

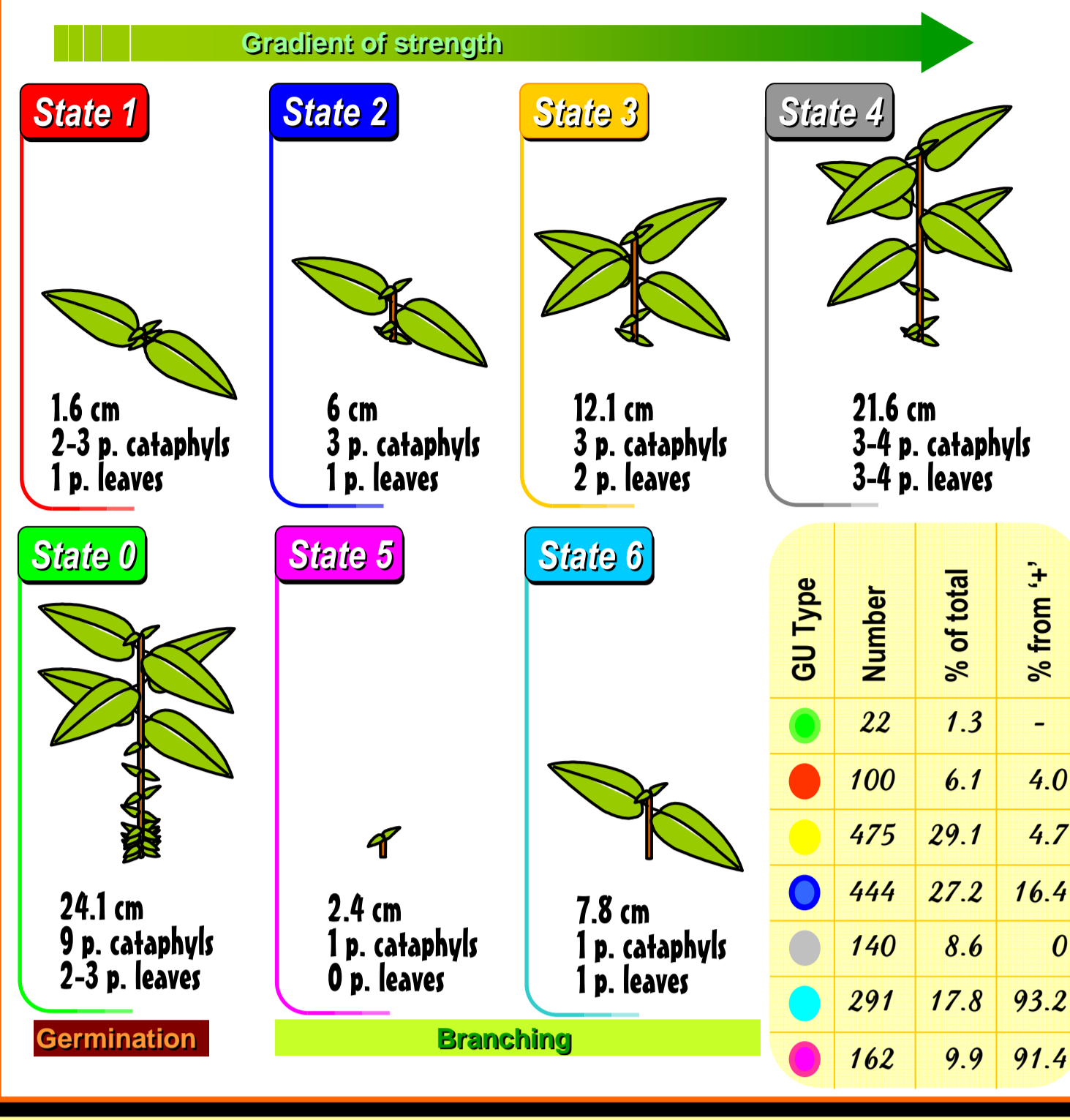
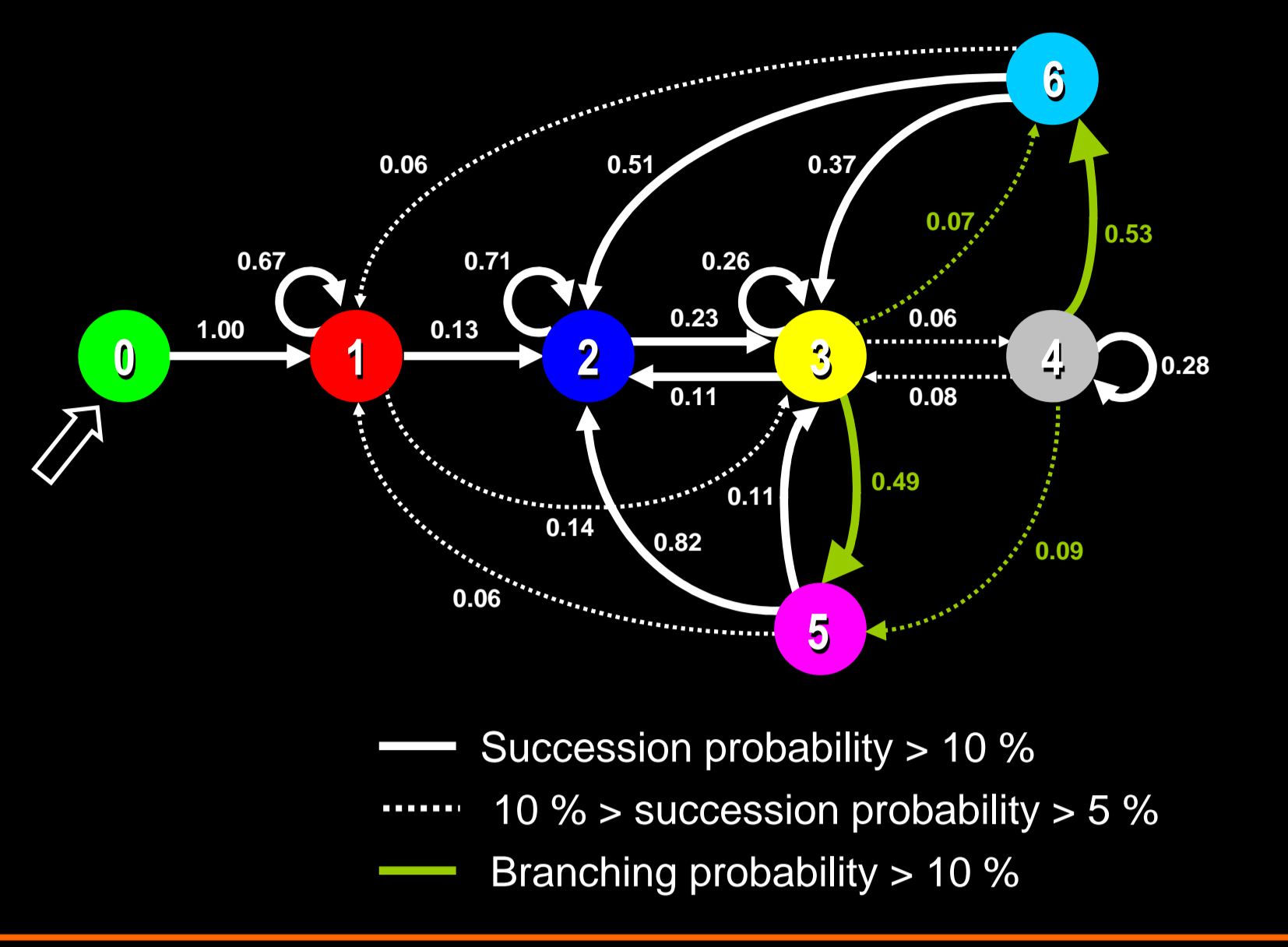
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INTRODUCTION

Plants are **modular organisms** that develop by the **repetition** of elementary botanical entities or constructional units through the three main and fundamental morphogenetic processes of growth, branching and reiteration [1]. Repetition of these entities induces **gradual or abrupt changes** in their characteristics. These characteristics are quantified through several variables, called the entity attributes. On the one hand, differences between entities reflect different stages of differentiation in the meristems, which are ordered in time and correspond to the notion of **physiological age of meristems** [1]. The changes of one attribute through the plant structure are referred to as morphogenetical gradient. On the other hand, part of the entity differences can be imputed to environmental factors. Based on this botanical model of plant functioning, our approach jointly relies on categories of entities with **similar characteristics**, a description of those within-category characteristics and the category topological organisation within the plant. This constitutes a useful summary of the plant architecture, which is the basis for **1) highlighting hidden regularities** in plant structures, for a better understanding of the gradients and organisation rules; **2) comparing** plant structures according to environmental factors.

