Contrasted spatial, demographic and genetic structures of a light-demanding African timber species, *Cylicodiscus gabunensis* Harms – Implications for a sustainable management of its populations

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A R T I C L E   I N F O

A B S T R A C T

Most Central African rainforest canopies consist of light-demanding tree species that hold high commercial value but also suffer locally from regeneration deficits, raising concerns about the sustainability of logging. Regeneration is influenced by factors such as past perturbations (including human activity), mating systems, and seed/pollen dispersal processes that impact demographic, spatial, and genetic structures within populations. To gain a better understanding of these interactions, we studied the spatial distribution and trunk diameter structure of *Cylicodiscus gabunensis* (Fabaceae) - a wind-dispersed, insect-pollinated, timber species - in three plots ranging from 400 to 839 ha situated in various environmental contexts (e.g. forest types and elephant densities) across Central Africa. We also genotyped adults and juveniles using microsatellite markers to analyze the spatial genetic structure of each population and infer the selfing rate, seed and pollen dispersal capacities and selection gradients using the 'neighborhood model'. The selfing rate was low (3 – 4 %), and seed dispersal distances ($ds = 184$ m) were much shorter than pollen dispersal distances ($dp > 2$ km). The three populations displayed contrasted spatial, demographic and genetic structures. One population showed no spatial aggregation or genetic structure, and a multimodal diameter structure indicating pulses of regeneration events. Two populations showed strong spatial aggregation and genetic structures. One exhibited a unimodal diameter structure indicating one ancient pulse of regeneration, while the other displayed a 'reverse J-shaped' diameter structure, typical of ongoing regeneration. In the latter, reproductive success appeared leptokurtic, three mother trees accounting for over 90 % of the regeneration and no tree below the minimum cutting diameter implemented by logging companies had offspring. The idiosyncratic nature of population characteristics observed in *C. gabunensis* suggests that, for sustainable management, a nuanced approach is needed. This involves protecting productive seed trees in areas where natural regeneration is occurring and actively supporting regeneration in areas exhibiting deficits, especially in contexts with low elephant densities.

1. Introduction

The canopy of many Central African rainforests is characterized by a high abundance of long-living light-demanding tree species (van Gemerden et al., 2003) that regenerated abundantly by the end of the nineteenth century (Morin-Rivat et al., 2017; Vleminckx et al., 2014). Today many of these species have a regeneration deficit while they are logged for their high commercial value, thus questioning the

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sustainability of their exploitation (Engone Obiang et al., 2014; Hardy et al., 2019; Ndonda Makemba et al., 2019). Tree regeneration is a key process in forest dynamics as it ensures the establishment of the next generation of overstory trees (Clark, 1986; Ebert et al., 2014). It typically depends on various biotic and abiotic factors such as pollination, dispersal, seed predation and germination success (Connell, 1971; Janzen, 1970; Wright, 2002). Moreover, regeneration success of light-demanding species also depends on natural and anthropogenic disturbances (Morin-Rivat et al., 2017; Sola et al., 2022; Tappeiner et al., 1997). By disrupting ecosystem structure and changing resource availability, and especially access to light, disturbances create the conditions for a new succession of species (Yamamoto, 2000). Colonization and establishment of long-lived light-demanding trees is thus indicative of past canopy openings following natural or anthropogenic disturbances (Vlam et al., 2017). A popular explanation for their current dominance in the canopy in Central Africa is that these forests are still recovering from slash-and-burn shifting cultivation over extensive areas that lasted until the 19th century (Morin-Rivat et al., 2017; van Gemerden et al., 2003; Vleminckx et al., 2014). Since Europeans started colonize the region, slash-and-burn agriculture in the hinterland was reduced because people were relocated along main communication roads. The resulting new environment might be less favorable for the regeneration of light-demanding species, which need large gaps to regenerate. This explanation is supported by the fact that present-day natural or logging gap size has been shown to be insufficient for many light-demanding species to regenerate underneath in Central African forests (Dupuy & Chazdon, 2008; van Gemerden et al., 2003). Anthropogenic disturbances that lead to the creation of forest openings spanning several ares or hectares thus seem to enhance the natural regeneration of long-lived light-demanding species (Ndonda Makemba et al., 2022a). However, it has been observed that herbivores, such as the African forest elephant (*Loxodonta cyclotis* Matscie), frequently visit plantations and logging gaps where they cause damage to light-demanding species by trampling seedlings and consume or beak the most vigorous stems, thereby lowering regeneration rate (Scalbert et al., 2022).

Regeneration success of light-demanding species also depends on intrinsic factors such as the mating system and the extent of seed and pollen dispersal (Hardy et al., 2019), processes affecting in turn the demographic, spatial and genetic structures of tree populations (Luambua et al., 2021; Sola et al., 2022). Most tropical tree species are allogamous but self-compatible and occur at low population density (Duminil et al., 2016a; Duminil et al., 2016b; Hardy et al., 2019). Pollen dispersal is therefore crucial to maintain within-population genetic diversity and among-populations connectivity (Monthe et al., 2017). Pollen movement of long-lived light-demanders is often insect-mediated and occurs over longer distances than seed dispersal. However, self-compatibility and the usually low population densities in tropical forests make these species vulnerable to inbreeding and assortative mating (Duminil et al., 2016b; Monthe et al., 2017). Compared to shade-tolerant species, light-demanders usually produce greater number of non-zoochoric, smaller seeds that are dispersed by wind over tens or hundreds of meters, making them efficient gap colonizers (Peres et al., 2016). However, low recruitment level of long-lived light-demanders suggests that traits favoring seed dispersal might disfavor the subsequent seedling establishment and survival (competition-colonization trade-off) in small gaps (Dalling et al., 2002; Dupuy & Chazdon, 2008).

In nature, the spatial distribution of individuals of a single plant species is driven by different factors such as seed dispersal capacity, light-requirement, as well as biotic factors (competition/facilitation, herbivores and pathogens) and habitat heterogeneity and can either be random, regular or aggregated (Fibich et al., 2016; Réjou-Méchain et al., 2011). Under spatially limited pollen and/or seed dispersal, strong spatial genetic structure (SGS), i.e. the non-random distribution of genotypes, is expected within population. SGS can be reinforced if selfing occurs (Angbonda et al., 2021; Hardy et al., 2019) and/or if the reproductive success is very heterogeneous among adults. Spatial aggregation

in low population density is also predicted to increase the magnitude of SGS if mating between near neighbors within aggregates occurs, which could potentially lead to biparental inbreeding (i.e., mating between related individuals) (Duminil et al., 2016b). Hence, comparative analyses of demography, spatial distribution and SGS of a single species across sites or populations can provide important insights to trace the imprint of past disturbances, to investigate colonization history and genetic consequences of seed and pollen dispersal (Fibich et al., 2016; Hardy & Sonké, 2004; Pardini & Hamrick, 2008).

In Central Africa, 26 % of the remaining tropical forest is conceded to logging companies (de Wasseige et al., 2014; Karsenty, 2016). Forests are usually exploited through selective logging. Legally managed concessions target only few timber tree species and only harvest one or two trees per hectare. Harvesting is done every 25 to 30 years and concessions must respect species-specific legal minimum cutting diameters (LMCD) (Karsenty & Ferron, 2017). Despite being regulated, selective logging is expected to reduce population density and to increase distance between mature conspecifics which could impact the natural regeneration of timber tree species (Cascante et al., 2002; Ghazoul et al., 1998; Hardy et al., 2019; Stacy et al., 1996).

Cylicodiscus gabunensis Harms (Fabaceae - Caesalpinioideae), commercially known as 'Okan', is one of these long-lived light-demanding tree species of high commercial value. It is ranked as the sixth most exploited species in Central Africa (Karsenty & Ferron, 2017; Seka et al., 2018). This species often shows a regeneration deficit and low population density in closed-canopy evergreen forests which suggests that particular precautions should be taken to achieve sustainable exploitation (Ndonda Makemba et al., 2019). It is thus a good model to infer the impact of logging on light-demanding, wind-dispersed, insect-pollinated timber species.

Comprehensive understanding of demographic and genetic factors and their influence on population dynamics is crucial to evaluate the impacts of present human disturbances such as selective logging on the natural regeneration of commercial species (Degen et al., 2006; Dupuy & Chazdon, 2008; Sola et al., 2022). To better understand how mating systems, gene flow and disturbances shape the regeneration success of long-lived light-demanding species and how these processes affect demography, spatial distribution and spatial genetic structure (SGS) of tree populations, we compared three distinct populations of *C. gabunensis* located in various environmental contexts. More specifically, the objectives of our study are to: (i) compare diametric distribution, spatial distribution and SGS of *C. gabunensis* between populations and discuss different environmental factors contributing to the variability in demographic characteristics, (ii) characterize mating system, seed and pollen dispersal and determinants of reproductive success, and (iii) evaluate the impact of selective logging on the natural regeneration of *C. gabunensis*.

