

Article

Differential Performance between Two Timber Species in Forest Logging Gaps and in Plantations in Central Africa

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Abstract: To develop silvicultural guidelines for high-value timber species of Central African moist forests, we assessed the performance of the pioneer *Milicia excelsa* (iroko, Moraceae), and of the non-pioneer light demander *Pericopsis elata* (assamela, Fabaceae) in logging gaps and in plantations in highly degraded areas in south-eastern Cameroon. The survival and size of each seedling was regularly monitored in the silvicultural experiments. Differences in performance and allometry were tested between species in logging gaps and in plantations. The two species performance in logging gaps was significantly different from plantations and concurred with the expectations of the performance trade-off hypothesis but not with the expectations of species light requirements. The pioneer *M. excelsa* survived significantly better in logging gaps while the non-pioneer *P. elata* grew significantly faster in plantations. The high mortality and slow growth of *M. excelsa* in plantations is surprising

for a pioneer species but could be explained by herbivory (attacks from a gall-making psyllid). Identifying high-value native timber species (i) with good performance in plantations such as *P. elata* is of importance to restore degraded areas; and (ii) with good performance in logging gaps such as *M. excelsa* is of importance to maintain timber resources and biodiversity in production forests.

Keywords: light requirement/shade tolerance; *Milicia excelsa*; *Pericopsis elata*; forest restoration; performance trade-off; tropical silviculture

1. Introduction

Central African moist forests extend over 180 million hectares, constituting the world's second largest continuous forest area after Amazonia. They provide an irreplaceable source of ecological, social and economic services for local populations, states and the international community [1,2]. Since the 1950s most of these forests have been granted to private logging companies and have been impacted by selective logging [3,4]. Today, approximately 26% of the forested area in Central Africa is licensed to logging companies contributing significantly to national economies [1,2]. With mismanagement and the conversion of large tracts of West African forests to agricultural production, Central African forests are experiencing increased harvesting pressures, and this is particularly true for the few timber species targeted by the extremely selective logging [5]. National regulations impose minimum cutting diameters for each targeted species and 20–30-year felling cycles, but barely on sound biological bases. Management plans based on tree inventories and the computation of timber stock recovery has been mandatory in most Central African countries, yet these are inadequate to ensure the sustainability of production forests [6]. Instead, after several felling cycles, timber resources of the targeted populations, *i.e.*, the number of trees with a diameter superior to the minimum cutting diameter, have in places dramatically decreased over the long-term [7]. In addition, other potential threats including anthropogenic (e.g., fragmentation, conversion) and climatic (e.g., drought events) disturbances may impact the populations of timber species in the coming decades. Thus, there is an urgent need to develop silvicultural techniques to maintain the sustainable harvest of timber resources.

Most African timber species are widespread light-demanding species [8–10] that require high light environments at the seedling stage for survival and growth [11]. The selective logging treatments generally applied in Central Africa [3,6] do not open the canopy sufficiently to promote their regeneration [5] although tree regeneration is controlled by more than just gap size [12]. Forest companies engaged in sustainable forest management and certification need to secure sufficient regeneration of the timber species which are abundant in the canopy and yet suffer from a lack of regeneration [13,14]. Silvicultural techniques can be applied to promote the regeneration of light-demanding timber species [12,15]. Planting timber species in logging gaps or restoring degraded forest areas are effective techniques that have the potential to maintain ecosystem diversity and resilience while protecting sensitive species of high commercial value [16]; however, only if based on sound silvicultural knowledge and practices. Enrichment techniques have been tested in several tropical contexts with promising results for forest restoration while promoting timber resource sustainability [17–22].

In Cameroon, the artificial canopy gaps created by selective logging were enriched through planting with nursery-raised seedlings of *Baillonella toxisperma* Pierre (moabi, Sapotaceae) an emblematic African tree [23]. The technique appeared to be relatively cheap (5.5 EUR per gap), and introduced seedlings showed a high growth and survival rate in logging gaps (>90% after 30 months, $n = 410$ 7-month-old seedlings distributed in 15 logging gaps). Although the technique of enriching logging gaps showed promising results for *B. toxisperma*, two essential issues must be addressed before extending to other timber species. First, logging gaps are difficult to monitor long-term, and the good performance in the early stage of tree life may be reduced by competition in later stages. Indeed, several events of growth suppression and release are usually identified across the lifetime of tropical trees using tree ring analysis [24]. Second, logging gaps may not be suitable for light demanding species at the high end of the irradiance spectrum [25] and plantations may thus be considered for true pioneers, as well as for the restoration of highly degraded areas and for reforestation. Large plantations following natural forest conversion were promoted up to the 1970s and often showed very encouraging results. Nevertheless, all of them were abandoned, mainly because they were too expensive to maintain [26,27]. If large industrial plantations of native species are no longer a priority, they could be usefully replaced by smaller plantations in degraded forests [26–28]; several logging companies under the independent FSC (Forest Stewardship Council) certification have to implement regular planting activities (FSC-STD-CB-01-2012 Regional Standard). However, to be implemented by the forest sector, practical guidelines need to be developed, tailored to the socio-economic context and to the autoecology of each timber species, and species need to be matched to the specific biophysical conditions of the site.

