Variation in growth unit morphology in Khaya senegalensis (Desr.) A. Juss. (Meliaceae) and Pterocarpus erinaceus Poir. (Fabaceae) according to habitat and climate

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Photo 1.
Fine counting of axes growth markers in the crown of a *Khaya senegalensis* tree using binoculars.
Photo B. I. Adji.

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RÉSUMÉ

Variation de la morphologie des unités de croissance des essences *Khaya senegalensis* (Desr.) A. Juss. (Meliaceae) et *Pterocarpus erinaceus* Poir. (Fabaceae) selon l'habitat et le climat

L'analyse rétrospective repose sur l'accès à des chronoséries longues sur la croissance permettant de comprendre et d'interpréter le fonctionnement structurel des houppiers, comme l'exige la gestion durable des peuplements. L'objectif de cette étude était d'évaluer le développement et l'adaptation des houppiers de *Khaya senegalensis* et *Pterocarpus erinaceus* à un environnement changeant, afin de préparer l'établissement de parcelles permanentes. Les morphologies des unités de croissance (UC) des axes de 420 individus jeunes, adultes et âgés ont été analysées en plein soleil ou à l'ombre pendant la saison des pluies et la saison sèche dans sept sites en Côte d'Ivoire. Les résultats montrent que la morphologie de ces unités de croissance est un indicateur à la fois de l'expression du développement et des difficultés de développement des essences. L'hétérogénéité des habitats n'avait aucun effet significatif sur la morphologie des unités de croissance (P > 0,05) des deux essences. La morphologie des UC varie d'un endroit (climat) à l'autre en raison des caractéristiques environnementales distinctes (P < 0,05). La partie sud du gradient (Toumodi et Bouaké dans la région centrale du pays) offre des zones favorables et donc prioritaires pour les programmes de reboisement basés sur ces deux essences. L'âge des individus influence le nombre de phytomères par unité de croissance (P < 0,05). Les individus jeunes (boutures) sont de bons idéotypes pour la sélection de génotypes suffisamment résistants. Quelle que soit l'essence, la saison des pluies augmente le taux de réussite de l'établissement des parcelles. Les unités de croissance des deux essences sont pratiquement de la même taille (P > 0,05). Nos résultats pourraient servir de guide pour la prise de décision en vue de sélectionner des environnements appropriés pour la mise en œuvre de programmes de reboisement ou d'agroforesterie basés sur *K. senegalensis* et *P. erinaceus* et visant à conserver et à gérer durablement ces essences dans le contexte actuel de changement climatique.

Mots-clés : *Khaya senegalensis*, *Pterocarpus erinaceus*, environnement, morphologie, unité de croissance (UC), Côte d'Ivoire.

ABSTRACT

Variation in growth unit morphology in *Khaya senegalensis* (Desr.) A. Juss. (Meliaceae) and *Pterocarpus erinaceus* Poir. (Fabaceae) according to habitat and climate

Retrospective analysis relies on access to long-term growth series to understand and interpret the structural functioning of tree crowns, as required for their sustainable management. The aim of this study was to assess the development and adaptation of crown shoots in *Khaya senegalensis* and *Pterocarpus erinaceus* to a changing environment, to prepare for the establishment of permanent plots. The growth unit (GU) morphologies of the axes of 420 young, adult and old individuals were analysed in full sunlight or shade during the rainy and dry season in seven locations in Côte d'Ivoire. The results show that the morphology of these growth units is an indicator of both development expression and developmental difficulties in tree species. Heterogeneous habitat had no significant effect on growth unit morphology (*P* > 0.05) in either species. The morphology of the growth units varied from one location (climate) to another due to their distinct environmental characteristics (*P* < 0.05). The southern part of the gradient (Toumodi and Bouaké in the central region of the country) offers favourable and hence priority areas for reforestation programmes based on the two species. The age of the individuals influenced the number of phytomers per growth unit (*P* < 0.05). Young individuals (cuttings) are good ideotypes for the selection of suitably resistant genotypes. Whatever the species, the rainy season increased the success rate of plot establishment. The growth units of the two species are of practically the same size (*P* > 0.05). Our results could be a guide to decisions for the selection of suitable environments for the implementation of reforestation or agroforestry programs based on *K. senegalensis* and *P. erinaceus* and aiming to conserve and sustainably manage these species in the current climate change context.

Keywords: *Khaya senegalensis*, *Pterocarpus erinaceus*, environment, morphology, Growth Unit (GU), Côte d'Ivoire.

RESUMEN

Variación de la morfología de la unidad de crecimiento en *Khaya senegalensis* (Desr.) A. Juss. (Meliaceae) y *Pterocarpus erinaceus* Poir. (Fabaceae) según el hábitat y el clima

El análisis retrospectivo se basa en el acceso a series de crecimiento a largo plazo para comprender e interpretar el funcionamiento estructural de las copas de los árboles, tal y como se requiere para su gestión sostenible. El objetivo de este estudio era evaluar el desarrollo y la adaptación de los brotes de copa en *Khaya senegalensis* y *Pterocarpus erinaceus* a un entorno cambiante, para preparar el establecimiento de parcelas permanentes. Se analizaron las morfologías de las unidades de crecimiento (UC) de los ejes de 420 individuos jóvenes, adultos y viejos a plena luz solar o a la sombra durante la estación lluviosa y la estación seca en siete localidades de Costa de Marfil. Los resultados muestran que la morfología de estas unidades de crecimiento es un indicador tanto de la expresión del desarrollo como de las dificultades de desarrollo de las especies arbóreas. El hábitat heterogéneo no tuvo un efecto significativo en la morfología de la unidad de crecimiento (*P* > 0,05) en ninguna de las especies. La morfología de las unidades de crecimiento varió de un lugar (clima) a otro debido a sus distintas características ambientales (*P* < 0,05). La parte sur del gradiente (Toumodi y Bouaké, en la región central del país) ofrece zonas favorables y, por tanto, prioritarias para los programas de reforestación basados en ambas especies. La edad de los individuos influyó en el número de fitómeros por unidad de crecimiento (*P* < 0,05). Los individuos jóvenes (esquejes) son buenos ideotipos para la selección de genotipos adecuadamente resistentes. Independientemente de la especie, la temporada de lluvias aumentó la tasa de éxito del establecimiento de las parcelas. Las unidades de crecimiento de las dos especies son prácticamente del mismo tamaño (*P* > 0,05). Nuestros resultados podrían orientar en la toma de decisiones hacia la selección de entornos adecuados para implementar programas de reforestación o agroforestales basados en *K. senegalensis* y *P. erinaceus* que tengan como objetivo la conservación y gestión sostenible de estas especies en el contexto actual de cambio climático.

Palabras clave: *Khaya senegalensis*, *Pterocarpus erinaceus*, entorno, morfología, unidad de crecimiento (UC), Costa de Marfil.

