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EXPLORING MORPHOGENETICAL GRADIENT VARIABILITY USING HIDDEN MARKOV TREE MODELS IN YOUNG INDIVIDUALS OF THE TROPICAL SPECIES *Symphonia globulifera* (CLUSIACEAE).

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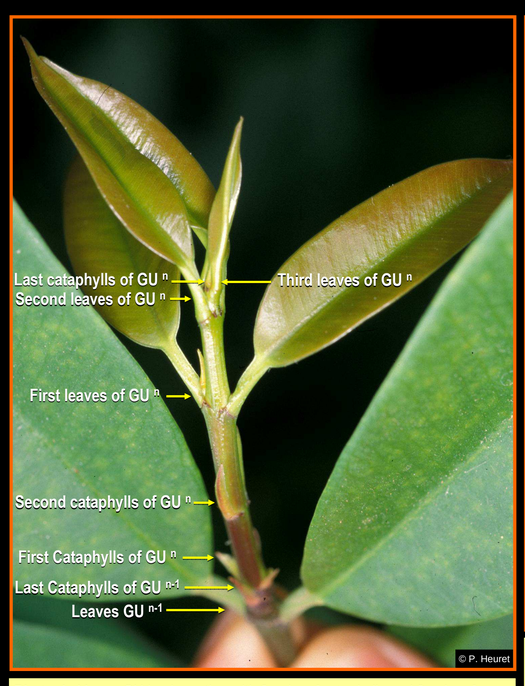

Photo 4 : Young GU in elongation with 3 pairs of cataphylls and 3 pairs of leaves : C-C-L-L-L-C.

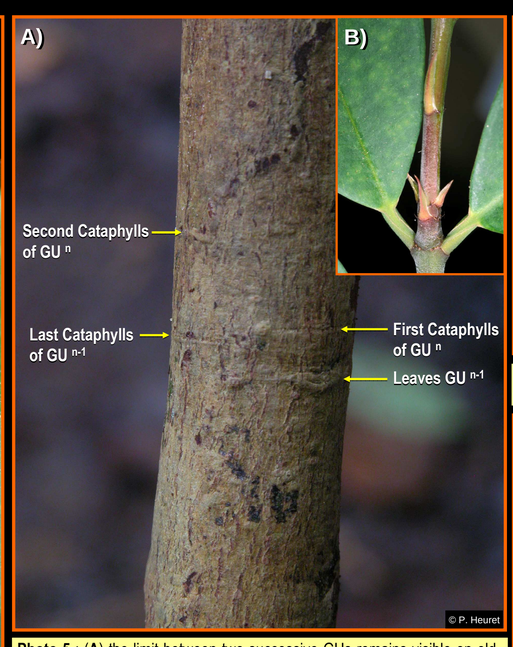

Photo 5 : (**A**) the limit between two successive GUs remains visible on old axis. We have been able to retrieve more than 70 GUs on the trunk of 3.50 m tall tree with an incertitude of 20 cm at the base. (**B**) Detail of the corresponding morphology when the axis was younger.

Photo 1 : Experimental nursery in 2003. A young *Symphonia* is indicated with a white arrow.

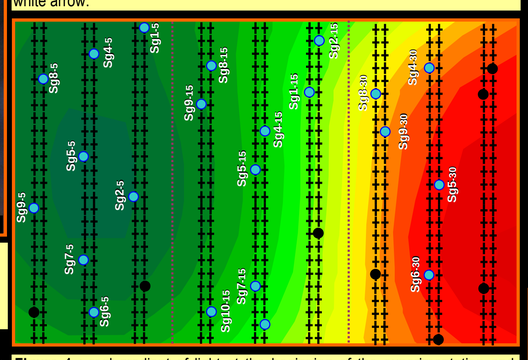

Figure 1 : real gradient of light at the beginning of the experimentation and localization of the whole plants of different species (black crucifix) and the position of the *Symphonia globulifera* studied (blue points, black ones correspond to the individuals who died during the experimentation).

