frontiers in Forests and Global Change

TYPE Original Research
PUBLISHED 05 March 2026
DOI 10.3389/ffgc.2026.1800379

OPEN ACCESS

EDITED BY
Ana Cristina Gonçalves,
University of Evora, Portugal

REVIEWED BY
Girmay Darcha,
Mekelle University College of Dryland Agriculture and Natural Resources, Ethiopia
Abu Mulatu,
Ethiopian Environment and Forest Research Institute, Ethiopia

*CORRESPONDENCE
Hidirou Orou
orouhidirou1996@gmail.com

RECEIVED 30 January 2026
REVISED 18 February 2026
ACCEPTED 19 February 2026
PUBLISHED 05 March 2026

CITATION
Orou H, Assèdé ESP, Ponette Q and Biaou SSH (2026) Structural heterogeneity modulates the effects of stem density on standing biomass in mature dry *Isoberlinia* woodlands. *Front. For. Glob. Change* 9:1800379. doi: 10.3389/ffgc.2026.1800379

Structural heterogeneity modulates the effects of stem density on standing biomass in mature dry *Isoberlinia* woodlands

Hidirou Orou[1,2]*, Eméline Sêssi Pélagie Assèdé[1,3], Quentin Ponette[2] and Samadori Sorotori Honoré Biaou[1]

[1]Laboratory of Ecology, Botany and Plant Biology, Université de Parakou, Parakou, Benin, [2]Earth and Life Institute, Université catholique de Louvain (UCLouvain), Louvain-la-Neuve, Belgium, [3]Department of Plant and Soil Sciences, University of Pretoria, Pretoria, South Africa

Introduction: While the impacts of forest structural attributes on above-ground biomass (AGB) has been largely documented in closed-canopy forests, much less is known in dry forests, where water rather than light drives biomass accumulation. In particular, little is known about how AGB of *Isoberlinia* spp. stands, a dominant ecosystem of dry West Africa, is shaped by structural attributes.
Methods: To overcome this gap stem density, summed crown projection area (SCPA), and tree diameter at breast height (DBH) were measured in forty 400 m^2 plots established in young and mature *Isoberlinia* spp. stands in the Sudano-Guinean zone of Benin. AGB was estimated using an allometric model, and a piecewise structural equation model (pSEM) was developed to analyze the direct and indirect effects of stem density, SCPA, and the coefficient of variation of the diameter at breast height (CVDBH) on AGB.
Results: In young stands (442.50 $\pm$ 34.51 stems/ha on average), higher stem density had a significantly negative direct effect on AGB ($\beta = -0.95$, $p < 0.001$), while SCPA influence remained non-significant. In mature stands (255 $\pm$ 32.04 stems/ha on average), increase in stem density also had a significant direct negative effect on AGB. In addition, higher CVDBH significantly reduced AGB ($\beta = -0.32$, $p = 0.04$), while denser SCPA showed a positive but non-significant trend ($\beta = 0.19$, $p = 0.49$). Whatever the stand stage, there was no indirect effects of stem density through SCPA and CVDBH.
Discussion: Our results provide actionable insights for managing *Isoberlinia* woodlands: density regulation is critical in young stands to optimize individual growth, while maintaining moderate diameter heterogeneity (intermediate CVDBH values at 15%) is essential in mature stands, as excessive structural variability can reduce AGB. These findings contribute to both local resource needs and broader climate mitigation goals by enhancing standing AGB while preserving ecosystem integrity.

KEYWORDS
developmental stages, natural stands, stand stocking, Sudano-Guinean zone, tropical silviculture, West African dry forests

Introduction

African tropical dry forests play a crucial role in biodiversity conservation and carbon storage, serving essential ecological functions in climate regulation and wildlife conservation, while providing a primary source of wood products for local populations (Kouassi et al., 2021; Axer et al., 2022). However, these ecosystems face increasing anthropogenic pressures from growing demand for fuelwood and timber, necessitating a deeper understanding of the structural factors that drive standing above-ground biomass (AGB) to ensure sustainable forest management (Bellefontaine et al., 2015; Sanon et al., 2019).

Understanding how forest structural characteristics influence AGB is critical for developing effective management strategies in tropical dry forests. Three key structural parameters have been identified as major drivers of AGB: stem density, canopy structure, and size heterogeneity (Gadow et al., 2012; Zhang and Chen, 2015). The relationship between stem density and AGB is complex and context-dependent. In closed-canopy forest, the self-thinning law predicts that initially high stem density triggers intense intraspecific competition for resources, resulting in density-dependent mortality and stands composed of numerous small individuals with lower total AGB than less dense stands with larger trees (Pretzsch and Biber, 2016). However, the sign and magnitude of density effects on AGB vary across forest types, developmental stages, and environmental conditions (Ali et al., 2019; Mensah et al., 2023). Canopy structure, quantified through summed crown projection area (SCPA the sum of individual tree crown projection areas scaled to stand level), reflects the stand's light interception capacity and photosynthetic potential. Greater SCPA is generally associated with higher AGB in light-limited forests (Sharma et al., 2008; Pretzsch, 2014; Nam et al., 2018). Structural heterogeneity, commonly measured by the coefficient of variation of diameter at breast height (CVDBH), captures the coexistence of trees at different developmental stages within a stand. According to the selection effect hypothesis, high diameter variation in monospecific stands reflects asymmetric competition where dominant individuals monopolize resources at the expense of suppressed individuals, leading to suboptimal resource use at the stand level and potentially lower total AGB (Grime, 1998; Poorter et al., 2015; Abbasi et al., 2023).

Tropical dry woodlands dominated by *Isoberlinia* spp., known as miombo-type formations in West Africa, present distinct ecological characteristics that may alter these well-established AGB-structure relationships. These ecosystems experience pronounced seasonal water stress, with a dry season lasting 5 to 7 months and monthly rainfall below 50 mm during the driest period, making water the primary limiting resource (Frost, 1996; Sankaran et al., 2005). This water limitation results in characteristically open canopy structures, with typical crown coverage below 25–30%, contrasting sharply with closed-canopy tropical moist forests where canopy closure often exceeds 80–90% (Chidumayo, 2013). Tree regeneration in *Isoberlinia* woodlands occurs primarily through vegetative root suckering rather than seed establishment, leading to spatially aggregated patterns of densely clustered stems originating from shared root systems (Dourma et al., 2009, 2012). This clonal regeneration strategy creates a distinctive stand structure characterized by patches of high stem density interspersed with more open areas. Additionally, fire is a recurrent disturbance that maintains the open structure, stimulates vegetative regeneration, and influences demographic processes and size distributions (Holdo, 2007; Staver et al., 2011).

Therefore, unlike closed-canopy temperate or tropical moist forests where light competition predominantly structures communities and drives productivity patterns (Pacala et al., 1996), *Isoberlinia* woodlands are characterized by a fundamental shift toward belowground competition for water and nutrients as the primary limiting factors (Sankaran et al., 2005; February et al., 2013). This ecological difference has critical implications for understanding AGB-structure relationships in these systems. In closed forests, self-thinning operates at the stand level as dense canopies trigger stem density-dependent mortality through light limitation (Weiner, 1990). By contrast, in *Isoberlinia* woodlands where most of the ground surface receives direct sunlight, self-thinning likely occurs locally within regeneration clusters through belowground competition rather than at the stand scale (Ryan and Yoder, 1997). This localized competitive dynamic suggests that stem density effects on AGB may be mediated more by belowground resource limitation than by aboveground light competition. The implications extend to canopy structure as well. In light-limited forests, trees in dense stands develop narrow, vertically-elongated crowns to compete for canopy space, leading to strong negative relationships between stem density and individual crown area (Pretzsch, 2014). However, in water-limited woodlands, lateral crown expansion may be less constrained by neighbors in terms of light interception but more fundamentally limited by the belowground resources needed to support crown maintenance (February et al., 2013). Consequently, the stem density-SCPA relationship may differ substantially from patterns observed in closed forests. Similarly, the interpretation of size heterogeneity requires careful consideration in these systems. While CVDBH in closed forests typically reflects competitive hierarchies driven by differential light access (Coates et al., 2009; Binkley et al., 2010), in *Isoberlinia* woodlands it may primarily reflect the clustered regeneration pattern dense aggregations of small vegetative shoots adjacent to scattered large seed-origin trees rather than purely competitive suppression. This distinction is crucial for interpreting CVDBH-AGB relationships, as high structural heterogeneity may result from regeneration strategy rather than indicating intense ongoing competition.