Introduction

Plant architectural retrospective analyses, which describes the historical growth strategy of tree's species (Barthélémy and Caraglio, 2007), has been used for the phenotypic description and diagnosis of tree condition in several studies (Rutishauser *et al.,* 2011; Nicolini *et al.,* 2012; Sabatier *et al.,* 2014). It has also been used in many countries to understand and detect the impact of climate on the growth phases, development difficulties and adaptation of trees to a changing environment (Chaubert-Pereira *et al.,* 2009; Taugourdeau *et al.,* 2011). Indeed, the interpretation of primary growth markers is often neglected, despite the fact that it provides long time series on the development of tree crowns, i.e., the conditions required for sustainable management (Nicolini *et al.,* 2012). Retrospective analysis provides a better understanding in the coordination of growth processes (elongation, thickening) in the crown, in the morphology and anatomy during the long-term development of trees and in the causes of observed variations (Nicolini and Caraglio, 1994; Nicolini *et al.,* 2012). Although retrospective analysis has been proven to be very effective in assisting foresters in the diagnosis of tree condition and sustainable management of many plant genetic resources in Europe and South America, it has not been frequently applied to native forest species in sub-Saharan Africa. Yet, data acquired through the use of such a methodology can help contributing to the conservation of forest genetic resources, and thus to the resilience of forest ecosystems.

In sub-Saharan Africa, biodiversity is threatened by unhealthy and environmentally unsustainable agriculture following deforestation (REDD+, 2017). Several multiple-use species are overexploited and are consequently threatened with extinction (Ake-Assi, 1999; Kouassi *et al.,* 2019). After sharply reducing tropical rainforests, these practices are now spreading to savannah areas (54% of the surface area of Côte d'Ivoire). Reforestation and agroforestry based on local species are the two solutions chosen by Ivorian decision-makers to restore forest cover and conserve the country's wood resources (Akaffou *et al.,* 2019; REDD+, 2020). *Pterocarpus erinaceus* Poir. and *Khaya senegalensis* (Desr.) A. Juss. are species highly appreciated by the populations of the savannah zones for the quality of their wood, their use as fodder, their ability to restore the soil (as leguminous plants) and their medicinal properties. Moreover, *P. erinaceus* is a CITES-listed endangered species as well as included in the IUCN Red List (CITES, 2016; Goba *et al.,* 2019; Dumenu, 2019; Issa *et al.,* 2017; Adji *et al.,* 2020, 2021b) due to their intensive exploitation. Including them in reforestation and agroforestry programmes is one solution for their preservation and sustainable use.

In the current context of climate change, the functioning of tree crowns, genomic and environmental signatures and the species adaptation mechanisms to a changing climate all need to be taken into account to ensure their sustainable management (Nicolini, 2000; Kushwaha *et al.,* 2010; Sabatier *et al.,* 2014). Applying the retrospective method to endangered species such as *K. senegalensis* and *P. erinaceus* will provide information on their difficulties in developing in a given environment, enable the selection of genotypes that are resistant or adapted to certain habitats, and of priority areas favourable for forest management or agroforestry programmes (Segla *et al.,* 2020; Adji *et al.,* 2021c).

The aim of this study was to use retrospective analysis to study the development of growth units of *K. senegalensis* and *P. erinaceus* as a function of habitat (full sun and shading) and cohorts of individuals (saplings, adult tree and old tree) in the rainy and dry seasons. In this aim different individuals of these two species were analysed across a North-South bioclimatic gradient in Côte d'Ivoire. This approach allowed to: (i) identify the development mode of the two species, their difficulties in developing and adapting to climate change; (ii) identify environments or locations conducive to their cultivation; (iii) identify resistant genotypes adapted to climate variations for use in more severe environments; (iv) assess the variability of shoots according to the size of the individuals and the optimal conditions for development, and (v) Identify and characterise architectural markers that can be used to optimise reforestation success (precision forestry). The latter could help to reduce dieback of stands based on these species, and lead to their conservation and sustainable management.

Material and methods

Plant material

Observations were made on the axes of 420 individuals per species of young (age: 1 to 5 year, height: 0.1 to 6 m, dbh: 1 to 9 cm for *K. senegalensis* and age: 1 to 5 years, height: 0.1 to 5 m, dbh: 1 to 9 cm for *P. erinaceus*), adult (age: 6 to 20 years, height: 7 to 20 m, dbh: 10 to 49 cm for *K. senegalensis* and age: 6 to 20 years, height: 10 to 15 m, dbh: 10 to 39 cm for *P. erinaceus*) and old trees (age: ≥ 21 years, height: ≥ 21 m, dbh: ≥ 50 cm for *K. senegalensis* and age: ≥ 21 years, height: ≥ 16 m, dbh: ≥ 40 cm for *P. erinaceus*) arbitrarily chosen in naturally regenerated individuals by species in shady undergrowth or crowded with other surrounding species and in the full sun or isolated (table I). Dendrometric characteristics and visual architectural appearance (physiological condition, decay, crown appreciation and visual aspect, ring colour, etc.) were used to estimate the age of trees and categorized them into the three development stages, *i.e.* young, adult and old ones. The number of individuals per type of habitat and per age category, as well as the types of axes assessed are detailed in table I.

Study sites

The study took place in seven sites locations along a north-south bioclimatic gradient in Côte d'Ivoire (table II). These locations were chosen according to a decreasing gradient of vegetation density harbouring stands of *K. senegalensis* and *P. erinaceus* (figure 1).

Table I.
Dendrometric and age criteria, number of material and type of axis evaluated as a function of age and habitat in the two-target species.

Species	Development stage	Habitat/ environment	Tree height (m)			Tree diameter (cm)			N° of indiv.	Axis examined
			Min	Max	Mean	Min	Max	Mean		
Khaya senegalensis	Young-tree (1-5 Yr) H (m): 0.1-6; D (cm): 1-9	Full sunlight	0.33	5.7	1.71 ± 0.29	0.52	9.74	3.54 ± 1.29	70	Main stem
		Shade	0.52	4.8	2.54 ± 0.15	1.18	8.85	5.39 ± 1.07	70	Main stem
	Adult-tree (6-20 Yr) H (m): 7-20; D (cm): 10-49	Full sunlight	7.5	17	14.09 ± 5.6	14.3	49.62	34.97 ± 4.01	70	Branch
		Shade	7.4	18.5	11.6 ± 6.18	12.3	45.92	29.08 ± 2.97	70	Branch
	Old-tree (≥21 Yr) H (m): ≥21; D (cm): ≥50	Full sunlight	21	37	31.46 ± 4.4	44	276.08	100.02 ± 57.	70	Branch
		Shade	20.5	34	28.76 ± 5.5	34.3	129.3	80.44 ± 34.8	70	Branch
Pterocarpus erinaceus	Young-tree (1-5 Yr) H (m): 0.1-5; D (cm): 1-9	Full sunlight	0.27	3.8	1.83 ± 0.51	0.38	9.59	3.21 ± 0.49	70	Main stem
		Shade	0.28	4.3	2.32 ± 0.59	0.54	9.20	3.93 ± 0.69	70	Main stem
	Adult-tree (6-20 Yr) H (m): 10-15; D (cm): 10-39	Full sunlight	10.1	15.6	12.18 ± 2.3	21.4	36.62	27.37 ± 4.93	70	Branch
		Shade	10.8	14.5	11.94 ± 3.1	14.2	38.1	24.6 ± 6.28	70	Branch
	Old-tree (≥21 Yr) H (m): ≥16; D (cm): ≥40	Full sunlight	16.5	19.5	17.78 ± 1.8	40.3	71.4	53.82 ± 12.1	70	Branch
		Shade	17	22	19.3 ± 3.2	41.7	63	50.51 ± 10.7	70	Branch

Yr = age in years: Tree-diam = diameter of tree or diameter of tree at breast height; Min = minimum; Max = maximum; m = meter; cm = centimetre; N° of indiv. = number individuals evaluated.

