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Beda Innocent Adji

adjibedainnocent@gmail.com

Université Jean Lorougnon Guédé

Research Article

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Beyond the large mother tree: a multi-approach modeling framework reveals the predominance role of site conditions on *Parkia biglobosa* seedling growth, with a maternal effect limited to germination

Beda Innocent Adji[1*]

[1]Jean Lorougnon Guédé University, Agroforestry Department, BP 150 Daloa, Côte d'Ivoire

Corresponding author : Beda Innocent Adji

Email : adjibedainnocent@gmail.com

ORCID : https://orcid.org/0000-0002-8423-1126

Abstract

Parkia biglobosa (Jacq.) R. Br. ex G. Don (Fabaceae), the néré or African locust bean, is a major agroforestry species of West Africa whose natural regeneration is declining sharply in Sudano-Sahelian agroforestry parklands. A previous study, conducted across three contrasting environments, had qualitatively suggested that seed trees of larger diameter produce heavier seeds generating more vigorous seedlings, without formally testing this causal chain. The present study fills this gap by employing six complementary analytical approaches (continuous regression, linear mixed models with a site × seed-tree interaction, seed-mass mediation analysis with Sobel test, non-linear growth modelling of « height and diameter », between-site phenotypic plasticity, and multi-predictor allometric equations), across two contrasting bioclimatic sites in Côte d'Ivoire (dry zone: Korhogo; humid zone: Daloa) and six seed-tree categories. Site exerts a decisive influence on growth at all ages (4, 6, 12 and 24 months) and on germination (73.3% at Korhogo versus 62.8% at Daloa; χ^2=4.14; p=0.042). No direct effect of seed-tree DBH is detected on growth (continuous regression and mixed model, p>0.20). By contrast, the mediation analysis statistically confirms, for the first time in this species, the causal chain previously suggested: seed-tree DBH is associated with seed mass (r=0.75; p=0.090), which is itself strongly associated with germination rate (r=0.90; p=0.014), with a significant overall indirect effect (Sobel test, z=1.97; p=0.049). This indirect effect does not, however, propagate through to final growth (p=0.39). The exponential growth model provides the best fit for height and diameter at both sites, and two-predictor allometric equations explain 91.5% of biomass variance compared with 85.6% for the single-predictor model. *Parkia biglobosa* thus stands out through the rigorous statistical confirmation of an indirect maternal effect, limited however to the germination stage. A finding that calls for prioritising provenance diversity in conservation seed orchards over the selection of the largest seed trees.

Keywords: *Parkia biglobosa*, forest restoration, mediation analysis, phenotypic plasticity, allometry, Côte d'Ivoire

Introduction

African tropical forests and agroforestry parklands, exceptional reservoirs of plant genetic diversity, are eroding under the combined effect of deforestation, unsustainable agricultural expansion, and climate change (Choat et al., 2012; De Wasseige C et al., 2012; Sosef et al., 2017). In Côte d'Ivoire, this dynamic threatens local woody genetic resources (Adji et al., 2023), with particularly marked consequences for species of Sudano-Sahelian agroforestry parklands (Hérault et al., 2020; Louppe and Ouattara, 1996; Mapongmetsem et al., 2011). *Parkia biglobosa* (Jacq.) R. Br. ex G. Don (Fabaceae), commonly known as néré or African locust bean, illustrates this issue with particular acuity (Kew Science, 2026). A major agroforestry species of West Africa, valued for its fruit (pulp and seeds fermented into soumbala, a highly prized condiment), its timber, its pharmacopoeia, and its central role in Sudano-Sahelian parkland systems (Houndonougbo et al., 2020). Néré further shows a strong

ethnobotanical value that differs across sociocultural groups, with some communities in northern Benin making simultaneous food, medicinal, and ritual use of the species, which intensifies harvesting pressure on natural stands (Koura et al., 2011). Despite this major socio-economic importance, néré suffers from a worrying decline in its natural regeneration. Ræbild et al. (2012), in Burkina Faso, measured extremely low seedling densities (11 to 24 seedlings per hectare) that were declining over several consecutive years in agroforestry parklands, raising the question of the factors limiting seedling establishment despite abundant seed production. Adji et al. (2021), using a design comparing three contrasting environments (Korhogo, Daloa, and a controlled greenhouse in Montpellier), suggested that Parkia biglobosa seed trees of larger diameter produce heavier seeds, themselves associated with more vigorous seedlings. This was a qualitative observation based on the descriptive comparison of the best-performing seed trees, without a formal statistical test of the causal chain DBH → seed mass → germination → growth. The same authors further showed, by analysis of variance, that seed trees had no overall influence on any germination or development parameter once the three sites were combined (P>0.05), whereas the planting site significantly influenced all of these parameters (P<0.05). This contrast (absence of a direct seed-tree effect, but the suggestion of an indirect effect never formally tested) constitutes the central question addressed by the present study. In addition, work on the genetic variability of the species (Bouda et al., 2013; Ouedraogo et al., 2012; Teklehaimanot et al., 1998) has documented differentiation among provenances at a broad geographic scale. Ouedraogo et al. (2012), in a multi-provenance trial comparing 25 néré populations from across the Sudano-Sahelian gradient at two sites in Burkina Faso, demonstrated substantial genetic differentiation: survival rate varied from 35% to 61% depending on the site, and height growth differed strongly according to provenance. This work, although informative on genetic structuring at a broad geographic scale, did not isolate the effect of individual seed-tree size within a single local population (the spatial scale specifically targeted by the present study).

These results, although convergent, remain incomplete and methodologically limited. They call for a study simultaneously testing, within a single experimental design and using statistical tools of adequate power, the effect of individual seed-tree dendrometric characteristics and that of the planting site. The present study formulates three research questions: (i) does the planting site influence the germination and juvenile growth of *Parkia biglobosa*? (ii) do individual seed-tree dendrometric characteristics exert a direct or indirect effect (via seed mass) on the performance of their offspring? and (iii) is this effect, or its absence, consistent with the pattern reported by Adji et al. (2021), or does it change with seedling age? Three hypotheses are tested: H1, the site has a significant effect on germination and growth; H2, individual seed-tree characteristics have no direct effect on growth; H3, an indirect seed-tree effect via seed mass is expected, and must be formally tested through a mediation analysis with Sobel test. Six complementary analytical approaches are used to test these hypotheses: continuous regression, linear mixed models with a site × seed-tree interaction, mediation analysis, non-linear modelling of growth trajectories, between-site phenotypic plasticity indices, and multi-predictor allometric equations compared by AIC (Akaike, 1974). By clarifying this determinism, this study aims to provide managers of conservation seed orchards and agroforestry programmes with a directly applicable scientific basis: should limited efforts be focused on selecting large seed trees, or on the judicious choice of planting site?

Materials and methods

Study sites

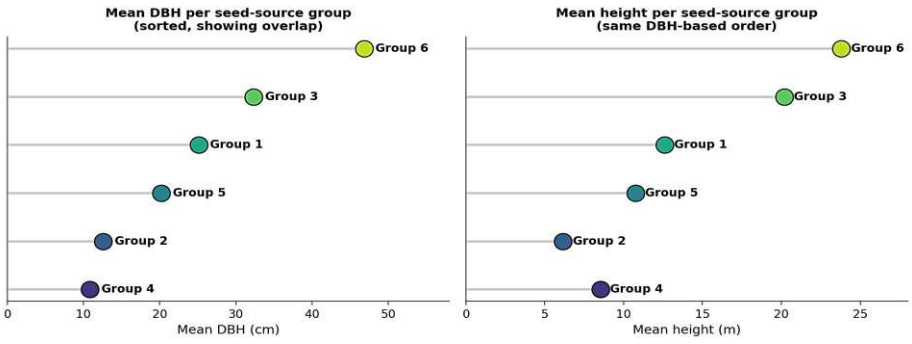
The study was conducted between May 2019 and July 2025, with several repetitions, in two experimental nurseries in Côte d'Ivoire, selected for their marked bioclimatic contrast along a north-south climatic gradient. The Diabaté Kmonon forestry research station (9°57'0.556" N; 5°54'2.889" W) near Korhogo (northern Côte d'Ivoire) is fairly representative of the Sudanian region. It lies between 360 and 390 m in altitude. Covering 100 ha, it is dominated by an outcropping granitic dome surrounded by shallow gravelly soils and, further out, deep gravelly soils with a heavy texture (clay-sandy) to sandy loam on the lower slopes. Soil pH is close to 6; the soils are poor in organic matter (former cultivated land), strongly desaturated, poor in calcium, magnesium, potassium and phosphorus, and bordering on boron deficiency. The climate is tropical, with a rainy season (April to October) and a dry season. Mean annual evapotranspiration is 1,764 mm and mean annual rainfall is 1,216 mm (range 140–1494 mm). Atmospheric humidity is high from April to October (above 70%). Annual sunshine duration is 2,270 h and mean annual temperature ranges from 26.6 to 35.7 °C. The climate has become globally drier over the past 30 years and mean temperatures have risen (+0.09 °C/decade for the hottest days), linked to local land-use change and global climate change (Hérault et al., 2020; Louppe and Ouattara, 1996). The natural vegetation is open forest

(with species such as *Isoberlinia doka*, *Afzelia africana*, *Anogeissus leïocarpa*, *Terminalia spp*.) and dense dry forest (of which sacred forests are the only remaining relics). The station's vegetation has been shaped by numerous parklands featuring *Vitellaria paradoxa* (shea) and *Parkia biglobosa* (néré). The station site has been under strict protection since 1988. The Jean Lorougnon Guédé University in Daloa (6°9'6.363" N; 6°43'8.1157" W), in the west-central part of the country, is representative of the sub-equatorial dense humid forest zone, with rainfall of 1000 to 1900 mm/year, temperatures of 21 to 34 °C, and deep, acidic ferralitic soils, desaturated in exchangeable bases but rich in organic matter (Adji et al., 2023; Akaffou et al., 2021). This pedoclimatic contrast makes it possible to test the site effect independently of the origin of the plant material, which is identical at both sites.

