Plant architecture reveals contrasting developmental strategies in two threatened West African timber species (Khaya senegalensisand Pterocarpus erinaceus): implications for conservation and sustainable forest management

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Plant architecture reveals contrasting developmental strategies in two threatened West African timber species (*Khaya senegalensis* and *Pterocarpus erinaceus*): implications for conservation and sustainable forest management

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***** *In this document, complex and unfamiliar architectural terms are defined in a glossary appended to the article before the reference list, to facilitate understanding. Indeed, the vocabulary used differs from that commonly used by foresters.*

Key Message

First formal architectural description of two threatened West African timber species identifies distinct developmental models and pinpoints, via a Favourable Development index, optimal localities for reforestation:

- First complete architectural description of *Khaya senegalensis* and *Pterocarpus erinaceus* ;
- Contrasting developmental strategies follow Rauh and Troll architectural models ;
- Architectural plasticity reveals adaptation across West African ecological gradients ;
- Architectural traits maps optimal sites for restoration and reforestation ;
- Plant architecture supports conservation and sustainable management of threatened trees.

Abstract

Architectural analysis provides a powerful analytical framework for understanding the ontogenetic trajectories of tree species and their adaptive responses to environmental constraints. Despite their ecological, economic, and cultural importance in West African agroforestry systems, the architectural development of *Khaya senegalensis* (Desr.) A. Juss. (Meliaceae) and *Pterocarpus erinaceus* Poir. (Fabaceae), two overexploited taxa classified as Vulnerable on the IUCN Red List, had never been formally described. This study presents the first complete characterization of their architectural development, from the seedling stage to senescence, based on architectural and retrospective analyses conducted on 360 individuals per species across seven localities along a south-north bioclimatic gradient in Côte d'Ivoire, covering contrasting vegetation zones ranging from dense humid forest to dry Sudanian savanna. Both species display well-defined ontogenetic trajectories comprising four phases: juvenile establishment, architectural construction, reproductive transition, and crown restructuring associated with ageing. Distinct architectural models were identified: *K. senegalensis* conforms to Rauh's model, characterized by a monopodial orthotropic trunk with indefinite growth and rhythmic acrotonic branching; *P. erinaceus* follows Troll's model, in which the orthotropic trunk progressively gives rise to a sympodial plagiotropic system with mixed terminal and lateral flowering. Architectural units, defined as the minimal structural organization enabling a species to reach reproductive maturity, were established at the adult stage: that of *K. senegalensis* comprises four axis categories and five branching orders, while that of *P. erinaceus* comprises three axis categories and up to six branching orders in old trees. Significant variation in growth-unit morphology among habitats and localities ($P<0.05$) revealed the architectural plasticity of both species in response to ecological gradients. The calculated Favourable Development indices (*FDi*) identified Bouaké and Katiola as optimal zones for *K. senegalensis*, and Bouaké and Toumodi for *P. erinaceus*, providing objective spatial criteria for reforestation planning. These findings demonstrate that architectural traits are robust indicators of development, adaptive strategies, and crown functioning. By linking structural organization to productivity, resilience, and regeneration potential, this study provides a scientific basis for integrating architectural analysis into reforestation programmes, sustainable forest management, and the design of agroforestry systems for threatened African tree species facing growing climatic and anthropogenic pressures. Complementary regression analyses further showed that phytomer number, rather than internode elongation, primarily governs growth-unit length in both species, and that growth unit diameter scales positively with growth unit length; a multivariate analysis of variance (MANOVA) confirmed that ontogenetic stage and locality, but not habitat alone, robustly structure growth-unit morphology.

Keywords: Tree architecture plasticity, Ontogenetic trajectory, architectural unit, agroforestry species conservation, West Africa

Introduction

West African forest and savanna ecosystems are undergoing rapid degradation as a result of agricultural expansion, uncontrolled logging, climatic variability, and increasing demographic pressure (Amani et al., 2022; Lykke et al., 2025). These pressures have led to a significant reduction in woody biodiversity, particularly affecting multi-purpose tree species that play essential ecological and socio-economic roles (Adji et al., 2023; Amani et al., 2022; Lykke et al., 2025). Plant architecture is one of the most powerful, yet least used, tools in forest management. Defined as the way in which a plant constructs its aerial structure, through its growth pattern, branching, axis differentiation, and the position of reproductive organs, it constitutes the visible expression of a species' genetic programme and of its adaptive response to the environment (Barthélémy and Caraglio, 2007; Hallé et al., 1978). Over more than five decades, from the foundational work of Hallé et Oldeman, (1970) in tropical forests to contemporary applications in European silviculture and South American forest management, architectural analysis has demonstrated its value as a diagnostic, predictive, and management tool for understanding and sustaining forest resources (Anest et al., 2021; Sabatier et al., 2014). Yet in West Africa this discipline remains practically unknown. Reforestation programmes, agroforestry schemes, and national forest management plans continue to be designed without any reference to the architectural development of target species. No architectural unit « the minimal stem structure necessary and sufficient for a species to reach sexual maturity and thereby complete its biological or life cycle » (Barthélémy, 1991), has ever been formally established for the major native tree species of the region. Yet understanding this unit is essential for interpreting tree functioning, productivity, and adaptive capacity. This therefore constitutes a serious knowledge gap. Without understanding how a tree builds itself from seedling to senescence, foresters cannot reliably identify optimal growing areas, diagnose tree health, forecast productivity, select high-performing genotypes, or prescribe relevant silvicultural interventions.

This gap is particularly critical for *Khaya senegalensis* (Desr.) A. Juss. (Meliaceae), the African mahogany or caïlcédrat or dry-zone mahogany, and *Pterocarpus erinaceus* Poir. (Fabaceae), African rosewood or vène, two emblematic agroforestry tree taxa that are overexploited and threatened in the Guinean-Sudanian savanna zone of West Africa, raising concerns about their long-term sustainability. Both species are listed on the IUCN Red List: *Pterocarpus erinaceus* is classified as Vulnerable (Dumenu, 2019; CITES, 2016), while *Khaya senegalensis* is

under growing overexploitation pressure and has recently been classified as Vulnerable (Centre, 1998). They are among the most socio-economically important species for rural populations in northern Côte d'Ivoire and the wider sub-Saharan region, providing timber, food, fodder, medicine, fuelwood, and cultural services (Bouka Dipelet et al., 2019; Goba et al., 2019). Despite this ecological, economic, and cultural importance for rural populations, the literature on both species remains limited to germination studies, basic morphological characterizations, dendrometric inventories, and studies of regeneration, population dynamics, or ecological distribution. Little attention has been paid to the endogenous developmental processes that determine their morphology. Their architectural and organizational developmental sequences (from seedling to senescent tree), their genetic programme, their architectural units, and their adaptive responses to climatic and edaphic gradients have never been formally described. At a time of intensive deforestation and climate change, this knowledge gap compromises rational management, reforestation programmes, and the conservation of these two key resources.

This study fills this gap by examining, for the first time, the complete characterization of the architectural development and architectural unit of these two species. Based on a retrospective morphological analysis of 360 individuals per species, covering all ontogenetic stages (young, adult, old) and observed across seven localities along a bioecological gradient extending from the humid forest zone to the dry Sudanian savanna of Côte d'Ivoire, we establish (i) the complete ontogenetic sequence of architectural development of *Khaya senegalensis* and *Pterocarpus erinaceus*, from juvenile to senescent stages; (ii) their respective architectural models and architectural units; (iii) the influence of habitat and locality on growth-unit morphology as indicators of species adaptation; and (iv) a conceptual framework for integrating architectural knowledge into forest management decision-making in West Africa. This work represents the first architectural study of these two species and advances a broader argument: architectural analysis should become a standard pillar of agroforestry and reforestation policy in West Africa, as it has become in Europe (France) and South America. To reinforce this argument, we further complement the categorical ANOVA/MANOVA framework with continuous regression, allometric, and multivariate analyses of the same dataset.

Materials and methods

Species studied

Khaya senegalensis (Desr.) A. Juss. (Meliaceae), commonly known as African mahogany or dry-zone mahogany, is a large deciduous tree of the Guinean-Sudanian savanna, reaching 25-35 m in height with a trunk diameter

exceeding 2 m in old trees (Adji et al., 2022c; Tre et al., 2025). It occurs naturally from Senegal to Uganda and is valued for its high-quality durable timber, as well as its bark, which is used in traditional pharmacopoeia. It is a heliophilous species adapted to deep, well-drained soils, and is heavily exploited for charcoal, carpentry, and construction (Bouka Dipelet et al., 2019; Issa et al., 2018). *Pterocarpus erinaceus* Poir. (Fabaceae), African rosewood or vène, is a medium to large tree (15-25 m in height) of the West African savanna, classified as Vulnerable by the IUCN following massive and uncontrolled commercial timber extraction, notably for export to Asia (Dumenu, 2019). It provides a valuable red hardwood, edible leaves used as fodder and food, and compounds used in traditional medicine (Dumenu, 2019; Goba et al., 2019). Both species are emblematic of the wooded parklands of the savanna of northern Côte d'Ivoire and are listed as priority species in national reforestation programmes, but neither has been the subject of an architectural study.

Study sites

The study was conducted in seven localities along a south–north bioecological gradient in Côte d'Ivoire, covering four vegetation zones (Fig. 1): the dense humid forest sector (Daloa), the transitional mesophilous sector (Toumodi, Bouaké), the sub-Sudanian sector (Katiola, Niakara), and the Sudanian sector (Korhogo, Ferkessédougou). These localities span a rainfall gradient from 1,900 mm/year in the south to 1,200 mm/year in the north and represent the full range of natural habitats of the two target species (Table 1).

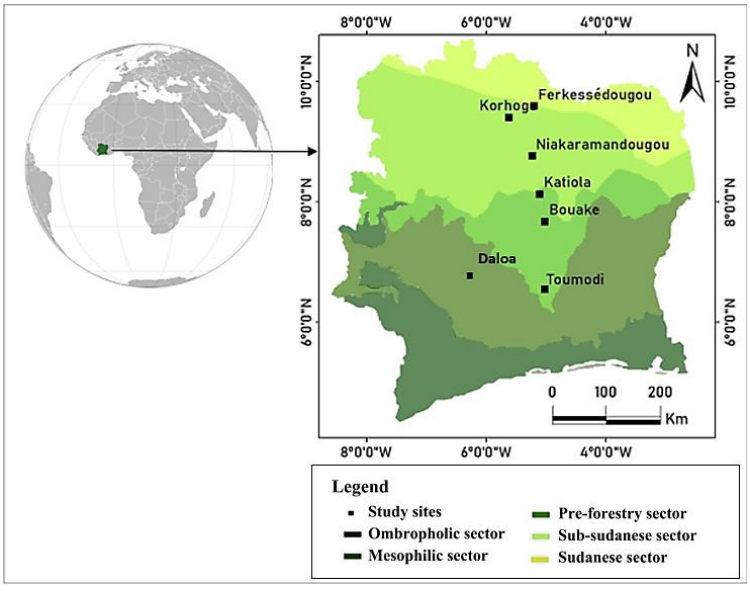


Fig.1. Map of the study sites along the south-north bioecological gradient in Côte d'Ivoire, showing the seven localities and their vegetation zones

Table 1. Soil and climatic characteristics of the experimental sites

Sites/localities	GPS coordinates	Vegetation	Climate	Temperature (°C)	Rainfall (mm/yr)	Soil type
Ferké	5°23'43.40" W; 9°36'1.87" N	Wooded and shrub savanna	Dry tropical	27 - 40	263-1200	Ferralitic soils (ferrisols, Cambisols, Fluvisols, Luvisols), strongly to moderately desaturated.
Korhogo	5°36'12.40" W; 9°33'24.69" N	Open forest (wooded savanna)	Dry tropical	26.6 - 35.7	817-1216	Ferruginous (90%) and Ferralitic (10%): shallow gravelly soil, deep gravel with heavy texture, poor in organic matter, strongly desaturated.
Niakara	5°18'40.74" W; 8°40'47.98" N	Wooded and grassy savanna	Dry tropical	24.7 - 38	800-1230	Complex of weakly desaturated ferralitic soils and tropical eutrophic brown soils derived from basic rocks.
Katiola	5°7'35.81" W; 8°13'53.94" N	Wooded and grassy savanna	Humid tropical	24 - 36	1100-1200	Moderately to strongly desaturated ferralitic soils.
Bouaké	5°5'47.33" W; 7°40'45.34" N	Open forest (wooded savanna)	Humid tropical	23.6 - 34	1100-1200	Gravelly ferralitic, moderately saturated, reworked, shallow, derived from granitic weathering material with a sandy-clay texture.
Toumodi	5°1'34.96" W; 6°22'42.68" N	Open forest (wooded, grassy savanna and gallery forests)	Humid tropical	26.6 - 30	1092-1200	Ferralitic soil on granitic bedrock (sandy-clay soil), characterized by weak differentiation and friable horizon consistency.
Daloa	6°26'9.20" W; 6°54'32.06" N	Dense humid tropical forest	Humid tropical	21 - 34	1000-1900	Ferralitic, deep, acidic, and desaturated in exchangeable bases, rich in organic matter.

°C = degrees Celsius**, mm** = millimeters**, W** = west**, N** = north.

(Adji et al., 2022b)

Sampling design

For each species and each of the three ontogenetic stages (young: 0-5 years; adult: 6-20 years; old: ≥ 21 years) growing under variably sized forest cover, 10 wild individuals were arbitrarily selected in open habitat (full sun) and 10 in closed habitat (understorey/canopy cover) in each of six localities (excluding Daloa, where individuals were monitored and observed in a nursery context at 1 and 2 years of age, and therefore not included in the study). Only architectural analyses concerned the locality of Daloa (young nursery grown plants); retrospective analyses did not include this locality, as natural or wild populations of the species are not distributed there. This yielded a total of 360 individuals from wild, naturally regenerating, freely growing populations observed per species, distributed by stage, habitat, and locality (Table 2). All individuals were in good physiological condition and free of major 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, and type of axes measured on the tree. The stages (young, adult, and old) were arbitrarily chosen on the basis of their dendrometric size (height and diameter), based on individuals raised in nurseries and those present in plots established in the 1970s and 1980s by the Côte d'Ivoire National Agricultural Research Centre (CNRA).

Table 2. Dendrometric characteristics and number of individuals observed by species, stage, and environment

	Ages	Habitats	H (m)			D or DBH (cm)			N-individual	Axes examined
			Min	Max	Mean	Min	Max	Mean		
Khaya senegalensis	Young trees (0-5 yr)	Full sun	0.33	5.7	1.71±0.29	0.52	9.74	3.54±1.29	60	Main trunk
		Understorey/shade	0.52	4.8	2.54±0.15	1.18	8.85	5.39±1.07	60	Main trunk
	Adult trees (6-20 yr)	Full sun	7.5	17	14.09±5.6	14.3	49.62	34.97±4.01	60	Branch
		Understorey/shade	7.4	18.5	11.6±6.18	12.3	45.92	29.08±2.97	60	Branch
	Old trees (≥ 21 yr)	Full sun	21	37	31.46±4.4	44	276.08	100.02±57.23	60	Branch
		Understorey/shade	20.5	34	28.76±5.5	34.3	129.3	80.44±34.8	60	Branch

Pterocarpus erinaceus	Young trees (0-5 yr)	Full sun	0.27	3.8	1.83±0.51	0.38	9.59	3.21±0.49	60	Main trunk
		Understorey/shade	0.28	4.3	2.32±0.59	0.54	9.20	3.93±0.69	60	Main trunk
	Adult trees (6-20 yr)	Full sun	10.1	15.6	12.18±2.3	21.4	36.62	27.37±4.93	60	Branch
		Understorey/shade	10.8	14.5	11.94±3.1	14.2	38.1	24.6±6.28	60	Branch
	Old trees (≥ 21 yr)	Full sun	16.5	19.5	17.78±1.8	40.3	71.4	53.82±12.1	60	Branch
		Understorey/shade	17	22	19.3±3.2	41.7	63	50.51±10.7	60	Branch

H = Height, **D** or **DBH** = collar diameter or diameter at breast height, **Min** = minimum, **Max** = maximum, **Mean** = mean, **m** = meter, **cm** = centimeter, **N** = number of individuals evaluated.

Choice of axis type and habitat

Axis types were selected according to crown accessibility in the two different habitats. In young trees, the axes evaluated concerned the trunk. For adult and old trees, evaluations focused on primary, secondary, and tertiary branches, as well as short shoots. Observations were made in situ for young trees, whereas for adult and old trees, axes were cut and transported to the laboratory for evaluation. Two habitat (environment) types were considered: understorey and full sun. The former concerns individuals living in a heavily shaded environment with forest cover, or in an overcrowded environment, or benefiting from an upper canopy shelter. The latter concerns isolated individuals in full sun or in an open environment in direct contact with sunlight.

Architectural and retrospective analysis

For each individual, a complete architectural description of the aerial branching system was carried out in the field and supplemented by laboratory observation of harvested branch samples. Retrospective analysis, which uses morphological markers arising from meristem activity and imprinted in the bark and wood anatomy (bud-scale scars, cataphylls, growth arrests (GA) or growth stop (GS), pith constrictions, apex death zones, growth rings) to reconstruct past growth history, was applied to delimit growth units (GU), count phytomers, and measure the dimensions (length and mean diameter) of growth units on the first two GUs from the apex of each sampled axis.

Collected axes were split (longitudinal and transverse sections) in order to identify growth arrests that were not visible on the bark of the axes. Indeed, under certain environmental conditions, growth arrests were less visible on the bark (smooth bark) along the axes. Data were collected during both the rainy and dry seasons, at different age stages, and in two distinct habitats (full sun and understorey).

In order to identify environments favourable to the cultivation of the target species, we calculated the Favourable Development index (*FDi*). It corresponds to the mean of the sums of the quotient of growth-unit length (L_{GU}) divided by the number of phytomers it carries ($Nbr_{\text{-}Internode}$) at each GU rank (i), contained within the physiological ages (φ) of the numbers of axis populations ($N_i^{\varphi}(p)$) sampled for each locality and habitat (P). or *FDi* aggregates the ratio between GU length (L_{GU}) and the number of internodes per GU (N_{int}) across the four physiological ages φ examined, averaged across the sampled axes of a population P in a given locality-habitat combination P:

$$FD_i = M \,.\, \sum_{n=1}^{P} \sum_{\varphi=1}^{mx\varphi} N_i^{\varphi}(p) \,.\, \left(L_{GU} \,.\, \frac{1}{Nbr{\sim}Intrenode}\right)_i \varphi p.$$

Where M is a normalization factor (inverse of the total number of axes sampled in P) and $mx\varphi = 4$ is the maximum physiological-age rank examined. Higher *DFi* values indicate longer, less-fragmented GUs in the considered population. Importantly, *FDi* is an inter-individual or/and inter-site ranking metric under the present sampling scheme. It has not been validated against independent fitness data (survival, fecundity) and is not intended as an absolute, cross-study fitness predictor. This limit is further discussed below. In a population of individuals with rhythmic growth, individuals with higher *FDi* values show better development. Consequently, an environment comprising individuals with a higher *FDi* relative to individuals from another environment indicates that this environment is more favourable to development. We then compared the number of growth arrests (GA) of each axis; the fewer GAs an axis contains, the better the development of the individual.

