RESEARCH ARTICLE

Competition and site weakly explain tree growth variability in undisturbed Central African moist forests

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Abstract

1. Identifying and quantifying factors that influence tree growth are crucial issues to ensure sustainable forest management, particularly in moist tropical forests. Tree growth depends on several factors comprising ontogenic stage, competition by neighbours and environmental conditions. Several studies have focused on one or two of them, but very few have considered all three, especially in Central Africa. We investigated the effects of diameter and competition on tree growth, in four Central African sites characterized by their soil physicochemical properties, at both tree community and population levels.

2. We calibrated growth models using diameter data collected on 29,741 trees between 2015 and 2018, on twelve 4 or 9-ha plots spread over the four sites. These models included diameter, wood density, competition indices and site effect as explainable variables at the community level and excluded wood density at the population level.

3. At the community level, the best models explained 11% of growth variability with a decreasing effect of species wood density, diameter, site and competition. Our results show that even if low, site effect can result from different soil nutrients depending on both tree size and species wood density. We observed higher tree growth on sites with (i) high exchangeable K, organic C, total N and total P for low wood density species; (ii) high available P and C:N for small trees, high exchangeable Ca and Mg for medium to large trees, all belonging to medium and hard wood

density species. At the population level, the best models explained between 0 to 43% of growth variability, with significant competition effect (resp. site effect) for 21 (resp. 9) of the 43 species studied. Site ranking varied greatly between the 9 species concerned, probably reflecting different sensitivities to the scarcity of particular soil nutrients.

4. *Synthesis*. Our study provides original results on the factors influencing tree growth in Central Africa, showing that the potential effect of soil nutrients depends on tree size and species wood density. Remaining highly unpredictable at the population level, this effect makes it essential to increase the number of dynamics monitoring systems in logging concessions.

1 | INTRODUCTION

Identifying and quantifying factors that influence tree growth are essential to better understand how trees function and to guide forest management towards sustainability. This requires the implementation of forest dynamics monitoring systems, which have been widely used for a long time in temperate forests. This is much less the case in dense lowland moist tropical forests, given the investments and organization required for settlement and monitoring (Blundo et al., 2021; Forni et al., 2019).

Tree growth depends on the genetic inheritance (captured in part by its membership in a species), the ontogenic stage (characterized by tree size), and the local environmental conditions including competition, the physical and chemical properties of the soils and the climatic characteristics of the site (Baker et al., 2003; Baribault et al., 2012). Growth models developed for trees in moist tropical forests generally incorporate some of the first two factors, species and ontogenic stage but much more rarely environmental factors and their various interactions.

Tree neighbours, competing for access to light, water and mineral elements, generally have a negative influence on tree growth. Existing growth models all include tree diameter in their explanatory variables, but much less the effect of competition, particularly because this requires monitoring and characterizing the competitive environment around each studied tree. This can be done only using large plots. Where such plots exist, different types of competition indices have been tested, ranging from simple indices such as basal area in a circle centered on the studied tree with a 10 to 30 m radius, to more complex indices involving neighbours crown or trunk size, their distance from the studied tree or their specific identity or belonging to species groups (Dawkins, 1966; Gourlet-Fleury & Houllier, 2000; Kunstler et al., 2016; Moravie et al., 1999; Rueger et al., 2011; Uriarte et al., 2004; Vanclay, 1991).

Soil chemical properties are expected to be important determinants of tree growth. At the community level, several studies have highlighted the positive effect of soil phosphorus content on increasing total biomass (Quesada et al., 2012, in Amazonia), biomass increment (Paoli & Curran, 2007, in Indonesia) or above-ground net primary productivity (Cleveland et al., 2011; Paoli & Curran, 2007 over the entire intertropical zone). This positive effect is followed by those of cation exchange capacity, CEC, one or more exchangeable cations (calcium, Ca, magnesium, Mg, potassium, K) and nitrogen or carbon-nitrogen ratio (N or C:N) (Paoli & Curran, 2007; Quesada et al., 2012).

However, relationships observed at the community level may not be observed at the tree level. Changes in tree community biomass integrate the whole dynamics process (growth, recruitment and mortality) and thus mask the effects of explanatory variables on tree growth (Gourlet-Fleury et al., 2013). Turner et al. (2018) showed in Panama that soil phosphorus content had no effect on tree community biomass increment, while it was positively correlated with tree diameter increment for most of the species present. Changes in the floristic composition of these communities explain this phenomenon, with less phosphorus-demanding species tending to replace more demanding ones on soils with lower phosphorus content. Baribault et al. (2012) also showed in Costa Rica that the observed effects differed depending on whether the analyses were performed at the community, species group or species level: while at their sites, soil P, K and Ca had an average positive effect on tree community basal area increment, this effect varied by species group. Phosphorus and K only had an effect on species with low wood density, while Ca had a greater effect on species with high wood density. The legume group appeared insensitive to soil nutrient content. Finally, only K had a slight effect on individual tree diameter growth.

Few studies have combined the effects of competition and other environmental variables on individual tree growth. However, there may be an interaction between these factors, the structure and floristic composition of the tree community and therefore the neighbourhood of a tree. The positive effect of nutrient-rich soil on tree growth may be hidden by the competition of a larger number of

neighbours. It may also be hidden by their characteristics, linked to their size or their belonging to a particular species or group of species. The few authors who have incorporated this effect into their models have reached different conclusions: in Costa Rica, Baribault et al. (2012) found a very weak effect of competition on tree diameter growth in contrast to those observed with soil characteristics, while in Panama, Zemunik et al. (2018) found the opposite effect. Other authors have tested these effects directly on competition at the community level (Rozendaal et al., 2020) and compared plots in the Amazon, West Africa and West Central Africa. They showed that the strength of competition was weakly related to topsoil total exchangeable bases ($Ca + Mg + K + sodium Na$) in Amazonia and Africa.

Little work has been done on individual tree growth in Central African forests, and even less on the effects of competition and soil characteristics on this growth. Some studies have quantified diameter increments of particular species and their variability using tree-ring analyses (Groenendijk et al., 2017), others by combining tree-ring analyses and repeated measurements of tree diameter (De Madron et al., 2000; Ligot et al., 2019) but without investigating the effects of competition. To our knowledge, the only works that have studied the effect of competition on individual tree growth are those of Feteke et al. (2015) in Cameroon, Kunstler et al. (2016) in the Central African Republic and Rozendaal et al. (2020) in Cameroon and Gabon. But none of these studies worked on the detailed physicochemical characteristics of soils as potential explanatory factors for this growth.

In this study, we investigated the effects of competition on individual tree growth at both community and population levels, at four sites in Central Africa (distant between 100 and 1000 km), characterized by their soil physicochemical properties. We acquired data from 2015 to 2018 on large permanent plots located in the Central African Republic, the Congo Republic and the Democratic Republic of the Congo, on four contrasting geological substrates, in areas considered climatically homogeneous. We tested the following hypotheses: (i) competition and site have a significant explanatory power on individual tree growth; (ii) effects of competition on individual tree growth are consistent among sites. We also examined whether (iii) the ranking of sites according to growth rates is related to exchangeable Ca for medium and high wood density species and to exchangeable K and available P for low wood density species.

2 | MATERIALS AND METHODS

2.1 | Study sites

We selected four sites that have never been harvested for timber and are currently under very little human pressure. These four sites (Table 1) are located in the northern part of the Central African forests, dominated by semi-deciduous (M'Baïki in the Central African Republic, Loundoungou in the Republic of Congo), semi-deciduous evergreen (Mokabi in the Republic of Congo) and semi-deciduous

evergreen transition (Yoko in the Democratic Republic of the Congo) forest types (Réjou-Méchain et al., 2021).

The climate is humid tropical across sites, with mean annual rainfall varying between 1500 and 1800 mm. Rainfall values were obtained from several sources (Table 1): rain gauges, often located several 10 km from the sites, and satellite sources. Satellite data allowed us to compare the sites over similar periods (2015–2018, see Section 2.2) and to evaluate seasonal drought stress by estimating the climatic water deficit (CWD). CWD is the sum of the monthly differences between evapotranspiration and precipitation when these differences are negative (Table 1).

The four sites are located on plateaus of similar altitude and on sedimentary or metamorphic rocks of different ages (from Precambrian to Quaternary; Table 1). The soils of M'Baïki, Mokabi, Loundoungou and Yoko are classified using the WRB soil classification (IUSS Working Group WRB, 2014) as Plinthosols, Arenosols, Ferralsols and Ferralsols, respectively (Jones et al., 2015).

2.2 | Plots data

We settled plots at each of the sites (Table 1). In the plots, trees larger than 10 cm in diameter at breast height (DBH) were located, botanically identified and their diameter measured almost every year since 1982 in M'Baïki (Gourlet-Fleury et al., 2013), and since 2015 in Mokabi, Loundoungou (Forni et al., 2019) and Yoko.

