Vertical structure of trees in the Tai forest (Ivory Coast) : a morphological and structural approach

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PATRICK S. BOURGERON
&
JEAN-LOUIS GUILLAUMET

RÉSUMÉ

BOURGERON, P. S. & J.-L. GUILLAUMET (1982). Structure verticale des arbres dans la forêt de Tai (Côte-d'Ivoire): une approche morphologique et structurale. *Candollea* 37: 565-577. En anglais, résumé français.

La description des forêts tropicales est difficile parce que les méthodes utilisées sont intrinsèquement liées au concept de stratification. L'identification ou le rejet d'un modèle de distribution verticale est une conséquence de l'acceptation, ou du rejet, de l'une des trois définitions du concept de stratification. Le but de cet article est de proposer une méthode descriptive de la structure verticale des arbres de la forêt tropicale, qui est rapide, ne porte aucun jugement à priori sur cette distribution, et qui présente plusieurs avantages par rapport aux méthodes actuelles de description des arbres. Nous présentons et discutons les résultats d'une étude de vingt quadrats, échantillonés dans la forêt de Tai (Côte-d'Ivoire).

ABSTRACT

BOURGERON, P. S. & J.-L. GUILLAUMET (1982). Vertical structure of trees in the Tai forest (Ivory Coast): a morphological and structural approach. *Candollea* 37: 565-577. In English, French abstract.

Description of vertical structure in tropical forests is made difficult because there is an intrinsic link between the descriptive methods and the concept of stratification. Recognition or rejection of a pattern of vertical distribution is a tautological consequence of the acceptance or the rejection of this concept, in any of its three definitions. This paper is aimed at providing a fast method of description of vertical distribution of trees in tropical forests, which do not

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convey any a priori assumption about stratification, in any of its definitions, and has several advantages upon the existing methods of description of individual trees. We present and discuss the results from the study of twenty stands in the Tai forest (Ivory Coast).

Introduction

Vertical structure of plants has been, and still is a central concept of plant ecology. Vertical structure in forests has been sought to be divisible into generalized strata, as expressed by three definitions describing three different phenomena: stratification of leaf mass, stratification of individuals, and stratification of species (see review and bibliography in SMITH, 1973). Authors are divided between those who do not see any evidence of regular patterns of vertical distribution, regardless of the definition (e.g. CAIN & CASTRO, 1959; SCHULZ, 1960; GRUBB & al., 1963; PAIJMANS, 1969; HOLDRIDGE & al., 1971; GORDON & al., 1974), and those who describe those patterns (e.g. DAVIS & RICHARDS, 1933, 1934; RICHARDS, 1952; WEBB, 1959; ODUM & al., 1970; OLDEMAN, 1974a, b; HALLE & al., 1978). However, there is no consensus among the latter authors on the definition of the phenomena described. Furthermore, data needed to falsify relevant hypotheses on vertical distribution of vegetation require an extensive knowledge of the floristics, and/or extensive sampling.

Descriptive methods of vertical distribution of trees in tropical forests are intrinsically linked to the acceptance or the rejection of the concept of stratification, in any of its definitions. This state of affairs is confusing for researchers in tropical forests, whose work needs a fast description of the vegetation, but who (1) are not necessarily familiar with the floristics, and (2) do not know, or are not interested in, the controversy about vertical distribution. This paper is aimed at providing these workers with a tool, which (1) does not require any knowledge of the floristics, and (2) does not make any a priori assumptions about the vertical distribution of the vegetation. This work is a logical extension of the paper of GUILLAUMET & KAHN (1979), in which these authors proposed a non-interpretative, morphological, and structural method of description of the vegetation, based on the concepts of plant architecture (HALLE & OLDEMAN, 1970; OLDEMAN, 1974a, b; HALLE & al., 1978). We describe herein how we recognized a pattern of vertical distribution of trees in the Tai forest (Ivory Coast), by using Guillaumet & Kahn's method. We briefly discuss our results in the light of a detailed bioclimatic study.

1. Methods

1.1. Localization of the study area

The study area is located in the southwestern Ivory Coast, several kilometers from the city of Tai, outside the national park, which covers a part of the forest. The region has been studied qualitatively in its whole (GUILLAUMET, 1967; GUILLAUMET & ADJANOHOUN, 1971), and quantitatively in the Tai area (HUTTEL, 1977; BOURGERON, unpublished). The study area is hilly (20-40 m), and, while all around the park industrial exploitation of tall trees progresses rapidly, human pressure within it is negligible.