Regarding architectural analysis, based on the morphological concepts and criteria of Barthélémy et al. (1995, 1989), Barthélémy and Caraglio (2007), and Sabatier (1999), the overall, precise, and complete morphology of the aerial branching system of individuals was described across varied environments (understorey and full sun). For each species, axis categories of the architectural unit were identified according to morphological and functional properties. Individuals were characterised using a set of architectural criteria. The spatial arrangement and structure of the different constituent axes were captured by means of drawings and architectural analysis sheets. The categorization of axis types of the architectural units, as well as the establishment of architectural characteristics, were carried out using the following qualitative traits:

- leafy axis (phyllotaxis and leaf type);
- growth strategy or mode (definite/indefinite, monopodial/sympodial, polycyclism);
- preferential direction and differentiation of axes (orthotropic, plagiotropic, mixed, ageotropic);
- branching mode (branching order, immediate/delayed, rhythmic/continuous/diffuse, acrotonic/mesotonic/basitonic, epitonic/hypotonic/amphitonic);
- size of GUs and annual shoots (in number of phytomers and GUs);
- polycyclism and monocyclism (number of GUs per annual shoot);
- position of sexuality (terminal/lateral/mixed/absent);
- leaf deciduousness (period during which leaves fall from the tree, phenology);
- axis taper (cylindrical/conical shape, height and diameter);
- axis complexity (branching orders, bearer–borne relationship);
- type of reiteration (total/partial/sequential/traumatic).

Quantitative parameters included: basal length and diameter of the GU (cm); number of phytomers per GU; and number of growth arrests (GA or GS) per axis.

For each age category (young, adult, and old), the fundamental morphological and architectural characteristics of each target tree species were described in the field with the naked eye. Binoculars were used to describe the tallest trees. Observation began with the youngest individuals (unbranched seedling stage) and progressed to increasingly complex and older individuals (adults and old trees). The whole plant was taken into account. In some cases, parts of trees were collected after felling, in order to make detailed observations on site and in the laboratory. Notes specifying scale, plant location, and certain facts were marked on each drawing. Each drawing was a synthesis of observations made on several individuals that had reached the same developmental stage.

Statistical analyses

Quantitative data were subjected to one and two-way analyses of variance (ANOVA/MANOVA) to compare the parameters evaluated between habitats and localities, using *SAS* software v.9.4. Post-hoc comparisons used the Student-Newman-Keuls test at a significance threshold of *alpha = 5%.* Differences were considered significant at $P < 0.05$. Because several individuals were sampled within the same locality, and because this hierarchical sampling structure could inflate the significance of habitat and age comparisons if treated as fully independent

(pseudoreplication), a post hoc robustness check was additionally performed: for each growth unit variable, linear mixed-effects models were fitted with locality included as a random intercept (habitat and age as fixed effects; *REML* estimation, Python statsmodels *v.0.14*), and the resulting significance levels were compared with those of the original *ANOVA* framework.

In addition to this categorical framework, complementary regression analyses were performed on the individual-level dataset to test specific architectural hypotheses (section 3.2). For each bivariate relationship, five candidate models (linear, quadratic, logarithmic, power, exponential, plus a saturating asymptotic growth model) were fitted and compared using the coefficient of determination (R^2) and Akaike's Information Criterion (*AIC*), both computed on the original response scale for fair comparison across model forms; quadratic fits whose vertex fell within the observed predictor range (implying a biologically implausible reversal) were excluded in favour of the best monotonic alternative. Because the dataset provides only the rainfall range reported per locality (Table 1) rather than a single annual normal, the midpoint of each range was used as an approximate rainfall proxy for exploratory gradient regressions; given the overlap between several localities' ranges, this proxy should be interpreted as a coarse, ordinal approximation rather than a fine-grained continuous covariate. One *P. erinaceus* record with a growth-unit diameter exceeding the individual's own trunk diameter was identified as a probable data entry anomaly and excluded from analyses involving growth unit diameter (n = 133 for these analyses). Multivariate analysis of variance (MANOVA, Wilks' lambda) was additionally used to jointly test the effects of habitat, ontogenetic stage, and locality on the vector of growth-unit length, growth-unit diameter, and phytomer number.

Results

Retrospective analysis

Habitat effect on marker morphology

Across all ages and localities combined, the results (Table 3) indicated that the number of growth arrests varied from one habitat to another ($P < 0.05$). In *Khaya senegalensis*, the mean number of growth arrests was 7.74 in full sun versus 9.06 in understorey; in *Pterocarpus erinaceus*, the mean was 7.51 in full sun versus 8.82 in understorey. The number of phytomers counted per growth unit varied between habitats only in *Pterocarpus erinaceus* ($P < 0.05$), at 15.05 in full sun versus 17.84 in understorey. The Favourable Development indices (*FD*i) calculated for the target species were higher in full-sun habitats regardless of species (Table 3). In *Khaya*

senegalensis, they were 1.27 versus 1.1. In *Pterocarpus erinaceus*, they were 1.5 versus 1.22. Moreover, the number of growth arrests along the axes was reduced in this habitat. Overall, the full-sun environment was more favourable to shoot development in both species. In general, individuals observed in the understorey showed growth difficulties (Table 3).

Table 3. Influence of habitat on the morphology of primary growth markers

Species	Habitats	Nbr-growth arrests/axis	GU-length (cm)	GU-diameter (cm)	Nbr phytomers/GU	*FDi*
Khaya senegalensis	**Full sun**	7.74±0.3 b	21.89±1.91 a	1.33±0.06 a	17.3±0.59 a	**1.27**
	Understorey	9.06±0.55 a	19.34±1.15 a	1.39±0.06 a	17.5±0.73 a	1.1
	Pr > F	**0.0379**	**0.2315**	**0.5950**	**0.8572**	
Pterocarpus erinaceus	**Full sun**	7.51±0.39 b	22.81±1.13 a	1.11±0.06 a	15.08±0.64 b	**1.5**
	Understorey	8.82±0.54 a	21.94±1.01 a	1.26±0.18 a	17.84±0.71 a	1.22
	Pr > F	**0.0451**	**0.5871**	**0.3739**	**0.0056**	

Values sharing the same letter within the same column are not statistically different at the 5% threshold. **Full sun** = open, exposed environment in direct sunlight; **Understorey** = crowded environment or under forest canopy cover

Locality effect on marker morphology

Across localities, the northernmost (driest) sites generally produced shorter growth units in both species, whereas southern localities (wetter, closer to the forest zone) tended to produce longer GUs. This trend was clearest in *Khaya senegalensis*, where the effect of locality was highly significant for all GU parameters ($P < 0.001$; Table 4). These locality-scale variations provide quantitative architectural markers for identifying ecologically favourable growing areas for each species, a key result for reforestation planning. Analyses of variance (Table 4), across all habitats and ages combined, showed that regardless of species, the observed marker variables varied statistically from one locality to another ($P < 0.05$). The number of growth arrests was 8.95 at Ferké, 9.13 at Korhogo, 8.39 at Niakara, 6.44 at Katiola, 10.64 at Bouaké, and 5.5 at Toumodi for *Khaya senegalensis*; for *Pterocarpus erinaceus*, this number was 10.24 at Ferké, 8.5 at Korhogo, 9.28 at Niakara, 7 at Katiola, 8.21 at Bouaké, and 8.35 at Toumodi. The calculated Favourable Development index (*FDi*) values, combined with the number of growth arrests along axes, indicate that the localities of Bouaké (*FDi*: 1.86) and Katiola (*FDi*: 1.5) are

favourable areas for the development of shoots in *Khaya senegalensis*. The localities of Bouaké (*FDi*: 1.7) and Toumodi (*FDi*: 1.54) are favourable areas for *Pterocarpus erinaceus*.

Table 4. Influence of locality on the morphology of primary growth markers

Species	Localities	Nbr-growth arrests/axis	GU-length	GU-diameter	Nbr phytomers/GU	*FDi*
Khaya senegalensis	**Ferké**	8.95±0.5 ab	16.68±1.51 c	1.44±0.07 b	15.77±0.68 b	1.06
	Korhogo	9.13±0.88 bcd	18.75±1.72 c	1.39±0.1 b	17.64±0.86 ab	1.06
	Niakara	8.39±0.35 bcd	18.09±1.5 c	1.21±0.06 b	20.46±1.23 a	0.88
	Katiola	6.44±0.87 d	25.82±2.87 b	1.4±0.1 b	17.19±1.17 ab	**1.5**
	Bouaké	10.64±0.73 a	29.68±11.14 a	1.91±0.26 a	15.89±1.33 b	**1.86**
	Toumodi	5.5±0.38 cd	19.65±2.41 c	1.07±0.09 b	14.44±1.18 b	1.36
	Pr>F	**0.001**	**0.001**	**0.001**	**0.001**	
Pterocarpus erinaceus	**Ferké**	10.24±0.94 a	22.94±1.49 bc	1.19±0.1 ab	17.05±1.07 ab	1.35
	Korhogo	8.5±0.61 ab	20.49-1.7 bc	0.98±0.06 ab	15.62±0.97 b	1.31
	Niakara	9.28±0.62 a	25.83±1.74 bc	1.25±0.09 ab	22.29±1.02 a	1.15
	Katiola	7±1.13 c	20.56±1.3 bc	1.02±0.08 ab	15.09±1.29 c	1.36
	Bouaké	8.21±1.08 ab	27.45±4.08 a	1.37±0.19 ab	16.09±2.06 c	**1.7**
	Toumodi	8.35±0.59 ab	25.17±2.12 ab	1.8±0.46 a	16.39±0.64 b	**1.54**
	Pr>F	**0.001**	**0.0015**	**0.0166**	**0.001**	

Values sharing the same letter within the same column are not different at the 5% threshold.

Individus age effect on marker morphology

Analysis of variance showed that in *Khaya senegalensis*, GU length and the number of phytomers per GU differed between ages ($P < 0.05$), whereas the number of GAs per axis and mean GU diameter remained unchanged ($P > 0.05$). GU length was highest in young individuals (23.45 cm) and lower in adults (17.38 cm) and old trees (18.02 cm). As for the number of phytomers per GU, it increased from the youngest individuals (16.31) to adults (17.75) and older trees (19.77) (Table 5). Age influences the primary growth markers in this species (Table 5). In *Pterocarpus erinaceus*, most of the parameters evaluated (Table 5) did not vary statistically between ages ($P > 0.05$), except for the number of phytomers carried per GU, which increased from the youngest (14.99) to adult

(17.28) and old (20.26) individuals ($P < 0.05$). Age also influences the number of phytomers per GU in this species.

Table 5. Influence of individual age on marker morphology

Species	Ages	Nbr-growth arrests/axis	GU-length	GU-diameter	Nbr phytomers/GU
Khaya senegalensis	**Vieux-arbre**	8.25±0.33 a	18.02±1.09 b	1.37±0.05 a	19.77±0.82 a
	Arbre-adulte	8.25±0.43 a	17.38±1.42 b	1.33±0.08 a	17.75±1.01 ab
	Jeune-arbre	7.95±0.41 a	23.45±2.28 a	1.34±0.06 a	16.31±0.64 b
	Pr>F	**0.87**	**0.0213**	**0.9463**	**0.0103**
Pterocarpus erinaceus	**Vieux-arbre**	9.22±0.54 a	22.9±1.76 a	1.09±0.09 a	20.26±1.43 a
	Arbre-adulte	7.63±0.34 a	24.44±1.4 a	1.25±0.07 a	17.28±0.71 b
	Jeune-arbre	7.94±0.47 a	21.66±1.06 a	1.16±0.12 a	14.99±0.62 c
	Pr>F	**0.3324**	**0.3520**	**0.8528**	**0.0007**

Values sharing the same letter are not statistically different at the 5% threshold within the same column.

Robustness check: linear mixed-effects reanalysis

Because several sampled individuals shared the same locality, the habitat and age comparisons reported above (Tables 3 and 5) could be affected by pseudoreplication if locality-level non-independence is ignored. To evaluate this, each growth unit variable was re-analysed using linear mixed-effects models with locality included as a random intercept, and the resulting significance levels were compared with those of the original, « naive » ANOVA framework (Fig. 2). This comparison shows that most conclusions are robust, but three results lose statistical significance once locality is accounted for: the habitat effect on the number of growth units per axis (a proxy for growth arrests) in both *K. senegalensis* (naive $P = 0.038$ vs. mixed-model $P = 0.765$) and *P. erinaceus* (naive $P = 0.045$ vs. mixed-model $P = 0.543$), and the age effect on the number of phytomers per GU in *P. erinaceus* (naive $P < 0.001$ vs. mixed-model $P = 0.352$). By contrast, the habitat effect on the number of phytomers per GU in *P. erinaceus* remains significant in both frameworks, although markedly weaker once locality is modelled (naive $P = 0.006$ vs. mixed-model $P = 0.049$). Locality alone accounted for 10 to 31% of the total variance across variables (intraclass correlation, Fig. 3), confirming that the clustering of individuals within localities is a non-negligible source of non-independence in this dataset. Full mixed-model coefficients are reported in Table S7 (Appendix).

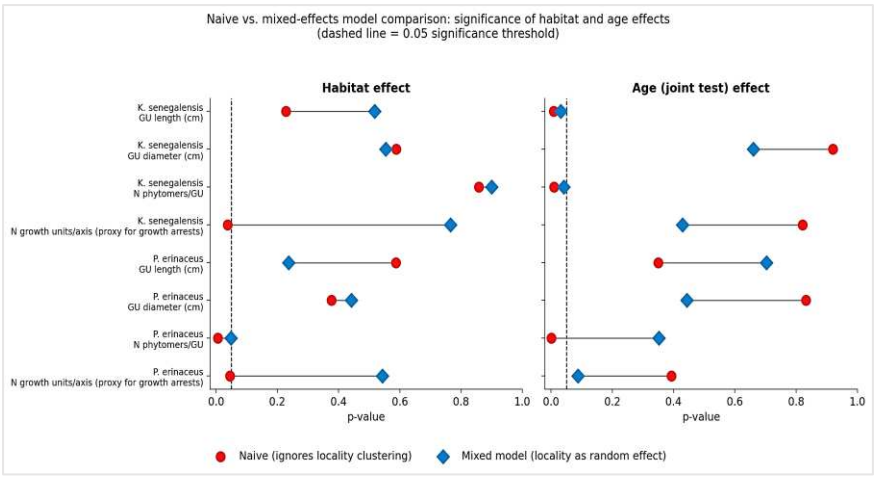


Fig. 2. Comparison of significance levels (*P-values*) between the original « naive » ANOVA framework (red circles), which does not account for locality clustering, and linear mixed-effects models with locality as a random intercept (blue diamonds), for the habitat effect (left) and the age effect (right) on growth-unit variables. The dashed line marks the $P = 0.05$ significance threshold.

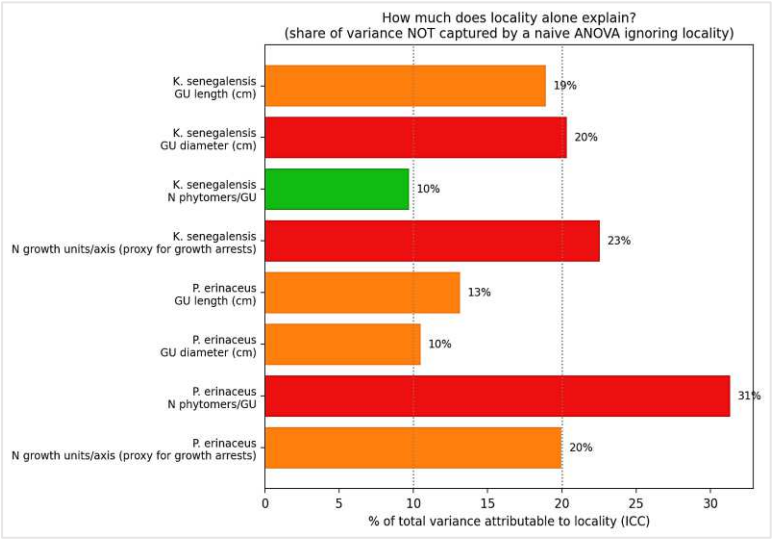


Fig. 3. Proportion of total variance in each growth-unit variable attributable to differences between localities (intraclass correlation, *ICC*), independent of habitat and age. Values of 10-31% indicate a non-negligible grouping structure that is not accounted for by the original ANOVA framework.

Detailed results on the influence of the factors explored above (habitat, locality, and habitat × locality) on growth unit morphology at each age stage (young, adult, and old) for each target species are presented in the appendices as supplementary information to this document.

Complementary regression, allometric, and multivariate analyses

To complement the categorical ANOVA/MANOVA framework presented above, we tested a set of specific architectural hypotheses using continuous regression, allometric, and multivariate analyses on the same individual-level dataset (n = 135 for *K. senegalensis* and n = 134 for *P. erinaceus,* Figs.4-12). For each bivariate relationship, five candidate models (linear, quadratic, logarithmic, power, exponential, plus a saturating asymptotic growth model) were compared by *AIC* on the original response scale.

Height increased with trunk diameter in both species (Fig.4), but the shape of the relationship differed markedly. In *K. senegalensis*, height rose steeply and then plateaued near 35-37 m from approximately 100 cm *DBH* onward, best described by a saturating asymptotic model ($H = 37.2 \times (1- e^{-0.025 \cdot D})$; $R^2 = 0.95$), consistent with Rauh's model, in which the monopodial trunk achieves most of its height early while radial growth continues largely independently in older individuals. In *P. erinaceus*, height increased more continuously across the sampled diameter range without a clear plateau, best described by a monotonic quadratic model ($R^2 = 0.95$), consistent with Troll's model, in which height accrues through the progressive stacking and straightening of successive relay axes. A conventional log-log power-law fit, the usual allometric convention, performed poorly for *K. senegalensis* ($R^2 = 0.26$) precisely because the relationship saturates, underlining the value of comparing several candidate models rather than assuming a single allometric form a priori.

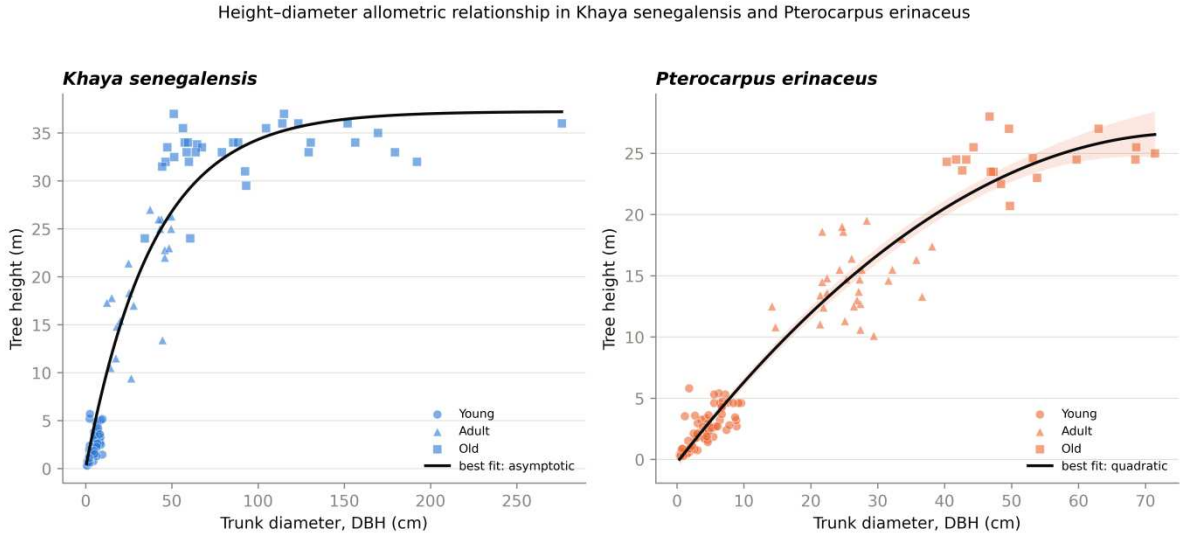


Fig. 4. Height-diameter allometric relationship in *K. senegalensis* and *P. erinaceus* (n = 135 and 134). Marker shape denotes ontogenetic stage (young, adult, old). Curves show the best-supported monotonic model with 95% confidence band.

