Changes and determinants of the shape of irregular trunk trees over time in a semi-deciduous forest in Central Africa

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Abstract

A better understanding of the determinants behind changes in the shape of irregular trunk trees over time is needed to predict likely changes in carbon stocks and biodiversity when environmental conditions change. To investigate this question, we studied the changes and determinants of irregular trunk shape in 6 tree species (72 trees) from a semi-deciduous forest in Central Africa. The change in trunk shape of each tree over time was assessed from the Deficit Basal Area Index (DeBA) using photogrammetric point cloud data and conventional measurements over a 7-year period. DeBA quantifies trunk irregularity, with values ranging from zero for a perfectly circular cross-section to one for highly irregular shapes. By comparing DeBA values for 2014 and 2021, we have tracked the evolution of trunk shape. A reduction in DeBA indicates a trend towards a more irregular shape. For all species, significant differences were observed in trunk shape between 2014 and 2021, with a mean change of 0.55±0.16, suggesting that these trees are evolving towards a more irregular shape. Among the species, *Triplochiton scleroxylon* showed a lower mean variation, indicating an evolution towards a more irregular shape. Notably, trees developing highly irregular shapes over time were generally large canopy trees with expansive crowns. Species with very irregular shapes tend to be large trees with wide, deep crowns, low wood density, deciduous trees, trees that don't require light and are dispersed by the wind. These results provide insight into the life-cycle strategy of tropical tree species.

Keywords: Close-range photogrammetric approach; Growth; Irregular trunk trees; Republic of Congo; Tropical forests

1. Introduction

Tree growth is a complex process involving increases in the length, diameter and thickness of different parts of the tree, including the stem, roots and branches [1,2]. These changes in shape and size are the result of a series of biological processes that occur throughout the tree's development cycle [2,3]. Previous studies have already shown that tropical tree growth is influenced by a combination of genetic and environmental factors. For example, tree growth is influenced by both intrinsic factors – ontogeny [4] and genotype [5] - and extrinsic factors such as climate, altitude [6,7], soil nutrients [8,9], competition with surrounding trees [10,11], strong winds [12] and disease [13]. The growth of these trees can be assessed by observing changes in the tree's most typical morphological parameters, including diameter and height, the two most characteristic tree variables. Observed changes in tree shape are key indicators of tree growth and are often used to assess the impact of global change on tropical forests and to propose alternative management practices for the conservation and production of forests that are resilient to environmental change [14].

From a morphological point of view, there are several types of tropical tree trunk shape, the most notable of which are regular trunk and irregular trunk trees [15]. Regular trunk trees are those with a generally cylindrical trunk, while irregular trunk trees are those that develop particular structures at the base of the trunk, such as buttresses and other

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deformations [16]. Importantly, irregular trunk trees make up the majority of large canopy trees in tropical forests [17]. These trees play an important role in the stability of forest ecosystems and in providing habitats for many plant and animal species [18–24]. In addition, they fix large amounts of carbon due to their high wood volume, making them interesting for climate adaptation research [25,26]. The development of irregularities on the trunk of these trees is an adaptive response to the harsh conditions of tropical environments [21,27–30]. As the tree matures, these irregularities gradually form at the base, increasing the stability of the trunk under the effect of gravity [31]. The presence of these irregularities therefore influences the way trees tolerate the difficult conditions typical of tropical regions.

The shape and size of irregular trunk trees are essential for determining the assortments of wood that can be sawn from each stem [32]. They are therefore of particular interest to forest management and the timber industry [33]. Thus, growth-induced changes in the shape and size of irregular trunk trees affect timber availability [32]. Sustainable forest management is an important issue from both an economic and environmental point of view. Whatever the objectives of forest management, there is a constant need for more accurate and up-to-date information on forest resources, such as the amount of wood available, forest growth, biomass quantity and carbon sequestration [3]. Monitoring changes in the shape and size of irregular trunk trees can also be achieved through the use of shape indices, which are derived from cross-sectional analyses of the trunk to describe irregularities along the tree [16,25,34–36]. These shape indices, as defined by Russ [37], measure the deviation from an ideal circular shape, providing valuable information about trunk compactness and structural anomalies. Although these methods have been widely applied in temperate forests, particularly in Europe, where they have been used to examine changes in tree shape over time [2,3], studies of irregular trunk trees in tropical forests remain limited.

Changes in the shape and size of irregular trunk trees are influenced by a combination of tree characteristics and abiotic factors. The growth of irregularities on tree trunks has been positively related to crown asymmetry in regions such as South and Central America [30,38–40]. Similarly, it has been positively associated with tree diameter, height and wood density in tropical Africa, South America, East Asia and Europe [21,38,39,41–46]. Abiotic factors, such as soil properties, slope, altitude and wind, also play an important role. For example, irregular trunk trees are often found on shallow, waterlogged soils [27,28,47] and tend to be located at medium altitudes and on steep slopes in tropical Africa, South America and Europe [29,38,40,41,43,46]. Wind direction has also been positively associated with the development of trunk irregularities in regions such as South America [31,48], Europe [29,49] and East Asia [50].

A better understanding of the drivers behind changes in the shape and size of irregular trunk trees is needed to predict the likely changes in carbon stocks and biodiversity when environmental conditions change. Despite the importance of this issue, few studies have explored the dynamics of how these drivers influence the shape of irregular trunk trees over time. As a result, knowledge of the growth responses of these trees is limited, particularly in the understudied region of Central Africa. This study aims to examine changes and determinants in the shape of irregular trunk trees over time in Central Africa, addressing two main research questions: (i) Is it possible to detect changes in the shape of irregular trunk trees over a 7-year period? (ii) What are the determinants of changes in the shape of irregular trunk trees over a 7-year period?