Sampling

Choice of individuals

In each species and tree development stage (young, adult and old), 10 individuals were arbitrarily and randomly selected in open and closed areas in the seven above-mentioned locations (Ferké, Korhogo, Niakara, Katiola, Bouaké, Toumodi and Daloa) during the rainy season (optimal conditions) and the dry season (limiting conditions) (Nicolini and Caraglio, 1994). Thus, we obtained: 10 individuals * 2 zones (Undergrowth/Shade and Full sun) * 3 stages (young, adult and old) * 7 localities = 420 individuals (table I). The development stages (young, adult and old) were chosen arbitrarily based on the height and diameter (dbh) of individuals grown in nurseries and from individuals present in former plots established by the National Center for Agronomic Research (CNRA) of Côte d'Ivoire in the 1980s, then by a field survey questionnaire containing the approximate age of the sampled trees, submitted to the rural populations who owned the plots surveyed in the forest.

Choice of habitats

Although both species are heliophiles (tree savannah/open forest and grassy savannah species), two types of environments were considered: undergrowth and full sun. Individuals in the undergrowth lived in a very shady environment with a forest cover or in an overcrowded environment or benefited from more shelter. Individuals in the second category were growing isolated in full sun or in an open environment with direct access to sunlight.

Choice of axis types

Observations were made on different types of axis in two different habitats depending on the accessibility of the

Table II.
Characteristics of the locations surveyed.

Sites/ locations	GPS coordinates	Vegetation	Climate	Temperature (°C)	Rainfall (mm/year)	Soil type
Ferké	5°23'43,39644"W; 9°36'1,87056"N	Grassy savannah	Dry tropical	27-40	263-1200	Ferralitic soils (Ferrisols, Cambisols, . Fluvisols, Luvisols), highly to moderately desaturated
Korhogo	5°36'12,39612"W; 9°33'24,68988"N	Open forest (wooded savannah)	Dry tropical	26,6- 35,7	817 - 1216	Ferruginous (90%) and Ferralitic (10%): superficial gravelly soil, deep gravel with a heavy texture, low in organic matter, highly desaturated
Niakara	5°18'40,73544"W; 8°40'47,97912"N	Wooded and grassy savannah	Dry tropical	24,7-38	800-1230	Complex of slightly desaturated ferrallitic soils and eutrophic brown tropical soils derived from basic rocks
Katiola	5°7'35,814"W; 8°13'53,94"N	Wooded and grassy savannah	Dry tropical	24-36	1100-1200	Moderately and highly desaturated ferrallitic soils
Bouaké	5°5'47,3289"W; 7°40'45,335"N	Clear forest (wooded savannah)	Wet tropical	23,6-34	1100-1200	Gravelly, moderately saturated, reworked, shallow ferralitic gravel from a granitic alteration material with a sandy-clay texture
Toumodi	5°1'34,95576"W; 6°22'42,67848"N	Open forest (wooded savannah, grassland and gallery forests)	Wet tropical	26,6-30	1092-1200	Ferralitic soil on granitic bedrock (sandy-. clayey soil), characterised by the weak differentiation and friable consistency of their horizons
Daloa	6°26'9,19788"W; 6°54'32,058"N	Tropical rainforest	Wet tropical	21-34	1000 -1900	Ferralitic, deep, acidic and desaturated in exchangeable bases, rich in organic matter

°C = Celsius degree; mm = millimetre; W = west; N = north.

crowns. In young trees, the axes evaluated were the main trunks due to the ease of access and the rareness of secondary branches on all individuals in this category. In adult and old trees, the axes evaluated were branches, tertiary branches and short twigs depending on accessibility. Young trees were assessed on site; whereas the branches of adult and old trees were cut and transported back to the laboratory for assessment (Nicolini and Caraglio, 1994; Adji *et al.*, 2021a).

Identification and observation of growth units

The growth unit is defined based on morphological markers which result from the functioning of meristems and which remain unchanged for several years. These morphological

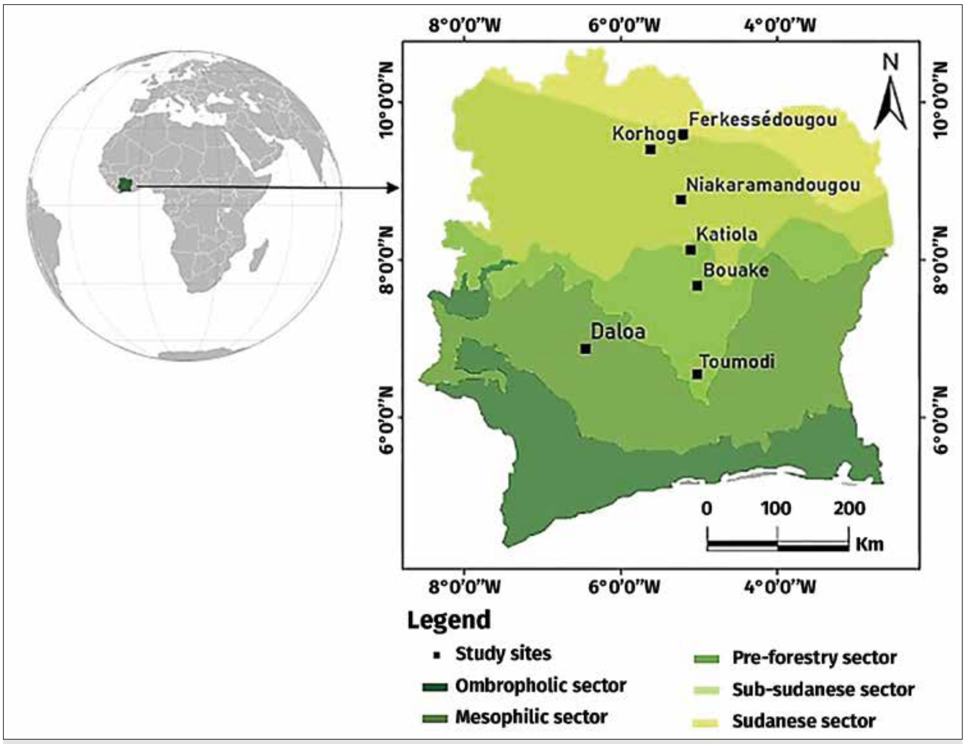

Figure 1.
Geographical location of the study area.

markers include the scars left by the scales of a bud, cataphylls and deciduous leaves, naturally pruned twigs, a bend in the axis at the site of apical necrosis or trauma, and the texture of the bark. The growth unit or elongation unit or morphological unit or extension unit (Hallé and Martin, 1968; Sabatier, 1999; Barthélémy and Caraglio, 2007; Millan, 2016) corresponding to all the organs initiated by the apical meristem during an uninterrupted organogenesis and elongation phase is delimited at its base by a large number of scars or pairs of scales (7 to 16) left by the terminal bud. This character can thus retrospectively enable identification of the successive growth units arranged along a leafy stem.