Contrary to the expectation that architecturally more developed (taller) trees would produce longer growth units, raw tree height was a weak predictor of GU length in both species (Fig.5 ; *K. senegalensis*: $R^2 = 0.06$, Pearson r

= -0.20, $P = 0.018$; *P. erinaceus*: $R^2 = 0.17$ under a saturating model, linear term not significant, $P = 0.12$). GU length was instead highest in young individuals and declined or plateaued thereafter (Table 5), indicating that ontogenetic stage and site, rather than height per se, are the primary drivers of GU length.

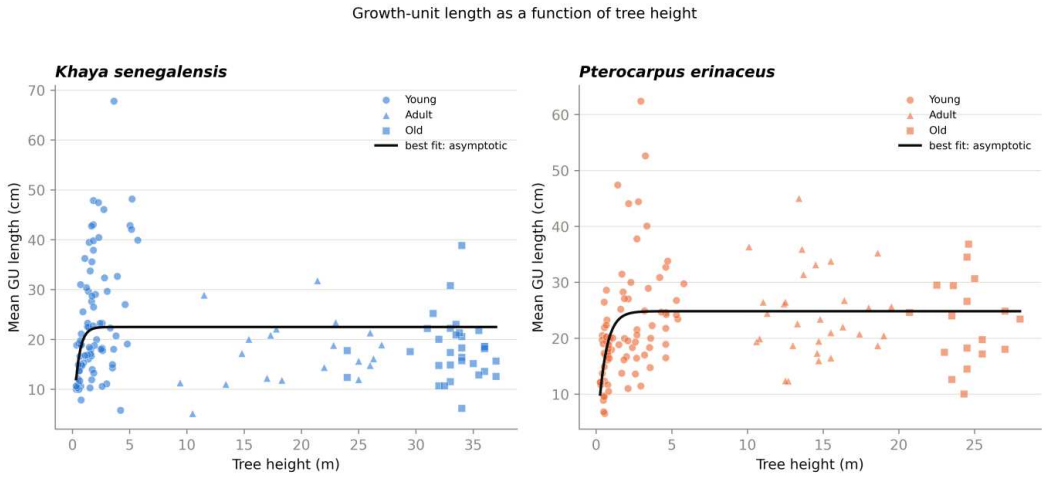


Fig. 5. Mean growth unit (GU) length as a function of tree height in *K. senegalensis* and *P. erinaceus*.

Phytomer number increased significantly with GU length in both species (Fig.6 ; *K. senegalensis*: $R^2 = 0.24$, $P < 0.001$, best fit saturating; *P. erinaceus*: $R^2 = 0.30$, $P < 0.001$, best fit quadratic with a downturn beyond ~35 cm). Longer growth units are therefore built primarily by adding phytomers rather than by proportionally elongating internodes; the marginal gain in phytomer number diminishes at the largest GU lengths, implying relatively longer internodes in the longest GUs of both species, a pattern directly relevant to the internode-length logic underlying the Favourable Development index (*FDi*).

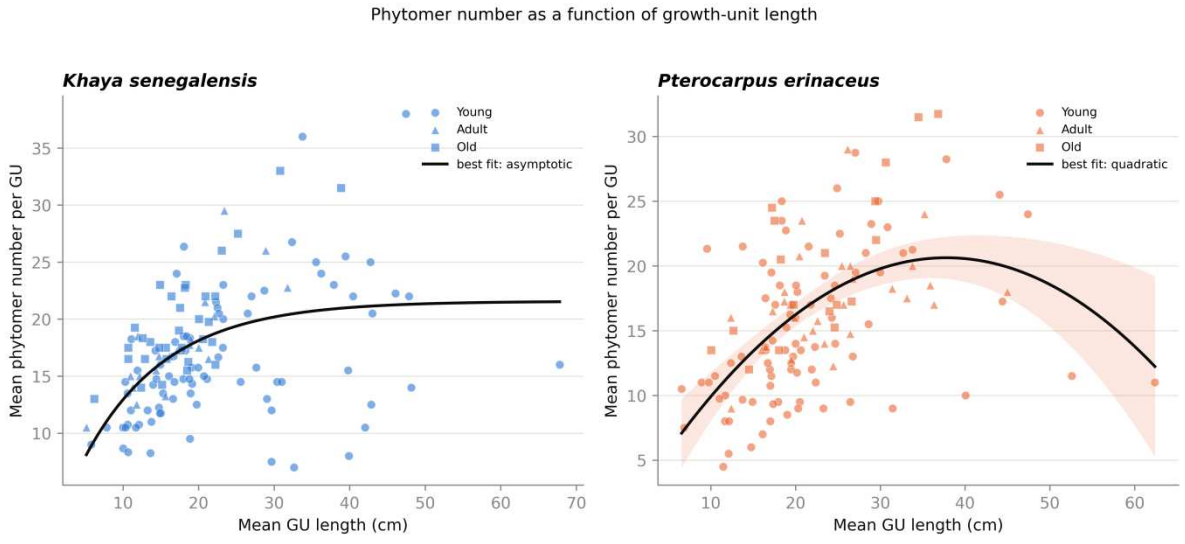


Fig. 6. Mean phytomer number per growth unit as a function of mean growth-unit (GU) length in *K. senegalensis* and *P. erinaceus.*

GU diameter increased significantly and positively with GU length in both species (Fig.7 ; *K. senegalensis*: R^2 = 0.17, $P < 0.001$; *P. erinaceus*: R^2 = 0.36, $P < 0.001$), indicating a positive structural coupling rather than a length/diameter trade-off: longer growth units are, on average, also thicker, with a steeper slope in *P. erinaceus*.

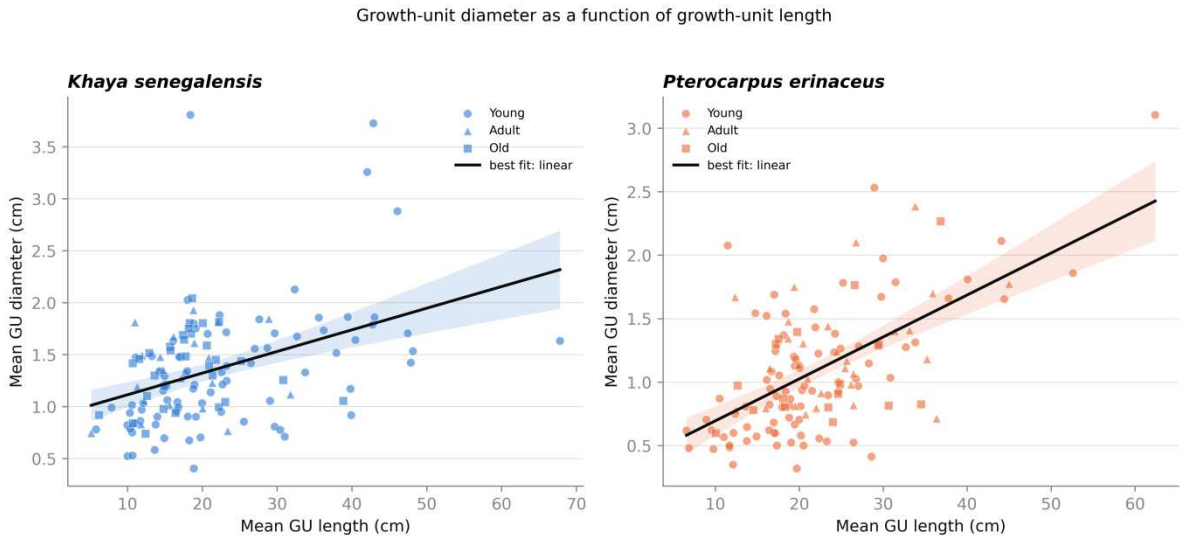


Fig. 7. Mean growth-unit (GU) diameter as a function of mean GU length in *K. senegalensis* and *P. erinaceus*. One *P. erinaceus* record showing a GU diameter exceeding the individual's own trunk diameter was treated as a probable data-entry anomaly and excluded *(n = 133)*.

GU length increased significantly with the rainfall proxy in *K. senegalensis* (Fig.8 ; r = 0.28, P = 0.003; best model logarithmic, R^2 = 0.07), consistent with the wetter-longer / drier-shorter pattern already reported across localities (Table 4). No significant relationship was found in *P. erinaceus* (r = 0.06, P = 0.56), consistent with phytomer number, not GU length, being the climate-sensitive marker in this species (see below).

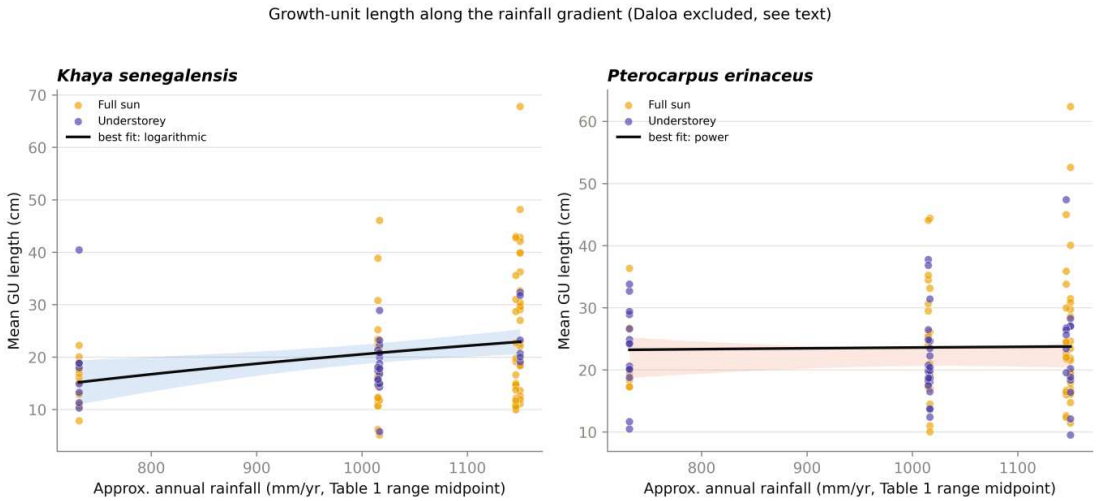


Fig. 8. Mean GU length as a function of an approximate rainfall gradient (locality range midpoint, Table 1) in *K. senegalensis* and *P. erinaceus*; Daloa (nursery seedlings) excluded.

In both species, phytomer number was better described by a hump-shaped (quadratic) model than a monotonic one along the rainfall proxy (Fig.9 ; *K. senegalensis*: $R^2 = 0.10$, $P = 0.002$; *P. erinaceus*: $R^2 = 0.06$, $P = 0.028$), peaking near the intermediate rainfall level corresponding to Bouaké-Katiola-Toumodi, consistent with Bouaké being identified as the locality with the highest Favourable Development index (*FDi*) for both species (Table 4).

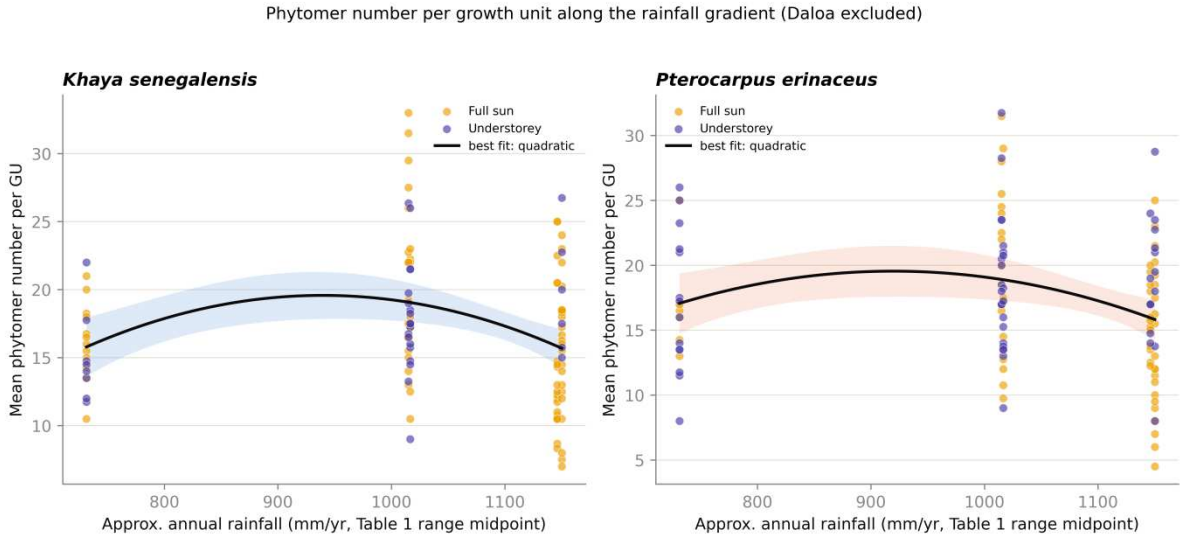


Fig. 9. Mean phytomer number per GU as a function of an approximate rainfall gradient in *K. senegalensis* and *P. erinaceus*; Daloa excluded.

Using the *FDi* values already reported in Table 4, *FDi* showed a positive but statistically non-significant relationship with the rainfall proxy in both species (Fig.10 ; *K. senegalensis*: $r = 0.62$, $P = 0.19$; *P. erinaceus*: $r = 0.43$, $P = 0.39$), reflecting the small number of localities available (n = 6) rather than an absence of pattern; Bouaké, the site with the highest *FDi* in both species, drives much of the apparent trend. This analysis is presented as descriptive and exploratory rather than confirmatory.

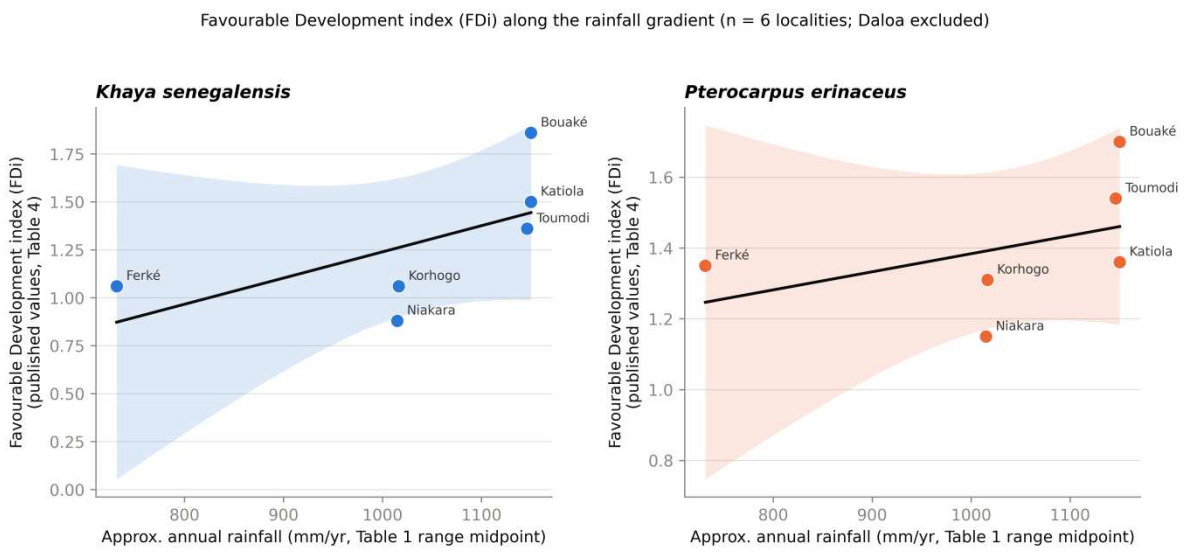


Fig. 10. Favourable Development index (*FDi*; published values, Table 4) as a function of an approximate rainfall gradient across the six wild-population localities, for *K. senegalensis* and *P. erinaceus* (exploratory, $n = 6$ localities per species).

A one-way *MANOVA* on the joint vector of GU length, GU diameter, and phytomer number confirmed a significant effect of ontogenetic stage in both species (Fig.11 ; *K. senegalensis*: Wilks' λ, $P < 0.001$; *P. erinaceus*: Wilks' λ, $P = 0.005$). Univariate follow-up tests indicate this effect is driven mainly by phytomer number in both species and, in *K. senegalensis*, also by GU length, while GU diameter did not vary significantly with stage in either species ($P > 0.16$), corroborating with a joint multivariate test the age effects already reported in Table 5.

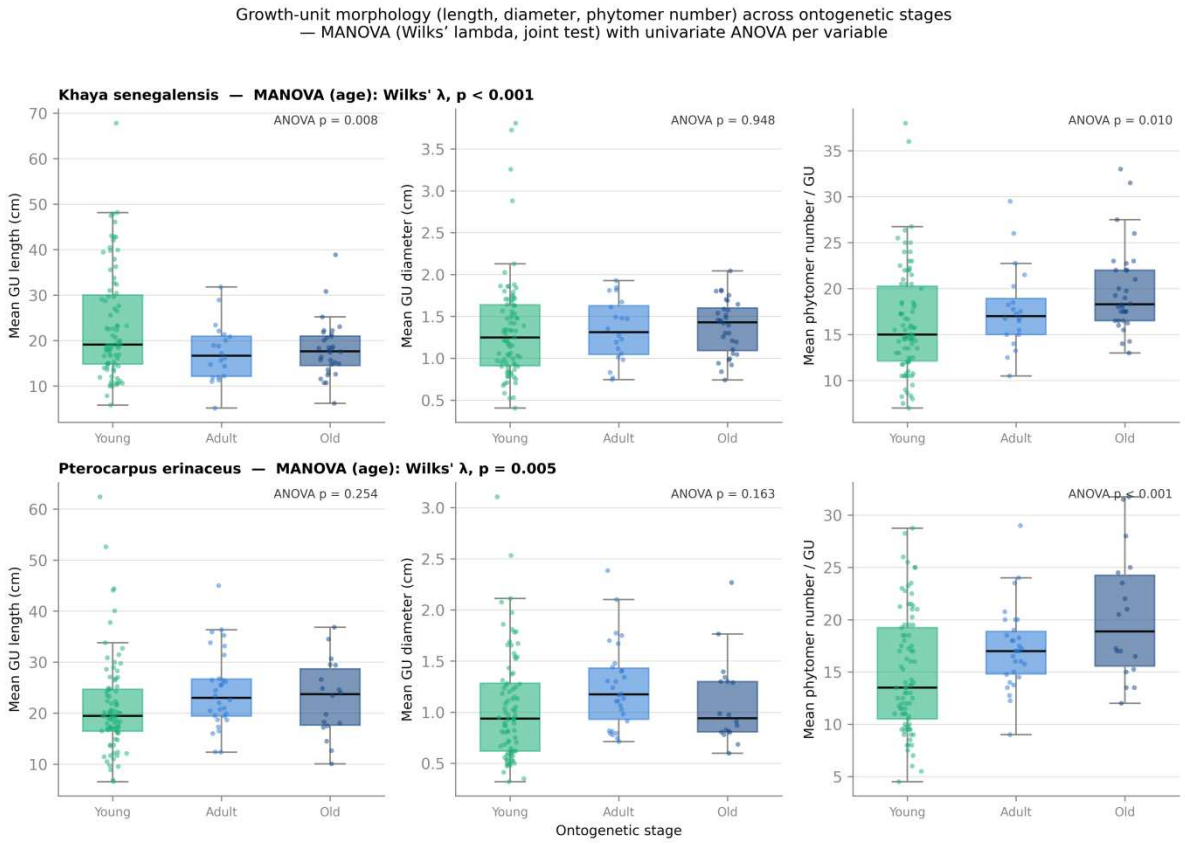


Fig. 11. Growth-unit length, diameter, and phytomer number across ontogenetic stages in *K. senegalensis* and *P. erinaceus*. Boxes show median and interquartile range; points are individual trees. Joint effect tested by one-way *MANOVA* (*Wilks' lambda*); per-variable *P-values* from univariate *ANOVA* are annotated on each panel.