2. Material and methods

2.1. Study site and sampling

The study site was located in the Loundoungou-Toukoulaka forest concession (17°31’17°34’’ E, 02°18’02°22’’ N) managed by the company CIB-Olam in the north of the Republic of Congo (Figure 1). Annual rainfall averages 1600 mm with a distinct dry season (December to March), and the average annual temperature is 25°C. The topography is slightly undulating, with an altitude varying between 400 and 460 m. The geological substratum consists of alluvial deposits [51]. The vegetation of the area belongs to the Central African rainforests [52] and, more specifically, to the *Celtis* semi-deciduous forest [53].

On this site, fieldwork was carried out in an 800-ha experimental set-up (DynAfFor project, www.dynaffor.org), which was described by Forni et al. [54]. Using DynAfFor forest inventories, we targeted 6 species of irregular trunk trees belonging to 6 genera and 4 families in 2014 and 2021 (Figure 1, Appendix S1, Table S1). For each species, we sampled an average of 12 individuals (range: 10 - 13 trees), representing a total of 72 trees.

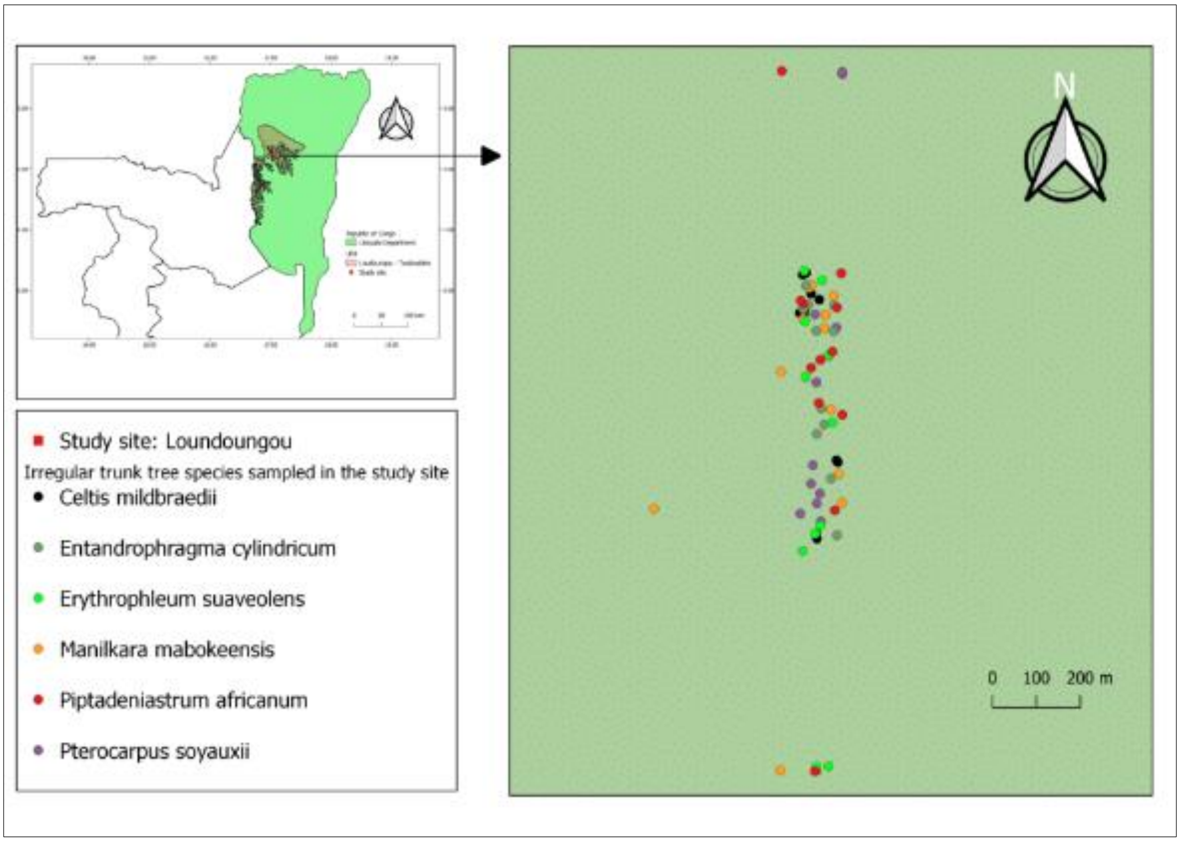

Figure 1 Location of the study site in the north of the Republic of Congo

2.2. Photogrammetric measurements and processing

The images were acquired twice at the study site to cover a period of 7 years. The first was carried out in 2014 and the second in 2021. The same image acquisition procedure was followed for both periods. The procedure involved removing all small plants and vines up to 2 m high around each tree within a 3 m radius, prior to image acquisition. Four photogrammetric targets were placed at the four cardinal points around each tree at a distance of less than 1m. The reference target was placed to the south to avoid backlighting and its height was measured using a pentadecameter. The targets were used to improve the alignment and scaling of the images. The diameter at breast height (DBH) was marked with blue paint, which provided additional information during model calibration.

For image acquisition, two Nikon D90 and Nikon D5600 digital SLR cameras with a fixed zoom lens with a focal length of 16 mm were used in 2014 and 2021, respectively. The cameras (focus, ISO and shutter speed) were set in automatic mode. All trees were photographed with these settings. A series of photographs were taken all around each tree following an image acquisition method similar to the "one panorama at each step" approach of Wenzel et al. [55]. At each step around the tree (1 m), photographs were taken with a high overlap (vertical panorama) and converging images. The lateral shooting distance around the tree was 2-3 m.