In this study, we analyzed the survival and growth of two timber species, *Milicia excelsa* (Welw.) C.C. Berg (iroko, Moraceae) and *Pericopsis elata* (Harms) Meeuwen (assamela, Fabaceae), in enriched logging gaps and in plantations. *M. excelsa* is widely distributed across tropical African forests in West, Central and East Africa, but shows a low local abundance. Although recorded as near threatened in the IUCN Red List *M. excelsa* is currently logged in Cameroon, Gabon, Congo, Democratic Republic of Congo and Central African Republic, and is the fifth largest species in terms of harvestable volume in Cameroon [1]. *P. elata* is a gregarious species extremely abundant locally that shows a patchy distribution in Central Africa. The species is almost extinct in West Africa due to forest mismanagement and overexploitation [9]. The harvest of *P. elata* is strongly regulated since the species is included in the CITES Appendix II and is recorded as “Endangered A1cd” on the IUCN Red List [29,30]. Here, we investigated whether there was a difference in the performance of the two species in logging gaps *versus* plantations. Given that the two focal species, *M. excelsa* and *P. elata* have different light requirements [9], we expect the pioneer species *M. excelsa* in the high light environment of plantations to have greater growth and survival while the non-pioneer light demanding species *P. elata* to perform better in the relatively low light environment of logging gaps. Based on the inter-specific performance trade-off [31] that has been widely reported between fast growth in high light and high survival in low light [32–34] we expect to find evidence of a rank reversal in performance between the two species between the two light environments. To corroborate the previous expectations, we examined the differences in seedling architecture among species and silvicultural experiments by regressing the relative growth rate (RGR, hereafter) in height with that in diameter, which is theoretically equivalent of fitting allometric relationships between height and diameter [35]. We expect seedlings grown in the relatively competitive

environment of logging gaps to be more slender, and thus, have greater height for a given diameter, than the seedlings grown in the higher light environment of plantations.

2. Methods

2.1. Study Area

The study area is located in the East province of Cameroon, east of the Dja reserve (3°01' N and 3°44' N; and 13°20' E and 14°31' E). The enrichment of logging gaps and plantations after clearance in degraded forests was performed in the Forest Management Units (FMUs) 10-041, 10-042, 10-044, 10-030 and 10-031, managed by the Pallisco company. The annual rainfall is 1640 mm, with two distinct rainy seasons (August to November and March to June) alternating with two dry seasons, and the mean annual temperature is 23.1 °C, according to the Worldclim data [36]. The topography is undulating with elevation varying between 500 and 650 m. The geological substrate consists of volcanic intrusions and metamorphic rocks, and soils have been identified as Ferralsols [37]. Forests in the area are mostly semi-deciduous with a canopy dominated by species of the Meliaceae, Sterculiaceae (now included in Malvaceae) and Ulmaceae families [38,39].

2.2. Study Species

Two focal species, a pioneer and a non-pioneer light demander of particular interest for the forest sector in Central Africa were selected for this study. The pioneer, *M. excelsa* is dioecious, small-seeded (3 mg, according to the Seed Information Database [40]) and animal-dispersed [41]. The non-pioneer light-demanding, *P. elata* is hermaphroditic, large-seeded (333 mg) and wind-dispersed [26,27]. Both species can exceed 130 cm in diameter and greater than 40 m in height. Both species have moderate wood specific gravity, with an average of 0.561 and 0.636 g·cm⁻³ in [42], respectively for *M. excelsa* and *P. elata*, and both show valuable wood mechanical properties. In the study area, and according to the management inventory data performed in 2003 (FMUs 10-041, 10-042, and 10-044) and in 2007 (FMUs 10-030 and 10-031) (J.-L. Doucet, unpublished data), the two study species show unimodal diameter distributions (lots of medium-sized trees) typical of the long-lived light-demanding species that currently suffer from a regeneration shortage (Figure 1).

