



# Seed and pollen dispersal and fine-scale spatial genetic structure of a threatened tree species: *Pericopsis elata* (HARMS) Meeuwen (Fabaceae)

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## Abstract

Seed and pollen dispersal are important for defining sustainable forest management practices. By reducing population density, selective logging could affect not only the seed production of timber species but also the selfing rate and the patterns of seed and pollen rains. To assess these risks, we characterized seed and pollen dispersal patterns and the fine-scale spatial genetic structure (FSGS) of *Pericopsis elata*, a gregarious, wind-dispersed legume tree which is highly logged in Central Africa and threatened by overexploitation. Eleven microsatellite markers were used to genotype 189 adults and 664 seedlings in a 4 km<sup>2</sup> plot in the Democratic Republic of Congo (DRC). According to the neighbourhood model, seed dispersal was extremely leptokurtic, with 80% of seeds dispersal distances <75 m, 15% >500 m. Pollen dispersal was locally more extensive (median distance 260 m), but pollen immigration was not detected, and the selfing rate (54%) appeared particularly high compared to other tropical tree species. Limited gene dispersal resulted in remarkably high FSGS ( $S_p = 0.072$ ). A decay of inbreeding with age also suggests that the species is prone to inbreeding depression. The reproductive success of trees was positively related to their diameter at breast height (dbh), with half of the progeny mothered by trees with dbh > 97 cm and fathered by trees with dbh > 119 cm. Our study highlights that (1) seed sources must be diversified for plantation or population reinforcement to limit consanguinity, and (2) the legal minimum cutting diameter in DRC (60 cm) should be increased to maintain enough post-logging reproductive potential.

**Keywords** Seed and pollen dispersal · Consanguinity · Inbreeding depression · Spatial genetic structure · *Pericopsis elata* · Minimum cutting diameter

## Introduction

Seed and pollen dispersal are key processes in the dynamics and evolution of tree populations (e.g. Dick et al. 2008; Kremer et al. 2012). The ability to colonize new sites depends

on seed dispersal (e.g. Muller-Landau et al. 2008; Nathan and Muller-Landau 2000). Inbreeding depends on the mating system (e.g. autogamy) and pollen dispersal (e.g. biparental inbreeding). Both seed and pollen dispersal determine gene flow between populations and their fine-scale spatial genetic

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structure (FSGS; e.g. Dutech et al. 2002; Hufford and Hamrick 2003; Kettle et al. 2011; Robledo-Arnuncio 2011). When both seed and pollen dispersal are spatially very restricted, a strong FSGS is expected and can be enforced further if autogamy occurs (Dutech et al. 2002; Vekemans and Hardy 2004). Limited pollen dispersal is combined with substantial FSGS results in biparental inbreeding (Fenster et al. 2003; Monthe et al. 2017). Inbred progeny, resulting from autogamy or biparental inbreeding, suffers lower fitness if inbreeding depression occurs, a phenomenon commonly observed in tree species (Duminil et al. 2009, 2016b). So far, these processes have been characterized in few tropical tree species from Africa (e.g. Bizoux et al. 2009; Born et al. 2008; Duminil et al. 2016a, 2016b; Hardy et al. 2019; Lourmas et al. 2007; Monthe et al. 2017; Ndiade-Bourobou et al. 2010). However, their knowledge is important to better assess how forestry activities affect natural populations of timber species and evaluate if logging practices are sustainable (e.g. André et al. 2008; de Lacerda et al. 2008; Lourmas et al. 2007; Wickneswari et al. 2004).

In Central Africa, forests are usually exploited through selective logging. This process typically removes one or two trees per hectare and targets only a few commercial species — each of which can be legally exploited above a minimal cutting diameter (MCD, de Wasseige et al. 2014). By removing sexually mature trees, selective logging affects population dynamics in various ways, including the following: (1) a general reduction of seed production due to the lower number of seed trees, (2) a reduced availability of pollen that can decrease seed production per seed tree and/or increase self-fertilization (with a potential alteration of seed quality if inbreeding depression occurs), and (3) a reduced seed rain in favourable habitat areas situated far from surviving seed trees if seed dispersal is severely limited by distance (Hardy et al. 2019). To assess these risks and define sustainable management practices of tropical forests, data on dispersal, autogamy, consanguinity, inbreeding depression, and seed production are needed, especially for intensively logged species.

*Pericopsis elata* (Harms) Meeuwen (Fabaceae) is an emblematic species of the African rain forest and is one of the most traded species in the Congo Basin due to its high-quality lumber (Ampofo and Lawson 1972), which is among the most expensive in the world (Bourland et al. 2012b). Its commercial name is known as *Afrormosia*, *Assamela*, or sometimes, “African teak” as it is often used as a substitute for *Tectona grandis* Lf. However, *P. elata* is a light-demanding species that shows a strong deficit of natural regeneration throughout its range, which compromises the sustainability of its exploitation (Boyemba 2011; Ouédraogo et al. 2014). In the Democratic Republic of Congo (DRC), strategies to support natural regeneration and specific reforestation of *P. elata* are insufficiently developed. The autoecology of this hermaphroditic and wind-dispersed tree is also insufficiently known

(Bourland et al. 2012a), while *P. elata* is under increasing pressure from various actors (e.g. villagers, artisanal and industrial loggers). The overexploitation and lack of regeneration of *P. elata* has justified its inclusion in Appendix II of the annotation 17 of the Convention on International Trade of Endangered Species (CITES) and the IUCN Red List of endangered species where it is considered “endangered” (<http://www.iucnredlist.org>). As an emblematic species, *P. elata* has attracted much interest from international and subregional organizations for conservation and sustainable management. However, many aspects of its biology and reproductive cycle remain poorly documented.

Today, genetic markers greatly facilitate the study of seed and pollen dispersal. For example, scientists can use parentage analyses to identify the parent(s) of natural regeneration and reconstruct seed and pollen dispersal movements and/or to model them (Gerber et al. 2003). This requires an exhaustive sampling and genotyping of all adult trees within a defined area in which the progeny (seeds or established juveniles) is also sampled and genotyped. The spatially explicit neighbourhood model (Chybicki and Burczyk 2010; Chybicki 2018) can model simultaneously forward seed and pollen dispersal kernels and estimate the selfing rate, as well as immigration rates (proportion of fathers and mothers situated outside the sampled area). This method also models how reproductive success is explained by the attributes of individuals, such as their size (Chybicki and Burczyk 2010), which is useful to assess the relative contributions of exploitable and non-exploitable trees to the overall reproductive potential of a local population (Hardy et al. 2019).

To enhance our knowledge on natural reproduction and gene flow in *P. elata*, we genotyped adult trees and juveniles in a 400 ha plot to (i) compare the level of consanguinity between juveniles and adults to assess if the species is subject to inbreeding depression, (ii) determine the self-fertilization rate, (iii) characterize seeds and pollen dispersal distances, (iv) test whether the male and female reproductive successes of individual trees are related to the trunk diameter or the dominance of the trees with respect to the surrounding canopy, and (v) characterize the FSGS to compare it with other rainforest tree species.