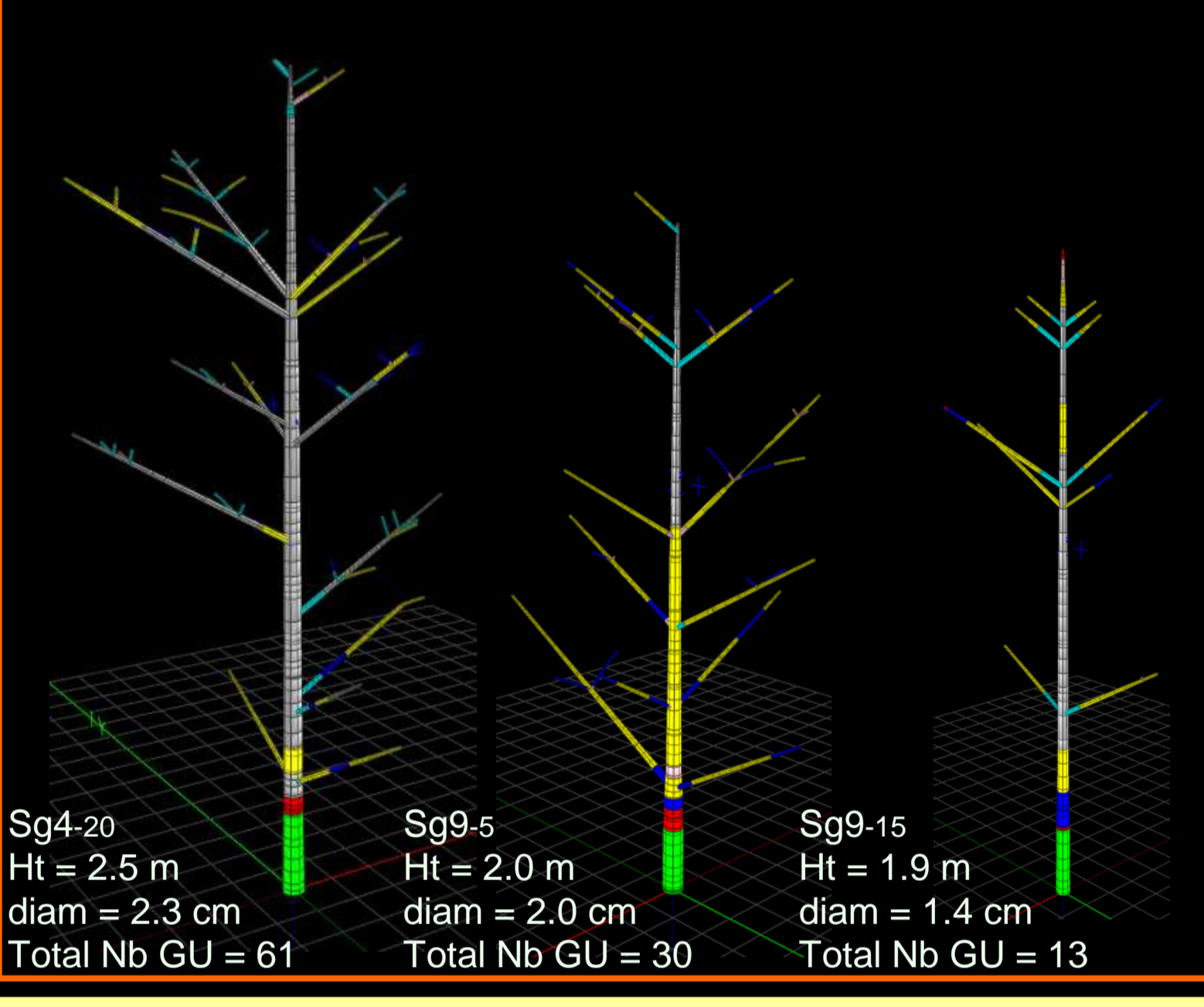
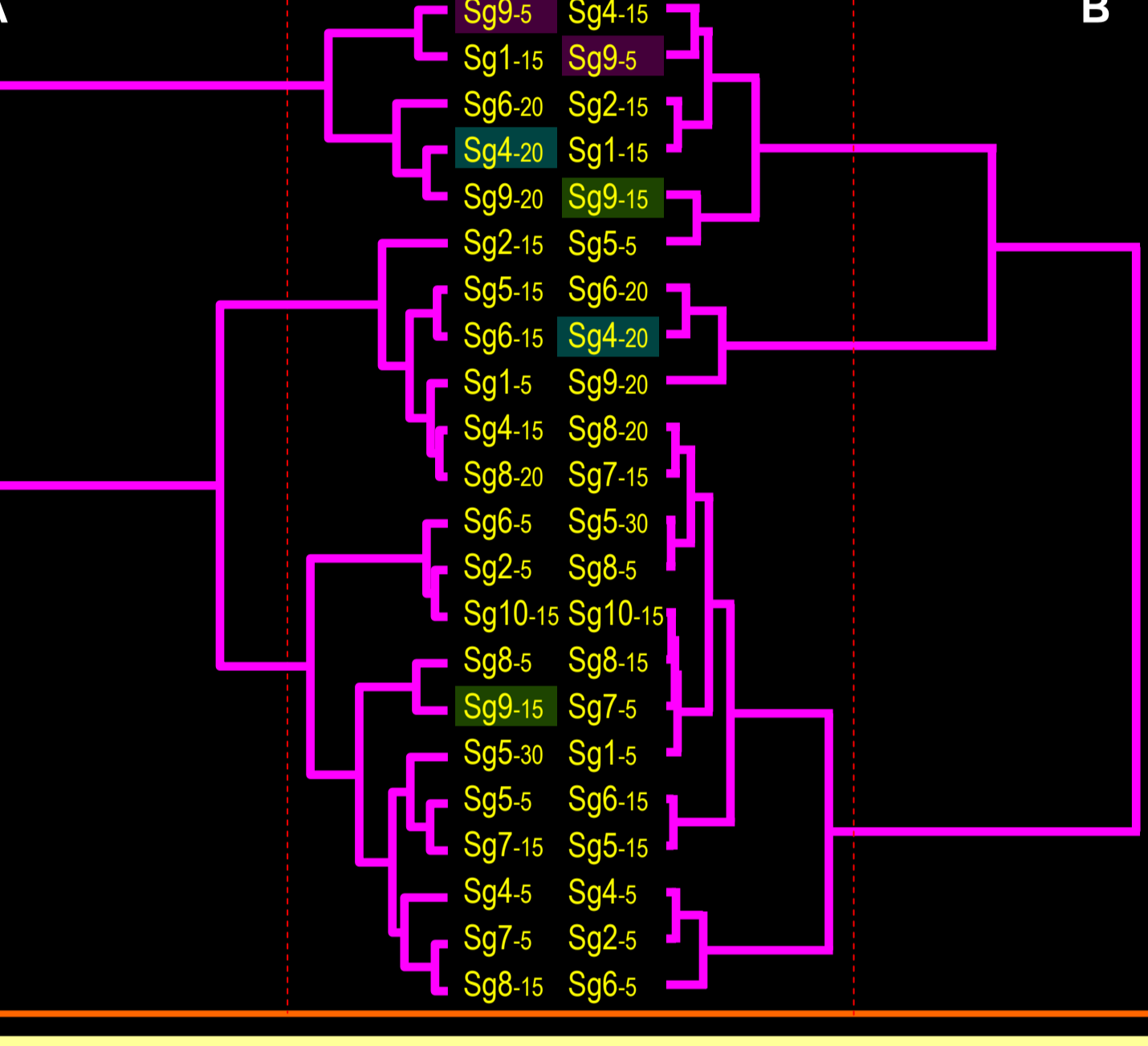
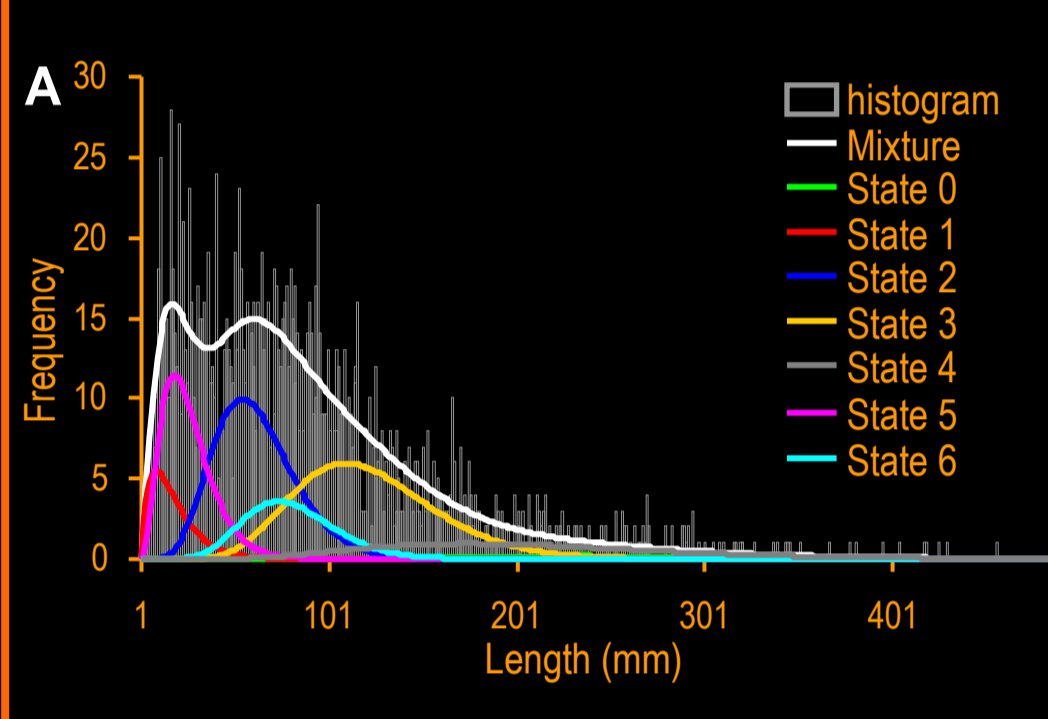
In this work, the methodology for tree architecture analysis is based on the study of **invariants and regularities** through identification of entity categories. This is achieved using a **hidden Markov tree (HMT)** model, in which local dependencies only (*i.e.* interactions between bearing and borne entities) are accounted for [2]. An HMT model is estimated from a dataset of botanical entities at a given scale (axes, annual shoots, growth units...). Having the largest sample of entities and exploring the broadest range of morphological expression requires the model to be estimated globally, on the whole sample (for instance, to regroup all individuals whatever the experimental plot they belong to). However, to better understand the variability at intermediate scales (axes, individuals, populations, experimental plots...), we use complementary methods as hierarchical classification and (edit distance algorithms). This methodology is illustrated on a temperate tree (*Fagus sylvatica*, *Fagaceae*) and a tropical tree (*Symphonia globulifera*, *Clusiaceae*).



MATERIAL AND METHODS

Symphonia globulifera: 22 two-years-old individuals grown in greenhouse under different light treatments (5%, 15% and 20% of incident light). Attributes=length, number of pairs of leaves and of cataphylls (phyllotaxy is opposite-decussate), completely measured at Growth Unit (GU) scale [5].
