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RESEARCH ARTICLE

Inbreeding depression, functional traits and phenotypic plasticity in an endangered tree species with a mixed mating system

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Abstract

1. Most tree species can suffer from inbreeding depression (ID), which they escape by reproducing predominantly through outcrossing. A remarkable exception is *Pericopsis elata*, an African timber species naturally producing 54% of self-fertilized seeds in the eastern Congo Basin. This species is highly logged and suffers from a deficit of natural regeneration, so that silviculture is needed for its sustainable management. While selecting good genetic material can increase the value of plantations, we lack fundamental biological knowledge on the effect of inbreeding and competition on growth potential, variability in leaf traits and phenotypic plasticity (PP). We hypothesize that ID in *P. elata* could result from the expression of deleterious mutations affecting functional traits, or from a reduction of adaptive PP in inbred genotypes.
2. To test our hypotheses, 540 *P. elata* seedlings were monitored for 4 years in a Nelder-type device, in which trees were planted along concentric circles to generate a density gradient. Nine leaf morphological traits (including specific leaf area, stomata density and size), eight leaf chemical traits, diameter and total height were measured regularly on 60 individuals, while paternity analyses allowed distinguishing inbred and outbred plants. To explain the observed ID on growth, we

tested whether inbreeding affected leaf traits and/or their plasticity expressed across years, across the density gradient or across sunlight exposure.

3. Outbred plants grew faster than inbred ones, demonstrating ID for each level of competition. Despite the significant correlation found between specific LA and growth, and the impact of planting density, plant age and leaf exposure to sunlight on multiple traits, mean leaf trait values did not differ according to inbreeding. However, a few leaf traits (chlorophyll content, maximum stomatal water vapour conductance and leaf fresh mass) showed significantly higher plasticity in outbred than inbred plants.
4. *Synthesis*. The observed ID on growth traits was not explained by a direct effect of inbreeding on the mean values of leaf traits but possibly by a reduction in PP with inbreeding. Additional studies on the interplay between ID, functional traits and plasticity should be conducted at the intraspecific level to identify general patterns.

KEYWORDS
functional traits, inbreeding depression, mating system, Nelder device, *Pericopsis elata*, phenotypic plasticity, silviculture

1 | INTRODUCTION

Inbreeding depression (ID), the negative impact of inbreeding on fitness, is a pervasive phenomenon in plants and animals, usually attributed to the expression of deleterious recessive mutations in more homozygous genotypes (Charlesworth & Willis, 2009; Hedrick et al., 2016). The first quantification of the harmful effects of inbreeding on plants was done by Charles Darwin who showed that inbreeding reduces the vigour and fertility of plant species (Darwin, 1876). This ID can be experienced from the earliest stages of the plant's life cycle (Hufford & Hamrick, 2003) but its severity tends to rise with age (Hardner & Potts, 1995). Harmful effects of inbreeding include a reduction of the seed production (Herlihy & Eckert, 2002), germination rates (Amorim et al., 2023; Ismail et al., 2014; Seltmann et al., 2009) and seeds weight (Hufford & Hamrick, 2003; Naito et al., 2005), albinism (Takeuchi et al., 2020), as well as a poor growth and high mortality (Burgess et al., 1996; Eldridge, 1983). While ID has been much studied in short-living plants (Winn et al., 2011), often comparing fitness components between inbred and outbred plants, it is less well characterized in long-living trees (but see Griffin et al., 2019; Hedrick et al., 2016; Nickolas et al., 2019).

Most tree species avoid ID by reproducing predominantly through outcrossing (Duminil et al., 2009), a pattern also documented in tropical trees (Dick et al., 2008). In most self-compatible tropical tree species, the estimated proportion of inbred adults is near to zero even when there is a non-negligible proportion of inbred seeds (e.g. Duminil, Daïnou, et al., 2016; Duminil, Mendene Abessolo, et al., 2016). This indicates that inbred offspring are less likely to reach adult age due to their higher rate of mortality (Costa e Silva et al., 2010; Eldridge, 1983). A remarkable exception is given by *Pericopsis elata* Harms, an African timber species which was shown to produce 54% of selfed seeds in the eastern Congo Basin (Angbonda et al., 2021), questioning how this threatened species copes with ID (Angbonda et al., 2024) and what the consequences are for managing its populations. Researches on ID in trees have generally evaluated the average fitness of inbred individuals in terms of fecundity, survival and growth rate (Amorim et al., 2023; Hufford & Hamrick, 2003; Ismail et al., 2014; Seltmann et al., 2009). However, we know little about the effect of inbreeding on the functional traits and their plasticity.

Trees adapt their physiology and life cycle according to environmental conditions (Sultan, 2000). These environmental responses can be assessed using functional traits—the morphological, physiological, biochemical and phenological characteristics of plants that can be measured at the individual level (Lavorel & Garnier, 2002; Pérez-Harguindeguy et al., 2013; Violle et al., 2007; Wang et al., 2022). These traits, being related to the different functions of the plants, account for important variations in the strategy and global functioning of plants (Richardson et al., 2013) and impact fitness through their effects on plant growth, reproduction and survival (Cornelissen et al., 2003; dos Santos & Ferreira, 2020). Functional traits can vary among species, conspecific genotypes and also clonemates subject to different environments (Fyllas et al., 2009; Richardson et al., 2013). This ability of a given genotype to express different phenotypes in different environments is a phenomenon known as phenotypic plasticity (PP) (Ren et al., 2020; Sultan, 2000; Valladares et al., 2006). PP is seen as one of the main processes by which plants might acclimate to changes in environmental conditions (Gratani et al., 2000; Vitasse et al., 2010).

While the functional trait approach has often been used to compare species, it has received less attention at the intraspecific level where the impact of ID on functional traits has rarely been investigated in tree species (Hajek et al., 2016; Violle et al., 2012). The PP of functional traits could affect fitness by allowing a genotype to better acclimate to fluctuating environmental conditions (adaptive PP). It has been hypothesized that inbreeding could reduce PP due to the reduced allelic diversity found in more homozygous genotypes (Reed et al., 2012; Swillen et al., 2015). Therefore, we hypothesize that ID could result from the expression of deleterious mutations affecting functional traits, and/or from a reduction of adaptive PP in inbred genotypes. Studies investigating the link between PP and inbreeding or ID found various results, including a positive correlation between PP and inbreeding (e.g. Auld & Relyea, 2010; Ratz et al., 2020), no association (e.g. Buckley et al., 2019; Murren & Dudash, 2012; Sandner et al., 2022; Schlichting & Levin, 1986) or even suggested a negative correlation following the concept of developmental stability (Charlesworth & Willis, 2009).

Better understanding the interplay between ID, functional traits and PP is particularly relevant for tropical trees threatened by overexploitation. The tropical rainforests of Central Africa are experiencing unprecedented episodes of deforestation and forest degradation to sustain the livelihood of an increasing population (Aleman et al., 2018; Tyukavina et al., 2018). Logging is also affecting timber species of high commercial value on the international market, some of which suffer from a deficit of natural regeneration, like *P. elata*. To exploit such species in a sustainable way and avoid the depletion of natural populations, silviculture is a promising pathway but which is still little developed on native species in Central Africa (but see Kouadio & Doucet, 2009; Ouédraogo et al., 2014). The selection of good genetic material can affect the success of plantations so that it is particularly important for *P. elata* with a mixed mating strategy where outbred seedlings showed higher growth than inbred ones (Angbonda et al., 2024). Hence, it is crucial to analyse how inbreeding affects the PP, leaf traits and the whole-plant traits associated with growth form and competitive vigour of endemic and endangered species (Gratani, 2014).

To understand the impact of inbreeding and competition on traits associated with growth form, leaf functional traits and PP, this study focused on *P. elata*. Firstly, using a common garden experiment of *P. elata* seedlings planted at different densities and followed during 4 years (Angbonda et al., 2024; Ilunga-Mulala et al., 2021), we show that inbreeding negatively affects the whole-plant traits associated with growth and competitive vigour (diameter and maximum height), leading to ID. Then, using a set of leaf trait measurements potentially affecting photosynthesis and growth, we test two hypotheses on the possible origin of ID from the perspective of functional traits: (H1) inbreeding directly affects leaf traits; (H2) inbreeding reduces the PP of leaf traits. To test these hypotheses, we regularly measured the diameter and total height of 540 *P. elata* seedlings, as well as various leaf characteristics and leaf mineral content (elementome) from the base and top of the crown of 60 seedlings.

