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The Architectural Unit Setting up and Architectural Characteristics of Néré, *Parkia biglobosa*, Jack, R. Br. (Fabaceae)

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Abstract

Parkia biglobosa is a much-loved and over-exploited African savannah species for its socio-economic importance. Knowing and taking into account its architectural unit, which is the basis for diagnosing phenology, productivity and tree health, could provide a new perspective on its sustainable management. The aim of this study is to establish the architectural development in *Parkia biglobosa* by retrospective analysis. To achieve this objective, 390 individuals of all sizes ranging from seedlings to senescent trees were observed and analysed under various soil and climatic conditions in Côte d'Ivoire. The results showed that *Parkia biglobosa* is a light plant but shading tolerant. It is a mixed vegetative axis plant, the stem is orthotropic* in its proximal part and plagiotropic* (collapsing) in its distal part in young stage. The tree then transitions to an adult and old stage into a tree with a plagiotropic* axis in the proximal and distal parts, the trunk is built up by superimposing collapsed relay axes that gradually straighten, branching is sympodial*, growth is defined and sexuality is terminal and lateral. The ontogeny takes place in three phases: initiation of development and establishment of the crown (young), then flowering and establishment of the architectural unity (adult) and finally the death of secondary axes in the crown, duplication of the architecture by a series of partial and total reiterations (old). The level of organisation is 5: the

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* *In this document, terms marked with an asterisk (*) are defined in a glossary appended to the article after the references in order to alleviate difficulties of understanding. Indeed, the vocabulary used differs from that commonly used by foresters.*

phytomere, the module or growth unit, the axis, the architectural unit and the reiterated complex. Retrospective analysis of the modules showed that the dimensions of the growth units are indicators of morphological variation and species adaptation to a changing climate ($P < 0.05$). However, the equations generated by the morphological and habitat dimension linkage models are not significant (R^2 and $r < 0.7$) to be used as a guide for field data collection. This study represents an initiation into the architectural study of this species and the information provided will serve as a basis for further research into the architecture in relation to the sustainable use of this species.

Keywords

Parkia biglobosa, Architectural Development, Architectural Unit, Côte d'Ivoire

1. Introduction

The architectural* study of a plant is a morphological approach that makes it possible to characterise the organisation of trees or groups of trees growing in different pedoclimatic contexts [1] [2] [3] [4]. In spite of this pedoclimatic variability, it nevertheless allows us to highlight a specific average architectural organisation that constitutes the species' sketch or architectural unit*. This sketch is the architectural expression of the plant that allows it to be visually differentiated from another tree species without having studied it, and in the second instance constitutes the pillar of its sustainable management in case of threat [5] [6] [7]. Indeed, the architectural unit constitutes the smallest stem structure necessary and sufficient for the plant to reach its sexual maturity phase (complete reproduction) and thus complete its life cycle by forming flowers and fruits [8] [9]. The plant then continues its growth by altering this architectural unit through the phenomenon of duplication; a series of axes of different categories are then reproduced in the adult plant [10] [11] [12]. It is, therefore, necessary and important to bring out this architectural unit hidden in the tree, as it is the basis for future diagnostics by foresters or observers to assess the difficulties, phenology, health, productivity and reproducibility of species in various geographical situations under stress or climate change.

Plant architecture* can be achieved through retrospective analysis, which analyses the structure of the plant using various morphological markers that allow the formation and successive increases in length of the axes to be limited and dated. It depends on the spatial and temporal arrangement of the plant parts (branched hierarchical system), and is based on these morphological traits at the shoot and branch level (axes grouped into categories characterised by morphological criteria, exploration and/or reproduction role); then affected by endogenous (genetic) and exogenous (environmental) factors [10] [13]. The growth pattern through which the plant develops its form is the architectural model* of the plant or the basic growth strategy of a plant. The main architectural parameters generally studied are growth, branching, morphological differentiation of axes and the position of reproductive structures [5] [11].

This discipline has long been recognised as an important scientific tool in horticultural crops, understanding plant function, yield assessment and for the development of crop models [14] [15] [16]. It has been used extensively and successfully in Europe and South America for yield optimisation, forest management, preservation of important species, understanding the adaptation of species to climate, sustainable exploitation and safeguarding of threatened species [1] [2] [6] [7] [17]. However, it has never been applied or applied to emblematic West African species, yet this area is a strategic carbon sink encompassing many important overexploited and threatened species.

This is the case of *Parkia biglobosa*, an agroforestry species indigenous to the savannahs of Africa. This species is much loved by the rural populations of this geographical area for its socio-economic role [18] [19] [20]. As a result, it is one of the most overexploited species among many others, but also the best documented to date [19] [21]. However, its architectural study does not exist in the literature to our knowledge. However, the knowledge of its architectural development sequence, its architectural characteristics and its architectural unity are very important for its phenological diagnosis, the evaluation of its productivity and its preservation. Indeed, in the first step, the architecture of this species completes its biological knowledge and in the second step, it allows access to the structure-function-time-environment relationship and thus can give a new point of view on the sustainable management of this species. The objective of this study is to establish the architectural development in *Parkia biglobosa* via retrospective analysis of various individuals from different environmental conditions in Côte d'Ivoire.

2. Material and Methods

2.1. Trees Studied

390 freely growing individuals in open and forest environments were arbitrarily selected and observed. These individuals of different ages (young, adult and old) were derived from wild individuals of natural regeneration (forest) and artificial regeneration (1- and 2-year-old individuals planted and monitored in a nursery) benefiting from a canopy of variable size. The number of individuals as well as the dendrometric characteristics per age category and environment, and the location of the growth units or modules studied are recorded in **Table 1**.

2.2. Study Sites

The study was carried out in seven locations along a bioecological gradient in Côte d'Ivoire (**Figure 1**). The soil and climate characteristics of the surveyed locations are shown in **Table 2**.

2.3. Observation Methods

2.3.1. Sampling of Individuals

For each stage of tree development (young, adult and old), 10 wild individuals

Table 1. Dendrometric characteristics and number of individuals used according to age and environment.

	Ages	Environments	Tree height (m)			Tree diameter (cm)			Indiv Nber	GU examined
			Min	Max	Mean	Min	Max	Mean		
Parkia biglobosa	Young trees	Opened	0.53	5.5	1.95 ± 0.11 **c**	0.56	18.96	4.35 ± 0.24 **c**	60	Main stem
		Closed	0.42	5.8	2.56 ± 0.05 **c**	1.26	17.83	7.06 ± 1.22 **c**	60	Main stem
		Nursery	0.44	1.7	0.52 ± 0.11 **c**	2.1	5.1	3.71 ± 0.21 **c**	30	Main stem
	Adult trees	Opened	7.5	11	9.68 ± 1.14 **b**	20.06	49.68	38.19 ± 3.02 **b**	60	Branches and axes
		Closed	8	13.7	12.02 ± 1.01 **b**	22.4	48.8	36.27 ± 1.53 **b**	60	Branches and axes
	Old trees	Opened	18	31.7	25.22 ± 3.21 **a**	61.3	178.44	85.51 ± 6.12 **a**	60	Branches and axes
		Closed	20.5	29.5	25.3 ± 3.32 **a**	60.1	115.61	76.98 ± 7.36 **a**	60	Branches and axes
		P			**0.0001**			**0.0001**		

Young trees = 1 to 5 years old, H (m) = 0.1 to 6 m and D or DBH (cm) = 1 to 19 cm; **Adult trees =** 6 to 20 years old, H (m) = 7 to 14 m and D or DBH (cm) = 20 to 50 cm; **Old trees** = ≥21 years old, H (m) = ≥15 m and D or DBH (cm) = ≥60 cm; **H** = height, **D ou DBH** = Tree diameter, **Min** = minimum, **Max** = Maximum, **Indiv Nber** = number of individuals observed, **GU** = growth units or modules.

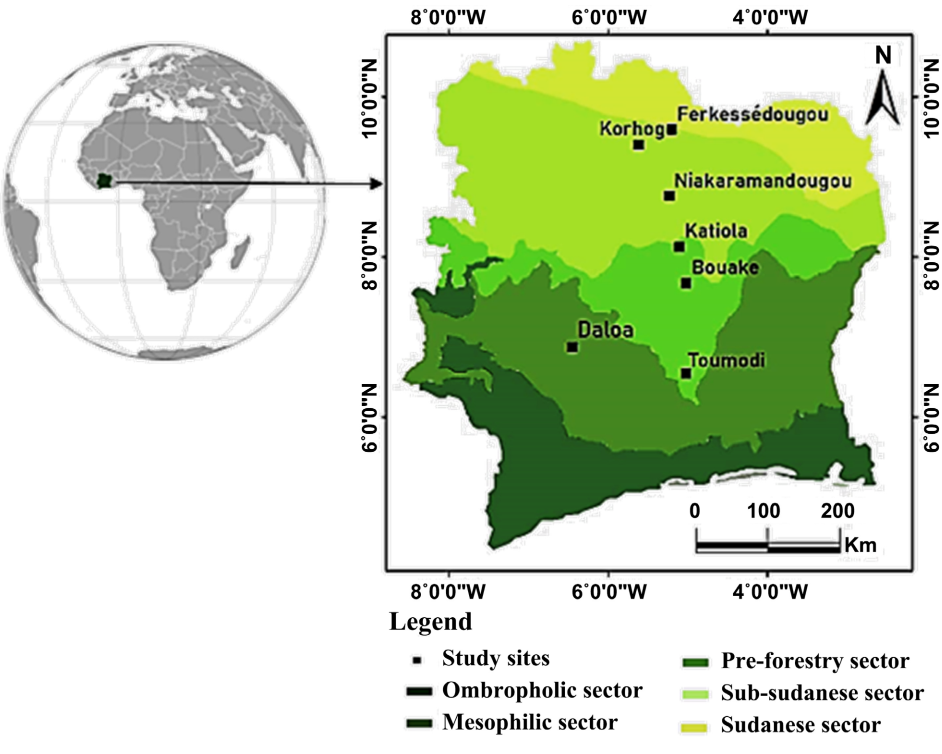


Figure 1. Geographical location of the study area.

were arbitrarily and randomly selected in open and closed areas in six localities mentioned above (Ferké, Korhogo, Niakara, Katiola, Bouaké and Toumodi). 15 individuals aged 1 year and 15 individuals aged 2 years resulting from the germination of seeds raised and monitored in the nursery were also selected in a locality outside the natural propagation area of origin of the species (Daloa): 15 trees + 15 trees = 30 trees. We therefore have: 390 trees (10 individuals × 2 areas

Table 2. Characteristics of surveyed localities [22].