In general, two types of shoots are produced by the establishment of growth units by the terminal bud in temperate zones: monocyclic shoots (a single growth unit during one year or a wave of growth in spring) and polycyclic shoots (several growth units during one year or in growth waves in spring and summer) (Thiébaut, 1982; Nicolini and Caraglio, 1994; Barthélémy and Caraglio, 2007). The first growth unit (spring growth wave) is qualified as pre-formed (in the sense of Hallé *et al.,* 1978: presence of all the leaf organs of the future growth units in the bud before budburst), whereas other organs in the growth unit are qualified as neo-formed (simultaneous prolonged establishment of the leaf organs by the apical meristem after the pre-formed organs). In the tropics, the majority of shoots are polycyclic due to the rhythmicity adopted by the species in this zone (Hallé *et al.,* 1978; Hallé and Keller, 2019). This is the case for *K. senegalensis* and *P. erinaceus*. Retrospective analysis allows to recognise and date different structures (axes and GU) in the crown of a plant, to quantify the development by measuring shoot dimensions, to qualify the expression of certain architectural characteristics of a species, to identify areas of favourable development for a species, to evaluate the capacity of a species to adapt to a changing climate, to apprehend the effects of environmental factors on the regeneration of a species, etc.

Parameters assessed

Retrospective analysis focused on the first four growth units starting from the apex of the sampled axis. The morphological parameters evaluated on each axis in each species were the total number of growth units in the axis, the length of each growth unit, the diameter at the beginning of the growth units, and the number of leaves or phytomers of the first four growth units (Nicolini *et al.,* 2012; Nicolini, 2000; Sabatier *et al.,* 1998; Godin and Caraglio, 1998). As a reminder, a phytomere is the most fundamental unit of organisation of a plant, generally composed of an internode and a node with a leaf and an axillary bud. The harvested stems and branches were split longitudinally and transversally to identify growth stops (delimiting portions of the growth units) that are invisible on the bark of the axes. Data were collected during the rainy season (June and July 2020) and again from exactly the same individuals during the dry season (January and February 2021).

Statistical analysis

Statistical analyses were first performed using univariate descriptive statistics methods with XLSTAT 2020 version 7.5. The effect of habitat, location, age of individuals, season and species on the morphological parameters of the growth units was evaluated by a one-way analysis of variance (ANOVA) after square root normalisation of the data in order to maintain the database, to decrease the complexity of the comparison models and to reduce the cases of redundant data (double value and outliers) in SAS version 9.4. The homogeneity of variances was validated and the Student-Newman-Keuls test at the 5% threshold was used for post-hoc comparisons (GLM).

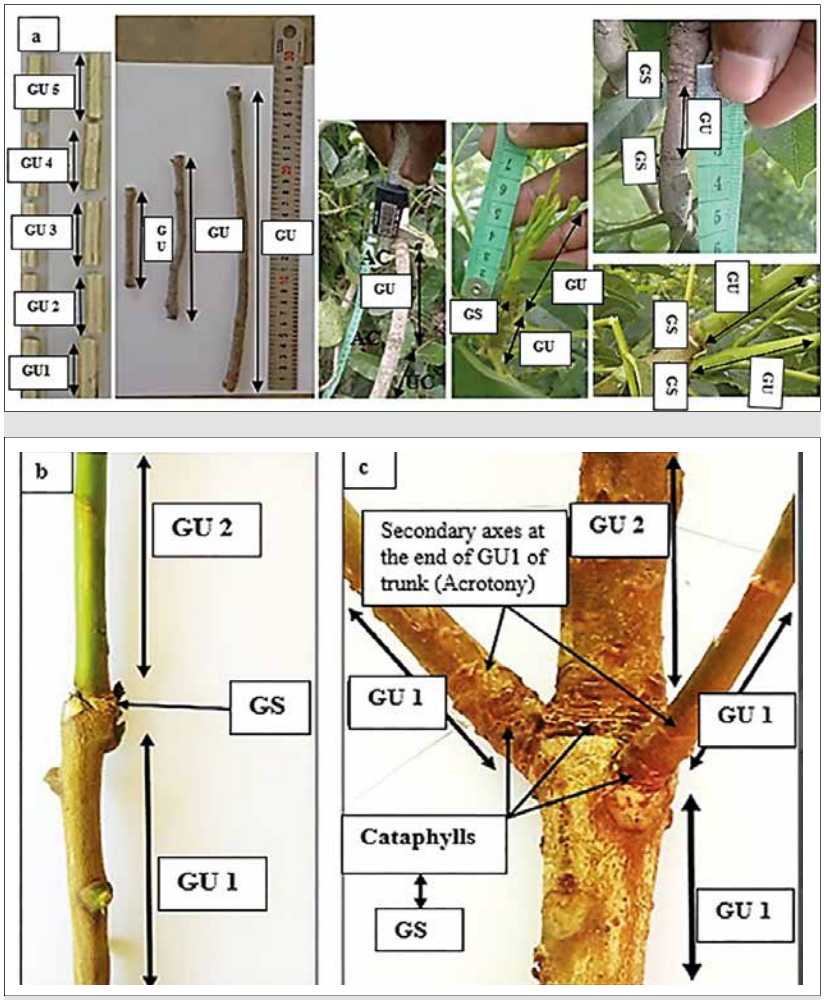

Figure 2.
a) Variation of the growth units (GU), b) Limit or growth stop (GS) of the growth units delimiting two physiological ages, c) Presence of cataphylls at the base of GUs, marking growth stop in *Khaya senegalensis*.

Results

Morphological description of the growth units (GUs)

Khaya senegalensis

Figure 2a shows variations in the size of the growth units along a foliar axis and the growth stops delimiting the portions of the growth units. figure 2b and 2c shows the growth stops (GS) between two (2) successive GUs along a leafy axis, identifiable by the cataphylls. figure 2b shows an axis consisting of two physiological ages (distinguished by colour change). These two physiological ages represent two successively formed GUs separated by an GS. The green age is the new GU, while the brown age represents the old GU. figure 2c shows cataphylls at the base of the GUs. This marks a cessation of meristem activity (GS) and the start of a new shoot (GU2).

All factors considered, in young trees of *K. senegalensis*, the number of growth units present on the observed axis ranged from 2 to 21 with an average of 7.95 ± 3.76; the length of growth units varied from 5.8 to 67.8 cm with an average of 23.46 ± 12.03 cm; the average diameter of the growth units ranged from 0.4 to 3.81 cm with an average of 1.34 ± 0.62 cm; the number of phytomers carried by growth units in this cohort ranged from 7 to 38 with an average of 16.32 ± 5.87.