2 | MATERIALS AND METHODS

Fieldwork conducted for this study did not require any specific permits or licences. The Nelder-type experimental design was developed and established by members of the research team, who are included as co-authors of this publication.

2.1 | Species and study site

Pericopsis elata, also known as Afrormosia or Assamela, is a tall tree of high commercial value of the moist semi-deciduous African forests (Bourland, Lambert, et al., 2012). The species can reach 60 m of total height and 150 cm of diameter at breast height (Kafuti et al., 2022). It regenerates with difficulty below the crown and its natural populations are declining (Laure et al., 2014). Its natural distribution is disjoint and ranges from the Ivory Coast to the Democratic Republic of Congo (Bourland, Lambert, et al., 2012). It is a light-demanding and wind-dispersed species easily recognizable by its cream or greyish scaly bark (with reddish brown spots), its compound leaves (7–11 leaflets) and its fruits (oblong indehiscent pods with 1–5 discoid seeds). The average diameter increment varies from 0.32 to 0.45 cm year^{-1} in Cameroon and can reach 0.80 cm year^{-1} in DRC (Bourland, Kouadio, et al., 2012; Daïnou et al., 2021). The species is listed in appendix II, CoP18#17 of CITES (https://speciesplus.net) and registered as endangered in the IUCN red list due to marked overexploitation in West Africa at the end of the 20th century (Bourland, Kouadio, et al., 2012; Hills, 2020). Silvicultural promotion of *P. elata* is therefore one of the best ways to support the sustainability of its populations, and to guarantee the long-term survival of the species (Ilunga-Mulala et al., 2021; Ouédraogo et al., 2014).

The plantation used for this study was installed in the suburbs of the city of Kisangani (25°15′58″ longitude East, 0°30′42″ latitude North and 495 m elevation). The seedlings for the Nelder device were obtained from seeds from 19 mother trees harvested in the Biaro forest, Tshopo province, DR Congo, where seed and pollen dispersal patterns had been studied in a 400 ha plot (Angbonda et al., 2021). Mother trees were selected based on (1) seed maturity and (2) sufficient isolation from other mother trees to ensure accuracy of seed provenance.

Seeds collected between December 2016 and January 2017 were first raised in a nursery on the campus of the Science Faculty of the University of Kisangani, planting individual seeds in 2 L plastic bags filled with forest soil. The region of Kisangani is covered with semi-deciduous forests, which are part of the Guineo-Congolian regional centre of endemism (White, 1986). The climate is of Af type, characteristic of areas without dry seasons, according to the Köppen classification. The average annual temperature is 25.1°C, and the thermal amplitude is less than 5°C. The average annual rainfall is 1672 mm with a slight decrease observed between January–February and June–July (De Ridder et al., 2014). The Kisangani region is made up of a mixture of sandstone, red clay, marl and limestone (Ilunga-Mulala et al., 2021; Mosango, 1983). Soils are Xanthic Ferralsol and Eutric Gleysols (Jones et al., 2013). The fertility is low and the cation exchange capacity (CEC) varies between 2 and 8 cmolc/kg. The soil is acidic with a pH varying between 3.5 and 5.5 (De Ridder et al., 2014).

2.2 | Sampling design, inbreeding and growth measurement

After a year in the nursery, when *P. elata* seedlings had reached heights of 40–160 cm (median around 65 cm), 648 seedlings from 19 mother trees were transplanted in October 2017 in three replicates following the Ia design proposed by Nelder (1962) and later applied in a context of research on monospecific tree plantations (Beeckman & Vander Mijnsbrugge, 1990). Each design occupies an area of 908 m^2 where seedlings are located along 12 concentric circles, each containing 18 evenly spaced saplings, ensuring a density gradient (Nelder, 1962). The saplings from the innermost and outermost circles, placed at a distance of 0.6 and 15.6 m from the centre of the circles, respectively, formed buffer zones and were not measured. Therefore, 180 out of 216 saplings were followed for each of the three replicates, totalling 540 surveyed seedlings. Local spacing between neighbouring plants ranged from 0.2 × 0.2 to 3.8 × 3.8 m (Figure 1). Each of five levels of competition illustrated on Figure 1 combines two concentric circles of the Nelder device.

The data used in this study were acquired in the first 4 years after planting. In October 2017 and then every 3 months from December 2017 to December 2021, we measured the total height (*H*max) from the collar to the terminal bud of the longest branch and the diameter at 10 cm from the collar of the 540 stems. A graduated ruler and a calliper were used to measure *H*max and diameter, respectively. The Telefix dendrometer was used from 2021 for the tallest plants. *H*max and diameter are whole-plant traits associated with growth form, the species position in the vegetation's vertical light gradient, competitive vigour, etc. (Pérez-Harguindeguy et al., 2013).

We assessed whether seedlings were inbred (i.e. resulting from self-pollination) or outbred (i.e. resulting from cross-pollination) following Angbonda et al. (2021) who characterized the mating system of the source population using 11 nuclear microsatellite markers. This data set has been completed with 250 additional genotyped seedlings (Angbonda et al., 2024).

2.2.1 | Leaf traits measurement

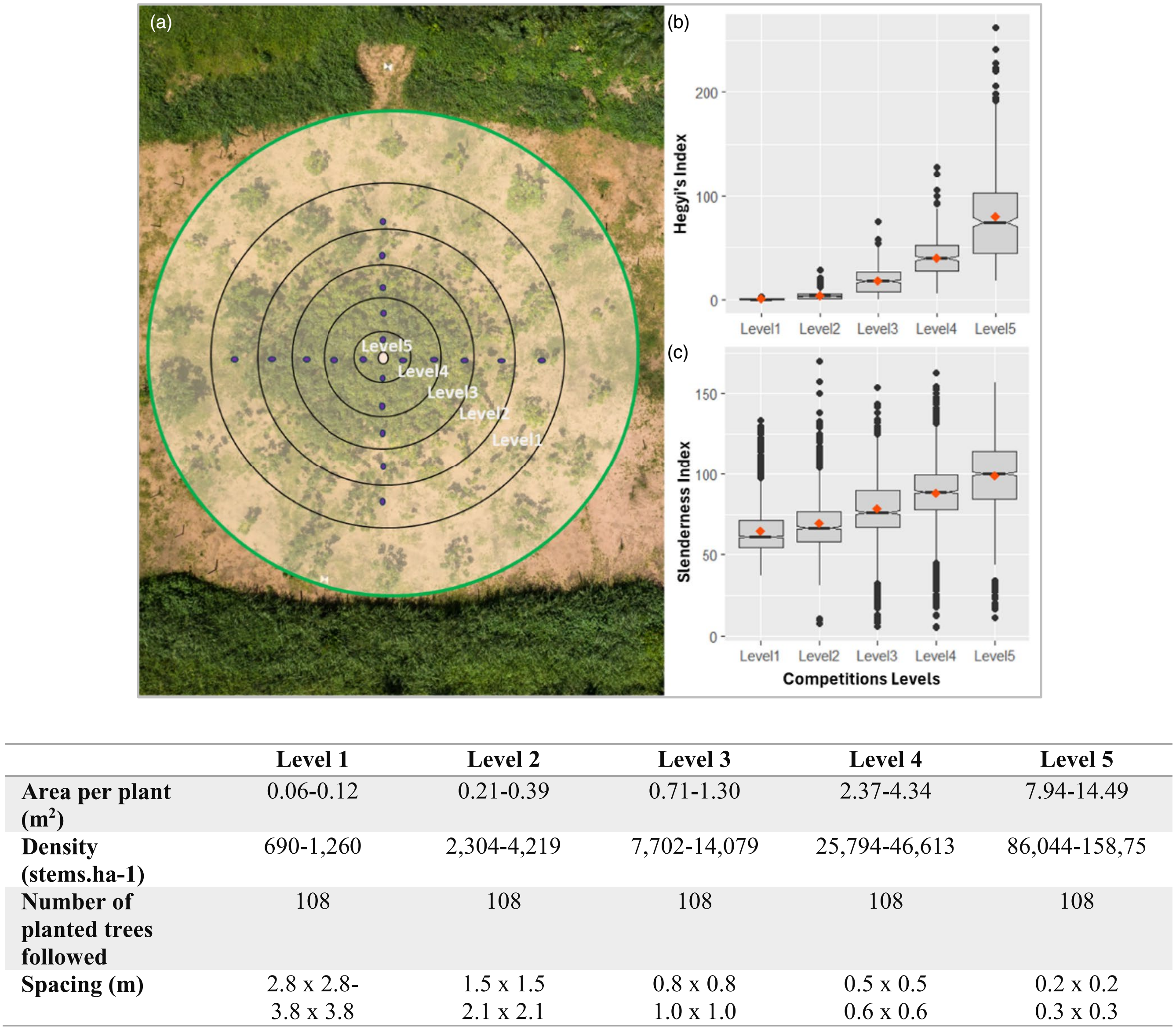
Foliar traits were collected on 60 saplings (33 inbred, 26 outbred and one for which the inbreeding status could not be assessed). We collected leaflet samples in March 2018, 2019, 2020 and 2021 from 20 saplings per Nelder device (two individuals per circle). These saplings were taken 2 by 2 from one circle to another, alternatively along the North–South and East–West axes, due to the staggered location (Figure 1a). For each sapling, whenever possible, we sampled one leaf directly exposed to the sunlight (from the top part of the crown) and another one not directly exposed to the sunlight (from the base of the crown; Kafuti et al., 2020). Each leaf bore 6 to 10 leaflets. It was not always possible to collect both exposed and shaded leaves, especially in 2021, when some plants stayed in the shade of neighbouring plants and others had only exposed leaves. In 2019, 2020 and 2021, chlorophyll content (Chl) was measured in the field before leaflet collection using a KONICA MINOLTA SPAD-502 chlorophyllometer plus (Coste et al., 2010; Rozendaal et al., 2006; Xiong et al., 2015). The chlorophyll content of leaves is one of the most significant parameters of the physiological state of plants, enabling them to absorb solar radiation and carry out the process of photosynthesis (Silla et al., 2010).