Sites/ locations	GPS coordinates	Vegetation	Climate	Temperature (˚C)	Rainfall (mm/year)	Soil type
Ferké	5˚23'43.39644"W; 9˚36'1.87056"N	Grassy and little wooded savannah	Dry tropical	27 - 40	263 - 1200	Ferralitics soil (Ferrisols, Cambisols, Fluvisols, Luvisols), highly to moderately desaturated.
Korhogo	5˚36'12.39612"W; 9˚33'24.68988"N	Open forest (wooded savannah)	Dry tropical	26.6 - 35.7	817 - 1216	Ferruginous (90%) and Ferralitic (10%): superficial gravelly soil, deep gravel with a heavy texture, low in organic matter, highly desaturated.
Niakara	5˚18'40.73544"W; 8˚40'47.97912"N	Wooded and grassy savannah	Dry tropical	24.7 - 38	800 - 1230	Complex of slightly desaturated ferrallitic soils and eutrophic brown tropical soils derived from basic rocks.
Katiola	5˚7'35.814"W; 8˚13'53.94"N	Wooded and grassy savannah	Dry tropical	24 - 36	1100 - 1200	Moderately and highly desaturated ferrallitic soils.
Bouaké	5˚5'47.3289"W; 7˚40'45.335"N	Clear forest (wooded savannah)	Wet tropical	23.6 - 34	1100 - 1200	Gravelly, moderately saturated, reworked, shallow ferralitic gravel from a granitic alteration material with a sandy-clay texture.
Toumodi	5˚1'34.95576"W; 6˚22'42.67848"N	Open forest (wooded savannah, grassland and gallery forests)	Wet tropical	26.6 - 30	1092 - 1200	Ferralitic soil on granitic bedrock (sandy-clayey soil), characterised by the weak differentiation and friable consistency of their horizons.
Daloa	6˚26'9.19788"W; 6˚54'32.058"N	Tropical rainforest	Wet tropical	21 - 34	1000 - 1900	Ferralitic, deep, acidic and desaturated in exchangeable bases, rich in organic matter.

˚C = Celsius degree, mm = millimeter, W = west, N = North.

(open or closed) × 6 localities × 3 stages + 30 in the nursery). All trees were in good physiological condition (free of trauma). The samples were classified according to the level of analysis. They were characterised by growth site, age of individuals, number of individuals or axes observed, type of axes measured in the tree. The stages (young, adult and old) were arbitrarily chosen on the basis of their dendrometric size (height and diameter) according to individuals raised in nurseries and those present in plots set up in the 1970s and 1980s by the Côte d'Ivoire National Agricultural Research Centre (CNRA).

2.3.2. Retrospective Analysis: Choice of Axis Type and Habitat

Observations were made on different types of axes depending on the accessibility of the crowns in two different habitats. For young trees, the axes assessed were the main trunks because of the easy access and the non-frequency of secondary branches on all individuals in this category. For mature and old trees, the axes assessed were only tertiary branches and short twigs due to accessibility. Assessments were carried out in situ for young trees; whereas, for mature and old trees, branches were cut and transported to the laboratory for observations (Figure 2). Two types of environments were considered: undergrowth and full sun. The former refers to individuals living in a very shaded environment with a forest canopy or in an overcrowded environment with superior shelter. The latter refers to individuals isolated in full sun or in an open environment in direct contact with sunlight.

2.3.3. Architectural Analysis Method

Based on morphological concepts and criteria [10] [23] [24], architectural analysis [8] [17] consists of a global representation of the aerial branching system of individuals of various âge and growing in various environments. This global representation is accompanied by a precise morphological description of some parts of the aerial branching system. This analysis makes it possible to identify the different categories of axes (trunk, branches, twigs, etc.) and to characterise them by a set of criteria (ability to branch, growth direction, flowering, etc.).

In order to identify these different characteristics of growth and branching modes, we started with a complete description of the aerial system of each individual, integrating the spatial arrangement and structure of the different axes constituting it by means of drawings and diagrams. We used the usual morphological markers of the functioning of the primary meristems, printed in the bark

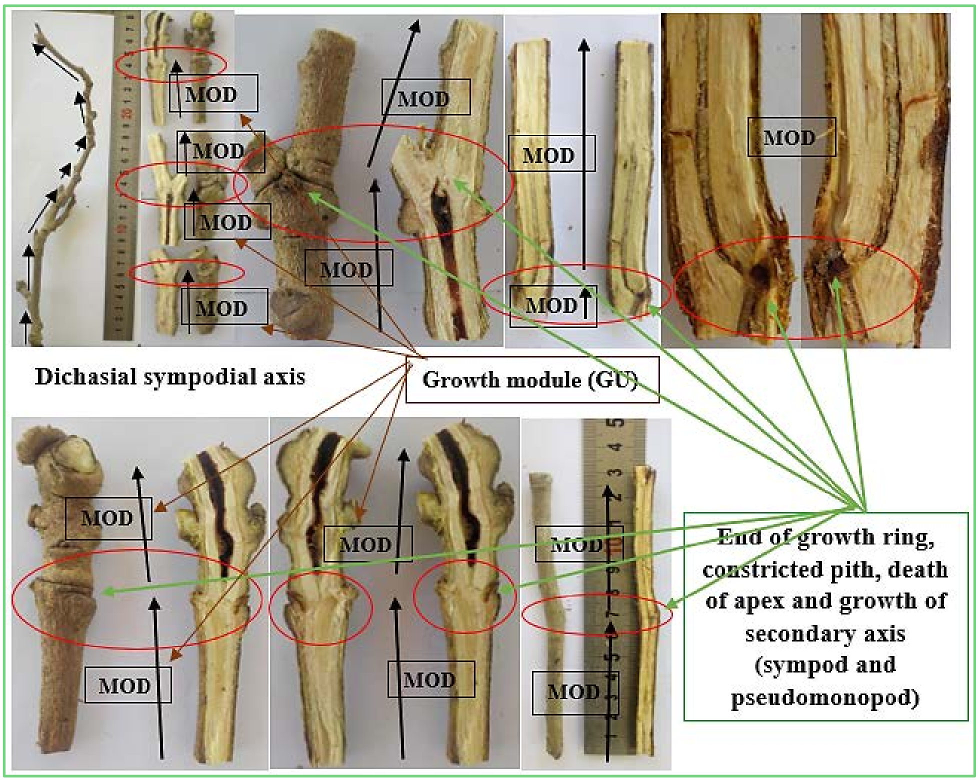


Figure 2. Images of fine morphological observations with retrospective analysis of growth units or modules in *Parkia biglobosa*. The labels or areas circled in red are the growth stops or trauma to meristem function and the limits of the growth modules (GU); the black labels named MOD are the lengths of the growth units or modules.

and anatomy of the different axes (**Figure 2**). We studied several individuals at various stages of development and in various environmental conditions, considering the organism at different scales from the level of organisation of the organ (node, internode and leaf) to that of the whole plant. We described the fundamental morphological and architectural characteristics of each of the standing plants with the naked eye and with binoculars for the larger ones by observation and drawings. The juxtaposition/comparison of these drawings/diagrams allowed us to characterise the architecture of the species and to reconstruct its development. More detailed morphological observations could be made by removing particular parts of trees after felling (**Figure 2**). First, we described younger individuals (seedling stage) up to older or taller, more complex individuals (structure with one or more branching order). The level of complexity was assessed by the maximum branching order of the aerial system. In the field, the individuals observed per stage depended on the structural variability expressed and the ability to generalise and synthesise the average architecture of the stage concerned. For the youngest and smallest individual we considered the whole plant and for larger individuals, we observed and drew the whole plant in situ and took parts of the plant for detailed observations in situ and in the laboratory. Notes specifying the scale, location of the plant and certain facts or events were marked on each drawing. The results were presented in the form of drawings characterising representative individuals at each stage of development, a set of diagrams revealing the developmental sequence of the species etc. Each diagram is a synthesis of the observations made and the results of the study. Each diagram is a synthesis of observations made on several individuals that have reached the same stage of development.

2.3.4. Parameters Assessed

To qualify (architectural analysis) and quantify (retrospective analysis) the axes in the architectural approach and to facilitate the drawings and subsequent description of the architectural characterisation, the following characteristics were used:

- Qualitative aspects: leafy axis (phyllotaxis*, internode), growth (definite*, indefinite*, monopodial* or sympodial*), direction and differentiation of axes (orthotropic* or plagiotropic*), growth (definite*, indefinite*, monopodial* or sympodial*, monocyclism, polycyclism), direction and differentiation of axes (orthotropic* or plagiotropic*, mixed*, ageotropic*), mode of branching (order of branching, immediate*, deferred*, delayed*; rhythmic*, continuous*, diffuse*, acrotone*, mesotone*, basitone*; epitone*, hypotone* and amphitone*), position of sexuality (terminal and lateral), life span of axes and leaves [5];
- Quantitative aspects: average length and diameter of growth units or modules (MODs), average number of phytomeres per MOD. These data were collected on the first two growth units or Modules from the tip (apex) of the shoots of the primary axes (young trees) and secondary and tertiary axes

(mature and old trees).

2.3.5. Statistical Data Analysis

Quantitative data were pooled and compared with each other (MANOVA) using SAS software version 9.4. The Student-Newman-Keuls test at the 5% threshold was used for post hoc comparisons. The links between the different quantitative parameters were made using XLSTAT 2020 version 7.5.