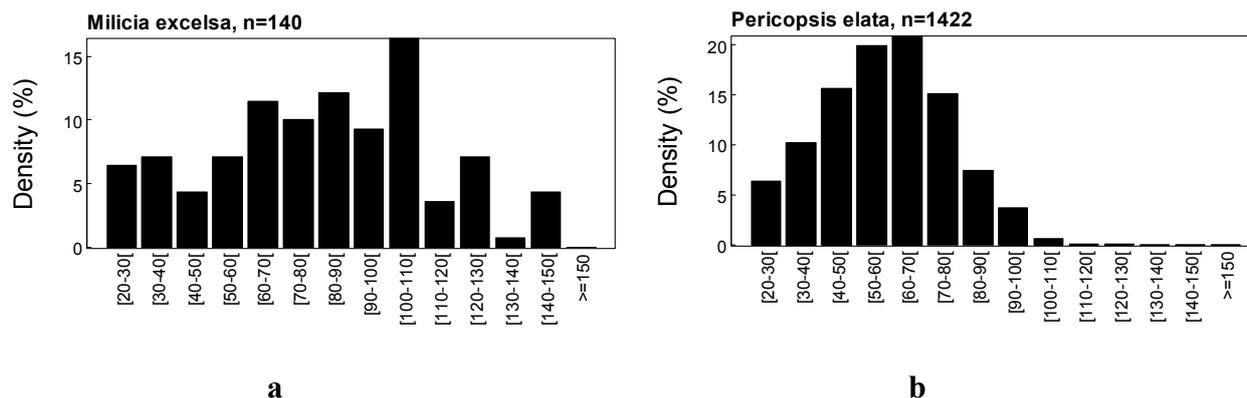


Figure 1. Diameter distribution of *M. excelsa* (a) and of *P. elata* (b) in the forest management units managed by the Pallisco logging company in south-eastern Cameroon. Each tree with a diameter at breast height (dbh) above 20 cm was measured and identified in the 5152, 0.5-ha plots inventoried prior to forest management in 2003 and in 2007.

2.3. Silvicultural Experiments

Within the study area, we analyzed the results of three distinct silvicultural experiments: briefly, (i) the enrichment of logging gaps with *M. excelsa* (K. Daïnou, unpublished data); (ii) the enrichment of logging gaps with *P. elata* (a subset of the data published in [43]); and (iii) plantations of high-value tree species, that included both *M. excelsa* and *P. elata*, after forest clearance in highly degraded forest areas (J.-L. Doucet, unpublished data). For the three experiments, the seedlings were germinated from seeds collected in the study area and raised in the same nursery before being transplanted in the logging gaps and in plantations. The survival, diameter and height of each individual seedling were regularly monitored from initial transplantation and up to 65 months (see below for details on the experimental designs). All field measurements were performed by the same field crew composed every year of the exact same 13 persons (1 manager, 2 nurserymen, and 10 technicians), which minimized measurement errors due to differences in crew members from year to year.

2.3.1. Enrichment in Logging Gaps

A total of 202 nursery-raised seedlings of *M. excelsa* were transplanted into ten logging gaps in 2004 and monitored over 65 months. A total of 95 nursery-raised seedlings of *P. elata* were transplanted into nine different logging gaps in 2007 and 2008, and monitored up to 60 months. In both enrichment experiments, seedlings were transplanted in 2×4 m grid cells in the proximal part of the logging gaps. The number of planted seedlings per logging gap (between 12 and 41 seedlings, with a mean of 20.2 seedlings and between 8 and 13 seedlings, with a mean of 10.6 seedlings per logging gap, for *M. excelsa* and *P. elata*, respectively) varied with the size of the gap (between 80 and 522 m², with a mean of 224 m² and between 94 and 234 m², with a mean of 145 m², for *M. excelsa* and *P. elata*, respectively). The mean height of the transplanted seedlings was 20 and 63 cm (standard deviation, SD = 8 and 20 cm) for *M. excelsa* and *P. elata*, respectively. Prior to all plantings, potentially competing vegetation with the exception of seedlings of high-value timber species was eliminated using a machete. In contrast with plantations, logging gaps are difficult to access and, hence, controlling the competition within logging

gaps is usually not performed as a treatment in long term monitoring of tree regeneration. The light levels were not assessed at the time of planting and no further maintenance was applied in the logging gaps. Thus, we considered the environment in the logging gaps as “with-competition”.

2.3.2. Plantations

From 2009 onwards, plantations with high-value tree species ($n = 23$) were regularly established in highly degraded forest areas (J-L. Doucet, unpublished data). Shifting cultivation, throughout the study area, and illegal logging activities, specifically in the FMUs 10-030 and 10-031, were the usual causes of forest degradation. In each plantation plot (between 0.2 and 1.2 ha, with a mean of 0.47 ha), species were planted in blocks of 25 or 30 seedlings and consecutive blocks were planted with different species to prevent parasitism and herbivory. Only a subset of these data concerning the two study species was considered in this study.

A total of 75 seedlings of *M. excelsa* were transplanted into one plantation plot in 2012 and monitored over 25 months. A total of 160 seedlings of *P. elata* were transplanted into three plantation plots, with 60 seedlings transplanted in 2009, 50 in 2010 and 50 in 2011, and monitored up to 57 months. Prior to plantation, the ground area was cleared but some standing trees (covering approximately 30% of plot area) were maintained to protect seedlings from photoinhibition. Seedlings were transplanted in 3×3 m grid cells in the plantation plots. The mean height of the transplanted seedlings was 37 and 54 cm (standard deviation SD = 13 and 22 cm) for *M. excelsa* and *P. elata*, respectively. Clearing maintenances were performed three times in the first year, twice in the second year, and once in the third year. The light levels were not assessed at the time of planting, but due to clearance, we considered the environment in plantations as “free-to-grow”.