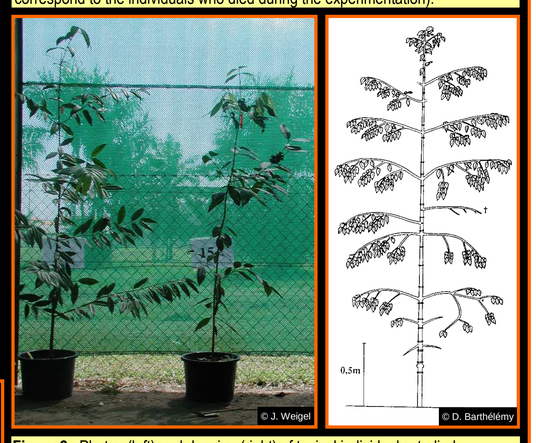

Figure 2 : Photos (left) and drawing (right) of typical individuals studied.

INTRODUCTION

In uneven-aged tropical rainforests, mechanisms of recruitment, *i.e.* the sustainable appearance of new individuals, rests on many mechanisms such as the phenology of flowering and dissemination, the survival of seedlings and their **waiting capacities in the understorey** **[1]**. To understand how long young trees can survive in the understorey before reaching the canopy and with which **morphological adaptations**, a precise study of their morphology and their architecture is capital. Objectives of such descriptive approaches are (i) to identify the **rules of plant construction**; (ii) to apprehend their **phenotypical plasticity** in light stress conditions and their waiting capacities; (iii) to determine morphological markers that can inform about the development potential of the considered individual; and finally (iv) to provide information on the plant environment and its life-history directly integrated in the perennial structure of the tree.

The aim of this work is to characterize the architectural variability in relation with light availability of young individuals of *Symphonia globulifera* L. f. (Clusiaceae), a species of South America and Africa tropical forests. To identify categories of growth units (GU) according their features (length, number of leaves and cataphylls) and understand their repartition in the whole architecture of the young trees we use **hidden-Markov tree models** (HMT, **[2, 3]**). A study of two-year-old individuals raised in a nursery allows us to make assumptions about the past growth and vigour of young trees issued from a natural French Guyana Forest.

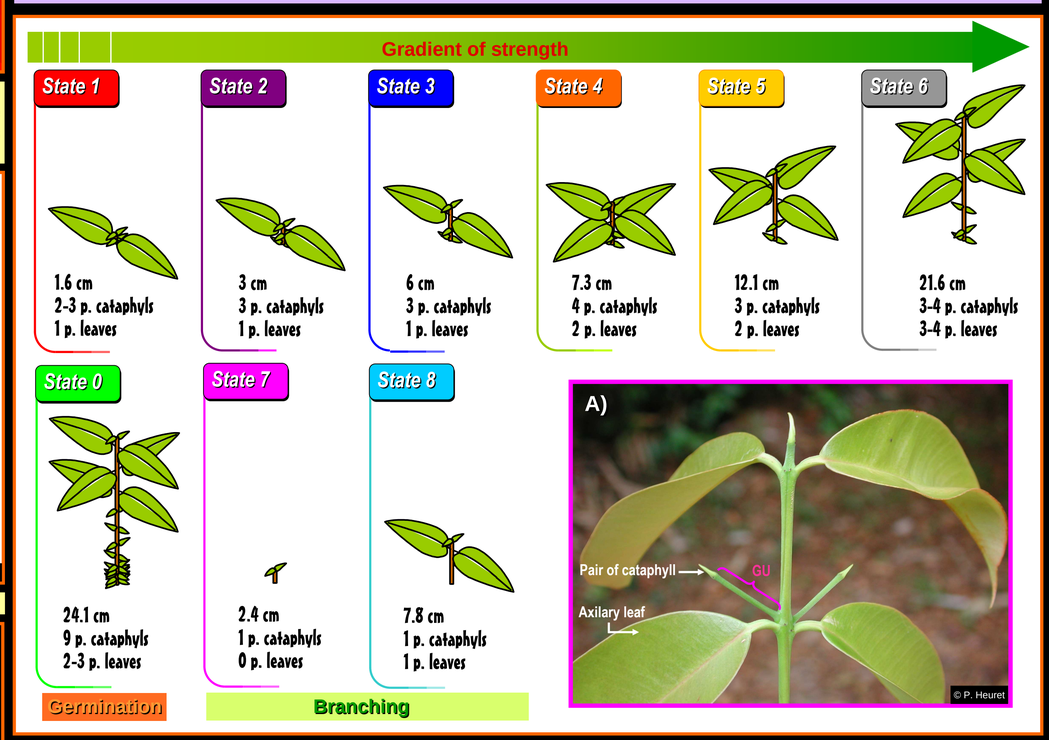

Figure 3: Representation of GUs in the different states identified by the HMT model. Mean of length, number of pairs of cataphylls and leaves are provided. (A) Example of GUs issued from immediate branching, comprising a unique pair of cataphyll and defined by state 7.