Locality had a significant joint effect on the three growth-unit variables in both species (Fig.12 ; Wilks' λ, $P < 0.001$ in each case), confirming and extending, with a proper multivariate test, the univariate locality effects already reported in Table 4. In *K. senegalensis*, every individual variable also varied significantly across localities (all $P < 0.01$); in *P. erinaceus*, GU length alone did not reach significance ($P = 0.12$) while GU diameter ($P = 0.049$) and phytomer number ($P < 0.001$) did.

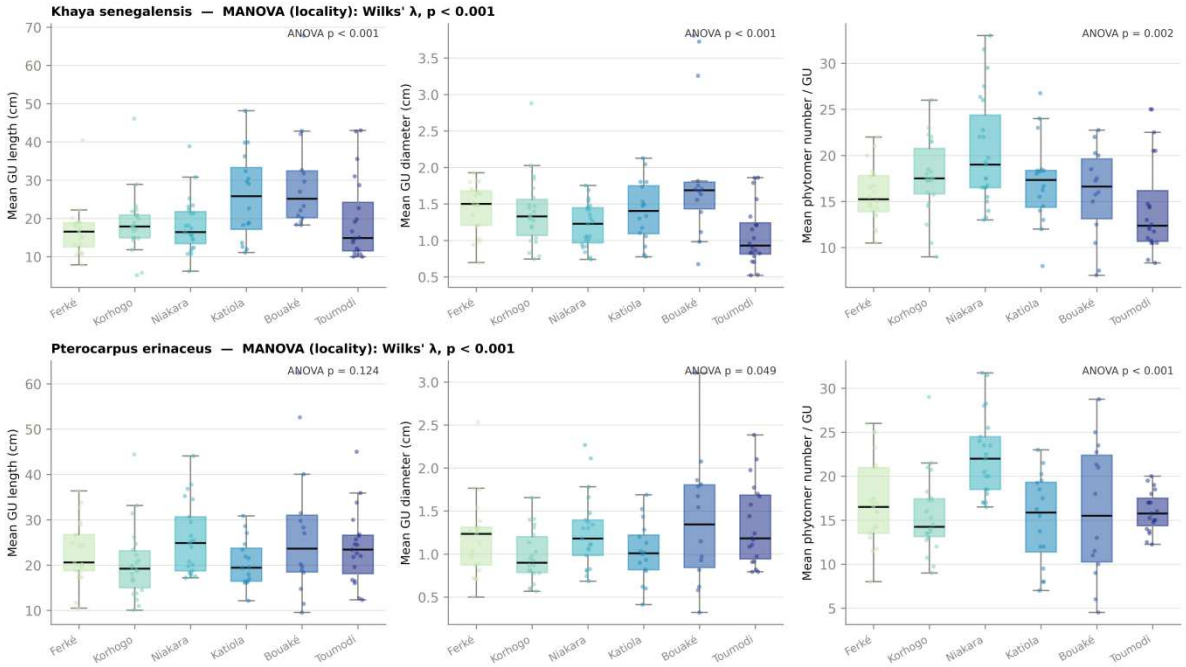


Fig. 12. Growth-unit length, diameter, and phytomer number across the six wild-population localities, ordered from driest (Ferké) to wettest (Toumodi), in *K. senegalensis* and *P. erinaceus*; Daloa excluded. Joint effect tested by one-way *MANOVA* (*Wilks' lambda*); per-variable *P-values* from univariate *ANOVA* are annotated on each panel.

A one-way MANOVA on habitat alone showed a significant effect in *P. erinaceus* (Wilks' λ, $P = 0.009$) but not in *K. senegalensis* ($P = 0.37$); once ontogenetic stage was added to the model, the habitat effect was no longer significant in either species (*K. senegalensis*: $P = 0.76$; *P. erinaceus*: $P = 0.74$). This instability mirrors, at the multivariate level, the sensitivity of the habitat effect to locality clustering already identified by the linear mixed-effects robustness check (Fig.2), and reinforces the conclusion that the habitat effect on growth-unit morphology is comparatively less robust than the effects of ontogenetic stage and locality.

Architectural units and characteristics

This work required the observation of numerous individuals of all sizes (from seedlings to senescent trees) by means of synthetic drawings, allowing the establishment of developmental stages (young, adult, and old). The following analysis presents the results of this description. There are therefore three main stages during the ontogeny of each species, each defined by precise morphological characteristics. First, we characterise the endogenous development of the young plant through to senescence, and then we analyse, where possible, certain

variations, whether these are natural variations within homogeneous stands or variations induced by stand management (density of forest cover) or the consequences of edaphic or climatic events.

Architectural developmental sequence in *Khaya senegalensis*

Young stage (0-5 years): Monopodial establishment

At the young stage, *Khaya senegalensis* appears as a slender, monopodial tree with a strictly vertical, orthotropic trunk (axis A1) whose apical meristem remains active and produces successive growth units with diffuse rhythmicity. Phyllotaxis is alternate spiral-distichous on orthotropic axes. The first leaves of seedlings are simple, penninerved, lanceolate, and entire; they progressively differentiate into imparipinnate compound leaves, then paripinnate leaves through regression and loss of the terminal leaflet at the end of the main rachis, as the tree matures. The trunk (A1) forms its first growth unit (GU) after 5 months on average; thereafter the terminal meristem successively produces GUs with diffuse rhythmicity. In the event of trauma (death of the apical bud, frequently observed in the field due to insect attack), the relay bud develops in continuation of the bearer axis, producing a monochasial sympode (pseudomonopode). Under optimal conditions, however, the trunk remains monopodial with indefinite growth. The trunk is upright and marked by clearly visible polycyclic GUs.

Branching (axis A2) appears in the upper crown at the tip of the growth units (pronounced acrotony), with delayed branching (without hypopodium), characterized by well-grouped cataphylls at the base of each newly developed and flushed shoot. Branches are initially orthotropic to ageotropic, then either rhythmic or diffuse. Their lateral shoots (A3) develop with a preferentially horizontal (amphitonic) direction in a delayed manner. Leaves on the branches show alternate spiral-distichous phyllotaxis (orthotropic axis) and alternate distichous phyllotaxis (ageotropic axis). The tree sheds its leaves in the lower part of the axes. The young tree shows a simple, hierarchical structure with 2-3 branching orders and, in most cases, 2 axis categories. It should be noted that *K. senegalensis* retains part of its foliage year-round under most conditions, an important adaptive trait in the dry savanna zone. It may lose much of its foliage during the dry season, and the crown may appear partially bare for a short period. In climates with a pronounced dry season, *Khaya senegalensis* may lose a large part of its leaves, giving the impression of a bare crown. However, this is neither systematic total deciduousness nor a permanently fully leafed tree; the behaviour is context-dependent (climate and water availability).

Adult stage (6-20 years): Establishment of the architectural unit and botanical model

At the adult stage, the architecture of *K. senegalensis* becomes complex, developing four axis categories (trunk A1, branches A2, long shoots A3-A4, and short shoots A5) and 5-6 branching orders, constituting the species' architectural unit (Table 6; Fig. 13). Lateral flowering, in the form of small panicle and raceme inflorescences, appears mainly on short shoots (A5) and, to a lesser extent, on long shoots (A3-A4) at the periphery of the crown, generally between the 7th and 8th year after planting. No additional axis category appears during ontogeny. The trunk constitutes a single axis within the moderately complex, branched system. In the tree crown, axes A3, A4, and A5 have specialized functions (photosynthesis and reproduction). It is at this stage that the trunk begins to lose its strictly monopodial character. At a certain point, the apical meristem eventually dies, triggering successive bifurcation events (vigorous relay axillary buds) that densify the crown and progressively transform the tree's shape from a well-hierarchized, single-stemmed structure into a broad, rounded crown. This transition marks the completion of the architectural unit and the onset of the reiteration phase. Figure 2 shows the developmental sequence of physiological ages or axis types (Figure 13a), as well as the axis categories, unit, and architectural model (Figure 13b) followed by *Khaya senegalensis*. Table 6 presents the architectural unit diagram of *Khaya senegalensis*.

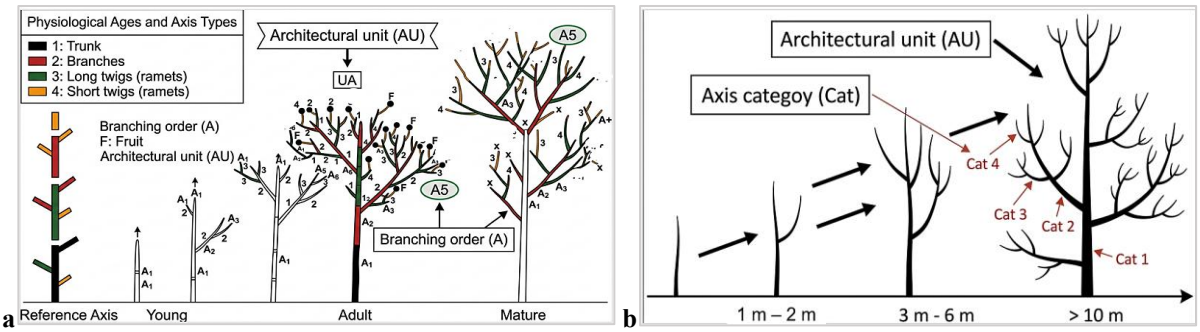


Fig. 13. **a**: Diagram of the developmental sequence from young to old tree and of the architectural unit diagram (adult stage), showing tree developmental progression with branching orders; **b**: Diagram of axis categories, illustrating the temporal progression of Categories 1 to 4 (Cat 1 to Cat 4) within the architectural unit and model

Table 6. Morphological and architectural description of axis categories within the architectural unit of *Khaya senegalensis*

	Trunk or main stem	**Branches**	**Long shoots**	**Short shoots**

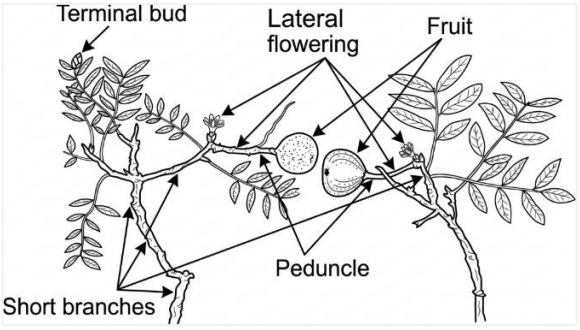
Phyllotaxis	Alternate spiral-distichous (radial symmetry)	Alternate spiral-distichous (axial symmetry)	Alternate spiral (minority) to alternate distichous (majority) (bilateral symmetry)	Alternate spiral-distichous (radial symmetry)
Leaf type *Note* : in young, adult and old shoots, the longer and more developed the leaf, the more the imparipinnate compound leaf differentiates into a paripinnate compound leaf.	Simple, entire, penninerved, lanceolate (seedling and young leaf) to imparipinnate compound (adult leaf) and paripinnate (old leaf).	Simple, entire, penninerved, lanceolate (proximal part) to imparipinnate then paripinnate compound (distal part)	Paripinnate compound	Simple, entire, penninerved, lanceolate (proximal) to imparipinnate then paripinnate compound (distal)
Growth	Indeterminate (indefinite)	Indeterminate (indefinite)	Determinate, long-term (definite)	Determinate, short-term (definite)
Preferential growth direction	Vertical	Vertical apically, to oblique	Inclined (oblique) to ageotropic	Vertical (majority) to oblique (minority)
Ramification or branching	Acrotonic (pronounced epitony)	Acrotonic (pronounced epitony)	None (seedling and young tree) and acrotonic (adult tree)	None (absent in sample observed)
Growth unit (GU) size	Variable: 7 to 56 leaf scars; long and short depending on location and	Variable: 9 to 38 leaf scars; long and short depending on location and	Variable: 9 to 27 leaves; short and very short depending on	Variable: 7 to 15 leaves; all moderately short (2.4 to 7 cm)

	ecological conditions (5.15 to 67.8 cm)	ecological conditions (6 to 53 cm)	location and ecological conditions (approx. 5 to 23 cm)	
Annual shoots	Polycyclic (2 to 6 GU)	Polycyclic (2 to 6 GU)	Polycyclic (2 to 5 GU)	Not observed
Sexuality	No flowering	No flowering	Lateral flowering	Lateral flowering
Leaf deciduousness	No (leaves not shed even in dry season)	No (persistent even in dry season)	No (persistent even in dry season)	No (persistent even in dry season)
Axis taper	Height: 0.54 m to 37 m; Diameter: 3.3 cm to 276.8 cm	Height: 0.62 m to 7 m; Diameter: 1.6 cm to 14 cm	Height: 0.33 m to 0.7 m; Diameter: 1.1 cm to 5.2 cm	Height: 0.07 m to 0.15 m; Diameter: 0.6 cm to 1.2 cm
Axis complexity	Bears branching orders 2 and long/short shoots	Bears branching orders 3, 4 and short shoots	Bears branching order 5 and short shoots	None (no branching)

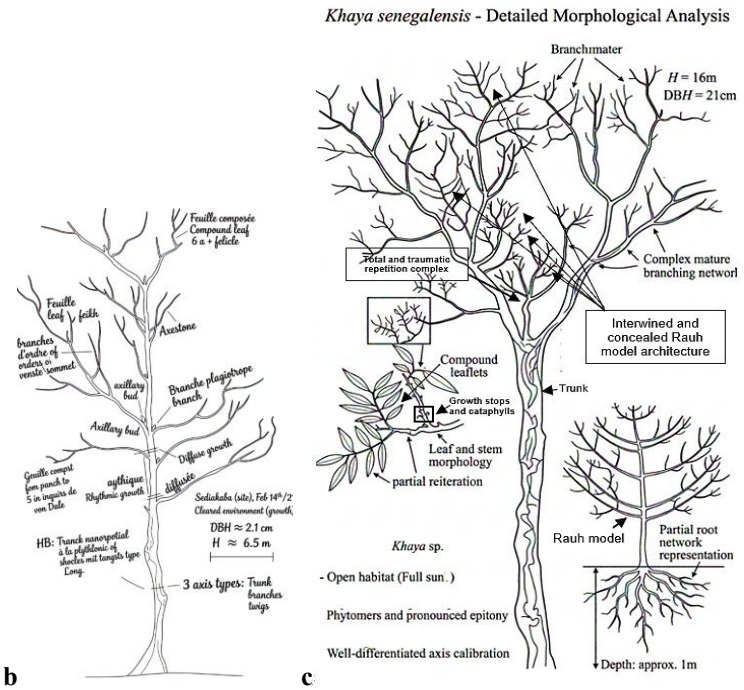
Old stage (> 20 years): Reiterated complex

In old trees, all primary branches progressively collapse under the effect of gravity. Dormant axillary buds in curvature zones develop into partial or total reiteration complexes. The whole tree progressively transforms into a reiterated complex in which the crown periphery is dominated by short, homogeneous sympodial structures. *K. senegalensis* can bear up to 6 branching orders in old trees, while retaining the 4 axis categories described in its architectural unit. Terminal buds increasingly die in the distal part of the leafy stems in the crown. This creates successive forks; the relay axes are short, rough, and formed of very short internodes. The main axis and the branches fork, while the long and short shoots develop by stacking of reiterated complexes. The unitary tree of the young and adult stages takes on the form of a colonial tree. Lateral flowering (Fig. 14a) persists and increasingly invades the crown periphery. The crown outline becomes elongated, open, and irregular, distinguishing old trees from the rounder, more compact crowns of adult individuals. Branching becomes epitonic and amphitonic. Phyllotaxis is alternate distichous on the most recent GUs along the main, perennial axes that have a horizontal direction, then alternate spiral-distichous on the small vertical and oblique axes. The crown is elongated, heterogeneous, and open. At this stage the tree's architecture is complex to describe; it regresses over

time due to total and partial reiterates on the trunk and branches. Senescence of the tree is frequently marked by a process of degeneration of the original crown (Fig. 14c).



a



b **c**

Fig. 14. Selected architectural drawings of *Khaya senegalensis*. **a**: lateral flowering (labels for terminal bud, lateral flowering, fruit, peduncle, and short branches); **b**: adult tree (with detailed scientific annotations); **c**: reiterated complex structure and senescent crown with open, irregular outline.

General architectural characteristics of *Khaya senegalensis*

Khaya senegalensis develops according to Rauh's architectural model (orthotropic trunk and branches, monopodial branching, rhythmic and continuous growth, lateral sexuality). Its structure is established in three phases: initiation of crown development, establishment of the architectural unit, and processes of partial and total reiteration (duplication of its architecture). The level of organization is 5: the phytomer, the growth unit, the axis,

483 the architectural unit, and the whole tree (reiterated complex). Table 7 summarizes the various architectural traits
484 of *Khaya senegalensis*.

485 **Table 7.** Architectural traits specific to *Khaya senegalensis*

1. **Growth mode**	2. **Branching mode**
- Indefinite - Rhythmic - Monopodial (pseudomonopode due to certain traumas: insect attack) - Pre- and neoformation of organs	- Delayed (absence of hypopodium and clearly marked growth arrests at the end of GUs) - Lateral - Terminal on the GU: acrotonic - Rhythmic (with branch tiers) - Supernumerary buds at the same node
3. Axis differentiation	**4. Sexuality position**
- Orthotropic in the apical (distal) part - Mixed in the median part (ageotropic) - Plagiotropic in the basal (proximal) part	-Lateral

486

487 **Architectural developmental sequence in *Pterocarpus erinaceus***

488 **Young stage (0-5 years): Orthotropic trunk and early branching**

489 At the young stage, *Pterocarpus erinaceus* appears as a tree with an upright, orthotropic, monopodial trunk with
490 indefinite growth under optimal conditions (nursery, full sun). The first leaves are simple, oval, entire, with 2
491 stipules per leaf sheath (Fig. 15a). Phyllotaxis is initially alternate distichous, then becomes alternate spiral as the
492 leaves differentiate into imparipinnate then paripinnate compound leaves. Under unfavourable conditions (dense
493 forest understorey, seasonal water stress), the young tree develops a bushy, multi-stemmed form (Fig. 15b) with
494 numerous reiterations from the root collar in oblique or horizontal directions without a fixed preferential direction.
495 It's a remarkable architectural plasticity, rarely documented in savanna species.

Branching appears at around 2 years of age in a delayed mode in the median zone of the growth units (mesotonic) and often immediately at the apex of the units (acrotonic, synchronous). Branches are plagiotropic and diffuse along the trunk (Fig. 15c). Under good conditions, growth unit boundaries are difficult to detect with the naked eye and require careful examination of bark colour transitions; under poor conditions, growth arrests are clearly visible as constriction zones (well-marked growth arrest). The young trunk eventually collapses in its distal part under gravity, due to the lack of lignin in new apical-bud shoots and the weight of new foliage, and 2-3 axillary buds take over, forming the first bifurcation events and the beginning of crown establishment (Fig. 15d). At this stage the tree comprises 2 axis categories (trunk and branches).