In adult *K. senegalensis* trees, the number of growth units on the assessed axes ranged from 5 to 14 with an average of 8.25 ± 1.94; the length of the growth units in this cohort ranged from 5.15 to 31.77 cm with an average of 17. 38 ± 6.38 cm; the diameter of growth units ranged from 0.74 to 1.93 cm with an average of 1.33 ± 0.37 cm and the number of phytomers counted per growth unit ranged from 10.5 to 29.5 with an average of 17.75 ± 4.53.

Finally, in old trees of *K. senegalensis*, the number of growth units present on the observed axis varied from 5 to 12 with an average of 8.25 ± 1.9; the length of growth units varied from 6.2 to 38.85 cm with an average of 18. 02 ± 6.2 cm; the average diameter of the growth units varied from 0.74 to 2.04 cm with an average of 1.37 ± 0.33 cm; the number of phytomers carried by growth units in this cohort varied from 13 to 33 with an average of 19.78 ± 4.67.

Pterocarpus erinaceus

Figure 3 shows the appearance of growth stops (GS), growth units (GUs) and variations in the size of the GUs along a leafy axis.

In *P. erinaceus* saplings, the number of growth units (GUs) present on the observed axis varied from 2 to 19 (average 7.94 ± 4.38); the length of the GUs varied from 6.55 to 62.4 cm (average of 21.67 ± 9.84 cm); the diameter of the GUs ranged

Figure 3.
A) Morphology of the growth units (GU), B) Indicators of growth stop (GS) along an axis in *Pterocarpus erinaceus*: a) external scars, b) narrowing of the pith.

Table III.
Comparison of morphological growth units according to habitat type.

Species	Habitat	Axis-GU-n°	GU-length (cm)	GU-diam (cm)	GU-phyto-n°
Khaya senegalensis	Full sunlight	7.74 ± 0.3b	21.89 ± 1.91a	1.33 ± 0.06a	17.3 ± 0.59a
	Min-Max	2-21	5.15-67.8	0.4-3.81	7-38
	Shade	9.06 ± 0.55a	19.34 ± 1.15a	1.39 ± 0.06a	17.5 ± 0.73a
	Min-Max	4-18	5.8-40.45	0.69-2.13	9-26.75
	Pr > F	**0.0379**	**0.2315**	**0.5950**	**0.8572**
Pterocarpus erinaceus	Full sunlight	7.51 ± 0.39b	22.81 ± 1.13a	1.11 ± 0.06a	15.08 ± 0.64b
	Min-Max	2-17	6,55-62.4	0.32-3.11	4.5-31.5
	Shade	8.82 ± 0.54a	21.94 ± 1.01a	1.26 ± 0.18a	17.84 ± 0.71a
	Min-Max	3-19	8.9-47.4	0.47-10.51	8-31.75
	Pr > F	**0.0451**	**0.5871**	**0.3739**	**0.0056**

Values with the same letters are not statistically different at the 5% threshold (SNK). Full sunlight = open and sunny environment; Shade = crowded environment or under forest cover; Axis-GU-n° = number of growth units per axis measured; GU-length = mean length of growth units in centimeters; GU-diam = mean diameter of growth units in centimeters; GU-phyto-n° = mean number of phytomers per growth unit; Min = minimum and Max = maximum.

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Table IV.
Variation in morphological parameters of the growth units according to the location.

Species	Locations	Axis-GU-n°	GU-length (cm)	GU-diam (cm)	GU-phyto-n°
Khaya senegalensis	Ferké	8.95 ± 0.5ab	16.68 ± 1.51c	1.44 ± 0.07b	15.77 ± 0.68b
	Min-Max	4-13	7.85-40.45	0.69-1.93	10.5-22
	Korhogo	9.13 ± 0.88bcd	18.75 ± 1.72c	1.39 ± 0.1b	17.64 ± 0.86ab
	Min-Max	5-21	5.15-46.07	0.74-2.88	9-26
	Niakara	8.39 ± 0.35bcd	18.09 ± 1.5c	1.21 ± 0.06b	20.46 ± 1.23a
	Min-Max	6-12	6.2-38.85	0.74-1.75	13-33
	Katiola	6.44 ± 0.87d	25.82 ± 2.87b	1.4 ± 0.1b	17.19 ± 1.17ab
	Min-Max	3-18	11.1-48.15	0.78-2.13	8-26.75
	Bouaké	10.64 ± 0.73a	29.68 ± 11.14a	1.91 ± 0.26a	15.89 ± 1.33b
	Min-Max	7-15	18.25-67.8	0.67-3.81	7.-22.75
	Toumodi	5.5 ± 0.38cd	19.65 ± 2.41c	1.07 ± 0.09b	14.44 ± 1.18b
	Min-Max	3-8	9.97-43	0.52-1.86	8.33-25
	Daloa	7.7 ± 0.69abc	24.35 ± 2.55b	1.21 ± 0.09b	19.07 ± 1.75a
	Min-Max	2-14	10.62-47.85	0.41-1.86	8.25-38
	Pr > F	**0.0001**	**0.0001**	**0.0001**	**0.0001**
Pterocarpus erinaceus	Ferké	10.24 ± 0.94a	22.94 ± 1.49bc	1.19 ± 0.1ab	17.05 ± 1.07ab
	Min-Max	3-19	10.5-36.35	0.5-2.53	8-26
	Korhogo	8.5 ± 0.61ab	20.49-1.7bc	0.98 ± 0.06ab	15.62 ± 0.97b
	Min-Max	5-19	10.05-44.4	0.57-1.66	9-29
	Niakara	9.28 ± 0.62a	25.83 ± 1.74bc	1.25 ± 0.09ab	22.29 ± 1.02a
	Min-Max	4-14	17.2-44.08	0.69-2.27	16.5-31.75
	Katiola	7 ± 1.13c	20.56 ± 1.3bc	1.02 ± 0.08ab	15.09 ± 1.29c
	Min-Max	3-17	12.13-30.85	0.41-1.69	7-23
	Bouaké	8.21 ± 1.08ab	27.45 ± 4.08a	1.37 ± 0.19ab	16.09 ± 2.06c
	Min-Max	2-16	9.53-62.4	0.32-3.11	4.5-28.75
	Toumodi	8.35 ± 0.59ab	25.17 ± 2.12ab	1.8 ± 0.46a	16.39 ± 0.64b
	Min-Max	4-15	12.35-47.4	0.79-10.51	12.25-24
	Daloa	4.35 ± 0.39bc	15.83 ± 1.24c	0.61 ± 0.04b	10.42 ± 0.6c
	Min-Max	2-8	6.55-26.45	0.35-1.25	5.5-19.5
	Pr > F	**0.0001**	**0.0015**	**0.0166**	**0.0001**

Values with the same letters are not statistically different at the 5% threshold (SNK). Axis-GU-n° = number of growth units per axis measured; GU-length = mean length of growth units in centimeters; GU-diam = mean diameter of growth units in centimeters; GU-phyto-n° = mean number of phytomers per growth unit; Min = minimum and Max = maximum.

from 0.32 to 3.11 cm (mean 1.05 ± 0.52 cm); and the number of phytomers carried by GUs in this cohort ranged from 4.5 to 28.75 (mean 15 ± 5.74). In adult *P. erinaceus* trees, the number of the GUs on the assessed axes ranged from 4 to 11 (average 7.63 ± 1.88); the length of the GUs in this cohort ranged from 12.35 to 45 cm (average 24. 44 ± 7.67 cm); the diameter of the GUs ranged from 0.71 to 2.39 cm (average 1.25 ± 0.41 cm) and the number of phytomers counted per GU ranged from 9 to 29 (average 17.28 ± 3.89). In old trees of *P. erinaceus*, the number of the GUs present on the observed axis varied from 5 to 14 (average 9.22 ± 2.32); the length of the GUs varied from 10.05 to 36.83 cm (average 22.91 ± 7.49 cm); the diameter of the GUs varied from 0.6 to 2.27 cm (average 1.09 ± 0.42 cm); the number of phytomers carried by the GUs of this cohort varied from 12 to 31.75 (average 20.26 ± 6.09).