2. Material & methods

2.1. Study species

Cylicodiscus gabunensis is distributed in the West African forest block (southern Ivory Coast and Ghana) and in the western part of the Central African forest block (southern Nigeria, Cameroon, Equatorial Guinea, Gabon), where it grows in semideciduous and evergreen moist forests (Louppe et al., 2008). This very large canopy tree species endemic to the Guineo-Congolian forests is the only species of the genus *Cylicodiscus*. It can reach 60 m high and a diameter at breast height (dbh) of 2 m (Hédin, 1929). The species is briefly deciduous (Hawthorne & Gyakari, 2006). It grows generally better in well-drained soils found in semideciduous forests. Diametric distribution and population density depend on the forest type and a deficit of regeneration can be observed in evergreen forests (bell-shaped stem diameter distribution) (Ndonda Makemba et al., 2019). Despite being a light-demanding species, seedlings tolerate shade in the first stages of development (Ndonda Makemba et al., 2019).

Inflorescences are spike-like false racemes up to 15 cm long, whitish to pale green yellow, grouped at the top of the branches (Fig. 1). They bear numerous densely packed actinomorphic and hermaphroditic fecal-scented flowers with small petals (c. 3 mm × 0.5 mm) and easily accessible pollen (Ndonda Makemba et al., 2019). This floral structure corresponds to a generalist pollination syndrome that could attract many small-sized pollinators, such as stingless bees, flies and small beetles but also larger nocturnal moths (Bhasin, unpublished results). Fruits (Fig. 1) are long and narrow brown-reddish dehiscent flat pods (up to 90 cm) containing numerous flat papery seeds (up to 7 cm) adapted to wind dispersal (Hédin, 1929). *Cylicodiscus gabunensis* effective fruiting diameter (DFR), which is an estimate of the diameter at which at least 50 % of the trees in the population produce seeds capable of germination, is 60 cm (Ndonda Makemba, 2023). The species is of high economical value and its dense and hard wood is harvested for heavy constructions including water-based constructions and heavy floor (Hédin, 1929; Louppe et al., 2008). Disregarded by the timber market a few decades ago, the interest for the species has recently increased rapidly as it can substitute *Lophira alata* Banks ex C.F.Gaertn. now in shorter supply (Karsenty & Ferron, 2017). The LMCD of *C. gabunensis* varies from 60 cm in Cameroon to 70 cm in Gabon (Ndonda Makemba et al., 2019). Its bark, which has medicinal properties, is highly prized by elephants which severely damage the base of the trees and consume the seedlings (Ndonda Makemba et al., 2022b).

2.2. Study sites and sampling

We inventoried *C. gabunensis* within 400 to 839 ha forest plots in three sites from Cameroon (sites A and B) and eastern Gabon (site C), hereafter referred to as populations (Fig. 2).

These populations are located in areas characterized by different forest types (semideciduous forest in site A, semideciduous-evergreen transition forest in site B, evergreen moist forest in site C; Fig. 2) and variable elephant densities. A recent study investigating how mammal predation affects performances of *C. gabunensis* seedlings in logging gaps pointed out important damages (destruction of 35 % of the seedlings) by the African forest elephant (*Loxodonta cyclotis*) (Ndonda Makemba et al., 2022b), which is rare in site A but moderately to very abundant in sites B and C (Table 1). All three locations have an equatorial climate with a consistent temperature averaging 24–25 °C throughout the year. Sites A and B receive around 1600–1700 mm of mean annual rainfall with two distinct rainy periods from March to June and September to November, separated by less humid intervals. Precipitation in site C also follows a bimodal distribution involving two rainy seasons during March–May and September–December along with relative dry spells during June-August and January-February and with c. 1700 mm of mean annual rainfall. An irradiance-centric analysis revealed that Gabon is strongly light-deficient due to high levels of cloud cover (Philippon et al., 2019). This characteristic contributes to a lower mean amount of solar radiation (hereafter referred as irradiance) received at the surface level in comparison to Cameroon (Table 1).

Site A is a 400-ha plot (2 × 2 km) located near the northern limit of the dense forest range of south-eastern Cameroon, in the Forest Management Unit (UFA) 10-051 managed by the logging company Alpicam/Grumcam (Société des grumes du Cameroun) (4.02°N, 14.69°E). The vegetation in the area consists of semi-deciduous forests (Fig. 2) (Letouzey, 1985). The density of human populations around the UFA is high (Lhoest et al., 2020). Elephants are absent from these forests (Brittain et al., 2020). No recent logging activity had occurred in the plot at the time of sampling (Zanguim et al., 2020).

Site B is also a 400-ha plot (2 × 2 km), located at the northern part of the Dja Faunal Reserve (3.27°N, 12.79°E), which is a protected area established in 1950 (Bruce et al., 2018). The area is characterized by a transition of vegetation formations between lowland evergreen and semi-evergreen moist tropical forest. This protected area has never been logged and the surrounding area has a low human density (Bruce et al., 2018). It still contains elephants, although their density is affected by poaching around and inside the 5260 km² protected area. As per the records of 2018, it was estimated that the forest elephant population in the Dja Faunal Reserve stood at approximately 15 % of its expected carrying capacity for the landscape (Bruce et al., 2018).

Site C is a 839-ha plot of irregular shape (see Fig. 3) located in western Gabon (0°49′N, 13°17′E), in the Forest Management Units 2 managed by the logging company CEB (Compagnie Équatoriale des Bois from Precious Woods Gabon). The surrounding area has a low human density (Haurez et al., 2014), so that the low hunting pressure allows the presence of elephants at a higher density than in site B (Fonteyn et al., 2021). No recent logging activity had occurred in the plot at the time of sampling (Van Hoef, 2019).

In each study plot, all *C. gabunensis* trees with a diameter at breast

Fig. 1. *Cylicodiscus gabunensis*. Flowering canopy (upper left, © O. Bhasin), flowers (upper right, © R. Ndonda Makemba), canopy of a mature tree with ripening fruits (lower left, © R. Ndonda Makemba), fruits and mature seeds (lower right, © J.-L. Doucet).
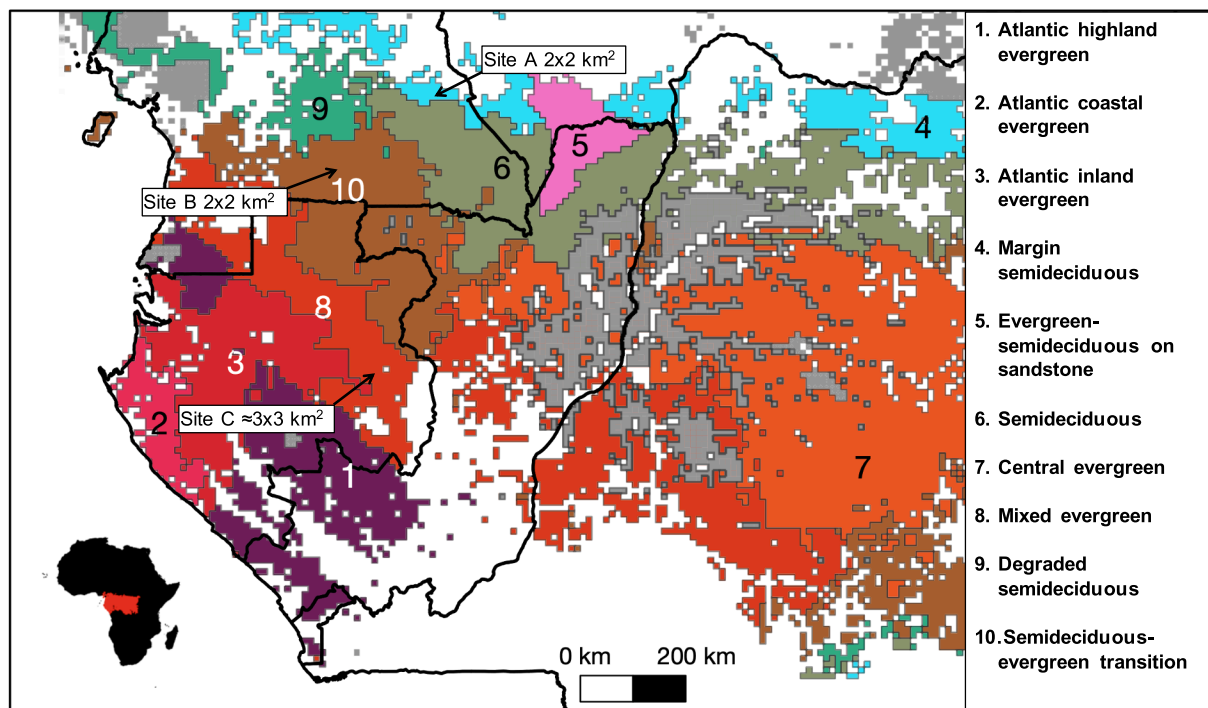
Fig. 2. Location of the three study sites (A, B and C) of *Cylicodiscus gabunensis* on a map showing 10 forest types recognized in Central Africa (Réjou-Méchain et al. 2021a,b), including type 4 ("Margin semideciduous") for site A, type 10 ("Semideciduous-evergreen transition") for site B and type 8 ("Mixed evergreen") for site C. The forest types differ in three main functional characteristics at the tree community level: wood density (low in type 4 – site A, medium in type 10 - site B, high in type 8 – site C), deciduousness (high in type 4 – site A, medium in type 10 - site B, low in type 8 – site C), and maximum diameter (high in type 4 – site A, medium in type 10 - site B, low in type 8 – site C) (modified from Réjou-Méchain et al. 2021a,b).