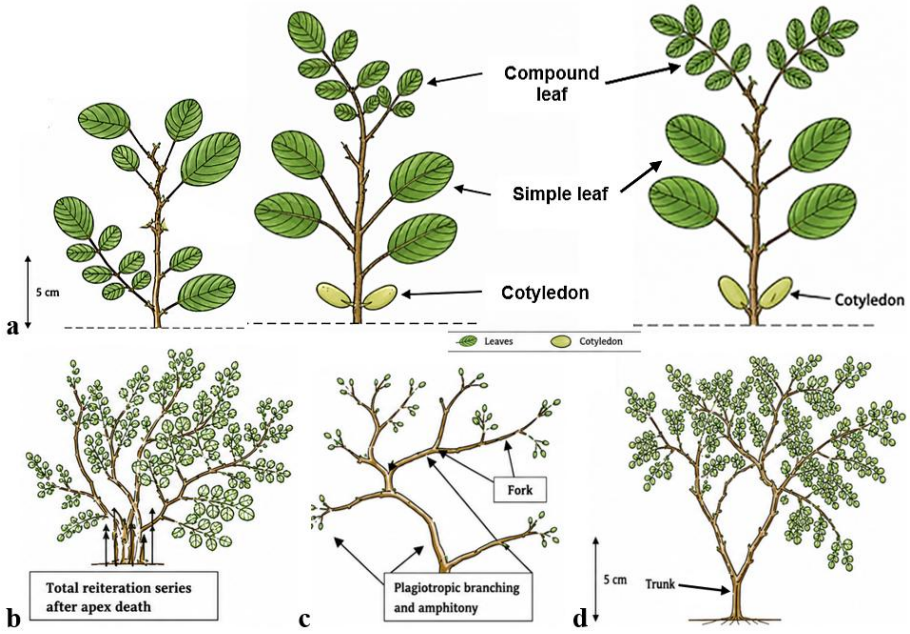


Fig. 15. Architectural drawings of young *Pterocarpus erinaceus*. **a**: young plants with orthotropic trunk showing different leaf types and phases; **b**: young plant developing a bushy, multi-stemmed form with numerous reiterations from the root collar; **c**: plagiotropic and diffuse branching along the trunk; **d**: first bifurcations and beginning of crown establishment.

Adult stage (6-20 years): Architectural unit and botanical model

The adult stage of *Pterocarpus erinaceus* is characterized by the establishment of 3 axis categories (trunk, branches/ramifications, and short floriferous shoots) forming the architectural unit (Fig. 16a, panel A; Table 8). Monocyclic floriferous shoots, both terminal and lateral (Fig. 16b), first appear between the 10th and 15th year, during the dry season (January-March). Apex death on the main axes (Fig. 16b, panel B) triggers the formation of successive bifurcations (vigorous relay buds), progressively converting the initially single-stemmed

hierarchical structure into a complex, dome-shaped colonial crown. Branching is delayed, with plagiotropic branches in the crown. Shoots and twigs are amphitonic and hypotonic in the crown, forming successively arched structures (arch-like structure). The crown colonizes its environment, often dominating neighbouring vegetation. At this stage, all axes are composed of a succession of growth units clearly delimited by growth arrests. Terminal flowering and apex death produce vigorous relays giving rise to successive forks. Fork formation also affects the trunk over time, thereby forming the crown of the adult tree. The tree becomes complex, moving from a structure hierarchized around a single main axis (single trunk) to a more complex structure. This species follows Troll's architectural model (Fig. 16c): all vegetative axes are fundamentally plagiotropic, and the trunk-like appearance is achieved through the progressive straightening of successive relay axes via secondary wood deposition (a pseudomonopode at the seedling stage transforming into a fully sympodial Troll architecture at maturity).

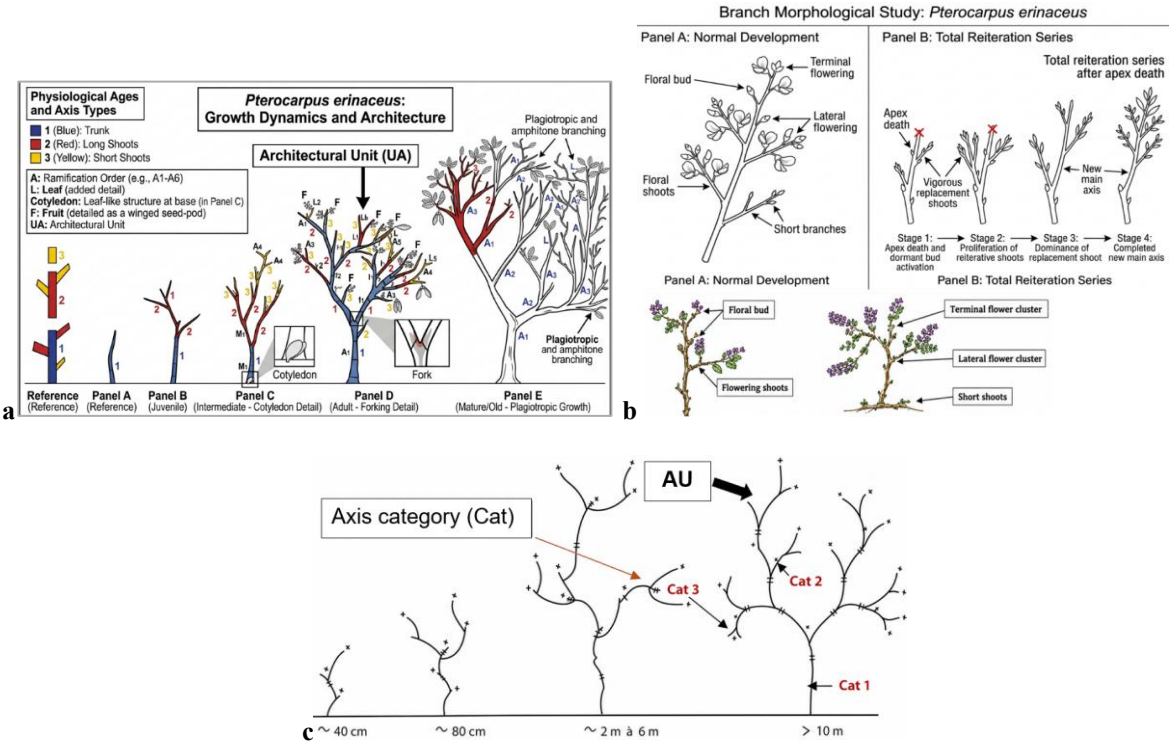


Fig. 16. a: Diagram of the developmental progression from young to senescent tree by physiological age and three axis types (trunk, branches, and short floriferous shoots) forming the architectural unit diagram (adult stage); **b**: diagram of monocyclic floriferous shoots in lateral and terminal position (panel A) and morphological study of branches: total reiteration series after apex death of main axes (panel B); **c**: diagram illustrating Troll's model followed by *Pterocarpus erinaceus* and its axis categories.

Table 8. Morphological and architectural description of axis categories within the architectural unit of *Pterocarpus erinaceus*

	Trunk or main stem	Shoots	Short shoots
Phyllotaxis	Alternate spiral (radial symmetry)	Alternate distichous (majority) and spiral (minority): mostly bilateral symmetry, minority axial	Alternate distichous (bilateral symmetry)
Leaf type	Simple, entire, oval, penninerved, with 2 stipules per sheath in young seedling, to imparipinnate compound (young leaf) with 2 stipules per sheath, to paripinnate (mature and old leaf) in trees.	Imparipinnate compound (young leaf) with 2 stipules per sheath to paripinnate compound (mature and old leaf).	Imparipinnate compound (young leaf) with 2 stipules per sheath to paripinnate compound (mature and old leaf).
Growth	Indeterminate (indefinite)	Determinate, very long-term (definite)	Determinate, short-term (definite)
Preferential growth direction	Vertical	Horizontal and oblique (majority), then oblique (minority)	Horizontal
Ramification or branching	Acrotonic apically and mesotonic (median) on GUs	Epitonic and amphitonic on GUs	None
Growth unit (GU) size	Variable: 4.5 to 40 leaf scars; long and short depending on location (3.55 to 62.4 cm)	Variable: 3 to 39 leaf scars; long and short depending on location (2.4 to 41.6 cm)	Variable: 3 to 26 leaves; short and very short depending on

			location (2.3 to 13.4 cm)
Annual shoots	Polycyclic (2 to 4 GU)	Polycyclic (2 to 4 GU)	Not observed
Sexuality	No sexuality	No sexuality	Terminal and lateral in dry season
Leaf deciduousness	Dry/flowering season (January, February, March)	Dry/flowering season (January, February, March)	Dry/flowering season (January, February, March)
Axis taper	Height: 0.5 m to 28 m; Diameter: 1.1 cm to 71.4 cm	Height: 0.15 m to 7.6 m; Diameter: 0.7 cm to 38.1 cm	Height: 0.04 m to 0.13 m; Diameter: 0.4 cm to 1.31 cm
Axis complexity	Bears only branching orders 2 and 3	Bears branching orders 3, 4 and short shoots	None (no branching), but bears clusters and floriferous shoots

Old stage (> 20 years): Progressive reiteration and crown degradation

In old trees, *P. erinaceus* maintains 5, often up to 6, branching orders while retaining its 3 fundamental axis categories (Fig. 17). Successive bifurcation events progressively fragment the crown. Dormant buds in curvature zones generate epitonic total reiteration complexes. All these reiterated complexes collapse over the course of further tree development. New complexes are generated once again in their curvature zone, and so on. Terminal and lateral flowering invades all axes located at the crown periphery. Fork formation becomes increasingly pronounced. Flowering occurs mainly on A4 axes (minority), A5, and short shoots (majority). With an irregular outline, the tree crown is open at its base, while its top is invaded by successive arched sympodial shoots (stacking). Over time, arched structures die, self-prune, and are replaced by fewer relay axes than at the young and adult stages. Old structures collapse and are replaced by shorter relay axes, mostly hypotonic and monocyclic, which bear sexuality during flowering. The final structure of a very old tree is a stack of reiterated complexes, each mimicking a simplified version of the architectural unit. The crown outline becomes irregular and open at the base, with apical clusters of arched sympodial branches.

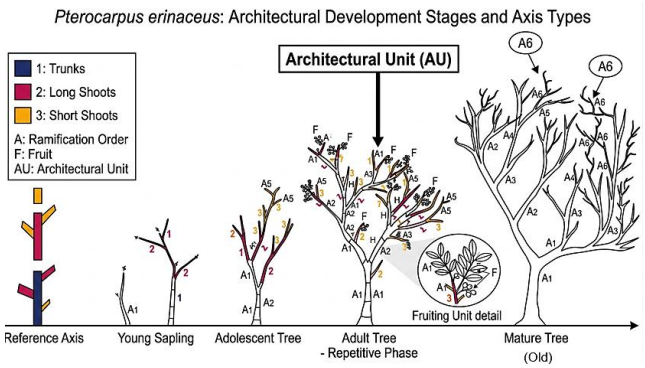


Fig. 17. Diagram of the developmental sequence of *Pterocarpus erinaceus* by stage, indicating branching orders, the architectural unit (AU), and the bifurcation phenomenon in the crown of the old tree

1.1.1.1. General architectural characteristics of *Pterocarpus erinaceus*

Pterocarpus erinaceus develops according to Troll's architectural model (a plant with mixed plagiotropic axes in both the proximal and distal parts; the trunk is built up by superposition of collapsed relay axes « stacking » that progressively straighten; sympodial branching; definite growth; mixed sexuality). Its structure is established in three phases: initiation of crown development, establishment of the architectural unit, and reiterated complex. The level of organization is 5: the phytomer, the growth unit, the axis, the architectural unit, and the whole tree. Table 9 presents the main architectural traits of *Pterocarpus erinaceus*.

Table 9. Architectural traits specific to *Pterocarpus erinaceus*

5. Growth mode	**6. Branching mode**
- Indefinite (trunk of young nursery trees) and definite (medium and short shoots on wild trees) - Colonial, rhythmic - Sympodial monochasial, dichasial, and very often polychasial (pseudomonopode for young wild trees and monopode for young nursery trees) - Preformation of organs	- Terminal (rarely lateral: mesotonic) - Rhythmic - Delayed or proleptic (absence of hypopodium)
7. Axis differentiation	**8. Sexuality position**

- Duplication of the main axis (fork) - Sympodial axis (pseudomonopode) - Most axes (A2 and A3) are plagiotropic, amphitonic, and ageotropic	- Terminal and lateral (generally synchronized)

Discussion

This study provides the first complete architectural description of *Khaya senegalensis* and *Pterocarpus erinaceus*, two emblematic and threatened tree species of the Guinean-Sudanian savannas of West Africa. By mobilizing architectural analysis (a well-established but strikingly under-used methodological framework in African tropical forestry) and combining it with a systematic retrospective approach across a complete bioclimatic gradient, our results reveal coherent ontogenetic trajectories, well-defined architectural units, and measurable environmental plasticity, which together open up relevant perspectives for the management and conservation of these species.

Architectural models as species-specific genetic signatures

The conformity of *K. senegalensis* to Rauh's model and of *P. erinaceus* to Troll's model is one of the fundamental findings of this study. These two models, originally defined by rhythmic growth and acrotonic branching, confer on *K. senegalensis* a hierarchized, dominant architecture particularly well suited to competition for light in wooded savanna formations and agroforestry parklands. This straight growth habit constitutes a major selective advantage for the production of high-quality timber, with a long, branch-free bole. This is a trait that has been exploited by silviculturists for decades but never before linked to the species' architectural basis. Major tree species such as Sipo (*Entandrophragma utile*), Tiama (*Entandrophragma angolense*), *Khaya anthotheca*, and even *Swietenia macrophylla* and *Swietenia mahogoni*, all belonging to the same family Meliaceae, likewise follow architectures close to Rauh's model (Hallé and Keller, 2019), suggesting that this family carries a genetic predisposition towards this type of structural organization.

Conversely, the Troll model followed by *P. erinaceus* reflects a radically different architectural strategy. The progressive straightening of successive, fundamentally plagiotropic relay axes, which simulates the appearance of a trunk without being one in the strict sense, is an elegant mechanism allowing the species to maximize light interception through horizontal stratification of the foliage from the juvenile stages onward. This mechanism, combined with synchronized mixed flowering (terminal and lateral) triggered in the dry season and with seasonal

leaf deciduousness, constitutes a coherent set of adaptations to Sudanian savanna conditions, as also seen in *Parkia biglobosa* (Adji et al., 2022b). Remarkably, this model is maintained in young nursery seedlings as a pseudomonopode that is sometimes difficult to distinguish, before the species expresses its true plagiotropic sympodial architecture at maturity. This ontogenetic transition between a juvenile pseudomonopode and an adult Troll architecture, rarely documented with precision for African savanna species, deserves to be integrated into nursery seedling-selection protocols. According to Hallé and Keller (2019), Troll's model is the most abundant among present-day floras. This model guides the growth of trees of all sizes, shrubs, bushes, lianas, epiphytes, and small perennial and annual plants. Indeed, all latitudes and vegetation types are concerned, but in closed vegetation, plants built in this way have horizontal leafy axes that are efficient energy-capture surfaces, whereas in open vegetation, such plants are either vertical or, conversely, prostrate on the ground. It should be noted that species of the three traditional legume families (Fabaceae « formerly Papilionaceae », Mimosaceae, and Caesalpiniaceae) are predominantly, though not exclusively, built according to Troll's model (Hallé and Keller, 2019).

The distinct nature of these two architectural models implies differential responses to silvicultural interventions and forest management (Heuret et al., 2003; Nicolini et al., 2012; Sabatier et al., 2014). Formative pruning in *K. senegalensis* can rely on the pronounced apical dominance of Rauh's model to extend the commercial bole, whereas any intervention on the main axes of *P. erinaceus* risks triggering massive, undesirable reiterations, owing to the frequent death of apices and the vigour of dormant relay buds characteristic of Troll's model.

This distinction is directly visible in the height-diameter allometric relationship (Fig. 4): height in *K. senegalensis* saturates early relative to diameter, consistent with a monopodial trunk that completes most of its vertical extension before subsequent growth is expressed mainly as radial increment, whereas height in *P. erinaceus* increases more continuously with diameter, consistent with height being built progressively through the stacking of successive relay axes rather than by a single indefinite apical meristem.

Ontogenetic sequence and architectural units: first formal descriptions

One of the most original contributions of the present study lies in the complete formalization of the architectural units (AU) of both species, a central concept in plant architecture (Barthélémy, 1991; Barthélémy et al., 1989; Hallé and Oldeman, 1970) but never before applied to native West African tree species. The AU of *K. senegalensis*, with its four axis categories (trunk A1, branches A2, long shoots A3-A4, short shoots A5) and five branching orders, is significantly more complex than that of *P. erinaceus* (three axis categories, up to six orders

610 in old trees). This differential structural complexity reflects distinct functional strategies: *K. senegalensis* invests
611 in a pronounced hierarchization of axes to optimize vertical light capture, whereas *P. erinaceus* multiplies
612 branching orders within a more horizontal, diffuse system. The description of the four ontogenetic phases (juvenile
613 establishment, architectural construction, reproductive transition, and senescent restructuring) offers a precise
614 interpretive framework for the developmental dynamics of both species. The reproductive transition phase is
615 particularly instructive: flowering in *K. senegalensis* occurs only in a lateral position on the short floriferous shoots
616 A5, which bear long peduncles, between the 7th and 8th year after planting, whereas *P. erinaceus* displays mixed
617 flowering (terminal and lateral) on short shoots between the 10th and 15th year (a longer delay that partly explains
618 the early harvesting pressure exerted on this species before it reaches sexual maturity). These architectural
619 phenological data constitute critical information for planning seed programmes (species-specific seed biology)
620 and assisted natural regeneration.

621 The senescence phase, characterized by duplication of the architecture through reiterated complexes, is consistent
622 with Oldeman (1990) concept of the « colonial tree » and with observations made on 193 Euphorbia species
623 representing all major subgenera and covering the worldwide distribution of the genus, with species originating
624 mainly from Africa, Eurasia, and the Americas (Anest et al., 2021). Indeed, according to these authors, mature
625 forest trees behave as « colonial trees » whose architecture results from the progressive accumulation of reiterated
626 complexes. In both species, the transition from unitary tree to colonial tree marks a major functional shift, in
627 which resilience takes precedence over structural extension. This reiteration capacity is biologically valuable: it
628 allows old trees to locally reconstitute their photosynthetic architecture after partial disturbance (insect attack,
629 drought, pruning, etc.), a property directly exploitable in the parkland agroforestry systems of northern Côte
630 d'Ivoire, where these species are regularly subjected to anthropogenic harvesting (Timite et al., 2023; Timité et
631 al., 2022).

632 **Architectural plasticity and response to environmental gradients**

633 The significant variation in the morphological parameters of growth units between localities and habitats ($P <$
634 0.001) eloquently illustrates the architectural phenotypic plasticity of both species in response to climatic and
635 edaphic gradients (Adji et al., 2022c). This plasticity is a well documented adaptive mechanism in tropical trees
636 (Adji et al., 2022c; Barthélémy and Caraglio, 2007; Hallé and Oldeman, 1970; Heuret et al., 2003; Nicolini et al.,
637 2012), but rarely quantified so systematically across such a wide gradient (1,900 to 1,200 mm/year rainfall) within
638 the same experimental design. The results show that this plasticity operates differently between species: in *K.*

senegalensis, it is mainly expressed as a change in growth-unit length (longer in the humid southern zones, shorter in the dry northern zones), whereas in *P. erinaceus*, it is the number of phytomers per growth unit that is most sensitive to the environment. These interspecific differences suggest distinct adaptive responses to water availability: *K. senegalensis* modulates the size of its growth segments (cell elongation), whereas *P. erinaceus* adjusts the number of leafy units (meristematic organogenesis). Both mechanisms are known in the literature to be complementary rather than mutually exclusive (Barthélémy and Caraglio, 2007; Hallé and Oldeman, 1970), but their relative importance is generally species-specific. Identifying these mechanisms in African savanna species opens new prospects for targeted genetic improvement and the selection of provenances adapted to specific climatic contexts, notably in the framework of climate-change projections for West Africa (Amani et al., 2022; Lykke et al., 2025; Timité et al., 2022).