Study species and plant material

Parkia biglobosa is a tree that can reach 20 m in height, exceptionally 30 m, with a broad, spreading, umbrella-shaped crown, characteristic of Sudano-Sahelian agroforestry parklands (Orwa, C et al., 2009). Les graines ont été récoltées sous 120 arbres semenciers, avec plusieurs campagnes de récolte (mai et juin 2019 ; avril et mai 2023), dans quatre localités disposées le long d'un gradient bioclimatique en Côte d'Ivoire : Katiola (5°7'35,814" W ; 8°13'53,94" N), Niakara (5°18'40,73544" W ; 8°40'47,97912" N), Korhogo (5°36'12,39612" W ; 9°33'24,68988" N) et Sinématiali (5°22'59,999" W ; 9°34'59,999" N). Seeds were collected from 120 seed trees, over several harvest campaigns (May and June 2019; April and May 2023), in four localities arranged along a bioclimatic gradient in Côte d'Ivoire: Katiola (5°7'35.814" W; 8°13'53.94" N), Niakara (5°18'40.73544" W; 8°40'47.97912" N), Korhogo (5°36'12.39612" W; 9°33'24.68988" N) and Sinématiali (5°22'59.999" W; 9°34'59.999" N). Seed trees were grouped into six distinct categories according to their dendrometric size. Six reference trees were selected at the CNRA forestry research station in Korhogo to represent a gradient of contrasting dendrometric characteristics (diameter at breast height and total height), and 19 additional seed trees with characteristics close to the reference tree of each group were then sought across all four provenance localities, forming six groups of 20 seed trees (Table 1). Seed trees from the same locality were approximately 150 m apart from one another within that locality.

The mean DBH and mean height of each group, calculated across the 20 seed trees, range respectively from 10.8 to 46.8 cm and from 6.2 to 23.8 m (Fig. 1). It should be noted that this dendrometric gradient is continuous rather than categorical, which retrospectively justifies the use, in the analyses presented, of continuous regression and mixed models treating DBH as a real variable rather than a simple categorical comparison. The age of the reference tree in each group, by contrast, was estimated through oral surveys of rural communities and technicians at the CNRA forestry research station. This information is therefore available only for this single reference tree, not for the other 19 seed trees in the group. Diameter was measured with a forestry tape and height was estimated using the lumberjack's eye method. The plant material used is the property of rural populations; authorisation to use it for this study was given orally by the orchard owners.



This continuous gradient motivates the use of continuous regression rather than categorical comparison

Fig. 1 Dendrometric gradient (mean DBH and height) among the six seed-tree groups of *Parkia biglobosa*, sorted by increasing DBH.

Table 1 Dendrometric characteristics of the six seed-tree groups of *Parkia biglobosa*

Seed-tree group	[a]DBH mean (cm)	[a]H mean (m)	[b]Reference tree age (Years)	GPS coordinates of reference tree		Number of seed trees	Seed mass (g)		
				Longitude	Latitude		Min	Max	Mean
1	25.12	12.6	20	-5.54872 W	9.56728 N	20	0.17	0.24	0.26 ± 0.04 **a**
2	12.56	6.17	14	-5.54763 W	9.56644 N	20	0.09	0.28	0.21 ± 0.04 **b**
3	32.34	20.18	20	-5.55056 W	9.56873 N	20	0.17	0.27	0.23 ± 0.02 **ab**
4	10.83	8.54	12	-5.54908 W	9.56742 N	20	0.14	0.33	0.20 ± 0.05 **b**
5	20.21	10.77	20	-5.55097 W	9.5687 N	20	0.11	0.27	0.19 ± 0.02 **b**
6	46.83	23.8	20	-5.55094 W	9.55686 N	20	0.21	0.31	0.26 ± 0.02 **a**
Pr > F									**0.003**

Mean DBH = Mean diameter at breast height of the tree groups in centimetres; **Mean H** = Mean height of the tree groups in metres; **W** = West; **N** = North; **Min** = Minimum; **Max** = Maximum. [a]Mean calculated across the 20 seed trees of the group (diameter measured with a forestry tape; height estimated using the lumberjack's eye method). [b]Age of the reference tree used to define each group (not a mean of the 20 seed trees). Since DBH and height served as the criteria for constituting the groups, no inter-group statistical test was applied to them; only seed mass (the outcome variable) was tested by ANOVA (values sharing the same letter: no significant difference, $p<0.05$, $Pr>F=0.003$).

Seedlings and plants derived from the germination of seeds from the six seed-tree categories were monitored at different ages (4 months, 6 months, 1 year, 2 years, 5 years and 7 years). Seeds intended for germination and growth trials were extracted manually, sorted by flotation, and air-dried until moisture stabilised (4.5-5%), following the ISTA (2009). The present study specifically uses germination and growth data collected at 4, 6, 12 and 24 months at the two contrasting sites of Korhogo and Daloa, constituting a subset of the broader experimental design described above; monitoring at 5 and 7 years, as well as the three other seed-collection localities (Katiola, Niakara and Sinématiali), are not covered by the analyses presented here (no provenance test).

Experimental design

Seeds from each seed-tree group were divided into two lots destined respectively for Korhogo and Daloa. After soaking in tap water for one day (24 hours) to break seed-coat dormancy, seeds were sown at a depth of 1.5-2 cm in polyethylene bags (20 × 10 cm) filled with local potting soil, at a rate of two seeds per bag, arranged in a block subdivided into six sub-blocks representing each seed-tree group. Each sub-block, containing 60 bags, was labelled with the serial number of the seed-tree group, i.e. 2 seeds × 60 bags × 6 groups × 2 sites = 1440 seeds for the trial. Seeds were collected and sown in subsequent years as experimental repetition and successive replacement. A phytosanitary treatment (granular FURADAN against rodents, DECIS against larval attacks) was applied, and maintenance consisted of daily watering and manual weeding.

Germination monitoring

Germination, defined by the appearance of the hypocotyl at the substrate surface, was monitored daily (cumulative kinetics over 60 days) at each site, allowing a cumulative germination model to be fitted and five classical parameters to be calculated (lag time, delay, rate, duration and germination percentage), following the definitions of Adji et al. (2023 ; 2021).

Growth and biomass monitoring

After germination, 30 vigorous seedlings were randomly selected per seed-tree group and per site for non-destructive growth monitoring at 6, 12 and 24 months: total height (from collar to apex), collar diameter, number and dimensions of leaves, root length and diameter, measured using a graduated ruler, electronic callipers and ImageJ software for leaf area. A subsample of plants was harvested at the same ages for destructive biomass

measurement (total, foliar, stem and root fresh and dry mass), after oven-drying (70 °C, 72 h) and weighing to the nearest 0.001 g, allowing allometric equations to be established.

Data quality control

A systematic consistency check revealed an anomaly in the 12-month biomass measurement file: mean total dry biomass at this age was, at both sites, lower than that measured at 6 months. This represents a growth regression that is physically impossible, indicating a likely systematic error in this specific file. Height and diameter data at 12 months, unaffected by this anomaly, were retained; only biomass variables at this age were excluded from the analyses. This anomaly, specific to the 12-month biomass measurement campaign, could be due to a balance calibration issue or a data-entry error occurring on that specific occasion. Detected outliers were treated as missing data rather than arbitrarily corrected. This step is presented here in the interest of reproducibility and scientific transparency.

Analytical strategy

Rather than comparing seed-tree categories using classical analysis of variance, six complementary statistical approaches were used to maximise the power to detect any seed-tree effect and to clearly distinguish it from the site effect:

- *Continuous regression*

Rather than comparing seed-tree groups against one another, as if tree size were a fixed category, we directly tested whether the actual diameter (DBH) and height of the seed tree can predict the performance of its offspring (much as one would test whether parents' height predicts that of their children, by plotting a scatter plot and fitting a line through it). Each growth parameter was regressed on DBH and then on seed-tree height, separately at each age, by simple linear regression. For each growth parameter Y (height, collar diameter, total biomass) and at each measurement age, a simple linear regression model was fitted separately on the actual DBH and height of the original seed tree, rather than on a categorical group variable:

$$Y = \beta_0 + \beta_1 \cdot X_semencier + \varepsilon \quad (1)$$

Where Y is the growth parameter, X_seed-tree is the seed tree's DBH or height, and β_1 is the tested coefficient (fitted by ordinary least squares, H0: $\beta_1 = 0$).

- *Linear mixed models*

Seedlings from the same seed tree are not entirely independent of one another: they share a common origin, much like siblings within the same family. The mixed model corrects for this by treating each seed tree as a « family » whose own variability is estimated, while simultaneously testing the effect of DBH, site, and their interaction (is the effect of DBH different at Daloa and Korhogo?) on growth:

$$Y_ij = \beta_0 + \beta_1 \cdot DBH_i + \beta_2 \cdot Site_j + \beta_3 \cdot (DBH_i \times Site_j) + \beta_4 \cdot \hat{A}ge + u_i + \varepsilon_ij \quad (2)$$

where *Y_ij* is the observed value for the individual from seed tree *i* at site *j*. *u_i* is the effect specific to seed tree *i* (random effect) and *ε_ij* is the individual residual. β_1 tests the direct effect of DBH; β_2 tests the main effect of site; β_3 tests the interaction between DBH and site; β_4 tests the effect of age. Models were fitted by restricted maximum likelihood (REML, Bates et al., 2015), using the lme4/lmerTest packages (*R*). For biomass, the response variable was log-transformed « log(total dry mass) » to stabilise variance, as the raw distribution was strongly right-skewed.