To avoid the effect of annual climate variation on comparison between sites, we calculated tree diameter increments between 2015 and 2018, the 2 years in which all plots were inventoried simultaneously (Figure 1). Only trees alive in 2015 and 2018 were selected for growth analysis, allowing to reduce possible effects related to recruitment—trees appearing above 10 cm between 2015 and 2018 could be younger, faster-growing trees and to mortality—trees disappearing between 2015 and 2018 could be older and/or injured or diseased trees. Among trees alive over the whole period, we filtered out those which point of measurement changed between censuses and those with abnormal annual diameter increment values (>6 cm and ≤−0.4 cm), which represent 0.1% and 1.2% of the data, respectively.

Finally, to study the effect of competition on tree growth, we retained only the trees for which we could compute the competition indices, i.e. being located at a certain distance from the edge of the plots (Table 2). In preliminary analyses, we tested three radii, 10, 15 and 20 m to define tree neighbourhood, and a 15 m value proved to be the most effective (see Section 2.4).

For population-level analyses, we retained the 43 species with at least 15 trees per site in at least three sites (Appendix S1: Table S1). Among these 43 species, 39, 43, 43 and 16 had more than 15 trees in M'Baïki, Loundoungou, Mokabi and Yoko, respectively.

Each species present on the sites was assigned a regeneration guild, distinguishing between pioneer, non-pioneer light-demanding and shade-bearing species (Appendix S1: Table S2) using information for regional databases (Bénédet et al., 2019; Hawthorne, 1995).

TABLE 1 Characteristics of the study sites including location, sampling and floristic, geological and climatic information.

Sites	Country	Location(elevation in m)	Number of plots	Size of plots	Dominant families	Number of tree species	Geological substrate*	Mean annual rainfall from rain gauges**	Mean annual rainfall from satellite (CHIRPS)***	Number of dry months (<100mm)	Mean annual CWD from satellite (CHIRPS)****	Mean monthly temperature from CFSR data***
M'Baïki	Central African Republic	3°54'N 17°56'E (550m)	3	4ha	Myristicaceae, Cannabaceae, Meliaceae, Fabaceae	262	Precambrian schists, sandstones and quartzites	1651mm (2007–2012)	1537mm (2015–2018)	3 to 6 (rain gauge) 3 to 4 (CHIRPS)	−233mm (2015–2018)	24.8°C (2015–2018)
Mokabi	Republic of Congo	3°09'N 16°58'E (530m)	4	9ha	Euphorbiaceae, Clusiaceae, Annonaceae, Sapotaceae	223	Mesozoïc Carnot sandstones	1534mm (2018–2019)	1554mm (2015–2018)	4 to 5 (rain gauge) 3 to 4 (CHIRPS)	−190mm (2015–2018)	25.0°C (2015–2018)
Loundoungou	Republic of Congo	2°22'N 17°05'E (430m)	4	9ha	Euphorbiaceae, Fabaceae, Meliaceae, Ebenaceae	232	Cenozoïc alluvium	1626mm (2012–2018)	1586mm (2015–2018)	2 to 5 (rain gauge) 2 to 4 (CHIRPS)	−150mm (2015–2018)	24.9°C (2015–2018)
Yoko	Democratic Republic of Congo	0°17'N 25°19'E (420m)	1	9ha	Fabaceae, Meliaceae, Euphorbiaceae, Malvaceae	168	Quaternary alluvium	1797mm (2012–2017)	1625mm (2015–2018)	3 to 6 (rain gauge) 1 to 3 (CHIRPS)	−96mm (2015–2018)	24.0°C (2015–2018)

Note: * Forni et al. (2019); **Rain gauges located at M'Baïki (ICRA, 3°53′N, 17°58′E), Lola (Mokabi SA, 3°16′N, 17°58′E), Pokola (CIB, 1°24′N, 16°44′E), Yangambi (INERA, 0°46′N, 24°28′E) *** CHIRPS: Climate Hazards Group InfraRed Precipitation with Station data, CFSR: Climate Forecast System Reanalysis (http://climateengine.org/), data extracted for each site location. **** Comparisons made with data from other sources taken from Climate Engine, estimating CWD from estimated rainfall and estimated evapotranspiration did not modify the rank of the sites on the dry/seasonal vs moist/less seasonal gradient (M'Baïki<Loundoungou<Mokabi<Yoko).

2.3 | Soil sampling

Soils were studied at the site level, not at the plot level, in two stages (Figure 2). First, auger holes down to 1.20 m were carried out to characterize the main soil types and their spatial distribution, based on field observations (e.g. texture, colour). A total of 59, 18, 15 and 13 auger holes were carried out for Mbaïki, Loundoungou, Mokabi and Yoko, respectively. This step led us to identify one to two representative soil types at each site. Second, two pits for each site were dug to a depth of 1.50 m to describe the profile of one or two representative soil types. Five soil samples were collected per profile at depths between (0–5 cm) and (130–150 cm), which were representative of the horizons in each soil profile.
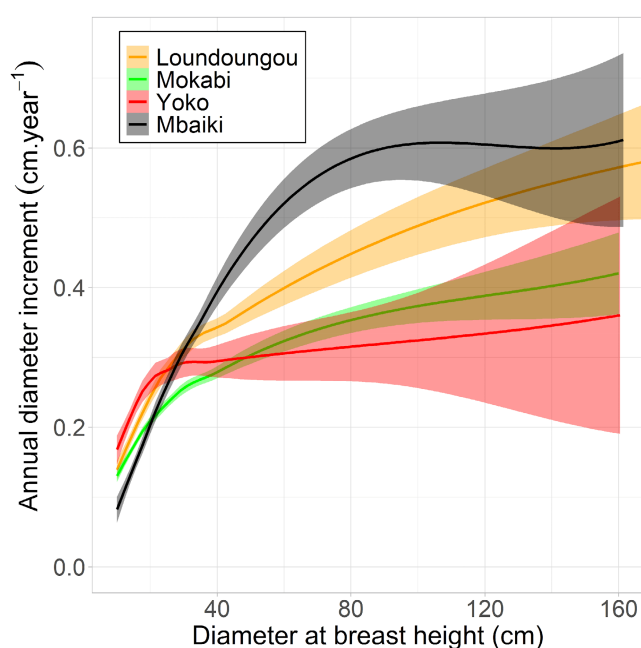

FIGURE 1 Tree mean diameter increments and 95% confidence intervals estimated with the loess method, according to diameter at breast height. Note that a very few number of trees, resp. 100, 31, 81 and 10 outpass 100 cm DBH at Loundoungou, Mbaiki, Mokabi and Yoko, respectively.

Soil samples were then dried, sieved at 2 mm and the subject of standard physical and chemical analyses at the Cirad laboratory in Montpellier, France: particle size in three classes (i.e. clay, silt, sand), pH in water, total organic C, total N, C:N, total P, available P (Bray2), CEC and exchangeable Ca, Mg, K, Na (Metson method, pH 7), Al and H (KCl method). The accuracy of the results given is estimated to be 10% by the laboratory. Results of the surface horizon at Loundoungou, Mokabi and Yoko were normalized to 0–15 cm depth to be compared with the surface horizon at M'Baïki. Specifically, we performed a linear interpolation from the values measured at 0–10 and 20 cm at Loundoungou, 0–5 and 15 cm at Mokabi and 0–5, 5–10 and 10–20 cm at Yoko (Appendix S2). We performed a principal component analysis (PCA) to compare the 8 surface horizons at 0–15 cm depth (4 sites × 2 replicates per site).

2.4 | Individual tree growth models

Tree growth was quantified by the annual diameter increment between 2015 and 2018 (Figure 1 for the community, Appendix S5: Figure S1 for each of the 43 species studied separately).

$$\Delta D = \frac{D_{2018} - D_{2015}}{(t_{2018} - t_{2015}) / 365.25},$$

with ΔD in cm.yr^{-1}, D_{2015} and D_{2018} the diameter at the same point of measurement between 2015 and 2018 in cm, and t the date of measurement in days.

To predict ΔD we compared, at the population level, 150 models built from six growth functions, eight competition indices and three competition radius length plus six models without competition. We ranked all the combinations according to the BIC criterion (see details in Appendix S3).

These preliminary analyses showed that

- the most frequent best growth function was the one used by Rozendaal et al. (2020) (Appendix S3: Table S4), which reflects the classical hump-shaped pattern found when studying large sets of data on tree growth (Herault et al., 2011; Le Bec

TABLE 2 Number of trees present on the different sites and corresponding basal area, number of trees selected for the study, that is, located more than 15 m from the edge of the plots, and the number of species to which they belong.