Despite the ecological and economic importance of *Isoberlinia* woodlands covering approximately 2.7 million km^2 across sub-Saharan Africa and supporting millions of rural livelihoods (Gumbo and Dumas-Johansen, 2021) quantitative assessments of AGB-structure relationships in these systems remain limited. Most existing research on stand structure and AGB has focused on closed-canopy forests where light competition dominates (Zhang and Chen, 2015; Ali et al., 2019), leaving considerable uncertainty about whether these findings apply to open, water-limited woodlands where fundamentally different competitive regimes operate. Several critical questions remain unresolved. It is unclear whether stem density effects on AGB operate through similar mechanisms in open versus closed forests, or if the shift from light to water limitation fundamentally alters these relationships. The role of SCPA in water-limited systems where light is abundant, but water scarce also requires investigation, as does the effect of structural heterogeneity when CVDBH reflects regeneration patterns and clonal structure rather than purely competitive hierarchies. In West Africa, natural woodlands dominated by *Isoberlinia* spp. have become increasingly essential for local communities while experiencing progressive structural degradation and depletion of valuable tree species (Biaou et al., 2011; Bellefontaine et al., 2015; Adjahossou et al., 2019; Sanon et al., 2019). Understanding AGB-structure relationships in these ecosystems is therefore crucial for developing locally-adapted

management strategies that account for their specific ecological processes, improving AGB estimation models for carbon accounting in dry tropical regions, and predicting responses to intensifying anthropogenic pressures and climate change (Silman, 2014; Rozak et al., 2018).

This study aims to evaluate the effect of stem density, summed crown projection area, and structural heterogeneity (CVDBH) on AGB in natural *Isoberlinia* spp. woodland stands at different developmental stages (young VS. mature) in the Sudano-Guinean zone of Benin. Given the ecological specificities of these water-limited, open-canopy woodlands described above, we tested four specific hypotheses (Figure 1). We hypothesize that stem density has a negative direct effect on AGB across all developmental stages (H1). Despite low SCPA that minimizes aboveground light competition, we expect that high stem density intensifies belowground competition for water and nutrients, limiting individual tree growth and overall stand AGB (Pretzsch and Biber, 2016). We further hypothesize that stem density has a negative indirect effect on AGB through its negative influence on SCPA and positive influence on CVDBH (H2). Higher stem density constrains individual SCPA expansion, thereby reducing total light-capturing area at the stand level, while simultaneously increasing size inequality through stem density-dependent processes, both pathways reducing stand productivity. Regarding structural heterogeneity, we hypothesize that CVDBH has a negative effect on AGB, particularly in mature stands (H3), reflecting either asymmetric competitive suppression or the coexistence of many small juvenile clonal stems with few large seed-origin adults, both scenarios resulting in suboptimal resource use at the stand level (Grime, 1998; Poorter et al., 2015). Finally, we hypothesize that SCPA exerts a positive effect on AGB, particularly in mature stands (H4), as greater SCPA indicates enhanced photosynthetic capacity. However, we anticipate this effect may be weaker than in closed forests due to the reduced role of light competition in water-limited systems (Pretzsch, 2014). By explicitly testing these hypotheses in the context of open, water-limited *Isoberlinia* woodlands, this study contributes to filling critical knowledge gaps and provides empirical evidence to support sustainable forest management adapted to the specificities of dry tropical ecosystems.

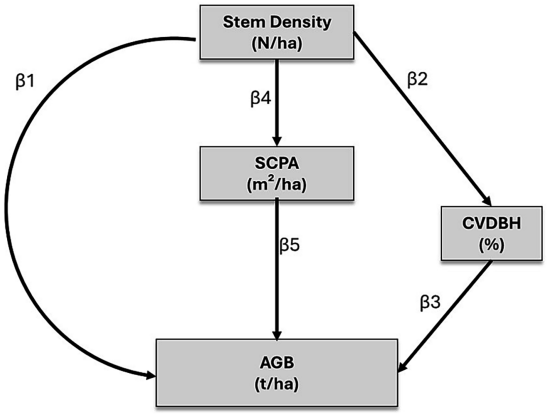

FIGURE 1
Piecewise structural equation model of the effects of Stem density, SCPA and CVDBH on AGB. AGB, above-ground biomass; CVDBH, coefficient variation of diameter at breast height; SCPA, summed crown projection area.

Materials and methods

Study area

The study was carried out in Benin in the Sudano-Guinean zone where more than 92.5% of the forest canopy cover is dominated by *Isoberlinia doka* and *Isoberlinia tomentosa* woodlands (Sokpon et al., 2006; Biaou, 2009) (Figure 2). This area has a tropical climate characterized by a progressive merging of the two precipitation peaks into one peak, which indicates a unimodal rainfall regime, and marks the transition toward a typical Sudanian climate (one rainy season from May to October and one dry season from October to April). The average annual precipitation is recorded at 1,200 mm (Adomou, 2005; Sinsin et al., 2010). This places the study area at the transition between the moist Guinean zone (with more than 1,400 mm per year) in southern part of the country and the semi-dry Sudanian zone (with less than 1,200 mm per year) in northern part of the country (White, 1983; Adomou, 2005; Assédé et al., 2020). The dominant soil type is tropical ferruginous. The vegetation consists of a patchy savannah mosaic including structurally distinct forest types: dense dry forests, woodlands, and gallery forests (Sokpon et al., 2006; Biaou, 2009; Hountondji et al., 2013). Following the ecological framework of Chidumayo and Gumbo (2010) for African dry forests and woodlands, these forest types differ primarily in canopy structure and continuity. Dense dry forests are characterized by relatively closed canopy with closely spaced trees and limited herbaceous layer development, while woodlands display more open canopy structure with substantial gaps between tree SCPA and well-developed grass understory typical of miombo type vegetation. Slash-and-burn agriculture dominated by cotton growing, timber logging, fuelwood harvesting, fire and grazing were pointed out as the main anthropogenic disturbances (Zida et al., 2007; Hountondji et al., 2013) that were shaping vegetation patterns (Kennedy and Potgieter, 2003; Biaou, 2009).

Sampling method and data collection

Sites were selected using a targeted approach based on two criteria: (i) dominance of *Isoberlinia* spp. as the dominant canopy tree species (>70% of stems), and (ii) minimal recent anthropogenic disturbance. Specifically, the selected sites are located within gazetted forest reserves managed by the national forestry service, where logging has been prohibited, as confirmed by local forestry officers and village management committees. Although low-intensity disturbances such as non-timber forest product collection and controlled burning persist, these do not substantially alter stand structure. Two vegetation units were delineated, representing two stages of *Isoberlinia* spp. woodland development. Stands in the study area (Assede et al., 2012; Geldenhuys et al., 2017). The AGB of these *Isoberlinia* spp. stands was assessed according to the following criteria:

i. Young stage: stands characterized by 70% of stems with a height ≥ 4 m and a DBH between 7 and 16 cm, not yet having reached the reproductive phase.
ii. Mature to advanced stage: stands characterized by 70% of stems with a height ≥ 11 m and a DBH > 18 cm, having begun their reproductive phase. It should be noted that the 18 cm DBH threshold is strictly a classification criterion based on the reproductive status of the dominant cohort, not an inventory exclusion limit; all trees with DBH ≥ 7 cm and height > 1.40 m

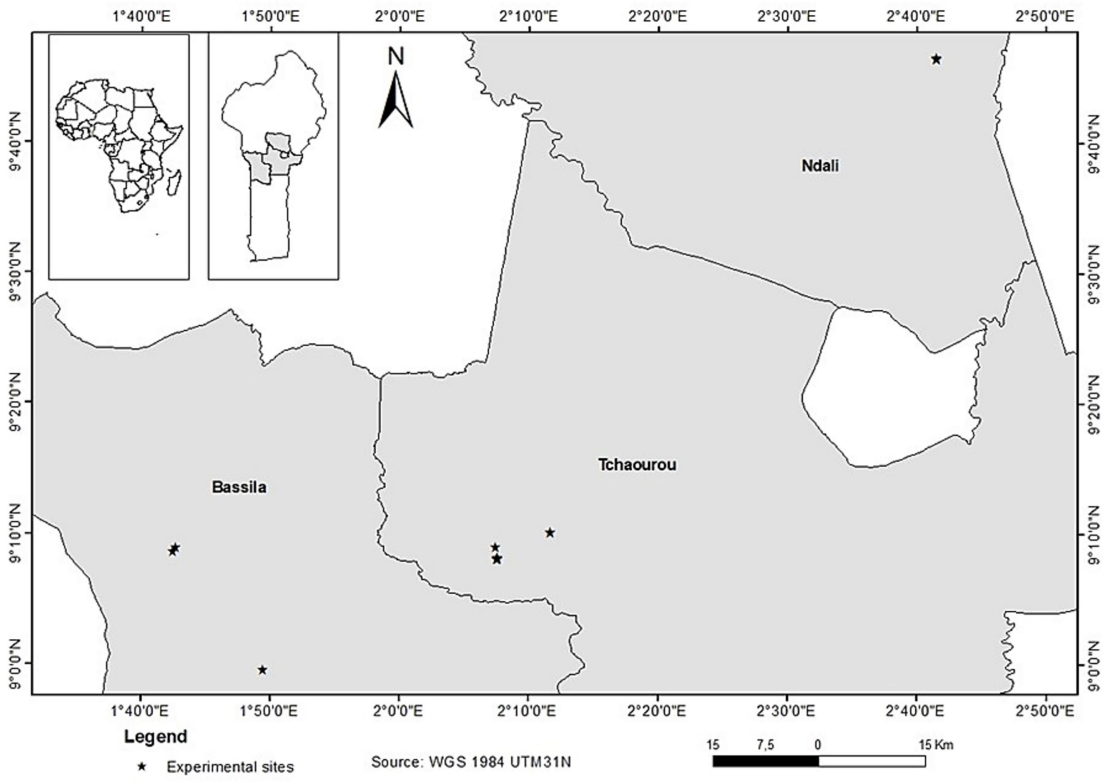

FIGURE 2
Map of study areas showing the experimental sites in Benin.

were measured across all plots regardless of developmental stage.