2.4. Data Analysis

To quantify species survival in logging gaps and in plantations, we estimated the survival function $S(t)$ over time using the non-parametric Kaplan-Meier estimator [44], which is the probability of an individual seedling to survive at least until time t , the time since the beginning of the experiment:

$$S(t) = \prod_{i|t_i \leq t} (1 - d_i/n_i) \quad (1)$$

where i indexes the time interval, d_i is the number of deaths that occur in the interval t_i , n_i is the number of seedlings that are alive at the end of the census interval t_i , and \prod is the product operator across all cases less than or equal to t . To quantify species growth in logging gaps and in plantations, we calculated the relative growth rate in height (RGR_H in $\text{cm} \cdot \text{cm}^{-1} \cdot \text{yr}^{-1}$) and diameter (RGR_D in $\text{mm} \cdot \text{mm}^{-1} \cdot \text{yr}^{-1}$) of each monitored seedling until the end of the experiment (surviving seedling) as follows:

$$\text{RGR} = (\ln(\text{size}_t) - \ln(\text{size}_0))/t \quad (2)$$

with size_t the height or diameter at time t , and size_0 the initial size of seedlings.

For practical reasons, we additionally calculated the annualized absolute changes in height and diameter of each seedling over the observation period (height and diameter increment, hereafter). We tested whether species significantly differ in performance in logging gaps compared to plantations

using log-rank tests and Welch's one-way analysis of variance for survival and growth, respectively. The period and frequency of monitoring were different for the three experiments but the non-parametric approach accommodates this caveat.

To examine the differences in seedling architecture between species and silvicultural experiments, we regressed the RGR_H to the RGR_D following Coomes and Grubb [35]. Assuming a power allometric relationship between seedling height (H , in cm) and diameter (D , in mm) that can be linearized with a log-transformation (see below Equations (3) and (4), respectively), the ratio of relative growth rates is theoretically equal to b_1 the scaling coefficient of the height-diameter allometric equation. A two-way analysis of covariance was conducted to assess the effect of silvicultural experiment, species, and the interaction between them on seedlings RGR ratios (*i.e.*, scaling coefficient).

$$H = \exp(b_0) \times D^{b_1} \quad (3)$$

$$\ln H = b_0 + b_1 \ln D \quad (4)$$

All statistical analyses were performed within the open source R environment (R version 2.14.1). We specifically used the survival package for the survival analysis [45].

3. Results and Discussion

3.1. Differential Performance between the Two Species

In contrast to our expectation based on each species' known light requirement, the pioneer species *M. excelsa* performed worse in plantations compared to the logging gaps, while *P. elata* showed the opposite pattern (Figure 2 and Table 1).

With 172 out of 202 (85.1%) surviving seedlings after 65 months *M. excelsa* showed a significantly higher survival than *P. elata* with 57 out of 95 (60%) surviving seedlings after 60 months in logging gaps-with-competition (Figure 2a, log-rank test $\chi^2 = 38.7$, $p < 0.001$). In contrast, with only 33 (44%) surviving seedlings after 25 months *M. excelsa* showed a significantly lower survival than *P. elata* with 115 (71.9%) surviving individuals after 57 months in plantations-free-to-grow (Figure 2b, log-rank test $\chi^2 = 14.8$, $p < 0.001$). Thus, we observed a rank reversal in survival between the two silvicultural treatments.

M. excelsa and *P. elata* showed almost similar diameter and height increment in logging gaps-with-competition but showed significantly different relative growth rates, with faster growth for *M. excelsa* than for *P. elata* (Table 1). In contrast, in plantations-free-to-grow *M. excelsa* showed significantly slower growth than *P. elata* for the whole of the growth variables considered. Thus, we observed a rank reversal in growth between the two silvicultural treatments.