Sites	Total number of trees in 2015	Number of trees per hectare in 2015	Mean basal area per hectare in 2015 (m².ha^{-1})	Number of trees living in 2015 and in 2018	Number of trees with normal diameters[a]	Number of trees with normal diameters located 15 m from the plot edge	Number of species to which they belong
M'Baïki	7204	600±67	37.9±4.0	6676	6555	4683	262
Mokabi	15,493	430±23	29.2±2.3	15,096	15,059	12,182	223
Loundoungou	12,603	350±36	28.5±3.3	12,057	12,001	9743	232
Yoko	4036	448±16	30.0±2.2	3898	3834	3133	168
Total	39,336			37,727	37,449	29,741	443

[a]Enchanged height of diameter measurement between 2015 and 2018.

FIGURE 2 Strategy adopted for soil sampling. The catena concept represents 'a regular repetition of soil profiles in association with a certain topography' (Milne, 1947).
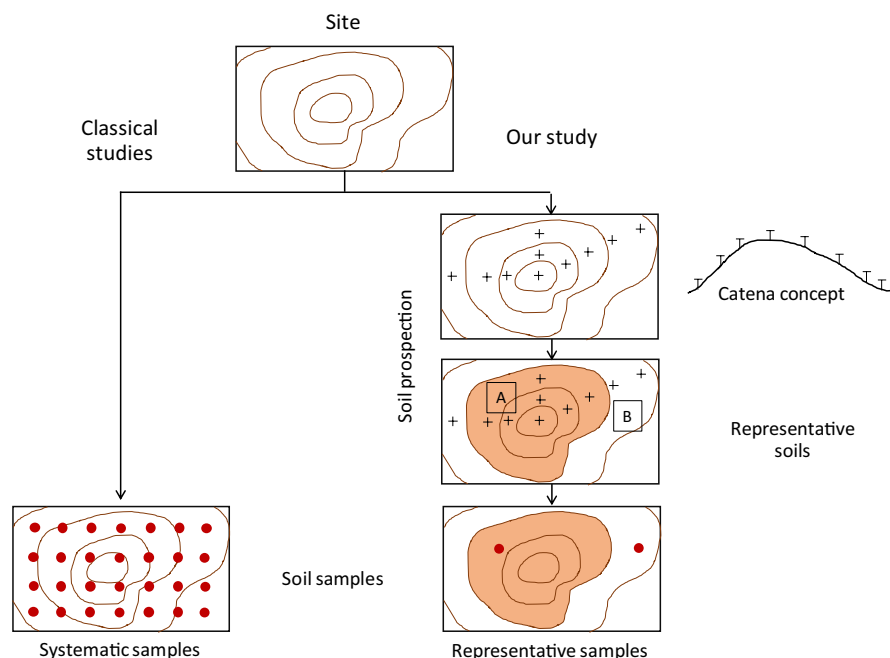
et al., 2015; Uriarte et al., 2004; Vanclay, 1991). This growth function has the advantage of being log-linear, thus simplifying statistical analysis.

- For almost all species, this growth function globally calibrated with a site effect was better than any combination of other growth functions calibrated separately on each site.
- The most frequent best competition indices were G (basal area), GD (basal area of dominant trees), NDt (number of dominant trees) or Nt (number of trees) where dominant trees mean trees with a greater diameter than the focus tree (Appendix S3: Tables S5–S7).
- The most frequent best radius length to quantify competition was 15 m (Appendix S3: Table S8).

Integrating these preliminary results in Appendix S3: Equation S2 leads us to model tree growth according to Equation 1:

$$\log(\Delta D + 1) = \alpha_{1,Site} + \alpha_{2,Site} \log(D) + \alpha_{3,Site} D + \beta_{Site} \times CI + \log(\varepsilon), \quad (1)$$

with $D = D_{2015}$, $Site = \{$Loundoungou, M'Baïki, Mokabi, Yoko$\}$, $\alpha_{1,Site}, \alpha_{2,Site}, \alpha_{3,Site}$ the $Site$ dependent parameters of the intercept, D and $\log(D)$, and β_{Site} the $Site$ dependent parameter of the competition index CI, ie G, GD, NDt or Nt computed using a 15 m radius. We tested the interaction between D and CI for CI not depending on D: the explained variance increased very little while increasing the AIC and BIC, so we did not include this interaction in the model (results not shown).

At the community level, to take into account interspecific growth variability, we added in all the models compared species random effects on all the parameters, and we added a wood density class factor ($CIWD$) as a fixed effect. $CIWD$ classified the wood density value of the studied tree within one of three classes [0.2; 0.4[($CIWD1$), [0.4; 0.6[and [0.6; 1[($CIWD3$). We chose this factorial variable instead of wood density because the curve of the average diameter increment as a function of wood density is clearly non-linear
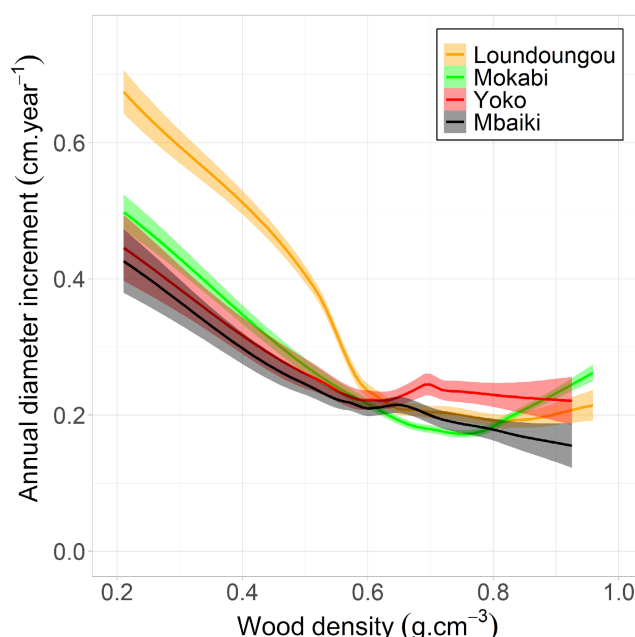

FIGURE 3 Tree mean diameter increments and 95% confidence intervals estimated with the loess method, according to wood density, per site.

and presents a threshold at a wood density of 0.6 (Figure 3). We also tried a factor variable with four regular classes in [0,2; 1] but it increased both BIC and R^2 very slightly. We, thus, modelled tree growth at the community level according to Equation 2:

$$\log(\Delta D + 1) = \left(\alpha_{1,Site} * a_{1,CIWD} + A_1\right) + \left(\alpha_{2,Site} + a_{2,CIWD} + A_2\right)$$
$$\log(D) + \left(\alpha_{3,Site} + a_{3,CIWD} + A_3\right) D + \left(\beta_{site} + b_{CIWD} + B\right) CI + \log(\varepsilon), \quad (2)$$

with $\alpha_{1,Site}, \alpha_{2,Site}, \alpha_{3,Site}, \beta_{Site}$ the $Site$ dependent parameters associated with the intercept, $\log\log(D)$, D and CI and $a_{1,CIWD}, a_{2,CIWD}, a_{3,CIWD}, b_{CIWD}$

the wood density classes parameters associated with the intercept, $\text{loglog}(D)$, D and CI. A_1, A_2, A_3 and B are the species random effects associated with the intercept, $\text{loglog}(D)$, D and CI, respectively.

We only considered the interaction between *Site* and *CIWD* for the intercept because interactions between three variables did not improve the models.

We did not include the regeneration guild in the models, both to limit the number of parameters to be estimated (qualitative variable), to avoid high correlation between explanatory variables (regeneration guild and *CIWD*) and because the number of species for which information is missing was site dependent (Appendix S1: Table S2). At the population level, however, we were able to compare the two variables, as all information was available (Section 2.5).

2.5 | Quantifying competition and testing site effect

2.5.1 | At the community level

We selected the best growth model according to the BIC criterion by an exhaustive comparison of a set of 3216 models using Equation 2. The models used the best explanatory variables identified in preliminary analyses: D and $\log(D)$, a competition index selected from G, GD, Nt or NDt, and site and/or wood density class effects on the above-listed variables.

We quantified the proportion of variance explained by competition, site effect and their interactions with other variables, by calculating the decrease in marginal R^2 (Nakagawa et al., 2017) when removing them from the best model.

We used the same approach with the subcommunity of legumes present on the four sites.

2.5.2 | At the population level

For each of the 43 species, we selected the best growth model according to the BIC criterion by an exhaustive comparison of a set of 304 models built using Equation 1.

For each species and all models compared, in addition to the BIC criterion, we computed the R^2 to indicate the part of variance explained. For species that best model integrated competition and site effect, we quantified their respective importance.

We also tested with Fisher's exact tests whether the existence of a competition and/or a site effect in each species growth model depended on the regeneration guild or on the wood density class of the species; we hypothesized a link between the guild and *CIWD* to help interpret the role played by *CIWD* in Equation 2. For this, we gathered pioneer and light-demanding species in the same class, given the low number of pioneer species selected (one, see Appendix S1: Table S1).