Table 1
Summary of the key environmental factors characterizing the populations of *C. gabunensis* in sites A, B, and C.

	Site A (Cameroon)	Site B (Cameroon)	Site C (Gabon)
Forest type	Margin semideciduous	Semideciduous-evergreen transition	Mixed evergreen
Elephant abundance	Low	Moderate	High
Mean normalized irradiance data (DNI)	155 W m^{-2}	132 W m^{-2}	105 W m^{-2}
Surrounding human density	High	Low	Low
Latest logging in the area	20–25 years ago	Never	20–25 years ago

height (dbh) ≥ 10 cm were systematically inventoried and georeferenced with a GPS. To ensure exhaustive sampling, six well-trained forest prospectors, spaced regularly between two lines 100 m apart, moved abreast to systematically sample the individuals found. Individuals with a dbh < 10 cm were also inventoried when encountered although we do not expect to have reached an exhaustive inventory for them. In site C we also collected seeds or recently germinated seedlings (usually found in dense patches) below the crown of the sampled trees when available. The dbh of each sampled tree was measured and in site A, the dominance status of each tree, indicating whether the position of the tree crown is below, within, or above relative to the surrounding canopy layer (dominant, co-dominant or dominated) was also recorded. For each individual we collected a sample of a few cm^2 of cambium or a leaf that was immediately dried with silica-gel to preserve DNA.

2.3. DNA extraction and genotyping

DNA was extracted using the NucleoSpin plant kit (Macherey-Nagel,

Deuren, Germany). When conducting genetic analyses, saplings and juveniles are not distinguished and instead categorized as juveniles due to their similar nature as individually dispersed plants in the genetic analyses. Distinguishing between saplings and juveniles is typically done while analyzing the demographics. Hereafter, we will refer to tree for individuals with a dbh ≥ 20 cm or juvenile for individuals with a dbh < 20 cm. Samples from site A (125 trees and 117 juveniles), site B (45 trees and 7 juveniles), and site C (140 trees, and 205 seeds and seedlings below 13 putative mother trees) were genotyped at 24 nuclear microsatellite loci (nSSR) following the protocol of a recent study developing and characterizing microsatellite markers in *C. gabunensis* (Bhasin et al., 2022).

2.4. Data analyses

2.4.1. Characterizing the demography of individuals and their diameter structure

We generated maps of each plot where individuals were classified in different size classes: i) seeds and recently germinated seedlings, i.e., found in dense patches below the crown of a conspecific tree during the 2019 fruiting period in site C; ii) saplings (established plants of dbh < 10 cm); iii) juveniles (dbh from 10 cm to < 20 cm) and iv) trees from 20 cm up to < 200 cm grouped by interval of 10 cm. For the trees we also generated histograms of frequencies per dbh class and computed the stand density.

2.4.2. Characterization of fine-scale spatial distribution and aggregation of trees

We characterized the spatial distribution of trees (dbh ≥ 20 cm) using the R package 'spatstat' (Baddeley et al., 2015) by the pair correlation function *g* (PCF), a distance-dependent correlation function related to the derivative of the widely used K-function (Ripley, 1976). The PCF is defined as the probability of observing a pair of points separated by a distance *r*, divided by the corresponding probability
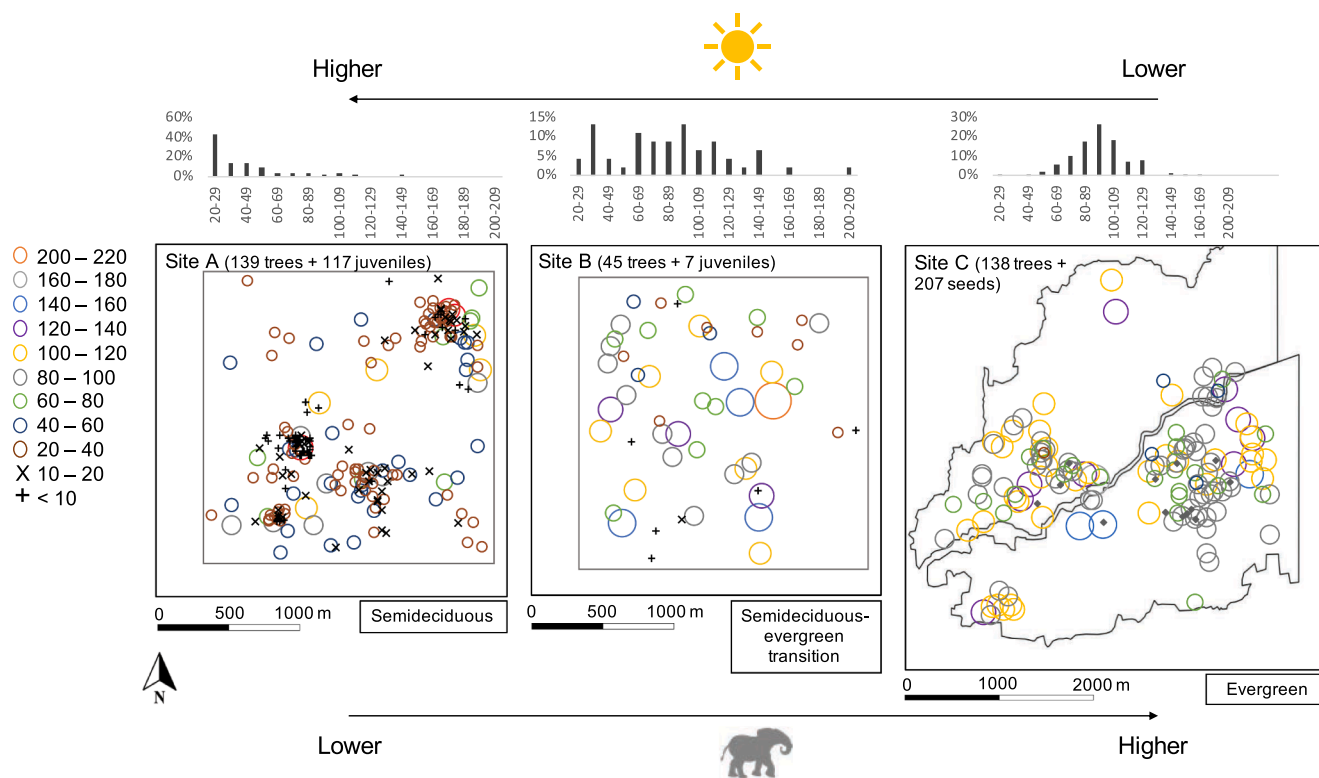
Fig. 3. Diametric distribution of trees with dbh ≥ 20 cm (upper panels) and spatial distribution maps of the different size classes (lower panels) of *Cylicodiscus gabunensis* in three Central African forest sites: site A (left), site B (center) and site C (right). The size and color of circles indicate the dbh class in cm of each tree while other symbols refer to juveniles, saplings, seedlings or seeds (see legend). The areas where trees with a dbh > 10 cm were exhaustively sampled are delimited by a line (400-ha squares in sites A and B, irregularly shaped 839-ha area in site C). In site A, three red circles correspond to three individuals responsible for 91.5 % of identified progenies and referred to as "super mothers" in the text. Upper and lower arrows indicate gradients of irradiance and elephant abundance, respectively.

under complete spatial randomness (uniform Poisson). Therefore, spatial aggregation will be marked by $g(r) > 1$ at small r and decreasing with *r*. Under complete spatial random distribution (CSR), $g(r) = 1$ at all distances. Deviation of the observed spatial pattern from the CSR null hypothesis was tested by comparing the observed distribution with 5 % critical value obtained from 399 Monte Carlo simulations of a Poisson process. Ripley's isotropic correction (Ripley, 1988) for edge effect was applied.

2.4.3. Characterization of fine-scale spatial genetic structure

The fine-scale spatial genetic structure (FSGS) of the three populations within their sampling area was characterized by the decay of the kinship coefficient, *Fij*, between trees (dbh ≥ 20 cm) with spatial distance (kinship–distance curve) following the procedure described by Vekemans & Hardy (2004), using SPAGeDi ver. 1.5d (Hardy & Vekemans, 2002). For each pair of individuals i and j from the same population, F_{ij} was estimated using J. Nason's estimator (Loiselle et al., 1995) and the set of F_{ij} values were regressed on the spatial distance $\ln(d_{ij})$ between individuals providing the regression slope b_{Ld}. The later can inform about the strength of FSGS through the statistic *Sp*, which synthesizes the decay of kinship coefficient between individuals with distance (Vekemans & Hardy, 2004). To visualize FSGS, F_{ij} values were also averaged for a set of nonoverlapping distance intervals (delimited by 50, 100, 200, 300, 500, 700, 1000, and 1500 m) to obtain the *F(r)* curve. Standard errors were provided by jackknifing loci (i.e. deleting information from one locus at a time). To test for FSGS, spatial positions of trees were permuted 999 times to draw 95 % confidence intervals of the *F(r)* curves under the null hypothesis (random spatial distribution of genotypes).