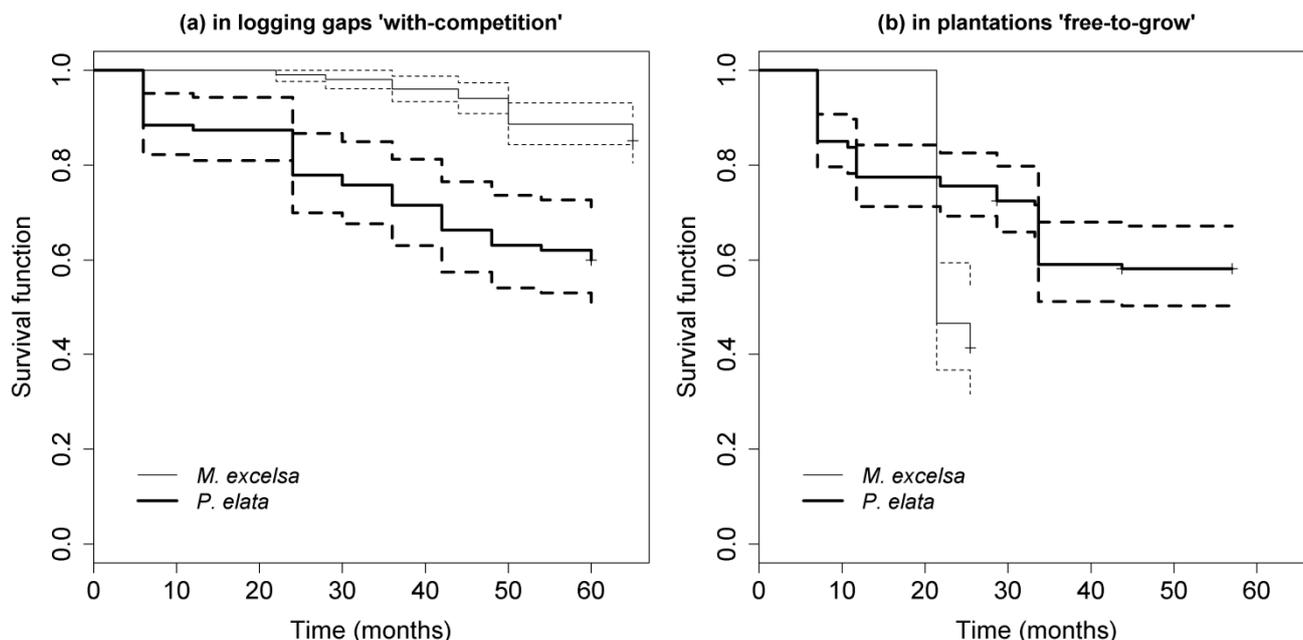


Figure 2. Kaplan-Meier survival estimates over time for *M. excelsa* and *P. elata* with their 95% confidence bounds in (a) logging gaps-with-competition; and (b) plantations-free-to-grow. The survival function of *M. excelsa* in plantations-free-to-grow may overestimate survival probability in the first 20 months due to the lack of monitoring during the first year.

Table 1. Growth performance of *M. excelsa* and *P. elata* in logging gaps-with-competition and in plantations-free-to-grow in south-eastern Cameroon. The mean and standard deviation (SD) of height and diameter increment, and relative growth rate in height (RGR_H) and diameter (RGR_D) are given for each species in logging gaps-with-competition and in plantations-free-to-grow. The number of seedlings (N) is also given. The letters (a, b) indicate significant differences between species using Welch’s one-way analysis of variance. The *T* and *P* values associated to the Welch’s tests are also given.

Growth Variable	<i>Milicia excelsa</i>			<i>Pericopsis elata</i>			<i>T</i> Value	<i>p</i> Value
	Mean	<i>SD</i>	<i>N</i>	Mean	<i>SD</i>	<i>N</i>		
(a) Logging Gaps-with-Competition								
Height increment (cm·yr ⁻¹)	39.96 a	30.76	172	45 a	23	57	-1.29	0.20
Diameter increment (mm·yr ⁻¹)	2.87 a	2.02	172	2.79 a	1.37	57	0.32	0.75
RGR_H (cm cm ⁻¹ ·yr ⁻¹)	0.40 a	0.16	172	0.29 b	0.09	57	6.81	<0.0001
RGR_D (mm mm ⁻¹ ·yr ⁻¹)	0.26 a	0.11	172	0.21 b	0.09	57	3.41	0.0009
(b) Plantations-Free-to-Grow								
Height increment (cm·yr ⁻¹)	19.96 a	20.87	33	86.43 b	42.96	115	-12.29	<0.0001
Diameter increment (mm·yr ⁻¹)	1.70 a	1.78	33	9.08 b	4.56	115	-14.03	<0.0001
RGR_H (cm cm ⁻¹ ·yr ⁻¹)	0.31 a	0.31	33	0.53 b	0.17	115	-3.83	0.0005
RGR_D (mm mm ⁻¹ ·yr ⁻¹)	0.24 a	0.21	33	0.47 b	0.13	115	-6.15	<0.0001

According to the performance trade-off hypothesis [31–34], we observed a differential performance of the two species in logging gaps-with-competition and in plantations-free-to-grow. This was however in contrast with species’ light requirement. We had expected better performance of the pioneer

M. excelsa in the high light environment of plantations and a better performance of the non-pioneer light demander *P. elata* in the relatively low light environment of logging gaps. Although the two study species have been assigned to two different regeneration guilds based on the ontogenic variations of the crown exposure index in Ghana [9], the difference in light requirement between the two species remains difficult to ascertain. In a light response experiment in Ghana, it has been demonstrated that both species showed an optimal growth at intermediate irradiance. The growth of *P. elata* was faster than the growth of *M. excelsa* and a negative growth rate was observed for *M. excelsa* at low irradiance [46]. A negative growth rate at low irradiance (<3%) is a typical characteristics of pioneer species [46,47], and pioneer species tend to show maximum growth at higher irradiance than shade-bearers, while non-pioneer light-demanders showed an intermediate response [48]. Thus, depending on the trait considered, *RGR* at low light or maximum growth (growth at optimal irradiance), the two species can be considered as either pioneer or non-pioneer light demanding species.