1.2. Description and sampling

Twenty rectangular stands of 20 × 50 m, located along five toposequences, from top hill to slope bottom, have been studied. Since we were interested in the structure of the closed forest, large gaps (constituting the building phases of the forest) have been avoided. Guillaumet & Kahn's method has been used to describe the vegetation. Following this method, the different elements of architecture (Fig. 1), their nature, structure and organization are described independently. Difference is made between assimilating and conducting systems, that is between the foliage on the one hand, and the free trunk (i.e. the part of the trunk between the main branches and the roots), main branches, and possible buttresses or stilt roots on the other hand. Distinction is made between the foliage of the trees of the present (i.e. trees still able to grow up). Foliage and trunks of lianas are described with different terms. Then, the forest is seen as a vertical succession of levels (GUILLAUMET & KAHN, 1979), each one being a lateral spatial continuum formed by the different architectural elements. Each level is differenciated from the upper and lower ones by the strong internal homogeneity of the constitutive elements. For a complete presentation of the method, of the vocabulary, and for some examples, we refer the reader to Guillaumet & Kahn's paper. On each of the study stands, description has been made above 2.5 m, and we recorded the maturity (i.e. future or present) and the height of all trees > 2.5 m.

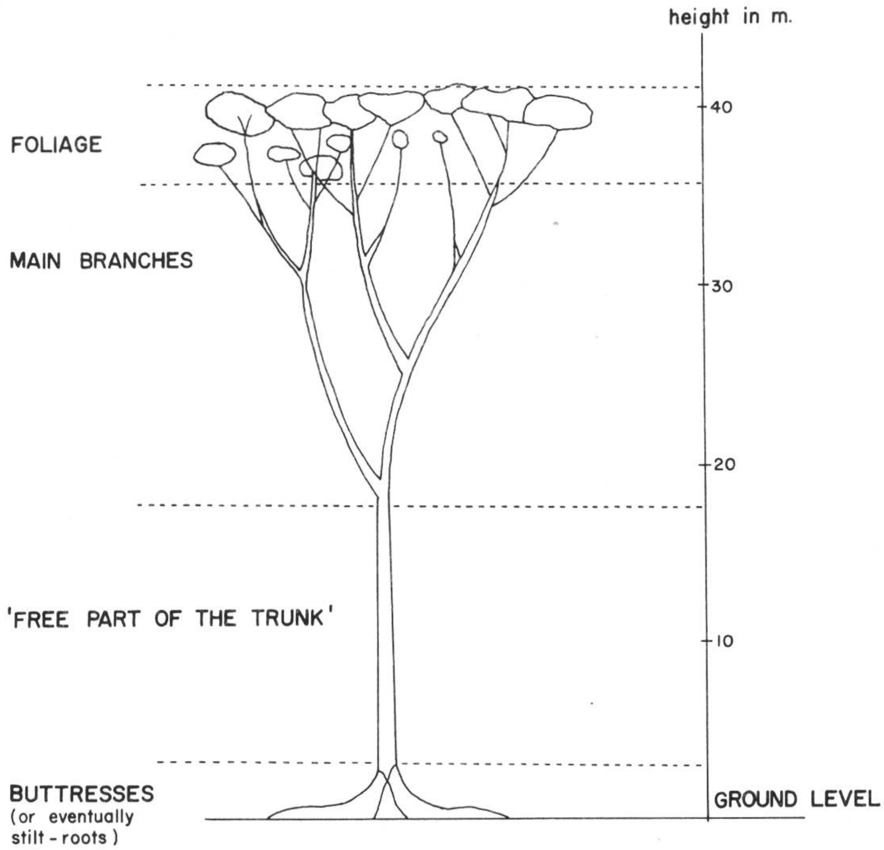

Fig. 1. – Architectural elements of a tree of the present (see text).

2. Results

2.1. Recognition of a pattern of vertical distribution of trees from the initial descriptions

Table 1 shows one of the twenty descriptions. The vertical succession of levels is fully exhibited. It should be emphasized two of the main advantages of this method over the profiles:

1. volumes in the distribution of the architectural elements are described (see Guillaumet & Kahn, and example below);
2. all elements of the vegetation are taken in consideration, while for purpose of clarity drawings do not, especially at the lower levels of the understory (profiles start very often above 10 m).