The effect of habitat (full sun vs. understorey) reveals a counter-intuitive but ecologically coherent result: individuals in full sun consistently show higher favourable development indices (*FDi*) (*K. senegalensis*: 1.27 vs. 1.1; *P. erinaceus*: 1.5 vs. 1.22), yet generally have shorter growth units than some understorey individuals. This apparent paradox is explained by the distinction between growth quality and growth quantity: in full sun, trees produce better-structured growth units, with an optimal length to phytomer ratio and fewer growth arrests, reflecting continuous, uninterrupted growth. In the understorey, elongation is sometimes artificially increased through etiolation but punctuated by numerous growth arrests, revealing irregular meristematic functioning. This result confirms that both species are fundamentally heliophilous, a characteristic that should be integrated into agroforestry management plans where these species are often planted in the understorey or under partial canopy cover.

It should be noted, however, that the mixed-effects reanalysis (Figure 2, Figure 3) indicates that not all of these habitat and age effects are equally robust to the sampling structure. The apparent effect of habitat on the number of growth arrests, in particular, does not withstand accounting for locality as a random effect in either species, suggesting that the pattern reported in Table 3 partly reflects differences between the localities sampled in each habitat rather than a direct physiological response to light availability per se. The habitat effect on the number of phytomers per growth unit in *P. erinaceus*, by contrast, persists after this correction, albeit with a reduced margin, and can therefore be considered a comparatively more robust signal of the species' heliophilous character. These nuances do not overturn the overall interpretation that both species respond to light availability, but they indicate that some of the underlying markers are more sensitive to this response than others, and they argue for interpreting locality-pooled comparisons of growth-arrest frequency with appropriate caution in future studies.

669 Mapping the zones favourable to species development, based on the *FDi* calculated per locality, constitutes a
670 notable methodological innovation compared with classical ecological zoning approaches based exclusively on
671 rainfall or pedology. By identifying Bouaké and Katiola as optimal zones for *K. senegalensis*, and Bouaké and
672 Toumodi for *P. erinaceus*, our data provide forest managers and national reforestation programmes with an
673 objective, architecturally grounded basis for the spatial allocation of planting efforts. These findings converge
674 with and complement the work of Sabatier et al. (2014), Drénou (2023) and Adji et al. (2022b) on the use of
675 architectural traits as indicators of planting-site quality in a tropical context (Adji et al., 2022c; Drénou, 2023;
676 Sabatier et al., 2014).

677 This species-specific mechanism is corroborated by the relationship between phytomer number and GU length
678 (Fig. 6): in both species, longer growth units are built primarily by adding phytomers rather than by proportionally
679 elongating internodes, with diminishing returns at the largest GU lengths. Along the rainfall gradient (Figs. 8-9),
680 GU length increased with rainfall in *K. senegalensis* but not in *P. erinaceus*, while phytomer number showed a
681 hump-shaped response peaking near Bouaké in both species, consistent with Bouaké being identified as the most
682 favourable locality by the *FDi* (Table 4). A direct regression of *FDi* against the rainfall proxy (Fig. 10) was
683 positive in both species but not statistically significant given the small number of localities ($n = 6$; $P = 0.19$ and
684 0.39), and should be regarded as descriptive rather than confirmatory.

685 **Implications for conservation and silvicultural management**

686 The results of this study have direct and immediate implications for the conservation of *K. senegalensis* and *P.*
687 *erinaceus*, two species classified as Vulnerable by the IUCN and subject to intensive commercial exploitation that
688 threatens their long-term viability. Identifying their architectural units provides a structural reference framework
689 for objectively diagnosing a tree's developmental state at any stage of its life (crucial information for defining
690 ecologically coherent minimum harvesting diameters). In particular, in *P. erinaceus*, whose flowering occurs only
691 between the 10th and 15th year, harvesting young trees that have not yet reached their architectural unit directly
692 compromises the species' sexual regeneration. Defining an architectural criterion of reproductive maturity, rather
693 than a purely diametric one, would represent a significant advance in regulating the exploitation of this species.
694 Furthermore, understanding reiteration processes opens up prospects for managing old trees in agroforestry
695 parklands. Old *K. senegalensis* and *P. erinaceus* trees, often considered unproductive and felled in favour of young
696 plantations, actually prove to be highly resilient, structurally complex architectures, capable of reconstituting their
697 photosynthetic and reproductive capital after disturbance. Their conservation within agroforestry parklands should

be reconsidered, not only for their heritage value but also as a seed reservoir, wildlife habitat, and structural model for naturally regenerating seedlings. It's an ecological function rarely taken into account in current management plans.

In the context of reforestation programmes currently being deployed in Côte d'Ivoire, notably within the framework of national commitments to restore degraded forests (Initiative AFR100, 2026), our results show that even minimal architectural knowledge of the target species would significantly improve seedling survival and growth rates. The choice of provenances, formative pruning practices, spacing schedules, and silvicultural interventions could be rationalized with reference to the architectural units and *FDi* values calculated in this study. In this respect, our results fit within the broader perspective of architecturally informed silviculture (Adji et al., 2022c, 2022b; Anest et al., 2021; Sabatier et al., 2014), whose integration into West African forest policy represents a major qualitative leap forward.

Positioning relative to the literature and originality of the study

Plant architecture as a forest-management tool has undergone considerable development in temperate Europe, notably in France with pioneering work on fruit trees (Coupel-Ledru et al., 2022; Grisafi et al., 2023; Rosati et al., 2024; Zhang et al., 2023), and forests (Barthélémy et al., 1995; Nicolini, 1998; Sabatier et al., 2014; Sabatier, 1999), and in tropical South America (Drénou, 2023; Heuret et al., 2003; Nicolini et al., 2012), with applications in precision silviculture for several species. In sub-Saharan Africa, this discipline remains virtually absent from forest research programmes, despite the wealth and importance of the region's woody species. To our knowledge, no previous study had formalized the architectural unit of a native tree species from the Sudanian savanna zone of West Africa, apart from that of Adji et al. (2022b). This gap is all the more concerning given that *K. senegalensis* and *P. erinaceus* have been the subject of substantial literature on their population ecology (Bouka Dipelet et al., 2019; Dumenu, 2019; Goba et al., 2019; Issa et al., 2018), pharmacognosy, and agroforestry uses, yet without ever integrating the architectural dimension, which is nonetheless essential for understanding their functioning and guiding their management. This study methodically fills this gap by adopting the standardized concepts and terminology of plant architecture (Barthélémy, 1991; Barthélémy and Caraglio, 2007), and applying them, for the first time, across a complete bioclimatic gradient and a sample of unprecedented size for this type of study (720 individuals in total, across all localities). The development of a quantitative favourable development index (*FDi*), calculated from growth-unit characteristics, constitutes an original methodological contribution that goes beyond the strictly qualitative framework of classical architectural analysis. By providing a synthetic score integrating

growth-unit length, number of phytomers, and frequency of growth arrests, the *FDi* enables an objective comparison between localities, habitats, and species, and paves the way for the operational use of plant architecture as a decision-support tool in reforestation programmes. This approach aligns with recent efforts to turn functional morphology into a quantitative forestry diagnostic tool (Anest et al., 2021; Drénou, 2023; Sabatier et al., 2014).

Limitations and perspectives

Although this study represents the most comprehensive architectural analysis ever conducted on these two species, several avenues deserve to be highlighted. First, the retrospective approach, which reconstructs growth history from morphological markers, introduces inherent uncertainty for older stages, particularly in old trees whose smooth bark can mask certain growth arrests. Complementary dendrochronological studies would allow these estimates to be calibrated and validated. Second, because several axes were sampled within the same individual tree, and several trees within the same locality, the ANOVA/MANOVA framework used here treats these observations as statistically independent; this hierarchical sampling structure introduces a risk of pseudoreplication that may inflate the significance of some comparisons. A post hoc linear mixed-effects reanalysis, with locality included as a random effect (Figure 2, Figure 3; Table S7), confirmed that this risk was not merely theoretical: three of the habitat and age effects reported in Tables 3 and 5 (the habitat effect on the number of growth arrests in both species, and the age effect on the number of phytomers per growth unit in *P. erinaceus*) lose statistical significance once locality-level non-independence is accounted for, while the habitat effect on the number of phytomers per growth unit in *P. erinaceus* remains significant but is markedly weaker. Locality alone explained 10 to 31% of the total variance across variables. Data allowing a similar correction at the level of multiple axes within the same individual tree were not available in the present dataset; future sampling designs should record a unique tree identifier for every measured axis so that this additional level of non-independence can also be modelled explicitly. Third, the genetic dimension of the architectural variation observed between localities was not explored in this work: genetic differentiation analyses between populations would be needed to distinguish genotypic plasticity from local genetic variation, particularly in the context of ongoing discussions on seed provenance for climate-adapted reforestation programmes. Fourth, interactions between architecture and associated faunal communities (notably pollinating insects, herbivores, and seed-dispersal agents) were not addressed, although they are likely to be influenced by the crown structure and floral phenology revealed in this study. Finally, integrating structure-function models and extending this approach to other priority tree species of the region (*Vitellaria paradoxa*, *Daniellia oliveri*, *Afzelia africana*, etc.) would represent a major step

towards an integrated architectural silviculture for West Africa. Such future work would help build a regional architectural database, comparable to those developed in Europe (the AMAP database, CIRAD-Montpellier) and South America, and would feed forest growth and productivity models currently calibrated without reference to architectural parameters.

A complementary multivariate analysis (MANOVA, Figs. 11-12) reinforces this picture: ontogenetic stage and locality had strong, consistent joint effects on the vector of growth-unit length, diameter, and phytomer number in both species, whereas the joint effect of habitat was not robust to the inclusion of ontogenetic stage in the model, an instability that parallels, at the multivariate level, the locality clustering sensitivity already identified by the linear mixed-effects robustness check. The approximate rainfall proxy used (range midpoints from Table 1 rather than single annual normals) is a further limitation of the present dataset; future work should draw on locality-specific climate normals to test the climate-gradient relationships reported here with finer resolution. The Python and R code used to reproduce the regression, allometric, and MANOVA analyses is provided as Supplementary Material to facilitate replication and extension to other species.

Conclusion

This study provides the first complete characterization of the architectural development of *Khaya senegalensis* and *Pterocarpus erinaceus*, two emblematic forest species of the Guinean-Sudanian savannas of West Africa. Our results show that these species follow distinct, genetically programmed ontogenetic trajectories that are adaptively consistent with the constraints of the Guinean-Sudanian savannas. *K. senegalensis* expresses Rauh's model (monopodial, acrotonic, four axis categories), conferring an upright habit favourable to timber production. *P. erinaceus* follows Troll's model (sympodial, plagiotropic, mixed flowering, three axis categories), reflecting a horizontal expansion strategy characteristic of open environments. The formalized architectural units, comprising four axis categories in *K. senegalensis* and three in *P. erinaceus*, constitute unprecedented structural reference frameworks for objectively diagnosing the developmental stage of individuals in the field, better understanding their adaptive strategies, and defining ecologically responsible harvesting thresholds. Beyond their fundamental interest, these findings offer direct applications for the sustainable management of forest resources. The architectural markers identified support the definition of ecologically responsible harvesting thresholds, particularly for *P. erinaceus*, whose reproductive maturity is reached only between the 10th and 15th year, as well as improving the selection of restoration sites through the Favourable Development indices (*FDi*). A post hoc mixed-effects reanalysis confirmed that the general pattern of heliophily in both species is robust, while showing that specific markers (notably growth-arrest frequency) are more sensitive than others to the clustering of

individuals within localities, underlining the value of accounting for locality as a random effect in future studies of this kind. The architectural plasticity observed along the bioecological gradient further supports, while also underscoring, the value of integrating the genetic variability of provenances into reforestation programmes in order to strengthen stand resilience to climate change. More broadly, this study shows that architectural analysis constitutes a quantitative, operational, and low-cost tool for linking tree development to conservation, restoration, and forest-management practices. Beyond these two species, this study calls for a paradigm shift: by demonstrating that architectural traits are reliable indicators of tree development and adaptation, it opens new prospects for integrating plant architecture (an operational, quantifiable, and low-cost tool), into more predictive, biologically grounded sustainable-management strategies for tropical forests, in a context of urgent ecological need. Complementary regression, allometric, and multivariate analyses reinforce these conclusions: the height–diameter allometry directly visualises the contrast between Rauh's and Troll's models, phytomer number rather than internode elongation governs growth-unit length in both species, and a joint multivariate test confirms that ontogenetic stage and locality, rather than habitat alone, robustly structure growth unit morphology.

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Author Contributions

B. I. A. designed the methodology, took the experimental measurements, analysed the data and wrote the paper. D. S. A., K.H.K., M.J., S.A.S., J.D. supervised the work. All authors have read and agreed to the published version ofthe manuscript.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The datasets generated during and/or analyzed in the current study are available on: Adji, Beda Innocent, 2022, "Growth unit morphology and biomass in *Khaya senegalensis* (Desr.) A. Juss. (Meliaceae), *Pterocarpus erinaceus* Poir. (Fabaceae) and *Parkia biglobosa* (Fabaceae) according to habitat and climate in Côte d'Ivoire", https://doi.org/10.7910/DVN/I37ABC, Harvard Dataverse, V1.

Appendix A. Supporting information

Annex-Glossary

Term	Definition
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 both the series of structural characteristics expressed by a plant during its development (ontogeny) and the method of study of the spatio-temporal organization of plant structure.
Architectural unit (AU)	A very stable elementary architecture of a plant. Each plant species has a small, 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, unconstrained ecological conditions, from germination to flowering, resulting from the expression of the plant's genetic heritage. The typology of architectural models is based on the observation of four main groups of morphological characters: growth (rhythmic or continuous), branching (absent or present, monopodial or sympodial, rhythmic, continuous, or diffuse), direction of axis growth, and position of sexuality. Each model corresponds to a particular combination of these architectural characteristics.
Growth unit (GU)	A portion of 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, phyllotaxis is said to be alternate. If successive leaves lie in the same plane and form a 180° angle in pairs, phyllotaxis is called alternate distichous. If leaves are arranged in several directions around the axis along a single virtual spiral, phyllotaxis is called

	alternate spiral. When several leaves are inserted at the same node, phyllotaxis is called whorled; a special case of whorled phyllotaxis is opposite phyllotaxis, where two leaves are inserted at the same node.
Monopodial development	An axis built by a single apical meristem; growth of the axis is ensured indefinitely by the same meristem or apical bud (mechanism of apical persistence without sexuality).
Pseudomonopodial development	A non-unique axis imitating monopodial development (masked sympode).
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.); construction of the axis is ensured by a succession of superimposed segments arising from different lateral buds (linear succession of elementary axes, each built by a short-lived meristem).
Sympode	In sympodial branching, the terminal meristem of the bearer axis dies or transforms into a structure that loses its capacity for vegetative growth. Further growth is then ensured by one or more lateral meristems, which build as many lateral or relay axes; the resulting branched whole is called a sympode. Depending on whether this branching produces one, two, or more relays, it is termed monochasial, dichasial, or polychasial, respectively.
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, are of the same age in the case of immediate branching; N+1 is younger than N in the case of delayed branching. This is the process by which a morphological unit of the plant body gives rise to one or more new units of the same fundamental nature as itself. The timing 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 axillary meristems of a stem give rise to a branch, branching is said to be continuous; when branches are grouped in distinct tiers, branching is said to be rhythmic; when the arrangement differs from both previous cases, branching is said to be diffuse.
Orthotropic axis	An axis whose direction of growth is vertical.
Plagiotropic axis	An axis whose direction of growth is horizontal.

Ageotropic axis	An axis whose direction of growth is oblique (mixed between vertical and horizontal).
Cataphylls	The scar of the leaf outline that protected the bud before bud-burst.
Continuous growth	Axes that do not show marked periodicity of endogenous elongation.
Rhythmic growth	Axes that show marked periodicity of endogenous elongation.
Immediate (or immediately developing) shoots	Shoots that develop without a dormancy phase of the bud; they develop on the elongating shoot and are generally located in the middle of this bearer shoot.
Delayed shoots (or delayed developing shoots)	Shoots preceded by a dormancy (resting) phase of the lateral bud; they develop the year after elongation of the bearer shoot.
Hypopodium	A very long internode set in the case of an immediate shoot; the length of internode between the base of the shoot and the first leaf.
Polycyclism	The annual shoot is composed of two 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 shoots at the base of the bearer entity or growth unit.
Mesotony	Shoots develop preferentially in the median zone of the bearer unit.
Hypotony	Large-diameter shoots are distributed on the lower part of the branches.
Epitony	Distribution of branches on the upper side of axes and branches.
Amphitony	Branches are borne preferentially in a horizontal plane on either side of the bearer axis. **NB**: *hypotony and amphitony are both involved in branch extension 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 reiteration is a young tree growing on an old bearer axis. The position of a reiteration is not predictable; it is determined by the presence of a local energy resource or by trauma. Reiteration has a dual function of exploiting light resources and ensuring resilience to trauma. It is said to be total if it appears on the trunk of the tree, and partial if it appears on another type of axis.
Forking	Formation of two or more morphologically identical relay axes on a sympode following apical trauma of a single axis.