- *Mediation analysis and Sobel test*

Even if seed-tree DBH has no direct effect on the growth of its offspring, it could have a hidden, indirect effect through an intermediate step: a large tree might produce heavier seeds, and these heavier seeds might in turn germinate better and produce more vigorous seedlings. This pathway (DBH → seed mass → germination → growth) was tested at the level of the six seed-tree groups through three successive sequential regressions, each testing one link in the chain (Baron and Kenny, 1986) :

Path *a*: $M = a_0 + a \cdot X + \varepsilon_1$ (3a) « seed mass (*M*) regressed on seed-tree DBH (*X*) » ;

Path *b*: $G = b_0 + b \cdot M + \varepsilon_2$ (3b) « germination rate (*G*) regressed on seed mass (*M*) » ;

Path *c*: $Cr = c_0 + c \cdot G + \varepsilon_3$ (3c) « mean growth (*Cr*) regressed on germination rate (*G*) » ;

Total effect: $Cr = c'_0 + c' \cdot X + \varepsilon_4$ « growth regressed directly on seed-tree DBH, with no mediator ». The indirect effect of *X* on *G* via *M* is estimated by the product of the coefficients ($a \times b$) and its significance tested by the Sobel test:

$z = (a \cdot b) / \sqrt{(b^2 \cdot SE_a^2 + a^2 \cdot SE_b^2)}$ (4)

where *SE_a* and *SE_b* are the standard errors of coefficients *a* and *b* respectively. The *z* statistic is compared against the standard normal distribution (two-tailed test, $\alpha = 0.05$ threshold).

- *Non-linear modelling of growth trajectories*

Plants do not necessarily grow at a constant rate over time. Three curve shapes (linear, power law, exponential) were compared, separately for height and diameter, and for each site, using Akaike's Information Criterion (*AIC*), which rewards the best trade-off between goodness of fit and simplicity:

Linear: $H = a + b \cdot t$ (5a)

Power law: $H = a \cdot t^{\wedge} b$ (5b)

Exponential: $H = a \cdot exp(b \cdot t)$ (5c)

The three models were compared using Akaike's Information Criterion, calculated from the residual sum of squares (*RSS*) on a common scale (raw, untransformed scale) to ensure a fair comparison between models:

$AIC = n \cdot ln(RSS/n) + 2k$ (6)

where n is the number of observations and k is the number of model parameters ($k = 2$ for the three models tested). The retained model is the one with the lowest *AIC* ($\Delta AIC > 2$ being considered a substantial difference in support between models; Burnham and Anderson, 2002).

Phenotypic plasticity index

Beyond mean performance, we sought to determine whether certain seed trees produce offspring that are more « sensitive » to site conditions than others. That is, offspring whose growth varies markedly depending on whether they grow at Daloa or Korhogo (high plasticity), as opposed to offspring that behave similarly at both sites (low plasticity). A between-site phenotypic plasticity index of the RDPI type (*Relative Distance Plasticity Index*, Valladares et al., 2006) was calculated for height, by seed-tree group *i* and age *t*:

$RDPI_{i,t} = |H_Daloa_{i,t} - H_Korhogo_{i,t}| / (H_Daloa_{i,t} + H_Korhogo_{i,t})$ (7).

where $H_Daloa_{i,t}$ et $H_Korhogo_{i,t}$ are the mean heights of seed-tree group *i* at age *t*, at Daloa and Korhogo respectively. The index ranges from 0 (no plasticity, identical performance at both sites) to 1 (maximum plasticity, if performance differs greatly). The relationship between this index and seed-tree DBH was then tested by regression and by one-way analysis of variance (seed-tree group).

Allometric equations

Measuring the biomass of a plant requires cutting and oven-drying it ; a destructive measurement, impossible to carry out across an entire nursery or reforestation trial. Allometric equations circumvent this problem by relating biomass to simple, non-destructive measurements (diameter, height). We compared a single-predictor model (diameter) with a two-predictor model (diameter and height) by log-log regression (Chave et al., 2014; Niklas, 1994) :

Simple model: $ln(B) = ln(a) + b \cdot ln(D) + \varepsilon$, i.e. $B = a \cdot D^{\wedge} b$ (8a)

Multiple model: $ln(B) = ln(a) + b \cdot ln(D) + c \cdot ln(H) + \varepsilon$, i.e. $B = a \cdot D^{\wedge} b \cdot H^{\wedge} c$ (8b)

The two models were compared by *AIC* (Equation 6, applied here directly to the regression residuals on the logarithmic scale, both models sharing the same transformed response variable, which makes the comparison directly valid). The retained model is the one that minimises *AIC* while maximising adjusted R^2 (Chave et al., 2014; Niklas, 1994).

All analyses were conducted in *R* and *Python 3.12* (pandas, numpy, scipy.optimize, statsmodels libraries), with a significance threshold set at $\alpha = 0.05$ for all tests. The complete scripts (*Python* and *R*) are available and will be provided upon reasonable request to the corresponding author to ensure full reproducibility of the study.

Results

Germination: overall phenology

Germination of *Parkia biglobosa* is hypogeal, with a generally thick-based epicotyl reaching an average collar diameter of 2.07 mm and an average length of 8.3 cm (approximately 22 days after sowing). The prophylls are compound and bipinnate, generally with 4 primary leaflets composed on average of 11 pairs of secondary leaflets. The leaves following the prophylls are generally composed of two primary leaflets; the seedling then develops bipinnate compound leaves with progressively more primary leaflets (up to ten primary leaflets, with an average of 36 pairs of secondary leaflets, at 3 months of development). Phyllotaxis is alternate-spiral at this stage, each leaf bearing two stipules, one at the leaf sheath and another at the end of the leaf (at the point of insertion of the last two leaflets, just at the end of the rachis).

Germination: a significant site effect

Cumulative germination kinetics differ markedly between sites (Fig. 2). The final rate reached 73.3 ± 3.3% at Korhogo (standard error, n=180 seeds) versus 62.8 ± 3.6% at Daloa (n=180 seeds) (χ^2=4.14; p=0.042), with contrasting dynamics: faster emergence at Daloa (*T50*=15.7 days) but a lower final rate than at Korhogo (*T50*=19.7 days). Germination proceeds faster at Daloa early in the cycle (*T50*=15.7 days) than at Korhogo (*T50*=19.7 days), but plateaus at a lower level. This result suggests that while Daloa's conditions favour early emergence, those at Korhogo ultimately allow a larger proportion of the seed lot to germinate.

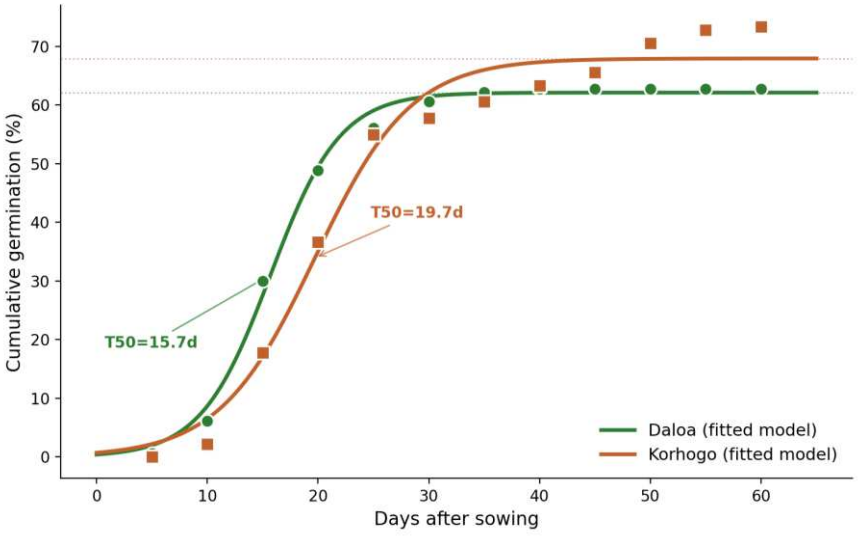


Fig. 2 Cumulative germination kinetics of *Parkia biglobosa* by study site, with fitted logistic models (*Gmax* = asymptotic germination rate; *T50* = time to reach 50% of final germination).

Analysis of variance (Table 2) indicates significant variability between sites for all germination parameters evaluated (P<0.05), whereas seed-tree group characteristics have no significant influence on these same parameters, whatever the parameter considered (P>0.05 for all five parameters, groups combined). These germination parameters (Table 2), derived from the main six-seed-tree-group design, are independent of the

cumulative kinetics presented in Figure 2, which relies on a distinct sub-sample used to characterise daily germination dynamics across all seed sizes combined.

Table 2 Overall influence of study sites and seed-tree groups on germination

Sites/Seed-tree group	Lag time	Germination delay	Germination rate	Germination duration	Germination percentage
Korhogo	17.83 ± 2.12 a	34.69 ± 1.32 a	39.83 ± 7.19 a	38 ± 3.58 a	64.44 ± 4.44 b
Daloa	10.50 ± 1.38 b	19.56 ± 1.34 b	19.33 ± 1.74 b	18.66 ± 2.33 b	94.58 ± 3.62 a
Pr > F	**0.0358**	**0.0001**	**0.0184**	**0.0004**	**0.0003**
Group-1	13.33 ± 3.84 a	24.07 ± 7.01 a	21.66 ± 5.24 a	23 ± 10.07 a	90 ± 5.77 a
Group-2	17 ± 2.08 a	27.63 ± 4.06 a	32.66 ± 8.97 a	25.33 ± 4.48 a	78.05 ± 14.37 a
Group-3	14.66 ± 1.20 a	25.92 ± 5.20 a	32 ± 11.13 a	28.33 ± 10.83 a	84.44 ± 12.37 a
Group-4	11 ± 5.57 a	25.32 ± 6.26 a	34 ± 13.74 a	31 ± 5.68 a	78.39 ± 11.02 a
Group-5	15 ± 3.05 a	26.55 ± 1.45 a	29 ± 3.05 a	24.66 ± 1.45 a	71.39 ± 3.20 a
Group-6	12.33 ± 2.02 a	26.56 ± 3.37 a	23 ± 4.58 a	25.67 ± 5.61 a	83.88 ± 8.73 a
Pr > F	**0.8281**	**0.9968**	**0.8637**	**0.9719**	**0.8278**

For each trait, values sharing the same letters are not statistically different at the 5% threshold.