Within each selected site, plots were randomly positioned to ensure unbiased spatial coverage of stand structural variability (Supplementary Figure S1). Sampling was carried out on forty 20 m × 20 m plots, comprising 30 plots spread over 6 experimental sites (5 plots per site) and 10 plots on a seventh experimental site. The unequal allocation of plots across sites (5 plots per site for 6 sites and 10 plots for the seventh site) reflects the greater structural heterogeneity observed at the seventh site, which warranted denser sampling to capture the full range of structural conditions. All the plots were divided into two equal groups: 20 plots in young stands and 20 in mature stands. Within each site, plots were placed at least 50 m apart to ensure spatial independence while capturing the variability of stand structures. This minimum distance was selected based on ecological considerations for Isoberlinia woodlands, where spatial autocorrelation in structural parameters typically decreases substantially beyond 30–40 m due to the patchy distribution of clonal regeneration clusters (Dourma et al., 2009; Chidumayo, 2013).

Quantification of structural variables

Stem density, defined as the number of individuals per unit area, was calculated by counting the number of *Isoberlinia* spp. individuals per plot with height > 1.40 m and DBH > 7 cm.

Coefficient of variation of DBH (CVDBH), was calculated as the ratio of the standard deviation to the mean DBH in each plot, expressed as a percentage (Mensah et al., 2023). This parameter reflects the heterogeneity of the stand's diameter structure and integrates both asymmetric competition between individuals and disturbance history. High CVDBH values indicate a highly heterogeneous structure with coexistence of contrasting size classes, while low values suggest a more homogeneous structure typical of even-aged stands.

Summed crown projection area (SCPA, m^2/ha) was calculated from crown diameter measurements taken in two perpendicular directions (north–south and east–west) for each tree. Crown diameter was measured by positioning one observer directly beneath the outermost extent of the crown in each cardinal direction while a second observer marked the corresponding ground position using stakes. Individual crown projection area was calculated assuming an elliptical crown shape, which provides a reasonable approximation for most tree crowns (Ganamé et al., 2021), using:

$$Crown\ area\_i\left(m^2\right) = \pi \times \left(\frac{Diameter\ North-South}{2}\right) \times \left(\frac{Diameter\ East-West}{2}\right)$$

SCPA was then calculated as

$$SCPA = EF \times \left(Crown\ area\_i\left(m^2\right)\right)$$

where.

$EF = \frac{A\_r}{A\_plot}$ is the expansion factor, with A_r being the reference area (10,000 m^2) and A_plot the plot area (400 m^2).

Basal area (m^2 ha^{-1}) was calculated from the diameters at breast height (1.30 m) using the following formula then converted to hectares:

$$Basal\ area = EF \times \sum \pi \times \left(\frac{DBH_i^2}{4} \right)$$

Estimation of AGB

Above-ground biomass (AGB) was estimated at the individual scale using the specific allometric equation for *Isoberlinia doka* established by Ganamé et al. (2021) for the diameter class 7–48 cm:

$$AGB_i\left(Kg\right) = e^{-3,36}\left(DBH_i^2 H_i\right)^{1,03}$$

where AGB_i is Above-ground biomass, DBH (cm) is diameter at breast height, and H (m) is total tree height.

This equation was selected because it covers the range of diameters observed in our study (7–45 cm) and was calibrated in an ecological context similar to Beninese savannah thus ensuring robust AGB estimation. Although this model was originally calibrated for *Isoberlinia. doka*, its application to *Isoberlinia. tomentosa* is justified by the close morphological and architectural similarity between the two species, which are often treated as a species complex (Dourma et al., 2009, 2012). The allometric equation is based on DBH and height as predictor variables and does not explicitly include wood density. Individual tree AGB values were summed at the plot level multiplicated by expansion factor to obtain total AGB expressed in tons per hectare (t/ha):

$$AGB\left(t/ha\right) = EF \times \sum \frac{AGB_i\left(Kg\right)}{1000}$$

Data analysis

Predictor selection and collinearity diagnostics

Prior to structural equation modeling, we performed multicollinearity diagnostics by calculating variance inflation factors (VIF) for each predictor. The VIF values greater than 5 indicate the presence of problematic collinearity that could compromise the interpretation of regression coefficients (Dormann et al., 2013; Ullah et al., 2021). This preliminary step is crucial in piecewise structural equation modeling (pSEM) analyses because the presence of strong collinearity between variables can lead to unstable parameter estimates and erroneous interpretation of causal relationships (Zuur et al., 2009). VIFs were calculated for each predictor variable in individual sub-models, separately for young and mature stands, to verify that relationships between structural variables do not introduce excessive redundancy in the models.

In young stands, basal area exhibited a VIF of 11.01, while stem density and mean DBH showed VIF values of 4.72 and 1.02, respectively. In mature stands, a similar pattern emerged with basal area (VIF = 12.53), stem density (VIF = 4.23), and mean DBH (VIF = 1.17). Basal area was excluded from all tested models it was inherently related to AGB through the use of the allometric model.

Piecewise structural equation modeling

Piecewise structural equation models were constructed separately for young and mature stands to test the formulated hypotheses and quantify causal relationships between structural variables and AGB (Ullah et al., 2021; Abbasi et al., 2023). The conceptual model structure postulates that (Figure 1): (i) stem density directly influences AGB; (ii) SCPA and CVDBH directly influence AGB; (iii) these structural variables can mediate the effect of stem density on AGB, thus creating indirect effects.

The models are expressed by the following system of equations (Equations 1–5):

$$AGB = \beta 1 \times \text{Stem density} \quad (1)$$

$$AGB = \beta 5 \times \text{SCPA} \quad (2)$$

$$AGB = \beta 3 \times \text{CVDBH} \quad (3)$$

$$SCPA = \beta 4 \times \text{Stem density} \quad (4)$$

$$\text{CVDBH} = \beta 2 \times \text{Stem density} \quad (5)$$

All variables were standardized by centering and scaling before analysis to: (i) facilitate comparison of effects between variables expressed in different units of measurement, (ii) improve numerical convergence of optimization algorithms, and (iii) allow direct interpretation of standardized coefficients in terms of change in standard deviation of the response variable for a one standard deviation change in the predictor variable (Zuur et al., 2009).

The goodness-of-fit of pSEM models was assessed using Fisher's C statistics, where a model is considered adequate for $0 \leq C/df \leq 2$ and $p > 0.05$ (Grace et al., 2016; Lefcheck, 2016). Direct effects were interpreted from standardized regression coefficients (β), while indirect effects were calculated as the product of coefficients along mediated paths (Lefcheck, 2016). Statistical significance of relationships was assessed using Wald tests at the $\alpha = 0.05$ threshold.

Analyses were performed in R 4.3.1 (R Core Team, 2022) using the piecewiseSEM, car, nlme, and ggplot2 packages.

Although ecological relationships are generally non-linear at large scales, the use of linear models can be justified when the study focuses on a restricted gradient of environmental conditions where relationships can be approximated by a linear function (Ullah et al., 2021). The appropriateness of linear models was assessed using comprehensive diagnostic plots for each structural equation. Observed versus predicted scatter plots, residual versus fitted values plots, and quantile-quantile plots confirmed that the linear models satisfied the assumptions of linearity, homoscedasticity and normality of the residuals for both developmental stages (Zuur et al., 2009). These results were corroborated by statistical tests (Shapiro–Wilk for normality and Breusch–Pagan for homoscedasticity; all $p > 0.05$), which validated the use of linear pSEM for quantifying structural-AGB relationships (Grace et al., 2016) (Supplementary Figures S2, S3).

Nonlinear effects of stand structure on AGB in all stages of development

Unlike stage-specific linear analyses, combining data from both developmental stages required a non-linear approach to capture potential curvilinear relationships across the full structural gradient.

We analysed the nonlinear effects of structural variables on aboveground biomass (AGB) using generalized additive models (GAMs) and generalized additive mixed models (GAMMs). AGB (t/ha) was modeled as a function of stem density (stems/ha), SCPA (m^2/ha), and CVDBH, combining data from young and mature stands. Nonlinear relationships were represented by thin plate regression splines, and ecologically relevant interactions were modeled using tensor products [te()], allowing interactive effects between structural variables to be captured. Smoothing parameters were estimated using restricted maximum likelihood (REML) with a limited base dimension to avoid overfitting. In GAMMs, the stage of development (young vs. mature) was incorporated as a random effect via a term s(Stage, bs = "re") to account for the hierarchical structure of the data. All models were compared using the Akaike information criterion (AIC), adjusted R^2, and explained deviance.