2.5.3 | Interpretation of results

We simplified the formulation of the results by interpreting the effects of the explanatory variables on tree diameter increment ΔD, instead of $\log(\Delta D + 1)$. This simplification did not distort the interpretation because the transformation is increasing and bijective.

We performed all statistical analyses with the R software (R Core Team, 2022) and with the package LME4 (Bates et al., 2015) for linear mixed modelling.

3 | RESULTS

3.1 | Competition and site effects on tree growth at the community level

Very little differences appeared in the best explanatory variables of the 10 best models (Appendix S3: Table S10). The best model calibrated at the community level reached a marginal R^2 of 11%. The variance explained by the different variables (Figure 4) were: 3.3% for D and $\log(D)$, 0.6% for competition index G, 1.5% for *Site*, and 6.2% for *CIWD*, 0.1% for the interaction between competition index and *CIWD*, 1.1% for the interaction between *CIWD* and *Site* and 0.2% for the interaction between *Site* and $\log(D)$, (Figures 4 and 5, Appendix S3: Table S9). We observed a significant positive and
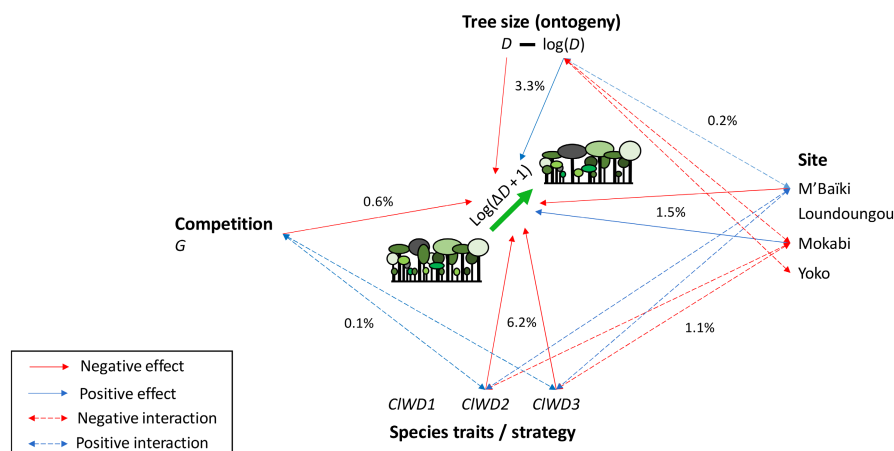

FIGURE 4 Tree growth determinants at the community level (Appendix S3: Table S9). Variances explained by each variable or by interacting variables were calculated using marginal R2, by deleting each of them from the best model. CIWD1 and Loundoungou are the reference levels for the CIWD and Sites factors, the effects of the other levels are relative to them.
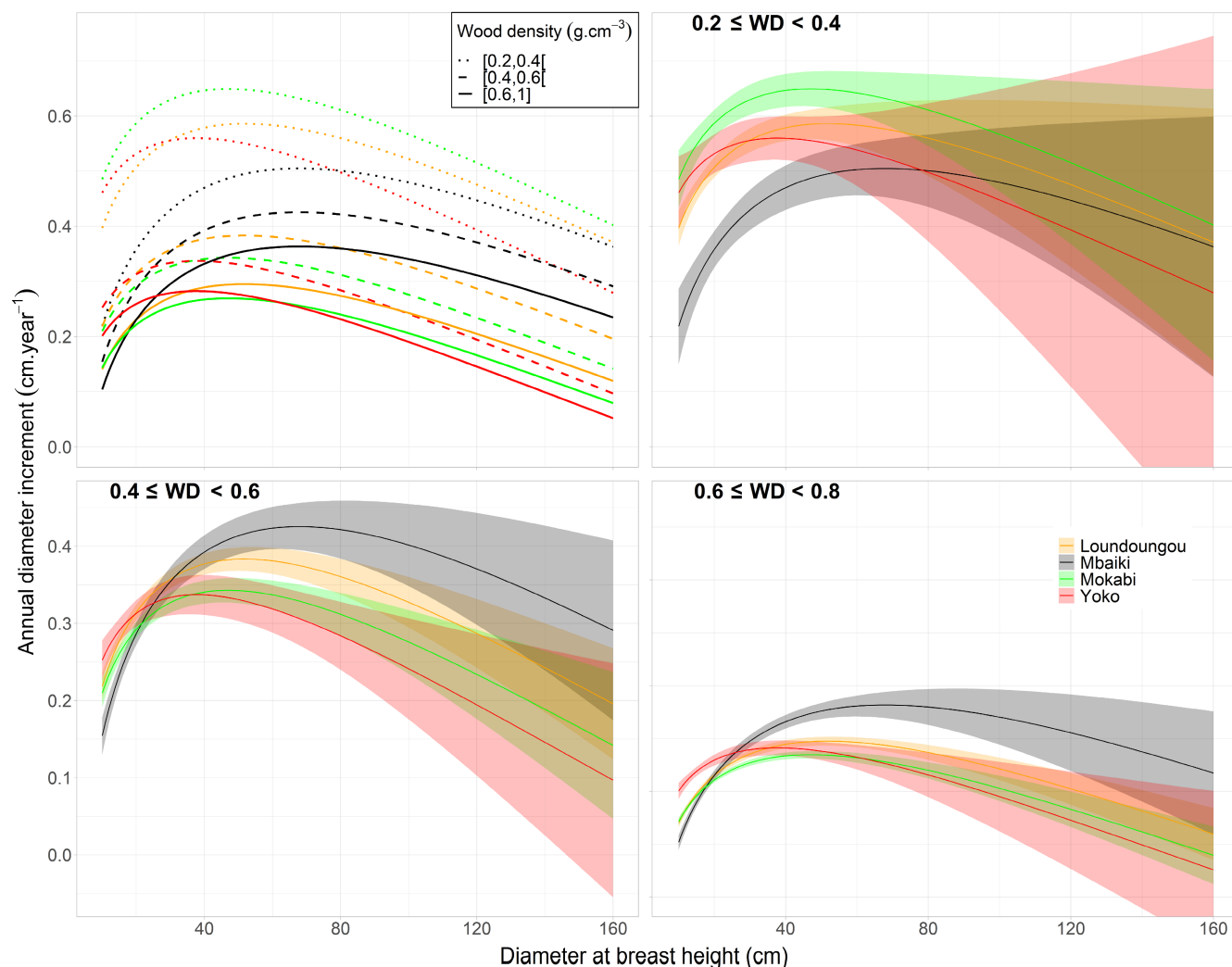
FIGURE 5 Mean tree diameter increment predicted by the community level model, without random effect according to tree diameter and wood density classes per site using the median G value for each diameter (up left); per WD class with a 95% estimated confidence interval (other).

negative effect of $\log(D)$ and D on tree diameter increment (Figure 5), producing a peak in diameter increment at intermediate diameter values (i.e. a hump-shaped pattern). We also observed a significant negative global effect of competition (Figure 6), a significant site effect as well as a significant negative effect of *ClWD* (Figure 5). Significant interactions appeared between:

- G and *ClWD*. While wood density had a negative effect on tree diameter increment, a decrease of this negative effect appeared with increasing competition and wood density, highly significant for *ClWD3* (Figure 6, Appendix S3: Table S9): the negative effect of G on diameter increment was higher on trees belonging to low wood density species, while it was lower on trees belonging to high wood density species;
- Site and $\log(D)$. This interaction showed a difference between the three sites of Loundoungou, Yoko, Mokabi, and the site of M'Baïki: for same values of G and *ClWD*, small trees ($D < 20$ cm) at these three sites tended to grow faster than at M'Baïki, whereas medium and large trees ($D > 30$ cm) tended to grow slower (Figure 5; Appendix S3:Table S9).

- Site and *ClWD*. This interaction showed that the difference between the three sites and M'Baïki highlighted above is more marked the higher the WD. However, for *ClWD1*, the results suffered from large confidence intervals because of the low number of trees in this class (4.5%, 18.2% and 77.3% for *ClWD1*, *ClWD2* and *ClWD3*, respectively).

The best growth model calibrated for the subcommunity of legumes did not include competition nor site effects (Appendix S3: Table S11), in line with the results of Baribault et al. (2012).