## Materials and methods

### Study species

*Pericopsis elata* occurs in West Africa (mainly Ghana) and between eastern Cameroon and the centre of DRC. The species is light-demanding (Ampofo and Lawson 1972; Veenendaal et al. 1996) and needs major disturbances (Boyemba 2011; Bourland et al. 2015) for its establishment and development. It is a gregarious species, forming dense

stands over areas up to a few ha (Bourland et al. 2012b; Bourland et al. 2015; Umunay et al. 2017). It reaches a diameter at breast height (dbh) of 170 cm and can be 30 to 50 m high. The fruit is a flat, thin pod, about 9 to 17 cm long and 2 to 5 cm wide. Pods are green, become brownish when ripe, and are easily recognizable with their oblong, linear, smooth, and loose wings at the edges, which allow them to be dispersed by wind. Each pod contains 1 to 4(6) seed discs (Dickson et al. 2005). The seed is reddish-brown, almost rectangular and about 15 mm wide (Toussaint et al. 1953). The flowers are bisexual, arranged in short terminal panicles on a hairy, thin, white rachis and usually 15 mm long and 13–14 mm wide (Boyemba 2011). They seem adapted for insect pollination (possibly bees), but thus far, the pollination biology of *P. elata* has not been characterized. The minimum fertility dbh observed in Cameroon is 32 cm (Bourland et al. 2012b). Adult trees do not yield ripe fruits each year (Bourland et al. 2012b). Their mortality rate is 0.85% in Eastern Cameroon while their average annual increase in diameter varies between 3.2 and 4.5 mm per year (Bourland et al. 2012b).

### Sampling

We performed parentage analyses in a forest plot of 400 ha ( $2 \times 2$  km) (Fig. 1), located in the Biaro forest ( $00^{\circ} 12' N$ ,  $25^{\circ} 20' E$ ), at an average elevation of 435 m. It is located in the Bakumu-Mangongo community, Ubundu territory in Tshopo province (DRC) (Lomba 2011). This forest has never been logged and benefits from an official conservation status; so, its vegetation has remained mostly undisturbed. The 400-ha study area was selected based on the presence of *P. elata* aggregates (Boyemba 2011; Lomba 2011). In 2015, all *P. elata* stems of  $dbh \geq 10$  cm were inventoried and georeferenced using a GPS. Their dbh and the status of their crown relative to the surrounding canopy (dominated, co-dominant or emergent) were recorded, as well as the position of dead *P. elata* trees. In the same year, we also sampled all the seedlings found in the central 100-ha square area and those found around *P. elata* aggregates. These seedlings measured  $< 1$  m in height but were at least 1 year old because the stand did not fruit in 2015. Leaves, or pieces of cambium (for some large trees), were sampled on living trees and seedlings and carefully dried with silica-gel to preserve DNA. The population did not produce ripe fruits in 2016, but fructification was good in 2017. We therefore searched for pods and seedlings below all trees during three systematic inventories conducted during the 2017 fruiting period, between October 6 and December 15, distinguishing seeds, recently germinated seedlings (usually found in dense patches), and  $>1$ -year-old seedlings. One *P. elata* tree situated 180-m west of the 400 ha plot, and nearby seedlings were also sampled, as well as 4 adults found at least 400 m from the plot. Seeds were germinated in a nursery, and two leaflets were collected on 8-month old seedlings and on the seedlings encountered in the field, to dry them

in silica gel. In total, we collected 853 individuals of *P. elata*: 160 adults ( $dbh \geq 30$  cm), 29 young trees (10 to 29 cm dbh), 236  $>1$ -year-old seedlings, and 428  $<1$ -year-old seedlings (355 from the nursery and 73 from the field). The observed density of trees ( $dbh \geq 10$  cm) within the plot was 0.46 trees/ha for an average dbh of 80 cm. This density is higher than the average of the surrounding forest, which should be close to 0.2 trees/ha, the density recorded in the adjacent CFT46/11 forest concession before logging (Compagnie Forestière et de Transformation, pers. communication).

### DNA extraction and genotyping

We used the NucleoSpin 96 Plant II Kit (Macherey-Nagel, Dürren, Germany) to extract DNA. We genotyped all 853 individuals at 11 nuclear microsatellite markers that were amplified in two multiplexes following the protocol of Micheneau et al. (2011). The PCR was performed on a TProfessional Basic thermocycler (Biometra, Göttingen, Germany) using the following cycle conditions: initial denaturation at  $95^{\circ} C$  for 15 min, then 22 cycles at  $94^{\circ} C$  for 30 s,  $57^{\circ} C$  for 90 s, and  $72^{\circ} C$  for 90 s, followed by 10 cycles at  $94^{\circ} C$  for 30 s,  $53^{\circ} C$  for 45 s, and  $72^{\circ} C$  for 45 s, and a final extension at  $60^{\circ} C$  for 30 min. Amplicons were analyzed on a 3730 ABI 48-capillary DNA analyzer (Applied Biosystems), using 0.8  $\mu$ l of PCR product, 12  $\mu$ l of Hi-Di formamide (Life Technologies), and 0.2  $\mu$ l of size marker (GeneScan 500 LIZ standard, Applied Biosystems).

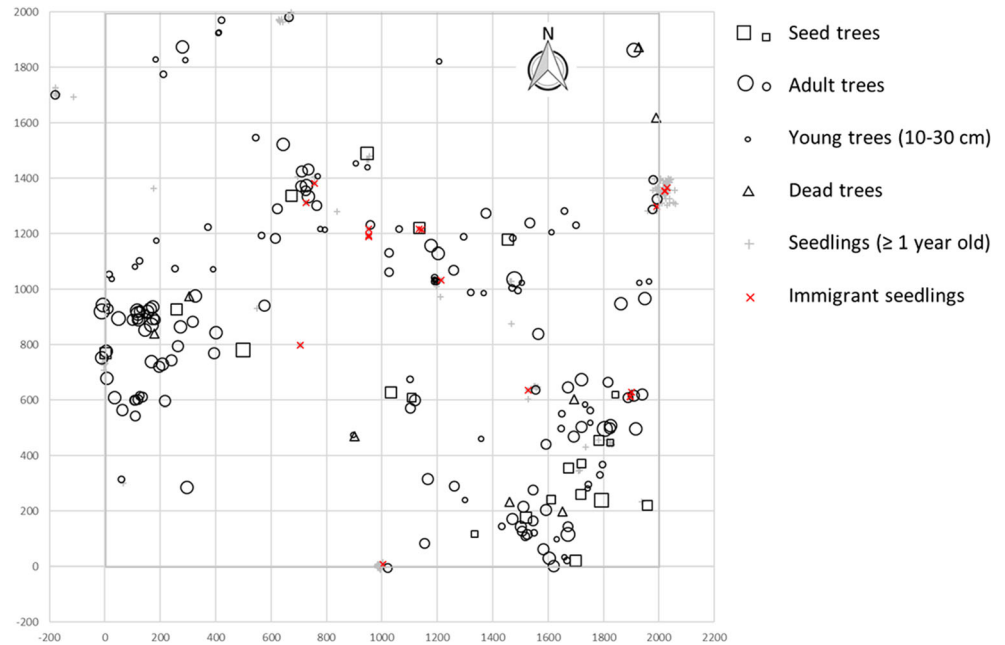
### Genetic diversity and fixation index

The following genetic diversity parameters were characterized using SPAGeDi1-5d (Hardy and Vekemans 2002) for three cohorts (trees of  $dbh \geq 10$  cm,  $>1$ -year-old seedlings, seeds, and  $<1$ -year-old seedlings from the 2007 fruiting period): the total number of alleles over loci ( $k$ ); the mean effective number of alleles (Nielsen et al. 2003); the standardized allelic richness, expressed as the expected number of alleles among  $k = 318$  gene copies ( $A_R$ ); the observed heterozygosity ( $H_O$ ); the unbiased expected heterozygosity ( $H_E$ , Nei's index of genetic diversity (Nei 1978); and the fixation index ( $F = 1 - H_O / H_E$ ). We also used INEST 2.2 (Chybicki and Burczyk 2009) to jointly estimate the frequencies of null alleles and genotyping failure per locus, as well as the inbreeding coefficient for each cohort, using a Bayesian method (model "nfb").