Agisoft Metashape Professional (Agisoft LCC, St Petersburg, Russia) was used to process the images. Each series of tree photos was loaded into the software without any additional information. The photogrammetric workflow of this software consists of six phases, namely (1) target detection, (2) image alignment and sparse cloud generation, (3) scaling of the constructed 3D point clouds, (4) optimization of the sparse point clouds, (5) densification of the point clouds and (6) mesh construction. More details on the reconstruction process of these three-dimensional trees are described in Bauwens et al. [16]. The final product is a dense three-dimensional (3D) point cloud containing XYZ coordinates. Finally, the mesh generated was saved and exported to Rstudio software to produce the cross-sections. The method used was carried out on a computer equipped with an AMD Ryzen 9 5900X processor (12 cores - 3.7/4.8 GHz - 70 MB cache) with an Asus Prime X570-Pro - AMD X570 chipset and 64 GB of DDR4 memory.

To make the cross-sections along the trunk, Rstudio software was used to obtain cross-sections along the trunk using the 'sp' [56], 'Raster' [57], 'lidR' [58] packages. Firstly, the skeleton of the trunk was created by digitising the contours of discs varying in thickness from 2 to 5 cm every 20 cm along the z axis of the trunk. The contours of the discs were delimited automatically. Each point cloud contour obtained using the splines function was then smoothed to generate a polygon. For sections of the disc where the smoothing was poorly adjusted due to occlusions, we proceeded by eliminating these occlusions and manually correcting the smoothing on the contour of the point clouds. The centre of each disc was automatically calculated as the point furthest from the edges of the polygon. All the resulting layers were saved in a "gpkg" file. The summary of the close-range photogrammetric process in this study is shown in Figure 2.

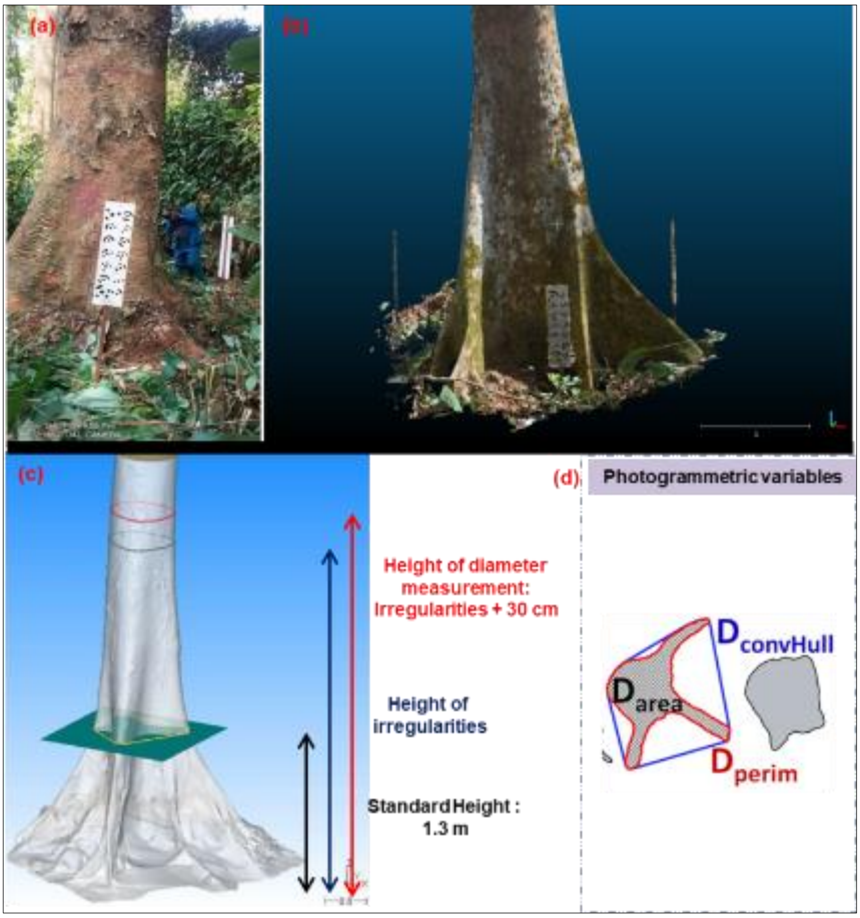

Figure 2 Diagram of the process for processing close-range photogrammetric data. (a) Acquisition of images all around the tree using a digital SLR camera in 2014 and 2021. (b) Result of the 3D dense point cloud with the location of the target. (c) Tree trunk skeleton generated in 3D with cross-sections at 1.30 m above ground, at the limit of the height of the irregularities and 30 cm above the irregularities. (d) On the basis of the cross-sections, the area (area) and the perimeter (perim) of the disc were estimated and then converted into diameters (Darea and Dperim)

2.3. Description of the shape of irregular trunk trees

To describe the trunk shape of irregular trunk trees, we first analysed the height of the trees generated in 3D in 2014 and 2021. Figure 3 shows the distribution of trees generated in 3D all along the trunk between 2014 and 2021. Examination of these frequency histograms reveals the greatest proportion of cross-sections between 1.30 and 5 m high in 2014 (63.05% with an average height of 2.48±1.69 m) and 2021 (50.70% with an average height of 4.14±2.80 m).