3.2 | Competition and site effects on tree growth at the population level

The performance (R^2) of the best specific models obtained according to BIC varied between 0—no significant explanatory variable, and 48.3% for *Entandrophragma candollei* (Table 3 and Figure 7).
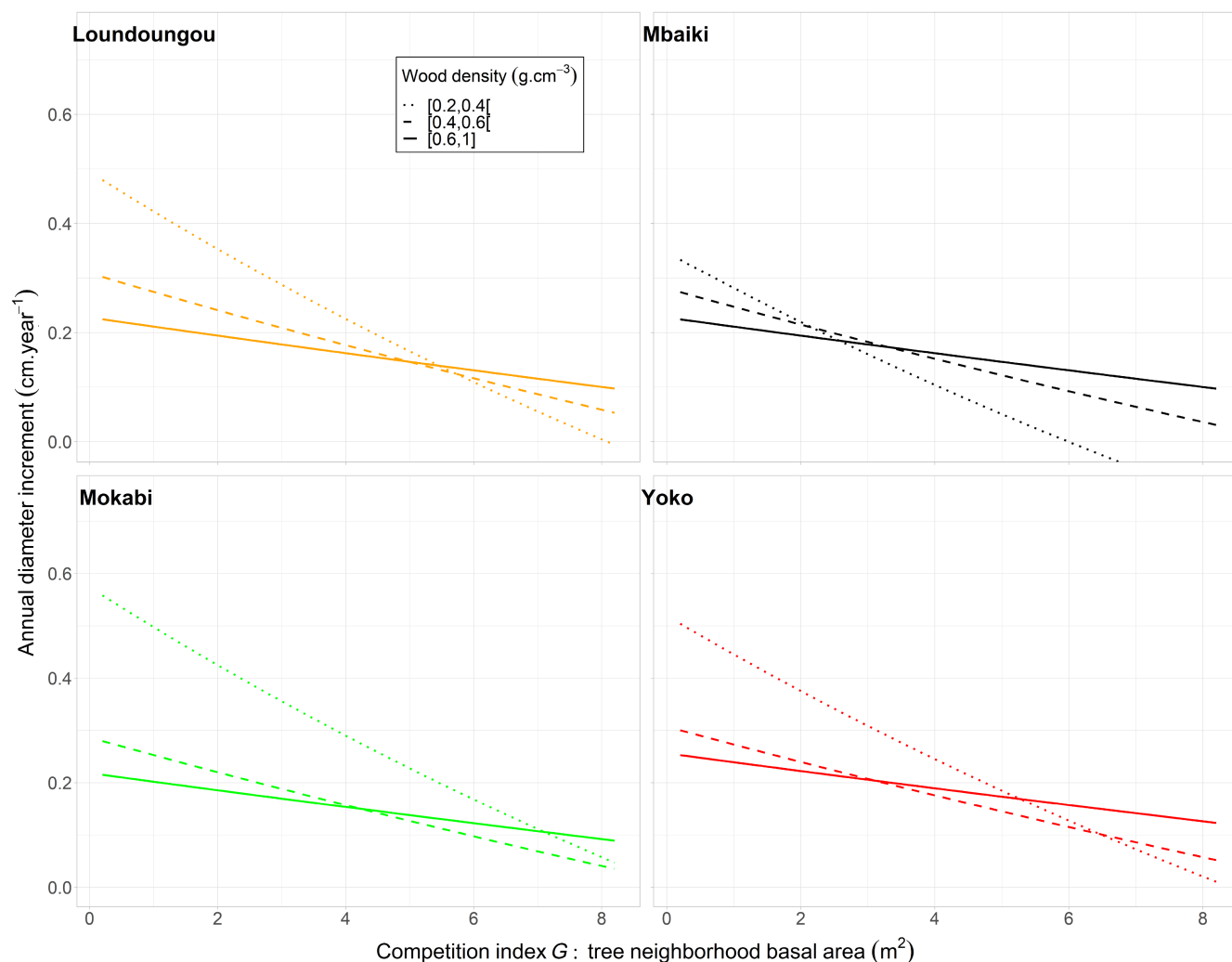
FIGURE 6 Mean tree diameter increment predicted by the community level model, without random effect according to competition index G and wood density classes on each site, for trees with DBH=20cm.

For 21 of the 43 species (48.8%), the best growth model included a competition index CI (i.e. *G*, *GD*, *NDt* or *Nt*), explaining 1.0% to 17.2% of the variance when alone (mean R^2: 6.7%) or adding 0.7% to 7.4% when combined with another variable (mean R^2: 4.1%, Appendix S3: Table S13). The competition indices *NDt* and *GD* were the most frequently selected: 10 and 5 species, respectively, vs 3 and 3 species for *Nt* and *G*. There was no effect of the regeneration guild nor of *ClWD* on the absence/presence and identity of *CI* (pv=0.60 and pv=0.71, respectively, Fisher exact test), these two variables being partly linked—88% of the species in *ClWD3* are shade bearers, but *ClWD1* and *ClWD2* equally gather light demanding (P+NPLD) and shade bearer species. For the 10 species including another explanatory variable than *CI* in their growth model, *CI* explained a mean additional part of 4.1% (min=0.7%, max=7.4%).

For 9 of the 43 species (20.9%), the best growth model included a site effect, explaining 2.0% to 8.3% of the variance when alone (mean R^2: 5.2%) or adding 0.8% to 9.9% when combined with another variable (mean R^2: 5.8%, Appendix S3: Table S13).

This effect appeared either independently, or in interaction with competition or in interaction with tree diameter (Appendix S3: Table S14). This effect appeared independently for 6 species (*Cleistanthus caudatus*, *Coelocaryon preussii*, *Diospyros iturensis*, *Drypetes gossweileri*, *Panda oleosa*, *Trichilia gilgiana*) with a site ranking varying according to the species. This effect appeared interacting negatively with competition (*Carapa procera*), with the higher Nt, the lower diameter increment at Mokabi and M'Baïki. This effect appeared interacting with tree diameter (*Leplaea thompsonii*, *Scottellia klaineana*), the larger being diameter, the faster being growth, with a site ranking varying according to the species. For the 6 species including another explanatory variable than *Site*, *Site* explained an additional part of 5.8% (min=0.8%, max=9.9%) (Appendix S3: Table S13).

For 3 of the 43 species, the best growth model included both a competition and a site effect (*Carapa procera*, *Cleistanthus caudatus*, *Drypetes gossweileri*, Appendix S3: Table S13). The competition indices, respectively, added at most 2%, 0.7% and 7% of the model variance, while the site added at most 4.3%, 0.8% and 6.8% of this variance. The two effects combined, respectively, explained 7.3%, 1.6% and 14.8% of tree growth variability. Using BIC as the decision criterion,

TABLE 3 Explanatory variables and species-specific performance of the best species growth models (see Appendix S3: Tables S12 and S13 for more details). CI is a competition index, among *G*, *GD*, *NDt* or *Nt*.

| Explanatory variables	Number of species concerned	Species	Mean R^2 (min-max)
None	9	*Anonidium mannii, Cola lateritia, Diospyros crassiflora, Garcinia smeathmannii, Lepidobotrys staudtii, Nesogordonia kabingaensis, Pancovia laurentii, Rinorea oblongifolia, Strombosia grandifolia*	0.000
D and log(*D*)	7	*Celtis mildbraedii, Dacryodes edulis, Drypetes leonensis, Entandrophragma candollei, Entandrophragma cylindricum, Hexalobus crispiflorus, Manilkara mabokeensis*	0.194 (0.049–0.483)
CI	11	*Celtis tessmannii, Dialium pachyphyllum, Drypetes occidentalis, Funtumia elastica, Garcinia punctata, Pausinystalia macroceras, Petersianthus macrocarpus, Pterocarpus soyauxii, Pycnanthus angolensis, Santiria trimera, Trichilia prieuriana*	0.067 (0.010–0.172)
Site	3	*Diospyros iturensis, Panda oleosa, Trichilia gilgiana*	0.052 (0.027–0.083)
D or log(*D*) and CI	7	*Angylocalyx pynaertii, Entandrophragma angolense, Polyalthia suaveolens, Macaranga barteri, Staudtia kamerunensis var. gabonensis, Strombosia pustulata, Strombosiopsis tetrandra*	0.132 (0.025–0.380)
D or log(*D*) and Site	3	*Coelocaryon preussii, Leplaea thompsonii, Scottellia klaineana*	0.129 (0.082–0.199)
CI and Site	3	*Carapa procera, Cleistanthus caudatus, Drypetes gossweileri*	0.079 (0.016–0.148)
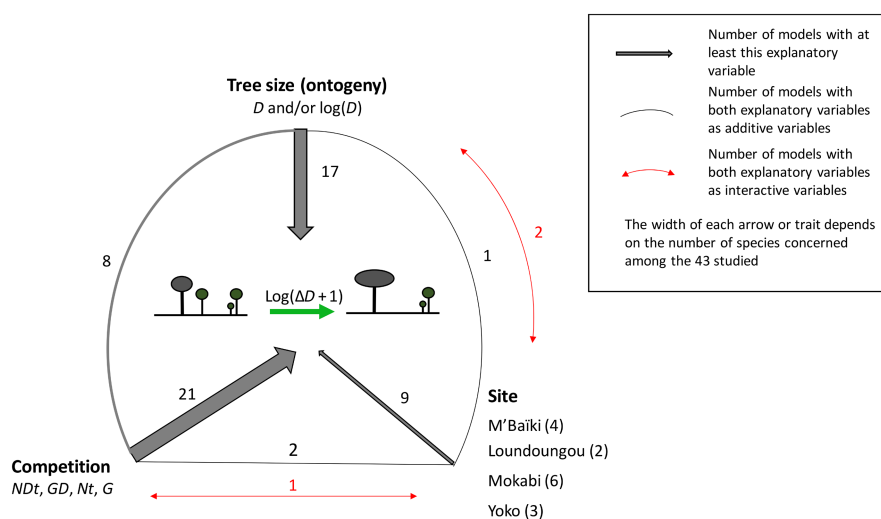
FIGURE 7 Tree growth determinants at the population level.