Objectives are:
 - to describe and model individual growth
 - to assess individual heterogeneity among tree population and to infer cluster of similar individuals
 - to assess the potential role of light treatment on tree architecture

Fagus sylvatica: (1) 16 forty-years-old individuals growing in 2 different density stands (8 + 8) and (2) 42 hundred-years-old individuals partially described (higher part of the trunk and one main branch per GU). Attributes=length, number of GUs per year and presence/absence of flowers, measured at Annual Shoot (AS) scale.
Objectives are:
 - to describe and model individual growth
 - to assess the effect of growth conditions on architecture – stages of development and vigor
 - to infer clusters of individuals with similar morphological characteristics
 - to highlight some morphological characteristics prior to flowering.

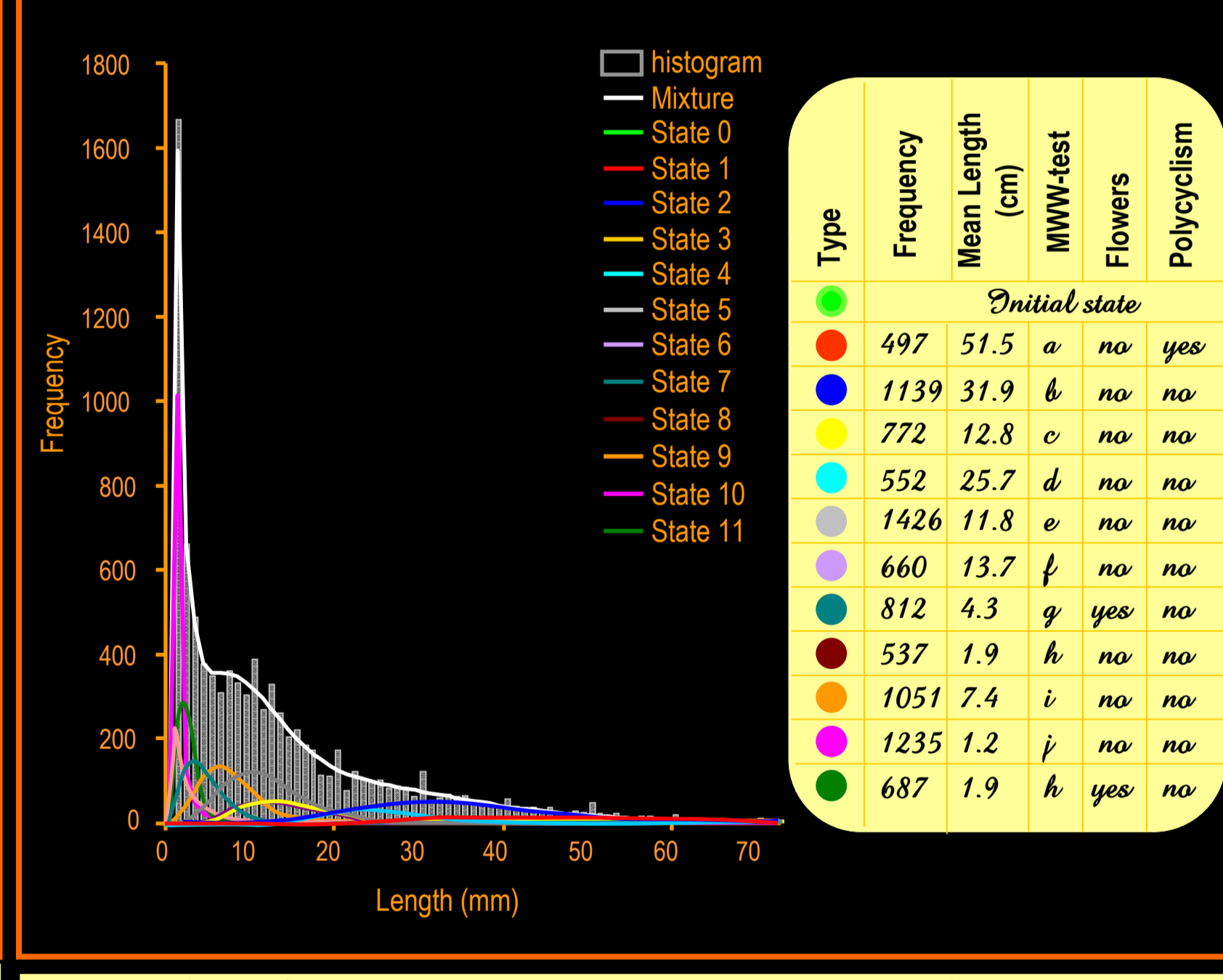
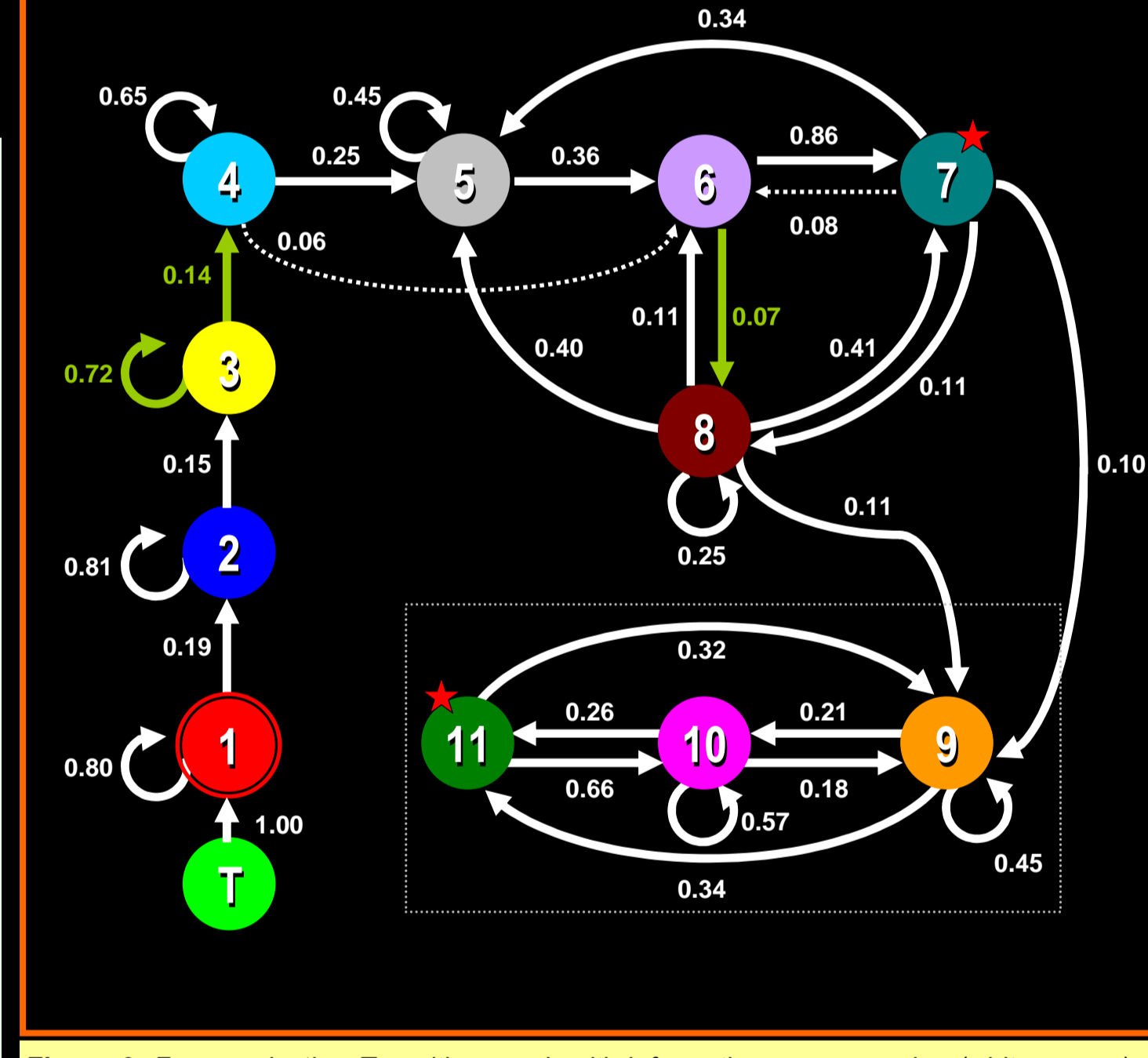


RESULTS

Symphonia globulifera: 7 well-differentiated states were identified using HMT models included in the OpenAlea software [6]. GUs in state 0 are the longest with a high number of cataphylls. They are always issued from germination. GUs in states 1 to 4 are respectively characterized by an increase of length and number of leaves (Fig. 1 and 2). They can be interpreted as levels of vigour. GUs in state 5 are leafless and are defined by a small number of cataphylls as GUs in state 6. They are mostly issued from immediate branching (Fig. 1 and 3). To assess light effect on plant architecture, the state frequencies were computed for each light treatment. As a result, GUs in state 1 and 2 (low vigour) are overrepresented in individuals growing under 5% of incident light, whereas GUs in states 3 and 4 (high vigour) are overrepresented in individuals growing under 20% of incident light. Hierarchical clustering of individuals was performed, firstly by