Influence of habitats on growth unit morphology

Variance analysis of morphological parameters evaluated according to habitat showed that the morphology of the growth units of axes in full sun and shade was statistically identical in *K. senegalensis* ($P > 0.05$) while only the number of growth units in the different axes differed ($P < 0.05$). The number of growth units was higher in axes growing in the shade than in full sun (table III). In *P. erinaceus*, the number of growth units per axis and the number of phytomers per growth unit differed from one environment to another ($P < 0.05$) and were higher in the shade (table III) whereas the length and diameter of the growth unit remained statistically unchanged whatever the environment considered ($P > 0.05$).

Influence of location on growth unit morphology

Comparison of the morphological dimensions of the growth units according to the vegetation and climatic gradient revealed highly significant differences ($P < 0.05$) between locations for each of the morphological parameters assessed, regardless of the species (table IV). The variation in these parameters neither increased nor decreased along the bioclimatic gradient and did not follow the order of the locations along the south-north gradient (table IV).

Influence of the tree development stage on the growth unit morphology of the individuals

Analysis of variance showed that in *K. senegalensis*, the length of the growth unit and the number of phytomers per growth unit differed according to the development stage ($P < 0.05$), while the number of growth units per axis and the mean diameter of the growth unit remained the same ($P > 0.05$). Indeed, the growth unit was longer in young individuals and shorter in adult and old individuals and the number of phytomers per growth unit increased from the youngest to the oldest individuals (table V). In *P. erinaceus*, most of the parameters evaluated did not vary from one development stage to another ($P > 0.05$), except the number of phytomers per growth unit, which increased from the youngest to the oldest individuals ($P < 0.05$).

Table V.
Variation in morphological parameters of the growth unit according to the age category of the individuals (size).

Species	Age category	Axis-GU-n°	GU-length (cm)	GU-diam (cm)	GU-phyto-n°
Khaya senegalensis	Old-tree	8.25 ± 0.33a	18.02 ± 1.09b	1.37 ± 0.05a	19.77 ± 0.82a
	Min-Max	5-12	6.2-38.85	0.74-2.04	13-33
	Adult-tree	8.25 ± 0.43a	17.38 ± 1.42b	1.33 ± 0.08a	17.75 ± 1.01ab
	Min-Max	5-14	5.15-31.77	0.74-1.93	10.5-29.5
	Young-tree	7.95 ± 0.41a	23.45 ± 2.28a	1.34 ± 0.06a	16.31 ± 0.64b
	Min-Max	2-21	5.8-67.8	0.41-3.81	7-38
	Pr > F	**0.8700**	**0.0213**	**0.9463**	**0.0103**
Pterocarpus erinaceus	Old-tree	9.22 ± 0.54a	22.9 ± 1.76a	1.09 ± 0.09a	20.26 ± 1.43a
	Min-Max	5-14	10.05-36.83	0.6-2.27	12-31.75
	Adult-tree	7.63 ± 0.34a	24.44 ± 1.4a	1.25 ± 0.07a	17.28 ± 0.71b
	Min-Max	4-11	12.35-45	0.71-2.39	9-29
	Young-tree	7.94 ± 0.47a	21.66 ± 1.06a	1.16 ± 0.12a	14.99 ± 0.62c
	Min-Max	2-19	6.55-62.4	0.32-10.51	4.5-28.75
	Pr > F	**0.3324**	**0.3520**	**0.8528**	**0.0007**

Values with the same letters are not statistically different at the 5% threshold (SNK). Axis-GU-n° = number of growth units per axis measured; GU-length = mean length of growth units in centimeters; GU-diam = mean diameter of growth units in centimeters; GU-phyto-n° = mean number of phytomers per growth unit; Min = minimum and Max = maximum.

Table VI.
Comparison of morphological parameters of the growth units according to the season.

Species	Season	Axis-GU-n°	GU-length (cm)	GU-diam (cm)	GU-phyto-n°
Khaya senegalensis	Dry season	7.73 ± 0.34a	18.12 ± 2.78b	1.34 ± 0.07a	16.36 ± 0.83b
	Min-Max	5-17	5.15-67.8	0.7-3.81	7-38
	Rainy season	8.4 ± 0.41a	24.46 ± 0.76a	1.34 ± 0.05a	18.34 ± 0.47a
	Min-Max	2-21	9.97-46.07	0.4-2.88	8.25-26.75
	Pr > F	**0.2227**	**0.0028**	**0.8883**	**0.0388**
Pterocarpus erinaceus	Dry- season	8.06 ± 0.5a	22.43 ± 0.87a	1.05 ± 0.15a	15.78 ± 0.68a
	Min-Max	3-19	6.55-44.40	0.32-2.53	4.5-31.5
	Rainy- season	8.08 ± 0.41a	22.47 ± 1.32a	1.29 ± 0.05a	16.64 ± 0.72a
	Min-Max	2-21	9.53-62.4	0.41-3.11	5.5-31.75
	Pr > F	**0.9617**	**0.9772**	**0.1525**	**0.3843**

Values with the same letters are not statistically different at the 5% threshold (SNK). Axis-GU-n° = number of growth units per axis measured; GU-length = mean length of growth units in centimeters; GU-diam = mean diameter of growth units in centimeters; GU-phyto-n° = mean number of phytomers per growth unit; Min = minimum and Max = maximum.

Influence of the season on growth unit morphology

In *K. senegalensis*, comparison of the morphological dimensions of the growth units according to the season revealed a significant difference between the rainy (optimal) and dry (constraining) seasons both in the length of the growth units and in the number of phytomers per growth unit ($P < 0.05$). The average diameter of the growth unit remained the same from one season to another ($P > 0.05$), whereas the growth units were longer and the number of phytomers per growth unit higher in the rainy season (table VI). In *P. erinaceus*, analysis of variance (table VI) revealed no significant difference between the rainy and dry seasons in all the morphological parameters assessed along the axes ($P > 0.05$).

Variation in growth unit morphology between target species

Table VII shows there was no significant difference between the two species in any of the morphological dimensions we measured ($P > 0.05$). All the morphological parameters of the axis-bearing growth units in *K. senegalensis* and *P. erinaceus* were almost identical ($P > 0.05$).