Results

Structural characteristics across developmental stages of *Isoberlinia* woodlands

The results of descriptive statistics of parameters such as stem density, DBH, SCPA, and AGB are presented in Table 1.

Young stands exhibit higher stem density (442.5 ± 34.51 stems/ha), with values ranging from 375 to 500 stems/ha. Mean DBH is 13.80 ± 3.76 cm with trees reaching an average height of 7.18 ± 1.18 m. The CVDBH is relatively low at 1.54%. SCPA averages 1732.73 ± 269.79 m^2/ha, while basal area reaches 7.10 ± 3.30 m^2/ha. AGB is, averaging 28.29 ± 13.67 t/ha.

In mature stands, stem density decreases substantially to 255 ± 32.04 stems/ha, with values ranging from 200 to 300 stems/ha. Mean DBH increases to 24.89 ± 6.91 cm, with trees averaging 12.47 ± 1.51 m in height. The CVDBH rises dramatically to 22.61%, reflecting considerable structural heterogeneity. SCPA nearly triples to 5000.91 ± 1,070 m^2/ha, and basal area increases to 13.36 ± 4.67 m^2/ha. AGB shows a pronounced increase, averaging 104.63 ± 47.72 t/ha.

Direct and indirect effects of stem density, CVDBH and SCPA on AGB in young and mature stage of development

In young stands, we observe a highly significant negative direct effect of stem density on AGB ($\beta = -0.95$; $p < 0.001$; Supplementary Table S1; Figure 3A). Although stem density significantly reduces SCPA development ($\beta = -0.89$; $p < 0.001$; Supplementary Table S1; Figure 3A), the influence of SCPA on AGB remains negligible ($\beta = 0.01$; $p = 0.93$; Supplementary Table S1; Figure 3A). Furthermore, CVDBH shows a non-significant negative effect on AGB ($\beta = -0.06$; $p = 0.39$; Supplementary Table S1; Figure 3A). The indirect effect via CVDBH was negligible ($\beta = 0.03 \times -0.06 = -0.002$; non-significant), while the indirect effect via SCPA was also minimal ($\beta = -0.89 \times 0.01 = -0.009$; non-significant). The total indirect effect remained very weak (β total indirect = −0.01; Figure 3C).

For mature stands, the direct negative effect of stem density on AGB is attenuated but significant ($\beta = -0.82$; $p = 0.01$; Supplementary Table S1; Figure 3B). The relationship between density and SCPA is strongly negative ($\beta = -0.79$; $p < 0.001$; Supplementary Table S1; Figure 3B), indicating that lower stem densities allow for greater SCPA expansion. However, the indirect effect via the SCPA ($\beta = -0.79 \times 0.19 = -0.15$) remains insignificant, as the effect of the SCPA is not significant ($\beta = 0.19$; $p = 0.49$; Supplementary Table S1; Figure 3B). Note that the

TABLE 1 Descriptive statistics including minimum, median, and standard deviation (SD) and maximum of structural parameters.

Structural parameter	Statistics	Young	Mature
Stem density (stem per ha)	Mean±SD	442.50 ± 34.51	255 ± 32.04
	Min	375	200
	Max	500	300
SCPA (m^2/ha)	Mean±SD	1732.73 ± 269.79	5000.91 ± 1,070
	Min	1204.18	3256.78
	Max	2185.73	7011.70
Coefficient of variation DBH (CVDBH) (%)	Mean±SD	1.54 ± 0.49	22.61 ± 7.22
	Min	0.56	10.87
	Max	2.37	36.74
Basal Area (m^2 per ha)	Mean±SD	7.10 ± 3.30	13.36 ± 4.67
	Min	5.60	7.50
	Max	8.51	22.22
AGB*(Ton per ha)	Mean±SD	28.29 ± 13.67	104.63 ± 47.72
	Min	9.31.	50.84
	Max	54.12	196.03
Mean DBH (cm)	Mean±SD	13.80 ± 3.76	24.89 ± 6.91
Mean height (m)	Mean±SD	7.18 ± 1.18	12.47 ± 1.51

AGB, above-ground biomass; CVDBH, coefficient variation of diameter at breast height, SCPA, summed crown projection area.
*AGB, above-ground biomass.

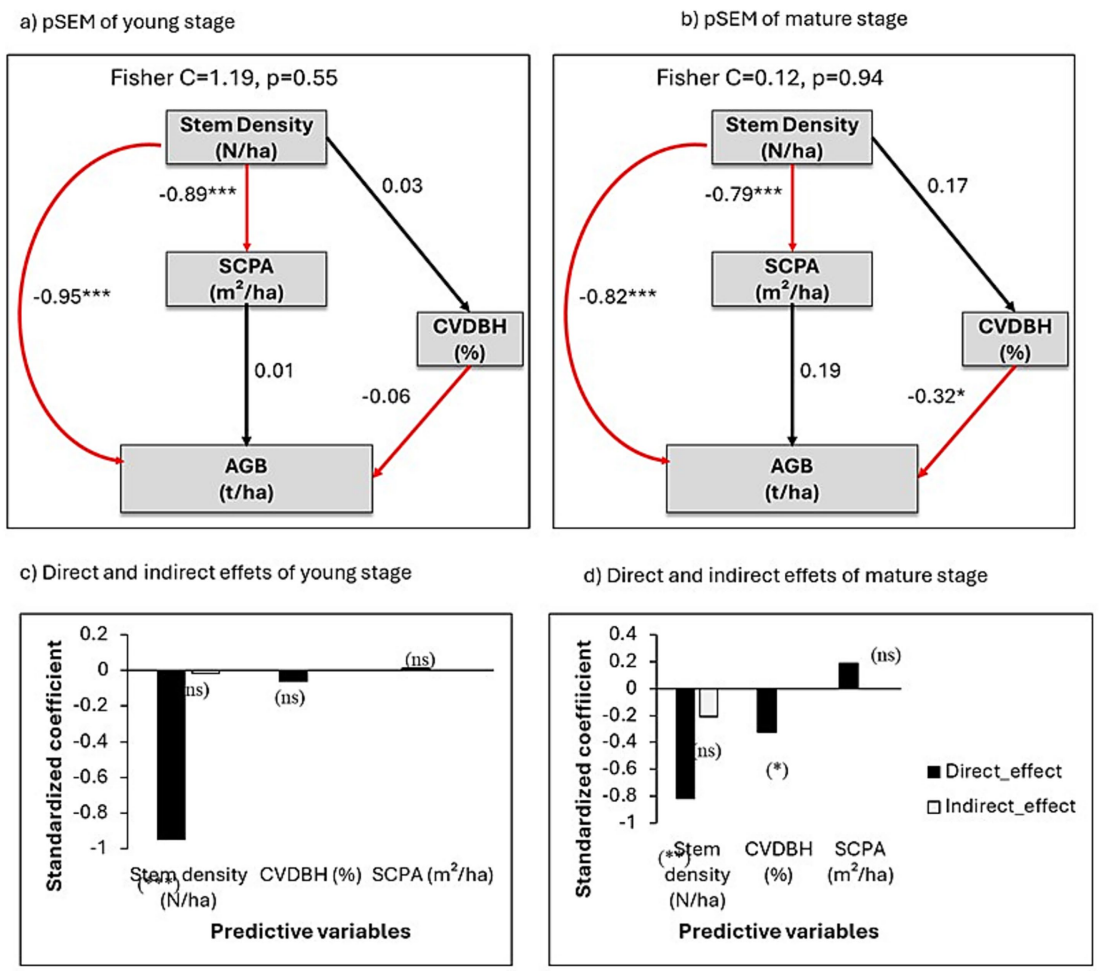

FIGURE 3
Structural equation model of the effects of stem density, SCPA and CVDBH on AGB in young stage of stand **(a)** and mature stage of stand **(b)**, and standardized coefficients of direct and indirect effects of structural variables on AGB in young stands **(c)** and mature stands **(d)**. AGB, above-ground biomass; CVDBH, coefficient variation of diameter at breast height; SCPA, summed crown projection area; *significant at 0.05; **significant at 0.01; ***significant at 0.001; ns, non-significant.

effect of CVDBH on AGB becomes significantly negative ($\beta = -0.32$; $p = 0.04$; Supplementary Table S1; Figure 3B), Underlining the increasing importance of horizontal stand structure with maturity. The indirect effect of stem density via CVDBH ($\beta = 0.17 \times -0.32 = -0.05$) is not significant. Combined, these indirect pathways yield a total indirect effect of −0.21 ($p = 0.42$), which is non-significant, representing approximately 27% of the direct effect magnitude (Figure 3D).