### Estimating seed and pollen dispersal

To estimate seed and pollen dispersal parameters, we used maximum likelihood estimates for parameters of the neighbourhood model implemented in the software NM $\pi$  (Chybicki and Burczyk 2010). To this end, we declared that seeds and  $<1$ -year-old seedlings collected below trees were

**Fig. 1** Map of the study area and sampling strategy of *P. elata*, showing the 400 ha plot (grey  $2 \times 2$  km<sup>2</sup> square) where trees with a dbh  $\geq 10$  cm were exhaustively inventoried. Seed trees (square) are those below which seed families or <1-year-old seedlings were sampled while circles represent the other trees. The size of symbols is proportional to the dbh class of trees (smallest = 10–30 cm, largest = 150–170 cm). Genotyped >1-year-old seedlings are shown (+), together with those inferred as immigrants (red x), as well as dead trees (triangles)



not dispersed (after checking that the overhanging tree was indeed genetically compatible as a mother tree) while >1-year-old seedlings were declared as dispersed (no parent known). Our field experience has convinced us that the large majority of <1-year-old seedlings found in dense patches below the crown of a conspecific adult do not survive more than a year, probably because of intense Janzen-Connell effect (DMAA and NB, pers. observations). By treating them as non-dispersed in NM $\pi$ , we ensure that seed dispersal estimates integrate at least one year of the seedling establishment phase. Young trees (dbh = 10 to 29 cm) were firstly declared as potential adults, but as none of them was inferred as a parent; they were subsequently added among the progeny generation, considering that adult trees have a dbh of at least 30 cm. Seeds and pollen were assumed to disperse according to power-exponential dispersal kernels. NM $\pi$  estimated the frequency of self-fertilization, the frequencies of seed and pollen immigration from surrounding sources ( $m_s$  and  $m_p$ , respectively), and the following parameters of the seed and pollen dispersal kernels: the mean distance ( $d_s$  and  $d_p$ ), the shape parameter ( $b_s$  and  $b_p$ ), the anisotropy ( $k_p$  and  $k_s$ , with  $k = 0$  under isotropic dispersal), and the azimuth of the prevailing dispersal direction ( $a_p$  and  $a_s$ , when  $k_p > 0$  or  $k_s > 0$ ). Finally, NM $\pi$  estimated the genotyping error rates as well as the effects of the dbh and the dominance status of trees on the male and female reproductive successes, using centred and standardized dbh and dominance values. Using seedlings for which a mother and/or a father was inferred with a posterior probability of the best genealogy ( $P$ ) of at least 0.8, we established the dbh distribution of the mothers and the fathers detected and compared it with the dbh distribution of the adults of the study plot, as well as with the legal minimum

cutting diameter of *P. elata* in RDC to assess the contribution of exploitable trees to the reproductive potential of the stand. We also considered the progeny with an inferred father and/or mother to compare seed and pollen dispersal events in a two-dimensional space and as cumulated distributions with distance. To assess the variability of the selfing rate among trees, we considered all mother trees with at least eight non-dispersed progeny for which selfing or outcrossing could be assessed at a  $P \geq 0.8$  and compared their respective selfing rates using chi-square tests. Finally, we used an indirect approach to estimate the frequency of selfing based on inter-locus identity disequilibrium (David et al. 2007). This method, implemented in SPAGeDi1-5d (Hardy and Vekemans 2002), allowed us estimating the proportion of selfed individuals for each cohort.

### Characterization of fine-scale spatial genetic structure, biparental inbreeding, and assortative mating

We assessed the fine-scale spatial genetic structure (FSGS) in the population by the relationship between genetic kinship and spatial distance (kinship-distance curve). To achieve this, we estimated pairwise kinship coefficients ( $F_{ij}$ ) between individuals using J. Nason's estimator (Loiselle et al. 1995) as implemented in the SPAGeDi1-5d software (Hardy and Vekemans 2002). Then, we regressed  $F_{ij}$  values on the natural logarithm of distance between individuals, obtaining the regression slope  $b$ . We also averaged  $F_{ij}$  values over a set of non-overlapping distance intervals ( $F_c$ , upper limit of the distance classes: 50, 100, 200, 300, 500, 700, 1000, and 1500 m) to graphically illustrate the trend of FSGS. FSGS was assessed within each cohort and was tested by permuting randomly

10,000 times the spatial positions of individuals to obtain the frequency distribution of the regression slope ( $b$ ) under the null hypothesis of a random spatial distribution of genotypes. Following the procedure described by Vekemans and Hardy (2004), we used the  $S_p$  statistic to compare the intensity of the FSGS with that of other studies:  $S_p = -b/(1-F_1)$ , where  $F_1$  is the average kinship between neighbours, measured as the kinship coefficient between adults separated by a distance <50 m.

Biparental inbreeding, which results from the mating between related individuals (excluding selfing events), was assessed by computing the  $F_{ij}$  values between identified mating pairs, considering progeny for which both parents were identified with a posterior probability of the best genealogy  $P \geq 0.8$  by NM $\pi$ . To assess if assortative mating occurs (Monthe et al. 2017), we compared  $F_{ij}$  values between mating pairs with (i) the distribution of  $F_{ij}$  values between all pairs of adults using a Wilcoxon rank sum test, and (ii) the expected  $F_{ij}$  value given the distance between each mating pair (i.e. the  $F_c$  value of the corresponding distance interval) using a Wilcoxon signed-rank test. The latter test allowed us to assess if the relatedness between mates was higher (under assortative mating), or lower (under inbreeding avoidance), than expected by chance while accounting for limited pollen dispersal and the FSGS.

## Results

### Genetic diversity and inbreeding

The analysis of the eleven loci for the total sample and each cohort showed moderate polymorphism levels (Table 1). The total number of alleles was 67, ranging from 2 ( $P$  12) to 12 ( $P$  55) per locus, with a mean of 6.09 alleles per locus. The effective number of alleles ranged from 1.05 to 5.83 (average of 2.55). The observed and expected heterozygosities varied from  $H_o = 0.02$  to 0.72 (average of 0.33), and from  $H_e = 0.46$  to 0.83 (average of 0.48). Similar genetic diversity parameters were observed in the different cohorts (Table 1). However, the average fixation index ( $F$ ), which was significantly higher than zero in all cohorts and over loci, was high in <1-year-old seedlings (0.351), slightly lower in >1-year-old seedlings (0.305) and much lower in trees with dbh  $\geq 10$  cm (0.188). This trend was also observed for each locus, except for P19 and P50, and paralleled with an inverse trend for the observed heterozygosity (Table 1).