A first set of traits included those often used to characterize the leaf economic spectrum: leaf fresh mass (LFM), leaf dry mass (LDM), leaf area (LA), specific leaf area (SLA), leaf dry matter content (LDMC), chlorophyll content (Chl), stomatal density (SD), stomatal size (SS) and maximum stomatal water vapour conductance (*G*max). These traits being involved in photosynthesis, they could express strategies of resource acquisition and phenotypic responses to environmental conditions affecting growth rate, as detailed below for each trait. They were measured each year on 60 plants, except Chl that was not measured in 2018 and stomatal traits that were collected on 30 trees in 2019 and 2020, and on 60 trees in 2021.

A second set of traits characterizing the elementome is the leaf composition in some key elements (Al, Ca, Fe, K, Mg, Mn, P and Zn), which were measured for 20 samples collected in 2020 to assess how element concentration was influenced by plant density, leaf exposure to light and inbreeding.

All leaflets collected were scanned using an HP Scanjet 5590P scanner. The high resolution images (1200 dpi) thus obtained were analysed with the software ImageJ-win64 (Schneider et al., 2012) to determine the LA (mm^2). Leaflets were oven-dried at 70°C for 72 h and then stored in the envelopes with dehydrated silica gel. The dry mass of leaflets without their petioles (LDM, mg) was weighed using a precision balance (0.001 g). The SLA ($mm^2\,mg^{-1}$) was calculated by dividing the leaf area by the dry mass (LA/LDM) (Pérez-Harguindeguy et al., 2013). SLA responds to a wide range of environmental stimuli (Díaz et al., 2016; Rozendaal et al., 2006; Velikova et al., 2020) and correlates with leaf chemical composition, photosynthesis rate, leaf longevity and carbon investment (Pierce et al., 2017). Leaflet dry matter content (LDMC = LDM/LFM) was also considered as it predicts leaf nitrogen content and soil fertility (Hodgson et al., 2011), and is sometimes better correlated with primary production than SLA in inter-species comparisons (Smart et al., 2017).

Stomatal characteristics of the abaxial surface of leaves were assessed in 2019 and 2020 on one or two leaflets (one exposed and one shaded) for each of 30 seedlings, and in 2021 on five or 10 leaflets (five exposed and five shaded) on each of 56 seedlings. To this end, a layer of clear nail polish was applied to the midsection of the leaflet, between the central vein and the leaflet margin. After the varnish dried overnight, the impression on the leaflet was



	Level 1	Level 2	Level 3	Level 4	Level 5
Area per plant (m^2)	0.06-0.12	0.21-0.39	0.71-1.30	2.37-4.34	7.94-14.49
Density (stems.ha-1)	690-1,260	2,304-4,219	7,702-14,079	25,794-46,613	86,044-158,75
Number of planted trees followed	108	108	108	108	108
Spacing (m)	2.8 x 2.8- 3.8 x 3.8	1.5 x 1.5 2.1 x 2.1	0.8 x 0.8 1.0 x 1.0	0.5 x 0.5 0.6 x 0.6	0.2 x 0.2 0.3 x 0.3

FIGURE 1 Nelder device. (a) Aerial view of one of the three replicates of the Nelder device. The black dots inside the competition circle represent the plants selected and monitored each year for leaf trait measurements. For each level of competition are given (b) the Hegyi's competition index (details in Ilunga-Mulala et al., 2021) and (c) the slenderness index: The ratio of total height to diameter (Kafuti et al., 2022). The slenderness index provides an expression of the social standing of trees in the Nelder device. With a declining slenderness index, the stability of trees in the system's competitive gradient rises. A slenderness value greater than or equal to 100 indicates that a tree is extremely mechanically weak. The red points in graphs (b and c) represent the average. The appended table reports information on the three Nelder replicates.

removed with tape, mounted on a glass slide and digitized using the Toupview UH-CMOS camera (Hangzhou Toup Tek Photonics Co., Ltd., Zhejiang, China) attached to the Olympus SZX-7 stereo microscope (Kafuti et al., 2020), taking five images for each leaflet. The length and width of stomata were measured on three stomata for each image, that is 15 stomata per leaflet and 7080 stomata for 472 leaflets sampled during the first 4 years of planting. Leaflets with poor quality prints were excluded from the stomatal measurements. Length (*Ls*, μm), width (*Ws*, μm) and SD (number per unit LA, mm^{-2}) were determined using the ObjetJ plug-in in ImageJ-win64 (Schneider et al., 2012). The SS was obtained from the length of the stomata: stomatal size $= 0.25 \times Ls^2$ (Taylor et al., 2012). The maximum stomatal conductance to water vapour (Gmax, en mole m^{-2} s^{-1}) was estimated as:

$$G\max = \frac{\mathrm{SD} * a\max * \frac{d}{v}}{dp + \frac{\pi}{2} * \sqrt{\left(\frac{a\max}{\pi}\right)}}$$

with SD, the stomatal density, *d* is the diffusivity of water vapour to air at 25°C (=2.43 10^{-5} $m^2 s^{-1}$), *v* is the molar volume of air at 25°C (0.024 m^3 $mole^{-1}$), *dp* is the depth of the ostiole. Since guard cells have an elliptical shape, *dp* is approximated by the stomatal width (*Ws*, μm) and the maximum pore area is calculated from the stomatal length (Ls, µm) using the formula of an ellipse: $amax = Ls \times Ws$ is the maximum surface of the completely open ostiole (µm^2) (Douhovnikoff et al., 2016; Kafuti et al., 2020). Note that the maximum stomatal conductance is higher (~20%) than the operating stomatal conductance (Douhovnikoff et al., 2016; Dow et al., 2014). The characteristics of stomata play a fundamental physiological role in the life of the plant (photosynthesis and transpiration) (Djinet et al., 2016). Stomatal conductance controls gas exchange between the leaves and the environment (Douhovnikoff et al., 2016; Flexas et al., 2009). This parameter is influenced by various environmental factors, such as light, temperature, humidity and water availability (Buckley, 2019).