3. Results

Through this work, which required the observation of several individuals of all sizes (from seedlings to senescent trees) by means of synthetic drawings, the development by stage (young, adult and old) was established. The following analysis is the result of such a description. There are therefore 3 main stages during the ontogeny of the species, each defined by precise morphological characteristics. Firstly, we characterise the endogenous development of the young plant until senescence and then we analyse, if possible, certain variations, whether they are natural variations within homogeneous plantations or variations induced by the management of the stands (density of the forest cover) or the consequences of pedological or climatic events.

3.1. Young Stage

In *Parkia biglobosa*, the seedling consists of an unbranched stem with bipinnate compound leaves. The phyllotaxy is alternate spiral. At this stage the leaf bears 2 to 6 leaflets with one stipule at the base of the petiole (leaf sheath) and another stipule at the end of the primary rachis. Each leaflet bears 9 to 16 pairs of secondary leaflets and the secondary rachis bear a single secondary stipule inserted at the end of the secondary rachis. The young stem tends to zig-zag (right-left-right-left) in the direction of the weight of the established leaves. After the formation of a phytomere, the stem continues to grow in the opposite direction to the previous leaf. This causes the main stem to twist and gives the impression that the leaves are distributed in an alternating spiral fashion along the leaf stem, but in reality the phyllotaxy is alternating distichous.

After 3 to 4 months of evolution, the apical meristem dies by desiccation, the part below the dead part swells by bulging, giving a water tower shape to the phytomere. At this point, the initially monopodial growth mode becomes sympodial. In the forest, nodule-like swellings appear on the leaf rachis and the main stem at this stage. The nearest axillary bud takes over in the direction of the main stem and after 2 to 6 phytomeres, it dies in turn, and so on. This system forms clearly visible modules along the stem. In most cases there is only one relay shoot and the structure is a monochasial* sympod. The stem is usually curved at the distal end and later straightens as the stem expands and loses its leaves. In fact, as the stem grows in height, the old leaves (in the base) are pruned off by themselves and in succession. The stem retains only the new leaves of the new module in the apical part. These leaves are larger and heavier than the phytomer, the module and often the stem; it is the weight of the leaves that causes the stem to collapse. After a year, when the main stem bends, the relay bud sets up in the bending part of the stem, the rest of the bent portion prunes and so on. The stem is a pseudomonopod* and the modules are clearly visible on the stem (growth arrest zones are marked by markers and well-swollen plateau-like areas).

The branching appears in the second year, the branches are short, deferred* and located in the middle of the tree. The branching is initially in a vertical direction and collapses, and then lengthens in the horizontal direction. It forms in the middle of most modules (mesotone*) and often at the end of the modules (acrotone*). The branching is not continuous, it does not follow any growth rhythm, it is diffuse* on the trunk. All the branches formed follow the same process of pruning the trunk and are all sympodes. This is the beginning of the establishment of the top. Observations on individuals of this stage revealed that the individuals cultivated and monitored in the nursery were larger and more vigorous than the wild individuals observed in the forest. The latter suffer more trauma (insect attacks) than those observed in nurseries.

Table 3 shows the comparison of the morphological parameters of the modules or GUs according to the habitat, the localities surveyed and according to the habitat per locality. The habitat does not statistically influence the morphology of the modules ($P > 0.05$). However, most of the morphological parameters vary from one locality to another ($P < 0.05$) and from one habitat to another per locality ($P < 0.05$).

3.2. Mature Tree and Flowering

The tree continues its development by setting up increasingly vigorous branches whose structure is a succession of amphitone* and hypotone* relay axes. At this stage, the tree still has a hierarchical structure around a single large trunk. The architectural unit is established at this stage after flowering with 3 categories of axes (Table 4) and 4 orders of branching. Surveys of rural populations revealed that the first flowering occurs between the 10th and 16th year after planting. Flowering is terminal and lateral in this species and occurs in the dry season. The flower buds grow longer and invade the whole tree. Flowering occurs only on the A4 (majority) and short branches (minority). The terminal inflorescence of the axes and trunk later leads to the production of successive forks (vigorous relays), one of which is established in the extension of the trunk (vertical) until a certain point. This direction then becomes oblique and then horizontal under the effect of gravity. When the tree reaches its maximum development, the contour of the crown is rounded and irregular; the periphery of this crown is composed of sympodial structures of almost identical size and morphology.

Table 4 shows the morphological and architectural description of the axis types constituting the architectural unit in *Parkia biglobosa*.

Table 5 presents the comparison of morphological parameters of modules or GUs according to habitat, surveyed localities and habitat by locality in adult

Table 3. Influence of habitat, locality and habitat by locality on the morphology of the first two modules in young trees of *Parkia biglobosa*.

Habitats/ Locality	Height (m)	Diam (cm)	MOD1-lenght (cm)	MOD1-diam (cm)	MOD1-leaf Nber	MOD2-lenght (cm)	MOD2-diam (cm)	MOD2-leaf Nber
Psol	1.95 ± 0.11 **b**	4.35 ± 0.24 **b**	18.53 ± 7.91 **a**	0.76 ± 0.43 **a**	10.47 ± 3.95 **a**	16.59 ± 4.59 **a**	1.13 ± 0.63 **a**	12.76 ± 3.85 **a**
Sbs	2.56 ± 0.05 **a**	7.06 ± 1.22 **a**	14.8 ± 7.06 **a**	0.88 ± 0.13 **a**	12.33 ± 4.5 **a**	19.52 ± 7.97 **a**	1.55 ± 0.55 **a**	15.17 ± 4.99 **a**
Pr > F	**0.0064**	**0.0036**	**0.5069**	**0.5522**	**0.3340**	**0.4953**	**0.1523**	**0.2181**
Bouaké	3.2 ± 7.89 **ab**	17.91 ± 8.43 **b**	29.65 ± 14.56 **a**	1.39 ± 0.34 **a**	15.28 ± 1.79 **a**	23.61 ± 9.4 **a**	2.04 ± 0.38 **a**	17.43 ± 3.45 **a**
Daloa	0.77 ± 0.11 **b**	1.41 ± 0.51 **c**	13.74 ± 8.27 **a**	0.43 ± 0.07 **b**	7 ± 2.06 b	15.98 ± 7.84 **a**	0.6 ± 0.09 **c**	9.78 ± 2.16 **a**
Katiola	3.72 ± 5.68 **ab**	11.09 ± 6.64 **bc**	12.95 ± 8.47 **a**	0.79 ± 0.25 **b**	11.5 ± 2.73 **ab**	13.95 ± 3.47 **a**	1.37 ± 0.28 **b**	14.5 ± 3.08 **a**
Korhogo	0.95 ± 3.32 **b**	11.06 ± 7.81 **bc**	9.8 ± 2.12 **a**	0.53 ± 0.03 **b**	13 ± 5.66 **ab**	18.5 ± 5.6 **a**	1.06 ± 0.47 **bc**	13.5 ± 3.53 **a**
Niakara	5.6 ± 1.41 **a**	17.98 ± 12.4 **a**	15.7 ± 3.8 **a**	0.73 ± 0.1 **b**	12 ± 4.4 **ab**	6.7 ± 2.3 **a**	0.81 ± 0.21 **bc**	14 ± 3.4 **a**
Toumodi	0.79 ± 1.28 **b**	6.14 ± 3.08 **bc**	16.85 ± 7.7 **a**	0.54 ± 0.17 **b**	8.5 ± 3.53 **ab**	14.5 ± 6.5 **a**	1.14 ± 0.37 **bc**	10.5 ± 4.94 **a**
Ferké	1.19 ± 1.3 **b**	5.74 ± 1.21 **bc**	11.45 ± 2.7 **a**	0.64 ± 0.21 **b**	9.6 ± 2.33 **ab**	16.1 ± 7.5 **a**	0.84 ± 0.6**bc**	15.4 ± 6.64 **a**
Pr > F	**0.0045**	**0.0001**	**0.0533**	**0.0001**	**0.0001**	**0.3127**	**0.0001**	**0.0621**
Psol-Bouaké	3.05 ± 5.79 **ab**	10.71 ± 11.36 **ab**	36.57 ± 16.28 **a**	1.5 ± 0.18 **a**	14.75 ± 1.7 **ab**	22.85 ± 6.19 **a**	2.12 ± 0.39 **a**	16.25 ± 3.5 **a**
Psol-Daloa	0.67 ± 0.11 **b**	1.41 ± 0.51 **b**	13.74 ± 8.27 **b**	0.43 ± 0.07 **b**	7 ± 2.06 **b**	15.98 ± 7.84 **a**	0.6 ± 0.09 **b**	9.77 ± 0.16 **ab**
Psol-Katiola	3.84 ± 4.82 **ab**	9.57 ± 6.15 **ab**	14.58 ± 8.34 **b**	0.84 ± 0.26 **b**	11.6 ± 3.05 **ab**	14.12 ± 7.58 **a**	1.36 ± 0.31 **b**	15.6 ± 1.67 **a**
Psol-Korhogo	3.3 ± 2.3 **ab**	11.59 ± 7.41 **ab**	8.3 ± 2.31 **b**	0.53 ± 0.21 **b**	17 ± 4.3 **a**	26 ± 6.63 **a**	1.4 ± 0.61 **b**	16 ± 3.33 **a**
Psol-Niakara	5.5 ± 6.31 **a**	17.98 ± 11.4 **a**	15.7 ± 1.7 **b**	0.73 ± 0.04 **b**	12 ± 3.4 **ab**	6.7 ± 1.73 **a**	0.81 ± 0.11 **b**	14 ± 2.36 **a**
Psol-Toumodi	1.48 ± 0.13 **b**	2.96 ± 1.31 **b**	22.3 ± 6.3 **ab**	0.66 ± 0.13 **b**	11 ± 3.4 **ab**	9.9 ± 0.83 **a**	0.88 ± 0.23 **b**	7 ± 1.7 **b**
Pr > F	**0.0133**	**0.0001**	**0.0378**	**0.0001**	**0.0005**	**0.3566**	**0.0001**	**0.0009**
Sbs-Bouaké	4.4 ± 2.27 **a**	15.5 ± 2.1 **a**	20.43 ± 3.92 **a**	1.26 ± 0.51 **a**	16 ± 2 **a**	24.63 ± 13.31 **a**	1.93 ± 0.41 **a**	19 ± 3.46 **a**
Sbs-Katiola	3.9 ± 7.3 **a**	16.69 ± 7.33 **a**	4.8 ± 1.33 **b**	0.6 ± 0.13 **a**	11 ± 3.4 **a**	13.1 ± 3.4 **b**	1.4 ± 0.31 **a**	9 ± 2.3 **b**
Sbs-Korhogo	4.6 ± 1.7 **a**	5.54 ± 1.83 **b**	11.3 ± 3.41 **ab**	0.53 ± 0.11 **a**	9 ± 2.51 **a**	11 ± 3.31 **b**	0.73 ± 0.23 **a**	11 ± 3.61 **b**
Sbs-Toumodi	4.3 ± 0.77 **a**	7.32 ± 3.1 **b**	11.4 ± 2.6 **ab**	0.41 ± 0.07 **a**	6 ± 1.81 **a**	19.1 ± 3.36 **a**	1.4 ± 0.2 **a**	14 ± 3.4 **ab**
Pr > F	**0.0697**	**0.0086**	**0.0091**	**0.5020**	**0.1161**	**0.0014**	**0.3248**	**0.004**