Growth: site outweighs seed-tree type

Morphology at four months of age

At 4 months of development, the results (Table 3) show that most morphological parameters differ significantly between sites (P<0.05): height (*HtPl*), collar diameter (*Dcol*), number of leaves (*NbreFe*), leaf length (*LgFe*), leaflet length (*LgFiol*) and internode length (*LgEntr*) are all higher at Daloa than at Korhogo. Only leaf width (*LaFe*), number of leaflets (*NbreFiol*) and leaflet width (*LaFiol*) remain statistically equivalent between sites (P>0.05). Regarding the effect of seed-tree group, sites combined, none of the nine parameters measured differs significantly according to group (P>0.05 in all cases), confirming, even at this early stage, the absence of a seed-tree effect on seedling morphology.

Table 3 Overall influence of study sites and seed-tree groups on seedling development

Sites/Seed-tree group	*HtPl (cm)*	*Dcol (mm)*	*NbreFe*	*LgFe (cm)*	*LaFe (cm)*	*NbreFiol*	*LgFiol (cm)*	*LaFiol (cm)*	*LgEntr (cm)*
Korhogo	19.51±0.74 b	2.21±0.15 b	3.52±0.12 b	9.37±0.49 b	9.01±0.47 a	4.65±0.34 a	6.69±0.31 b	3.12±0.32 a	2.45±0.2 b
Daloa	25.52±0.83 a	3.12±0.34 a	4.38±0.23 a	11.57±0.57 a	10.86±0.67 a	4.96±0.18 a	8.46±0.44 a	3.82±0.19 a	2.98±0.2 a
Pr > F	**0.0001**	**0.0147**	**0.0031**	**0.0015**	**0.0757**	**0.5447**	**0.0016**	**0.1383**	**0.0155**
Group-1	23.27±2.84 a	2.74±0.49 a	4.53±0.69 a	12.28±0.70 a	11.25±0.61 a	4.88±0.22 a	7.43±0.49 a	3.35±0.15 a	2.84±0.39 a
Group-2	23.41±2.27 a	2.45±0.34 a	3.94±0.34 a	11.05±1.59 a	10.78±1.61 a	4.59±0.02 a	8.27±1.15 a	3.47±0.39 a	3.15±0.31 a
Group-3	23.03±1.74 a	2.89±0.39 a	4.23±0.36 a	10.56±1.14 a	9.37±1.05 a	5.28±0.18 a	8.54±0.58 a	3.67±0.36 a	2.90±0.60 a
Group-4	22.89±3.05 a	2.93±0.46 a	3.76±0.38 a	9.83±1.13 a	9.08±0.87 a	5.07±0.38 a	8.46±1.12 a	3.81±0.2 a	2.87±0.51 a
Group-5	25.53±1.67 a	2.94±0.63 a	4.31±0.37 a	12.13±1.33 a	10.37±1.35 a	4.93±0.37 a	7.10±0.85 a	3.51±0.63 a	3.45±0.26 a
Group-6	26.61±2.56 a	3.31±0.52 a	4.31±0.29 a	11.50±0.69 a	11.33±0.86 a	4.52±0.64 a	9.50±1.11 a	3.70±0.77 a	2.74±0.54 a
Pr > F	**0.9610**	**0.8795**	**0.8117**	**0.6508**	**0.6105**	**0.6737**	**0.5374**	**0.9824**	**0.8832**

For each trait, values sharing the same letters are not statistically different at the 5% threshold. *HtPl*: Seedling height; *Dcol*: Seedling collar diameter; *NbreFe*: Number of leaves*; LgFe*: Leaf length; *LaFe*: Leaf width;

NbreFiol: Number of leaflets; *LgFiol*: Leaflet length; *LaFiol*: Leaflet width; *LgEntr*: Internode length; cm: centimetres; mm: millimetres

Growth and modelling at 6, 12 and 24 months

Site, not seed-tree type, determines growth

Three independent statistical approaches demonstrate that the growth of *P. biglobosa* is determined by the planting site rather than by the dendrometric characteristics of the seed tree.

Analysis of variance and boxplot

A classical ANOVA confirms the magnitude of the site effect on the three growth parameters at each age (Table 4; Figure 3). Note that at 6 months, the effect on diameter is at the borderline of significance (p=0.067), suggesting a later differentiation of this parameter in this species.

Table 4 Mean ± standard deviation of the main growth parameters of *Parkia biglobosa* by site and age. Biomass was not measured at 12 months

Age	Parameter	Daloa (mean±SD)	Korhogo (mean±SD)	*p*
6 months	Height (cm)	35.64 ± 5.69	29.18 ± 3.93	<0.001
6 months	Diameter (mm)	5.10 ± 1.06	4.66 ± 0.95	0.067
6 months	Biomass (g)	22.95 ± 13.18	8.51 ± 1.65	<0.001
12 months	Height (cm)	60.73 ± 13.92	31.63 ± 8.79	<0.001
12 months	Diameter (mm)	10.19 ± 2.49	5.99 ± 1.16	<0.001
24 months	Height (cm)	221.78 ± 53.66	176.74 ± 13.09	0.003
24 months	Diameter (mm)	27.37 ± 9.35	17.84 ± 2.98	<0.001
24 months	Biomass (g)	283.90 ± 138.84	196.52 ± 48.85	0.026

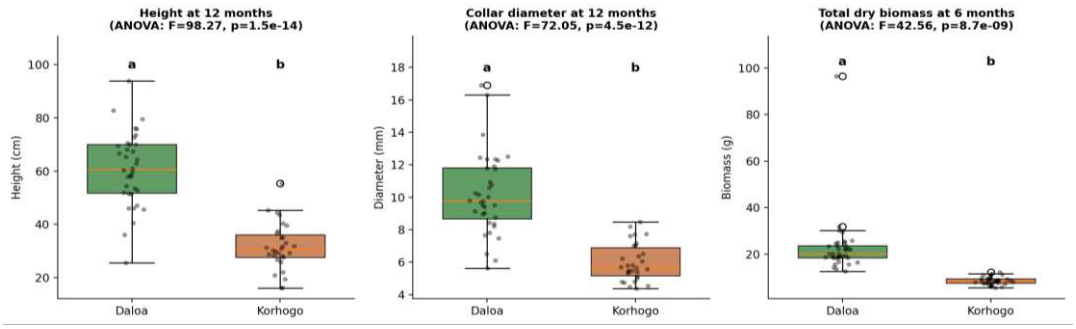


Fig. 3 Boxplots showing the effect of study site on height, collar diameter, and total dry biomass of *Parkia biglobosa*, with ANOVA results (letters denote significant differences, p<0.05).

For comparison, Fig. 4 shows the effect of seed-tree group on height at 12 months: no significant difference appears among the six groups, in contrast to the massive site effect observed above.

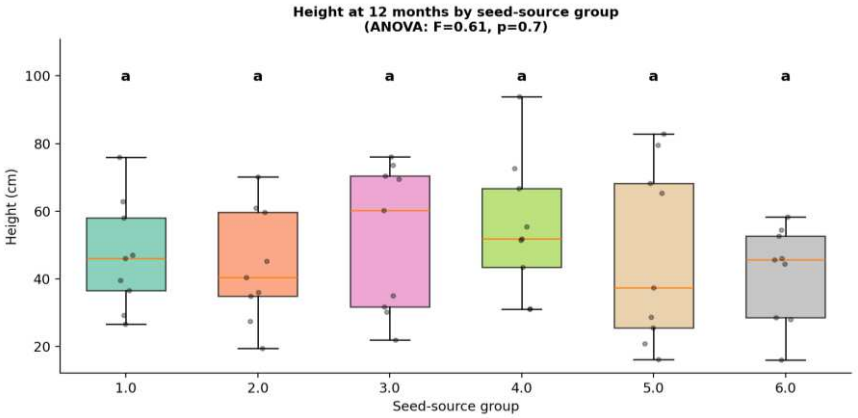


Fig. 4 Height at 12 months by seed-source group: no significant difference between mother-tree groups (boxplot with ANOVA).

Continuous regression

Rather than comparing seed-tree categories, each growth parameter was regressed directly on the actual DBH and height of the seed tree, separately at each age (Fig. 5). The vast majority of the 16 regressions tested are not significant (p>0.10), with the exception of an isolated association between seed-tree height and seedling height at 24 months (p=0.017; R^2=0.19; n=29), to be interpreted with caution given the number of tests performed (approximately 0.8 falsely significant result is statistically expected by chance across 16 tests at the 5% threshold).

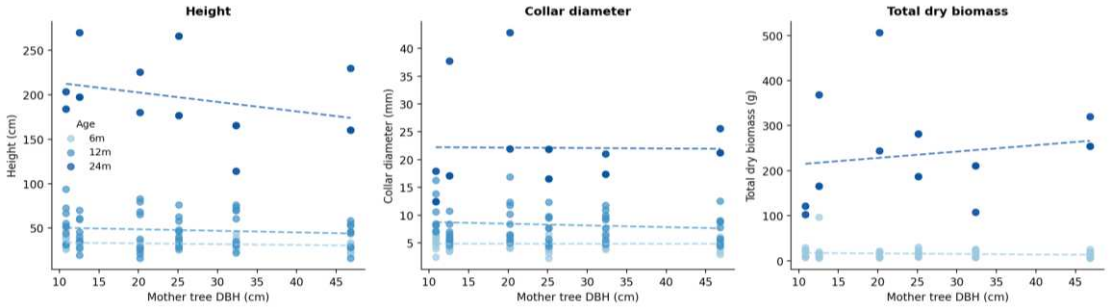


Fig. 5 Continuous regression of growth parameters against mother tree DBH, by age class. A single isolated association reaches significance (height at 24 months, p=0.017).