considering morphological characteristics (height, diameter, number of axis of each possible order, of GUs, internodes, leaves, cataphylls ...). A partition in 3 clusters highlighted well-differentiated groups relatively coherent with different light levels (Fig. 4). A second clustering based only on GUs type frequency did not change the clusters deeply. However, it revealed that some individuals were relatively small and poorly branched but developed long GUs (state 4) on the trunk (Fig. 5).

Fagus sylvatica: 12 states were identified using HMT models. ASs in state 0 correspond to the part of the trunk that was not measured as AS scale. ASs in States 1, 2, 4, and 3 respectively correspond to ASs of decreasing in length and are mostly represented in the young beech tree set. ASs in states 5 to 11 are involved in flowering process and are mostly represented in the old beech tree set (state characteristics shown in Fig. 6). Two groups of states (5 to 8 and 9 to 11) were defined by the fact they constitute a cycle (a recurrent class) from which going out is definitive. In a general way, ASs of the first class are longer than those of the second class as well the vegetative states (5, 6, 8 vs. 9, 10) as the flowering ones (7 vs. 11). The second class is mostly accessed to through states 7 and 8. Finally, the first class may be interpreted as a more vigorous flowering cycle, when compared to the flowering cycle of the second class.

To explore individual variability of growth and flowering with the HMT model point of view (Fig 7), a hierarchical clustering of individuals based on ASs type frequency was performed on the centenary trees. A partition in 4 clusters highlighted well-differentiated groups of individuals based on their growth and flowering abilities (Fig. 8).



DISCUSSION