2.4.4. Estimation of seed and pollen dispersal parameters and selection gradients

We used the 'neighborhood model' (parentage model) to estimate seed and pollen dispersal kernels, selfing rate and effects of phenotypic characters on reproductive success. The model is implemented in the software NMπ (Chybicki, 2018) that requires genotype data on progeny and their putative parents, their spatial coordinates, and optionally tree quantitative phenotypic characters to estimate their effects on male and female reproductive success. NMπ was run on plot A and C but not on plot B because there was not enough regeneration (only 7 juveniles found). In site C, seeds and recently germinated seedlings found in dense patches below the crown of a conspecific tree that were genetically compatible with the tree above (as a mother tree) were declared as 'non-dispersed' while seeds and recently germinated seedlings below the crown of a conspecific tree incompatible with the tree above were declared as 'dispersed'. In site A, saplings and juveniles (dbh < 20 cm) were assigned as dispersed progeny, considering that potential parental trees have a dbh of at least 20 cm. This data collection, with site A providing insights into female reproductive success and seed dispersal, and site C focusing on pollen dispersal and paternal reproductive success allows the study of both male and female contributions, as explained in the subsequent paragraph.

Pollen and seed dispersal were measured by: the selfing rate *s*, the proportion of pollen and seed immigration *mp* and *ms* (indicating that the father or both parents were located outside the sampled plot, or were missed during sampling) as well as four parameters of the exponential-power-von Misses distribution for modelling forward dispersal kernel (i. e., distribution of seed or pollen rains around parents). These kernel parameters are: the mean pollen and seed dispersal distance *dp* and *ds*, the shape parameter of the dispersal distribution *bp* and *bs* (i.e., $b = 2$ for a Gaussian distribution, $b = 1$ for an exponential distribution, $b < 1$ for a

fat-tailed distribution), the intensity of directionality (anisotropy) in dispersal kp and ks (with $k = 0$ under isotropic dispersal), and the azimuth of the prevailing dispersal direction ap and as (when $kp > 0$ or $ks > 0$). The effect of phenotypic characters on female and male reproductive success (selection gradients) was assessed through NMπ. This analysis involved centered and standardized dbh values and, for site A, centered and standardized dominance status (high values for trees dominating the surrounding canopy). Kendall's rank correlation coefficient (τ_b) was used to examine the relationship between dbh and tree dominance status.

Once all parameters were estimated, NMπ provided the most likely mother and father of each seed and seedling with an associated probability, accounting simultaneously for the spatial, genotypic and phenotypic character data. Considering the progeny (seedlings and juveniles) for which a father/mother was inferred with a probability of $P \geq 0.8$, the dbh structure was compared between all trees, inferred mothers and inferred fathers, computing the percentages of progeny produced by each dbh size class. The dbh distributions were then compared with the LMCD of *C. gabunensis* in Cameroon and Gabon to assess the contribution of exploitable trees to the reproductive potential of the stand and the implications for natural regeneration after selective logging.

We also plotted the two-dimensional dispersal distributions of seeds and pollen, using respectively the positions of juveniles with respect to their inferred mothers and the positions of mothers with respect to the fathers, considering dispersal events inferred with a probability of $P \geq 0.8$. Finally, we estimated the effective number of distinct fathers pollinating a mother tree (*Nep*) as the reciprocal of the level of correlated paternity within 11 maternal sibships collected in site C using Poldisp (Robledo-Arnuncio et al., 2007).

2.4.5. Genetic diversity and fixation index

Mean number of alleles (*Na*), standardized allelic richness, observed heterozygosity (*Ho*), expected heterozygosity (*He*) and Weir and Cockerham's fixation index (F_{IS}) were estimated with SPAGeDi 1.5 in each population and separately for three cohorts: adults, juveniles as well as seeds and recently germinated seedlings. We also jointly estimated the population inbreeding and the frequencies of null alleles for each population and for each cohort using INEst v2.2 with the Bayesian approach (model "nfb"). *Ho* estimates were compared between seeds, seedlings and adults to check if there was a reduction of observed heterozygosity with age, a sign of inbreeding depression. The selfing rate of the three cohorts in each population was also estimated with SPAGeDi 1.5 based on the standardized identity disequilibrium between loci (David et al., 2007).

3. Results

3.1. Spatial and diametric structures of each population

The three sites displayed contrasted population densities, diametric structures and spatial distributions of *C. gabunensis* (Fig. 3). Small-diameter trees were observed in site A (N = 139 trees with dbh $\geq$ 20 cm and 117 juveniles) and site B (45 trees and 7 juveniles) but not in site C (138 trees). Site A was characterized by a 'reverse J-shaped' dbh distribution (Fig. 3) with high number of individuals in the first dbh class and with gradual decrease of larger sized trees. In site B, the species showed a multimodal dbh distribution as small (dbh in the 30–39 class) and large (dbh in the 90–99 class) trees were the most abundant while very few trees had a dbh between 40 and 59 cm (Fig. 3). Site B is the only one where trees with a dbh > 200 cm were found. Site C is characterized by a 'bell-shaped' dbh distribution (Fig. 3) with fewer smaller and larger trees. Median of dbh decreased progressively from 90.0 cm in site C to 75.7 cm in site B and 33.2 cm in site A. Highest population density of *C. gabunensis* was found in site A (60.5 individuals km^{-2}) and decreased abruptly in site B (13 individuals km^{-2}) and site C (17 individuals km^{-2}).

3.2. Fine-scale spatial distribution and aggregation of trees

The spatial aggregation of trees was higher in site A (Pearson χ^2 test, p-value = 0.005) and site C (p-value = 0.005) than in site B (Fig. 3, Appendix 1a, b, c). In sites A and C, the spatial distribution of *C. gabunensis* exhibited aggregation at a small scale, with pairs of individuals separated by 50 m occurring 4.8 and 3.9 times more frequently, respectively, than under complete spatial randomness with the same average tree density. By contrast, the spatial distribution in site B was not statistically different (p-value = 0.05) from a random process ($g = 1$).

3.3. Fine-scale spatial genetic structure of trees and juveniles

The kinship–distance curves showed a regular decay, approximately linear with the logarithm of the spatial distance, in all sites (Fig. 4). However, FSGS was stronger in site C (mean b_{Ld} = -0.028 $\pm$ 0.002; *Sp* statistic = 0.033) and site A (b_{Ld} = -0.026 $\pm$ 0.005; *Sp* = 0.028) than in site B (b_{Ld} = -0.004 $\pm$ 0.003; *Sp* = 0.004) where no FSGS was detected.

3.4. Seed and pollen dispersal modelling

The selfing rate estimated by NMπ was low and very similar in both site A and site C (respectively, $s = 4$ % and 3 %) (Table 2). Pollen dispersal was very extensive as illustrated by the high immigration rates: $mp = 71$ % $\pm$ 3.2 % at site C and $mp = 94$ % $\pm$ 3 % at site A (Table 2). In the larger site C, we detected pollen dispersal events up to 2.5 km (mean distance of pollen dispersal events detected = 656 m) (Fig. 5a) while the fitted pollen dispersal kernel resulted in a mean dispersal distance $dp = 4923$ m and a fat-tailed distribution (exponent $bp = 0.38 \pm 0.31$; Table 2). The estimated dp had a very broad confidence interval (unbounded upward; Table 2) but when the shape of the kernel was fixed to $bp = 0.38$, the confidence interval indicates that the mean pollen dispersal distance dp should be at least equal to 2.5 km (Table 2). The mean correlated paternity per maternal sibship was 0.057, resulting in a mean effective number of fathers per outcrossed maternal sibship (*Nep*) = 17.5.

Seed dispersal parameters could only be estimated in site A given the low regeneration rate in the two other populations (48.3 % of individuals with dbh < 20 cm in site A, 13.5 % in site B and 0 % in site C). Seed dispersal appeared more restricted than pollen dispersal as the maximal distance of detected seed dispersal events was 311 m (mean dispersal distance = 96.2 m) (Fig. 5b). The seed immigration rate was also lower: $ms = 13$ % $\pm$ 4 % (Table 2). Moreover, the fitted seed dispersal kernel resulted in a mean $ds = 184$ m with 95 % CI from 26 to 526 m and a kernel which did not differ significantly from an exponential distribution ($bs = 1.16 \pm 0.40$). Seed dispersal anisotropy was not detected ($ks = 0.07 \pm 0.25$; Fig. 5b).