Linear mixed models with interaction: site × seed tree

Linear mixed models were fitted for height, collar diameter and total biomass (log-transformed), with seed tree as a random effect, site and age as fixed effects, and a *DBH* × *site* interaction term allowing a test of whether the seed-tree effect differs according to environment (Table 5). Seed-tree *DBH* is not significant in any of the three models (p=0.203 for height; p=0.454 for diameter; p=0.515 for biomass), nor is its interaction with site (p>0.19 in all three cases). The absence of significance of the interaction term confirms that the effect of *DBH* does not differ by site. The absence of a seed-tree effect is therefore not masked by a differential response between environments. The site effect, meanwhile, remains highly significant in these same models (p<0.01 for all three responses), confirming its predominance over growth.

Table 5 Results of linear mixed models (seed tree as random effect) for three growth responses of *Parkia biglobosa*

Response	Seed-tree DBH (p)	Interaction DBH×site (p)	Site (p)	Age (p)
Height	*0,203*	*0,736*	*<0,006*	*<0,001*
Collar diameter	*0,454*	*0,347*	*0,001*	*<0,001*
Total biomass (log)	*0,515*	*0,199*	*<0,001*	*<0,001*

Neither the main effect of seed-tree DBH nor its interaction with site is significant for any of the three responses. In other words, the absence of a seed-tree effect is not masked by a differential effect depending on site: it is robust in both environments.

Mediation analysis: an indirect seed-tree effect via seed mass, confirmed statistically for the first time

An alternative hypothesis is that seed-tree size could indirectly influence the performance of its offspring through the mass of the seeds it produces (a classical maternal effect in seed ecology). A mediation pathway was tested at the level of the six seed-tree groups: seed-tree DBH → mean seed mass → germination rate → mean seedling height (Fig. 6).

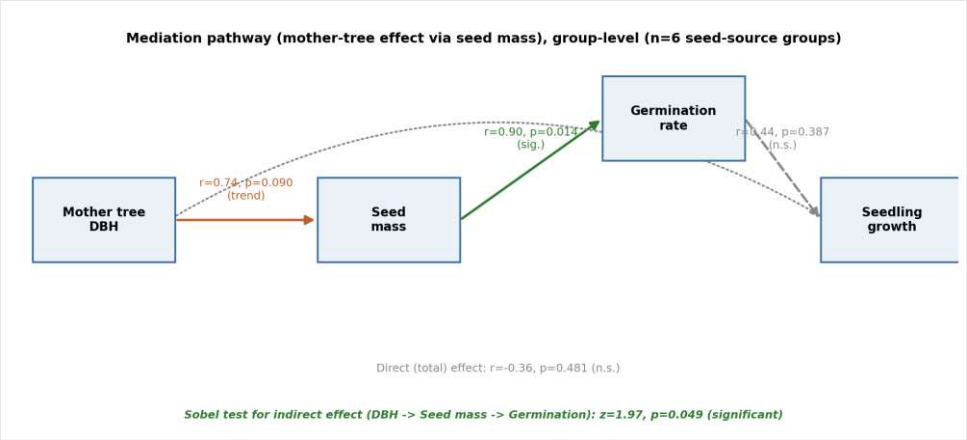


Fig. 6 Mediation path linking mother tree *DBH* to offspring growth through seed mass and germination rate (group-level analysis, *n*=6). Note the significant indirect effect on germination in this species.

The first link (*DBH* → seed mass) is close to the significance threshold (r=0.75; p=0.090), and the second link (seed mass → germination) is significant (r=0.90; p=0.014). The Sobel test confirms a significant overall indirect effect of DBH on germination via seed mass (z=1.97; p=0.049). The first formal statistical confirmation, to our knowledge, of this causal chain in this species. This effect does not, however, propagate through to final growth: the germination → growth link is not significant (r=0.44; p=0.39), and the total effect of *DBH* on growth remains non-significant (r=-0.36; p=0.48).

Non-linear modelling of growth trajectories

Three growth models (linear, power law, exponential) were fitted to individual height and collar-diameter data, separately by site, and compared by *AIC* calculated on a common scale (Tables 6 and 7). A Gompertz model was also tested on the individual height data, but its asymptote parameter proved poorly constrained, the three available age classes (6-24 months) covering only an ascending growth phase, with no indication of a slowdown allowing a plateau to be estimated; this model was therefore not retained.

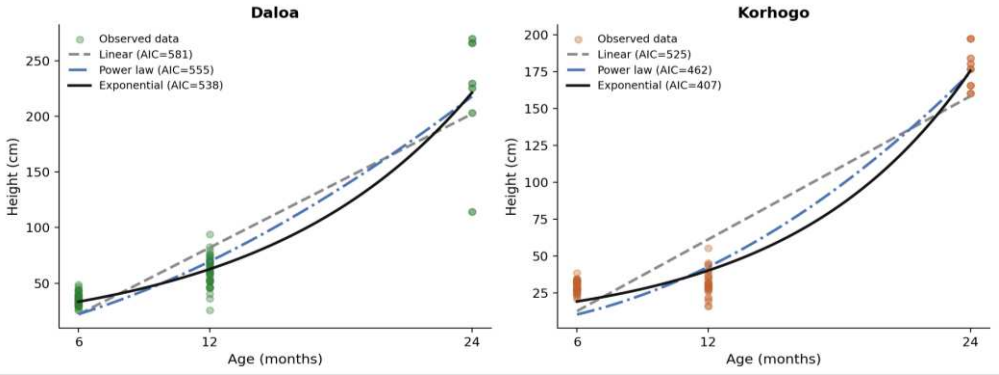
Height growth

The exponential model is the best fit at both sites, with a very clear advantage at Korhogo (ΔAIC=54.9 relative to the power law). The estimated parameters (Daloa: H=17.73×exp(0.105×age); Korhogo: H=9.21×exp(0.123×age)) show a slightly higher relative growth rate at Korhogo (12.3%/month) than at Daloa (10.5%/month), despite a markedly lower initial height at Korhogo. Most of the observed growth gap therefore stems from a difference in initial height rather than a difference in relative growth rate (Table 6, Fig. 7).

Table 6 Comparison of height growth models by *AIC* (common scale, see Fig. 7)

Site	Model	AIC	R^2
Daloa	Linear	581.3	0.817
Daloa	Power law	555.1	0.865

Daloa	Exponential	538.1	0.889
Korhogo	Linear	524.6	0.834
Korhogo	Power law	461.6	0.923
Korhogo	Exponential	406.7	0.960



The exponential model provides the best fit at both sites, with a particularly clear advantage at Korhogo.

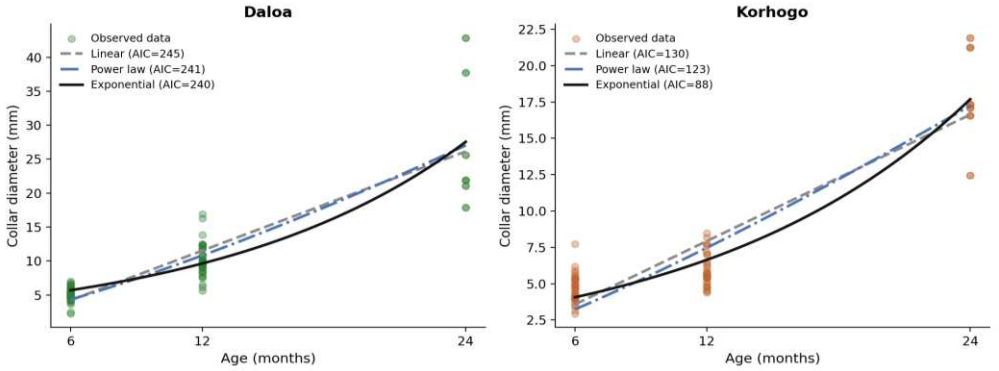
Fig. 7 Comparison of the three growth models (linear, power law, exponential) fitted to individual height data of *Parkia biglobosa*, by site.

Collar-diameter growth

As for height, the exponential model consistently dominates for diameter at both sites ; although the advantage over the power law remains modest at Daloa (ΔAIC=0.9). The estimated parameters (Daloa: D=3.37×exp(0.088×age); Korhogo: D=2.49×exp(0.082×age)) show very similar relative growth rates between sites (8.8%/month at Daloa versus 8.2%/month at Korhogo), in contrast to the more contrasted pattern observed for height (Table 7, Fig. 8).

Table 7 Comparison of collar-diameter growth models by *AIC* (common scale; see Fig. 8).

Site	Model	AIC	R^2
Daloa	Linear	245.2	0.767
Daloa	Power law	240.6	0.779
Daloa	Exponential	239.7	0.781
Korhogo	Linear	130.2	0.832
Korhogo	Power law	122.5	0.847
Korhogo	Exponential	88.3	0.899



The exponential model provides the best fit at both sites

Fig. 8 Comparison of the three growth models (linear, power law, exponential) fitted to individual collar-diameter data of *Parkia biglobosa*, by site.

Between-site phenotypic plasticity

A between-site phenotypic plasticity index (RDPI, *Relative Distance Plasticity Index*) was calculated for height, by seed-tree group and age, based on the relative difference between the Daloa and Korhogo means (Figure 9). This index ranges from 0.02 to 0.43 depending on the group and age considered (a markedly narrower range than reported for other species in the same design), but this variation is correlated neither with seed-tree DBH (r=0.19; p=0.45, all data combined), nor significantly different among seed-tree groups (ANOVA: F=0.25; p=0.93). This result indicates that, while mean seedling performance varies markedly between sites, the extent of this variation (plasticity itself) likewise does not depend on the size of the original seed tree. A result that closes one last possible door to a hidden seed-tree effect.