Values with the same letters are not statistically different at the 5% level. **Psol** = open and sunny environment, **Sbs** = crowded or forested environment, **Height (m) =** tree height in metres, **Diam (cm)** = diameter at the base of the tree in centimetres, **MOD** = Module or Growth Unit, **MOD1-length (cm) =** length of the first module or growth unit in centimetres, **MOD1-diam (cm) =** diameter at the base of the first module or growth unit in centimetres, **MOD1-leaf Nber** = number of leaves or phytomers carried by the first module or growth unit, **MOD2-length (cm), MOD2-diam (cm), MOD2-leaf Nber** = Parameters of the second growth unit or Modules. **MOD1** are the growth units or modules located at the shoot tip (apex or summit of the sampled axis); **MOD2** are the growth units or modules that directly follow **MOD1**.

Table 4. Summary table of the characteristics of the architectural unit in *Parkia biglobosa*.

	Trunk or main stem	Branche	Twigs
Phyllotaxy	Alternate spiral to distichous (axial and bilateral symmetry)	Alternate spiral to distichous with twisting of the leaf axis giving a spiral leaf appearance (axial and bilateral symmetry)	Alternate spiral to distichous with torsion of the module giving a spiral leaf appearance (axial and bilateral symmetry)

Continued

Leaves type NB: In the wild, nodosities (swellings) are common on the petiole and rachis of leaves	Paripinnate compounds with one stipule per leaf sheath and another stipule at the end of the primary rachis. The leaves are composed of 2 to 16 pairs of leaflets on the compound leaf and 11 to 52 pairs of secondary leaflets on each leaflet.	Paripinnate compounds with one stipule per leaf sheath and another stipule at the end of the primary rachis. The leaves are composed of 2 to 16 pairs of leaflets on the compound leaf and 11 to 52 pairs of secondary leaflets on each leaflet.	Paripinnate compounds with one stipule per leaf sheath and another stipule at the end of the primary rachis. The leaves are composed of 2 to 16 pairs of leaflets on the compound leaf and 11 to 52 pairs of secondary leaflets on each leaflet.
Growing	Determinate (defined)	Determinate (defined)	Determinate (defined)
Preferential growth direction	Vertical in the proximal part and oblique to horizontal in its distal part	Oblique (minority) and horizontal (majority)	Horizontal
Ramification	Mesotone (majority) and Acrotone (minority) on growth modules	Mesotone (majority) and Acrotone (minority) on growth modules	No
Size of growth units (GUs)	Variable: 4.5 to 35.5 leaf scars; Long and short in places (3.85 to 51.4 cm)	Variability: 4 to 27 leaf scars; Long and short in places (4.5 to 43.6 cm)	Variability: 3 to 16 leaves; Short and very short in places (2.1 to 11 cm)
Annual shoots	Polycyclic (2-5 GU)	Polycyclic (2 - 4 GU)	Polycyclic (2 - 3 GU)
Sexuality	-	Terminal and lateral in the dry season	Terminal and lateral in the dry season
Leaf caducity	Dry season flowering period (January, February and March)	Dry season flowering period (January, February and March)	Dry season flowering period (January, February and March)
Taper of the axis	Height: 0.64 m to 31.7 m Diameter: 2.8 cm to 178.44 cm	Height: 0.26 m to 9.5 m Diameter: 1.4 cm to 23.2 cm	Height: 0.08 m to 0.67 m Diameter: 0.7 cm to 4.4 cm
Axis complexity	Bears branching orders 2, 3 and short, greedy twigs	Bears only branching orders 3 and short gourmand branches	No (unbranched), but bears flowering clusters and shoots

Table 5. Influence of habitat, locality and habitat by locality on the morphology of the first two modules in adult *Parkia biglobosa* trees.

Habitats/ Locality	Height (m)	Diam (cm)	MOD1-lenght (cm)	MOD1-diam (cm)	MOD1-leaf Nber	MOD2-lenght (cm)	MOD2-diam (cm)	MOD2-leaf Nber
Psol	9.68 ± 1.14 **a**	38.15 ± 3.02 **a**	15.63 ± 5.15 **a**	0.76 ± 0.31 **a**	11.47 ± 5.97 **a**	16.15 ± 12.81 **a**	1.13 ± 0.58 **a**	14.14 ± 6.74 **a**
Sbs	12.02 ± 1.01 **a**	36.27 ± 1.53 **a**	14.25 ± 6.55 **a**	0.75 ± 0.11 **a**	10.89 ± 4.83 **a**	16.93 ± 7.98 **a**	1.23 ± 0.38 **a**	16.55 ± 5.63 **a**
Pr* > *F	**0.9971**	**0.4114**	**0.7956**	**0.9479**	**0.7968**	**0.8675**	**0.6768**	**0.3558**
Bouaké	9.66 ± 3.45 **b**	44.94 ± 7.56 **a**	14.6 ± 3.02 **a**	1.01 ± 0.25 **a**	11 ± 2 **a**	21.36 ± 12.99 **a**	1.8 ± 0.26 **a**	19 ± 4.58 **a**
Ferké	9.23 ± 5.47 **b**	39.39 ± 5.47 **a**	26.94 ± 12.47 **a**	1.06 ± 0.53 **a**	15.57 ± 7.41 **a**	15.62 ± 6.68 **a**	1.49 ± 0.77 **a**	13.57 ± 7.02 **a**
Katiola	13.1 ± 7.33 **a**	28.57 ± 8.6 **b**	7.8 ± 0.74 **a**	0.71 ± 0.1 **a**	8 ± 2.41 **a**	18.3 ± 7.4 **a**	1.7 ± 0.73 **a**	19 ± 5.4 **a**
Korhogo	10.77 ± 6.5 **b**	33.54 ± 15 **b**	10.95 ± 2.12 **a**	0.59 ± 0.12 **a**	10.87 ± 2.07 **a**	12.38 ± 3.56 **a**	0.81 ± 0.15 **a**	10.63 ± 2.65 **a**
Niakara	9.2 ± 8.29 **b**	35.09 ± 5.78 **b**	11.16 ± 3.47 **a**	0.69 ± 0.14 **a**	8.4 ± 2.08 **a**	15.14 ± 3.49 **a**	0.89 ± 0.08 **a**	15.6 ± 1.81 **a**
Toumodi	8.03 ± 3.73 **b**	21.28 ± 5.95 **c**	12.15 ± 4.48 **a**	0.57 ± 0.19 **a**	10 ± 2.96 **a**	20.83 ± 3.12 **a**	1.07 ± 0.24 **a**	18.66 ± 5.31 **a**
Pr* > *F	**0.0001**	**0.0001**	**0.1695**	**0.0596**	**0.2962**	**0.7971**	**0.0582**	**0.1745**
Psol-Bouaké	8.7 ± 1.83 **b**	45.92 ± 11.43 **a**	17 ± 1.83 **a**	1.3 ± 0.41 **a**	11 ± 2.41 **a**	32.3 ± 7.31 **a**	2.1 ± 0.13 **a**	23 ± 5.4 **a**

Continued

Psol-Ferké	12.3 ± 5.56 a	41.01 ± 5.89 ab	27.03 ± 10.05 a	1.11 ± 0.22 a	15.16 ± 3.28 a	15.4 ± 7.9 a	1.61 ± 0.31 ab	12.83 ± 3.01 a
Psol-Korhogo	8.68 ± 7.42 b	38.9 ± 15.64 b	9.8 ± 4.34 a	0.56 ± 0.12 b	10.33 ± 2.23 a	13.98 ± 4.65 a	0.79 ± 0.07 b	11.33 ± 3.55 a
Psol-Niakara	12.25 ± 2.65 a	45.54 ± 3.28 a	11.02 ± 4.48 a	0.64 ± 0.04 b	8.75 ± 2.65 a	14.32 ± 8.76 a	0.81 ± 0.11 b	15.75 ± 2.06 a
Psol-Toumodi	7.62 ± 1.66 b	21.1 ± 0.85 c	11.55 ± 2.71 a	0.52 ± 0.11 b	10.5 ± 1.65 a	18.32 ± 4.13 a	1.02 ± 0.11 b	16.5 ± 2.53 a
Pr* > *F	**0.0066**	**0.0006**	**0.3060**	**0.0331**	**0.5219**	**0.7787**	**0.0167**	**0.4820**
Sbs-Bouaké	9.65 ± 0.49 a	44.45 ± 10.62 a	13.4 ± 3.11 b	0.87 ± 0.05 a	11 ± 2.82 a	15.9 ± 8.9 a	1.65 ± 0.05 a	17 ± 3 a
Sbs-Ferké	10.6 ± 1.47 a	43.68 ± 11.4 a	26.4 ± 1.37 a	0.73 ± 0.11 a	18 ± 1.73 a	17 ± 2.43 a	0.78 ± 0.14 a	18 ± 4.1 a
Sbs-Katiola	9.1 ± 6.4 a	42.57 ± 7.4 a	7.8 ± 1.28 c	0.71 ± 0.04 a	8 ± 2.4 a	18.3 ± 7.1 a	1.7 ± 0.13 a	19 ± 2.7 a
Sbs-Korhogo	9.05 ± 2.05 a	38.44 ± 12.01 a	14.42 ± 7.97 b	0.69 ± 0.07 a	12.5 ± 6.5 a	7.6 ± 0.2 a	0.86 ± 0.03 a	8.5 ± 1.5 a
Sbs-Niakara	10 ± 3.4 a	43.31 ± 13.1 a	11.7 ± 1.43 b	0.91 ± 0.14 a	7 ± 2.4 a	18.4 ± 1.48 a	1.2 ± 0.13 a	15 ± 6.1 a
Sbs-Toumodi	12.85 ± 4.15 a	45.64 ± 7.48 a	13.35 ± 1.95 b	0.66 ± 0.03 a	9 ± 2.82 a	25.85 ± 3.46 a	1.18 ± 0.35 a	23 ± 2.82 a
Pr* > *F	**0.0702**	**0.3151**	**0.0039**	**0.1959**	**0.7584**	**0.4713**	**0.1132**	**0.1262**

Values with the same letters are not statistically different at the 5% level.

trees. According to the table, habitat and surveyed localities did not significantly influence the majority of the morphological parameters of the assessed modules ($P > 0.05$).

