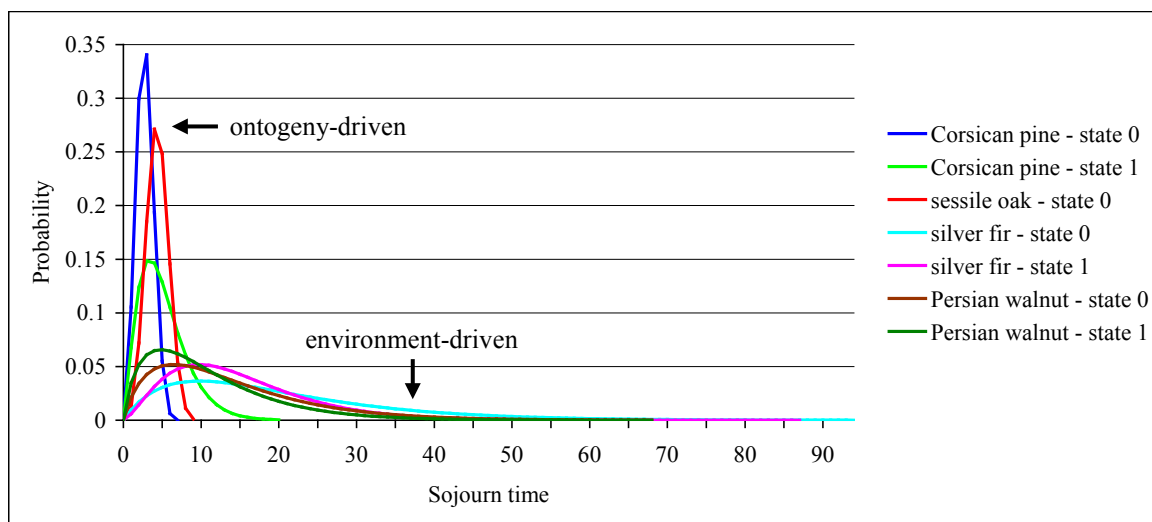|	State 0			State 1		
	Distribution	Mode	Skewness	Distribution	Mode	Skewness
Corsican pine	B(1, 6, 0.36)	3	0.26	NB(1, 3.26, 0.44)	3	1.15
Sessile oak	B(1, 9, 0.42)	4	0.11			
Silver fir	NB(1, 1.95, 0.092)	10	1.43	NB(1, 2.89, 0.17)	10	1.18
Persian walnut	NB(1, 1.83, 0.12)	6	1.48	NB(1, 1.74, 0.15)	5	1.52

Figure 1: Estimated state occupancy distributions.

All the estimated state occupancy distributions were 1-shifted binomial distributions $B(1, n, p)$ or negative binomial distributions $NB(1, r, p)$; see Table 1. The estimated state occupancy distributions were very different in terms of shape, ranging from bell-shaped distributions (state 0 for Corsican pine and sessile oak) to distributions tending toward reverse-J-shaped distributions (states 0 and 1 for Persian walnut, state 0 for silver fir); see Figure 1. The estimated state occupancy distributions can be compared on the basis of their coefficient of skewness and their shape parameter r for negative binomial distributions; see Table 1. The

coefficient of skewness is a dimensionless measure of the asymmetry of a distribution. In our case of positive skewness, the magnitude of this coefficient quantifies how the bulk of the values lies to the left of the mean. The proximity of the coefficient of skewness to 2 (approximate coefficient of skewness of the implicit geometric state occupancy distributions of the estimated HMCs in our case) can be interpreted in terms of proximity to the geometric distribution. In the case of a negative binomial distribution, the proximity of the shape parameter r to 1 (the shape parameter of the geometric distribution) can be also interpreted in terms of proximity to the geometric distribution. The estimated state occupancy distributions can be ranked from the closest to the farthest from geometric distributions:

1. states 0 and 1 for Persian walnut, state 0 for silver fir,
2. state 1 for silver fir and state 1 for Corsican pine,
3. state 0 for Corsican pine and sessile oak.

For 1-shifted binomial distributions (state 0 for Corsican pine and sessile oak), we have $\mu - 1 > \sigma^2$ while for 1-shifted negative binomial distributions (all the other states), we have $\mu - 1 < \sigma^2$. Hence, the three groups of state occupancy distributions defined above also correspond to different variance to mean ratios.

DISCUSSION

If it is assumed that forest gaps occur with a constant probability at a given location in unmanaged forest understorey (Spies et al. 1990), trees within the population will be randomly affected by a marked change in the light environment that suddenly will become favourable and likely induce a growth phase transition. In this case, we expect growth phase duration distributions to be close to geometric distributions, the unique discrete memoryless distribution, reflecting opportunistic development at the population scale. When tree development is mainly driven by changes in the local environment (mainly light environment), we will speak of environment-driven development. When the changes in the local environment are gradual, small in magnitude, and only slightly modulate tree ontogeny, we will speak of ontogeny-driven development. At first sight, the Corsican pine and sessile oak examples illustrate ontogeny-driven development while the Persian walnut and silver fir examples illustrate environment-driven development.

The modes of the two estimated growth phase duration distributions were similar in the different three-state models (Corsican pine, silver fir and Persian walnut); see Table 1. The four examples may be ranked in order of increasing mode of growth phase duration distributions:

- Corsican pine and sessile oak: trees growing in managed stands with a rather low level of competition;
- Persian walnut: trees growing in the understorey of a riparian forest;
- Silver fir: trees growing in the understorey of a mountain forest.

We therefore assume that the mode of growth phase duration distributions is an indicator of the growing potential of a species in a specific location (independently of competition level). In the case of a highly heterogeneous light environment, the growth phases lengthen for a certain proportion of the population and the growth phase duration distributions become highly right-skewed.

Since each example corresponded to a specific species growing in a specific environment, we focused on dimensionless characteristics of growth phase duration distributions such as the coefficient of skewness. An avenue for future work would be to study species with different adaptative strategies (e.g. shade avoidance and shade-tolerant species) in a given location or to compare the development of a given species in different environments in order to study the phenotypic plasticity of this species.

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