Half of each leaflet sampled for the year 2020 in one of the replicates of the Nelder device was used for chemical analyses at the Laboratory of Plant Ecology and Biogeochemistry of the 'Université Libre de Bruxelles'. Leaflet samples were dried at 65°C and ground into a cutting mill. About 0.5 g of plant sample was dry ashed for 12 h at 450°C in a muffle furnace. Ashes were dissolved in 1 mL of nitric acid (65%), heated on a hot plate for 10 min. The final clear solutions were filtered using Whatman filter paper No. 41 and diluted to 15 mL. Element concentrations Al, Ca, Fe, K, Mg, Mn, P and Zn of the solutions were measured by inductively coupled plasma optical emission spectrometry (iCAP PRO, Thermo Scientific, Cambridge, United Kingdom). The precision and accuracy of the analyses were monitored using a certified reference material (Peach Leaves, NIST 1547). Analyses agreed with certified values to within ±5%. The nutrient content in leaflets provides information on the ability of seedlings to acquire resources (Pérez-Harguindeguy et al., 2013).

2.3 | Statistical analyses

To assess the impact of ID on the whole-plant traits associated with growth form and competitive vigour (diameter and maximum height), we modelled the maximum height or diameter growth of each plant over time using logistic regression (using R package 'stats' version 4.1.3.), separately for each competition level and inbred versus outbred plants. The growth asymptote (parameter 'a') was compared between inbred and outbred plants. The maximum height and diameter measured during the four measurement campaigns of leaf traits was also modelled using two types of linear mixed models implemented in the R package 'lmerTest' version 3.1.3 (Kuznetsova et al., 2017) and 'lme4' version 1.1–31 (Bates et al., 2015). First, we considered all explanatory variables (year, level of competition, Nelder replicate, inbreeding and mother tree) as random factors in order to assess the proportions of variance explained by each of these factors. Second, we considered the variables year, level of competition and inbreeding as fixed factors, leaving the variables mother tree and Nelder replicate (plot) as random factors, in order to test the differences between states of the fixed factors using the R package 'emmeans' version 1.8.5 (Lenth et al., 2025).

For leaf traits, we performed two linear mixed models to assess the extent of intra- and inter-individual trait variation. The first model aimed to partition the variance of leaf traits among the different explanatory variables (year, level of competition, leaf exposure to light and inbreeding), which were all treated as random factors. In the case of elementomes, as they were measured in a single year, explanatory variables were restricted to level of competition, exposure to light and inbreeding. The second model was used to assess differences in means between states of explanatory variables of interest (levels of competition, leaf exposure to light, year and inbreeding), which were declared as fixed factors, with tree identifier and Nelder replicate used as random factors. The mother tree could not be included in these models due to the limited sample size for leaf traits (60 trees).

Phenotypic plasticity of leaf traits was quantified across years, exposure to light or the density gradient using the relative distance plasticity index (*RDPI*) ranging from 0 (no plasticity) to 1 (maximum plasticity) (Valladares et al., 2006):

$$\mathrm{RDPI} = \frac{1}{n} \sum_{\substack{i \neq i' \\ j, j'}}^{n} \frac{(x_{ij} - x_{i'j'})}{(x_{ij} + x_{i'j'})}$$

where i represents a given level of the environmental treatment (year, levels of competition or exposure to light), j refers to the individual number identification, x_{ij} is the trait value of j in condition i, and the sum is taken over all possible pairs of measures taken in distinct environments for different ($j' \neq j$) or the same ($j' = j$) individuals, making a total of n pairs. When estimating plasticity across years or exposure to light, we computed RDPI using only measures taken on the same individuals ($j' = j$), while we had to consider measures taken in different individuals to compute RDPI across competition levels ($j' \neq j$). RDPI was computed for each leaf trait, separately for inbred and outbred plants. To test whether RDPI was lower in inbred than outbred plants, we compared the difference with the one obtained after 1000 random permutations of the inbreeding status of seedlings. The permutation test was used to compare the plasticity of leaf traits.

To determine the link between photosynthetic capacity and growth, pairwise correlations were computed with the 'PerformanceAnalytics' version 2.0.4 R package to test the relationship between foliar traits and the height or diameter growth of inbred and outbred plants.

3 | RESULTS

The paternity analysis showed that of the 540 planted seedlings, 267 were inbred and 192 were outbred. The results were inconclusive or lacking for the remaining 81 seedlings, which were therefore not considered for statistical analyses.

3.1 | Stand competition and inbreeding effects on traits associated with growth

The total height (*H*max) and diameter were lower in inbred than in outbred plants (Figure 2, Table 1), a difference not observable until

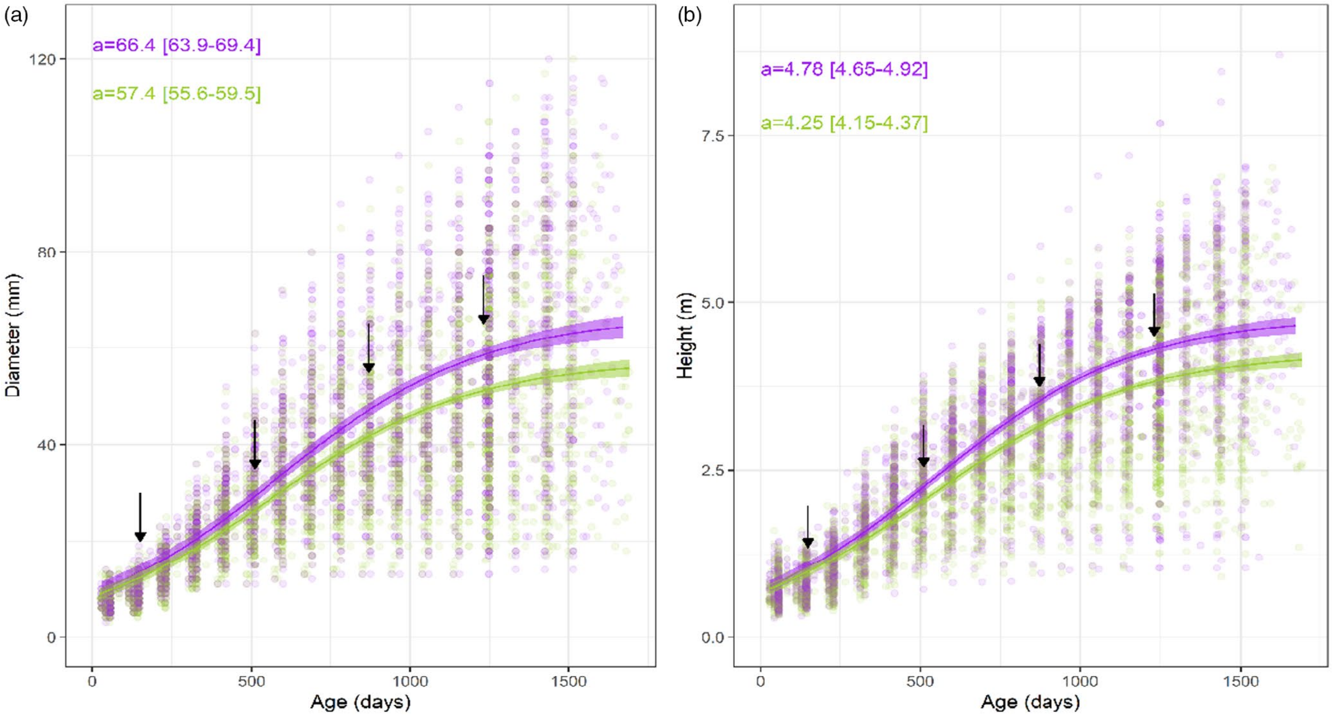


FIGURE 2 Diameter (a) and total height (b) of *P. elata* seedlings as function of the age for outbred (violet) and inbred plants (green). '*a*' is the estimator of the growth asymptote of the logistic model. Confidence bands were generated using bootstrapping procedure. Vertical arrows along the growth curves indicate when leaf traits measurements were taken: 150, 510, 870 and 1230 days after transplantation.

510 days after transplantation. Among the four measurement campaigns of leaf traits, the second one (2019, *c*. 510 days after transplantation) has recorded the highest mean growth rate in height and diameter (Figure 2).

As expected, diameter and height growth rates increased with less competition (Figure S1) and plants grew slowly after 1000 days under the highest competition levels (Figure S1A,F). According to the estimates of the asymptote (*a*) of the logistic models, the higher growth of outbred than inbred plants occurred at all competition levels, except at the intermediate level where *a* estimates had overlapping 95% confidence intervals (level 3, Figure S1C,H). The difference in growth between outbreds and inbreds tended to be highest at the lowest level of competition (Figure S1E,J).