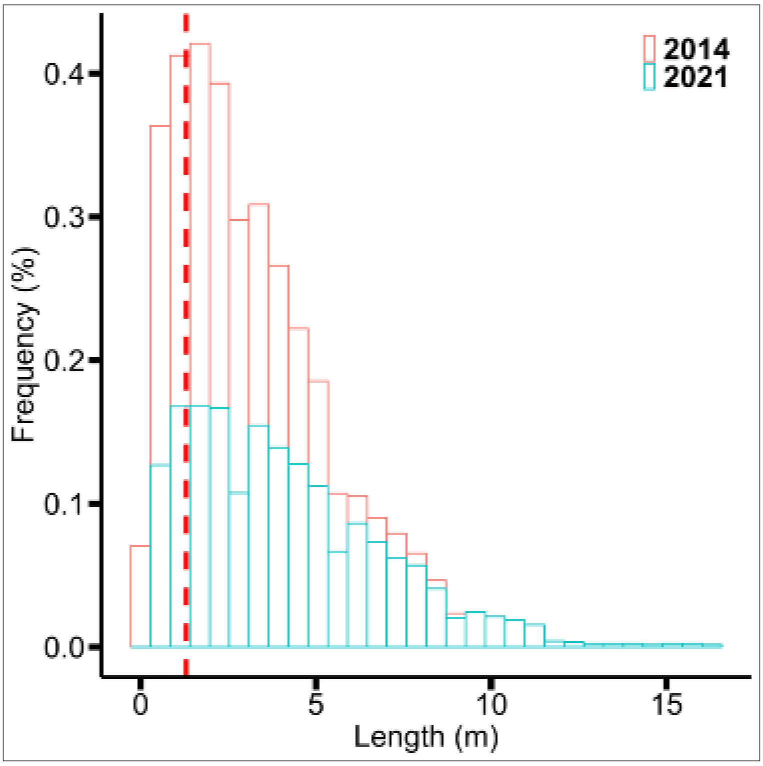

Figure 3 Distribution of cross-sections at different heights along the trunk in 2014 and 2021. The red line indicates the measurement point at 1.30 m from the ground

The imbalance in the height of the trees generated in 3D in 2014 and 2021 made it impossible to follow the cross-sections along the trunk during the growth period. This led us to consider the cross-sections at 1.30 m from the ground. In addition, the perimeter (perim) and the area (area) of the cross-sections) were calculated for each tree. Since diameter is the variable more frequently used than basal area to quantify tree size in forestry science, the area and perimeter of cross-sections were converted into diameter. The area and the perimeter of the cross-sections were converted into diameter by calculating the diameter of the disc with the same area as the area of the disc (D_{area}) and the diameter of the disc with the same perimeter as the perimeter of the disc (D_{perim}).

To describe the shape of irregular trunk trees, the deficit basal area index (DeBA) was estimated from cross-sectional data obtained at 1.30 m from the ground in semi-deciduous forest. DeBA characterizes cross-sectional shape. It is the most widely used of the many shape indices available [16,35,59,60]. DeBA is defined as minus the ratio of the basal area of the cross-section to the area of a circular disk of the same perimeter as the cross-section [16,25,35,59,60]. Consequently, DeBA is zero for a circular disk and tends towards one as the cross-section becomes more irregular [16,25,35,59,60]. According to Nölke et al. [25], a cross-section with a DeBA < 0.05 can be considered circular.

$$DeBA = \frac{BA_{perim} - BA_{area}}{BA_{perim}} = 1 - \left(\frac{D_{area130}}{D_{perim130}}\right)^2 \qquad \text{………………..} \ (1)$$

with BA_{perim} the area of a disc with the same perimeter as the perimeter of the cross-section (in m^2), BA_{area} the area of the cross-section (in m^2), and D_{area} and D_{perim} as defined above (in cm).

2.4. Tree measurements and species traits

In addition to photogrammetric measurement, non-destructive quantitative measurements and species traits have been obtained at tree and species levels, respectively in 2021. At the tree level, we measured tree diameter, total height, first branch height, horizontal projection of four crown rays and a qualitative measure (crown exposure index described below). Tree diameter (D; in cm) was measured with a tape at breast height for less irregular trunks or 30 cm above any deformation in 2014 and 2021. Total tree height (H, in metres) and first branch height (H_{fb}, in metres) were measured using a laser rangefinder device (VERTEX IV dendrometer). For crown measurements, we used the crown measurement protocol described in Loubota Panzou and Feldpausch [61]. The crown depth (Cd, in m) was defined as the difference between H and H_{fb}. The crown radius (Cr, in m) was defined as the average of the four projected perpendicular crown radii, measured along the four cardinal directions. The crown exposure index (CEI) describing the crown position in the canopy and exposure to light [62] was visually estimated using the following five classes [63], namely, (1) for lower canopy trees that are fully shaded vertically and laterally by other crowns; (2) for upper canopy trees that are fully shaded vertically but with some direct lateral light; (3) for lower canopy trees that are partially exposed and shaded vertically by other crowns; (4) for upper canopy trees that are fully exposed from above but complemented laterally by other crowns; and (5) for emergent trees that are free of competition for light, at least in the 90° inverted cone in which their crown is located.

Species trait were maximum diameter (Dmax), maximum height (Hmax), maximum crown depth (Cdmax) and maximum crown radius (Crmax) calculated as the 98th percentile of tree diameter, total tree height, crown depth and crown radius for each species. Species average wood density (WD, in $g.cm^{-3}$) which ranged from 0.57 to 0.88 $g.cm^{-3}$ – were retrieved from the global wood density database [64,65]. We extracted light requirements using CEI for juvenile plants (CEI_{juv}) in Loubota Panzou et al. [66]. Leaf habit, dispersal mode, and regeneration guild were also extracted from the literature. Among the 6 species of irregular trunk trees, one species were considered evergreen and five species were considered deciduous for leaf habit, one were animal-dispersed species, four were wind-dispersed species and one had unassisted dispersal modes [67–70]. Following Hawthorne's [71] definitions in Ghana, the regeneration guild was assigned to each species according to existing literature [69,72]. Of the 6 irregular trunk tree species, one were classified as shade-bearing (SB), four as non-pioneer light demanding (NPLD) and one as pioneer (P).