Figures 4 and 5 shows an average distribution pattern of the number of phytomer per growth unit and of the growth stops or limits (GS) of the growth unit along an axis in the two species studied. The growth stop zones are generally marked by small leaves or leaf scales or by successive very short internodes often identical in length.

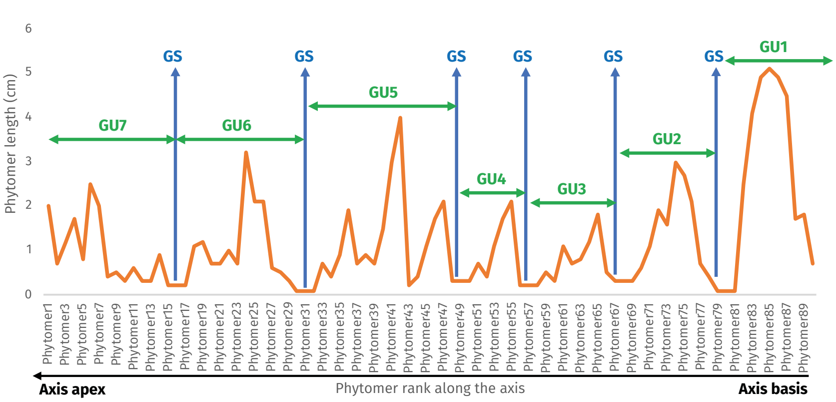
Discussion

The forms of plant growth have been the subject of many studies, but are still poorly defined and continually questioned because of the inconsistency and heterogeneity of the different methods used to analyze them. The sustainable management of plant genetic resources must take into account all possible aspects of methodological approaches including architectural concepts (retrospective analysis) and the phenological cycle of trees. This study dealt with the effect of different factors, *i.e.* the type of light type (full sunlight and

Table VII.
Comparison of growth unit morphology between target species.

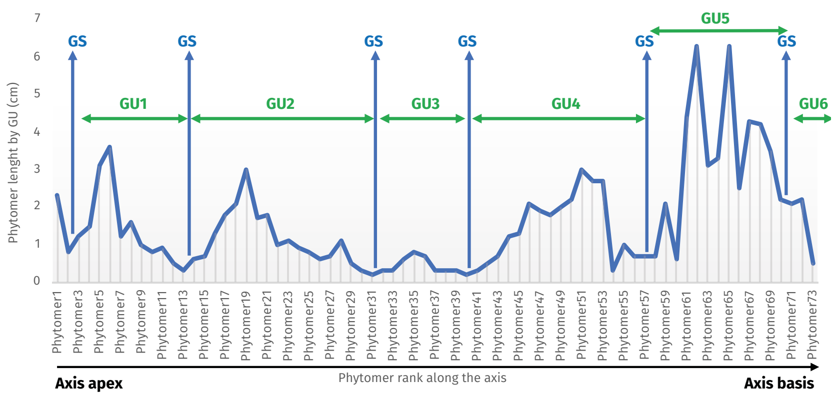
Species	Axis-GU-n°	GU-length (cm)	GU-diam (cm)	GU-phyto-n°
Khaya senegalensis	8.06 ± 0.27a	21.265 ± 1.47a	1.35 ± 0.04a	17.35 ± 0.48a
Min-Max	2-21	5.15-67.8	0.4-3.81	7-38
Pterocarpus erinaceus	8.04 ± 0.32a	22.45 ± 0.79a	1.1 ± 0.08a	16.22 ± 0.49a
Min-Max	2-19	6.55-62.4	0.32-3.11	4.5-31.75
Pr > F	**0.9587**	**0.9997**	**0.0595**	**0.1009**

Values with the same letters are not statistically different at the 5% threshold (SNK). Axis-GU-n° = number of growth units per axis measured; GU-length = mean length of growth units in centimeters; GU-diam = mean diameter of growth units in centimeters; GU-phyto-n° = mean number of phytomers per growth unit; Min = minimum and Max = maximum.



GU = growth unit, GS = growth stop.

Figure 4.
Variation in the size and number of phytomers per growth unit along the axes observed in *Khaya senegalensis*.



GU = growth unit, GS = growth stop, cm = centimeter.

Figure 5.
Variation in the size and number of phytomeres per unit of growth along a *Pterocarpus erinaceus* axis.

shade) in different locations along a gradient of climate; the age of individuals; and the seasonality (rainy *vs* dry season) on the growth unit morphology of the different types of axes in *K. senegalensis* and *P. erinaceus* in Côte d'Ivoire.

Morphology of growth units

Our results showed that whatever the species, growth stops are represented by very short successive internodes. The same observations have been made in many species in Europe and Latin America (Barthélémy and Caraglio, 2007), notably in Beech (*Fagus sylvatica* L.) (Nicolini, 2000), in Jacquot wood (*Laetia procera*) and Angelica (*Dicorynia guianensis*) (Heuret *et al.*, 2003), in Walnut (*Juglans regia* L.) (Sabatier *et al.*, 1998), in *Cedrus atlantica* (Sabatier and Barthélémy, 1999), in *Fagus sylvatica* (Nicolini and Caraglio, 1994), in *Parkia velutina* (Nicolini *et al.*, 2012). The shape of the growth units depends on the optimal growth conditions of the species driven by the functioning of the terminal meristems. If the growth conditions are limiting (lack of water, crowded environment, etc.), the growth units will be lean (short with a small diameter and many very short internodes per growth unit), in contrast to those in a favourable environment (long growth units, large diameter and a small number of very long internodes per growth unit). The morphology of the growth units is thus an indicator of environmental conditions.

Influence of habitats

Specifically, the number of growth units per axis and the number of phytomers per growth unit were high, and growth unit were shorter in the shade (individuals growing in undergrowth) than in individuals growing in full sun in both species. This means that the shady environment (undergrowth) is less favourable for the optimal development of the species. Indeed, when conditions are optimal, shoot development is harmonious, and continuous, with fewer large organs. Full sunlight favours the optimal development of the individuals and should be preferred for planting establishment. The crown diameter of the individuals developing in open environments in both species was wider and well-rounded with large oblique branches made up of leaves at the end and openings in the crown allowing sunlight to pass through. On the other hand, the trees developing in shady environments or in undergrowth had tapering, tufty crowns and vertical branches reaching for the light of the canopy. These results have also been reported in several studies (Nicolini and Caraglio, 1994; Tousignant and Delorme, 2006; Abidi, 2012; Calonnec, 2013). The individuals developed a large number of growth stops and phytomers per growth unit. These observations show that it is difficult to develop in undergrowth. Moreover, in these conditions the individuals are subject to possible attacks by various insect species. The more repetitive the stoppages along the axis, the less likely the plant to survive. In these cases, individuals struggle to develop and produce reliable reproductive entities. On the other hand, when there are few growth stops along an axis, this indicates harmonious development and successful growth. For this reason, the undergrowth habitat cannot be recommended for optimising the success of cultivation with these species.