3.5. Determinants of reproductive success and diameter distribution

The impact of dbh on the female reproductive success was only inferred in site A where a strong effect was detected ($g = 1.14 \pm 0.11$; Table 2). By contrast, the dominance status of the crown, although strongly correlated with the dbh (Kendall's rank correlation $\tau_b = 0.51$, P < 0.001), was uncorrelated with the female reproductive success when both the dominance status and the dbh are included in the model. The impact of dbh on the male reproductive success was only inferred in site C where a relatively weak effect was detected ($b = 0.24 \pm 0.14$; Table 2). It should be noted that the apparent lower impact of the dbh on the male than female reproductive success could be affected by the different dbh structures in the two sites: unimodal in population C versus "inverted J" in population A. Thus, the bell-shaped dbh structure in site C implies a relatively low variability of dbh among trees, limiting the power to detect a dbh effect (Fig. 3). The impact of dbh on reproductive success is further illustrated by comparing the distributions of dbh for all trees,
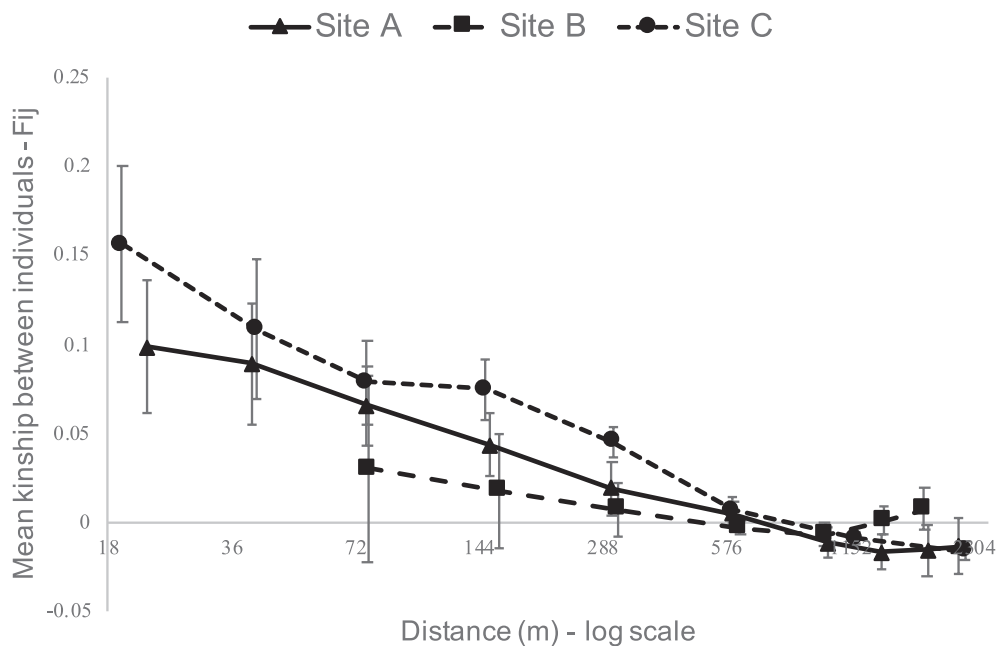
Fig. 4. Comparison of the fine-scale spatial genetic structures (FSGS) of *C. gabunensis* trees in the three study sites, as assessed by the kinship coefficient (F_{ij}) plotted against geographical distances (in meters, on a logarithmic scale). Symbols distinguish site A (triangles), site B (squares) and site C (circles).

Table 2

Seed and pollen dispersal parameters of *C. gabunensis* according to the 'neighborhood model' implemented in NMπ. Unless indicated, pollen dispersal parameters were inferred from the 839-ha plot of site C while seed dispersal parameters were inferred from the 400-ha plot of site A.

Neighborhood model parameter	Estimate ± standard error
Selfing rate (*s*)	0.03 ± 0.01 (site C)
	0.04 ± 0.01 (site A)
Pollen immigration rate (*mp*)	0.71 ± 0.03 (site C)
	0.94 ± 0.03 (site A)
Shape of pollen dispersal kernel (*bp*)	0.38 ± 0.31
Mean kernel pollen dispersal distance (*dp*)	4923 m [858 - ∞][a] [2563 – 62,249][b]
Pollen dispersal anisotropy (*kp*)	0.35 ± 0.19
Pollen dispersal prevailing direction (*ap*)	0.77 ± 0.12 (W)
Seed immigration rate (*ms*)	0.13 ± 0.04
Shape of seed dispersal kernel (*bs*)	1.16 ± 0.40
Mean kernel seed dispersal distance (*ds*)	184 m [26 – 526][a]
Seed dispersal anisotropy (*ks*)	0.07 ± 0.25
Seed dispersal prevailing direction (*as*)	0.45 ± 0.54
Effect of dbh on female fitness (*g*)	1.14 ± 0.11 (site A)
Effect of dbh on male fitness (*b*)	0.24 ± 0.14 (site C)

[a] 95% confidence interval when both the shape and mean distance of dispersal kernels are estimated.

[b] 95% confidence interval when the shape parameter *bp* is fixed to 0.38.

trees identified as mothers, and trees identified as fathers (Fig. 6).

In site A, results obtained for diameter structures of mothers were contrasted compared to site C and showed an extreme variance in reproductive success among trees (Fig. 6a). When considering juveniles for which at least one parent was detected at P ≥ 0.8 (N = 76), the smallest reproductive mother (OK207) had a dbh of 73 cm. Three "super mothers" (dbh = 105 cm, dbh = 107 cm, dbh = 144 cm) contributed disproportionally to the production of offspring as they mothered 91.5 % of the progenies. Individual OK79 itself (dbh = 144 cm) was responsible for 72.9 % of them, causing a much-aggregated distribution of seedlings (Fig. 3).

In site C, results obtained for diameter structures of reproductive trees were contrasted between mothers and fathers (Fig. 6b). When considering seeds for which at least one parent was detected at P ≥ 0.8 (N = 201), the smallest reproductive mother had a dbh of 70 cm.

Mothers with a dbh in the 80–89 cm and 90–99 cm classes contributed to more than half (53.7 %) of the production of seeds. Fathers with a dbh < 80 cm contributed more to the production of offspring (11.5 %) than the mothers and those with a dbh in the 90–109 cm range fathered more than half (53.8 %) of the progenies. However, the reproductive success of fathers dropped above 110 cm.

3.6. Genetic diversity, genotyping error rates, inbreeding and selfing rates

The 24 SSR loci showed 4 (Cyl05 and Cyl16) to 27 (Cyl27) alleles with a mean of 9.96 alleles per locus. The mean effective number of alleles (N_a) per population and cohort ranged from 6.33 to 7.58 (average of 6.90). Per population and cohort, mean H_o ranged from 0.49 to 0.56, and mean H_e from 0.51 to 0.58. Of the 24 loci studied, a weak multi-locus heterozygote deficit in site A (mean F = 0.046) and site C (mean F = 0.072) was mostly driven by nine loci (Cyl07, Cyl14, Cyl16, Cyl24, Cyl25, Cyl28, Cyl37, Cyl38, Cyl45), which significantly deviated from HWE in at least one of the populations. However, heterozygosity deficiency was associated with higher frequencies of null alleles indicating that it was mostly driven by null alleles rather than inbreeding which was absent in site A and C according to INEst, with the exception of site B (F = 0.106). Similar genetic diversity parameters were observed in the different cohorts but were more contrasted between populations (Table 3). The observed heterozygosity (H_o) did not differ among cohorts in site A (H_o = 0.50 in juveniles and 0.49 in adults) and in site C (H_o = 0.51 in seeds and 0.52 in adults). The indirect selfing rate estimates were very close to 0 in all populations and cohort, confirming the low level of selfing in this species (Table 3). Finally, there is no evidence of inbreeding depression in *C. gabunensis*, given the absence of increase in observed heterozygosity (H_o) and absence of decrease in heterozygosity deficiency (F) with age in sites A and C.