2.5. Assessment of changes in the shape of irregular trunk trees between 2014 and 2021

Changes in the shape of irregular trunk trees were quantified by subtracting the estimated ΔDeBA in 2021 with the ΔDeBA in 2014 (Equation 2). The decrease in DeBA indicates that the trunk is evolving towards a highly irregular shape, which can be interpreted as an increased allocation of biomass to the base of the trunk. This change in DeBA is related to a change in trunk shape: if more wood is allocated to the trunk base, the trunk will tend to adopt a conical rather than a cylindrical shape.

$$\Delta DeBA = DeBA_{2021} - DeBA_{2014} \qquad \text{………… (2)}$$

Where *ΔDeBA* is the absolute change in deficit basal area index, $DeBA_{2021}$ is the basal area deficit index in 2021 and $DeBA_{2014}$ is the basal area deficit index in 2014.

2.6. Data analysis

To detect differences in DeBA of irregular trunk trees between 2014 and 2021, we performed the Wilcoxon pairwise test for all species combined. To detect interspecific differences in De_{BA} between coexisting species, we performed a one-sample Student's t-test within and between tree species.

To assess the most critical factors in determining the shape of irregular trunk trees, the linear mixed-effects model was fitted at tree level. We used individual tree measurements (tree diameter, tree height, crown depth, crown radius, wood density and crown exposure index) as potential determinants of trunk irregularities. Before fitting the model, we assessed collinearity between determinants (i.e. fixed effects in linear mixed models) using the multicollinearity test. Due to high collinearity (i.e. ≥ 14.2), tree diameter was excluded from the list of fixed-effect determinants. Thus, for a tree *i* belonging to a species *S*, the tree level mixed effects model takes into account tree height (H), crown radius (Cr), crown depth (Cd), crown exposure index (CEI) and wood density (WD) as fixed effects and species as random effects (Equation 3).

$$\Delta DeBA = \beta + \alpha_1 H_i + \alpha_2 Cr_i + \alpha_3 Cd_i + \alpha_4 CEI_i + \alpha_5 WD_i + \beta species[S] \quad \text{……………. (3)}$$

Where α and β are the slope and intercept respectively.

To assess the most critical factors in determining the shape of irregular trunk trees, at species level, we analyzed covariations between ΔDeBA and species traits. We used pairwise Pearson's multiple correlation tests for quantitative variables and ANOVA analysis for qualitative variables. Covariations between ΔDeBA and traits were examined using principal correspondence analysis (PCA). Juvenile light requirement was excluded for lack of a value in *Piptadeniastrum africanum* (Hook. f.) Brenan (Appendix S2, Table S2).

All statistical analyses were performed with the open-source environment R [73] using the packages "lme4" for linear mixed model analysis [74], "ade4" for principal correspondence analysis (PCA) [75] and "ggplot2" for graphical output

[76]. The conditions of normality and homogeneity of variances were tested using the Shapiro-Wilk and Bartlett tests respectively before proceeding with the analyses.

3. Results

3.1. Change in shape of irregular trunk trees

Our results reveal that the mean DeBA increased significantly from 0.27±0.22 in 2014 to 0.82±0.062 in 2021, indicating a notable shift towards more irregular trunk shapes in 2021. This change is statistically significant (Wilcoxon pairwise test, P-value < 0.001), with an average increase of 0.55±0.16 in ΔDeBA over the study period.

Differences in trunk shape (DeBA) between 2014 and 2021 were significant for each species (Table 1), suggesting that changes in trunk shape occurred in different species. In addition, significant interspecific variation in ΔDeBA was observed (t = 11.86, df = 5, P-value < 0.001). For example, *Piptadeniastrum africanum* (Hook. f.) Brenan showed relatively smaller changes in trunk shape, implying a highly irregular trunk shape compared with the other species (Table 1).

Table 1 Change in deficit basal area index (ΔDeBA) within and between tree species

	$DeBA_{2014}$	**$DeBA_{2021}$**	**ΔDeBA**	***P - value***
Piptadeniastrum africanum (Hook. f.) Brenan	0.47±0.20	0.89± 0.05	0.41±0.15	<0.001
Celtis mildbraedii Engl.	0.39±0.23	0.85± 0.07	0.45±0.17	<0.001
Manilkara mabokeensis Aubrev.	0.05±0.04	0.76± 0.01	0.71±0.033	<0.001
Pterocarpus soyauxii Taub	0.28±0.21	0.82±0.05	0.54±0.15	<0.001
Entandrophragma cylindricum (Sprague) Sprague	0.30±0.19	0.83±0.04	0.53±0.14	<0.001
Erythrophleum suaveolens Brenan	0.15±0.09	0.80±0.03	0.64±0.068	<0.001

3.2. Determinants of trunk shape changes in irregular trunk trees during the growth period

At tree level, ΔDeBA was related to total height and crown radius (Figure 4a, Table S3), with a significant negative correlation with total height (Figure 4b) and crown radius (Figure 4c). Trees developing highly irregular shapes during the growing season tended to be high canopy trees with large crowns.