The analyses of variance used show that, overall, the environment (full sun and undergrowth) in which the trees of both species grow does not seem to affect all the morphological parameters assessed ($P > 0.05$). Only the number of growth units per axis was significantly influenced by the habitat in the two species ($P < 0.05$). As well as the number of phytomers per growth unit in *P. erinaceus* ($P < 0.05$). Normally, the type of light would be expected to have a significant effect on the morphology of the growth units. This is certainly due to the fact that the light available in the undergrowth was favourable and tolerable for the development of the species' shoots, and could also be due to the genetic programme of architectural development that was properly expressed by each species. According to Hallé and Keller (2019), architecture is the expression of the genetic programme of plant growth and development visible to the naked eye.

Influence of location

Analysis of the variance of the morphological parameters evaluated as a function of the location along a south-north vegetation and climate gradient revealed that location had a significant influence on the morphology of the growth units of the two-target species ($P < 0.05$). In fact, even if the locations surveyed were chosen along a decreasing gradient of vegetation density, each location has its own characteristics (climate, soil type, rainfall, relative humidity, etc.) that distinguishes it from the others. In addition, in the current context of climate change, the climatic and microclimatic parameters are very unstable, uncontrolled and show high daily variations. Sabatier (1999), Lauri *et al.* (2010) and Calonnec (2013) showed that the depth and fertility of the soil, the environment and the age of the individuals can influence the architectural development of a species. Maranz and Wiesman (2003), and Soloviev *et al.* (2004) also reported that climate or an ecological gradient had an effect on plant morphology. Similarly, Salazar and Quesada (1987) then Assogbadjo *et al.* (2006) reported that the origin of differences in tree morphology lies in factors such as soil type and the genetic characteristics of the sampled individuals.

In *K. senegalensis*, the lengths and diameters of the growth units were maximum in Bouaké. The environment in Bouaké could thus favour shoot development and improve the success of a forest management programme targeting this species. In *P. erinaceus*, large shoot sizes were obtained in Toumodi and Bouaké (i.e. in centre of the country). where locations are favourable for the successful establishment of *P. erinaceus* plantings.

Influence of the age of the individuals sampled (size of the individuals)

Our study showed that the majority of morphological dimensions differed in young, adult and old individuals of *K. senegalensis* ($P < 0.05$). Indeed, the plant function capacities (strength, adaptation and photosynthesis) for the establishment of organs differed depending on the age of the individual, and this also influenced the dimensions of the plant organs, whereas in the species *P. erinaceus*, only the number of phytomers per growth unit was influenced by the age of the individual ($P < 0.05$). Growth of *P. erinaceus* was very slow compared to that of *K. senegalensis*; in the former, the shoots of the crowns are synchronous and take time to develop whatever the growth stage. This gives the impression that the shoots of young and old individual have the same morphology. However, the difference in the number of phytomers per growth unit in each age category showed that adult and old individuals were better developed than younger ones. Indeed, even though some studies have shown that the age of individuals influences tree morphology (Sabatier, 1999; Assogbadjo *et al.,* 2006; Lauri *et al.,* 2010); it should be noted that the crown setting of trees and the organogenesis of macro-anatomical markers of a species is intrinsic to the genome of a plant (Hallé and Keller, 2019). Whatever the age of the plant, the expression or architectural development of a species may be plastic, but remains the same. In some cases, architecture can be influenced by environmental conditions, but this influence remains limited because, regardless of age, the majority of species follow their architectural programme and return to their original architectural development sequence.

In *K. senegalensis*, the growth units were longer in small (young) individuals with fewer internodes per growth unit, meaning that individuals develop most when young. Young individuals (cuttings) would be ideal for the selection of suitable genotypes for a natural or artificial forest regeneration programme based on this species, unlike *P. erinaceus,* in which selection could be conducted at all levels or in all age categories. In fact, the development of shoots of *P. erinaceus* is identical from one age to another, except for the number of phytomers per growth unit, which increases from the youngest to the oldest.

Influence of the season

In *K. senegalensis*, the season influenced the morphological development of the growth units, whereas the season had no influence in *P. erinaceus*. In *K. senegalensis,* in the rainy season, the length and number of phytomers per growth unit were greater than in the dry season. This is very logical since water is essential for plant growth and development. Water guarantees the physiological development and harmonious functioning (metabolism, photosynthesis, organogenesis, etc.) of all living beings, especially plants, while water stress slows down all physiological activity up to withering.

The rainy season is thus the most favourable period to establish agroforestry and reforestation programmes based on these species and to increase their survival rate after transplanting in Côte d'Ivoire.

Comparison of target species according to growth unit morphology

Our observations showed that *K. senegalensis* and *P. erinaceus* have practically identical growth unit morphologies. Even if the two species belong to different families (*K. senegalensis* to Meliaceae and *P. erinaceus* to Fabaceae), their architecture could be almost the same (Hallé and Keller, 2019), which we intend to verify in a future study (architectural development of the two-target species). In their study, Hallé and Keller (2019) indicated that most species in the Meliaceae family follow Werner Rauh's model of architectural development, as confirmed by our field observations in *K. senegalensis*. The same authors also showed that the majority but not all species belonging to three legume sub-families (Fabaceae, Caesalpiniaceae and Mimosaceae), particularly Fabaceae, follow Wilhelm Troll's model. However, we believe that *P. erinaceus* architectural model is more similar to the model of Paul Champagnat, as the species is a reiterated complex of unbranched axes and discrete branching with short branches. The axes are vertical at their base while their distal end represents a curve with a large radius, brought back to the horizontal or collapsed due to the gravity and flexibility of the wood. The leaves are spirally arranged while inflorescences can be either lateral or terminal like in *Parkia biglobosa*. This hypothesis will be tested in further studies.

Conclusions

This study allowed us to observe and identify a number of factors that influence the morphology of crown growth units in *Pterocarpus erinaceus* Poir. and *Khaya senegalensis* (Desr.) A. Juss. which are necessary for their sustainable management. Our results show that growth unit morphology is an indicator of the best environmental or climate conditions for growth. Different light conditions (full sunlight or shade) did not significantly alter the morphology of the growth units in either species, but full sunlight enabled good general development of the growth units, showing that full sunlight is favourable for plot establishment. The size of the growth units varied significantly from one location to another due to different environmental characteristics (microclimate, soil type, rainfall, etc.); the shoots were well developed in the southern part of the climate gradient selected for this study (central part of Côte d'Ivoire: Toumodi and Bouaké). This zone is more favourable for these two species and should be chosen over other possible zones for a reforestation program. The age of the individuals was seen to influence the number of phytomeres per growth unit. Young individuals (cuttings) are ideal for the selection of adapted and resilient genotypes due to the ability of their shoots to regenerate rapidly under optimal conditions (immediate synchronization). The size of the *K. senegalensis* growth units increased significantly in the rainy season. In contrast, the season had no significant effect on the size of the growth units in *P. erinaceus*. The growth units of *K. senegalensis* had almost the same dimensions as those of *P. erinaceus*, the two species may thus have identical architectural characteristics. This hypothesis will be tested in a comparative architectural study, as such information is important to complete the data required for the establishment of forest plantings under ongoing climate change. Our results contribute to understanding the functioning of the crown and the adaptation of the two species to global climate change and could guide the choice of environments and seasons for the implementation of reforestation or agroforestry programs based on these two species.

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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.

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