4. Discussion

The sample sizes and number of study sites, along with the contrasted forest types allow us to better understand factors influencing the range of demographic parameters (population density, spatial distribution and structure), gene flow and genetic structure in *C. gabunensis*. Hereafter, we discuss the mating system, pollen- and seed-mediated
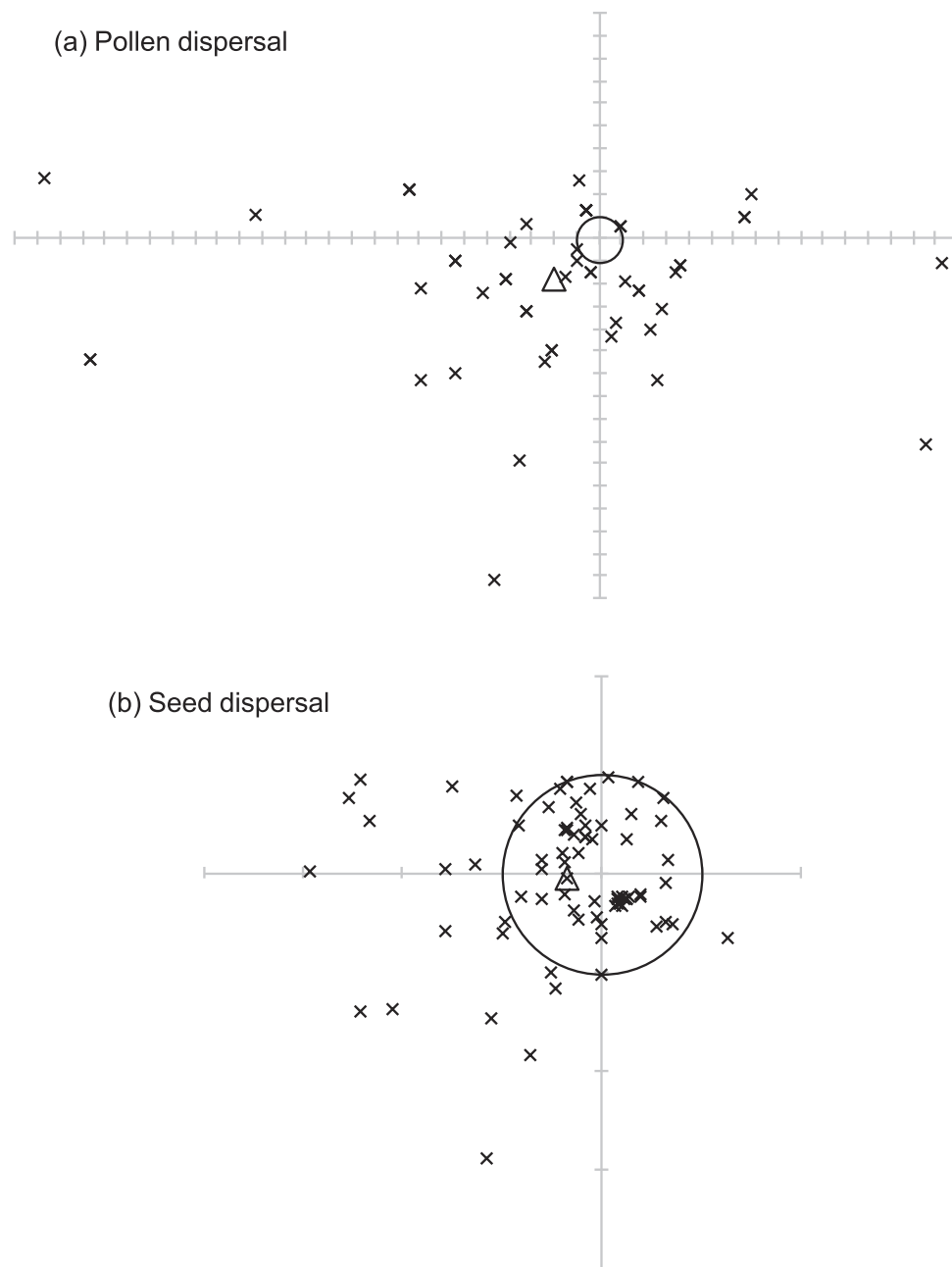
Fig. 5. Spatial representation of the dispersal events around the source inferred by parentage analyses for pollen (upper panel, site C) and for seeds (lower panel, site A). Propagule dispersal events (x symbols) inferred with a probability ≥ 0.8 are depicted after adjusting the latitudinal and longitudinal displacements based on the source (0, 0 coordinates). The circle centered on the source has a radius of 100 m. The triangles indicate the mean vector of all dispersal events.

gene flow and factors affecting the spatial distribution and spatial genetic structure within three populations as well as implications for sustainable logging of the species. Our results will also be compared with those obtained from other tropical tree species.

4.1. Insights into the drivers influencing the contrasted demographic characteristics of C. gabunensis populations

The examination of *C. gabunensis* across three sites revealed distinct stem diameter structures. Site C displayed a 'bell-shaped' dbh distribution, indicating a homogeneous even-aged stand, while site A exhibited a 'reverse J-shaped' dbh distribution, characteristic of a balanced uneven-aged stand due to abundant seedlings and saplings.

Site B presented a seemingly multimodal dbh distribution, suggesting coexisting age cohorts (Eichhorn, 2010).

The regeneration of light-demanding species in evergreen forests of Central Africa, such as *C. gabunensis*, is influenced by both environmental and anthropogenic factors (van Gemerden et al., 2003). Some of these factors include the specific light requirements of the species, as well as anthropogenic pressures and herbivory. Dense evergreen forests, more prevalent in the western regions of Central Africa, face lower light availability during dry seasons compared to the semideciduous forests in Cameroon. Ndonda Makemba's (2023) research indicated that the optimal irradiance for *C. gabunensis* seedling growth falls between 10 and 40 %, a range typically unavailable in evergreen forest understories. The regeneration and population dynamics in southeast Gabon's
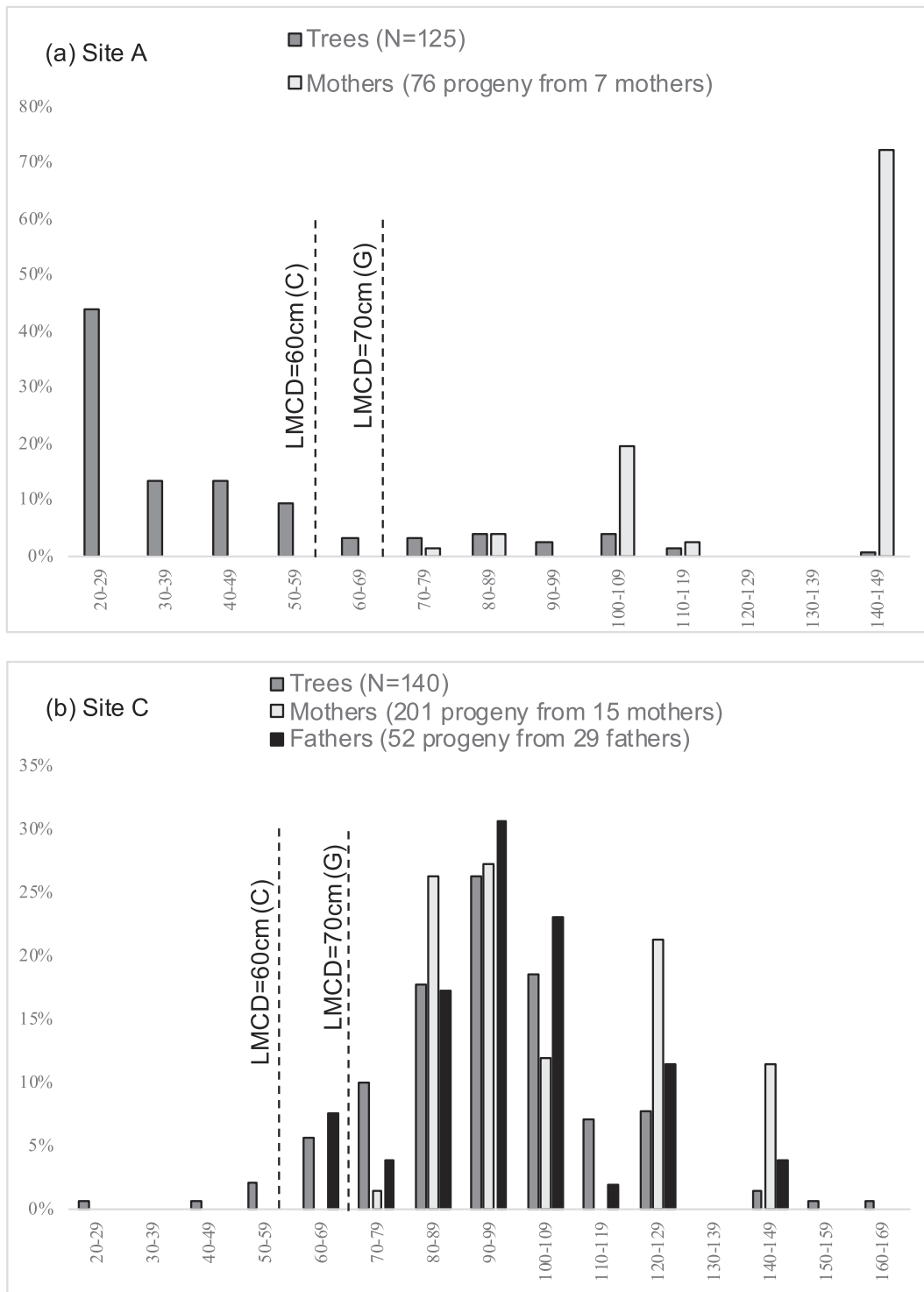
Fig. 6. Comparison of the dbh structures of all trees with that of inferred mothers and fathers of juveniles or seeds in the *Cylicodiscus gabunensis* populations of site A (above) and site C (below). The legal minimum cutting diameters (LMCD) for *C. gabunensis* in Cameroon (C) and Gabon (G) are also shown to envision the potential impact of selective logging on the reproduction potential.

evergreen forests (site C) might be further influenced by human activities and soil fertility, as reported by Ndonda Makemba et al. (2022a). However, the lack of large-scale human-induced disturbances, particularly due to the abandonment of slash-and-burn agriculture practices, has led to a decline in natural regeneration for this species (van Gemerden et al., 2003). Forest elephant herbivory has been identified as another significant factor influencing *C. gabunensis* regeneration in evergreen forests. Despite recent declines in forest elephant populations,

Gabon sustains relatively high densities of these animals (Laguardia et al., 2021). Elephants feed in plantations and logging gaps, causing damage to seedlings and significantly impacting the regeneration of light-demanding species (Scalbert et al., 2022). Ndonda Makemba et al. (2022b) conducted a study on *C. gabunensis* seedlings planted in felling gaps within our site C. They found that gap size significantly influenced diameter growth and survival rates, and the impact of elephants was substantial, with 35 % of seedlings destroyed after 18 months (Ndonda

Table 3

Parameters of genetic diversity and consanguinity for different populations and cohorts of *C. gabunensis* in three Central African forest sites.