MATERIAL AND METHODS

A first set of data was measured in a greenhouse nursery in French Guyana in semi-controlled conditions. For three conditions of incident light (5, 10 and 20%), 10 individuals of 15 species have grown during 2 years (from January 2003 to June 2006) that is 30 individuals per species and 450 plants in total (**Photo 1**, **Fig. 1**).Our sample concern 22 *Symphonia globulifera* still alive in 03/03/06 (**Fig. 2**). A second data set concerns 25 individuals of natural French Guyana understorey (**Photo 2, 3**) growing up to 3.50 m without knowledge about the age or the past growth of the trees. For the entire trees, we have delimited each GU and measured their length, their number of cataphylls and their number of leaves (by direct observations or observation of their scares, **Photos 4, 5**). The structure of the trees was coded and categories of GUs were obtained using an HMT model **[2, 3]** included in the OpenAlea software **[4]**.

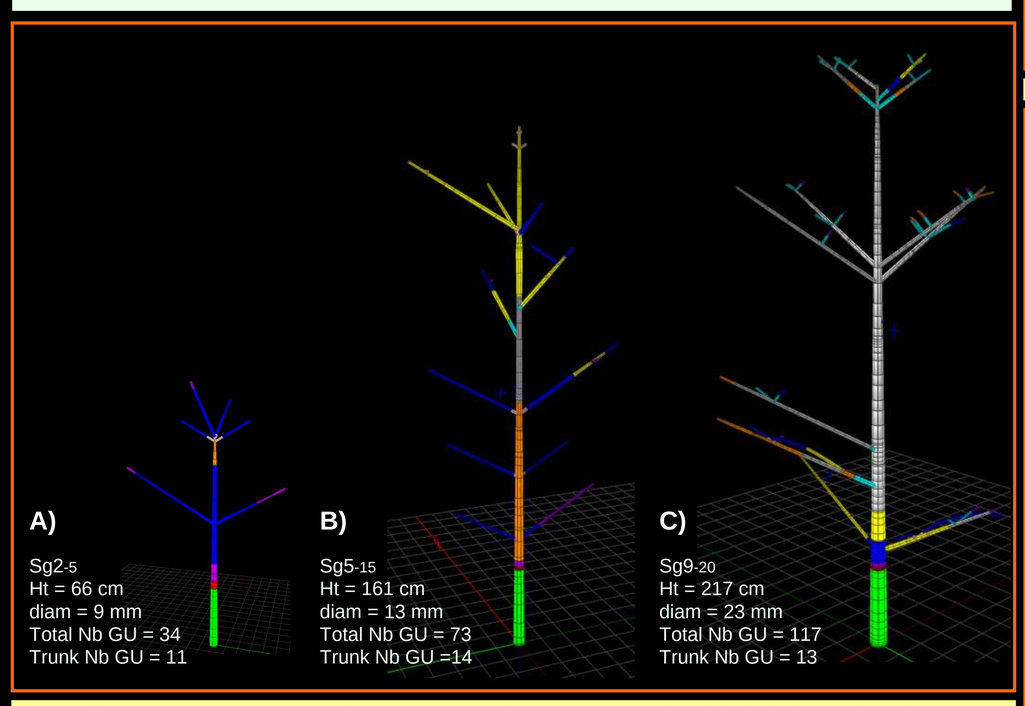

Figure 6: 3D representations of the architecture of three typical trees growing under (**A**) 5%, (**B**) 10% and (**C**) 20 % of incident light in the experimental nursery (see their localization on **Fig. 1**). The GUs in the different states are indicated by appropriated colors as defined in **Fig. 3**.