Effects of structural variables on AGB across all stages of development

Among the models tested (Supplementary Table S2), GAM5 achieved the lowest AIC (365.4), followed closely by GAM2 (AIC = 365.5, ΔAIC = 0.1). However, GAM2 model was selected as the final model based on parsimony (Zuur et al., 2009). While GAM5 included two tensor product interactions (stem density × SCPA and stem density × CVDBH), GAM2 achieved nearly identical fit with a simpler structure: one interaction (stem density × SCPA) and a univariate smooth term for CVDBH. Moreover, all smooth terms in GAM2 were statistically significant ($p < 0.05$), whereas the additional interaction in GAM5 was non-significant ($p = 0.071$). Given the negligible difference in AIC and the lack of significant improvement, GAM2 model was retained as the most parsimonious model. The interaction between stem density and SCPA has a significant non-linear effect on AGB ($F = 39.13$; $p < 2e\text{-}16$; Supplementary Table S3). The lowest AGB values (28.29 ± 13.67 t/ha on average) were observed in cases of high density (442.5 ± 34.51 stems/ha) coupled with limited SCPA (1732.73 ± 269.79 m²/ha), whereas the highest AGB values (104.63 ± 47.72 t/ha) were observed in stands with low stem density (255 ± 32.04 stems/ha) and extensive SCPA (5000.91 ± 1,070) (Figures 4A,B). Also, CVDBH showed a significant effect on AGB ($F = 4.59$; $p = 0.04$; Supplementary Table S3). Young stands with minimal diameter variation (1.54 ± 0.49%) showed low AGB, while mature stands with greater heterogeneity (22.61 ± 7.22%) achieved higher AGB (Figure 4C). However, AGB gains plateaued beyond 15% CVDBH, and within mature stands, CVDBH values above 20% were associated with reduced AGB (Figure 4C).

Discussion

Structural characteristics across developmental stages of *Isoberlinia* woodlands

The results of this study highlight marked structural differences between the developmental stages of *Isoberlinia* woodland in the Sudano-Guinean zone of Benin. The significant decrease in stem

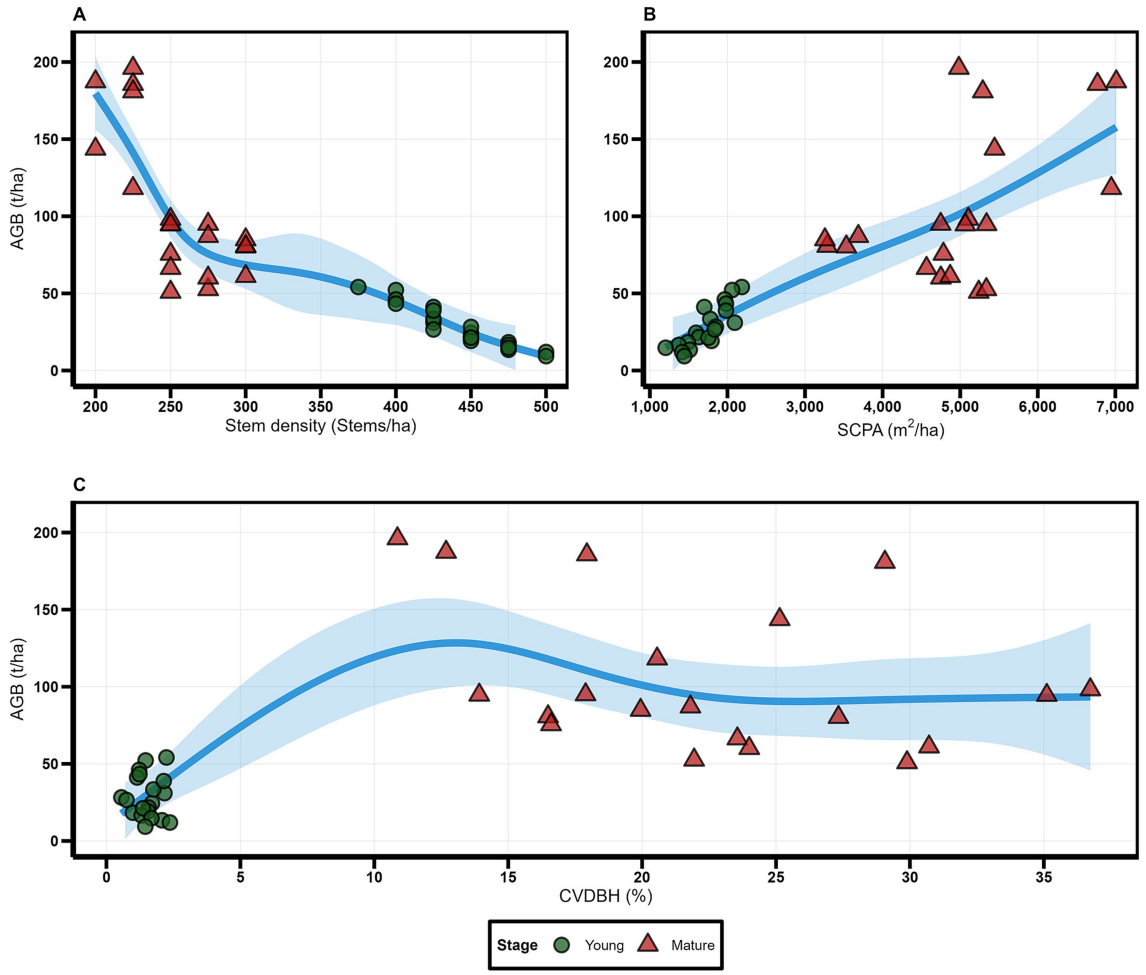

FIGURE 4
Nonlinear relationships between AGB and stem density **(A)**, SCPA **(B)**, and CVDBH **(C)** across all stand stages, associated with the GAM2 model (Supplementary Tables S2, S3). AGB, above-ground biomass; CVDBH, coefficient variation of diameter at breast height; SCPA, summed crown projection area.

density between young stands (442.50 ± 34.51 stems/ha) and mature stands (255 ± 32.04 stems/ha) primarily results from stem density-dependent mortality (Kouassi et al., 2021; Axer et al., 2022), where competition for limited resources (light, water, nutrients) progressively eliminates suppressed individuals.

The substantial increase in mean DBH between young (13.80 ± 3.76 cm) and mature stages (24.89 ± 6.91 cm) illustrates the progressive growth of surviving trees that benefit from increased resource access. This dimensional evolution in terms of both diameter and height explains the considerable increase in AGB, which rises from 28.29 ± 13.67 t/ha in young stands to 104.63 ± 47.72 t/ha in mature stands. Nam et al. (2018) observed similar patterns in other tropical forests in Vietnam, highlighting the universality of this relationship between structure and AGB. SCPA values also follow this developmental progression, increasing from 1732.73 ± 269.79 in young stands to 5000.91 ± 1,070 in mature stands, reflecting SCPA expansion with tree maturation and increased structural heterogeneity the latter allowing trees of different heights to expand their crowns laterally.

Effects of stem density, CVDBH and forest SCPA on AGB

In young stands, AGB is mainly controlled by stem density, which has a direct negative effect, consistent with hypothesis H1. This result can be explained by intense stem density-dependent competition typical of early stages of forest development, where individuals compete strongly for limited resources such as light, water, and nutrients (Franklin et al., 2002; Poorter et al., 2015; Ali, 2019). In the case of *Isoberlinia* spp., this dynamic is reinforced by vegetative regeneration through root suckering, which creates dense spatial aggregates of young stems sharing the same root system (Dourma et al., 2009; Bellefontaine et al., 2015). Although this mode of regeneration allows for rapid colonization of space, it increases intraspecific competition and limits individual growth, resulting in low AGB at the stand level. This negative relationship between stem density and AGB in young stages has been documented in different forest types. In Himalayan forests, Sharma et al. (2008) demonstrated that high densities intensify intraspecific competition for light, water, and nutrients, thereby limiting individual growth and stand level AGB. Similar patterns have been observed in temperate forests (Franklin et al., 2002; Ullah et al., 2021) and tropical forests (Poorter et al., 2015). However, the competitive mechanisms in *Isoberlinia* woodlands are expected to differ fundamentally from those in closed-canopy forests. Unlike closed forests where high stem density triggers stand-level self-thinning through light competition (Weiner, 1990; Pretzsch, 2014), *Isoberlinia* woodlands maintain open canopy structure with coverage rarely exceeding 25–30%, as indicated by our SCPA values below 3.000 m^2/ha in most stands. In these open conditions, light is abundant and competition

shifts primarily to belowground water and nutrients, especially during the prolonged dry season (Sankaran et al., 2005; February et al., 2013). This shift is compounded by the clonal regeneration strategy characteristic of *Isoberlinia* spp. Vegetative regeneration by root suckering produces densely aggregated clusters, with locally high stem densities that often exceed 1,000 stems per hectare, despite relatively low stand-level densities (Bellefontaine et al., 2015). Within these clusters, intense competition leads to early differentiation between dominant and suppressed stems, with selective mortality reaching 40% within five years (Dourma et al., 2012; Sanon et al., 2019). The shared root system plays a paradoxical role. Although theoretically facilitating resource sharing, stems originating from the same root system show highly variable growth rates, suggesting preferential allocation of resources to certain shoots at the expense of others (Dourma et al., 2012; Chidumayo, 2013, 2017). Simultaneously, spatial clustering creates localized shading that reduces individual photosynthetic efficiency despite the overall open canopy (Ryan and Yoder, 1997). This dual competitive regime characterized by intense belowground competition for water within clusters combined with paradoxical resource competition among root-connected stems explains the negative stem density-AGB relationship in our young stands. Unlike in closed forests, where there is stand-level light competition, the mechanisms primarily reflect localized belowground competition within regeneration clusters.