This method captures well the structural framework in which trees evolve. Let us examine in details the level 7.5/12 m of Table 1 as an example. The free part of the trunk ("stylage") is the main component. Then this level is characterized by the foliage of both the trees of the present ("palyphise") and of the future ("prophyse"). The ratio space occupied by the architectural elements / empty space is always high, from the total occupation of the space by the elements, to a total apportionement between elements and air ("stomaphique"). At this level, the general aspect is one of vertical structure ("erecloide"), due to the

28m/40 m Paliphyse, with phasis dendrigée with stigme ophiagé	stomaphique
24m/28m Pali-Dendrigé, with phasis stylagée with stigmes (ophiagé, pléiophysé)	stomaphique érécloïde
16m/24m Pali-Stylagé, prophysé, with phasis dendrigée with stigmes (ophiagé, pléiophysé)	stoma-isophique érécloïde
12m/16m Pro-Pali-Stylagé, with phases (ophiagée, pléio-physée) with stigme zoolithique	stoma-cléistophique érécloïde paliphyse with stigme nésoïde
7.5m/12m Pro-Pali-Stylagé, with phases (ophiagée, dendri-gée, pléiophysée)	stoma-iso-cléistophique érécloïde ophiagé:nésoïde paliphyse:améronésoïde prophyse isocléistophique
5m/7.5m Styla-Pro-Paliphyse, with phases (ophiagée, plé-iophysée) with stigmes (dendrigé, hypsonécrophytique) with stigme nécrumitique	stoma-cléistophique améronésoïde hori-érécloïde ophiagé: nésoïde
3m/5m Pali-Styla-Prophyse, with phases (ophiagée, plé-iophysée) with stigmes (nécrophytique (wood), hypsoné-crophytique, dendrigé)	cléistophique améronésoïde érécloïde with phasis laticloïde

Table 1. – Description of stand 7.

importance of free trunks, of foliage of trees of the future, and of trunks of lianas ("ophiage"). Foliage of trees of the future is always preponderant ("isophique" or "cleistophique"). Trunks of lianas form small blocks ("nesoide"), as does also, but without internal organization, the foliage of the trees of the present. Now, for the purpose of another study, we were interested in identifying, if possible, different sets of individuals sharing the same sets of constraints, as exerted by the trunks, the branches, or any other element of other trees, as well as by the presence or absence of lianas. The description of each recognized level allows to replace the trees having their crown at a specific level (this information being provided by the list of individuals which complement the description) in their "physical" environment, because each element is weighted within each level. During this analysis, it has been necessary both to regroup trees belonging to different levels, and to separate trees of the same level. For instance, levels 3/5 m, 5/7.5 m, 7.5/12 m, and 12/16 m correspond after this analysis to three sets of individuals located respectively between 3/5.5 m, 5.5/13 m, and 13/18 m. Let us detail the process for level 12/16 m. Trees between 12 and 13 m of this level (Table 2) have been regrouped with the trees of the level 7.5/12 m, because it appeared by reading the description that they share the same constrainst (as defined above) than the trees of level 7.5/12 m. Furthermore, the other trees of level 12/16 m were all higher than 15 m. We think that our regrouping is reasonable because as stated above, each element is weighted in the initial description (see GUILLAUMET & KAHN, 1979). It is clear that the recognition of sets 1, 2, and 3 would not have been easy, if not possible at all, because the general aspect of the understory at this level is one of dense vegetation without any clear pattern emerging readily. There is no discrepancy between such a rearrangement and the initial description, because the latter considers only sets of architectural elements, without any reference to the individuals, while we distinguished afterwards sets of individuals. Recognition of such a pattern of vertical distribution is a direct consequence of analyzing the description and the list of trees for each study stand. Same basic distribution has been recognized on each of the study stands (Table 3).