At species level, we first examined covariations between ΔDeBA and species traits (Table 2). We found that ΔDeBA and wood density were positively correlated (Pearson's r = 0.879, P - value < 0.05), as well as between wood density, light requirements for juveniles (Pearson's r = 0.922, P - value < 0.05) and regeneration guild (F - value = 41.33, P - value < 0.01). Maximum diameter was positively correlated with maximum crown radius (Pearson's r = 0.812, P - value < 0.05). Tree species that develop highly irregular shapes during the growing period tend to have large canopy sizes with wide crown radii, high light requirements in the juvenile stage and low wood density.

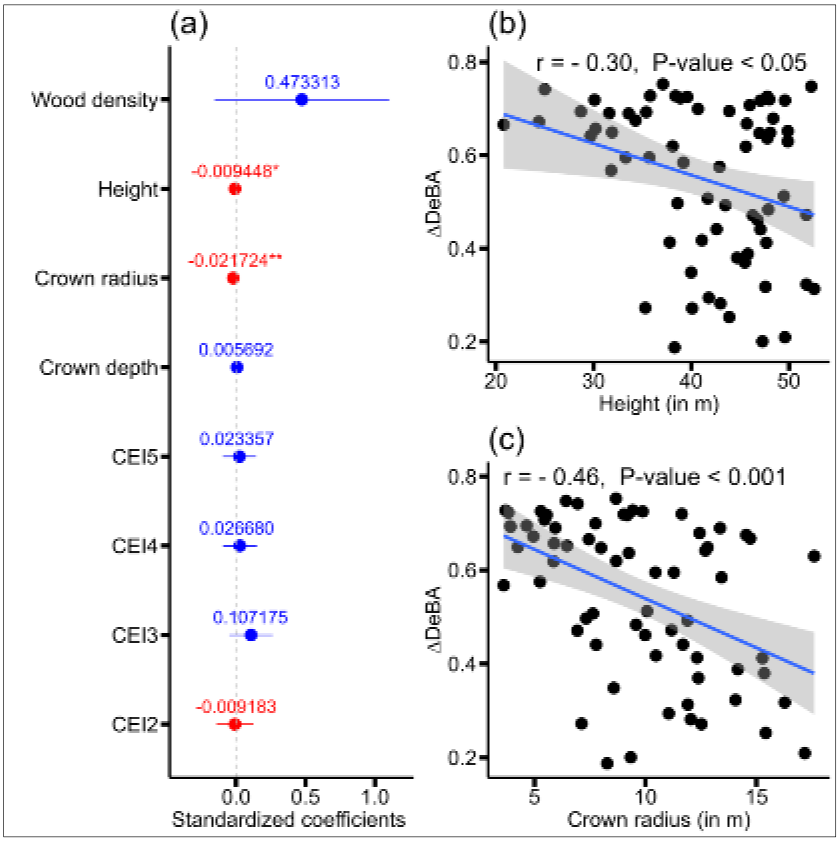

Figure 4 Determinants of ΔDeBA at tree level: (a) standardized coefficients of ΔDeBA with error bars indicating confidence intervals (* $p < 0.05$) and all coefficients for fixed and random effects are shown in Appendix S3: Table S3 (red indicates a negative coefficient and blue a positive coefficient); (b, c) bivariate relationships between ΔDeBA and significant variables with Pearson correlation coefficients (r^2). With CEI: Crown exposure index

Table 2 Bivariate relationships between ΔDeBA and species traits among 6 coexisting irregular trunk tropical tree species. Significant relationships are shown in bold (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$)

	ΔDeBA	**Dmax**	**Hmax**	**Crmax**	**Cdmax**	**WD**	**CEIjuv**
ΔDeBA	1						
Dmax	0.122	1					
Hmax	0.368	0.688	1				
Crmax	-0.382	**0.812***	0.210	1			
Cdmax	-0.277	0.738	0.446	0.749	1		
WD	**0.879***	-0.064	0.159	-0.435	-0.252	1	
CEIjuv	0.810	-0.109	-0.213	-0.279	-0.179	**0.922***	1
LH (df = 1)	4.037	0.006	1.046	1.644	0.01	2.756	0.679
MD (df = 2)	0.593	1.176	0.071	0.555	0.677	0.956	0.95
RG (df = 2)	6.551	0.041	0.396	0.62	0.046	**41.33****	2.783

Note. Change in deficit basal area index (ΔDeBA), architectural traits (H: height; Cr: crown radius and Cd: crown depth, in m) were calculated at maximum diameter (Hmax , Crmax and Cdmax). Pearson correlation coefficients are given between Change in deficit basal area index (ΔDeBA) and species traits, between architectural traits, and between architectural traits and the quantitative functional trait (wood density : WD in g/cm^3 and light requirements for juveniles: CEIJuv). F-values associated with ANOVA analysis are given for Change in deficit basal area index (ΔDeBA) or architectural traits and qualitative functional traits (dispersal mode, leaf habit and regeneration guild).

The PCA carried out on quantitative traits revealed a continuum of species on the first axis (describing 31.6% of variation), with species developing less irregular forms over time with high wood density (Figure 5a), being pioneer (P) and shade tolerant (SB), evergreen and unassisted dispersal (Figure 5b). Species developing highly irregular forms over time, i.e. those with negative PC1 scores, tended to be light-demanding and deciduous (Figure 5b). The second axis (describing 26.8% of the variation) highlighted a positive correlation between architectural traits, suggesting that tree species developing irregular forms over time tended to be large canopy species with a crown that was large, deep (Figure 5a) and wind-dispersed (Figure 5b). The latter species, i.e. those with negative PC2 scores, tended to be dispersed by animals (Figure 5b).