	N	*N_a*	*H_o/H_e*	*F_IS*	*F*	*s*	*b_Ld*	*Sp*
site A			*0.49/0.52*	*0.046***				
adults	125	6.33	0.49/0.51	0.047**	0.004 (0.000–0.013)	0.022 ± 0.030	−0.026 ± 0.005	0.028
juveniles	117	6.46	0.50/0.51	0.030	0.003 (0.000–0.010)	0.015 ± 0.030	−0.024 ± 0.005	0.030
site B			*0.56/0.58*	*0.042*				
adults	45	6.71	0.56/0.58	0.038	0.106 (0.068–0.144)	0.040 ± 0.033	−0.004 ± 0.003	0.004
site C			*0.51/0.55*	*0.072***				
adults	140	7.42	0.52/0.56	0.077**	0.004 (0.000–0.011)	0 ± 0.002	−0.028 ± 0.002	0.033
seeds	205	7.58	0.51/0.55	0.059**	0.009 (0.000–0.016)	0.017 ± 0.017	/	/

N Sample size.

N_a Effective number of alleles.

H_o/H_e Observed heterozygosity/ Expected heterozygosity.

F_{IS} Inbreeding coefficient (i.e. apparent heterozygote deficit).

F Inbreeding coefficient corrected for null alleles and 95% highest posterior distribution (INEST estimates).

s Selfing rate ± se (standard error) based on identity disequilibrium.

b_{Ld} Regression slope ± se of kinship coefficient values on the logarithm of the spatial distance between individuals.

Sp Degree of fine-scale spatial genetic structure (FSGS).

Makemba et al., 2022b). Notably, site A experiences higher levels of irradiance (Philippon et al., 2019; Seiwa, 1998; Tang & Dubayah, 2017) and the absence of elephants (Brittain et al., 2020), potentially promoting favorable conditions for seedling growth. By contrast, site B has intermediate conditions in terms of light and elephant density, which could contribute to a multi-story uneven-aged stand with episodic regeneration and a less aggregative distribution of trees.

Understanding the relative importance of various factors in determining species' population dynamics is crucial for developing effective management strategies. Nonetheless, this study did not specifically examine the influence of environmental factors and human activities on the natural regeneration of *C. gabunensis*. Further research is needed to explore the underlying reasons for the varying demographic characteristics of this species. A comprehensive assessment of the entire forest, considering species composition, total tree density, and dbh distribution, is crucial for accurate regeneration estimations. Such assessment would require multiple site replicates to test the various factors and assess if these findings can be generalized across different regions.

4.2. Fine-scale spatial distribution and genetic structure also vary with the regeneration history

The three study sites displayed contrasted spatial distributions of trees and spatial genetic structures, albeit not in the same sequence as their dbh structures. There was a shift from strong aggregation of *C. gabunensis* in sites A and C to a random distribution in site B. The degree of fine-scale spatial genetic structure followed the same trend and was thus well correlated with the degree of spatial aggregation.

Aggregation is common in tropical trees (e.g. Picard et al., 2009; Plotkin et al., 2002; Réjou-Méchain et al., 2011; Traissac & Pascal, 2014) and different factors can promote species aggregation (Luambua et al., 2021) such as: i) variation in local site characteristics and site history (spatial heterogeneity); ii) competition for light leading to regeneration of clustered offspring in tree gaps (mostly for light demanding-species); iii) spatially limited seed dispersal; iv) biotic factors (intra- or inter-competition and facilitation). Clustered distribution of this anemochorous species in evergreen (site C) and semideciduous forests (site A) suggested that aggregation was strongly driven by spatially limited seed dispersal (as discussed below) and light-requirements for the growth of seedlings. Studies have also highlighted the role of spatial heterogeneity, competition and facilitation in shaping species distribution, structure and pattern but these factors were not examined during this study (e.g. Eichhorn, 2010; Hardy & Sonké, 2004; Réjou-Méchain et al., 2011).

The fine-scale spatial genetic structures (FSGS) observed in *C. gabunensis* populations were consistent with isolation-by-distance models as the kinship coefficient decayed approximately linearly with

the logarithm of the distance (Vekemans & Hardy, 2004). Significant FSGS in *C. gabunensis* was found in populations of sites C and A, reflecting nonrandom distribution of the genotypes. Pairs of trees spaced by c. 18 m had a kinship coefficient as high as the value expected between half-siblings (c. 0.125; Fig. 4). By contrast, in site B, the FSGS did not depart significantly from a random distribution but this result must be taken cautiously because it could be a consequence of the small sample size (N = 45 trees), due to the low density of the species in this site, limiting the statistical power to detect a FSGS. Nevertheless, the amplitude of FSGS in site B is c. four times (4.2–5.0 with 95 % C.I.) less pronounced than in sites A and C, paralleling the differences in the degree of spatial aggregation of trees among sites.

While relatedness is controlled by mating system and pollen flow (Angbonda et al., 2021; Duminil et al., 2016b), the FSGS depends mostly on seed dispersal distance and population density (Duminil et al., 2016b; Dutech et al., 2002). Limited seed dispersal could thus be the main factor explaining both the high aggregation and strong FSGS observed in two of our sites. In addition, FSGS decreases with the effective population density, i.e. density of individuals weighted by their reproductive success (Hardy et al., 2006). In site A, we observed an extreme variance of female reproductive success as 73 % of seedlings were mothered by a single large tree. This phenomenon should decrease substantially the effective population density and, hence, increase the FSGS. Moreover, historical colonization events can also have lasting effects on FSGS (Pardini & Hamrick, 2008). The high values of *Sp* statistic in sites C (*Sp* = 0.033) and A (*Sp* = 0.028) denoted a strong spatial genetic structure. Thus, we hypothesize that the FSGS in both sites results from a colonization process involving a few seed trees, so that the low seed dispersal distance combined with low effective density of founders resulted in strong FSGS. In site B, the lower FSGS may suggest a higher effective density, despite the lower census density, if the current population was established by a more even distribution of reproducing trees over time.

4.3. Long-distance pollen dispersal but short-distance seed dispersal

We found that *Cylicodiscus gabunensis* is mainly an outcrossing species as direct and indirect estimates of selfing rate remained low (0 % up to 4 % in seeds, juveniles and trees from site A and site C). Selfing rate was not affected by limited pollen dispersal as suggested by the absence of impact of population density on selfing. Partial self-incompatibility systems or prezygotic factors, such as unsynchronized flowering (Loiselle et al., 1995) might limit autogamy. These mechanisms possibly also limit mating between near neighbors, which would otherwise lead to biparental inbreeding (i.e., mating between related individuals) (Angbonda et al., 2021; Monthe et al., 2017).

Seed and pollen dispersal characteristics were very contrasted in

C. gabunensis, so that pollen is the main vector connecting spatially distant stands. One of the most striking results is how far the pollen can travel. Within the 8.39 km^2 plot of site C, pollen dispersal distance ranged from 108 to 2481 m, and we still observed a very large amount of pollen immigration (c. 71 %). The best-fitting pollen dispersal kernel indicates a leptokurtic (i.e., fat-tailed) distribution with an average distance > 2 km, so that most pollen disperse over several kilometers. Such long-distance pollen dispersal ensures a high degree of genetic connectivity among populations of *C. gabunensis*. The large effective number of fathers per maternal sibship in site C (about 17 fathers) also indicates that each seed tree received pollen from many sources. Therefore, pollen is not a limiting factor for ovule fecundation despite the relatively low population density (22 trees of $\geq$ 20 cm dbh km^{-2}). The higher immigration rate in site A can be due to the smaller size of the inventoried area (400 ha instead of 839 ha for site C), indicating that 400 ha is too small to estimate pollen dispersal kernel or male selection gradient in *C. gabunensis*.