2.2. Ecological meaning

In order to know if the recognized sets of individuals in Tai forest were related in some way to one or more ecological factor(s), we used the results of a very detailed bioclimatic study of the Banco forest (CACHAN, 1963; CACHAN & DUVAL, 1963), located near Abidjan, some 200 miles east of the study area. CACHAN (1963) provided a profile of the study stand in Banco. By complementing it with the

Species	*State*	*Height*
Aidia genipaeflora	pr.	12
Berlinia grandiflora	fut.	10,5
Breya fasciculata	fut.	12
Calpocalyx brevibracteatus	fut.	10,5
	fut.	10
Corynanthe pachyceras	fut.	9,5
	fut.	10
	fut.	12
	fut.	8
Diospyros mannii	fut.	10
	fut.	8,5
	fut.	8,5
	pr.	10
	pr.	10
	pr.	9
	pr.	9
	fut.	8
	fut.	11
	fut.	8
	fut.	9,5
Diospyros soubreana	pr.	8
	pr.	11,5
	fut.	10
Drypetes principum	fut.	8
Enantia polycarpa	fut.	12
	fut.	10
Maesobotrya barteri	pr.	8
	pr.	8
	pr.	11
Mareya spicata	fut.	11
Memecylon golaense	fut.	8
Memecylon guineense	pr.	8
	pr.	9
Polyalthia oliveri	pr.	11
	pr.	10
	fut.	9
Sacoglottis gabonensis	fut.	11
Scotelia chevalieri	fut.	8
Strombosia glaucescens	fut.	8
	fut.	10
Xylopia parviflora	pr.	12
	fut.	11
	fut.	8
Xylopia quintasii	fut.	9
Xylopia standtii	fut.	9

Table 2A. – List of individuals having the top of their crown in layer 7.5-12 m of stand 7. *pr.* = trees of the present; *fut.* = trees of the future.

Species	*State*	*Height*
Corynanthe pachyceras	fut.	15
	fut.	16
Diospyros mannii	pr.	15
	pr.	15,5
	pr.	13
Diospyros sanzaminika	fut.	16
	fut.	12,5
Enantia polycarpa	fut.	14,5
Mareya spicata	pr.	14,5
Polyalthia oliveri	pr.	12
Xylopia parviflora	pr.	13
	pr.	12,5
Xylopia standtii	fut.	15
	fut.	16
	fut.	15

Table 2B. – List of individuals having the top of their crown in layer 12-16 m of stand 7. Same legend as Table 2A.

Stand	Stratum				
	1	2	3	4	5
1	3,5/5	5/12	12/18	18/22	22
2	2,5/4,5	4,5/12	12/19	19/25	25
3	3/4,5	4,5/11	11/18	18/22	22
4	3/4,5	4,5/12	12/18	18/22	22
5	3/6	6/12	12/18	18/26	26
6	3/5,5	5,5/12	12/18	18/27	27
7	3/5,5	5,5/13	13/18	18/25	25
8	3/5	5/12	12/19	19/24	24
9	3/5	5/12	12/19	19/25	25
10	2,5/5	5/12	12/20	20/25	25
11	3/5	5/13	13/18	18/26	26
12	3/4,5	4,5/13	13/20	20/26	26
13	2,8/4,5	4,5/12	12/20	20/29	29
14	3/5,5	5,5/12	12/20	20/26	26
15	3/5	5/10,5	10,5/18	18/25	25
16	2,75/4,75	4,75/12	12/18	18/27	27
17	3/5	5/12	12/20	20/28	28
18	2,75/5	5/10	10/20	20/28	28
19	3/5	5/12	12/20	20/26	26
20	2,8/4,5	4,5/12	12/17	17/22	22

Table 3. – Heights of the strata on the twenty stands.
The heights indicated are the minimum and maximum heights, in meters.