The partition of variance indicates that the level of competition, year and Nelder replicate (plot) had the highest impact on height and diameter growth (Figure 3c), often explaining 19% to 25% of the variation, while inbreeding and mother tree explained 4% to 5% of the variation.

3.2 | Determinants of leaf traits variation

Plant leaf characteristics varied substantially as a function of year, planting density, and/or leaf exposure to light (Figure 3; Table 1). On the contrary, inbreeding had no significant impact on any of the studied leaf traits (Table 1), despite the fact that about 4% to 5% of the variation in plant growth was explained by inbreeding and by the mother tree (Figure 3c).

Competition affected in particular SLA, explaining 11.2% of its variance, *H*max (24.5%), Diameter (19.5%) and iron concentration (Fe, 60.3%) (Figure 3a–c). SLA increased by about 50% from lowest to highest competition, an effect due to a decrease in leaf mass rather than a change in LA (Table 1). Similarly, leaf Fe concentration increased about twofold along the competition gradient (Table 1).

Year affected most of the leaf traits (e.g. 38% explained variance for dry mass content) but had a non-significant impact on stomata size or density (Table 1). There was no regular trend with year, as it was most often the Year 2019 that stood out from the other ones (higher leaf mass, dry mass content, LA, chlorophyll content and *G*max, lower SLA; Table 1; Figure S2).

Leaf exposure to light affected mostly SD (13.3%, albeit non-significantly), fresh leaf mass (higher for exposed leaflets) and all elements (28.7% to 69.8%) except Fe concentration. Leaflets well exposed to sunlight had lower concentration in Al, Ca, Mg and Mn, but higher concentration in K, P and Zn (Table 1).

3.3 | Phenotypic plasticity of inbred and outbred plants

Overall, PP was moderate for all leaf traits, with *RDPI* in the range 0.15–0.32 for most traits (Figure 4) but lower plasticity was found for chlorophyll content (CHL: 0.11), stomata size (SS: 0.04 to 0.06) and stomatal conductivity (Gmax: 0.04 to 0.05). Plasticity was nearly always slightly lower across exposure to sunlight (measured within year and tree) than across years (measured within tree and sun

TABLE 1 Means and standard errors of growth and foliar traits across years, competition levels, position of the leaf within the crown and inbreeding.

	Year				Competition					Exposure to sun		Inbreeding	
Traits	2018 [1.42 year]	2019 [2.42 year]	2020 [3.42 year]	2021 [4.42 year]	Level 1 [very low]	Level 2 [low]	Level 3 [medium]	Level 4 [high]	Level 5 [very high]	Shaded	Exposed	Inbred	Outbred
Growth traits													
Diameter	–	32 ± 1.47a	43.10 ± 1.47b	53.10 ± 1.47c	25.80 ± 1.96a	37.90 ± 1.93b	43.90 ± 1.94b	52.3 ± 1.94c	53.80 ± 1.74c	–	–	39 ± 1.62a	46.4 ± 1.55b
Height	–	263 ± 9.84a	342 ± 9.84b	402 ± 9.84c	275 ± 13a	360 ± 12.90b	357 ± 13b	351 ± 13b	335 ± 11.70b	–	–	316 ± 10.80a	355 ± 10.30b
Leaf structural traits													
LFM	0.29 a ± 0.01	0.34 ± 0.01b	0.26 ± 0.01a	0.24 ± 0.01a	0.34 ± 0.01a	0.30 ± 0.01ab	0.28 ± 0.01b	0.25 ± 0.02b	0.24 ± 0.01b	0.25 ± 0.01a	0.31 ± 0.01b	0.27 ± 0.01	0.29 ± 0.01
LDM	0.08 ± 0.01a	0.14 ± 0.01b	0.07 ± 0.01a	0.06 ± 0.01a	0.11 ± 0.01*a*	0.09 ± 0.01ab	0.08 ± 0.01b	0.08 ± 0.01ab	0.07 ± 0.01b	0.08 ± 0.01	0.09 ± 0.01	0.08 ± 0.01	0.09 ± 0.01
LDMC	0.28 ± 0.02a	0.41 ± 0.02b	0.28 ± 0.01a	0.29 ± 0.02a	0.33 ± 0.02	0.31 ± 0.02	0.30 ± 0.02	0.33 ± 0.02	0.31 ± 0.02	0.33 ± 0.02	0.30 ± 0.02	0.31 ± 0.02	0.31 ± 0.02
LA	17.20 ± 0.83a	21.30 ± 0.82b	15.00 ± 0.86a	18.40 ± 0.96ab	18.10 ± 1.01	17.70 ± 1.02	16.90 ± 1.04	17.90 ± 1.55	19.20 ± 0.90	17.40 ± 0.72	18.60 ± 0.72	17.40 ± 0.81	18.50 ± 0.76
SLA	22.50 ± 1.70a	15.60 ± 1.69ab	24.60 ± 1.72ab	32.6 ± 1.79b	18.10 ± 1.92a	21.08 ± 1.93ab	23.70 ± 1.95ab	25.80 ± 2.55ab	29.90 ± 1.80b	25.90 ± 1.62	21.80 ± 1.61	23.6 ± 1.66	24.40 ± 1.71
CHL	–	35.80 ± 0.86a	27.20 ± 0.90b	28.60 ± 0.99b	34.20 ± 1.07a	32.10 ± 1.04ab	28.60 ± 1.1b	28.00 ± 1.65b	30.10 ± 0.96ab	30.70 ± 0.82	30.80 ± 0.81	30.9 ± 0.81	30.5 ± 0.87
SS	–	97.70 ± 2.86	91.40 ± 2.88	92.50 ± 2.61	96.90 ± 3.17	91.7 ± 3.43	92.20 ± 3.01	94.00 ± 3.72	94.70 ± 3.58	95.10 ± 2.68	92.70 ± 2.69	93.6 ± 2.80	94.2 ± 2.90
SD	–	246 ± 16.30	264 ± 16.30	222 ± 12.20	268 ± 17	268 ± 21.30	221 ± 14.50	237 ± 21.10	227 ± 17.40	218 ± 12.70	259 ± 12.80	237 ± 13.40	240 ± 14.10
Gmax	–	1.74 ± 0.02a	1.71 ± 0.02ab	1.61 ± 0.01b	1.75 ± 0.02	1.69 ± 0.02	1.67 ± 0.03	1.65 ± 0.03	1.65 ± 0.03	1.67 ± 0.01	1.70 ± 0.01	1.68 ± 0.01	1.68 ± 0.01
Leaf chemical traits													
Al	–	–	117.61 ± 55.41	–	88.20 ± 13a	86 ± 14a	127.50 ± 18ab	124.70 ± 14ab	164 ± 13.50b	147 ± 9.34a	88.40 ± 8.94b	110 ± 10.81	126 ± 8.66
Ca	–	–	5342 ± 3598	–	6307 ± 882	6026 ± 913	4922 ± 1226	4258 ± 913	5458 ± 882	8022 ± 608a	2767 ± 582b	5536 ± 704	5253 ± 564
Fe	–	–	58.45 ± 27.01	–	36.50 ± 6.44a	40.20 ± 6.67ab	55.40 ± 8.85ab	66.50 ± 6.67ab	94.30 ± 7.6b	63 ± 4.20	54.20 ± 4.03	54.40 ± 5	62.80 ± 4.11
K	–	–	4211 ± 2141	–	4346 ± 636	5118 ± 659	4114 ± 885	3462 ± 659	4230 ± 637	3078 ± 439a	5430 ± 421b	4887 ± 508	3622 ± 407
Mg	–	–	1188 ± 522	–	990 ± 158	1588 ± 164	1091 ± 220	1074 ± 164	1256 ± 158	1424 ± 109	976 ± 105	1302 ± 126	1098 ± 101
Mn	–	–	13.49 ± 7.17	–	16.30 ± 1	13.80 ± 1	12.60 ± 2	12.40 ± 1	11.50 ± 1	17.90 ± 1a	8.80 ± 1b	11.60 ± 1	15.10 ± 1
P	–	–	1229 ± 392	–	1167 ± 110	1379 ± 113	1230 ± 152	1222 ± 113	1161 ± 110	980 ± 75a	1484 ± 72b	1302 ± 87	1161 ± 70
Zn	–	–	17.01 ± 7.16	–	16.80 ± 2.66	18.60 ± 2.76	13.60 ± 3.62	18.70 ± 2.76	15.90 ± 2.66	13 ± 1.67a	20 ± 1.60b	16.70 ± 2.12	16.70 ± 1.70

Note: The age mentioned here starts from the germination in the nursery until the date of measurement. Values in black indicates that significant differences occur according to factor of interest, while values in grey indicate no significant differences. The letters (a–c) indicates which means are significantly different at an $\alpha = 0.05$. All chemical traits are expressed in µg/g; leaf trait units are provided in Methodology Section 2.2.