3.3. Older Scene

In old and aged trees, all twigs tend to droop. New sympodial twigs develop from dormant buds by piling up in the bending zones in amphitone* and epitone* positions. These structures are in fact successive partial reiterations. The total reiterations occur later, giving the impression of rescuing the tree in distress. These new reiterations regenerate the top of the tree, while the old structures fall off the tree (the tree molts). The whole tree becomes a reiterated complex; in the periphery of the crown, the sympodial structures form successive arches (piling up). At this stage, the tree can carry up to 6 orders of branching with always three types of axis categories. The branching orders are the capacity to carry an axis (carrier-to-carrier ratio), while the axis category is a set of axes groupable by common botanical entity characteristics (size, diameter, number of GUs, phytomeres, flower buds, etc.). The tree can branch up to 6 times in order, but the axis categories are repeated in the successive branching at this stage. During flowering, the reiterations also bear terminal and lateral inflorescences. Flowering takes over the whole tree at this time; the outline of the crown is rounded but irregular.

Table 6 presents the analysis of variance of the morphological parameters of the modules by habitat and by locality in the sampled old trees of *Parkia biglobosa*. The former moduli were not influenced by the different localities surveyed in old trees ($P > 0.05$). However, they were influenced by habitat type ($P < 0.05$). Habitat (undergrowth and full sun) altered the morphology of the growth units at the shoot tips. However, the morphology of the growth units was statistically similar in all surveyed localities (Table 6).

Table 6. Influence of environment and locality on the morphology of growth units or modulus in old trees of *Parkia biglobosa*.

Habitats/ Locality	**Height (m)**	**Diam (cm)**	**MOD1-lenght (cm)**	**MOD1-diam (cm)**	**MOD1-leaf Nber**	**MOD2-lenght (cm)**	**MOD2-diam (cm)**	**MOD2-leaf Nber**
Psol	25.22 ± 3.21 **a**	85.51 ± 6.12 **a**	8.94 ± 1.42 **a**	0.64 ± 0.05 **b**	8.62 ± 0.7 **b**	13.76 ± 2.79 **a**	1.11 ± 0.11 **a**	14.12 ± 1.6 **a**
Sbs	25.3 ± 3.32 **a**	76.58 ± 7.36 **a**	15.46 ± 8.28 **b**	0.94 ± 0.09 **a**	12.4 ± 2.3 **a**	13.22 ± 5.81 **a**	1.53 ± 0.38 **a**	16.8 ± 6.26 **a**
Pr* > *F	**0.454**	**0.3359**	**0.003**	**0.0098**	**0.0095**	**0.8974**	**0.0611**	**0.3894**
Bouaké	21.7 ± 7.4 **a**	115.6 ± 11.4 **a**	6.4 ± 0.13 **a**	0.53 ± 0.08 **a**	8 ± 1.4 **a**	13.4 ± 2.4 **ab**	1.2 ± 0.04 **ab**	16 ± 3.4 **ab**
Ferké	27.5 ± 17.85 **a**	112.25 ± 36.73 **a**	12.67 ± 5.9 **a**	0.87 ± 0.27 **a**	11.25 ± 1.25 **a**	7.65 ± 2.14 **b**	1.4 ± 0.16 **ab**	11.25 ± 2.36 **b**
Korhogo	28.61 ± 2.81 **a**	69.04 ± 5.21 **b**	10.72 ± 1.70 **a**	0.58 ± 0.03 **a**	11.3 ± 1.76 **a**	14.61 ± 3.13 **ab**	0.86 ± 0.07 **b**	11.2 ± 2.16 **b**
Katiola	22.1 ± 11.23 **a**	76.48 ± 19.03 **b**	10.8 ± 3.37 **a**	0.88 ± 0.12 **a**	11 ± 0.58 **a**	16.46 ± 2.64 **ab**	1.77 ± 0.08 **a**	15.33 ± 1.45 **ab**
Niakara	26.2 ± 1.63 **a**	87.16 ± 3.91 **ab**	11.97 ± 5.08 **a**	0.64 ± 0.07 **a**	9.75 ± 2.17 **a**	14.55 ± 3.92 **ab**	0.8 ± 0.06 **b**	18.25 ± 3.98 **a**
Toumodi	23 ± 7.4 **a**	73.24 ± 8.4 **b**	11.4 ± 1.41 **a**	0.63 ± 0.13 **a**	6 ± 0.83 **a**	24.6 ± 3.4 **a**	1.23 ± 0.04 **ab**	17 ± 5.1 **a**
Pr* > *F	**0.3009**	**0.0098**	**0.9627**	**0.3962**	**0.4943**	**0.0079**	**0.003**	**0.008**

Values with the same letters are not statistically different at the 5% level.

3.4. Relationship between the Morphology Parameters of Modules Present on *Parkia biglobosa* Axes Observed

The analysis of the links between the morphological parameters of the modules evaluated (Table 7), indicates strong positive correlations between the lengths and diameters of module 1 ($r = 0.6986$), between the lengths and the numbers of leaves of module 1 ($r = 0.6375$) and between the diameters of modules 1 and 2 ($r = 0.7156$).

The relationships between the full-sun environment and the undergrowth environment in relation to the morphological parameters of the modules evaluated on the axes of the individuals are presented globally in Figure 3. This figure indicates very weak relationships ($R^2 = 0.028$; $r = 0.167$) between the lengths of the modules observed in full sun and those observed in undergrowth; then equally weak relationships ($R^2 = 0.078$; $r = 0.279$) between the numbers of leaves inserted on the modules of the axes evaluated in full sun and undergrowth. Although 57.19% of the diameters of the modules observed in full sun are related and 32.71% are explained by those observed in undergrowth (Figure 3(b)), the relationships remain weak and cannot be taken into account. The allometric equations of the models are:

- *Leng-MOD-psol* = 13.91 + 0.21**Leng-MOD-sbs* (*Leng-MOD-psol* = Length of modules or growth units in the full sun environment and *Leng-MOD-sbs* = Length of modules or growth units in the undergrowth environment);
- *Diam-MOD-psol* = 0.31 + 0.66**Diam-MOD-sbs* (*Diam-MOD-psol* = Diameter of modules or growth units in the full sun environment and *Diam-MOD-sbs* = Diameter of modules or growth units in the undergrowth environment);
- *Nber-leaf-MOD-psol* = 10.08 + 0.31**Nber-leafl-MOD-sbs* (*Nber-leaf-MOD-psol* = Number of leaves carried by the modules or growth units of the full sun environment and *Nber-leaf-MOD-sbs* = Number of leaves carried by the modules or growth units of the undergrowth environment).

Table 7. Correlation matrix (Pearson (*n*)).

Variables	MOD1-lenght	MOD1-diam	MOD1-leaf Nber	MOD2-lenght	MOD2-diam	MOD2-leaf Nber
MOD1-lenght	1					
MOD1-diam	**0.6986**	1				
MOD1-leaf Nber	**0.6375**	0.4968	1			
MOD2-lenght	0.0893	0.2184	−0.0071	1		
MOD2-diam	0.2690	**0.7156**	0.2327	0.4972	1	
MOD2-leaf Nber	0.3046	0.2840	0.2040	0.5418	0.2824	1

Values in bold are different from 0 at significance level alpha = 0.05.