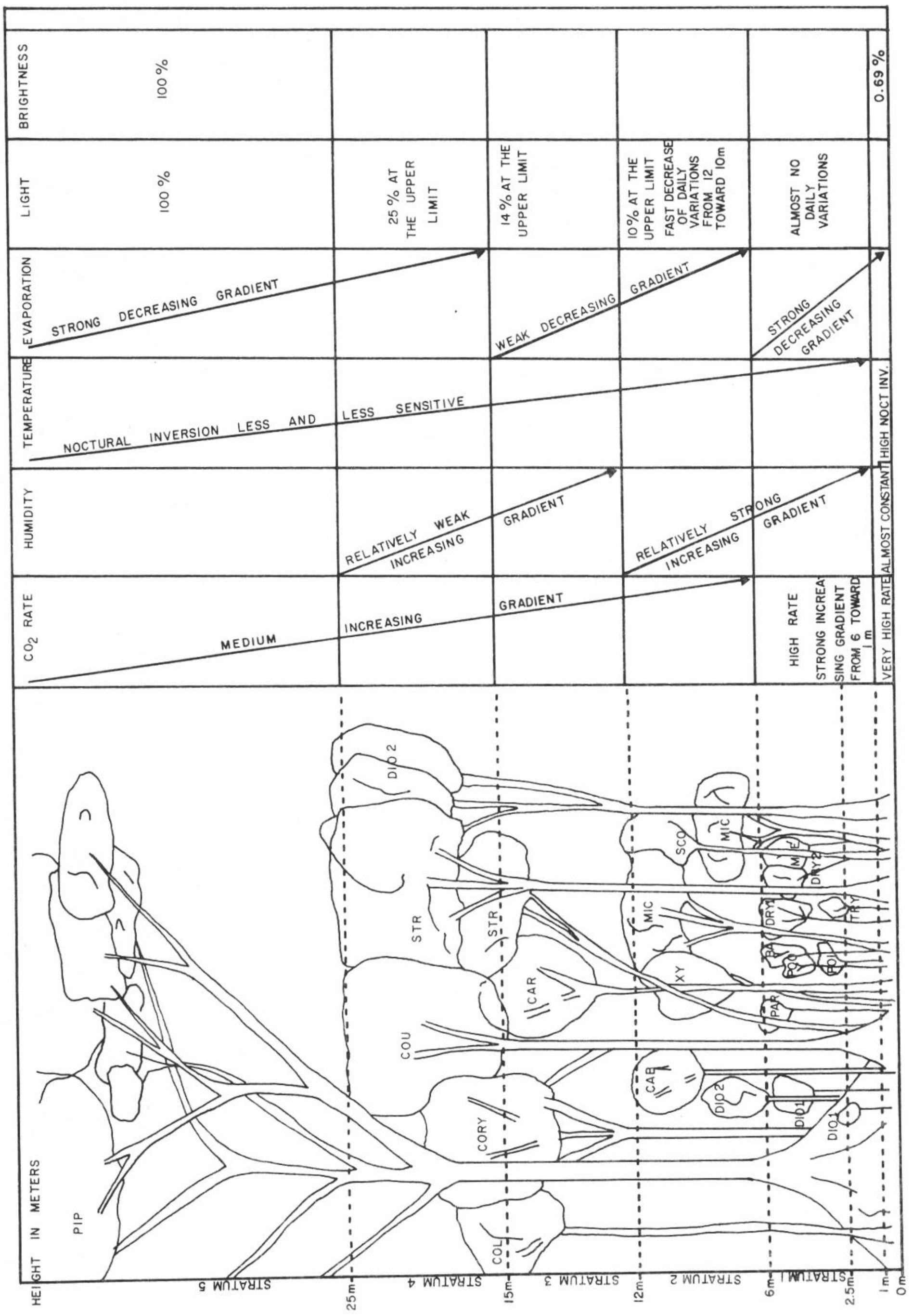

Fig. 2. – Recognized pattern of vertical distribution on one stand in Tai forest and correspondence with the variations of bioclimatic factors.

descriptions given in the text, we have been able to recognize a pattern of vertical distribution of trees similar to the pattern identified in Tai. Consequently, although differences in absolute values are expected, results dealing with daily and seasonal trends of the bioclimatic factors, as well as their relative importance, can be applied to Tai forest. In Figure 2, the table has been compiled from CACHAN (1963), and CACHAN & DUVAL (1963), while the profile is one of the twenty study stands. The table applies to any of these stands, because all exhibit the same basic pattern of vertical distribution (see above). Strata 1, 2, 4, and 5 correspond to the superposed "screen" of leaves described by CACHAN (1963), and stratum 3 to the empty space he described as only filled by trunks. Ecological meaning of the recognized pattern of vertical distribution emerged as follows (bioclimatic comments are excerpted from Cachan, and Cachan & Duval):

1. *Stratum 5:* trees are the emergents. Their height varies widely from 30 m to 55 m. There is not the continuity of foliage as at the lower level. These trees have the space they need to grow until their maximum expansion, except, of course, if they die before reaching it (e.g. fall by storms, etc.). They are under the conditions of open-field, with the particularity that they come under the influence of strong humidity from evaporation of the lower strata.