Studies have reported that small-flowered species attract smaller-sized insect pollinators (Dick et al., 2003) and have lower pollen dispersal distances (often < 300 m) in closed-canopy forests (Hardy et al., 2019) than large-flowered species (e.g. in Dipterocarpaceae species, Kettle et al., 2011). Hence, *C. gabunensis* appears as an exception as it bears very small flowers and yet disperse its pollen over long distances. Analysis of 27 h of video recordings from three cameras focused on a single tree in Gabon revealed that nocturnal moths visited *C. gabunensis*' flowers (Bhasin, unpublished results). Several moth species are known to travel for long distances (Hendrix et al., 1987) but additional evidences are needed to identify insects responsible for effective long-distance pollen dispersal. Additionally, smaller insects like stingless bees, flies, and small beetles (making up 84 % of potential pollination events according to video recordings) may be carried over longer distances by strong winds. This could explain the western direction of pollen dispersal in site C. The flowering period of *C. gabunensis* coincides with the rainy season from May to October, which is influenced by southwest monsoon winds (www.climate-data.org). Specialized fig wasps also utilize wind currents for extensive travel between sparse populations of specific fig species, promoting gene flow between populations (Ahmed et al., 2009; Nason & Hamrick, 1997). This results in a prevalent gene flow direction likely influenced by the dominant wind direction in these regions. While it is widely accepted that the roles, significance, and diversity of pollinators can vary significantly across different locations and time periods (Abrahamczyk et al., 2011; Herrera, 1988; Mertens et al., 2021), the lack of research on pollinators in sites A and B, along with observations limited to a single tree in site C, reveals a gap that requires further exploration. This is crucial in order to gain a thorough understanding of pollen-mediated gene flow. Population density can also strongly affect pollen dispersal distances and studies of low-density population trees in continuous forests and agroecosystems documented exceptionally long-distance insect-mediated pollen movement. In *Erythrophleum suaveolens* Brenan, another African legume tree which also bears small whitish to pale green-yellowish flowers densely packed in a spike-like false raceme up to 15 cm, pollen dispersal seems much more limited: mean pollen dispersal distance was estimated at 294 m while only c. 22 % immigrated in a 400-ha study plot (Hardy et al., 2019). However, Duminil et al. (2016a) showed that indirect estimates of *E. suaveolens* pollen dispersal increased from c. 200 to 1,000 m when the density of trees decreased from 175 to 11 trees km^{-2}. The longer pollen dispersal distance we observed in *C. gabunensis* than reported in *E. suaveolens* might thus at least partially be explained by the lower population density of the study plots (22 *C. gabunensis* trees km^{-2} versus 178 *E. suaveolens* trees km^{-2} (Hardy et al., 2019).

Seed dispersal distance was an order of magnitude shorter than pollen dispersal with a mean distance of 184 m. In the 400-ha plot (site A), only around 13 % of seeds immigrated and probably dispersed over > 500 m. These results combined with an exponential seed dispersal kernel (i.e., without fat tail) suggest that a major part of seeds disperses

locally, and that long-distance seed dispersal events are rare. Seed dispersal distance in *C. gabunensis* is similar to those reported for some other wind-dispersed tropical African tree species with fairly large winged diaspores (seed or fruits) (Angbonda et al., 2021; Hardy et al., 2019). While wind-dispersal of seeds is often not as extensive as dispersal by mobile animals in tropical forests, its efficiency strongly depends on the seed morphology and its adaptation to glide, e.g. reduced weight and increased surface area (Dick et al., 2008; Hardy et al., 2019; Nathan et al., 2008). In closed-canopy tropical forests, however, diaspores would usually fly down directly from the canopy layer and disperse at c. 100 m (Angbonda et al., 2021; Dick et al., 2008; Hardy et al., 2019). Dispersal events over kilometers would therefore be rare and limited to occasional strong winds or storms that can uplift diaspores above the forest canopy (Maurer et al., 2013; Nathan et al., 2008).

4.4. Logging implications and recommendations for the sustainable management of C. gabunensis

Selective logging can potentially impact the natural regeneration of exploited tree species (i) by increasing the distance between reproductive trees, which can affect cross-pollination and inbreeding, (ii) by reducing the seed production of the population and local seed rains, and (iii) by modifying local biotic/abiotic conditions affecting fruit production and/or seedling recruitment (Hardy et al. 2019). We discuss these potential impacts in turn.

The low selfing rate and long pollen dispersal distances observed in *C. gabunensis* should ensure extensive pollination and low inbreeding, even for isolated trees, provided that a few reproductive trees are available within a few kilometers around each seed tree. Thus, cross-pollination is not likely to be a limiting factor under selective logging. By contrast, seed dispersal being limited to c. 200 – 300 m around seed trees, a seed tree releases most of its seed rain over an area of approximately 10 ha (Fig. 5b). Hence, ideally, a density of minimum 10 seed trees km^{-2}, regularly distributed, should be maintained to ensure that favorable recruitment sites receive seeds. However, such conditions are actually not met even without logging in our sites A and C due to the low density of *C. gabunensis*, their aggregated distribution and the high heterogeneity of reproductive success (Fig. 3).

As reported for other African long-lived light-demanding species, our results showed that dbh had a significant effect on the female reproductive success of *C. gabunensis*. Plant size most likely represents a direct advantage for reproduction because height facilitates seed dispersal of wind-dispersed species (Angbonda et al., 2021; Hardy et al., 2019). The observed extreme heterogeneity in reproductive success in site A, with three large trees contributing to 91.5 % of juvenile production, raises concerns about the potential impact of selective logging on *C. gabunensis*. If this success is tied to seed production by these large trees, logging could reduce overall seed availability, hindering population regeneration. Alternatively, if success is linked to high seed survival, logging may bring favorable conditions for germination and seedling establishment in logging gaps. The high degree of inequality in sapling production suggests that special precautions should be taken for selective logging of large trees in *C. gabunensis*. Moreover, information regarding the production and survival of seeds from smaller trees in site A would be useful.

Current national regulations impose a LMCD for each timber tree species and FSC (Forest Stewardship Council) certification requires additional measures to improve the recovery rates like an increase of the LMCD and the preservation of seed trees (Karsenty & Ferron, 2017). Our results showed that no tree below the LMCD contributed to the reproduction, so it appears that LMCD in Cameroon and Gabon is too low to ensure any natural regeneration if all exploitable trees were harvested. A minimal cutting diameter of 90 or 100 cm would maintain 28 % to 55 %, respectively, of the seed production potential according to results from site C, but would still be insufficient for site A. Alternatively, the

regeneration potential could be maintained for the largest part by keeping untouched the most productive seed trees. Ideally, such measure would require appropriate field observations to identify the productive seed trees before logging operations. Many logging companies define a maximum cutting diameter (DMAX), especially for species whose dense wood can damage the logging equipment. Consequently, preserving *C. gabunensis* trees larger than 120 cm would help maintaining 34 % of the seed production potential in site C (71% in site A).

Post-logging environmental conditions can either aid or impede investment in reproductive organs, seedling establishment, and growth. For light-demanding species such as *C. gabunensis*, selective logging could improve the regeneration if the canopy gaps are large enough and if seedling growth is high enough to avoid competition from short-lived pioneer sun-loving species (Angbonda et al., 2021; Hardy et al., 2019). Nevertheless, the contrasted dbh distributions among sites (Fig. 3) highlight that *C. gabunensis* seedling recruitment seems to vary substantially from one site to the other. Hence, additional research should be conducted on the impact of logging on natural regeneration in different forest types to assess whether canopy opening effectively foster seedling recruitment. It must also be taken into account that the skidding trail network leading to felling gaps are used by elephants (Scalbert et al., 2022), which selectively forage on *C. gabunensis* seedlings (Ndonda Makemba et al., 2022b). Therefore, one might enrich logging gaps or other open areas like log yards (Ndonda Makemba, 2023) to compensate for reduction in reproductive trees but such measures may be effective only in areas with low elephant densities (Ndonda Makemba et al., 2022b).

Two recommendations can be made in order to limit the impact of logging on *C. gabunensis*: i) in areas where natural regeneration occurs, increasing the LMCD to 90 or 100 cm or preserving the most productive seed trees to keep enough potential for natural regeneration and/or fixing a DMAX at 120 cm, ii) in areas where a regeneration deficit is observed, assisting *C. gabunensis* regeneration by enriching methods with nursery-raised seedlings but only in large gaps located in forests with low elephant densities.

5. Conclusion

The comparison of different tree populations in variable environmental conditions allows to better understand the population dynamics of timber species, which is crucial for developing sustainable management practices. Long-lived light-demanding timber species, such as *C. gabunensis*, are expected to experience a population decline in Central Africa in forests with closed canopies. Logging activities can exacerbate this situation by removing productive seed trees, or conversely, slow down or reverse the process by promoting higher fruit production through increased access to sunlight by the crown and the seedling recruitment. In this study we have shown that pollen dispersal and inbreeding of *C. gabunensis* are not limiting factors but that limited seed dispersal and the high heterogeneity of reproductive success among trees can be critical for natural regeneration. To improve the management of *C. gabunensis*, it is necessary (i) to conduct an objective assessment of logging's impact on species regeneration, and (ii) to implement suitable and targeted measures to support effective regeneration when deficiencies arise.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

https://doi.org/10.5061/dryad.0zpc8674f.

Author Contributions

OB and OJH designed the study. OB, RNM, JFG and VD contributed to collection of plant material. OJH, JLD, JFG and BS contributed to the technical and financial support. OB performed the laboratory analyses. OB and OJH conducted the data analyses. OB wrote the first draft and all authors contributed to the final version of the manuscript.

Appendix

Appendix 1: Contrasted spatial distribution of *Cylidodiscus gabunensis* trees (dbh ≥ 20 cm) in site A (left), site B (middle), site C (right). The pair correlation function, denoted *g*(*r*), is a function of an inter-point distance (*r*). The black solid line represents the pair correlation observed for the data, the red dotted line represents point pattern generated from a homogenous Poisson process (i.e. spatially random distribution of trees) and the grey area indicate the 95 % critical envelope under this process.

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