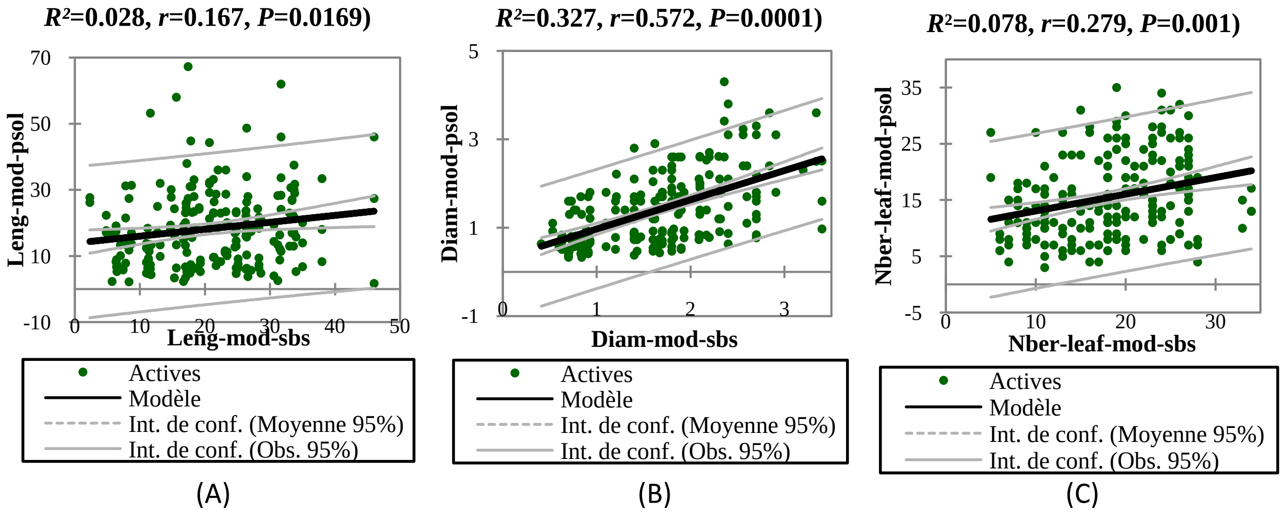
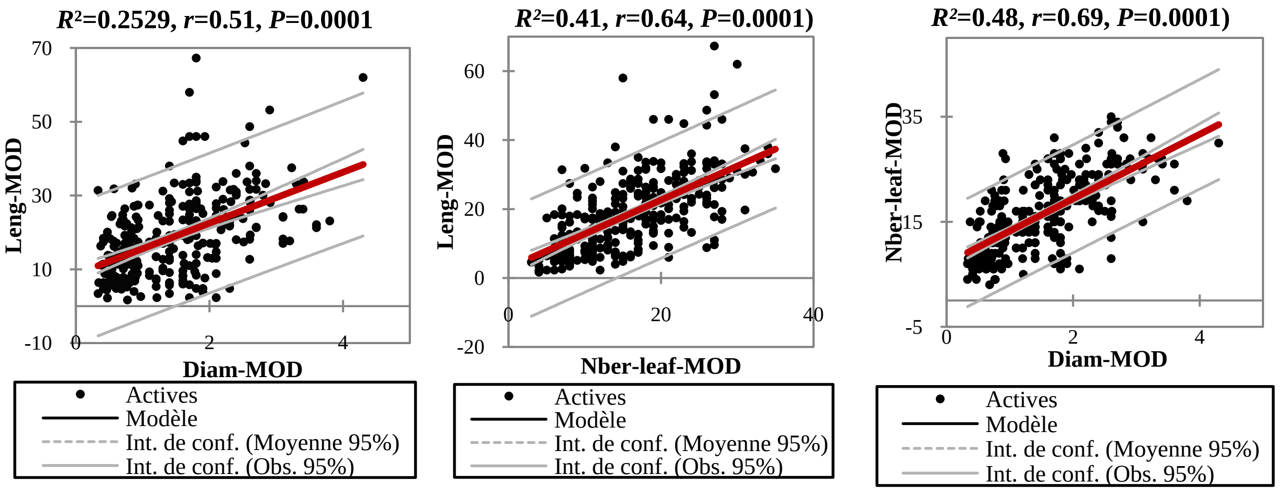


Figure 3. regressions between module lengths observed in full sun and undergrowth (A), between module diameters observed in full sun and undergrowth (B) and between the number of leaves carried by modules in full sun and undergrowth (C).

Figure 4 shows the correlations between the different module morphology parameters. Despite the significance of the parameters, the low correlation coefficients (R^2 and $r < 0.8$) indicate negligible links in the set between the evaluated parameters. The equations of the models are as follows:

- *Leng-MOD* = 8.7 + 6.91**Diam-MOD* (*Leng-MOD* = Length of modules or growth units and *Diam-MOD* = Module or growth unit diameter);
- *Leng-MOD* = 2.97 + 0.98**Nber-leaf-MOD* (*Nbr-leaf-MOD* = Number of leaves on modules or growth units) and
- *Nber-leaf-MOD* = 7.12 + 6.14**Diam-MOD*

Parkia biglobosa is a tree identical to Champagnat's model at the young tree stage (plant with a mixed vegetative axis, the main stem is orthotropic in its proximal part and plagiotropic "sags" in its distal part). The tree then transits to the Troll model at the adult and old stage (plant with a plagiotropic axis in the proximal and distal parts, the trunk is built by superimposing collapsed relay axes that gradually straighten, sympodial branching, amphitone* and epitone*, definite growth, terminal and lateral sexuality). Its structure is set up in three



(A) (B) (C)

Figure 4. Representation of the relationships between module length and diameter (A), module length and leaf number (B) and leaf number and module diameter (C) in *Parkia biglobosa*.

phases: initiation of development and establishment of the top, then establishment of the architectural unit and finally duplication of the architecture by a series of partial and total reiterations. The level of organisation is 5: the phytomere, the module or growth unit, the axis, the architectural unit and the reiterated complex. Table 8 shows the main architectural characters in *Parkia biglobosa*.

Figure 5 shows some drawings and diagrams summarising the architectural development in *Parkia biglobosa*.

4. Discussion

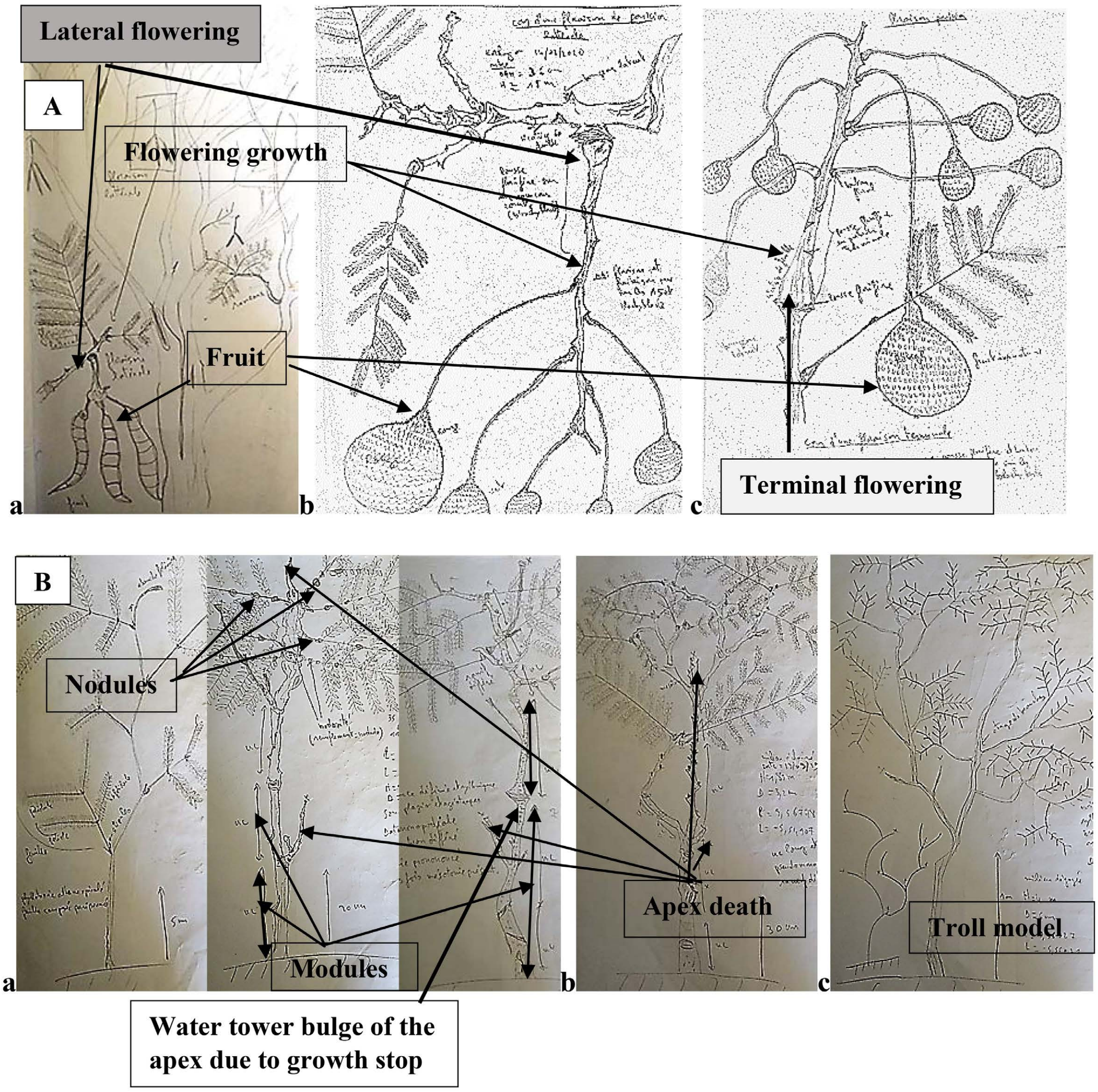
Each plant follows a succession of morphological development stages throughout its life with a precise sequence ordered by different elementary entities (composition of the tree axis structure): phytomere, growth unit [5] [12] [25]. This scientific discipline has several advantages: it allows us to understand the functioning and shape of plants, to describe the biological phenomena that gave rise to them and to translate the non-linear aspect of their reaction dynamics to certain stresses [7]. In this study, the architectural analysis carried out on *Parkia biglobosa* along a climatic gradient made it possible to highlight its architectural characteristics. The analysis of the morphology of the modules informed us about the adaptability and the evolution of the species in relation to a changing environment. These results are an introduction to the architectural study of this species, in order to open up short, medium and long-term research perspectives.

4.1. Architectural Analysis

In *Parkia biglobosa*, from the young stage, the leaves are already bipinnate and do not differentiate. Modules are formed in the very young stage by the death of the apex (trauma), which forms a monochasial sympod*. The boundaries of the modules are well marked by bulging areas on the main stem and the young tree forms a collapsed pseudomonopod in the apical part under the weight of the leafy cap of the terminal modules. In the young stage the species adopts the Champagnat

Table 8. Architectural characteristics of *Parkia biglobosa* species.