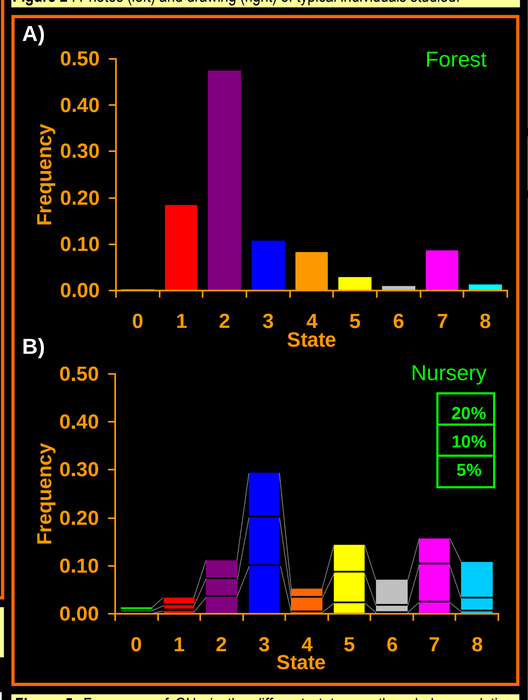

Figure 5: Frequency of GUs in the different states on the whole population measured in (**A**) the natural forest and (**B**) the nursery. In **B**, the three levels separated by a black line correspond to the expressed proportion in 5%, 10% and 20% of incidence light (respectively from the base to the top of the histogram).

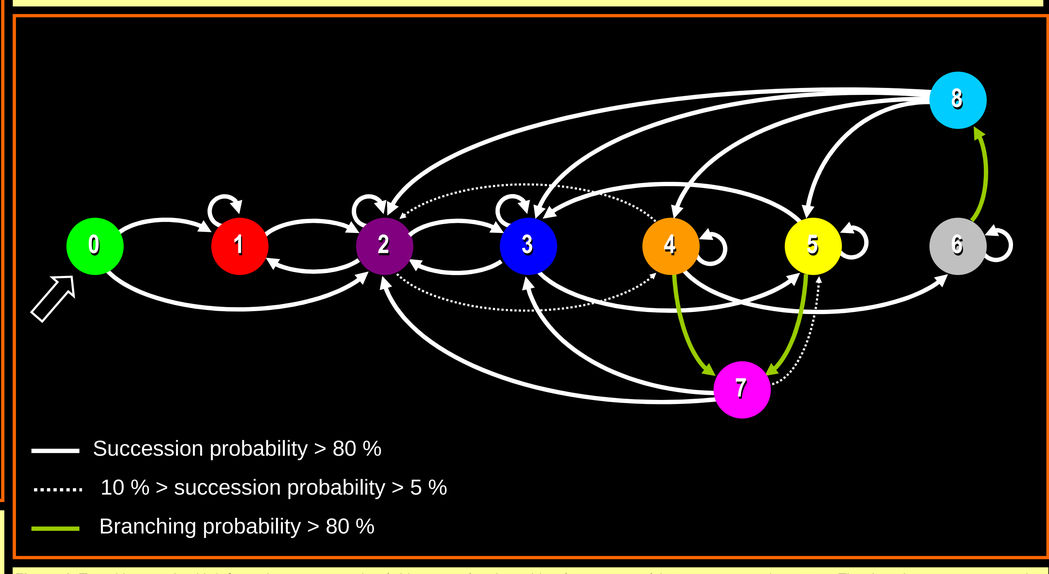

Figure 4: Transition graph with information on succession (white arrows) or branching (green arrows) between successive states. The dotted arrows correspond to transition probabilities. Only the transitions with probability > 0.05 are represented. Code for states is in **Fig 3**.

RESULTS

9 well-differentiated states were identified on the whole trees (from nursery and natural understorey). The HMT parameters and structure (**Fig 3, 4**) allows theses states to be interpreted as follows: GUs in state 0 are the longest with a high number of cataphylls. They are always issued from germination.