CI was found to be more important than *Site* in modelling tree diameter growth for *Carapa procera* and *Cleistanthus caudatus*, while it was found to be less important than *Site* for *Drypetes gossweileri*.

No *Site* effect was found for the legume species (*Angylocalyx pynaertii, Dialium pachyphyllum, Pterocarpus soyauxii*, Appendix S3: Table S12), confirming the results obtained at the community level (Section 3.1).

3.3 | Comparison of soil properties between the four sites

The soils of the four sites were acidic (pH < 4.8) and had low CEC values (<6.7 cmolc kg^{-1}; Appendix S2: Table S3). Two axes were retained from the PCA, which explained 73% of the total variability (Figure 8). Axis 1 (41% of the variability) discriminated Yoko soil samples with a high percentage of sand (i.e. loamy sand texture), and the highest available P, C:N and exchangeable H, in contrast to M'Baïki samples with the highest exchangeable Ca and Mg. Axis 2 (33% of the variability) discriminated Mokabi samples with the highest organic C, N, exchangeable K and CEC, in contrast to other samples. The PCA also illustrates a low variability within M'Baïki and Yoko soils and a higher variability within Loundoungou and Mokabi soils. The two soils of Mokabi are variable in texture (sandy clay loam vs sandy loam). Surprisingly, they did not have a sandy texture, although they developed on Carnot sandstone, a geological substrate classically associated with such a texture (Boulvert, 1986). The presence of large termite mounds of *Macrotermes* in this site
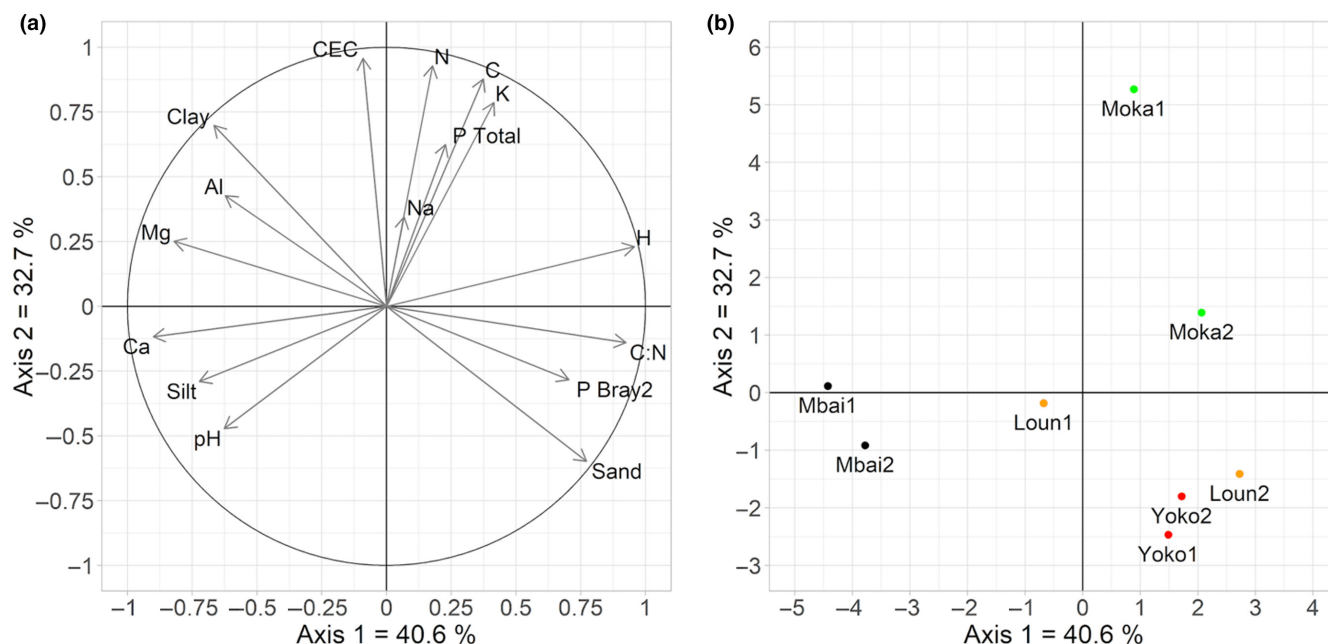
FIGURE 8 Principal component analysis using data of Appendix S2: Table S4 (a) Ordination of 16 soil properties in the factorial plane defined by axes 1 and 2; (b) projection of the 8 soil samples at 0–15 cm depth onto the factorial plane.
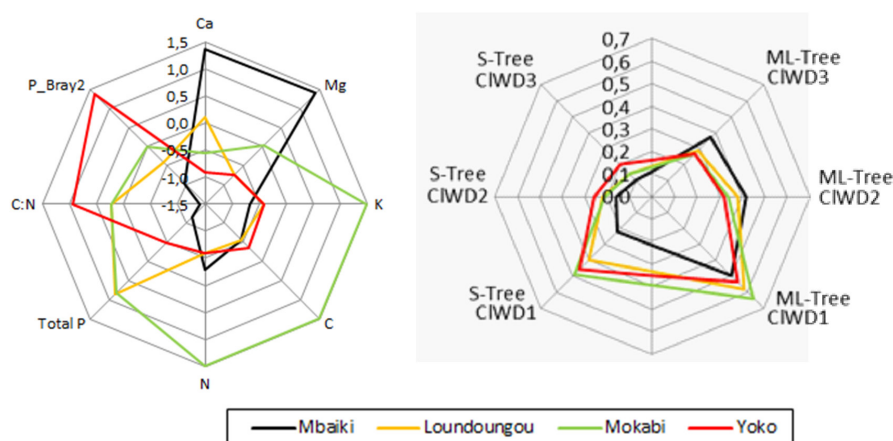

FIGURE 9 Ranking of the four study sites according to (left) each of the eight soil nutrients that discriminate the sites in the principal component analysis (values are standardized means calculated from values given in Appendix S2: Table S4); (right) tree growth regarding tree size (small S-Tree $D < 20$ cm vs. medium and large ML-Tree $D > 30$ cm) and wood density classes (ClWD1 [0.2,0.4], ClWD2 [0.4,0.6] and ClWD3 [0.6,1]).

could explain a more clayey than sandy soil texture as shown in savannahs (Abe et al., 2009).

Although we could not perform statistical tests because the number of soil samples was too small, the results of the PCA (shown in Appendix S2: Table S4) suggested trends to rank the sites according to eight soil nutrients that discriminate them in the PCA and are classically studied in tropical ecology (Figure 9).

3.4 | Comparison of sites ranking according to soil properties and tree growth

We compared site ranking according to soil properties and tree growth (Figure 9, a synthesis from Figure 5). First, this comparison suggests that for small trees, especially with low wood density, the diameter growth gradient (Loundoungou, Yoko, Mokabi > M'Baïki) matched with a decrease of P (available, total) and C:N ratio. Second, this comparison suggests that for medium and large trees, with medium to large wood density, the diameter growth gradient (M'Baïki > Loundoungou, Yoko, Mokabi) matched with a decrease of Ca and Mg content. Due to wide confidence intervals for medium and large trees with low density (Figure 5), we could not relate differences in tree growth between sites to soil properties. However, medium trees with low density at Mokabi tended to grow better than at the other sites (Mokabi > Loundoungou, Yoko > M'Baïki). This site had higher exchangeable K concentration, organic C and total N content than the other sites.