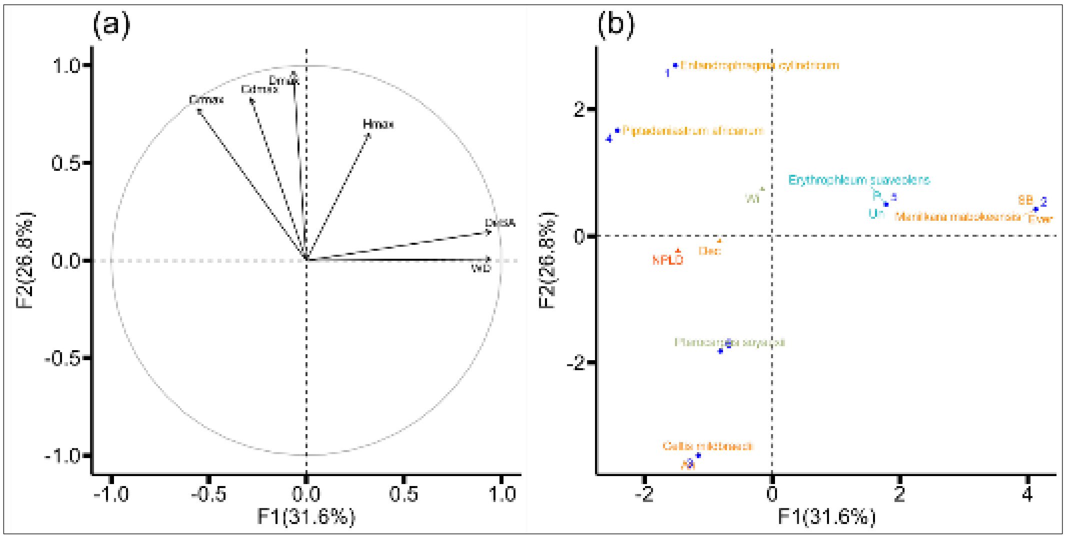

Figure 5 Covariations between traits and the Change in deficit basal area index (ΔDeBA) of the 6 irregular trunk tropical tree species for which trait data were available. The correlation circle resulting from PCA on quantitative traits is shown in (a) with the ΔDeBA and quantitative traits of the species. Species scores (b) have been colored according to dispersal mode, leaf habit and regeneration guild

4. Discussion

The results indicate a clear trend towards increasing trunk irregularity over time, with significant differences observed both within and between species. The relationship between changes in trunk shape and various tree- and species-level traits highlights the complex interplay of factors influencing trunk irregularity. The results suggest that the structural characteristics of certain species, such as crown size and wood density, play a crucial role in the evolution of trunk shape.

4.1. Irregular trunk trees evolve towards a more irregular shape

Our results showed significant differences in DeBA between 2014 and 2021 for all species, indicating changes in the shape of irregular trunk trees in 2021. The mean change in ΔDeBA was 0.55±0.16, indicating an evolution from irregular trunks to a very irregular shape at 1.30 m above ground in 2021. This is the first time such an observation has been made in Central Africa. These results are similar to those obtained by Luoma et al. [3] in boreal forests, who also detected changes in the normal shape quotient using the Terrestrial Laser Scanner (TLS) point cloud at two different dates. It is accepted that trees develop more irregularities at the base of the trunk to reassure their anchorage over time on poor soils, shallow substrates for root growth or water saturation, as well as locations subject to strong winds, resulting in a greater proportion of the total biomass allocated to the base of the trunk and to the roots of these trees [27–29,47]. In addition, evolution towards a more irregular form can provide micro-habitats for a variety of organisms, thereby increasing biodiversity at the individual level [18–20,22,23].

At species level, our results revealed specific differences in ΔDeBA between coexisting species, with a smaller mean change for *Piptadeniastrum africanum* (Hook. f.) Brenan indicating that the trunk evolves more towards an irregular shape. The evolution of the trunk towards an irregular shape implies a greater change in trunk taper. These differences in ΔDeBA evolution between species could sometimes be explained by the diversity of growth strategies that exist in response to light availability [77]. These growth strategies should in turn limit tree architecture [78].

4.2. Tree species traits determine change in irregular trunk shape in semi-deciduous forest

At tree level, the determining factors in the shape change of irregular trunk trees are height and crown radius. Trees that develop highly irregular shapes during the growing period tend to be large canopy trees, with large crowns. Large canopy trees developing large crowns have been observed in Southeast Asia [77,79] and South Asia [80]. Large canopy trees with large crowns have the advantage of increasing carbon uptake, intercepting light and eliminating competition with neighboring canopies [81]. The response of large canopy trees to light availability reflects changes in growth allocation rules that probably have strong adaptive significance [79]. Most of these fast-growing canopy trees have low wood densities in the tropics [80]. These low wood density values indicate the heliophilic nature of the wood in these trees [82].

Species traits, including maximum diameter, maximum height, maximum crown radius, maximum crown depth, wood density, leaf habit, regeneration guild and dispersal mode, significantly influenced changes in the shape of irregular trunk trees over the growing period. These results suggest that tropical canopy tree species developing very large irregularities over the growing period tended to be tall species with large, deep crowns and low wood density. Tall canopy tree species developing large, deep crowns have been observed in Central Africa [72]. These large canopy species develop large crowns to maximize light interception [83].