Paired  $t$ -tests between cohort pairs using single-locus values as replicates show that there is no significant difference between >1-year-old and <1-year-old seedlings for  $H_o$  ( $P = 0.590$ ) and  $F$  ( $P$ -value = 0.966), while the difference is significant between adults and >1-year-old or <1-year-old seedlings, for  $H_o$  ( $P$ -value = 0.046,  $P$ -value = 0.003, respectively) and  $F$  ( $P$ -value = 0.015,  $P$ -value = 0.038).

According to INEST results, there is no evidence of genotyping failure but null alleles were detected in six loci

using the whole dataset with the following percentages: 8.6% in P12, 2.8% in P32, 4.2% in P13, 1.6% in P19, 2.6% in P52, and 35.7% in P66. Subdividing the dataset by cohorts, the inbreeding coefficients, which are here corrected for the presence of null alleles, contrary to  $F$ , again decrease with the age of cohorts: mean estimates of 0.298 in <1-year-old seedlings, 0.223 in >1-year-old seedlings, and 0.155 in trees with dbh > 10 cm (Table 1).

### Selfing rate

We estimated the selfing rate of progenies at  $0.54 \pm 0.02$  (standard error), based on the direct approach provided by NM $\pi$ . Using the identity disequilibrium method implemented in SPAGeDi1-5d, we observed variations in rates of selfing among cohorts:  $0.26 \pm 0.10$  for trees with dbh > 10 cm,  $0.31 \pm 0.12$  for >1-year-old seedlings, and  $0.48 \pm 0.10$  for <1-year-old seedlings. The differences of selfing rates are thus coherent with differences in inbreeding levels between cohorts.

In total, 17 mother trees had from 8 to 56 non-dispersed offspring for which selfing or outcrossing could be established. Their selfing rate ranged for 0.11 to 0.81 (mean  $\pm$  standard deviation:  $0.54 \pm 0.23$ ). According to chi-square tests ( $\alpha \leq 0.05$ ), four families showed lower than average selfing rates (from 0.11 to 0.43), and two families showed higher than average selfing rates (0.80 to 0.81). Although one mother tree was particularly homozygous (only one locus heterozygous), suggesting that it may have resulted from a selfing event, and displayed a particularly high selfing rate (0.8 among 46 offspring); there was no significant correlation between the selfing rate of families and the mean heterozygosity of the mother tree.

### Modelling seed and pollen dispersal

Single-locus genotyping error rates estimated by NM $\pi$  (including errors due to null alleles) ranged from 0.2 to 8.4% (mean 2.5%). The neighbourhood model (NM $\pi$ ) analysis estimated seed immigration rate at  $m_s = 0.104 \pm 0.022$  (estimate  $\pm$  standard error) but did not detect pollen immigration ( $m_p = 0$ ). The NM $\pi$  algorithm suffered from convergence problems to adjust the shape of the exponential-power dispersal kernel for seeds ( $b_s$  parameter); so, we ran the analysis for fixed values of  $b_s$  by step of 0.01 and obtained the highest likelihood for  $b_s = 0.03$ , indicating a very leptokurtic kernel. By contrast, the pollen dispersal kernel was moderately leptokurtic with  $b_p = 0.55 \pm 0.15$ . The resulting predicted mean dispersal distances of seeds and pollen reached  $d_s = 539$  km (95% CI 125 km– $\infty$ ) and  $d_p = 942$  m (95% CI 547–2958 m) according to the fitted forward dispersal kernels. These mean distances actually hide very distinct dispersal kernels as revealed by the 0.25, 0.5, 0.75, and 0.9 quantiles, which reach, respectively, 25 m, 417 m, 6950 m, and 300 km for seeds, and 320 m, 650

**Table 1** Parameters of genetic diversity and consanguinity for different cohorts of *P. elata* in the study population

Cohort	$N^a$	$NA_E^b$	$A_R^c$	$He^d$	$Ho^e$	$F^f$	$f^g$
All samples	853	2.55	5.00	0.480	0.326	0.322	
Trees (dbh $\geq$ 10 cm)	189	2.62	4.94	0.488	0.396	0.188	0.155 (0.103–0.189)
>1-year-old seedlings	236	2.40	4.99	0.463	0.322	0.305	0.223 (0.194–0.264)
<1-year-old seedlings	428	2.36	4.51	0.457	0.297	0.351	0.298 (0.255–0.341)

<sup>a</sup> Sample size<sup>b</sup> Effective number of alleles<sup>c</sup> Allelic richness ( $k = 318$ )<sup>d</sup> Gene diversity corrected for sample size (expected heterozygosity)<sup>e</sup> Observed heterozygosity<sup>f</sup> Inbreeding coefficient (i.e. apparent heterozygote deficit)<sup>g</sup> Inbreeding coefficient corrected for null alleles and 95% highest posterior distribution (INEST estimates)

m, 1220 m, and 2020 m for pollen. The tail of the adjusted kernel for seeds is unrealistic, and the size of the 400 ha plot does not allow us to reliably infer the shape of a kernel beyond approximately 2 km, but it highlights that while a significant proportion seed disperse at short distances; long-distance dispersal also occur. There was a trend toward anisotropy for seed dispersal ( $k_s = 0.91 \pm 0.20$  in the SSE direction,  $a_s = 214^\circ \pm 13^\circ$ ) but not for pollen dispersal ( $k_p = 0$ ). The trunk diameter had more effect on the reproductive success for the male ( $b = 0.82 \pm 0.12$ ) than the female ( $g = 0.27 \pm 0.20$ ) functions, while the dominance status had no significant effect ( $b = g = 0$ ). When considering only offspring for which the mother and/or the father was identified with a posterior probability  $P \geq 0.8$ , we detected 142 offspring dispersed up to 2.1 km from their mother (mean seed dispersal distance = 100 m, median = 37 m), and 76 cross-pollination events between adults separated by up to 1305 m (mean pollen dispersal distance = 332 m, median = 260 m). The distribution of dispersal events around their sources illustrates the contrast between seeds, which are mostly dispersed at <100 m from the mother tree, preferentially in the S-E direction, with a few long-distance dispersal events, and pollen, which is often dispersed over several hundreds of meters, without preferential direction (Fig. 2). A total of 18 progeny were inferred as immigrant at  $P \geq 0.8$ , meaning that the genotyped adults are unlikely to include their mother. They were distributed throughout the 400 ha plot and did not cluster around dead trees (Fig. 1), suggesting they are true immigrants. None of four adult trees sampled >400 m from the plot was inferred as a parent of the sampled progeny.