In comparison with other studies reporting a performance trade-off [31–34] or with the natural variation within tropical forests between gaps and the understory [49], the light gradient considered here between logging gaps and plantations is most probably rather restricted. The number of species is also limited to properly test the rank reversal hypothesis. For instance, high light growth (number of years to reach 3 m high) has been shown to be negatively correlated with low light survival (<10%) for seedlings/saplings of ten major tree species spanning a range of presumed shade tolerances in transition oak-northern hardwood forests of North America [32]. Additionally, with our experimental design, we could not disentangle the effects of light availability from that of competition with vegetation regrowth. Within the conditions of our study area and for the two study species, the control of competition might be more important than light availability. Our early results however offer a new perspective on the light requirement and on the planting behavior of the two study species. This is an important first step to developing silvicultural guidelines, and those guidelines are currently lacking to develop strategies for the sustainable management of Central African forest stands and species.

The differential survival of *M. excelsa* between logging gaps-with-competition and plantations-free-to-grow, and specifically the high mortality of this tree species in plantations-free-to-grow, is surprising for a pioneer species, and may be due to the parasitic attacks of the psyllid *Phytolyma lata* (J.-L. Doucet and P. Tekam, personal observations). Repeated attacks in the same season have indeed been responsible for high mortality [50]. The survival and growth of *M. excelsa* has been demonstrated to be higher in forest than in a degraded ecosystem, and the number of galls has been shown to be positively correlated with irradiance [51]. The number of galls have also been shown to be higher and earlier in large than in small gaps [52]. As a consequence, it has been previously recommended to maintain the seedlings of *M. excelsa* in the shade during the first 12–18 months to minimize the development of galls and associated dieback. These results, although preliminary, tend to argue in favor of the growth-survival-herbivory tradeoff recently demonstrated in Sri Lanka [34]. Thus, to define practical guidelines it is of importance to take into account species' light requirement (and tolerance to shade) but also, for some species, their susceptibility to attacks from pests and pathogens.

3.2. Tree Architecture in Logging Gaps and in Plantations

To further examine the variability of seedling morphology in response to light availability, and the differences between the two study species when grown in logging gaps-with-competition and in plantations-free-to-grow, we regressed RGR_H to RGR_D [35]. Although the two study species showed a differential performance in logging gaps-with-competition and in plantations-free-to-grow, they responded similarly to the variation in light availability (Figure 3). A significantly higher RGR ratio (*i.e.*, slope of RGR_H on RGR_D) was reported in logging gaps-with-competition than in plantations-free-to-grow for both species (Figure 3, analysis of covariance $F_{2375} = 1671, p < 0.0001$), thus indicating that seedlings of both species tended to be taller in logging gaps-with-competition than in plantation-free-to-grow for the same diameter. This result tended to suggest a similar strategy for the two study species to escape competition, and to confirm their high light requirement. The differential response of tree allometry between light-demanding and shade tolerant species has been previously reported in tropical forests of Panama [53]. According to the two major principles of silviculture that (i) tree height reflects the site fertility/productivity [54]; and (ii) tree density and diameter depends on the intensity of competition (and the self-thinning line) [55], seedling morphology thus reflected the strong intensity of competition in non-cleared logging gaps due to the relatively low light.