1) Growth mode - Defined - Colonial, rhythmic - Sympodial (mono, di and polychasial and modulated) - Organ preformation	**2) Branching mode** - Terminal and median (acrotone and mesotone on modules) - Rhythmic - Delayed or proleptic (without hypopodium, the terminal meristem dies, the relay bud(s) are delayed)
3) Differentiation of axes - Rapid slowing of meristematic activity and death of the terminal bud in the short term - Orthotropic-like trunk (pseudomonopod) - Most axes (branches) are plagiotropic and ageotropic	**4) Sexuality position** - Terminal and lateral (synchronised)



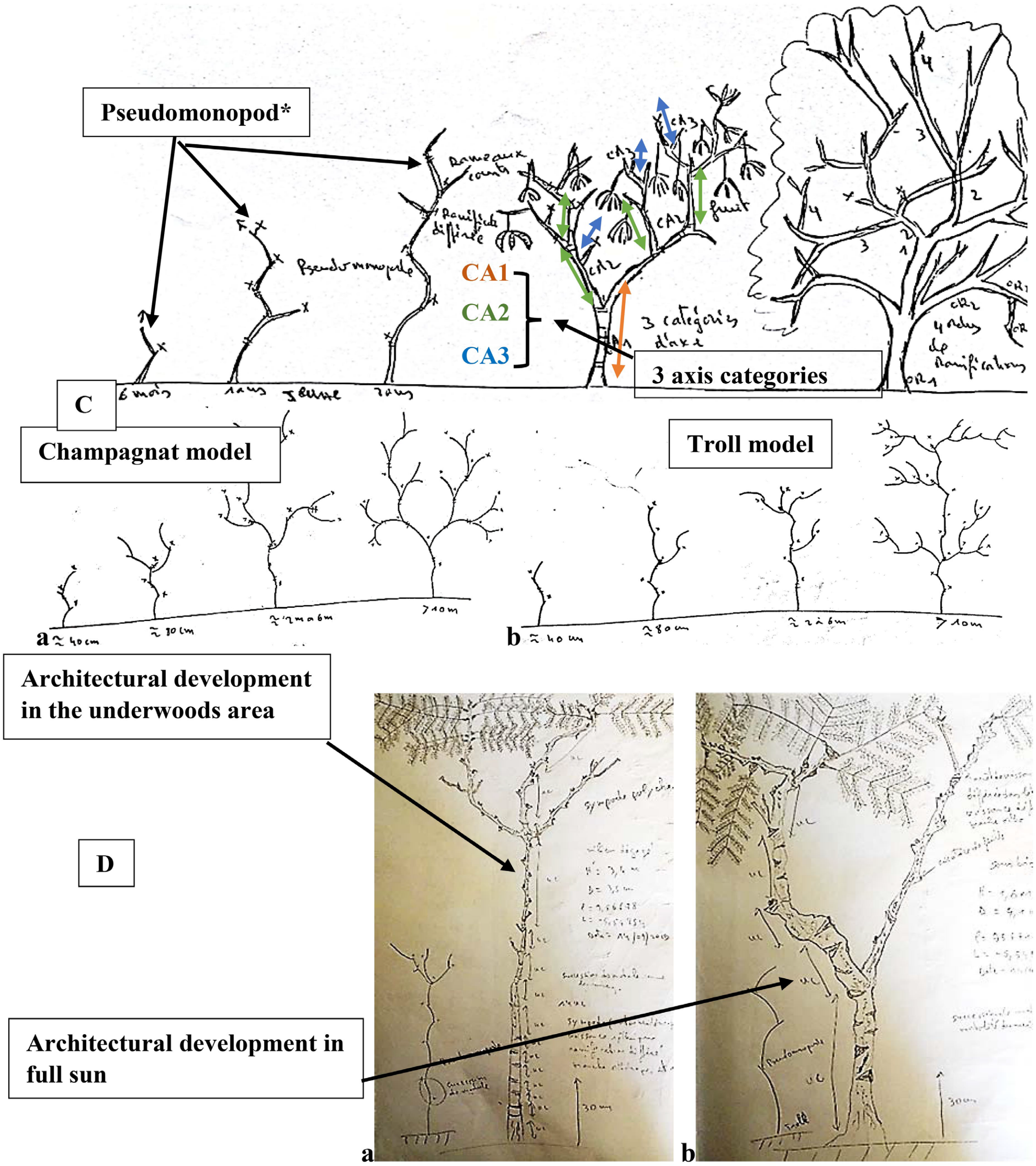


Figure 5. drawings and diagrams relating to types of flowering (A), a and b: lateral flowering, c: terminal flowering; traumatic phenomena often encountered (B), a: drawing of young plants with nodosities on the rachis of leaves in the understory and length of growth units or modules, b: trauma of the apical meristem leading to the death of the bud and the establishment of growth modules, c: drawing and diagram of an adult individual developing according to Troll's model; the sequence of architectural development from seedling to senescent tree (C), a: development according to Champagnat's architectural model and b: architectural development according to Troll's model; the influence of habitat on architectural development (D), a: architectural development in a closed or covered environment and b: in an open or sunny environment.

architectural model and transits to the Troll model in the adult and old stage after flowering. In fact, in the young stage, the stem is built as a repetitive stack of unbranched and discretely branched axes (short branches on the stem). The main axis is vertical at the base with the distal (younger) end curved at a large radius and brought back to the horizontal (collapsed) often to the ground due to gravity and the flexibility of the wood. The growth of the distal tips retains the vertical tendency and the leaves are spirally inserted with terminal and lateral flowering. The plant bears up to 6 orders of branching grouped into 3 categories of axes. This is the result of an intensive reiterative complex at the old stage. The architectural unit appears in the adult stage after flowering. According to [4], Champagnat's pattern is not known in ferns, Gymnosperms and Monocotyledons. This pattern appears in more than 30 families in the Dicotyledons. In the adult and old stage, the leafy axes overlap indefinitely in a horizontal fashion and secondary growth straightens the base vertically (pseudomonopod). The sympodial structures that form by superposition often go in all directions by piling up. This species is colonial and dominates its environment. The Troll model is not represented in ferns, Gymnosperms or Monocotyledons. However, more than 50 families of Dicotyledons are concerned by this model and the species of the three families of Leguminosae are built mainly, but not exclusively, according to the Troll model [4].

Architectural analysis has been undertaken mostly on temperate and South American species and has proven to be highly effective and successful in managing plant genetic resources in these areas [3] [7] [26]. This is the case of *Laetia procera* and *Dicorynia guianensis* [2]; *Juglans regia* and *Juglans nigra* [12]; *Fraxinus excelsior*, *Populus alba*, *Prunus padus*, *Quercus robur*, *Tilia cordata*, *Ulmus laevis*, *Cornus sanguinea*, *Corylus avellana*, *Prunus spinosa*, *Crataegus monogyna*, *Euonymus europaeus*, *Sambucus nigra*, *Viburnum opulus* [16]; *Fagus sylvatica* [1], etc.

Generally, architectural analysis on each individual is most frequently used because of its effectiveness in clearly illustrating the developmental pattern of a species. However, it is possible to analyse the three-dimensional organisation of a forest in a global way based on dendrometric data and graphical representations of plant architecture [16]. This makes it possible to develop the general architectural model of a forest [27] in order to identify the interest in forest interpretation and management or to illustrate the interest of the architectural model in the interpretation of biodiversity [16]. Indeed, the criteria used to characterise the architectural state of a plant are not always relevant and applicable to other species. It is therefore necessary to develop architectural approaches by grouping species by first studying the development sequence of key species under various stresses and behaviours in order to generalise or attribute it to a vegetation [2]. This mechanism would provide a global architectural vision of a forest for its rapid management.

Plant architecture holds many keys to understanding the ecological performance of species because resources (water, light, nutrients) are spatially variable and disturbances (e.g. frost, fire and herbivory) also impact on plants [3] [28] [29]. The main drivers of the evolution of architectural traits probably include water stress in deserts. Plant architecture strongly influences ecological performance and its role in plant evolution has recently been studied in depth by [30] on the genus *Euphorbia*. The reason for their study was that plant architecture in relation to environmental and biotic variables was until now poorly understood. They therefore tested both phylogenetic and environmental signals to separate architectural traits into four categories. Their study showed that architectural traits explain the structural evolution of species and that this evolution is influenced by climatic constraints.

4.2. Growth Units or Modules Morphology

Parkia biglobosa is a light species and native to arid areas (savannah). However, it is shade tolerant, as the results of this study revealed that individuals observed in the nursery were taller and more vigorous than young wild individuals observed in the forest. This may be due to trauma from insect and herbivore attacks in the forest than in the nursery. Furthermore, analysis of variance showed that in young trees, the largest individuals were found in the undergrowth for all surveyed localities. This is due to the search for light; the stems elongate by means of intense apical meristematic activity induced by auxin (phytohormone) in order to reach the canopy. The majority of these trees develop fewer branches and have a tapered monopodial trunk. The majority of these trees benefit from a humid environment due to evapotranspiration of leaves from trees with higher strata. In contrast to the young wild trees, which are exposed to full sun and have less of a microclimate that is favourable to their functioning (drier soil and environment). The latter are short and very often develop reiterations that are confused with branches. Their height is smaller because the race for light is not necessary and urgent in addition to the lack of water (dry soil). The effects of light and environment on development and growth have been demonstrated in several studies [31] [32] [33] [34] [35]. The results showed that the two environments considered (undergrowth and full sun) had no influence on the morphology of the growth units in young trees. Regardless of the environment, meristem function may depend on the plant genome and therefore cannot be significantly influenced by the environment in many cases. The expressed phenotype is therefore purely related to the plant genotype. Indeed, according to [4], the genetic programme for plant growth and development, of which the architecture is the visible expression, may not vary from one environment to another in several families of species. Locality has had influences on the morphology of growth units in young trees. This is due to the difference in climate, soil type and rainfall between localities. Indeed, observations on the morphology of growth units were made along a south-north drought gradient. It is obvious that some localities have more severe (drier) conditions than others. [12] [36] and [31] have shown in their research that soil depth and fertility, environment and age of individuals can influence the architectural development of a species. [37] and [38] have indicated in their studies that climate or ecological gradient has an effect on plant morphology. Similarly, the studies of [39] [40] and [41] indicated that the origin of differences in tree morphology is due to factors such as soil type, age and genetic characteristics of individuals.