822 **Appendix B. Supplementary information**

823 **Table. S1:** Influence of habitat, locality, and habitat × locality on growth-unit morphology in young *Khaya*
824 *senegalensis* trees

Habitats/Localities	Height (m)	Diam. (cm)	GU1 length (cm)	GU1 diam. (cm)	GU1 leaf N	GU2 length (cm)	GU2 diam. (cm)	GU2 leaf N
Full sun	1,71±**0**,15 **b**	5,39±2,27 **b**	16,78±14,16 **a**	0,66±0,29 **a**	11,41±5,64 **a**	20,17±10,55 **a**	0,97±0,46 **a**	14,54±4,17 **a**
Understorey	3,54±**1**,24 **a**	3,54±**1**,56 **a**	16,46±10,9 **a**	0,83±0,33 **a**	12,23±4.10 **a**	17,92±8,59 **a**	1,22±0,42 **a**	15.23±3,63 **a**
Pr > F	**0,001**	**0,0034**	**0,9461**	**0,1126**	**0,6506**	**0,5207**	**0,1175**	**0,6262**
Ferké	0,96±0,56 **ab**	3,08±1,7 **b**	17,1±5,30 **a**	0,56±0,19 **a**	12,33±5,03 **ab**	15,9±3,63 **a**	0,92±0,38 **ab**	13±1 **ab**
Korhogo	5,64±4,87 **a**	9,63±6,04 **a**	21,83±18,57 **a**	0,91±0,34 **a**	14±3,46 **ab**	21,94±15,51 **a**	1,36±0,51 **ab**	15,75±3,69 **ab**
Katiola	1,61±1,07 **ab**	3,73±1,27 **b**	24,7±6,51 **a**	0,88±0,27 **a**	18±3,61 **a**	27,9±9,24 **a**	1,57±0,21 **a**	19±3,46 **a**
Bouaké	4,68±1,58 **ab**	6,11±1,11 **ab**	11,32±3,92 **a**	0,86±0,36 **a**	8,2±2,39 **b**	19,92±2,87 **a**	1,12±0,46 **ab**	18±3,94 **ab**
Daloa	1,20±0,54 **ab**	2,37±1,44 **b**	17,38±15,71 **a**	0,67±0,3 **a**	11,56±6,27 **ab**	17,98±8,64 **a**	0,91±0,37 **ab**	13,56±3,78 **ab**
Toumodi	0,52±0,17 **b**	1,53±0,6 **b**	10±5,43 **a**	0,48±0,16 **a**	8,86±4,05 **b**	15,48±7,33 **a**	0,72±0,24 **b**	8±2,58 **b**
Niakara	0,49±0,1 **b**	1,33±0,6 **b**	9±3,33 **a**	0,6±0,26 **a**	8,71±1,07 **b**	17,58±5,43 **a**	0,65±0,22 **b**	9±3,28 **b**
Pr > F	**0,0022**	**0,0003**	**0,4063**	**0,0696**	**0,0387**	**0,5048**	**0,0177**	**0,0186**
Full sun × Bouaké	3,6±1,41 **a**	7,16±0,67 **a**	12,7±6,64 **a**	0,58±0,34 **a**	8±4,24 **a**	22,3±1,84 **b**	0,88±0,64 **ab**	20,5±3,53 **a**

Full sun × Daloa	1,20±0,54 **b**	2,37±1,4 4 **b**	17,38±15,74 **a**	0,67±0,29 **a**	11,55±6,27 **a**	17,98±8,6 4 **b**	0,91±0,37 **ab**	13,56±3,78 **ab**
Full sun × Katiola	1,02±0,4 **b**	2,99±0,18 **b**	1,35±4,17 **a**	0,96±0,33 **a**	17,5±4,9 5 **a**	22,65±2,3 3 **b**	1,45±0,07 **ab**	17 **ab**
Full sun × Korhogo	2,68±0,09 **a**	6,97±1,9 8 **a**	37,25±27,51 **a**	0,98±0,30 **a**	17±2,82 **a**	41,8±15,9 8 **a**	1,71±0,72 **a**	19,5±3,5 3 **ab**
Full sun × Toumodi	0,51±0,17 **b**	1,53±0,5 9 **b**	10±5,42 **a**	0,48±0,16 **a**	8,86±4,0 5 **a**	15,48±7,3 4 **b**	0,72±0,23 **b**	12±2,58 **b**
Pr > F	**0,0001**	**0,0001**	**0,1812**	**0,1012**	**0,1592**	**0,0160**	**0,0260**	**0,0125**
Understorey × Bouaké	5,4±1,4 4 **a**	5,41±0,6 4 **a**	10,4±2,36 **a**	1,05±0,28 **a**	8,33±1,5 3 **b**	18,33±2,3 1 **b**	1,28±0,35 **a**	16,33±3,78 **b**
Understorey × Ferké	0,96±0,56 **a**	3,08±1,7 **a**	17,01±5,3 **a**	0,56±0,19 **a**	12,33±5,03 **ab**	15,90±3,6 2 **b**	0,92±0,38 **a**	13±1 **b**
Understorey × Katiola	2,8±0,3 2 **a**	5,19±0,3 5 **a**	31,4±10,5 6 **a**	0,71±2,3 **a**	19±12,0 4 **a**	38,4±5,61 **a**	1,8±0,5 3 **a**	23±9,87 **a**
Understorey × Korhogo	6,62±5,34 **a**	10,52±6,82 **a**	16,68±14,3 **a**	0,88±0,37 **a**	13±3,22 **ab**	15,32±8,6 8 **b**	1,25±0,45 **a**	14,5±3,0 2 **b**
Pr > F	**0,3033**	**0,2491**	**0,4689**	**0,3477**	**0,01120**	**0,0458**	**0,3641**	**0,0347**

Values sharing the same letter are not statistically different at the 5% threshold. **Full sun/Full sun** = open, sun-exposed environment; **Understorey** = crowded environment or under forest canopy cover. **Height (m)** = tree height, **Diam. (cm)** = diameter at tree base, **GU** = growth unit, **GU1 length/diam**. = length/basal diameter of the first growth unit, **GU1 leaf N** = number of leaves (phytomers) borne by the first growth unit; **GU2 length, GU2 diam., GU2 leaf N** = corresponding parameters of the second growth unit.

Table. S2: Influence of habitat, locality, and habitat × locality on growth-unit morphology in young *Pterocarpus erinaceus* trees

Habitats/Localities	**Height (m)**	**Diam. (cm)**	**GU1 length (cm)**	**GU1 diam. (cm)**	**GU1 leaf N**	**GU2 length (cm)**	**GU2 diam. (cm)**	**GU2 leaf N**

Full sun	1,83±0, 5 **b**	3,21±0, 49 **a**	17,73±8,4 9 **a**	0,51±0, 2 **a**	11,45±4, 29 **a**	21,64±9,3 8 **a**	0,82±0, 34 **a**	16,33±6, 64 **a**
Understorey	2,32±0, 59 **a**	3,93±0, 13 **a**	24,51±14, 71 **a**	0,57±0, 33 **a**	12,76±5, 62 **a**	17,4±7,51 **a**	0,78±0, 31 **a**	17,22±5, 26 **a**
Pr > F	**0,018**	**0,8225**	**0,0671**	**0,4673**	**0,6458**	**0,1237**	**0,7127**	**0,6426**
Ferké	3,49±2, 85 **a**	5,35±1, 35 **ab**	28,74±16, 56 **a**	0,69±0, 46 **a**	12±7,05 **ab**	17,32±7,0 6 **a**	0,88±0, 44 **a**	15,12±4, 99 **bcd**
Korhogo	4,28±2, 59 **a**	7,16±1, 58 **a**	22,05±13, 98 **a**	0,45±0, 14 **a**	11,5±3,0 1 **ab**	21,32±10, 08 **a**	0,75±0, 3 **a**	12,33±3, 72 **cd**
Niakara	1,53±0, 78 **a**	3,25±1, 75 **ab**	19,23±11, 14 **a**	0,45±0, 11 **a**	12,16±3, 86 **ab**	22,03±12, 38 **a**	0,97±0, 29 **a**	23±5,55 **a**
Katiola	2,79±1, 69 **a**	5,31±3, 08 **ab**	18,59±9,0 8 **a**	0,58±0, 14 **a**	12,78±4, 96 **ab**	19,55±5,6 5 **a**	0,74±0, 14 **a**	18,77±4, 49 **abc**
Bouaké	2,07±0, 88 **a**	1,08±0, 56 **b**	15,46±5,3 8 **a**	0,49±0, 25 **a**	12,66±4, 13 **ab**	21±13,78 **a**	0,79±0, 47 **a**	21,16±2, 31 **ab**
Daloa	0,53±0, 17 **a**	0,82±0, 52 **b**	15,04±6,8 6 **a**	0,33±0, 07 **a**	6,4±1,34 **b**	19,08±7,3 3 **a**	0,55±0, 06 **a**	8,6±2,97 **d**
Toumodi	3,35±1, 76 **a**	4,26±1, 8 **ab**	26,9±4,94 **a**	0,77±0, 06 **a**	16,5±2,1 2 **a**	18,3±4,1 **a**	1,14±0, 22 **a**	15±2,82 **bcd**
Pr > F	**0,0634**	**0,0018**	**0,3365**	**0,1376**	**0,01834**	**0,9721**	**0,2737**	**0,0001**
Full sun × Bouaké	3,1±2,7 **ab**	1,09±0, 99 **b**	12,25±8,2 7 **a**	0,59±0, 38 **a**	11±5,6 **a**	36,9±5,51 **a**	1,08±0, 93 **a**	21,5±3,5 3 **a**
Full sun × Daloa	0,53±0, 18 **b**	0,82±0, 53 **b**	15,04±6,8 5 **a**	0,33±0, 07 **a**	6,4±1,34 **b**	19,08±7,3 3 **a**	0,55±0, 06 **a**	8,6±2,96 **b**
Full sun × Ferké	1,32±0, 77 **ab**	2,85±1, 51 **ab**	18,5±0,14 **a**	0,54±0, 02 **a**	9,5±3,53 **a**	15,6±8,2 **a**	0,77±0, 13 **a**	16±4,24 **ab**
Full sun × Katiola	3,43±1, 3 **ab**	6,58±1, 51 **a**	19,27±9,2 3 **a**	0,64±0, 1 **a**	14,7±3,2 **a**	20,43±5,6 4 **a**	0,79±0, 1 **a**	19,57±4, 54 **ab**

Full sun × Korhogo	2,7±0,5 5 **ab**	6,58±2, 04 **a**	13,36±3,9 5 **a**	0,43±0, 21 **a**	12,66±3, 05 **a**	19,43±9,6 6 **a**	0,76±0, 46 **a**	9,66±2,0 8 **b**
Full sun × Niakara	1,34±0, 66 **ab**	7,06±2, 28 **ab**	20,85±12, 75 **a**	0,42±0, 08 **a**	11,5±4,6 5 **a**	24,12±15, 42 **a**	1,03±0, 35 **a**	22,75±5, 56 **a**
Full sun × Toumodi	4,6±1,3 3 **a**	5,54±3, 32 **a**	30,4±14,1 1 **a**	0,82±0, 3 **a**	15±9,31 **a**	21,2±14,2 3 **a**	1,31±0, 81 **a**	17±5,43 **b**
Pr > F	**0,0134**	**0,0001**	**0,5726**	**0,0616**	**0,0252**	**0,3292**	**0,2262**	**0,0007**
Understorey × Bouaké	1,56±0, 38 **a**	1,08±0, 44 **a**	17,07±10, 66 **a**	0,44±0, 04 **a**	13,5±3,8 7 **a**	13,05±7,3 3 **a**	0,65±0, 06 **a**	21±2,16 **a**
Understorey × Ferké	4,22±2, 96 **a**	6,18±4, 99 **a**	32,15±18, 11 **a**	0,75±0, 53 **a**	12,83±7, 98 **a**	17,9±7,4 **a**	0,92±0, 52 **a**	14,83±5, 56 **a**
Understorey × Katiola	0,57±0, 22 **a**	0,86±0, 13 **a**	16,2±11,5 9 **a**	0,4±0,0 1 **a**	6±4,24 **a**	16,5±6,35 **a**	0,55±0, 06 **a**	16±4,24 **a**
Understorey × Korhogo	5,87±3 **a**	7,26±0, 99 **a**	30,73±15, 71 **a**	0,47±0, 06 **a**	10,33±3, 05 **a**	23,2±12,2 5 **a**	0,74±0, 12 **a**	15±3 **a**
Understorey × Niakara	1,9±0,1 3 **a**	4,14±2, 7 **a**	16,10,05 **a**	0,5±0,1 8 **a**	13,5±2,1 2 **a**	17,85±0,2 1 **a**	0,84±0, 09 **a**	23,5±7,7 7 **a**
Understorey × Toumodi	2,1±1,4 **a**	2,99±0, 47 **a**	23,4±8,11 **a**	0,73±0, 07 **a**	18±4,8 **a**	15,4±6,11 **a**	0,97±0, 21 **a**	13±7,01 **a**
Pr > F	**0,1565**	**0,1454**	**0,5345**	**0,7042**	**0,5760**	**0,7222**	**0,7265**	**0,1753**

Values sharing the same letter are not statistically different at the 5% threshold. **Full sun/Full sun** = open, sun-exposed environment; **Understorey** = crowded environment or under forest canopy cover. **Height (m)** = tree height, **Diam. (cm)** = diameter at tree base, **GU** = growth unit, **GU1 length/diam**. = length/basal diameter of the first growth unit, **GU1 leaf N** = number of leaves (phytomers) borne by the first growth unit; **GU2 length, GU2 diam., GU2 leaf N** = corresponding parameters of the second growth unit.

Table. S3: Influence of habitat and locality on growth-unit morphology in adult *Khaya senegalensis* trees

Habitats/Localities	**Height (m)**	**Diam. (cm)**	**GU1 length (cm)**	**GU1 diam. (cm)**	**GU1 leaf N**	**GU2 length (cm)**	**GU2 diam. (cm)**	**GU2 leaf N**

Full sun	14,09±8,05 **a**	34,97±11,43 **a**	8,08±1,89 **a**	0,76±0,24 **a**	7,5±2,39 **a**	15,13±6,46 **a**	1,14±0,32 **a**	18,37±2,56 **a**
Understorey	11,6±6,33 **b**	29,08±12,12 **b**	18,1±13,48 **a**	0,72±0,10 **a**	13,75±7,89 **a**	19,3±10,85 **a**	0,94±0,25 **a**	16±3,46 **a**
Pr > F	**0,0073**	**0,0422**	**0,0554**	**0,7543**	**0,0577**	**0,4174**	**0,3097**	**0,2051**
Ferké	14,83±6,86 **ab**	49,62±14,28 **a**	13,37±13,02 **a**	0,79±0,15 **a**	10,66±5,68 **a**	11,8±3,96 **b**	1,25±0,39 **a**	17,66±2,52 **a**
Korhogo	8,45±5,31 **b**	17,96±5,06 **b**	7,3±3,02 **a**	0,78±0,56 **a**	9±4,21 **a**	17,3±6,51 **ab**	0,93±0,24 **a**	18±8,12 **a**
Niakara	18,5±8,66 **a**	48,82±13,91 **a**	7,67±1,86 **a**	0,62±0,14 **a**	5,5±1 **a**	13,9±2,43 **ab**	0,93±0,12 **a**	15,25±1,71 **a**
Katiola	13,6±9,21 **ab**	47,58±15,21 **a**	8,7±4,31 **a**	0,77±0,11 **a**	12±4,03 **a**	7±2,31 **b**	1,3±0,51 **a**	20±6,05 **a**
Bouaké	7,9±3,02 **b**	20,01±4,86 **b**	16,73±12,48 **a**	0,85±0,34 **a**	13,33±8,5 **a**	27,66±6,51 **a**	1,08±0,46 **a**	19,66±4,16 **a**
Pr > F	**0,0079**	**0,0182**	**0,7590**	**0,7275**	**0,4770**	**0,0121**	**0,6899**	**0,3648**
Full sun × Bouaké	9,86±8,20 **b**	15,13±6,51 **b**	11,4±6,64 **a**	1,24±0,34 **a**	7±2,3 **a**	28±4,32 **a**	1,68±0,31 **a**	23±8,65 **a**
Full sun × Ferké	17,85±6,29 **a**	27,49±10,09 **ab**	5,85±0,64 **a**	0,76±0,19 **a**	7,5±2,12 **a**	12,2±5,51 **a**	1,21±0,54 **a**	19±1,41 **a**
Full sun × Katiola	16±8,96 **a**	46,58±9,15 **a**	8,70±2,31 **a**	0,77±0,12 **a**	12±5,12 **a**	7±2,33 **a**	1,3±0,07 **a**	20±7,52 **a**
Full sun × Korhogo	8,8±7,82 **b**	17,96±9,25 **b**	7,3±1,05 **a**	0,78±0,30 **a**	9±4,21 **a**	17,3±15,98 **a**	0,93±0,72 **a**	18±3,53 **a**
Full sun × Niakara	17,69±3,42 **a**	44,72±16,39 **a**	8,5±1,06 **a**	0,59±0,16 **a**	5,66±1,15 **a**	14,8±2 **a**	0,96±0,12 **a**	**16**±1 **a**
Pr > F	**0,0485**	**0,01952**	**0,0805**	**0,2299**	**0,1692**	**0,1097**	**0,5505**	**0,0610**
Understorey × Bouaké	15,4±4,24 **a**	42,45±3,38 **a**	19,4±16,4 **a**	0,65±0,03 **a**	16,5±9,19 **a**	27,5±9,19 **a**	0,82±0,08 **a**	18±4,24 **a**

Understorey × Ferké	16,8±7,82 **a**	45,92±13,2 **a**	28,4 **a**	0,87±0,11 **a**	17±5,03 **a**	11±5,12 **a**	1,32±0,38 **a**	15±1,21 **a**
Understorey × Niakara	16±6,24 **a**	43,15 **a**	5,2 **a**	0,71±0,23 **a**	5±1,24 **a**	11,2±4,23 **a**	0,82±0,03 **a**	13±3,14 **a**
Pr > F	**0,1267**	**0,0882**	**0,7027**	**0,1552**	**0,6727**	**0,4889**	**0,1923**	**0,7071**

Values sharing the same letter are not statistically different at the 5% threshold.

Table. S4: Influence of habitat and locality on growth unit morphology in adult *Pterocarpus erinaceus* trees

Habitats/Localities	**Height (m)**	**Diam. (cm)**	**GU1 length (cm)**	**GU1 diam. (cm)**	**GU1 leaf N**	**GU2 length (cm)**	**GU2 diam. (cm)**	**GU2 leaf N**
Full sun	12,18±2,3 **a**	27,37±**4**,93 **a**	15,68±2,73 **a**	0,48±0,17 **a**	11,16±6,43 **a**	26,82±13,27 **a**	0,72±0,16 **a**	15,5±6,94 **a**
Understorey	11,94±**3**,1 **a**	24,6±**6**,28 **a**	19,56±9,37 **a**	0,53±0,13 **a**	11,14±3,53 **a**	27,96±10,29 **a**	0,79±0,07 **a**	21,28±8,76 **a**
Pr > F	**0,4542**	**0,2197**	**0,5407**	**0,6110**	**0,9934**	**0,8645**	**0,2847**	**0,1287**
Bouaké	11,4±0,18 **a**	16,27±0,91 **b**	16,81±10,37 **a**	0,45±0,16 **ab**	12,17±3,97 **a**	19,1±11,01 **a**	0,65±0,15 **ab**	21,5±2,88 **ab**
Ferké	12,85±3,47 **a**	21,39±6,2 **ab**	28,59±5,17 **a**	0,72±0,43 a	12,22±6,63 **a**	16,62±6,93 **a**	0,94±0,45 **ab**	14,88±4,73 **c**
Katiola	10,79±1,69 **a**	17,31±3,07 **b**	18,59±9,08 **a**	0,58±0,13 **ab**	12,78±4,96 **a**	19,55±5,65 **a**	0,74±0,14 **ab**	18,79±4,49 **ab**
Korhogo	12,37±7,12 **a**	22,99±6,7 6 **ab**	20,07±11,81 **a**	0,49±0,15 **ab**	10,7±2,58 **a**	22,47±11,58 **a**	0,78±0,23 **ab**	15,7±6,83 **c**
Niakara	11,15±4,9 **a**	21,26±5,16 **ab**	22,67±3,66 **a**	0,5±0,16 **ab**	13,2±4,96 **a**	29,12±17,94 **a**	0,96±0,27 **a**	25,3±7,66 **a**
Toumodi	11,53±5,42 **a**	34,52±12,49 **a**	15,43±7,86 **a**	0,58±0,2 **ab**	11,33±4,33 **a**	25,56±6,29 **a**	0,79±0,25 **ab**	14,89±3,55 **bc**
Pr > F	**0,0997**	**0,0103**	**0,1894**	**0,0494**	**0,1994**	**0,2014**	**0,0481**	**0,0001**

Full sun × Korhogo	14,1±4,71 **a**	25,32±0,43 **a**	7,8±2,43 **a**	0,43±0,07 **a**	8±3,51 **a**	9,7±4,31 **a**	0,78±0,22 **a**	11±5,1 **a**
Full sun × Niakara	12,6±7,4 **a**	21,68±11,3 **a**	39,6±7,4 3 **a**	0,62±0,11 **a**	22±4,31 **a**	49,8±13,3 **a**	0,86±0,33 **a**	27±11 **a**
Full sun × Toumodi	13,1±2,25 **a**	29,91±10,06 **a**	11,67±6,11 **a**	0,46±0,21 **a**	9,25±4,64 **a**	25,35±4,1 **a**	0,67±0,18 **a**	13,75±5,05 **a**
Pr > F	**0,3370**	**0,4771**	**0,0514**	**0,7861**	**0,1752**	**0,0137**	**0,6521**	**0,1792**
Understorey × Korhogo	12,76±3,72 **a**	20,54±3,8 **a**	20,2±7,2 7 **a**	0,61±0,16 **a**	10±1 **a**	29,03±4,13 **a**	0,84±0,08 **a**	24±5,19 **a**
Understorey × Niakara	12,01±2,98 **a**	22,12±2,75 **a**	26,65±13,5 **a**	0,43±0,01 **a**	12,5±3,78 **a**	22,5±9,1 9 **a**	0,78±0,06 **a**	23±7,07 **a**
Understorey × Toumodi	11±2,12 **a**	27,38±1,35 **a**	11,5±2,68 **a**	0,5±0,13 **a**	11,5±2,12 **a**	31,8±7,63 **a**	0,74±0,09 **a**	15,5±0,7 **a**
Pr > F	**0,1708**	**0,0937**	**0,3141**	**0,4158**	**0,8011**	**0,7297**	**0,4436**	**0,2746**