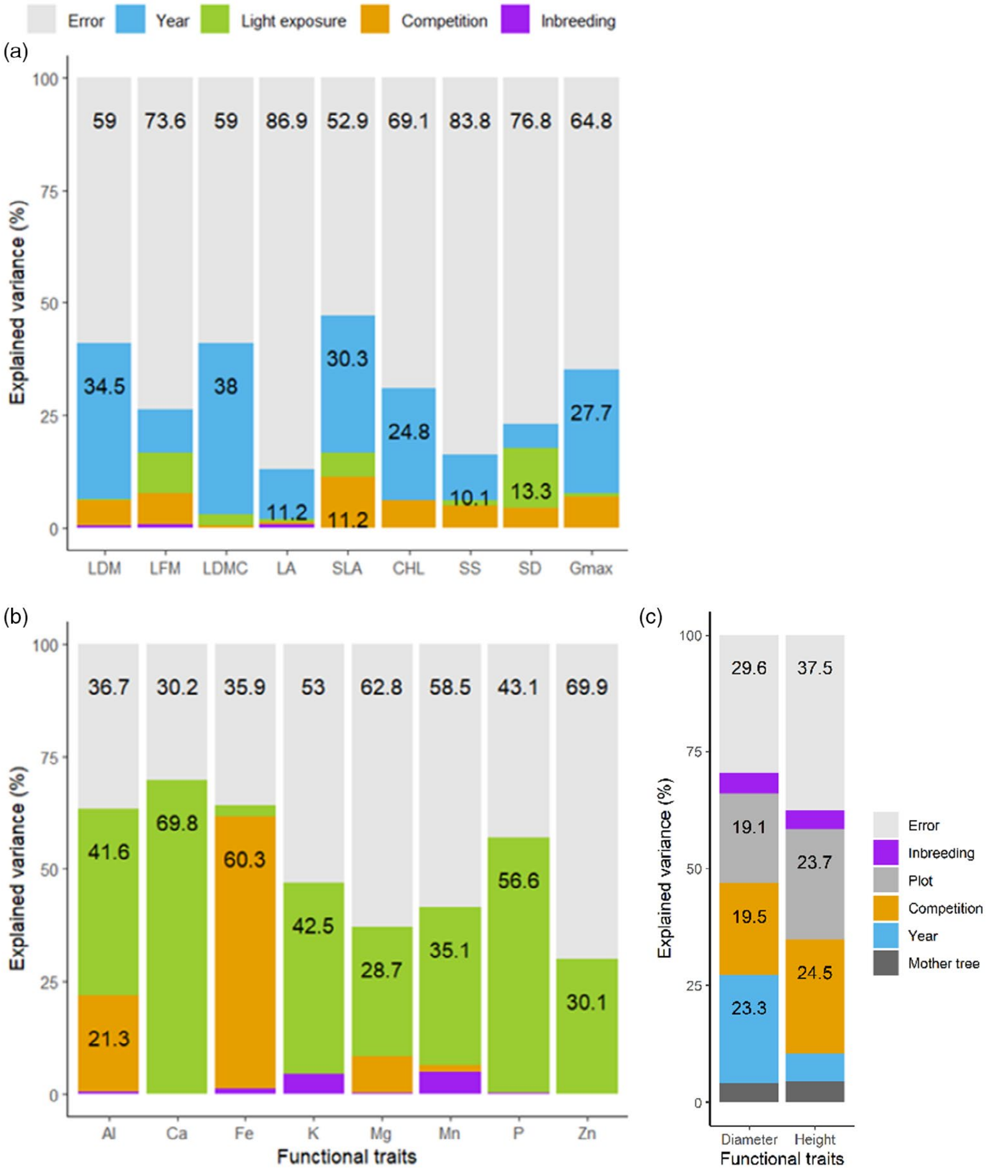


FIGURE 3 Variance partitioning of (a) nine leaf morphological and physiological traits (CHL, chlorophyll content; Gmax, maximum stomatal conductance; LA, leaf area; LDM, leaf dry mass; LDMC, leaf dry matter content; LFM, leaf fresh mass; SD, stomatal density; SLA, specific leaf area; SS, stomatal size), (b) leaf concentration of eight elements and (c) two traits associated with growth (stem diameter and height) across five explanatory categorical variables expressing the effect of age (Year, except for elements which were measured on a single year), light exposure (leaves from top or bottom of the crown, except for height and diameter), competition (five levels of stand density), inbreeding (inbred versus outbred plants) and mother tree (only for height and diameter). The residual variation (Error) includes unexplained variation within and between individuals. For each level where the explained variance is higher than 10%, the value is printed on the corresponding stacked bar.

exposure level) or competition levels (measured within year and sun exposure level). Plasticity across years and competition levels was similar, except for SLA showing higher plasticity across competition levels (0.25) than across years (0.21) and across exposure to sunlight (0.16).

Permutation tests found higher plasticity in outbred than inbred plants (one-sided tests) only for chlorophyll content (CHL) across years ($p=0.029$) and competition levels ($p=0.032$), for fresh leaf mass (LFM) across exposure to sunlight ($p=0.020$) and competition levels ($p=0.062$, marginal significance), and for stomatal conductivity (Gmax) across competition levels ($p=0.072$, marginal significance). The sole case of a statistically significant reverse pattern—higher plasticity for inbred than outbred plants—was found for leaflet dry mass content (LDMC) across competition levels ($p=0.028$).

3.4 | Relationship between leaf traits and growth

Correlations between leaf traits for inbred and outbred plants are presented in Table S1. Growth in diameter was negatively related to

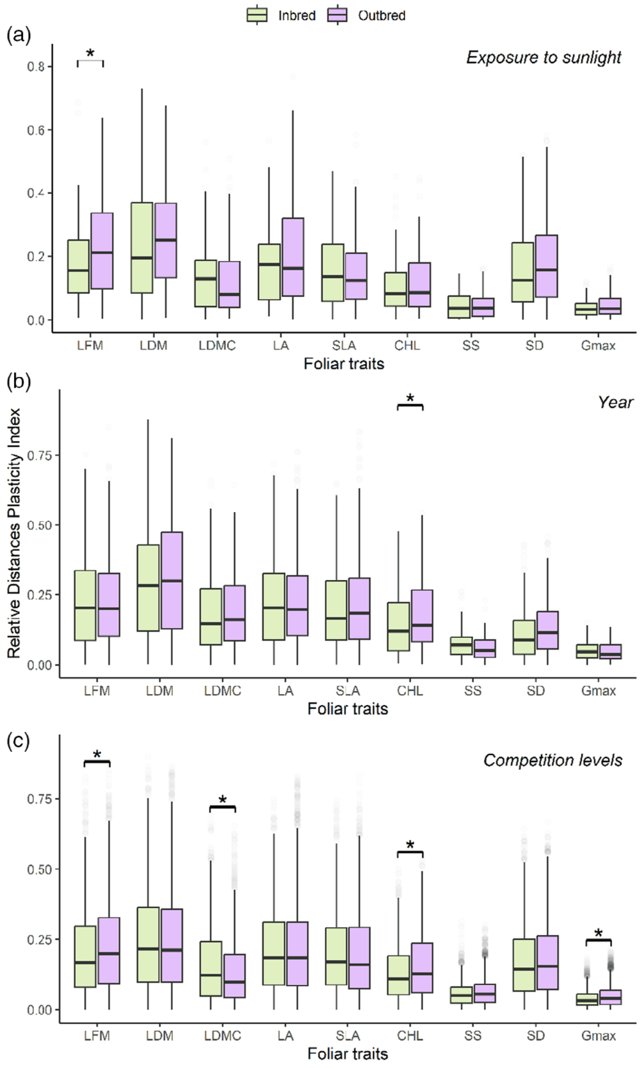


FIGURE 4 Phenotypic plasticity of leaf traits estimated as the relative distance plasticity index (*RDPI*) and its 95% confidence interval, according to three environmental gradients: (a) between upper and lower leaf position in the crown (sunlight gradient), (b) across year (ontogenetic plasticity) and (c) across different levels of competition (environmental plasticity). For each trait, the average *RDPI* is compared between inbred (green) and outbred (purple) individuals, and tested following a permutation test. *: significant difference ($p < 0.05$).