2. *Stratum 4:* it is the upper foliage continuum, discontinuous in respect to the occurence of gaps of different sizes, resulting from a wide variety of accidents. Competition for space is strong. It is at this level that most of the bioclimatic factors start varying very strongly. Trees are mainly trees of the present, with some trees of the future (potential emergents).

3. *Stratum 3:* it is the level which is relatively "empty". This indeed refers to the absence of leaves. This level has been described by other authors (e.g. RICHARDS, 1952; CACHAN, 1963; PAIJMANS, 1969; OLDEMAN, 1974a). The rare trees having their crown at this level are mostly at the upper limit of this stratum, in what may be a transient state when they grow from stratum 2 to stratum 4. There is at this level a double phenomenom related to the penetration in the understory (CACHAN, 1963): (1) obstacles to the centripetal penetration of external conditions, and (2) influence of the ground on the milieu located above it.

4. *Stratum 2:* the density of foliage is high again. Main characteristics are that daily variations of light waves stop being perceptible, and that the humidity gradient is strong. Trees are a mixture of trees of the present (species of small size), and of the future.

5. *Stratum 1:* the set of trees, both of the present and of the future, is dense. Bioclimatic factors vary again strongly.

It appears clearly that each one of the recognized sets of individuals is under the influence of a different set of environmental factors. As we consider the whole set of factors as being determinant, and not a single factor, trees not only grow along non-monotonic gradients of factors, but must adaptively respond to the different sets of them, as they grow up.

Conclusion

This approach respects the complexity of the different phenomena involved in the vertical distribution of trees, because our recognition of a pattern of vertical distribution resulted from field work. Vegetation was not expected to follow a rigid framework of vertical distribution, a predetermined so-called pattern of stratification. Some aspects of forest dynamics were respected. Trees of the present go toward their death, according to species characteristics (OLDEMAN, 1974a and b, 1978). If there is no drastic changes, trees of the future may grow up, depending upon competition and changes in forest structure. So the recognized pattern of distribution may change with time accordingly to these minor structural changes. There are many such changes, from the ground to the canopy, which are likely to influence quantitatively the forest structure. For instance, the fall of leaves, or of branches, may allow for the opportunistic growth of some individuals of the future. In short, the vegetation of tropical forests act upon the environmental factors (as light, humidity, etc.) and modify them, because of its large biomass (e.g. RICKLEFS, 1977). As forest builds up, heterogeneities are more numerous, and more individuals, with different requirements, can become established. Vertical distribution can best be seen as a self-begeting process: the more heterogeneities are found, the more individuals can fit different portions of the habitat, and, in turn, these new individuals generate new heterogeneities, and so on.

We made no a priori assumptions about the recognition of a pattern, assumptions which, in turn, would have led to the tautological recognition or rejection of this pattern. The pattern recognized in Tai does not convey any statement about stratification as defined in the introduction. It might be possible that, in terms of any of the three definitions, there is another pattern, or no pattern at all. It provided us with a workable "picture" of the study stands, compatible with the needs of other studies. This work complements Guillaumet & Kahn's paper, as a second step in the description of forest structure, step consistent with the philosophy of these authors. As already stated, recognition of the different sets of individuals in the understory would have been very difficult, if we did not have had the method of Guillaumet & Kahn. The relationship of the recognized pattern with different sets of bioclimatic factors show that the different identified strata indeed correspond to very different environments for the individual trees. The set of bioclimatic factors and the interactions with other trees require a different adaptive response of the individual, depending upon the level where it is actually found. Finally, another feature of this approach is the time required to collect data (half a day maximum for each stand).

In conclusion, our approach provides a framework of the vegetation, whether interpretation of the ecological factors is sought or not. Fact that the pattern of vertical distribution in Tai corresponds to different sets of bioclimatic factors show that this method gives a reasonable account of these ecological interactions, without making any untested hypotheses. We believe that this approach can be used for a variety of purposes, when little time can be devoted to the analysis of the vertical distribution of the vegetation per se. It is not a substitute to testing hypotheses about stratification, because, if this is the purpose of the study, other data are clearly needed to answer the addressed questions.

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Addresses of the authors: P. S. B.: School of forest and conservation IFAS, University of Florida, 118 Newins-Ziegler Hall, Gainesville, Fla-32 611 U.S.A.

J.-L. G.: Botanist – ORSTOM, 24, rue Bayard, F-Paris 4.