The one-way ANOVA nonetheless reveals a significant variation in this index according to seedling age (F=19.58; p<0.001), though not following a simple linear progression: the mean index rises from 0.10 ± 0.04 at 6 months to a peak of 0.31 ± 0.08 at 12 months, before falling back to 0.15 ± 0.06 at 24 months (linear correlation with age not significant, r=0.009; p=0.97). This bell-shaped profile, distinct from a simple progressive increase in plasticity with age, suggests that the performance gap between sites widens temporarily around 12 months (likely during a growth phase particularly sensitive to local conditions), before narrowing relatively as the most established seedlings converge towards a growth trajectory specific to each site.

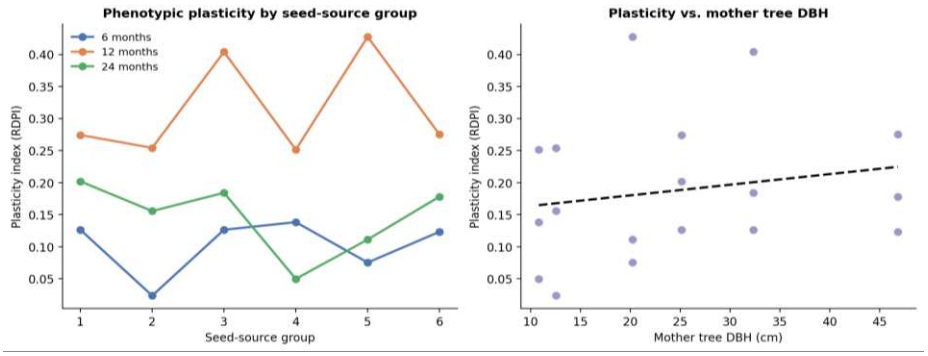


Fig. 9 Between-site phenotypic plasticity index (*RDPI*) for height, by seed-source group and age, and its relationship with mother tree DBH

Allometric equations and model comparison

The allometric relationship between collar diameter and total dry biomass is strong and highly significant (R^2=0.86; Fig. 10), following a power law with an exponent of 1.75, close to the classical cubic value expected in juvenile woody plants, but more moderate than in other species within the same design. The relationship with leaf area is also solid (R^2=0.63), as is that with leaf biomass (R^2=0.71). Root biomass, by contrast, shows a markedly weaker relationship with diameter (R^2=0.34), consistent with the reduced dataset available for this organ following the exclusion of 12-month biomass measurements and the correction of physically impossible values. This equation should therefore be considered preliminary rather than a reliable prediction tool for this species. The root-to-shoot ratio could only be reliably calculated at 6 months (0.96 ± 0.88 on average, n=66), data at 12 and 24 months being insufficient, as they were affected by the anomalies already noted. This ratio, already close to 1 at this early stage, suggests substantial root investment in young seedlings of this species, but cannot be tracked over time with the data currently available.

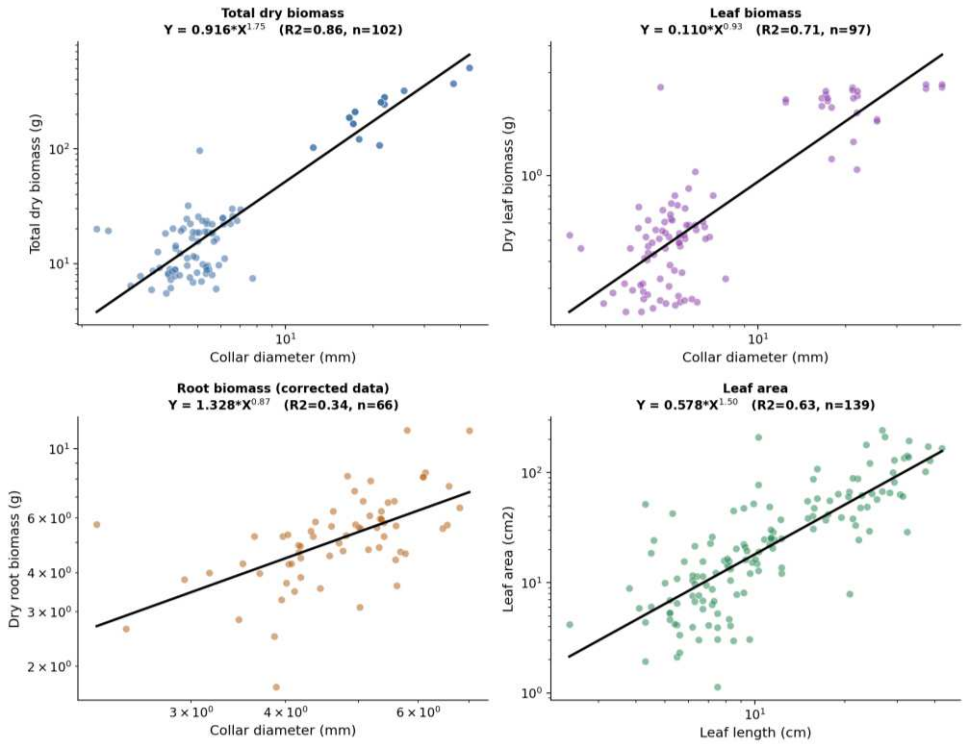


Fig. 10 Allometric equations (log-log regression) relating collar diameter or leaf length to the various biomass components and to leaf area in *Parkia biglobosa* seedlings (6-24 months, sites combined).

A single-predictor allometric model (total biomass ~ diameter alone) was then compared with a two-predictor model (diameter and height), by *AIC* calculated on a logarithmic scale (Table 8). The two-predictor model is markedly superior (ΔAIC=51.9 relative to the single-predictor model), with a substantial reduction in residual error (R^2 raised to 0.915). The retained equation is: $ln(Biomass) = -2.23 + 0.44 \times ln(Diameter) + 1.20 \times ln(Height)$, providing a non-destructive estimation tool substantially more accurate than the single-predictor equation for nursery and reforestation-trial monitoring.

Table 8 Comparison of allometric models of total dry biomass of *Parkia biglobosa*, by *AIC* (logarithmic scale).

Model	AIC	R^2
Power law (diameter only)	157.2	0.856
Quadratic log-log (diameter only)	155.9	0.860
Multiple allometry (diameter + height)	105.3	0.915

Correlation structure of morphological traits

The correlation matrix (Fig. 11) shows strong phenotypic integration among height, collar diameter and total biomass (r=0.89 to 0.97), while leaf area is more moderately correlated with the other traits (r=0.68 to 0.73). Root traits show a more contrasted pattern: root biomass is strongly correlated with diameter (r=0.62) but more weakly with height (r=0.23), and root length even shows a negative correlation with total biomass (r=-0.26). This looser structure for the root compartment is consistent with the reduction and correction of the dataset specifically affecting this organ, and calls for caution when interpreting relationships involving root traits.

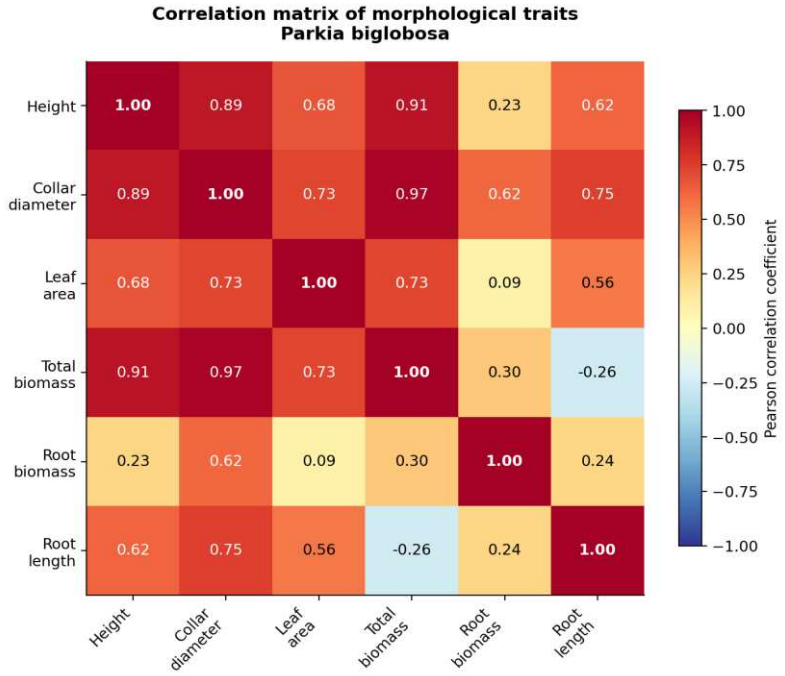


Fig. 11 Pearson correlation matrix of the main morphological traits measured on *Parkia biglobosa* seedlings.

Discussion

Site remains the major determinant of growth and regeneration in *Parkia biglobosa*

The results obtained here, converging across classical ANOVA, continuous regression and mixed models, unambiguously confirm hypothesis H1 and largely corroborate hypothesis H2: the planting site very largely dominates the germination and growth of *Parkia biglobosa*, whereas no dendrometric characteristic of the seed tree has a detectable direct effect, at any age. This result is already observed at the early 4-month stage, where six of the nine morphological parameters measured already differ significantly between sites, against none according to seed-tree group (Table 3). A site-driven differentiation that is faster and more complete than that typically reported at this stage in other savanna woody species, suggesting a particularly marked early sensitivity to edaphic and climatic conditions from the very first months of development in this species. This result is consistent with the finding of Adji et al. (2021), who had already shown, through classical analysis of variance across three environments, that seed trees had no overall influence on any germination or development parameter once sites were combined, whereas the planting environment significantly influenced all of these parameters. A result obtained, however, through a limited categorical analysis, without testing the continuous relationship with actual tree size.