The twelve-state HMT model was achieved using the whole beech-tree sample (young and old) in order to include a great diversity of AS expression. Thus the states could be interpreted as a quantification of physiological age, because of their stability (number and the nature) versus the population diversity (age and conditions of growth) used in the estimation process. The complex patterns (two classes) in the state succession leading to flowering result not only from young and old trees but also can assess variability inside one sample (old trees) on which the hierarchical classification was applied. Apparent regularities were observed on segmented plants (Fig. 9), which could be explored using variable-order Markov chains applied to selected paths within the trees. We intend to carry other approaches to validate this methodology, by assessing how increasing the population diversity (for example diverse social status), or selecting different sets of attributes to build the HMT model, affects the state number or dynamics. Entity segmentation has a polyvalent status in the above studies: firstly, this provides a synthetic overview of the gradients, represented in the model through attribute distributions within each state, and the transition probabilities between states. Adding the state as a new synthetic variable in the data, allows complementary approaches for benefiting from a reduction of complexity (dimensionality), and some denoising. Secondly, the state-based approach reinforces the botanical notion of physiological age, since the state number remains very low, given the large complexity of measured trees, the number of individuals and of entities (hence the entity diversity). However, our model is not appropriate to model patterns, to relate the states with the topological growth, nor to resume the characteristics of whole branched systems. This is why HMT-based segmentation has to be combined with those complementary approaches, to precise and characterize states of architectural development.