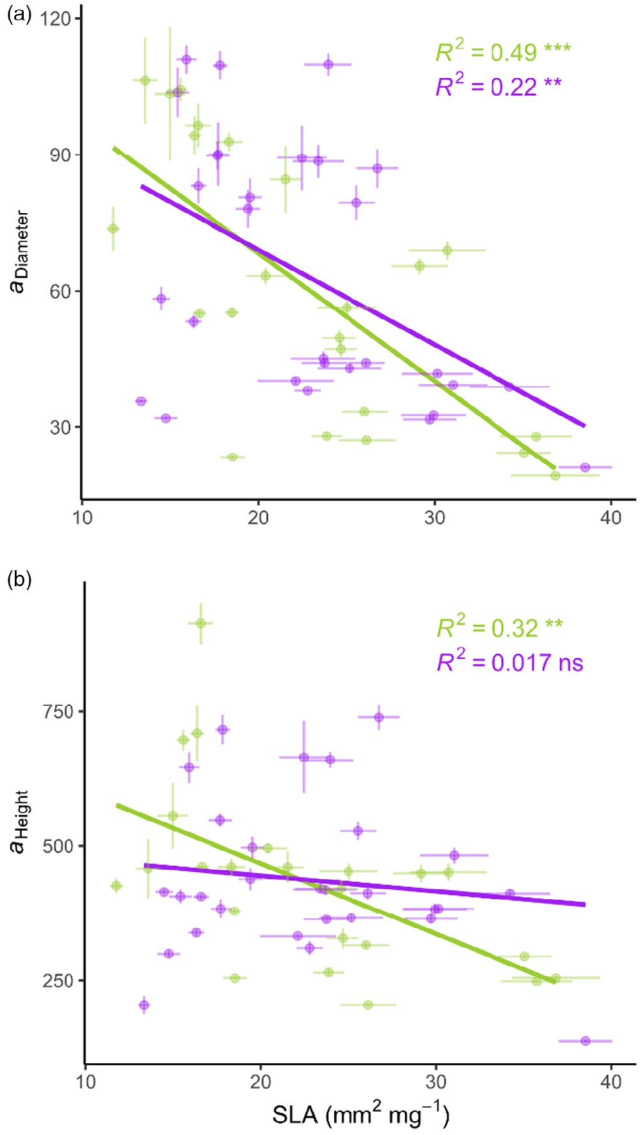


FIGURE 5 (a) Diameter (a_{Diameter}) and (b) height (a_{Height}) growth estimates of *Pericopsis elata* as function of the specific leaf area (SLA) for outbred (violet) and inbred (green) saplings. Regression line, coefficient of determination (R^2) and statistical significance: *** for $p < 0.001$; ** for $p < 0.01$; ns for non-significant. Horizontal and vertical bars indicate the standard errors of means.

SLA, both in inbred plants ($R^2 = 0.49$, $p < 0.001$) and in outbred plants ($R^2 = 0.22$, $p < 0.01$) (Figure 5). Growth in height was significantly related to SLA in inbred plants ($R^2 = 0.32$, $p < 0.01$) but not in outbred plants ($R^2 = 0.017$, $p > 0.05$).

4 | DISCUSSION

This study shows that inbreeding and competition (planting density) have a significant impact on the height and diameter growth of 1- to 4-year-old *P. elata* saplings. While leaf traits varied with competition, age and/or leaf exposure to direct sunlight, they were not affected by inbreeding. However, the PP of some leaf traits was slightly lower in inbred than outbred saplings. On the contrary, the SLA of inbred saplings was more correlated with height and diameter growth than that of outbred saplings. The various effects observed are discussed below.

4.1 | Higher growth performance of outbred saplings

The significant impact of competition on sapling growth has been reported by other authors in a natural environment (Rozendaal et al., 2020) or in plantations (Angbonda et al., 2024; Ilunga-Mulala et al., 2021). These results underline the relevance of density control in forest plantations (Pommerening & Grabarnik, 2019). High planting density affects the diameter growth more than the height growth (Figure S1) so that slenderness increases with planting density (Figure 1c). This confirms an important theory in dendrometry, according to which tree species generally respond to light competition by investing more energy in height growth than in diameter growth (Brunner & Nigh, 2000).

After 53 months in plantation, outbred *P. elata* plants showed higher growth performance in height and diameter than inbred plants for all levels of competition, a result also reported in Angbonda et al. (2024). Similar results were reported in *Prunus dulcis* (Oukabli et al., 2001) and *Shorea laxa* seedlings (Takeuchi et al., 2020). All these studies show that outbred plants outperform inbred plants, confirming a strong link between inbreeding and growth (Burgess et al., 1996). Furthermore, our results showed no significant difference between inbred and outbred plants until around 510 days after transplantation. These results suggest that the deleterious effects of ID are only observable around a year and a half after transplanting *P. elata* seedlings. Similar observations were reported by Stacy (2001) on the growth of *Syzygium rubicundum* and *Shorea cordifolia*, where no effect of the cross or parent tree was observed on growth in the first year after sowing. Hardner and Potts (1995) also reported a trend for ID to increase with age in *Eucalyptus globulus* seedlings. In *Eucalyptus regnans* plants, the growth of inbred and outbred did not differ significantly up to the age of 2 years, with very high mortality in inbred families from the age of 13 (Eldridge, 1983). The effects of inbreeding are most apparent at the seed formation stage, and less at the seed germination and early seedling growth stages (Stacy, 2001). This phenomenon was not tested in *P. elata* because it was not possible to follow the fate of inbred versus outbred ovules before seed dispersal. In view of these observations, we confirm that inbreeding negatively affects the height and diameter growth of young *P. elata* plants. Furthermore, the impact of inbreeding increases with seedling age.

4.2 | Leaf traits determined by environmental conditions but not by inbreeding

We found considerable variation in chemical and foliar traits of *P. elata* trees that were mostly explained by plant development stage (year), light exposure and the level of competition. By contrast, inbreeding had no measurable impact on these leaf traits, refuting our hypothesis H1 that inbreeding negatively affects leaf traits.

We must remain cautious with the later interpretation because while growth was measured on more than 500 plants, leaf traits were measured on 60 plants (20 for leaf elementome), limiting the statistical power to detect ID. The acquisition of functional traits is time consuming and costly, so we opted firstly to take repeated measurements on a limited number of plants to be able to assess the sources of PP (i.e. variation within each genotype). Nevertheless, our data are conclusive enough to affirm that inbreeding has a negligible impact on leaf trait values compared with the impact of year, competition or light exposure (Figure 3).

For most leaf traits, notably LDM, LDMC, LA, SLA, CHL and *G*max, the first source of explained variation is year, where measurements made in 2019, about 510 days after transplantation, often departed from the other ones (Table 1; Figure S2). This is concomitant with the highest growth rates recorded (Figure 2). These results are in line with previous studies reporting that the characteristics of the leaves and/or the whole plant change with age (e.g. Laforest-Lapointe et al., 2014), including leaf chlorophyll content (Wang et al., 2020), and independently of the competitive and light environment (Coleman et al., 1994).

Some leaf traits responded to the competition gradient. With increasing plant density, we observe in particular a decrease in leaf dry and fresh mass (LDM and LFM), increasing SLA, a decrease in chlorophyll concentration (CHL) and an increase in Fe concentration, the sole element responding to the density gradient. These variations are explained by the fact that different levels of competition create different microenvironments (Ren et al., 2020). According to Ackerly et al. (2002), low SLA contributes to leaf survival and nutrient retention, the situation observed under low competition. Silvicultural practices therefore affect the mineral retention capacity of *P. elata* saplings (Ebuy et al., 2016).