### Fine-scale spatial genetic structure, biparental inbreeding, and assortative mating

A particularly strong FSGS was detected in the population ( $S_p = 0.072$ ), whereby the kinship coefficient between individuals separated by <50 m was close to  $F_{ij} = 0.25$  and decayed approximately linearly with the logarithm of the spatial

distance (Fig. 3). The kinship-distance relationships were very similar for all cohorts (Fig. 3). Hence, the FSGS between young trees already corresponded to the FSGS observed between adults.

Considering the outcrossing events for which both parents were identified, the mean kinship coefficient between mates was  $0.036 \pm 0.021$ , a value significantly larger than the distribution of pairwise kinship coefficients between adults (Wilcoxon rank sum test, unilateral:  $W = 513749$ ,  $P$ -value = 0.026). This level of biparental inbreeding is not significantly different from the mean kinship coefficient between adults separated by the same distance classes, which is 0.072 (Wilcoxon test for paired samples:  $V = 1386$ ,  $P$ -value = 0.123). Hence, there is neither evidence of assortative mating nor of inbreeding avoidance, but biparental inbreeding occurs in outcrossed progeny due limited pollen dispersal distances and the FSGS.

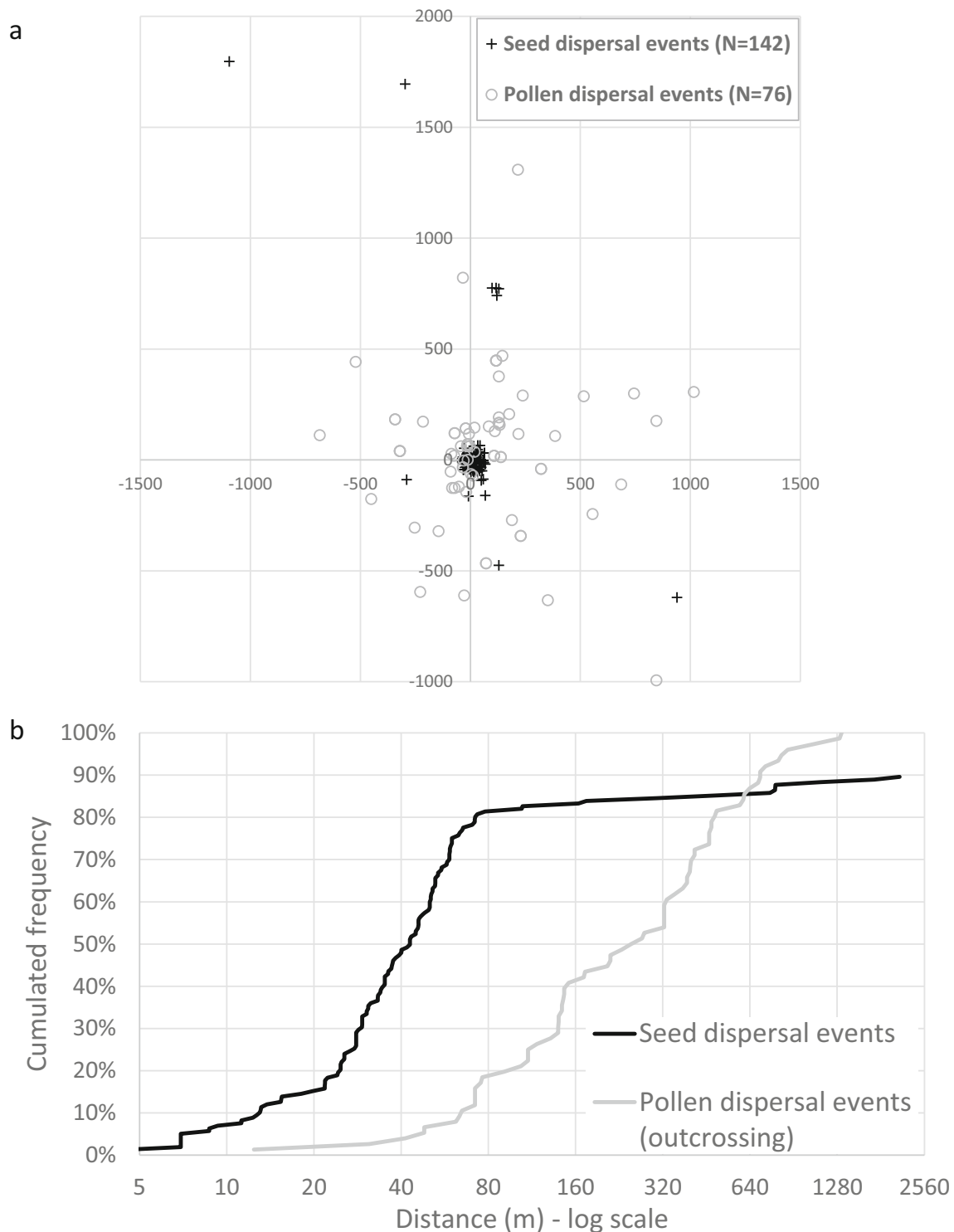
### Diameter structures of reproductive trees

The diameter structure of adult trees indicates similar proportions per diameter class from 30 to 130 cm, with a drop in the 50–70 cm class and above 130 cm (Fig. 4a). When considering offspring for which at least one parent was detected at  $P \geq 0.8$ , the two smallest reproductive trees had dbh of 33 cm (mother of one progeny) and 40 cm (father of one progeny). However, the reproductive success of trees with a dbh < 50 cm was very low while trees with a dbh > 110 cm contributed disproportionately to the production of offspring (Fig. 4a). Half of the progeny were mothered by trees with a dbh > 97 cm and fathered by trees with a dbh > 119 cm (Fig. 4b).

## Discussion

### Consanguinity and inbreeding depression

A peculiar genetic feature of the studied *P. elata* population is its high level of inbreeding (deficit of heterozygotes reaching



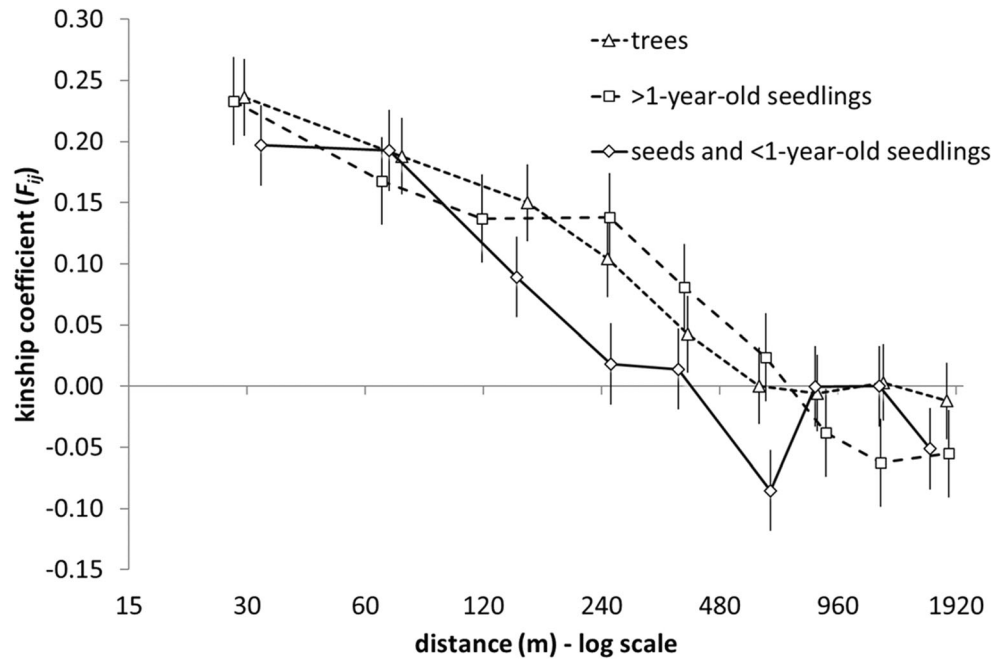
**Fig. 2** Distribution of seed and pollen dispersal events in a two-dimensional space around the source (**a**) or as a function of the distance crossed (**b**), according to parentage analyses (parents identified at a  $P \geq 0.8$ ). For seed dispersal, we also considered that 10% seed immigration