Interestingly, although stem density significantly reduces SCPA in young stands ($\beta = -0.89$, $p < 0.001$), this did not translate into a significant indirect effect on AGB (indirect effect = −0.009, $p > 0.05$). These results provide only partial support for hypothesis H2, as the negative relationship between stem density and SCPA exists but does not significantly influence AGB. This SCPA-AGB relationship suggests that light is not the primary limiting resource in these water-limited open woodlands when canopy coverage remains below 30%. In systems where water rather than light constrains productivity, reductions in SCPA caused by high stem density have limited consequences for AGB accumulation, as the capacity to intercept light exceeds the amount that can be converted into AGB given water constraints.

In mature stands, stem density continues to negatively affect AGB even as mean stem density declines from 442.5 to 255 stems/ha. This persistent effect, which further confirms hypothesis H1 across developmental stages, reflects continued localized competition within clonal regeneration clusters (Dourma et al., 2012). By contrast, Ullah et al. (2021) found that stem density had a positive effect on AGB through enhanced SCPA packing and efficient light capture in mixed-species stands. Similarly, Nam et al. (2018) reported that high stem density promoted AGB through optimized species composition and SCPA space utilization in logged evergreen forests of Vietnam. Both studies examined closed-canopy, multi-species forests where light was the primary limiting resource and niche complementarity could buffer competitive effects. Our contrasting results can be explained by the monodominant nature of *Isoberlinia* stands. In monospecific forests, the absence of interspecific complementarity eliminates the niche differentiation that would otherwise mitigate the effects of competition (Zhang and Chen, 2015). Under these conditions, AGB is primarily governed by intraspecific competitive dynamics and resource allocation patterns rather than structural diversity alone. According to the selection hypothesis (or mass-ratio effect), AGB is primarily determined by the functional characteristics of dominant individuals, regardless of overall stand diversity (Grime, 1998; Poorter et al., 2015). Within this framework, high diameter variation in monospecific stands reflects asymmetric competition, whereby dominant individuals monopolize resources at the expense of suppressed individuals (Abbasi, 2025). This leads to suboptimal resource utilization at the stand level. Consequently, stands with lower stem density but composed of larger, more productive individuals may accumulate greater total AGB than dense stands with numerous small individuals competing for the same resources. The relative importance of these competitive processes varies according to the developmental stage of the stand, environmental conditions and species-specific regeneration strategies (Ullah et al., 2021).

In mature stands, horizontal structural heterogeneity (CVDBH), also has a significant negative effect on AGB. This finding supports hypothesis H3, which predicted such a negative effect particularly in mature stands. High diameter variability reflects the coexistence of trees from different cohorts with contrasting developmental stages (Gadow et al., 2012), which could reduce to stand AGB in the mature phase for several reasons. Size-asymmetric competition creates a competitive hierarchy in which larger trees monopolize resources, particularly light and nutrients, at the expense of smaller trees (Binkley et al., 2010; Pretzsch and Biber, 2016). This disproportionate capture of resources slows the growth of small stems without proportionally benefiting large ones, thereby reducing overall stand productivity (Coates et al., 2009; Forrester and Albrecht, 2014). Additionally, high diameter heterogeneity may reflect poorly synchronized regeneration phases resulting from past disturbances (e.g., harvesting, fire, windthrow), leading to the coexistence of younger cohorts with limited contribution to total stand biomass (Iida et al., 2011).

SCPA has a positive but insignificant influence on AGB in mature stands. These results do not provide statistical support for hypothesis H4, which predicted a positive effect of SCPA on AGB. This could be due to a functional SCPA closure threshold beyond which increased light interception no longer leads to a proportional increase in AGB. In Sudano-Guinean ecosystems, this functional saturation may be reinforced by edaphic and water constraints limiting the response of primary production to increases in leaf area (Sankaran et al., 2005; Chu et al., 2019).

Effects of structural variables on AGB at all stages of development

When the patterns are considered across all development stages, it appears that the effect of stem density on AGB depends heavily on the level of SCPA development, while diameter heterogeneity plays a secondary but significant role.

The interaction between stem density and SCPA primarily reflects a developmental stage effect, with young dense stands characterized by low SCPA and mature stands with lower stem density characterized by extensive SCPA. This pattern also illustrates how SCPA development modulates the effects of stem density on AGB. In young stands with limited SCPA expansion, high stem density can intensify competition for resources, reducing individual growth and cumulative AGB (Forrester et al., 2017). In contrast, the extensive SCPA of mature stands allows for more efficient utilization of airspace and resources (Jucker et al., 2015). However, the relatively open structure of these *Isoberlinia* woodlands suggests that there is moderate light competition compared to closed-SCPA. Our results reveal a threshold effect for CVDBH, with AGB peaking at approximately 15% before declining at higher values. This nonlinear pattern suggests the presence of competing mechanisms operating at different developmental stages (Figure 3). In young stands,

CVDBH is low and exhibits limited variability, explaining the absence of significant effects at this stage. In contrast, mature stands display higher and more variable CVDBH, with a threshold dependent negative effect on AGB. While low-to-moderate levels of heterogeneity (CVDBH <15%) might enhance the efficiency with which resources are used through vertical stratification and niche differentiation (Jucker et al., 2015), higher heterogeneity (>20%) might be associated with asymmetric size distributions, where few large individuals trees reduce the functioning of smaller individuals (Getzin et al., 2008).

Study limitations

Several limitations of this study need to be considered. The sample size (40 plots: 20 young and 20 mature stands) meets the requirements for piecewise structural equation modeling but remains relatively small for capturing the full variability of *Isoberlinia* woodlands across West Africa. Our reliance on temporary rather than permanent plots prevents us from directly accounting for temporal changes and limits our capacity to confirm causal links between stand structure and AGB. Repeated measurements over time would be needed to validate the mechanisms identified here. Finally, as we did not measure stand age, we cannot completely rule out some age effect behind stem density within a given stand stage; however, mean stand height, which can be considered as a rough indicator of stand age, was not correlated with stem density within neither young nor mature stands.

Implications for sustainable management

These results have important practical implications for the management of *Isoberlinia* woodland. In young stands, we suggest that silvicultural interventions should be concerned with stem density regulation for individual growth optimization. These management recommendations align with recent findings on the importance of stand structure regulation for optimizing AGB allocation during forest development (Cudjoe et al., 2025). However, it should be noted that, while the reduction in stem density achieved by thinning results in an increase in the growth of individual trees, the resulting standing AGB at the stand level is likely to be less than that of an unthinned stand of similar age immediately following the intervention. In the longer term, however, thinned stands could achieve higher AGB than unthinned ones, as the remaining trees benefit from accelerated individual growth and better access to resources, resulting in larger individuals and, ultimately, potentially higher total AGB. This is consistent with the findings of Sokpon et al. (2006), who recommend early thinning to reduce competition. For mature stands, our results suggest that management should focus on maintaining a moderate structural heterogeneity (CVDBH) around 15%, while avoiding overly uniform (CVDBH <10%) or excessively heterogeneous (CVDBH >20%) distributions. It is important to ensure sufficient space for SCPA development. This adaptive approach, taking into account the stage of development, seems crucial to ensure the sustainability of these forest ecosystems.

Conclusion

This study reveals fundamental differences in the relationships between structure and biomass in water-limited, open-canopy *Isoberlinia* woodlands compared to the closed-canopy, light-limited forests in which most forest ecology theory has been developed. Stem density reduces aboveground biomass (AGB) consistently across all developmental stages. Importantly, stand canopy projection area (SCPA) shows no significant relationship with AGB, suggesting that light-mediated pathways central to productivity in closed forests are less functionally relevant when water is limiting and canopy coverage remains below 30%. Instead, structural heterogeneity (CVDBH) emerges as the key modulator of productivity in mature stands. It exhibits a threshold effect whereby AGB peaks at moderate heterogeneity (approximately 15%), but then declines beyond 20% probably as a result of size-asymmetric competition. These findings highlight the fact that forest management strategies optimised for closed-canopy systems cannot be directly applied to water-limited, open woodlands. The sustainable management of *Isoberlinia* woodland requires the regulation of stem density in young stands and the maintenance of moderate structural heterogeneity in mature stands, adapted to prioritize water over light limitation. These findings have broader implications for ecosystem service provision in West African dry forests. Accurate biomass estimation, informed by structural heterogeneity rather than canopy density alone, is essential for reliable carbon stock assessment under REDD+ and voluntary carbon market mechanisms. Furthermore, optimized stand management that balances density regulation and moderate structural heterogeneity can enhance the sustained provision of timber and non-timber forest products, including fuelwood, construction material, and medicinal plants, that underpin rural livelihoods across the region. Community-based management approaches integrating these structural guidelines could thus simultaneously contribute to carbon credit generation and income diversification for local communities.