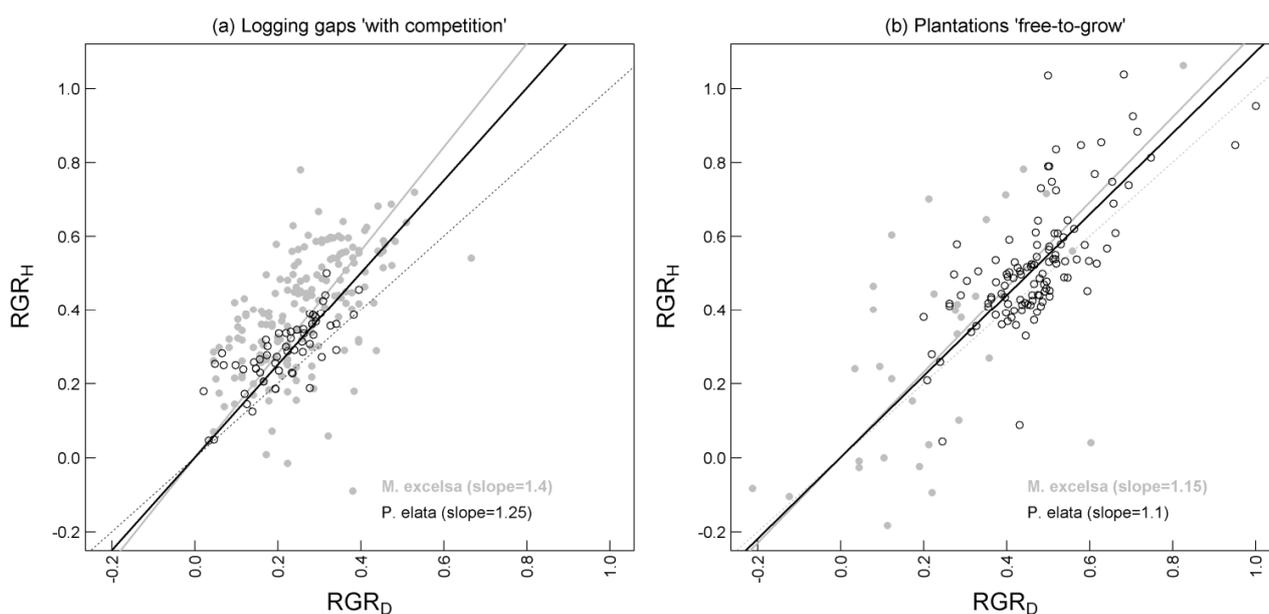


Figure 3. Variations in seedling architecture between *M. excelsa* (grey dots) and *P. elata* (black open circles) when grown in logging gaps (a) and in plantations (b). Seedlings relative growth rate in height (RGR_H , in $\text{cm} \cdot \text{cm}^{-1} \cdot \text{yr}^{-1}$) was regressed against that in diameter (RGR_D , in $\text{mm} \cdot \text{mm}^{-1} \cdot \text{yr}^{-1}$) between species and silvicultural experiments. The RGR ratio is equivalent to the scaling coefficient of the power allometric relationship between seedling height and diameter [35]. The dashed grey line corresponds to the 1:1 line.

4. Conclusions

The relatively good performance of the two native species, *M. excelsa* in logging gaps and *P. elata*, in plantations, have profound applied perspectives to maintain or restore biodiversity, ecological functioning, and the supply of goods and ecological services in Central African moist forests. Identifying high-value native timber species with good performance in plantation is of extreme importance to restore degraded areas since plantations can facilitate forest succession in the understory through modification of both physical and biological site conditions [56]. This is an alternative approach to exotic monocultures for reforestation in Central African moist forests [17] and the rather sensitive, highly light-responsive *P. elata* [29,30] appeared to be a good candidate species. Identifying high-value native timber species with good performance in logging gaps, such as *M. excelsa* in this study, or *B. toxisperma* in a former study on the same site [23] is important to maintain biodiversity in production forests, and favor the recovery of light-demanding timber species that do not naturally regenerate in Central African moist forests. However, it is important to remember that the time period of up to 65 months, although adequate for the assessment of seedling performance, may not be enough to assess the timber potential of the two species especially because several events of growth suppression and release occur later over the lifetime of tropical trees [24]. Despite these limitations, our results highlighted the good performance of *M. excelsa* in logging gaps and of *P. elata* in plantations. Although encouraging, these early results argue in favor of further experiments, which will need long-term monitoring, in order to define practical guidelines adapted to the autoecology of each timber species.

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Author Contributions

Adeline Fayolle, Dakis-Yaoba Ouédraogo, Gauthier Ligot and Jean-Louis Doucet conceived the ideas; Jean-Louis Doucet, Kasso Daïnou, Nils Bourland and Patrice Tekam collected the data; Adeline Fayolle and Dakis-Yaoba Ouédraogo analysed the data and led the writing. All authors commented on the manuscript.

Conflicts of Interest

The authors declare no conflict of interest.