should correspond to long-distance dispersal events (the tail of the curve in panel **b** is therefore undefined). For pollen dispersal, it must be accounted that with a selfing rate of 54%, about half of pollen does not disperse at all

$F = 0.35$  in <1-year-old seedlings) in comparison to most other tropical tree species (e.g.  $F = 0.06$  for *Distemonanthus benthamianus* and  $F = 0.003$  for *Erythrophleum suaveolens*

(Hardy et al. 2019)). Strong deficit of heterozygotes in *P. elata* was already reported by Micheneau et al. (2011) using samples from eastern Cameroon and was detected in other

**Fig. 3** Fine-scale spatial genetic structure of *P. elata* in the 400 ha plot, expressed by the kinship-distance relationship on a log(distance) scale within each cohort. Error bars represent standard errors estimated by jackknifing over loci



populations from the Congo basin (unpublished data). This high inbreeding results predominantly from a high self-fertilization rate, reaching 54% at the seed or young seedling stage in the studied population while it is usually <10% in other tropical rainforest trees (Dick et al. 2008; but it reached c. 20% in *E. suaveolens* and 30% in *Baillonella toxisperma*; Duminil et al. 2016a, 2016b). In addition, biparental inbreeding occurs as c. 80% of outcrossing events happened between adults separated by <500 m (Fig. 2b) which are significantly more related than random individuals (Fig. 3). Nevertheless, for all loci, adults had a lower inbreeding coefficient than seedlings, a common feature found in other inbred tree species (e.g. André et al. 2008; Monthe et al. 2017; Cloutier et al. 2007; Doligez and Joly 1997; Hufford and Hamrick 2003; Jones et al. 2005), which is an indicator of inbreeding depression. In *P. elata*, however, inbreeding depression does not preclude all selfed individuals from reaching adulthood as we estimated that c. 26% of adults resulted from self-fertilization. Thus, if we assume that the selfing rate of new progeny has remained stable over generations, our results would indicate that selfed progeny is two times less likely to reach adulthood than outcrossed progeny. Further studies are needed in order to investigate how inbreeding affects the growth and mortality of *P. elata* trees at different stages, but preliminary results already indicate that outcrossed seedlings grow faster than selfed seedlings (unpublished results).

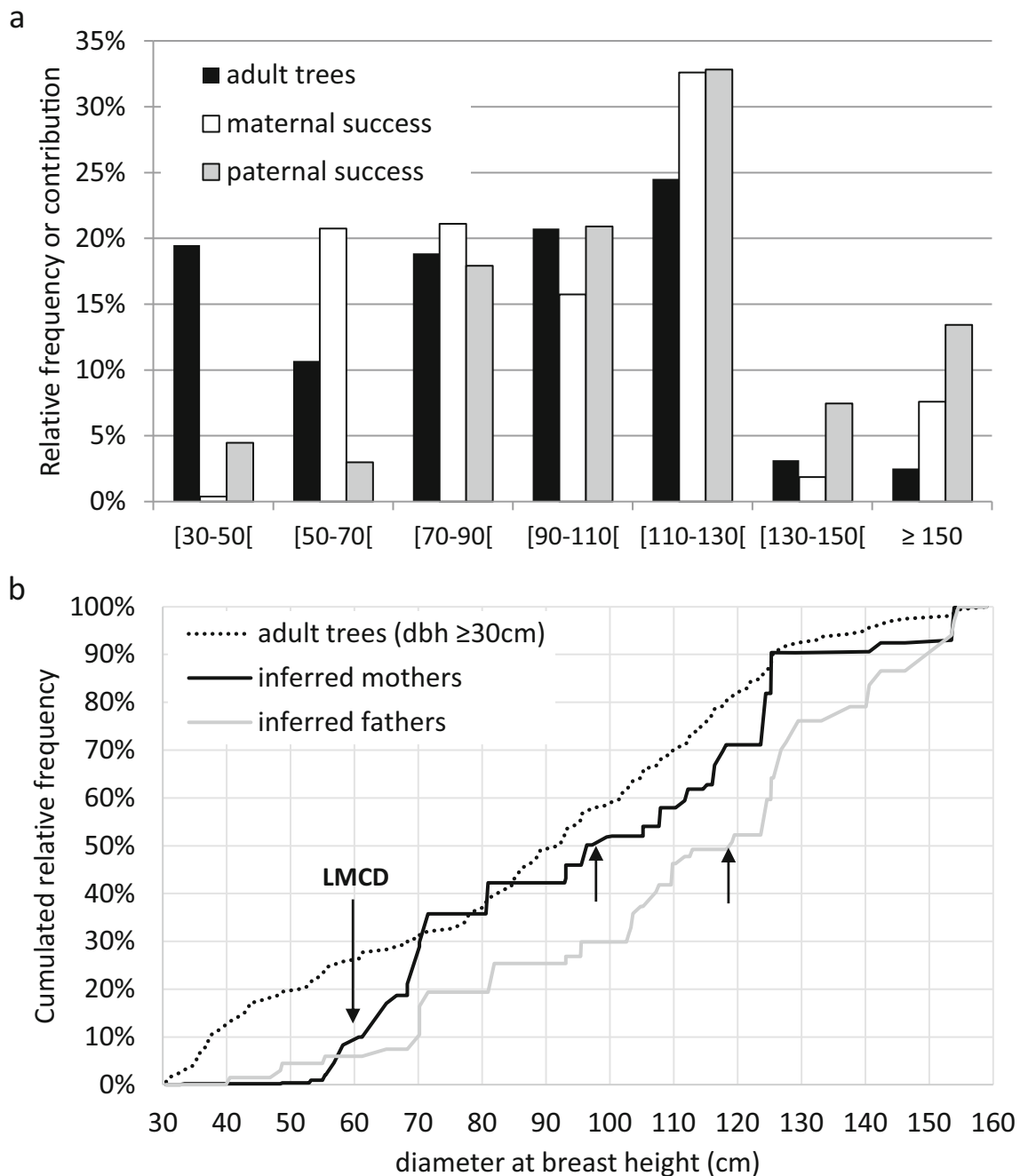
Inbreeding depression is primarily due to the expression of recessive deleterious alleles. However, in species with a mating system favouring regular inbreeding, theory predicts that selection should eliminate these deleterious alleles more efficiently, eventually reducing inbreeding depression (but not genetic load) and favouring selfing over outcrossing, so that

the maintenance of an intermediate selfing rate is difficult to explain from an evolutionary point of view (Porcher and Lande 2005). In *P. elata*, the selfing rate varied among seed trees, but none of them was relying only on selfing or only on outcrossing. Moreover, there was no significant association between the selfing rate and the heterozygosity of the mother tree, so that there is no evidence of a heritable component. As a pioneer tree species, *P. elata* probably benefits from selfing as a reproductive insurance after a long-distance seed dispersal event. This potential ability to establish a new stand from a single individual may favour the maintenance of a mixed-mating strategy despite the occurrence of inbreeding depression. Other factors, like pollen discounting or lack a genetic determinism controlling the rate of geitonogamous selfing (i.e. pollen transfers between flowers from the same individual), may also explain the origin of the peculiar mating system of *P. elata* (Porcher and Lande 2005).