Data availability statement

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

Author contributions

HO: Formal analysis, Writing – review & editing, Data curation, Writing – original draft, Methodology, Software, Conceptualization. EA: Methodology, Visualization, Conceptualization, Supervision, Validation, Writing – review & editing. QP: Supervision, Writing – review & editing, Formal analysis, Data curation, Software, Methodology, Conceptualization, Validation. SB: Data curation, Formal analysis, Validation, Methodology, Writing – review & editing, Software, Conceptualization, Supervision.

Funding

The author(s) declared that financial support was received for this work and/or its publication. The authors would like to thank the Académie de Recherche et d'Enseignement Supérieur (ARES) and the University of Parakou for awarding the first author a research grant to carry out this study.

Acknowledgments

The authors also acknowledge Bill Agassounon for his valuable contribution to the data collection in the field.

Conflict of interest

The author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Generative AI statement

The author(s) declared that Generative AI was not used in the creation of this manuscript.

Any alternative text (alt text) provided alongside figures in this article has been generated by Frontiers with the support of artificial intelligence and reasonable efforts have been made to ensure accuracy, including review by the authors wherever possible. If you identify any issues, please contact us.

Publisher's note

All claims expressed in this article are solely those of the authors and do not necessarily represent those of their affiliated organizations, or those of the publisher, the editors and the reviewers. Any product that may be evaluated in this article, or claim that may be made by its manufacturer, is not guaranteed or endorsed by the publisher.

Supplementary material

The Supplementary material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/ffgc.2026.1800379/full#supplementary-material

References

Abbasi, E. (2025). Integrated thermocatalytic and photocatalytic valorization of *Hermetia illucens* biomass for renewable fuel and chemical production. *Cleaner Circular Bioeconomy* 12:100168, 1–9. doi: 10.1016/j.clcb.2025.100168

Abbasi, U. A., Gilani, H., Hussain, K., and Ali, A. (2023). Increasing stand stature weakens the positive effects of tree richness and structural imbalance on aboveground biomass in temperate forests: the stand stature hypothesis. *For. Ecol. Manag.* 539:121040, 1–8. doi: 10.1016/j.foreco.2023.121040

Adjahossou, S. G. C., Houéhanou, D. T., Toyi, M., Salako, V. K., Ahoyo, C. C., Lesse, P., et al. (2019). Dépendance socioculturelle des connaissances locales des usages de Isoberlinia spp. au Moyen-Bénin, Afrique de l'Ouest. *Bois Forets Des Tropiques* 339:33. doi: 10.19182/bft2019.339.a31702

Adomou, A. C. (2005). Vegetation patterns and environmental gradients in Benin: Implications for biogeography and conservation. Wageningen University ,Wageningen. Available online at: https://search.proquest.com/openview/6d220f1ecda2856491d92e086daa162b/1?pq-origsite=gscholar&cbl=44156 (Accessed March 21, 2024).

Ali, A. (2019). Forest stand structure and functioning: current knowledge and future challenges. *Ecol. Indic.* 98, 665–677. doi: 10.1016/j.ecolind.2018.11.017

Ali, A., Lin, S.-L., He, J.-K., Kong, F.-M., Yu, J.-H., and Jiang, H.-S. (2019). Climatic water availability is the main limiting factor of biotic attributes across large-scale elevational gradients in tropical forests. *Sci. Total Environ.* 647, 1211–1221. doi: 10.1016/j.scitotenv.2018.08.072

Assede, E. S., Adomou, A. C., and Sinsin, B. (2012). Secondary succession and factors determining change in soil condition from fallow to savannah in the Sudanian zone of Benin. *Phytocoenologia* 42, 181–189. doi: 10.1127/0340-269x/2012/0042-0506

Assédé, E. S. P., Azihou, A. F., Geldenhuys, C. J., Chirwa, P. W., and Biaou, S. S. H. (2020). Sudanian versus Zambezian woodlands of Africa: composition, ecology, biogeography and use. *Acta Oecol.* 107:103599. doi: 10.1016/j.actao.2020.103599

Axer, M., Kluckow, F., and Wagner, S. (2022). Evaluation of a restoration approach after one century–effects of admixed European beech on the natural regeneration potential and humus condition in spruce stands. *Front. Forests Global Change* 5:826186. doi: 10.3389/ffgc.2022.826186

Bellefontaine, R., Meunier, Q., Aboubacar, I., and Bouler, H. L. (2015). Multiplication végétative à faible coût au profit des paysans et éleveurs des zones tropicales et méditerranéennes. *VertigO*. doi: 10.4000/vertigo.16516

Biaou, S. S. H. (2009). Tree recruitment in West African dry woodlands: The interactive effects of climate, soil, fire and grazing. Wageningen University, Wageningen. Available online at: https://search.proquest.com/openview/f5dfddc94c8de26b327f32880ba7bdb2/1?pq-origsite=gscholar&cbl=2026366&diss=y (Accessed February 10, 2025).

Biaou, S. S. H., Holmgren, M., Sterck, F. J., and Mohren, G. M. J. (2011). Stress-driven changes in the strength of facilitation on tree seedling establishment in West African woodlands: seedling facilitation in West African woodlands. *Biotropica* 43, 23–30. doi: 10.1111/j.1744-7429.2010.00642.x

Binkley, D., Stape, J. L., Bauerle, W. L., and Ryan, M. G. (2010). Explaining growth of individual trees: light interception and efficiency of light use by Eucalyptus at four sites in Brazil. *For. Ecol. Manag.* 259, 1704–1713. doi: 10.1016/j.foreco.2009.05.037

Chidumayo, E. N. (2013). Forest degradation and recovery in a miombo woodland landscape in Zambia: 22 years of observations on permanent sample plots. *For. Ecol. Manag.* 291, 154–161. doi: 10.1016/j.foreco.2012.11.031

Chidumayo, E. N. (2017). Biotic interactions, climate and disturbance underlie the distribution of two *Julbernardia* tree species in miombo woodlands of Africa. *J. Trop. Ecol.* 33, 1–11. doi: 10.1017/S0266467416000584

Chidumayo, E. N., and Gumbo, D. J. (2010). *The dry forests and woodlands of Africa*. London, UK: Earthscan.

Chu, C., Lutz, J. A., Král, K., Vrška, T., Yin, X., Myers, J. A., et al. (2019). Direct and indirect effects of climate on richness drive the latitudinal diversity gradient in forest trees. *Ecol. Lett.* 22, 245–255. doi: 10.1111/ele.13175

Coates, K. D., Canham, C. D., and LePage, P. T. (2009). Above- versus below-ground competitive effects and responses of a guild of temperate tree species. *J. Ecol.* 97, 118–130. doi: 10.1111/j.1365-2745.2008.01458.x

Cudjoe, E., Bravo, F., Pretzsch, H., Bettinger, P., and Ruiz-Peinado, R. (2025). Competition in mixed scots pine and Pyrenean oak stands modifies allometry and partially affects biomass allocation during early stand development. *Ecol. Indic.* 176:113713. doi: 10.1016/j.ecolind.2025.113713

Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., et al. (2013). Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 36, 27–46. doi: 10.1111/j.1600-0587.2012.07348.x

Dourma, M., Batawila, K., Wala, K., Kokou, K., Guelly, K. A., Bellefontaine, R., et al. (2009). Régénération naturelle des peuplements à *Isoberlinia* spp. en zone soudanienne au Togo. *Acta Bot. Gallica* 156, 415–425. doi: 10.1080/12538078.2009.10516167

Dourma, M., Wala, K., Guelly, K. A., Bellefontaine, R., Deleporte, P., Akpavi, S., et al. (2012). Typology, structural characteristics and dynamics of fragile *Isoberlinia* spp. woodlands to support their management in Togo. *Bois et Forêts des Tropiques*, 313, 19–33.

February, E. C., Higgins, S. I., Bond, W. J., and Swemmer, L. (2013). Influence of competition and rainfall manipulation on the growth responses of savanna trees and grasses. *Ecology* 94, 1155–1164. doi: 10.1890/12-0540.1

Forrester, D. I., and Albrecht, A. T. (2014). Light absorption and light-use efficiency in mixtures of Abies alba and *Picea abies* along a productivity gradient. *For. Ecol. Manag.* 328, 94–102. doi: 10.1016/j.foreco.2014.05.026

Forrester, D. I., Benneter, A., Bouriaud, O., and Bauhus, J. (2017). Diversity and competition influence tree allometric relationships – developing functions for mixed-species forests. *J. Ecol.* 105, 761–774. doi: 10.1111/1365-2745.12704

Franklin, J. F., Spies, T. A., Van Pelt, R., Carey, A. B., Thornburgh, D. A., Berg, D. R., et al. (2002). Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *For. Ecol. Manag.* 155, 399–423. doi: 10.1016/s0378-1127(01)00575-8

Frost, P. (1996). The ecology of miombo woodlands. *Miombo Transit. Woodl. Welf. Afr.* 266, 11–57.