Exposure to sunlight had little impact on most leaf traits, except that exposed leaves had higher fresh mass (LFM). By contrast, sun exposure had a very strong impact on the concentration of most leaf elements, except Fe, and in different directions according to the specific element considered. More specifically, Al, Ca, Mg and Mn were more concentrated in the shaded foliage at the base of the crown, while K, P and Zn were more concentrated in the well-exposed foliage at the top of the crown. A similar observation was reported by Hedde et al. (2007), where leaves exposed to full sunlight had lower nutrient levels and a more capacitive antioxidant system than leaves in the shade. The abundance of these three elements (K, P and Zn) in leaves fully exposed to sunlight is explained by their relevance to primary growth, given that potassium controls water pressure (opening and closing of stomata) (Santiago et al., 2012), phosphorus and zinc improve photosynthetic pigment production and growth (Richardson & Simpson, 2011; Walker et al., 2014; Zhang et al., 2023). Furthermore, Fyllas et al. (2009) show that mean annual temperature is negatively correlated with leaf concentrations of nitrogen, phosphorus and potassium. This might also explain why leaves exposed to sunlight contain more nutrients for photosynthetic growth than leaves located at the base of the canopy. Soil fertility plays a major role in determining the chemical properties of the leaves of specific tree species, in particular their N, P, K, Mg, Cu and Al content (Fyllas et al., 2009; Heineman et al., 2016). However, in the relatively homogeneous pedological environment where the Nelder devices were installed (unpublished results), the variability of the leaf chemical traits does not appear correlated with local soil variability and would depend primarily on the strategy of capture and conservation of resources affected by the position of the leaves in the crown and access to light.

In contrast to the results of Aranda et al. (2001), where the SD of *Pinus sylvestris* is positively correlated to light exposure, we found no impact of sunlight exposure, competition and seedling age on SD or size (SS and SD; Table 1). Only Gmax, which depends on SD and size, showed significant variation according to age. However, tree identity explained a large portion of the variation in SD and size, both for inbred and outbred seedlings (Figure S3), suggesting that these traits have a strong genetic determinism (i.e. high broad-sense heritability). In Amazonia, Camargo and Marenco (2011) have suggested that stomatal variation depends on the genetic background of each species. Our results suggest furthermore that the importance of the genetic background also applies at the intraspecific level.

4.3 | Phenotypic plasticity of some leaf traits is slightly higher in outbred plants

For most traits and environmental contrasts, PP did not differ significantly between inbred and outbred plants (Figure 4) and there was no dominant trend either. However, we found that PP was slightly but significantly higher for outbred than inbred plants for CHL across years and the competition gradient, for Gmax across the competition gradient, and for LFM across the light exposure and competition gradients (but LDMC showed higher plasticity for inbreds across the competition gradient). Hence, we find only moderate support for hypothesis H2 stating that inbreeding reduces PP.

Auld and Relyea (2010) report an effect of inbreeding on PP while Murren and Dudash (2012) found no significant differences between inbred and outbred plants. It is usually argued that plants with greater morphological plasticity are better able to adapt to heterogeneous environments (Abdusalam & Li, 2018), possibly contributing to ID if inbred plants showed lower plasticity due to a reduction of their allelic diversity at functional genes. Our results indicate that the higher plasticity of outbred *P. elata* plants for some foliar characteristics, particularly chlorophyll content, maximum water vapour conductance and fresh mass, might confer a higher potential for acclimation in a changing environment. We can, however, not demonstrate that such an effect is responsible for the ID detected on *H*max and diameter.

For tree species to survive rapid anthropogenic climate change, they must adapt their phenotypes through plasticity (Nicotra et al., 2010) by adjusting trait values to suit specific conditions (Anderson et al., 2012). Further work on the PP of *P. elata* and other tree species is still needed to better understand how ongoing environmental changes will affect tree populations.

4.4 | Relationship between growth and foliar traits

In this study, we found significantly negative correlations between SLA and both maximum height growth ($R^2 = 0.32^{**}$) and diameter growth ($R^2 = 0.49^{***}$) in inbred seedlings, and weaker relationships in outbred seedlings (Figure 5). These results suggest that SLA may be a better indicator of growth in inbred plants than in outbred plants. These relationships are opposite to those typically found at the interspecific level, where growth rate and SLA are positively correlated (Poorter et al., 2008; Poorter & Bongers, 2006). SLA is an indicator of the efficiency of investment in biomass for light interception. When evaluating the field performance of seedlings of 53 Neotropical tree species, Poorter and Bongers (2006) found that SLA was a reasonable predictor of interspecific variation in height growth ($R^2 = 0.18$) and interpreted their results as an adaptive consequence of the growth–survival trade-off. The negative relationship between SLA and growth reported in our study possibly originates from the fact that we consider the growth–SLA relationship at the intraspecific level and that our measures were taken along a steep gradient of competition. High competition reduces the growth rate of diameter, due to resource limitation, but the latter could also limit the development of thick leaves, resulting in high SLA. Hence, we suggest that the negative growth–SLA correlation found in *P. elata* would result from environmental constraints rather than reflect an adaptive strategy.

The fact that this negative relationship manifests more strongly in inbred seedlings than outbred ones (Figure 5) is more difficult to interpret. It may reflect a higher capacity of outbred plants to compensate for environmental constraints, reflecting higher plasticity, but our plasticity measure did not detect a difference in plasticity between inbred and outbred plants for SLA, and our sample size is too small to demonstrate that the growth–SLA correlation truly differs according to inbreeding.

5 | CONCLUSION

The aim of this study was to evaluate the impact of inbreeding and planting density on the whole-plant traits associated with growth form and competitive vigour, the variability of leaf functional traits and their PP, using young individuals of *P. elata*. We found lower height and diameter for inbred seedlings compared with outbred seedlings. This ID was not clearly reflected in the values of leaf traits. However, some leaf traits had slightly higher PP in outbred seedlings. Whether this difference in plasticity could explain, or at least contribute, to ID remains unclear. Our results highlight the importance of taking into account the selfed/outcrossed origin of *P. elata* seeds and density control when establishing sustainable forest plantations in a context of environmental change. The implications for management and conservation of *P. elata* are discussed by Angbonda et al. (2024). Few studies have investigated so far the potential interplay between ID, functional traits and PP at the intraspecific level. We argue that such studies should be replicated in different biological models to assess whether general patterns emerge.

AUTHOR CONTRIBUTIONS

Hans Beeckman and Nils Bourland conceived and implemented the plantations under Nelder designs. Dieu-Merci Assumani Angbonda collected the seeds in the Biaro forest, set up and monitored the saplings in the nursery under Nils Bourland's and Olivier J. Hardy's supervision. Jean Pierre Ngongo, Crispin Ilunga-Mulala, Espoir Ibrahim and Hulda Hatakiwe collected data in the field. Jean Pierre Ngongo and Espoir Ibrahim carried out laboratory treatment of leaf traits. Dieu-Merci Assumani Angbonda and Olivier J. Hardy genotyped the seedlings to identify the ones resulting from selfing. Jean Pierre Ngongo analysed the phenotypic data with the support of Olivier J. Hardy, Chadrack Kafuti, Nils Bourland, Hans Beeckman, Thomas Drouet, Léopold Ndjele and Yves Brostaux. Jean Pierre Ngongo wrote the manuscript under the supervision of Olivier J. Hardy. The final draft of the manuscript received contributions from all authors. All authors have read and agreed to the published version of the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.70082.

DATA AVAILABILITY STATEMENT

Data used in this study were collected between 2017 and 2021 and can be found at https://doi.org/10.5281/zenodo.13927593 (Ngongo, 2024).

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SUPPORTING INFORMATION

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

Table S1. Correlation matrix between leaf and chemical traits, separately for outcrossed (top value printed in black) and selfed (bottom value printed in grey) seedlings.

Figure S1. Evolution of diameter (A–E) and total height (F–J) of Pericopsis elata plants for 4 years since transplantation across five competition levels (high to low from A–E and from F–J) for outbred (violet) and inbred (green) individuals.

Figure S2. Distribution of the values of nine leaf traits of *Pericopsis elata* during the first 4 years in plantation.

Figure S3. Variance partitioning of nine foliar traits (LFM, leaf fresh mass; LDM, leaf dry mass; LDMC, leaf dry matter content; LA, leaf area; SLA, specific leaf area; CHL, chlorophyll content; SS, stomatal size; SD, stomatal density; and Gmax, maximum stomatal conductance) across four explanatory variables for outbred (A) and inbred (B) trees.

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