In tropical Africa, it has been shown that species with low wood density are species with large canopies [84]. Wood density is an important indicator of a species' ability to respond to temporal changes in light availability [83,85–88]. Our results show that *Piptadeniastrum africanum* (Hook. f.) Brenan, a non-pioneer light-demanding species, tended to develop more irregular forms (ΔDeBA, 0.41±0.15) than *Manilkara mabokeensis* Aubrev. (ΔDeBA, 0.71±0.033), which is a shade-tolerant species. These low wood densities are advantageous for light-demanding species that need to monopolize space by growing rapidly upwards and completing their life cycle before being overtaken by competing neighboring plants [83].

In addition, tropical canopy tree species developing very irregularities over the growing period tended to be deciduous, non-pioneer light-demanding and wind-dispersed. In Central Africa, the deciduous, non-pioneer light-demanding and wind-dispersed species proved to be the large-canopy species [72]. In addition to the advantage of reducing hydraulic stress through leaf fall during the dry season [85], large-canopy deciduous species in seasonal rainforests could be explained by their higher photosynthetic capacity than that of evergreen species [89,90]. Non-pioneer light-demanding species are also known to be fast-growing species with high photosynthetic capacity in tropical forests [86,91–93]. Wind dispersed wide-canopy species could be explained by the shape and mass of their seeds [94], as well as by the fact that they colonize environments disturbed by windthrow [95,96]. Wind dispersal over distant distances may be of disproportionate importance for seeds colonizing bright spaces and avoiding distance- and/or density-dependent mortality [94].

4.3. Advantages and limitations of the close-range photogrammetric approach for extracting physical tree parameters

In this study, the close-range photogrammetric approach was used to capture very high-resolution images of irregular trunk trees, resulting in detailed 3D models of their structure. This new source of data may improve our ability to characterise growth processes determined by interactions with the environment and during ontogeny. Consequently, the analysis of the shape of irregular trunk trees during the growth period using the point cloud makes this approach potentially revolutionary for better integration into large-scale ecological studies of the concept of tree shape. This approach could also be useful in studies aimed at monitoring tree growth in complex forest structures, such as mangroves or peat swamp forests, where traditional methods struggle to capture the complexity of trunk shapes.

Although this approach is promising, the use of the close-range photogrammetric approach is affected by forest situations, lighting conditions under the canopy and the standardisation of shots. Images of the upper part of the tree are often tilted and the degree of overlap between photos is difficult to maintain. All these factors limit the height of the reconstructed point cloud and affect the accuracy of extracting individual tree parameters. This approach requires significant training and expertise to capture and process the data efficiently, which could limit its widespread adoption. The development of user-friendly software tools and the provision of on-the-job training could help to alleviate these obstacles. Future research should therefore develop ways of efficiently acquiring sequential images in order to increase the accuracy of the reconstructed point cloud.

5. Conclusion

This study is, to our knowledge, the first to show the evolution of the shape of irregular trunk trees over a 7-year period in Central Africa. Significant differences were detected in the shape of irregular trunk trees over the growth period at tree and species level, indicating that irregular trunk trees tend to allocate more of their growth to the base of the trunk. The changes observed are consistent with current knowledge of how trees distribute their growth. At tree level, changes in the shape of irregular trunk trees are determined by the height and crown radius. Trees that develop highly irregular shapes during the growing period tend to be tall canopy trees with large crowns. At species level, changes in the shape of irregular trunk trees are influenced by maximum diameter, maximum height, maximum crown radius, wood density, leaf habit, regeneration guild, and dispersal mode. These results suggest that tropical canopy tree species that develop very large irregularities over the growth period tend to be species with large canopy heights, large and deep crowns, low wood density, deciduous leaves, non-pioneer light-demanding and wind-dispersed. Our results support the idea that raiped-growing species are light-demanding, deciduous, wind-dispersed species that invest in low-density wood to reach the canopy quickly. These life-history traits affect irregular trunk tree architecture and plant performance in different ways, contributing to the coexistence of tree species in tropical forests.

Despite the relevance of our results, certain limitations must be taken into account. Although the evolution of irregular trunk shape was observed over several years, the ΔDeBA measurements are based on data points collected 1.30 m above the ground. This approach, although indicative, does not take into account potential variations over the full height of the trunk, which could underestimate or overestimate the evolution of tree shape. Future studies should consider analyses at different heights to obtain a more complete picture of trunk morphology. Furthermore, our conclusions are based on a limited sample of sites and species, which may limit the generalisation of our results to other tropical forests or other biomes. Another limitation is the duration of the study. The evolution of trunks towards more irregular shapes is a potentially long process, and the changes observed over a limited period may not fully reflect long-term dynamics. It would be appropriate to broaden the sample to include more species and more tropical forest sites, particularly those with marked climatic and edaphic variations. This would provide a better understanding of how different environmental factors influence the evolution of trunk shape.

5.1. Supplementary materials

- Appendix 1, Table S1. Irregular trunk tree species, including family, number (n) of samples, mean diameter above irregularity (DPOM) values for each species in 2014 and 2021.
- Appendix 2, Table S2. Study species traits: Scientific names, functional traits including regeneration guild (pioneer, P, non-pioneer light-demanding, NPLD, and shade-bearing, SB), leaf habit (deciduous, Dec, and evergreen, Ever); dispersal mode (unassisted dispersal, Un, wind dispersal, Wi and animal dispersal, An); light requirements for juveniles (CEIjuv), wood density (WD in g.cm-3) and architectural traits including height (H in m), crown depth (Cd in m) and crown radius (Cr in m) at maximum diameter (Hmax, Crmax and Cdmax) are given for the 6 coexisting irregular trunk tree species.
- Appendix 3, Table S3. Determinants of ΔDeBA of irregular trunk trees at the trees level according to the results of linear mixed model. With CEI: Crown Exposure Index.

Compliance with ethical standards

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Data availability

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

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