Gadow, K. V., Zhang, C. Y., Wehenkel, C., Pommerening, A., Corral-Rivas, J., Korol, M., et al. (2012). "Forest structure and diversity" in *Continuous cover forestry*. eds. T. Pukkala and K. Von Gadow (Dordrecht: Springer Netherlands), 29–83.

Ganamé, M., Bayen, P., Ouédraogo, I., Balima, L. H., and Thiombiano, A. (2021). Allometric models for improving aboveground biomass estimates in West African savanna ecosystems. *Trees Forests People* 4:100077. doi: 10.1016/j.tfp.2021.100077

Geldenhuys, C. J., Atsame-Edda, A., and Mugure, M. W. (2017). Facilitating the recovery of natural evergreen forests in South Africa via invader plant stands. *For. Ecosyst.* 4:21. doi: 10.1186/s40663-017-0108-9

Getzin, S., Wiegand, K., Schumacher, J., and Gougeon, F. A. (2008). Scale-dependent competition at the stand level assessed from crown areas. *For. Ecol. Manag.* 255, 2478–2485. doi: 10.1016/j.foreco.2008.01.007

Grace, J. B., Anderson, T. M., Seabloom, E. W., Borer, E. T., Adler, P. B., Harpole, W. S., et al. (2016). Integrative modelling reveals mechanisms linking productivity and plant species richness. *Nature* 529, 390–393. doi: 10.1038/nature16524

Grime, J. P. (1998). Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *J. Ecol.* 86, 902–910. doi: 10.1046/j.1365-2745.1998.00306.x

Gumbo, D. J., and Dumas-Johansen, M. (2021). The role of miombo woodlands in the three Rio conventions. *Clim. Dev.* 13, 107–114. doi: 10.1080/17565529.2020.1729686

Holdo, R. M. (2007). Elephants, fire, and frost can determine community structure and composition in kalahari woodlands. *Ecol. Appl.* 17, 558–568. doi: 10.1890/05-1990

Hountondji, Y.-C., Gaoué, O. G., Sokpon, N., and Ozer, P. (2013). Analyse écogéographique de la fragmentation du couvert végétal au nord Bénin: paramètres dendrométriques et phytoécologiques comme indicateurs in situ de la dégradation des peuplements ligneux. *Geo-Eco-Trop. Rev. Int. Géol. Géogr. Écol. Trop.* 37, 53–70.

Iida, Y., Kohyama, T. S., Kubo, T., Kassim, A. R., Poorter, L., Sterck, F., et al. (2011). Tree architecture and life-history strategies across 200 co-occurring tropical tree species. *Funct. Ecol.* 25, 1260–1268. doi: 10.1111/j.1365-2435.2011.01884.x

Jucker, T., Bouriaud, O., and Coomes, D. A. (2015). Crown plasticity enables trees to optimize canopy packing in mixed-species forests. *Funct. Ecol.* 29, 1078–1086. doi: 10.1111/1365-2435.12428

Kennedy, A. D., and Potgieter, A. L. F. (2003). Fire season affects size and architecture of *Colophospermum mopane* in southern African savannas. *Plant Ecol.* 167, 179–192. doi: 10.1023/a:1023964815201

Kouassi, J.-L., Gyau, A., Diby, L., Bene, Y., and Kouamé, C. (2021). Assessing land use and land cover change and farmers' perceptions of deforestation and land degradation in south-west Côte d'Ivoire, West Africa. *Land* 10:429. doi: 10.3390/land10040429

Lefcheck, J. S. (2016). piecewiseSEM: piecewise structural equation modelling in r for ecology, evolution, and systematics. *Methods Ecol. Evol.* 7, 573–579. doi: 10.1111/2041-210X.12512

Mensah, S., Noulèkoun, F., Salako, V. K., Lokossou, C. S. M. J., Akouété, P., Seifert, T., et al. (2023). Structural and taxonomic diversity predict above-ground biomass better than functional measures of maximum height in mixed-species forests. *Appl. Veg. Sci.* 26:e12732. doi: 10.1111/avsc.12732

Nam, V. T., Anten, N. P. R., and Van Kuijk, M. (2018). Biomass dynamics in a logged forest: the role of wood density. *J. Plant Res.* 131, 611–621. doi: 10.1007/s10265-018-1042-9

Pacala, S. W., Canham, C. D., Saponara, J., Silander, J. A., Kobe, R. K., and Ribbens, E. (1996). Forest models defined by field measurements: estimation, error analysis and dynamics. *Ecol. Monogr.* 66, 1–43. doi: 10.2307/2963479

Poorter, H., Jagodzinski, A. M., Ruiz-Peinado, R., Kuyah, S., Luo, Y., Oleksyn, J., et al. (2015). How does biomass distribution change with size and differ among species? An analysis for 1200 plant species from five continents. *New Phytol.* 208, 736–749. doi: 10.1111/nph.13571

Pretzsch, H. (2014). Canopy space filling and tree crown morphology in mixed-species stands compared with monocultures. *For. Ecol. Manag.* 327, 251–264. doi: 10.1016/j.foreco.2014.04.027

Pretzsch, H., and Biber, P. (2016). Tree species mixing can increase maximum stand density. *Can. J. For. Res.* 46, 1179–1193. doi: 10.1139/cjfr-2015-0413

R Core Team (2022). R: A language and environment for statistical computing. R Found. Stat. Comput. Available online at: https://www.R-project.org/ (Accessed December 24, 2025).

Rozak, A. H., Rutishauser, E., Raulund-Rasmussen, K., and Sist, P. (2018). The imprint of logging on tropical forest carbon stocks: a Bornean case-study. *For. Ecol. Manag.* 417, 154–166. doi: 10.1016/j.foreco.2018.03.007

Ryan, M. G., and Yoder, B. J. (1997). Hydraulic limits to tree height and tree growth. *Bioscience* 47, 235–242. doi: 10.2307/1313077

Sankaran, M., Hanan, N. P., Scholes, R. J., Ratnam, J., Augustine, D. J., Cade, B. S., et al. (2005). Determinants of woody cover in African savannas. *Nature* 438, 846–849. doi: 10.1038/nature04070

Sanon, Z., Yameogo, J. T., Rabiou, H., and Hien, M. (2019). Pression anthropique et dynamique des peuplements de *Isoberlinia doka* Craib et Stapf et *Isoberlinia tomentosa* (Harms) Craib et Stapf dans le domaine soudanien du Burkina Faso. *Int. J. Biol. Chem. Sci.* 13:911. doi: 10.4314/ijbcs.v13i2.27

Sharma, R. K., Sankhayan, P. L., and Hofstad, O. (2008). Forest biomass density, utilization and production dynamics in a western Himalayan watershed. *J. For. Res.* 19, 171–180. doi: 10.1007/s11676-008-0032-5

Silman, M. R. (2014). Functional megadiversity. *Proc. Natl. Acad. Sci.* 111, 5763–5764. doi: 10.1073/pnas.1402618111

Sinsin, B., Kampmann, D., Thiombiano, A., and Konaté, S. (2010). Atlas de la biodiversité de l'Afrique de l'Ouest. *Tome Benin Cotonou FrankfurtMain*. Available online at: http://www.goethe-university-frankfurt.de/50800968/CI_01_Cover_Preface_Introduction.pdf (Accessed February 10, 2025).

Sokpon, N., Biaou, S. H., Ouinsavi, C., and Hunhyet, O. (2006). Bases techniques pour une gestion durable des forêts claires du Nord-Bénin: rotation, diamètre minimal d'exploitabilité et régénération. *Bois For. Trop.* 287, 45–57.

Staver, A. C., Archibald, S., and Levin, S. A. (2011). The global extent and determinants of savanna and Forest as alternative biome states. *Science* 334, 230–232. doi: 10.1126/science.1210465

Ullah, F., Gilani, H., Sanaei, A., Hussain, K., and Ali, A. (2021). Stand structure determines aboveground biomass across temperate forest types and species mixture along a local-scale elevational gradient. *For. Ecol. Manag.* 486:118984. doi: 10.1016/j.foreco.2021.118984

Weiner, J. (1990). Asymmetric competition in plant populations. *Trends Ecol. Evol.* 5, 360–364. doi: 10.1016/0169-5347(90)90095-U

White, F. (1983). The vegetation of Africa. *Nat. Resour. Res.* 20, 1–356.

Zhang, Y., and Chen, H. Y. H. (2015). Individual size inequality links forest diversity and above-ground biomass. *J. Ecol.* 103, 1245–1252. doi: 10.1111/1365-2745.12425

Zida, D., Sawadogo, L., Tigabu, M., Tiveau, D., and Odén, P. C. (2007). Dynamics of sapling population in savanna woodlands of Burkina Faso subjected to grazing, early fire and selective tree cutting for a decade. *For. Ecol. Manag.* 243, 102–115. doi: 10.1016/j.foreco.2007.02.013

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., and Smith, G. M. (2009). "Mixed effects modelling for nested data" in *Mixed effects models and extensions in ecology with R* (New York, NY: Springer New York), 101–142.