### Seed and pollen dispersal

Seed and pollen dispersal were assessed using the neighbourhood model, which has the advantage of estimating simultaneously all dispersal parameters, including immigration and selfing rates. The immigration rate was higher for seeds ( $m_s = 0.10$ ) than for pollen ( $m_p = 0$ ), suggesting that seed dispersal is the main component connecting local stands. However, the median distance of inferred dispersal events within the plot was much higher for pollen (260 m) than for seeds (37 m). This is explained by the contrasted shape of the inferred exponential-power dispersal kernels, which is much more leptokurtic (fat-tailed) for seeds ( $b_s = 0.03$ ) than for pollen ( $b_s = 0.55$ ). The cumulative probability of seed and





**Fig. 4** Relative frequencies of adult trees and their relative maternal and paternal contributions to the production of offspring according to the diameter of trees at breast height (dbh). Values are represented by dbh class (**a**) or as cumulated relative frequencies for increasing dbh (**b**). The distributions for adult trees are based on the  $N = 156$  trees with a dbh  $\geq 30$  cm found in the 400 ha plot. The distributions for maternal and paternal successes are based  $N = 540$  progeny with an inferred mother

and  $N = 67$  outcrossed progeny with an inferred father, considering only seedlings for which the parent(s) could be assessed at a probability  $\geq 0.8$  according to parentage analyses (the weight of each parent is proportional to the number of offspring produced). The arrows highlight the legal minimal cutting diameter (LMCD) of *P. elata* in DRC (60 cm) in comparison with the median dbh of mothers and fathers of seedlings

pollen dispersal as a function of distance, based on dispersal events detected at  $P \geq 0.8$  and accounting for the immigration rates shows that more than 80% of seeds disperse less than 75 m while 12% disperse over a long distance at the scale of the 400 ha, hence probably over more than 1 km (Fig. 2b), resulting in highly leptokurtic seed dispersal. For pollen, on

the other hand, 54% of pollen grains do not disperse due to autogamy (including geitonogamy), while 80% of the rest disperse less than 500 m (Fig. 2b). Given the large mean dispersal of the adjusted kernel (924 m), it remains paradoxical that no pollen immigration was detected. Whether prezygotic factors, such as phenological delay, limit mating

between aggregates of *P. elata* remains to be investigated. The behaviour of pollinators might also matter but pollinators remain to be identified.

Seed dispersal distance in *P. elata* is similar to values reported in the literature for other wind-dispersed tropical tree species. In *Aucoumea klaineana* (Burseraceae), seed dispersal distances ranged from 20 to 258 m, with an average of 118 m (Born et al. 2008). In *Jacaranda copaia* (Bignoniaceae), most seeds (75%) dispersed within 100 m while some long-distance dispersal events ( $\geq 700$  m) were also detected (Jones et al. 2005). In *D. benthamianus* (Fabaceae), which produces pods similar in size to *P. elata* pods, 70% of seeds dispersed within the study plot at a mean distance of 71 m while c. 20% immigrated and had dispersed over >500 m (Hardy et al. 2019). The short dispersal range of the bulk of *P. elata* seeds can be explained by the fact that the slightly winged pods can easily be dispersed by strong winds but not efficiently in the absence of strong winds (Boyemba 2011). As suggested to explain fat-tailed seed dispersal in *D. benthamianus*, strong winds (e.g. during thunderstorms) might be responsible for c. 15% long-distance dispersal of *P. elata* seeds that are taken in turbulent flows over the canopy, while the rest falls over much shorter distances because, once a seed falls below the canopy, wind is much reduced. It should also be noted that, as for *D. benthamianus*, anisotropy is expected under wind-dispersal and tends to reflect the main direction of winds (Fig. 2a; Hall et al. 2003).

### Determinants of individual reproductive success

In light of our results, trunk diameter has shown a positive effect on the reproductive success, as reported in other species (e.g. Lourmas et al. 2007; Monthe et al. 2017; Hardy et al. 2019), and this effect seems stronger for the male than the female function. Our results show that all diameter classes from 30 cm contribute to reproduction, the minimum diameter to be mother or father being 34 cm and 40 cm, respectively (Fig. 4). This is in line with our field observations showing that most fruiting trees with a dbh  $\leq 35$  cm produce pods that fall before reaching maturity. In Cameroon, Bourland et al. (2012b) showed that, over 5 years of observation, only 15% of stems flowered at least once, and no stem yielded mature fruits over this period. Contrary to *Entandrophragma cylindricum* which reaches a maximum individual reproductive success in the dbh classes of 100 to 120 cm and declines in larger classes (Lourmas et al. 2007; Monthe et al. 2017), we did not observe a senescence effect in *P. elata*. In contrast to the dbh, the dominance status had no impact on the reproductive success, at least when the dbh effect was already accounted for. This is consistent with the behaviour of *E. suaveolens* but in sharp contrast with *D. benthamianus* where dominance played a more important role than dbh (Hardy et al. 2019).