In adult trees, the results showed that neither the environment nor the locality has a global and statistical influence on the morphology of the growth units. In fact, these trees were grouped by category on the basis of their dendrometric size without precise knowledge of the age of each individual. This remains a major weakness for this study. Furthermore, the axes evaluated were randomly selected at the top of the trees without sorting by axis category. It was found that on the secondary axes selected from adult trees, regardless of the environment and locality surveyed, the majority of terminal buds were synchronous (generalized bud break). In French Guiana, [42] had observed the same phenomenon on *Parkia velutina*. According to them, at the tree level the phenological cycle (leaf fall, elongation of growth units and formation of growth rings) was synchronous and affected all axes, whereas at the population level trees could be desynchronised. They later concluded that it was possible to date a branch by counting the number of growth units or growth rings over many years with reasonable error. However, it was still difficult to estimate the exact month of their formation in order to study climatic influences.

In old trees, the analyses of variance showed that the two habitats considered and the locations surveyed had no significant effect on the dendrometric parameters and the morphology of the growth units. This is due to the age and physiological state of these individuals. Indeed, all individuals of this age were confused due to the high intraspecific similarity. All old individuals observed in any environment had almost identical qualitative and quantitative aspects (dendrometry and morphology of growth units). At this stage the architecture can evolve, the structure of the tree is degrading and homogeneous from one individual to another. According to [4], whatever the age of the plant, young or old, the distribution of aerial and underground organs (leaves, internodes, phytomeres, growth units) is a conflict between two contradictory influences: firstly, the genetic programme for growth and development dictates architectural rules; inherent in the genome, these rules are stable and predictable in the species considered. On the other hand, adverse ecological factors (light, wind, animals, etc.), which are naturally random, often distort the architectural programme.

The Pearson matrix showed a strong positive correlation between the morphological parameters evaluated on the modules. This means that as one variable increases, the second variable also increases. For example, as module 1 gets longer, their diameter increases and the number of leaves increases. The correlation between the different dimensions of organ morphology has been demonstrated in the studies of [43] and [44]. Also, [45] and [46] obtained similar results on *Tectona grandis* and African coffee species respectively. However, in their studies, relationships between organ sizes of individuals from different environments were not established as was the case in our study. The allometric equations established by the linear model could be used to reduce the effort of collecting field data between the variables used and the two habitats considered if the relationships (R^2 and r) were strong (R^2 and $r > 0.7$). This is not the case.

5. Conclusions

This work firstly allowed us to understand and characterise architectural development in *Parkia biglobosa* and secondly to highlight the variability of morphological markers at the end of the axes in the crown of the trees. Thus, the architectural development of a plant is a succession of ordered and precise sequences of morphological differentiations that can be translated into a modification in the expression of meristem function during ontogeny. The establishment of this sequence results in a repetition of homologous elementary entities during key stages corresponding to the degrees of complexity of the plant's structure. The specific average architectural organisation constitutes the architectural unit of the species. *Parkia biglobosa* follows the Champagnat architectural model (plant with a mixed vegetative axis, the main stem is orthotropic in its proximal part and plagiotropic "collapses" in its distal part) before transiting to the Troll model in the adult and old stage (plant with a plagiotropic axis in the proximal and distal part, the trunk is built up by superimposing a collapsed relaying axis that gradually straightens, sympodial branching, amphitone and epitone, defined growth, mixed sexuality). This species has up to 6 orders of branching due to several reiterated sympodial structures forming arches. The architectural unit consists of three categories of axes. Its structure is established in three phases: initiation of development and establishment of the crown, then establishment of the architectural unit and finally duplication of the architecture by a series of partial and total reiterations.

The level of organisation of the species is 5: the phytomere, the growth unit or module, the axis, the architectural unit and the whole tree (reiterated complex). This information allows us to understand the sequential development of the overall structure of *P. biglobosa*. Its architectural unit is thus its smallest stem structure necessary to reach its sexual maturity stage and thus complete its life cycle by forming flowers and fruits. This study is an introduction to the architectural study of this species and the information provided will serve as a basis for further research into the architecture in relation to the sustainable use of this species.

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Author's Declaration

Beda Innocent Adji took the experimental measurements, analyzed the data and wrote the article. **Yves Caraglio** provided ideas of the paper. **Doffou Sélastique Akaffou, Véronique Letort, Mengzhen Kang, Xiujuan Wang, Marc Jaeger, Philippe De Reffye and Sylvie Annabel Sabatier** supervised the work. **Jerôme Duminil, Kouadio Henri Kouassi and Yao Patrice Houphouet** are the project coordinators.

Conflicts of Interest

The authors have no conflicts of interest to declare.

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Annex—Glossary

Plant architecture: the way in which the plant builds its structure at a given moment of its existence (mode of growth, branching, differentiation of axes and position of sexuality); this expression designates the series of structural characteristics expressed by a plant during its development (ontogeny) but also the method of study of the spatio-temporal organisation of the plant structure.

Architectural unit (AU): A very stable elementary architecture of a plant. Each plant species has a small and finite number of axis categories. All these categories, with their precise functions, constitute the Architectural Unit of the species.

Architectural model: a series of architectures that follow one another under stable and unconstrained ecological conditions, from germination to flowering, and which result from the expression of its genetic heritage. The typology of architectural patterns is based on the observation of four main groups of morphological characters: growth (rhythmic or continuous), branching (absence or presence, monopodial or sympodial, rhythmic, continuous or diffuse), direction of growth of the axes and position of sexuality. Each model corresponds to a particular combination of these architectural characteristics.

Growth unit: a portion of the stem established during an uninterrupted period of elongation.

Phyllotaxis: the arrangement of leaf organs along an axis. When a single leaf is borne at each node, the phyllotaxy is said to be alternate. In this case, if the successive leaves are positioned in the same plane and form an angle of 180˚ in pairs, the phyllotaxy is called distichous alternating. Conversely, if the leaves are arranged in several directions around the axis in a single virtual spiral, the phyllotaxy is called spiral alternation. When several leaves are inserted at the same node, the phyllotaxy is called whorled. A special case of whorled phyllotaxy is the opposite phyllotaxy where two leaves are inserted at the same node.

Monopodial development: axis built by a single apical meristem; the growth of an axis is ensured indefinitely by the same meristem or apical bud (mechanism of apical abscission without sexuality).

Pseudomonopodial development: non unique axis imitating monopodial development (masked sympod).

Sympodial development: not a single axis but a set of axes (succession of elementary axes with apical flowering or terminated by apical structures related to flowers, spines, tendrils, parenchyma domes, etc.); the construction of an axis is ensured by a succession of superimposed segments originating from different lateral buds (linear succession of elementary axes, each of which is built by a short-lived meristem).

Sympode: In sympodial or sympodial branching the terminal meristem of the supporting axis dies or is transformed into a structure that loses its ability to grow vegetatively. Further growth is then ensured by the functioning of one or more lateral meristems which will build as many lateral axes or relay axes, and the branched whole will be called a sympod. Depending on whether this branching leads to the formation of one, two or more relays, we speak respectively of a **monochasial**, **dichasial or polychasial sympod**.

Branching: the appearance of a branch on the trunk and, more generally, of an N + 1 axis on an N axis. The two axes, N and N + 1, have the same age in case of immediate branching; N + 1 is younger than N in case of delayed branching. This is the fact that a morphological unit of the plant body gives rise to one or more new units of the same fundamental nature as itself. The moment of development of a lateral branch is described as delayed or immediate, depending on whether or not it follows a resting phase after initiation of the lateral meristem by the terminal meristem. When all the axillary meristems of a stem give rise to a branch, the branching is said to be **continuous**; when the branches are grouped in distinct stages, the branching is said to be **rhythmic**; finally, when the arrangement of the branches is different from the two previous cases, the branching is said to be **diffuse**.

Rhythmicgrowth: axes that show a marked endogenous periodicity of elongation.

Orthotropic axis: when the direction of the axes is vertical.

Plagiotropic axis: when the direction of the axes is horizontal.

Ageotropic axis: when the direction of the axes is oblique (mixed between vertical and horizontal directions).

Cataphylls: the scar of the leaf outline that protected the bud before budburst.

Continuous growth: axes that do not show a marked periodicity of endogenous elongation and are said to be continuously growing.

Rhythmic growth: axes that show a marked periodicity of endogenous elongation.

Immediate or immediately developing shoots: growth without dormancy phase of the bud, the shoots develop on the shoot that is elongating and are generally located in the middle of this bearing shoot.

Delayed twigs or delayed developing shoots: dormancy (resting) phase of the lateral bud, the twigs develop the year after the elongation of the bearing shoot.

Hypopoduim: very long internode set in the case of an immediate shoot, length of internode between the base of the shoot and the first leaf.

Polycyclism: the annual shoot is composed of 2 or more growth units.

Monocyclism: the annual shoot is composed of a single growth unit.

Acrotony: preferential development of lateral axes at the top of a shoot or at the end of the growth unit.

Basitony: preferential development of twigs at the base of the bearing entity or growth unit.

Mesotony: the twigs develop in a privileged way in the median zone of the bearing unit.

Hypotony: twigs with a large diameter are distributed on the lower part of the branches.

Epitony: distribution of branches on the upper side of the axes and branches.

Amphitony: when the branches are carried preferentially in a horizontal plane on either side of the bearing axis.

NB: **hypotony** and **amphitony** are involved in the extension of the branches and may overlap.

Epicormic shoot (offshoot or supplanter): a shoot developing from a dormant lateral bud on the trunk or on main branches.

Reiteration: A reiterationis a youngtreegrowing on an oldsupporting axis. The position of reiterationis not predictable, itisdetermined by the presence of a local energyresource, or trauma. The reiteration has a dual function of exploiting light resources and ensuringresilience to trauma. It issaid to be total if itappears on the trunk of the tree and partial if itappears on other types of axis.

Forking: formation of two or more morphologically identical relay axes in a sympod from the apical trauma of a single axis.