4 | DISCUSSION

4.1 | Competition and site have significant explanatory powers on individual tree growth at the community level

At the community level, we found a significant explanatory power of both competition and site on tree growth, validating our first hypothesis. The growth model selected explained 11.0% of the variance, mainly due to wood density which partly reflects a species effect, and of diameter, revealing a strong ontogenic stage effect (Clark & Clark, 1999). Competition index and site explained, respectively, 0.6% and 1.5% of this variance. Very few studies like ours, analysing both the effect of competition and site on tree growth in tropical or subtropical undisturbed moist forests, have been conducted on such large plots, located on different geological substrates and soils (Appendix S4: Table S15). The most comparable study is by Rozendaal et al. (2020, on a very large number of sites but smaller plots), but they did not specify the part of variance explained by their models. Most of the studies on the subject have been carried out on a few small plots (sometimes <1 ha) located on different substrates or a single large plot (50 ha), but with a high level of soil sampling to quantify physical and chemical soil properties. In Costa Rica, Baribault et al. (2012) growth model explained 9.1% of the variance, with only 1.0% mainly explained by soil nutrients rather than by competition. In Panama, Zemunik et al. (2018) growth model explained 23.5% of the variance, with competition, DBH and both soil nutrients and potential toxins all playing a significant decreasing part. In China, Chi et al. (2015) growth model explained 22% of the variance, with no significant effect of competition nor of soil resources. It is interesting to note that, despite a high effort to detail soil characteristics at a large spatial scale, the part of variance explained in those studies remains low.

4.2 | ... but these explanatory powers are highly variable at the population level

At the population level, the best growth models selected could explain 0% to 48.3% of the variance, mainly due to diameter. Almost half of the 43 species included a significant competition index in the calibrated models, explaining 1.0% to 17.2% of the variance when alone or adding 0.7% to 7.4% when combined with another variable; while less than a quarter included a significant site effect, explaining 2.7% to 8.3% of the variance when alone or adding 0.8% to 9.9% when combined. Similar results were obtained in Costa Rica by Baribault et al. (2012) for 15 species: the part of variance explained by their specific models ranged between 1.1% and 30.9%, but with a more important part (between 1.9% and 15.4%) contributed mainly by soil nutrients. In India, Le Bec et al. (2015) explained 34% ±13% of the variance of about 50 species with both DBH, competition and topographic variables—reflecting more a light effect than soil characteristics effects on a site with steep slopes. In

Cameroon, Feteke et al. (2015) could explain 9.2% to 44.7% of the variance for four species, largely due to diameter, with an included 5.5% to 9.1% part added by the competition index for three of them; they detected no effect from topographic nor hydrological variables. Their results for *E. cylindricum* were quite comparable with those obtained in this study, further east: diameter as the only explanatory variable, but with a lower part of the variance explained (24.4% vs 36.5%, Appendix S3: Table S12). One reason could be that in their study, about half of the trees were located in an area logged 5 to 10 years before, which changes the explanatory variables and their performance.

4.3 | These explanatory powers bring interesting insights into tree growth in several Central African forests

4.3.1 | Competition and site interact indirectly through wood density at the community level

Competition and site were found to interact indirectly through wood density, invalidating our second hypothesis which was, the effects of competition on individual tree growth are consistent among sites. Both the best competition index selected, G, and the wood density of the studied tree had a significant negative effect on tree diameter increment as currently shown in the literature, also explaining the high positive effect of the ratio light index/wood density used by King et al. (2005). Interestingly, we found a significant positive interaction between G and wood density of the studied tree, which means that trees belonging to higher wood density species tend to better withstand increased competition. Our results confirm those found by Kunstler et al. (2016) on five biomes across the world, and by Rozendaal et al. (2020) on their African forest plots.

4.3.2 | The site effect on tree growth could mainly result from Ca, Mg, K, P, C and N content but depends on tree wood density and ontogenic stage

We examined whether trees belonging to species with medium to high wood density tended to grow faster on soil Ca-rich sites (third hypothesis). We concluded that this could be right for medium and large trees but not for small trees.

Our result could suggest that for medium and high wood density species, the soil-limiting factors for growth depended on the ontogenic stage: Ca and Mg for medium and large trees and C:N and available phosphorus for small trees (Figure 9). Our result could be consistent with that of Baribault et al. (2012) who found that the growth of species with high wood density in Costa Rica correlated more strongly with soil Mg and Ca (if we consider that these trees were medium to large trees). This result could also be consistent with those of Alvarez-Clare et al. (2013) and Li et al. (2018): these authors found, respectively, that P addition increased the growth of small

trees but not of larger trees in Costa-Rica, and in a subtropical forest in China (if we consider that these small trees had medium or high wood density). One explanation of limiting soil nutrients varying with tree size could be that medium to large trees in the overstory are more efficient at trapping nutrients from atmospheric deposition in contrast to small trees in the understory. Indeed Bauters et al. (2022) showed for a secondary forest in the DRC that these atmospheric depositions were sufficient to meet the phosphorus needs of the trees but insufficient for their calcium needs.

We examined whether trees belonging to species with low wood density tended to grow faster on soil K and P-rich sites (third hypothesis). Our observations partially confirmed this hypothesis, but only for small trees in P-rich sites, while medium and large trees showed no significant trend due to the large confidence intervals. Our results were consistent with those of Baribault et al. (2012) but with some nuances since they found that the growth of species with low wood density correlated more strongly with K and available P. In Sarawak, (Russo et al., 2005) found that only the growth of pioneer tree species (i.e. supposed to have low wood density) was positively linked with total P and N but also Mg and Ca. In Sabah, (Aoyagi et al., 2016) found that total P and N acted significantly only on the growth of small trees belonging to the Dipterocapaceae species (but with no information on their wood density).

One possible explanation that soil nutrient limitation on growth varies with wood density could be that low- and high-wood-density species do not have the same requirements to build their tissues for meeting their water needs. Heineman et al. (2016) showed in Panama that wood P concentration decreased with increasing wood density. Lira-Martins et al. (2022) showed in the Amazon that lower wood density trees store more water in their woody tissues and have high K concentrations, certainly to regulate this reservoir. As Heineman et al. (2016) also showed a good correlation between soil nutrients and wood nutrients, these results could in turn explain why lower wood density trees are limited by P and K soils, in contrast to higher wood density trees.

Finally, our results suggest that soil properties that influence growth are different depending on species wood density, and on tree ontogenic stage. To our knowledge, such an interacting effect between these variables has not been described in the tree growth literature. These nuanced results challenge, at least for the forests of Central Africa, the traditional paradigm that considers plant growth to be mainly P-limited in tropical forests (Vitousek et al., 2010). Other factors (environmental, historical, …), could also explain differences in growth between sites.

4.3.3 | The competition effect is more frequent than the site effect at the population level and not all species grow faster at the same site

At the population level, 48.8% of the species studied included a competition effect, 21% included a site effect and only 7% included both effects. This suggests that species tend to be more sensitive to

competition than to the physicochemical characteristics of the soil. Our conclusions must be taken with some caution, as the often small numbers and their uneven distribution between the sites affect the results presented here.

While, as found in other studies, *G* has been selected as the best competition index at the community level, we expected that the best one selected for each species would depend on its regeneration guild and wood density, but this was not the case. One-sided indices, *NDt* and *GD*, were more frequently selected than the two-sided *Nt* and *G*, whatever their trait; this indicates that access to light even if assessed indirectly remains a key for the most abundant species, gathering about 54% of all trees at the community level. This may partly explain why light indices are often found to be more efficient to explain growth at the species level (see Section 4.4.1).

Size and competition being taken into account, we expected that the site ranking observed at the community level would not translate in the same way at the population level, given the variability of species ecological niches (Baribault et al., 2012; Turner et al., 2018). This was the case. Among the nine species concerned, height were shade-bearers with medium and high wood density, perhaps illustrating a greater sensitivity of shade-bearers to soil resources even if two of them were also sensitive to light (*C. caudatus* and *D. gossweileri*, see Section 3.2). Four species (resp. three, two) had higher diameter growth at Yoko (resp. M'Baïki, Mokabi) while five species (resp. three, two) had lower diameter growth at Mokabi (resp. Loundoungou, M'Baïki). Even if comparisons cannot be correctly done between sites as several species present at M'Baïki were not at Yoko and vice versa, the better performance of some species observed at Yoko could be explained by a high phosphorus affinity: these performing species in Yoko would be less competitive at the other sites and replaced by species with low phosphorus affinity (Turner et al., 2018).

Interestingly, we did not detect any effect of competition nor site on diameter growth for more than one-third (37.2%) of the species studied, while at least competition frequently appears in the literature as a significant explanatory variable in specific growth models. This could result from the particularly low tree density encountered in moist Central African forests compared with moist tropical forests on the other continents, possibly linked with the presence of large herbivorous mammals in these forests (Lewis et al., 2013; Sheil & Salim, 2004).

4.4 | What should be further explored on these sites

4.4.1 | Should we use light indices rather than competition indices?