Contrary to what is sometimes observed in other woody species of the region, germination itself is here strongly structured by site: all five detailed germination parameters (lag time, delay, rate, duration, rate) differ significantly between Korhogo and Daloa (Table 2), with none influenced by seed-tree group. This germinative sensitivity to the pedoclimatic contrast may reflect the fact that soaking in water alone (without mechanical or acid scarification, methods usually required to effectively break seed-coat dormancy in this species; Aliero, 2003) leaves residual dormancy in place, making germination more dependent on prolonged substrate moisture and temperature conditions. Indeed, in contrast to Pterocarpus erinaceus, where only germination escaped the site effect (Adji et al., 2021a), *Parkia biglobosa* shows here a sensitivity to site that extends across the entire germination process as well as post-germination growth, suggesting a more integrated ecological response in this species to the pedoclimatic contrast tested.

One isolated signal warrants cautious mention: seed-tree height is associated with seedling height at 24 months in continuous regression (p=0.017; R^2=0.19; n=29). Given the number of tests performed (16 regressions), this single result could reflect a statistical false positive rather than a genuine biological effect (with 16 tests at the

5% threshold, approximately one falsely significant result is statistically expected by chance). It is not reproduced for either diameter or biomass, nor at other ages, and is not confirmed by the corresponding mixed model (p=0.203). We report it in the interest of full scientific transparency, but recommend its replication before any causal interpretation.

An indirect maternal effect confirmed statistically for the first time

The most notable result of this study is the confirmation, through a formal mediation analysis with Sobel test, of a causal chain previously only sensed qualitatively: seed trees of larger diameter produce significantly heavier seeds, themselves associated with a better germination rate, with a statistically significant overall indirect effect (z=1.97; p=0.049). This result aligns with the classical literature on maternal effects in seed ecology, which frequently documents a relationship between mother-tree size, the mass of seeds produced, and the germinative vigour of the offspring (Norden et al., 2009; Roach and Wulff, 1987).

It is essential to note, however, that this indirect effect, although statistically confirmed, remains confined to germination: it does not propagate through to post-germination growth, where the site effect remains very largely dominant. This dissociation between a maternal effect on germination and an absence of effect on subsequent growth is consistent with the idea that seed reserves primarily influence initial seedling establishment, while external environmental conditions subsequently take over to determine the growth trajectory. This result is consistent with the very low natural regeneration densities reported for this species in agroforestry parklands (Ræbild et al., 2012), which could result from the combination of several successive bottlenecks rather than a single factor.

It is useful to place this variation structure at two distinct scales. At a broad geographic scale, Ouedraogo et al. (2012) demonstrated, in a multi-provenance trial comparing 25 néré populations from across the entire Sudano-Sahelian gradient, substantial genetic differentiation among provenances: survival rate varied by almost a factor of two depending on the trial site (35% to 61%), and height growth differed strongly according to the geographic origin of the seeds. At the finer scale adopted here (that of individual seed trees within a single local population), our results show that this genetic variability documented at a broad scale does not necessarily translate into a detectable effect of individual mother-tree size, except via the indirect and modest pathway of seed mass demonstrated here. This distinction has a direct practical implication for conservation seed orchards, which should prioritise the diversity of source provenances rather than the sole selection of the largest individuals within a given population.

Rapid exponential growth, with contrasting allocation patterns between organs

The exponential model consistently dominates for both height and diameter, at both sites. The relative growth pattern nonetheless differs between organs. For height, the gap between sites stems mainly from a difference in initial size rather than relative growth rate, whereas for diameter, relative growth rates are nearly identical between sites despite distinct initial sizes. This difference in behaviour between height and diameter is consistent with a classical allocation trade-off between vertical growth (light access) and radial investment (structural stability and resistance to water stress), already documented in tropical tree seedlings facing contrasting environmental constraints (Markesteijn and Poorter, 2009). On a more applied level, the marked superiority of the two-predictor allometric model over the diameter-only model (R^2 raised to 0.915) confirms, as widely established for tropical trees, that incorporating height substantially improves the accuracy of biomass equations compared with diameter alone (Chave et al., 2014). The relatively higher weight of the height coefficient (1.20) than the diameter coefficient (0.44) in the retained equation suggests, in this species, a biomass allocation proportionally more linked to elongation than to radial thickening during the juvenile phase studied. The correlation matrix of morphological traits confirms this differentiation between compartments: aboveground traits (height, diameter, total biomass) are strongly intercorrelated (r=0.89 to 0.97), reflecting coordinated aboveground growth, while root traits show a markedly looser structure, even a negative correlation between root length and total biomass (r=-0.26). This partial dissociation between aboveground and root growth is consistent with the reduction and correction of the dataset specifically affecting the root compartment, and calls for caution in the biological interpretation of this apparent decoupling rather than viewing it as a genuine and robust allocation strategy.

A bell-shaped phenotypic plasticity, non-linear with age

An unexpected result of this study concerns the temporal dynamics of between-site phenotypic plasticity: rather than a progressive, linear increase with age, the plasticity index follows a bell-shaped profile, peaking at 12 months before declining at 24 months. This type of non-monotonic variation in plasticity over the course of development, although rarely reported in tropical forest species, fits within an emerging field of research on the ontogenetic dimension of plant functional ecology, which emphasises that the expression of phenotypic plasticity can vary substantially according to developmental stage rather than following a monotonic trajectory (Barton, 2024). A plausible explanation is that a phase of heightened sensitivity to local conditions manifests transiently around 12 months (perhaps an architectural or physiological transition period in this species), before the most established seedlings converge relatively towards more stable, site-specific growth trajectories. This hypothesis nonetheless remains to be tested directly, notably through finer-resolution architectural monitoring around this pivotal age.

Implications for conservation and study limitations

Taken together, these results call for a two-pronged recommendation for restoration and agroforestry programmes based on Parkia biglobosa: the choice of planting site remains by far the most determining lever for growth and overall plantation success, but the selection of seed trees with larger diameter can legitimately be incorporated into conservation seed orchards as a secondary, modest but real lever to specifically improve initial germination rates ; without, however, expecting a benefit for the subsequent growth of the plants.

This study has several limitations. The anomaly detected in the 12-month biomass data affects the precision of the root and leaf allometric equations, which rely on a reduced sample after exclusion of suspect data. The number of seed-tree groups (six) inherently limits the power of the mediation analysis; replication on a larger sample would allow the *DBH-seed mass* relationship, currently significant only at the p=0.090 threshold, to be consolidated. The bell-shaped plasticity profile, although robustly observed across the three available age classes, would benefit from confirmation through higher-resolution temporal monitoring around 12 months. Finally, this study was conducted at only two sites; replication across a larger number of sites would allow the conclusion to be generalised to the species' entire Sudano-Sahelian distribution range.

Conclusion

In *Parkia biglobosa*, the planting site constitutes the major determinant of germination and juvenile growth, from the 4-month stage through to 24 months. This study, however, brings an important nuance beyond a simple confirmation of « site rather than seed tree »: the mediation analysis confirms, statistically for the first time in this species, a genuine indirect maternal effect (seed trees of larger diameter producing heavier seeds with better germination capacity), although this effect remains confined to germination and does not propagate through to growth. Converging across six complementary approaches, from classical variance testing to formal mediation, these results methodically close off the avenues through which a direct seed-tree effect on growth might have manifested. The unexpected bell-shaped profile of phenotypic plasticity, peaking at 12 months before declining, further opens a research avenue on critical developmental windows in this species. The multi-predictor allometric equations developed here, substantially more accurate than the diameter-only model, also provide a non-destructive monitoring tool directly applicable in nurseries and seed orchards. Ultimately, these results call on managers of conservation and agroforestry programmes to focus their efforts on the choice of planting site as the absolute priority, while reserving a more modest but legitimate place for the dendrometric selection of seed trees in the establishment of seed orchards aimed specifically at optimising germination. A fine but decisive distinction for the efficient allocation of limited conservation resources.

Author Contributions

BIA: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Resources, Software, Validation, Visualization, Writing – original draft, Writing - review & editing.

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Declaration of competing interest

The author declare no competing interests.

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Data availability

The datasets analysed as part of this study are available at: ADJI, B. I. (2026). Supporting Dataset for the document of Germination, morphology and biomass of *Khaya senegalensis*, *Pterocarpus erinaceus* and *Parkia biglobosa* seedlings according to mother-tree dendrometric characteristics and planting site in Côte d'Ivoire (2018-2025). https://doi.org/10.5281/zenodo.21435509

References

Adji, B.I., Akaffou, D.S., Kouassi, K.H., Houphouet, Y.P., Duminil, J., Sabatier, S.A., 2021a. Bioclimate influence on seed germination and seedling morphology parameters in Pterocarpus erinaceus Poir., 1804 (Fabaceae). Int. J. Environ. Agric. Biotechnol. 6, 001–015. https://doi.org/10.22161/ijeab.63.1

Adji, B.I., Akaffou, D.S., Sabatier, S., 2021b. Ecological environment effects on germination and seedling morphology in Parkia biglobosa in nursery (Côte d'Ivoire) and greenhouse (France). Int. J. Hortic. Agric. Food Sci. 5, 01–13. https://doi.org/10.22161/ijhaf.5.5.1

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

Akaffou, S.D., Kouame, A.K., Gore, N.B.B., Abessika, G.Y., Kouassi, H.K., Hamon, P., Sabatier, S., Duminil, J., 2021. Effect of the seeds provenance and treatment on the germination rate and plants growth of four forest trees species of Côte d'Ivoire. J. For. Res. 32, 161–169. https://doi.org/10.1007/s11676-019-01064-y