GUs in states 1 to 6 are respectively characterized by an increase of length and number of leaves (**Fig. 3**). They can be interpreted as levels of vigour. GUs in state 7 are leafless and are defined by a small number of cataphylls. GUs in state 8 are also defined by a small number of cataphylls but bear one pair of leaves. GUs in state 7 and 8 are mostly issued from immediate branching. States 0, 1, 2 cannot be branched and branching is very rare in state 3. State 4 and 5 can bear immediate branching constituted by a first GU in state 7. Only GU in state 6 can bear immediate branching with a first GU in state 8. For the trees raised in the nursery, the global size, the frequency and the succession of GUs in the different states can be related to the different light treatments. In restricted light conditions, trees desynchronize and develop more GUs on the branches than on the trunk, thus forming a plate (**Fig. 6A**). Those trees are mainly constituted by GUs in states 0, 1, 2 and 3 (**Figs. 5B**, **6A**). The architecture of individuals growing under 15 % of incident light is mainly composed of GUs in states 3, 4 and 5 (**Fig. 5B**, **6B**) while individuals growing under 20 % of incident light develops GUs with a high proportion in state 6 and are indeed highly branched. The trees of the forest sample are mainly composed by GUs in states 2 and 1 and are often desynchronized between the trunk and the branches (**Fig. 5A**, **Photo 3**). However a high inter-individual variability is observed in the relation between the height of the trunk and the number as well as the state of the GUs that composed the trunk. An example is given in the **Fig. 7** for two trees with a similar height (3.51 and 3.20 m). The trunk of the first one is composed by 33 GUs which are mainly in states 4, 5 and 6. The trunk of the second one is composed by 66 GUs which are, for the 40 first GUs, in states 1 and 2 and after, mainly in state 4. On the whole observed population, this individual has emitted the longest GU with a length of 45.5 cm associated to 12 pairs of leaves (62th GU classified in state 6).

Photo 2 : Understorey where the *S. globulifera* population was studied.

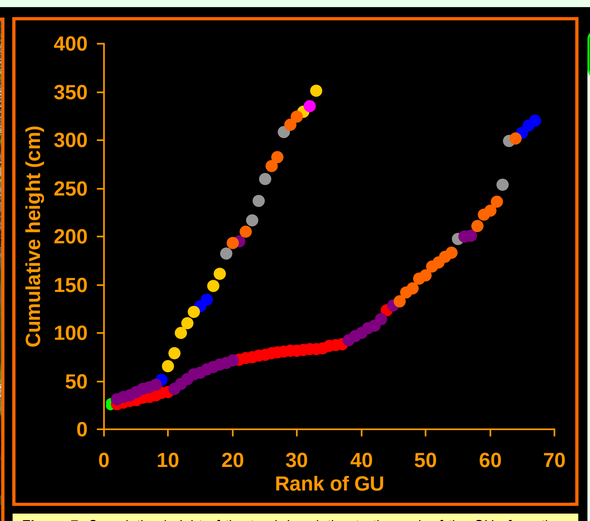

Figure 7: Cumulative height of the trunk in relation to the rank of the GUs from the base to the top for two trees issued from the natural forest. The GUs in the different states are indicated by appropriated colors as defined in Fig. 3.

DISCUSSION - CONCLUSION

Trees growing under low light conditions do not differentiate, from the germination, GUs in a state higher than state 3. They are indeed small and poorly branched. However, trees from nursery in the 5% of incidence light treatment are mainly constituted of GU with a higher degree of vigour than trees in the forest understorey. As light measurements were not performed in forest, it is well-known that 5% of incidence light is a very high level in natural understorey; 1 % seems to be more usual. An important question concerns the relation between the time separating the growth of two successive GUs and their associated state. In the nursery, first results shows that GUs in state 1 and 2 are emitted with a lower frequency than GUs in state 3 to 6. Considering this information, the two trees presented in **Fig. 7** must have very different histories and ages despite similar global dimensions. It presumes that this specie has very high waiting capacities in understorey. This result is consistent with other studies on lifespan of leaves, study of their morphological and chemical characteristics as well as their photosynthetic capacities **[5]**.

Photo 3 : example of one young tree in the understorey. This individual is growing in very limitative light resources and is desynchronized; the last GU on the trunk bear branches with 4 GUs forming thus a plate.

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