### Fine-scale spatial genetic structure

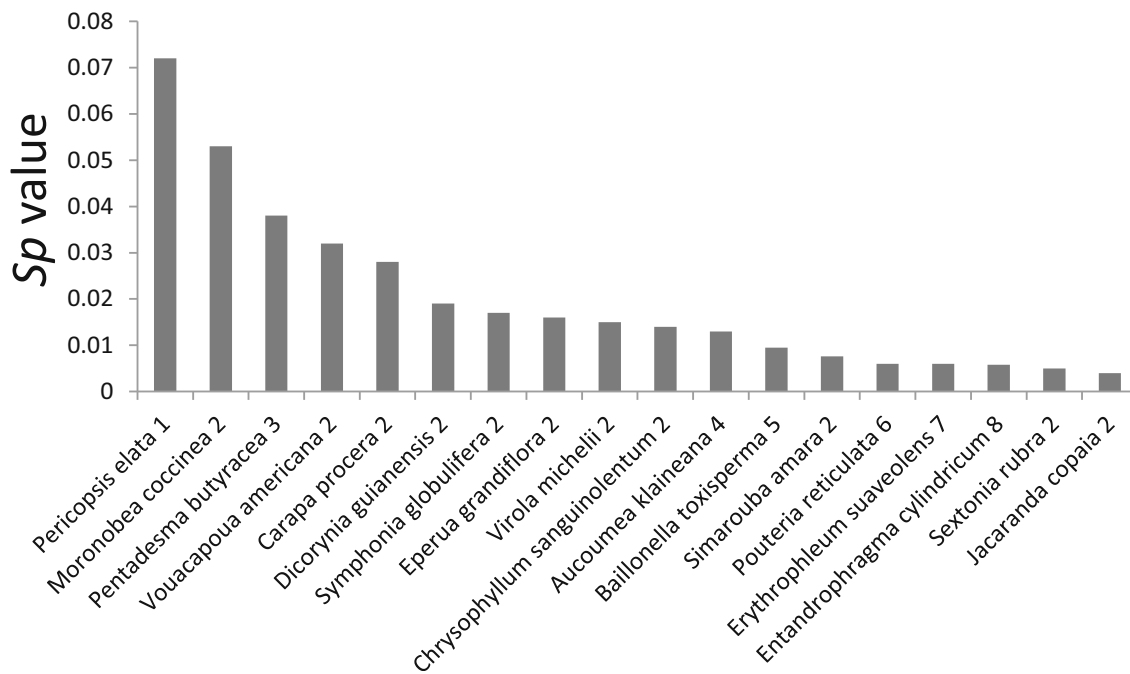
*Pericopsis elata* has a very strong spatial genetic structure, characterized by a steep decline of the mean kinship coefficient between individuals with spatial distance ( $S_p = 0.072$ ; Fig. 3). Trees distant by c. 30 m have a kinship coefficient as high as the value expected between full brothers or between parent and offspring in the case of an outbred population (c. 0.25). The kinship between adults decays approximately linearly with the logarithm of the distance, at least up to c. 500 m (Fig. 3), as predicted by isolation by distance models (Vekemans and Hardy 2004). This strong FSGS is mainly explained by the combination of limited seed dispersal with a relatively high rate of autogamy, causing substantial inbreeding (Bittencourt and Sebbenn 2007; da Silva Carneiro et al. 2007; Eduardo et al. 2008). The stability of the observed FSGS among the different cohorts indicates that it has reached a steady-state, perpetuated from generation to generation (Fig. 3).

Under FSGS and limited pollen dispersal, biparental inbreeding is expected because trees that are within the pollen dispersal curve tend to be related. However, biparental inbreeding can also be enforced by assortative mating, a phenomenon first detected by Monthe et al. (2017) in rain forest trees and appearing in nearly half of the tree species, possibly due to more synchronous phenology between related individuals (Ismail and Kokko 2020). In *P. elata*, we detected significant biparental inbreeding due to limited pollen dispersal but no assortative mating.

Compared to the  $S_p$  statistics reported in the literature for 17 other tropical forest species (Fig. 5), *P. elata* displayed the highest value (0.072), which remains even high compared to the mean value of tropical trees dispersed at short distances by wind, gravity or rodents ( $S_p = 0.023$ ) (Dick et al. 2008). The main reason for this seems to be related to the high selfing rate of *P. elata*, while the large majority of tropical rain forest trees are predominantly allogamous (Dick et al. 2008). The relatively low population density, at least compared to temperate tree species, also contributes to high local genetic drift and strong FSGS. Hence, *P. elata* appears to be an extreme example of a gregarious species subject to very strong FSGS.

### Implications for forest management

Logging is an important economic activity (Arnhem et al. 2008), which is gaining increasing momentum in recent decades in the Congo Basin countries (de Wasseige et al. 2012). It contributes to a gross domestic product in several wood-producing countries committed to development (Haurez et al. 2013). This lucrative activity is unfortunately accompanied by several negative impacts (Doucet and Kouadio, 2007), in particular for populations of exploited species (Doucet et al. 2007; Doucet et al. 2016). It modifies the original abiotic and biotic features of the habitat (Lee 2000; Wickneswari et al.



**Fig. 5** Comparison of the degree of fine-scale spatial genetic structure ( $S_p$  statistic) in tropical trees species. Note: (1) This study, (2) Hardy et al. (2006), (3) Ewédjè et al. (2017), (4) Born et al. (2008), (5) Duminil et al. (2016b), (6) Schroeder et al. (2014), (7) Duminil et al. (2016a), (8) Monthe et al. (2017)

2004), ecosystem structure, and composition (Clark et al. 2009). It can also cause significant losses in terms of allelic richness of target species due to its selective nature, which may lead to some genetic skimming (André et al. 2008; Nanson 2004; Sebbenn et al. 2011).

This study has direct implications for the conservation of woody genetic resources and the sustainable management of *P. elata* stands. First, the observed decline of inbreeding with age suggests that *P. elata* is subject to inbreeding depression. Inbreeding must be taken into account for a good selection of seed collection sources in the context of reforestation or planting *P. elata* and maintain the regeneration potential of the species. To avoid excessive inbreeding, seed sources used in nurseries should be diversified and seed trees should be separated by at least 500 m to avoid sampling closely related individuals and ensure sufficient genetic diversity (Bittencourt and Sebbenn 2008). Second, our analysis of the relative reproductive success of trees according to their diameter can inform on the minimal legal cutting diameter (MLCD) to adopt without compromising the natural regeneration of the species. Our results show that the median diameter of the parents of offspring reached c. 97 cm for mothers and 119 cm for fathers. This means that, if all trees above these median diameters were exploited, the reproductive output of the population would be halved. Currently, the MLCD for *P. elata* is 60 cm in RDC and 90 cm in Cameroon. According to our results, if all trees >60 cm were cut, >90% of the reproductive potential of the stand would vanish (Fig. 4b), strongly compromising the natural regeneration of the species. A minimal cutting

diameter of 80 or 90 cm would maintain 35 to 42% of the seed production potential, which may still be limiting, especially given the general deficit of natural regeneration of the species, which demands large openings for its regeneration. Hence, we recommend the following: (1) an increase of the MLCD in RDC to keep enough potential for natural regeneration, and (2) the development of programs of reforestation and/or enrichment of logged forests (Ouédraogo et al. 2014; Fayolle et al. 2015; Doucet et al. 2016) to compensate for the low natural regeneration of *P. elata*.

## Conclusion

*Pericopsis elata* is an exceptional tree species because it shows a high level of selfing (54% of selfed seeds or seedlings in the studied population) probably combined with a moderate inbreeding depression (survival to adulthood of selfed progeny seems to be half of outcrossed progeny). The resulting inbreeding combined with limited dispersal distances for most seeds is contributing to its aggregative distribution and results in an exceptionally strong fine-scale spatial genetic structure. We find a typical selection pattern in the population, favouring heterozygotes between seedling and adult stages, suggesting that inbreeding depression progressively eliminates the most consanguineous individuals. Hence, the genetic resources of the species should be carefully managed by developing practical regeneration protocols using well-diversified sources of reproductive material.

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**Code availability (software application or custom code)** Not relevant here

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**Data availability** The genotypes, diameters, and spatial coordinates of the trees within the 400 ha plot are available in the TreeGenes Database under code TGDR368 (<https://treegenesdb.org/completed-submission/TGDR368>).

## Declarations

**Conflict of interest** The authors declare no competing interests.

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