Akaike, H., 1974. A new look at the statistical model identification. IEEE Trans. Autom. Control 19, 716–723. https://doi.org/10.1109/TAC.1974.1100705

Aliero, B.L., 2003. Effects of sulphuric acid, mechanical scarification and wet heat treatments on germination of seeds of African locust bean tree, Parkia biglobosa. Afr. J. Biotechnol. 3, 179–181. https://doi.org/10.5897/AJB2004.000-2031

Baron, R.M., Kenny, D.A., 1986. The moderator–mediator variable distinction in social psychological research: Conceptual, strategic, and statistical considerations. J. Pers. Soc. Psychol. 51, 1173–1182. https://doi.org/10.1037/0022-3514.51.6.1173

Barton, K.E., 2024. The ontogenetic dimension of plant functional ecology. Funct. Ecol. 38, 98–113. https://doi.org/10.1111/1365-2435.14464

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting Linear Mixed-Effects Models Using **lme4**. J. Stat. Softw. 67. https://doi.org/10.18637/jss.v067.i01

Bouda, Z.H.-N., Bayala, J., Markussen, B., Jensen, J.S., Ræbild, A., 2013. Provenance variation in survival, growth and dry matter partitioning of Parkia biglobosa (Jacq.) R.Br. ex G.Don seedlings in response to water stress. Agrofor. Syst. 87, 59–71. https://doi.org/10.1007/s10457-012-9521-9

Burnham, K.P., Anderson, D.R. (Eds.), 2004. Model Selection and Multimodel Inference. Springer, New York, NY. https://doi.org/10.1007/b97636

Burnham, K.P., Anderson, D.R. (Eds.), 2002. Information and Likelihood Theory: A Basis for Model Selection and Inference, in: Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. Springer, New York, NY, pp. 49–97. https://doi.org/10.1007/978-0-387-22456-5_2

Chave, J., Réjou-Méchain, M., Búrquez, A., Chidumayo, E., Colgan, M.S., Delitti, W.B.C., Duque, A., Eid, T., Fearnside, P.M., Goodman, R.C., Henry, M., Martínez-Yrízar, A., Mugasha, W.A., Muller-Landau, H.C., Mencuccini, M., Nelson, B.W., Ngomanda, A., Nogueira, E.M., Ortiz-Malavassi, E., Pélissier, R., Ploton, P., Ryan, C.M., Saldarriaga, J.G., Vieilledent, G., 2014. Improved allometric models to estimate the aboveground biomass of tropical trees. Glob. Change Biol. 20, 3177–3190. https://doi.org/10.1111/gcb.12629

Choat, B., Jansen, S., Brodribb, T.J., Cochard, H., Delzon, S., Bhaskar, R., Bucci, S.J., Feild, T.S., Gleason, S.M., Hacke, U.G., Jacobsen, A.L., Lens, F., Maherali, H., Martínez-Vilalta, J., Mayr, S., Mencuccini, M., Mitchell, P.J., Nardini, A., Pittermann, J., Pratt, R.B., Sperry, J.S., Westoby, M., Wright, I.J., Zanne, A.E., 2012. Global convergence in the vulnerability of forests to drought. Nature 491, 752–755. https://doi.org/10.1038/nature11688

De Wasseige C, De Marcken P, Bayol N, Hiol Hiol F, Mayaux P, Desclée B, Nasi R, Billand A,, Defourny P, Eba`A Atyi R, 2012. Les forêts du bassin du Congo : état des forêts 2010. Publications Office, LU. https://doi.org/10.2788/48830

Hérault, B., N'Guessan, A.K., Ouattara, N., Ahoba, A., Bénédet, F., Coulibaly, B., Doua-Bi, Y., Koffi, T., Koffi-Konan, J.-C., Konaté, I., Tiéoulé, F., Wourro, F., Zo-Bi, I.C., Louppe, D., 2020. The long-term performance of 35 tree species of sudanian West Africa in pure and mixed plantings. For. Ecol. Manag. 468, 118171. https://doi.org/10.1016/j.foreco.2020.118171

Houndonougbo, J.S.H., Kassa, B., Mensah, S., Salako, V.K., Glèlè Kakaï, R., Assogbadjo, A.E., 2020. A global systematic review on conservation nd domestication of Parkia biglobosa (Jacq.) R. Br. ex G. Don, an indigenous fruit tree species in Sub-Sahara African traditional parklands: current knowledge and future directions. Genet. Resour. Crop Evol. 67, 1051–1066. https://doi.org/10.1007/s10722-020-00892-w

ISTA, I.S.T., 2009. International Rules Seed Testing | Official ISTA Guidelines [WWW Document]. Int. Seed Test. Assoc. URL https://www.seedtest.org/en/publications/international-rules-seed-testing.html (accessed 7.31.26).

Kew Science, 2026. Parkia biglobosa (Jacq.) R.Br. ex G.Don | Plants of the World Online | Kew Science [WWW Document]. Plants World Online. URL http://powo.science.kew.org/taxon/urn:lsid:ipni.org:names:941491-1 (accessed 8.12.26).

Koura, K., Ganglo, J.C., Assogbadjo, A.E., Agbangla, C., 2011. Ethnic differences in use values and use patterns of Parkia biglobosa in Northern Benin. J. Ethnobiol. Ethnomedicine 7, 42. https://doi.org/10.1186/1746-4269-7-42

Louppe, D., Ouattara, N., 1996. Les arboretums d'espèces locales en Nord Côte d'Ivoire. Résultats des mesures de 1996. Communication présentée à l'occasion de la sixième réunion tripartite Burkina Faso - Côte d'ivoire - Mali. Kaya - Burkina Faso - 17-21 juin 1996 [WWW Document]. URL https://agritrop.cirad.fr/581418/ (accessed 7.31.26).

649 Mapongmetsem, P.M., Nkongmeneck, B.A., Rongoumi, G., Dongock, D.N., Dongmo, E.B., 2011. Impact des
650 systémes d'utilisation des terres sur la conservation de *Vitellaria paradoxa* Gaerten. F. (*Sapotaceae*)
651 dans la région des savanes soudano-guinéennes. Int. J. Environ. Stud. 68, 851–872.
652 https://doi.org/10.1080/00207233.2011.587259
653 Markesteijn, L., Poorter, L., 2009. Seedling root morphology and biomass allocation of 62 tropical tree species in
654 relation to drought- and shade-tolerance. J. Ecol. 97, 311–325. https://doi.org/10.1111/j.1365-
655 2745.2008.01466.x
656 Niklas, K.J., 1994. Plant Allometry: The Scaling of Form and Process. University of Chicago Press, Chicago, IL.
657 Norden, N., Daws, M.I., Antoine, C., Gonzalez, M.A., Garwood, N.C., Chave, J., 2009. The relationship between
658 seed mass and mean time to germination for 1037 tree species across five tropical forests. Funct. Ecol.
659 23, 203–210. https://doi.org/10.1111/j.1365-2435.2008.01477.x
660 Orwa, C, Mutua, A, Kindt, R, Jamnadass, R, Simons, A, 2009. Agroforestree Species profile [WWW Document].
661 URL https://apps.worldagroforestry.org/treedb2/speciesprofile.php?Spid=1255 (accessed 8.12.26).
662 Ouedraogo, M., Ræbild, A., Nikiema, A., Kjær, E.D., 2012. Evidence for important genetic differentiation between
663 provenances of Parkia biglobosa from the Sudano-Sahelian zone of West Africa. Agrofor. Syst. 85, 489–
664 503. https://doi.org/10.1007/s10457-011-9463-7
665 Paine, C.E.T., Marthews, T.R., Vogt, D.R., Purves, D., Rees, M., Hector, A., Turnbull, L.A., 2012. How to fit
666 nonlinear plant growth models and calculate growth rates: an update for ecologists. Methods Ecol. Evol.
667 3, 245–256. https://doi.org/10.1111/j.2041-210X.2011.00155.x
668 Ræbild, A., Hansen, U.B., Kambou, S., 2012. Regeneration of Vitellaria paradoxa and Parkia biglobosa in a
669 parkland in Southern Burkina Faso. Agrofor. Syst. 85, 443–453. https://doi.org/10.1007/s10457-011-
670 9397-0
671 Roach, D.A., Wulff, R.D., 1987. Maternal Effects in Plants. Annu. Rev. Ecol. Evol. Syst. 18, 209–235.
672 https://doi.org/10.1146/annurev.es.18.110187.001233
673 Sosef, M.S.M., Dauby, G., Blach-Overgaard, A., van der Burgt, X., Catarino, L., Damen, T., Deblauwe, V.,
674 Dessein, S., Dransfield, J., Droissart, V., Duarte, M.C., Engledow, H., Fadeur, G., Figueira, R., Gereau,
675 R.E., Hardy, O.J., Harris, D.J., de Heij, J., Janssens, S., Klomberg, Y., Ley, A.C., Mackinder, B.A., Meerts,
676 P., van de Poel, J.L., Sonké, B., Stévart, T., Stoffelen, P., Svenning, J.-C., Sepulchre, P., Zaiss, R.,
677 Wieringa, J.J., Couvreur, T.L.P., 2017. Exploring the floristic diversity of tropical Africa. BMC Biol. 15,
678 15. https://doi.org/10.1186/s12915-017-0356-8
679 Teklehaimanot, Z., Lanek, J., Tomlinson, H.F., 1998. Provenance variation in morphology and leaflet anatomy of
680 Parkia biglobosa and its relation to drought tolerance. Trees 13, 96–102.
681 https://doi.org/10.1007/PL00009742
682 Valladares, F., Sanchez-Gomez, D., Zavala, M.A., 2006. Quantitative estimation of phenotypic plasticity: bridging
683 the gap between the evolutionary concept and its ecological applications. J. Ecol. 94, 1103–1116.
684 https://doi.org/10.1111/j.1365-2745.2006.01176.x
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