In this study, we used competition indices based on the dendrometric characteristics of the studied tree and/or of its neighbours, instead of a direct light index (Rueger et al., 2009, 2011) or an indirect one (Clark & Clark, 1999; Dawkins, 1958). Some authors have

combined the two types of indices in their models or compared the part of growth variance explained by one or the other type (King et al., 2005; Laurans et al., 2014; Moravie et al., 1999; Ndamiyehe Ncutirakiza et al., 2020; Zambrano et al., 2019, see Appendix S4: Table 14). Although these light indices attempt to measure the amount of light received by the tree, thus being closer to the actual underlying mechanism, their explained variance was comparable with that of the classical competition indices. A detailed comparison (Grote et al., 2013) of the complex light index developed and used in Panama by Rueger et al. (2009) with a conventional competition index showed that these indices were highly correlated and provided nearly identical species rankings and between-species variation in response to light availability.

The data collection efforts required for such light indices make them difficult to apply in practice, without necessarily achieving a large part of explained variance in growth models: mean R^2 of 12% when combining diameter and light index, and no significant effect for more than one-third of the species studied at BCI (Rueger et al., 2011). The Dawkins index is quicker to collect, but it is based on a partly subjective estimate, making comparisons between sites surveyed by different field teams unreliable: this is the reason why we did not use it in our study. However, the current development of aerial imagery using UAV cameras, which allows a better characterization of tree crowns and their degree of lighting (Araujo et al., 2020; Ndamiyehe Ncutirakiza et al., 2020), could bring important improvements in the medium term.

4.4.2 | Influence of environmental variables

Climatic conditions can influence tree growth in moist tropical forests, particularly through soil water availability (Baker et al., 2003; Hubau et al., 2020; Turner et al., 2018). In Amazonia, Rozendaal et al. (2020) showed that competition pressure increases with CWD (i.e. water availability) because G tends to increase in wetter forests, but they did not observe this in tropical Africa. In this study, we considered our sites to be climatically homogeneous as their location was selected to maximize potential soil effects on tree growth and to limit soil/climate interactions. However, the ranking of our sites according to CWD did not follow their ranking according to G and tree growth, which tends to confirm the results (Rozendaal et al., 2020). More in-depth studies are needed on this subject.

Soil properties have been shown to significantly influence tree growth in moist tropical forests. The limited number of samples we collected on each site constrained us to use *Site* rather than soil characteristics as an explanatory variable in our models. This can have resulted in the low part of growth variance explained. However, our results are similar to those of studies that have invested more heavily in soil characterization (e.g. Baribault et al., 2012; Chi et al., 2015). It would be useful to develop less expensive sampling strategies, similar to the one we used, but with more repetitions allowing statistical tests.

4.5 | Implications for monitoring tree growth at the regional scale

Managing and sustainably harvesting forests require, among other things, access to quantified information on species growth and the determinants of that growth. Small plots (1 ha) are the most frequent in existing networks in Central Africa (Hubau et al., 2020; Rozendaal et al., 2020), limiting the possibility to study in detail the effect of neighbourhood on tree growth. The large plots used in this study allowed for a more thorough test of this effect but are unfortunately expensive to settle and maintain over the long term, limiting their extension on the regional scale. The need to monitor the growth of species, and particularly commercial species in large size Central African forest concessions is leading to the increased use of species-specific trail-type devices (i.e. group of trees of the same species, within a block, numbered and measured regularly DYNAFAC, 2022; Ligot et al., 2022). These devices should be improved, by supplementing the diameter measured on each tree with a neighbourhood inventory of all trees located within a 15 m radius: this will allow us to quantify the four competition indices that were found to be most effective in this study. A recommendation of this type should be made mandatory in all certification systems currently used in the region.

5 | CONCLUSIONS

Our study quantified the effect of factors influencing tree growth in Central African forests using data from a network of large permanent plots. These large plots allowed us to model growth at the community and population levels by integrating various factors, including competition between trees. At the population level, the best growth models were highly variable for the 43 species studied, explaining between 0% and 48% of the variance, with tree diameter emerging as the strongest predictor of tree growth. The competition effect was more frequent than the site effect (for 49% vs. 21% of the species studied), while these two factors had no effect for 37% of the species studied. At the community level, the best model explained 11% of the growth variability. This model included the following variables in order of decreasing importance: wood density, diameter, site and competition. Although site explained only 1.5% of the growth variability, its effect could result from different soil nutrients (not only P but also Ca and Mg) depending on wood density and ontogenic stage. Our study is one of the first in Central Africa to cross-reference, on a large scale, the factors influencing growth with soil characteristics. It contributes, along with those of other authors, to questioning the traditional paradigm that considers plant growth to be mainly P-limited in tropical forests.

AUTHOR CONTRIBUTIONS

Sylvie Gourlet-Fleury: design of the study and the experimental plots, plots settlement and field measurements, data analysis, drafting of the paper. Vivien Rossi: design of the experimental plots, plots settlement and field measurements, data analysis, co-drafting of

the paper. Eric Forni: design of the experimental plots, plots settlement and field measurements, data gathering. Félix Allah-Barem: field measurements, data gathering. Fidèle Baya: field measurements, data gathering. Fabrice Bénédet: data control, data inclusion in a database. Faustin Boyemba: field measurements, data gathering. Guillaume Cornu: data gathering and first data analysis. Jean-Louis Doucet: proofreading and helping to improve the manuscript. Adeline Fayolle: proofreading and thoroughly helping to restructure the manuscript. Jean-François Gillet: plots settlement and field measurements and proofreading. Gauthier Ligot: proofreading and helping to improve the manuscript. Mathurin Mazengue: field measurements and data gathering. Michel Mbasi Mbula: field measurements and data gathering. Yorick Van Hoef: field measurements and data gathering. Isaac Zombo: field measurements and data gathering. Vincent Freycon: conception of the soil study, data collection, characterization and analysis of soil physicochemical properties and co-drafting of the paper.

CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.14152.

DATA AVAILABILITY STATEMENT

Data are available on the CIRAD Dataverse: https://doi.org/10.18167/DVN1/T0DMFJ (Sylvie et al., 2023). The metadata are openly available, and the data are available upon request, due to the fact that data are co-owned by forestry companies and national research structures.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Description of tree species communities.

Table S1. Main characteristics of the species used to study competition and site effects on individual tree diameter growth. Final analysis was done on 43 species with at least 15 trees in each of at least three of the sites, located 15 m from the border of their plot. The number of trees used for the primary analysis (38 species, trees located 20 m from the border of the plots) are within brackets. Regeneration guilds are taken from Hawthorne (1995) and completed from several sources (Bénédet et al., 2019). Mean wood density values come from the Biomass R package (in bold: mean wood density at the genus level, in italic: mean wood density at the African Data Base level).

Table S2. Species distribution according to regeneration guilds (Hawthorne, 1995) and wood density classes (*ClWD*), all sites included and site by site. The corresponding number of trees is indicated in brackets.

Appendix S2. Soil properties.

Table S3. Physical and chemical properties of the eight soil profiles. CEC: cation exchange capacity, Ca, Mg, K, Na (Metson Method, pH7), Al, H (KCl Method).

Table S4. Physical and chemical properties of the eight soil profiles, normalized at 0–15 cm depth. CEC: cation exchange capacity, Ca, Mg, K, Na (Metson Method, pH7), Al, H (KCl Method).

Appendix S3. Models selection and use.

Table S5. Models tested for estimating the mean growth function ΔD_{mean}.

Table S6. Competition functions tested for estimating CI. The competition functions were computed using the set of trees in the neighborhood (NBH) of the focal tree.

Table S7. Number of trees per site used to compare mean growth models and competition functions.

Table S8. Preliminary analysis. Best components of the individual growth models calibrated at the population level for the 38 selected species: mean diameter growth functions, competition indices used in the competition function, and competition radius.

Table S9. Coefficients estimates of fixed effects of the best growth model calibrated at the community level (based on Equation 2).

Table S10. The 10 best growth models selected according to the BIC rank for all trees at the community level (fixed effects + random effects, syntax of the LME4 package (Bates et al., 2015). $R^2c = R^2$ conditionnel, $R^2m = R^2$ marginal (Nakagawa et al., 2017).

Table S11. The 10 best growth models selected according to the BIC rank for all legume trees at the community level (fixed effects + random effects, syntax of the LME4 package (Bates et al., 2015). $R^2c = R^2$ conditionnel, $R^2m = R^2$ marginal (Nakagawa et al., 2017).

Table S12. Best growth model selected (according to the BIC rank) for each of the 43 species studied.

Table S13. Part of the variance explained by CI and site in the best growth model selected for each of the 27 species concerned. To estimate the part added by competition, site, or competition and site, we compared each best growth model to models eliminating each of the target variables.

Table S14. Coefficients estimates of the best growth model for the nine species which included a site effect (based on Equation 1).

Appendix S4. Short description of experimental designs and model used in other studies. NB. There are many limitations to the relevance of comparisons between our results and those obtained in these studies as working protocols, experimental design and modelling methods—comprising predicted variables used to quantify growth—can differ a lot.

Table S15. Studies analysed and main information available.