841 Values sharing the same letter are not statistically different at the 5% threshold.

842

843 **Table. S5 :** Influence of habitat and locality on growth unit morphology in old *Khaya senegalensis* trees

Habitats/Localities	**Height (m)**	**Diam. (cm)**	**GU1 length (cm)**	**GU1 diam. (cm)**	**GU1 leaf N**	**GU2 length (cm)**	**GU2 diam. (cm)**	**GU2 leaf N**
Full sun	31,46±10,99 **a**	100,02±65,45 **a**	8,78±6,67 **a**	0,81±0,16 **a**	7,81±2,82 **a**	15,41±4,49 **a**	1,28±0,27 **a**	16,54±3,41 **a**
Understorey	28,76±13,9 **a**	80,44±32,99 **a**	8,33±3,1 **a**	0,88±0,08 **a**	9±2,64 **a**	17,5±4,62 **a**	1,19±0,21 **a**	18±6,54 **a**
Pr > F	**0,8146**	**0,2752**	**0,9154**	**0,4639**	**0,5282**	**0,4928**	**0,5857**	**0,4877**
Ferké	35,62±16,22 **a**	204,22±48,78 **a**	12,37±10,69 **a**	0,71±0,16 **a**	9,5±3,69 **a**	18,5±4,91 **a**	1,3±0,36 **a**	17±3,27 **a**
Korhogo	32,7±3,24 **a**	85,54±5,64 **b**	5,8±1,86 **a**	0,97±0,14 **a**	6±1,03 **a**	18,7±2,43 **a**	1,4±0,12 **a**	18±1,71 **a**

Niakara	30,96±10 ,22 **a**	89,3±41,3 7 **b**	8,18±2,3 6 **a**	0,87±0, 15 **a**	8,33±2, 06 **a**	14,5±4,5 **a**	1,2±0,2 8 **a**	15,5±2,8 1 **a**
Katiola	31±3,6 **a**	122,6±8,2 4 **ab**	5,7±0,98 **a**	0,83±0, 07 **a**	6,33±2, 52 **a**	14,13±3, 54 **a**	1,3±0,1 **a**	19±3,46 **a**
Bouaké	32,12±4, 26 **a**	133,6±10, 24 **ab**	7,7±0,48 **a**	0,94±0, 16 **a**	7,44±4, 62 **a**	16,14±2, 44 **a**	1,4±0,2 1 **a**	17,2±6,4 4 **a**
Pr > F	**0,5959**	**0,0074**	**0,5150**	**0,3287**	**0,4427**	**0,4587**	**0,8844**	**0,4682**

Values sharing the same letter are not statistically different at the 5% threshold.

Table. S6: Influence of habitat and locality on growth-unit morphology in old *Pterocarpus erinaceus* trees

Habitats/Localities	**Height (m)**	**Diam. (cm)**	**GU1 length (cm)**	**GU1 diam. (cm)**	**GU1 leaf N**	**GU2 length (cm)**	**GU2 diam. (cm)**	**GU2 leaf N**
Full sun	17,78±1, 8 **a**	53,82±1 2,1 **a**	15,4±7,3 **b**	0,34±0, 1 **b**	9±3,51 **b**	28,4±5,1 1 **b**	0,62±0, 04 **b**	18±4,44 **b**
Understorey	19,3±3,2 **a**	50,51±1 0,7 **a**	22,9±6,3 6 **a**	0,89±0, 03 **a**	13±1,41 **a**	37,6±26, 6 **a**	1,4±0,2 **a**	27,5±14, 5 **a**
Pr > F	**0,3452**	**0,0973**	**0,0002**	**0,0006**	**0,021**	**0,0045**	**0,0001**	**0,0098**
Ferké	18,7±6,3 **a**	59,71±1 0,4 **ab**	27,4±11, 3 **a**	0,92±0, 04 **ab**	14±6,4 **ab**	11±5,4 **c**	1,4±0,7 **ab**	13±5,4 **c**
Niakara	19,7±11, 4 **a**	53,18±2 3,4 **b**	18,4±7,4 **b**	0,87±0, 01 **ab**	12±3,31 **ab**	64,2±11, 4 **a**	1,4±0,0 7 **ab**	42±7,6 **a**
Toumodi	18,7±7,3 3 **a**	54,74±6, 6 **b**	15,4±4,3 3 **b**	0,34±0, 06 **b**	9±5,3 **b**	28,4±7,6 **ab**	0,62±0, 04 **b**	18±1,8 **bc**
Katiola	16,79±1, 69 **a**	55,31±3, 07 **b**	19,56±8, 89 **b**	0,91±0, 18 **ab**	16,56±6, 32 **ab**	24±5,83 **b**	1,47±0, 33 **ab**	23,87±4, 12 **b**
Korhogo	19,37±7, 12 **a**	67,99±6, 7 6 **a**	20,49±9, 51 **b**	1,23±0, 45 **a**	15,1±3,7 3 **ab**	28,29±9, 22 **ab**	1,77±0, 72 **ab**	18,4±6,7 3 **bc**

Bouaké	16,4±0,1 8 **a**	51,27±0, 91 **b**	17,86±6, 69 **b**	0,89±0, 24 **ab**	22,6±3,9 1 **a**	22±3,29 **b**	2,36±1, 59 **a**	30,67±8, 33 **ab**
Pr > F	**0,751**	**0,0073**	**0,0327**	**0,0113**	**0,0043**	**0,0001**	**0,0134**	**0,001**

847 Values sharing the same letter are not statistically different at the 5% threshold.

848 **Table. S7:** Linear mixed-effects model coefficients (locality as random intercept) for the effects of habitat and
849 age on growth-unit variables by species

Species	Variable	Term	Estimate	SE	*p*
Khaya senegalensis	GU length (cm)	Understorey (vs Full sun)	-2.53	2.23	0.256
Khaya senegalensis	GU length (cm)	Old (vs Adult)	0.39	2.90	0.894
Khaya senegalensis	GU length (cm)	Young (vs Adult)	5.85	2.67	0.028
Khaya senegalensis	GU diameter (cm)	Understorey (vs Full sun)	-0.05	0.12	0.669
Khaya senegalensis	GU diameter (cm)	Old (vs Adult)	0.13	0.15	0.363
Khaya senegalensis	GU diameter (cm)	Young (vs Adult)	0.07	0.14	0.600
Khaya senegalensis	N phytomers/GU	Understorey (vs Full sun)	0.73	1.19	0.538
Khaya senegalensis	N phytomers/GU	Old (vs Adult)	1.88	1.56	0.229
Khaya senegalensis	N phytomers/GU	Young (vs Adult)	-1.42	1.42	0.318
Khaya senegalensis	N growth units/axis	Understorey (vs Full sun)	0.02	0.70	0.983

Khaya senegalensis	N growth units/axis	Old (vs Adult)	0.42	0.85	0.622
Khaya senegalensis	N growth units/axis	Young (vs Adult)	1.06	0.82	0.199
Pterocarpus erinaceus	GU length (cm)	Understorey (vs Full sun)	-1.86	1.61	0.249
Pterocarpus erinaceus	GU length (cm)	Old (vs Adult)	-2.13	2.72	0.434
Pterocarpus erinaceus	GU length (cm)	Young (vs Adult)	-1.38	2.19	0.531
Pterocarpus erinaceus	GU diameter (cm)	Understorey (vs Full sun)	0.12	0.17	0.485
Pterocarpus erinaceus	GU diameter (cm)	Old (vs Adult)	-0.04	0.29	0.883
Pterocarpus erinaceus	GU diameter (cm)	Young (vs Adult)	0.26	0.24	0.295
Pterocarpus erinaceus	N phytomers/GU	Understorey (vs Full sun)	1.82	0.89	0.041
Pterocarpus erinaceus	N phytomers/GU	Old (vs Adult)	0.90	1.51	0.552
Pterocarpus erinaceus	N phytomers/GU	Young (vs Adult)	-1.14	1.24	0.357
Pterocarpus erinaceus	N growth units/axis	Understorey (vs Full sun)	0.23	0.63	0.714
Pterocarpus erinaceus	N growth units/axis	Old (vs Adult)	1.43	1.05	0.174
Pterocarpus erinaceus	N growth units/axis	Young (vs Adult)	1.93	0.89	0.031

Model: response variable ~ habitat + age, with locality included as a random intercept (n = 7 localities). Reference levels**: habitat** = Full sun, **age** = Adult. ***SE*** = standard error. Bold-worthy effects ($P < 0.05$) are discussed in the main text (Results, « Robustness check » section, and Discussion).

Références

Adji, B.I., Akaffou, D.S., De Reffye, P., Sabatier, S., 2022a. Maternal environment and seed size are important for successful germination and seedling establishment of Pterocarpus erinaceus (Fabaceae). J. For. Res. 33, 977–990. https://doi.org/10.1007/s11676-021-01412-x

Adji, B.I., Akaffou, D.S., Letort, V., Kang, M., Wang, X., Jaeger, M., De Reffye, P., Kouassi, K.H., Houphouet, Y.P., Duminil, J., Caraglio, Y., Sabatier, S., 2022b. The Architectural Unit Setting up and Architectural Characteristics of Néré, <i>Parkia biglobosa</i>, Jack, R. Br. (Fabaceae). Am. J. Plant Sci. 13, 109–136. https://doi.org/10.4236/ajps.2022.131008

Adji, B.I., Akaffou, D.S., Sabatier, S., 2022c. Variation on growth unit morphology in Khaya senegalensis (Desr.) A. Juss., 1830 (Meliaceae) and Pterocarpus erinaceus Poir., 1804 (Fabaceae) according to habitat and climate. BOIS FORETS Trop. 354, 41–54. https://doi.org/10.19182/bft2022.354.a36768

Adji, B.I., Letort, V., Wang, X., Kang, M., De Reffye, P., Jaeger, M., Cilas, C., Kouassi, K.H., Duminil, J., Sabatier, S., Akaffou, D.S., 2023. Rethinking Iconic Species Reforestation in West Africa: Seed Shape Harnessing Is Strategic for Enhanced Germination and Vigorous Growth in Khaya senegalensis and Parkia biglobosa. Forests 14, 1311. https://doi.org/10.3390/f14071311

AFR100, 2026. AFR100 [WWW Document]. URL https://afr100.org/ (accessed 6.28.26).

Amani, B.H.K., N'Guessan, A.E., Van Der Meersch, V., Derroire, G., Piponiot, C., Elogne, A.G.M., Traoré, K., N'Dja, J.K., Hérault, B., 2022. Lessons from a regional analysis of forest recovery trajectories in West Africa. Environ. Res. Lett. 17, 115005. https://doi.org/10.1088/1748-9326/ac9b4f

Anest, A., Charles-Dominique, T., Maurin, O., Millan, M., Edelin, C., Tomlinson, K.W., 2021. Evolving the structure: climatic and developmental constraints on the evolution of plant architecture. A case study in *Euphorbia*. New Phytol. 231, 1278–1295. https://doi.org/10.1111/nph.17296

Barthélémy, D., 1991. Levels of organization and repetition phenomena in seed plants. Acta Biotheor. 39, 309–323. https://doi.org/10.1007/BF00114184

Barthélémy, D., Caraglio, Y., 2007. Plant Architecture: A Dynamic, Multilevel and Comprehensive Approach to Plant Form, Structure and Ontogeny. Ann. Bot. 99, 375–407. https://doi.org/10.1093/aob/mcl260

879 Barthélémy, D., Edelin, C., Hallé, F., 1989. Architectural concepts for tropical trees. Academic Press, p. 89.
880 Barthélémy, D., Sabatier, S., Pascal, O., 1995. Le développement architectural du noyer commun , Juglans regia
881 L. (Juglandaceae).
882 Bouka Dipelet, U.G., Doumenge, C., Loumeto, J.J., Florence, J., Gonmadje, C., Mckey, D., 2019. Des confusions
883 entre espèces préjudiciables à la gestion durable des essences forestières : l'exemple des acajous
884 d'Afrique (Khaya, Meliaceae). BOIS FORETS Trop. 339, 17–32.
885 https://doi.org/10.19182/bft2019.339.a31714
886 Centre, W.C.M., 1998. IUCN Red List of Threatened Species: Khaya senegalensis. IUCN Red List Threat.
887 Species.
888 Coupel-Ledru, A., Pallas, B., Delalande, M., Segura, V., Guitton, B., Muranty, H., Durel, C., Regnard, J., Costes,
889 E., 2022. Tree architecture, light interception and water-use related traits are controlled by different
890 genomic regions in an apple tree core collection. New Phytol. 234, 209–226.
891 https://doi.org/10.1111/nph.17960
892 Drénou, C., 2023. La methode ARCHI Quebec Vert 2023.
893 Dumenu, W.K., 2019. Assessing the impact of felling/export ban and CITES designation on exploitation of
894 African rosewood (Pterocarpus erinaceus). Biol. Conserv. 236, 124–133.
895 https://doi.org/10.1016/j.biocon.2019.05.044
896 Goba, A.E., Koffi, K.G., Sié, R.S., Kouonon, L.C., Koffi, Y.A., 2019. Structure démographique et régénération
897 naturelle des peuplements naturels de Pterocarpus erinaceus Poir. (Fabaceae) des savanes de Côte
898 d'Ivoire. BOIS FORETS Trop. 341, 5–14. https://doi.org/10.19182/bft2019.341.a31750
899 Grisafi, F., Farinelli, D., Costes, E., Boudon, F., Durand, J.B., Tombesi, S., 2023. Architecture and yield
900 relationship in hazelnut tree. Acta Hortic. 331–336. https://doi.org/10.17660/ActaHortic.2023.1366.40
901 Hallé, F., Keller, R., 2019. Mais d'où viennent les plantes? Actes Sud Editions.
902 Hallé, F., Oldeman, R., 1970. Essai sur l'architecture et la dynamique de croissance des arbres tropicaux.
903 Httpshorizondocumentationirdfrexl-Docpleinstextesdivers20-0804497pdf.
904 Heuret (Patrick), Nicolini (Eric), Edelin (Claude), Roggy (Jean-Chirstophe), 2003. Approche architecturale pour
905 l'étude des arbres de la forêt tropicale humide guyanaise. Rev. For. Fr. 158.
906 https://doi.org/10.4267/2042/5769

Issa, I., Wala, K., Dourma, M., Atakpama, W., Kanda, M., Koffi, A., 2018. Valeur ethnobotanique de l'espèce, Khaya senegalensis (Desr.) A. Juss (meliaceae) auprès des populations riveraines de la chaine de l'Atacora au Togo.

Louppe, D., Ouattara, N., N'Guessan Kanga, A., Zo-Bi, I., Tiéoulé, F., Ahoba, A., Coulibaly, B., Hérault, B., 2021. Vingt-deux espèces d'arbres autochtones plantées en arboretum à Korhogo au nord de la Côte d'Ivoire : trois décennies de suivi. BOIS FORETS Trop. 348. https://doi.org/10.19182/bft2021.348.a36399

Lykke, A.M., Rømer, N., Gonzalez, P., Glèlè Kakaï, R., Rabiou, H., Amegnaglo, K.B., Ganaba, S., Sambou, B., Niang, F., Herault, B., Guuroh, R.T., Ouoba, P., Yaméogo, J.T., Traoré, L., Sinsin, B., Amahowe, O.I., Bay, S.S., Houehanou, T.D., Houessou, L.G., Gouwakinnou, G.N., Yetein, M.H., Tankoano, B., Ouédraogo, A., Ouédraogo, I., Taita, P., Amani, B.H.K., Coulibaly, B., Kouyaté, A.M., Van Damme, P., Vanhove, W., Mahamane, A., Bonache, C., Sambou, S., Soumana, I., Amani, A., Maârouhi, I.M., Barfod, A.S., 2025. Tree populations show low regeneration of valued species in West Africa. Biol. Conserv. 301, 110891. https://doi.org/10.1016/j.biocon.2024.110891

Nicolini, E., 1998. Architecture et gradients morphogénétiques chez de jeunes hêtres *Fagus sylvatica* L. Fagaceae) en milieu forestier. Can. J. Bot. 76, 1232–1244. https://doi.org/10.1139/b98-053

Nicolini, E., Beauchêne, J., De La Vallée, B.L., Ruelle, J., Mangenet, T., Heuret, P., 2012. Dating branch growth units in a tropical tree using morphological and anatomical markers: the case of Parkia velutina Benoist (Mimosoïdeae). Ann. For. Sci. 69, 543–555. https://doi.org/10.1007/s13595-011-0172-1

Oldeman, R.A.A., 1990. Forests: Elements of Silvology. Springer Berlin Heidelberg, Berlin, Heidelberg. https://doi.org/10.1007/978-3-642-75211-7

Rosati, A., Paoletti, A., Lodolini, E.M., Famiani, F., 2024. Cultivar ideotype for intensive olive orchards: plant vigor, biomass partitioning, tree architecture and fruiting characteristics. Front. Plant Sci. 15, 1345182. https://doi.org/10.3389/fpls.2024.1345182

Sabatier, S., Caraglio, Y., Drénou, C., 2014. L'architecture des arbres au service des forestiers. Innov. Agron. 41, 119–128.

Sabatier, S.-A., 1999. Variabilité morphologique et architecturale de deux espèces de noyers : Juglans regia L., Juglans nigra L. et de deux noyers hybrides interspécifiques (thesis). UM2.

Timite, N., Koua, K.A.N., Kouakou, A.T.M., Barima, Y.S.S., 2023. Dynamiques spatio-temporelles des parcs agroforestiers dans la zone soudanienne de la Côte d'Ivoire de 1990 à 2020 dans un contexte d'expansion

de l'anacarde: Spatio-temporal dynamics of agroforestry parks in the Sudanian zone of Côte d'Ivoire from 1990 to 2020 in a context of cashew expansion. Int. J. Biol. Chem. Sci. 17, 484–504. https://doi.org/10.4314/ijbcs.v17i2.16

Timité, N., Kouakou, A.T.M., Bamba, I., Barima, Y.S.S., Bogaert, J., 2022. Climate Variability in the Sudanian Zone of Côte d'Ivoire: Weather Observations, Perceptions, and Adaptation Strategies of Farmers. Sustainability 14, 10410. https://doi.org/10.3390/su141610410

Tre, B., Koffi, Kg, Kouonon, L., Koffi, Ka, Pereda-Loth, V., Sie, R., 2025. CHARACTERISATION OF THE DEMOGRAPHIC AND SPATIAL STRUCTURES OF THREE NATURAL POPULATIONS OF KHAYA SENEGALENSIS IN CÔTE D'IVOIRE. J. Trop. For. Sci. 37, 475–483. https://doi.org/10.26525/jtfs2025.37.4.475

Zhang, X., Chen, X., Wang, K., Li, X., Bai, R., Feng, J., Zhao, B., Costes, E., Yang, W., 2023. Effect of floral differentiation on shoot morphology and consequences on canopy light interception and photosynthetic capacity based on 3D virtual plants. Acta Hortic. 337–344. https://doi.org/10.17660/ActaHortic.2023.1366.41