References

1. De Wasseige, C.; Devers, D.; de Marcken, P.; Eba'a Atyi, R.; Nasi, R.; Mayaux, P. *Les Forêts du Bassin du Congo—Etat des Forêts 2008*; Office des publications de l'UE: Luxembourg, Luxembourg, 2009.
2. De Wasseige, C.; de Marcken, P.; Bayol, N.; Hiol Hiol, F.; Mayaux, P.; Desclée, B.; Billand, A.; Nasi, R. *Les Forêts du Bassin du Congo—Etat des Forêts 2010*; Office des publications de l'UE: Luxembourg, Luxembourg, 2012.
3. Nasi, R.; Billand, A.; van Vliet, N. Managing for timber and biodiversity in the Congo Basin. *For. Ecol. Manag.* **2012**, *268*, 103–111.
4. Ruiz Pérez, M.; Ezzine de Blas, D.; Nasi, R.; Sayer, J.A.; Sassen, M.; Angoué, C.; Gami, N.; Ndoye, O.; Ngono, G.; Nguinguiri, J.C. Logging in the Congo Basin: A multi-country characterization of timber companies. *For. Ecol. Manag.* **2005**, *214*, 221–236.
5. Hall, J.S.; Harris, D.J.; Medjibe, V.; Ashton, P.M.S. The effects of selective logging on forest structure and tree species composition in a Central African forest: Implications for management of conservation areas. *For. Ecol. Manag.* **2003**, *183*, 249–264.
6. Fargeot, C.; Forni, É.; Nasi, R. Réflexions sur l'aménagement des forêts de production dans le bassin du Congo. *Bois For. Trop.* **2004**, *281*, 19–34.
7. Karsenty, A.; Gourellet-Fleury, S. Assessing sustainability of logging practices in the Congo Basin's managed forests: The issue of commercial species recovery. *Ecol. Soc.* **2006**, *11*, 26.
8. Bongers, F.; Poorter, L.; Rompaey, R.S.A.R.; Parren, M.P.E. Distribution of twelve moist forest canopy tree species in Liberia and Côte d'Ivoire: Response curves to a climatic gradient. *J. Veg. Sci.* **1999**, *10*, 371–382.
9. Hawthorne, W.D. *Ecological Profiles of Ghanaian Forest Trees*; Tropical Forestry Papers, Oxford Forestry Institute, Department of Plant Sciences, University of Oxford: Oxford, UK, 1995.
10. Doucet, J.-L. L'alliance délicate de la gestion forestière et de la biodiversité dans les forêts du centre du Gabon. Ph.D. Thesis, Faculté Universitaire des Sciences Agronomiques de Gembloux, Gembloux, Belgique, 2003.
11. Makana, J.-R.; Thomas, S.C. Effects of Light Gaps and Litter Removal on the Seedling Performance of Six African Timber Species. *Biotropica* **2005**, *37*, 227–237.
12. Sist, P.; Brown, N. Silvicultural intensification for tropical forest conservation: A response to Fredericksen and Putz. *Biodivers. Conserv.* **2004**, *13*, 2381–2385.
13. Van Gemerden, B.S.; Olf, H.; Parren, M.P.E.; Bongers, F. The pristine rain forest? Remnants of historical human impacts on current tree species composition and diversity. *J. Biogeogr.* **2003**, *30*, 1381–1390.
14. Engone Obiang, N.L.; Ngomanda, A.; Hymas, O.; Chézeaux, É.; Picard, N. Diagnosing the demographic balance of two light-demanding tree species populations in central Africa from their diameter distribution. *For. Ecol. Manag.* **2014**, *313*, 55–62.
15. Grogan, J.; Landis, R.M.; Ashton, M.S.; Galvão, J. Growth response by big-leaf mahogany (*Swietenia macrophylla*) advance seedling regeneration to overhead canopy release in southeast Pará, Brazil. *For. Ecol. Manag.* **2005**, *204*, 399–412.

16. Coates, K.D.; Burton, P.J. A gap-based approach for development of silvicultural systems to address ecosystem management objectives. *For. Ecol. Manag.* **1997**, *99*, 337–354.
17. Lamb, D.; Erskine, P.D.; Parrotta, J.A. Restoration of Degraded Tropical Forest Landscapes. *Science* **2005**, *310*, 1628–1632.
18. Schulze, M. Technical and financial analysis of enrichment planting in logging gaps as a potential component of forest management in the eastern Amazon. *For. Ecol. Manag.* **2008**, *255*, 866–879.
19. Stanturf, J.A.; Palik, B.J.; Dumroese, R.K. Contemporary forest restoration: A review emphasizing function. *For. Ecol. Manag.* **2014**, *331*, 292–323.
20. Keefe, K.; Schulze, M.D.; Pinheiro, C.; Zweede, J.C.; Zarin, D. Enrichment planting as a silvicultural option in the eastern Amazon: Case study of *Fazenda Cauaxi*. *For. Ecol. Manag.* **2009**, *258*, 1950–1959.
21. Korpelainen, H.; Ådjers, G.; Kuusipalo, J.; Nuryanto, K.; Otsamo, A. Profitability of rehabilitation of overlogged dipterocarp forest: A case study from South Kalimantan, Indonesia. *For. Ecol. Manag.* **1995**, *79*, 207–215.
22. Ashton, M.S.; Goodale, U.M.; Bawa, K.S.; Ashton, P.S.; David Neidel, J. Restoring working forests in human dominated landscapes of tropical South Asia: An introduction. *For. Ecol. Manag.* **2014**, *329*, 335–339.
23. Doucet, J.-L.; Kouadio, Y.L.; Monticelli, D.; Lejeune, P. Enrichment of logging gaps with moabi (*Baillonella toxisperma* Pierre) in a Central African rain forest. *For. Ecol. Manag.* **2009**, *258*, 2407–2415.
24. Brienen, R.J.; Zuidema, P.A. Lifetime growth patterns and ages of Bolivian rain forest trees obtained by tree ring analysis. *J. Ecol.* **2006**, *94*, 481–493.
25. Goodale, U.M.; Ashton, M.S.; Berlyn, G.P.; Gregoire, T.G.; Singhakumara, B.M.P.; Tennakoon, K.U. Disturbance and tropical pioneer species: Patterns of association across life history stages. *For. Ecol. Manag.* **2012**, *277*, 54–66.
26. Brunck, F.; Grison, F.; Maitre, H.F. *L'Okoumé: Monographie*; Centre Technique Forestier Tropical (CIRAD-Forêt): Montpellier, France, 1990.
27. Koumba Zaou, P.; Nze Nguema, S.; Mapaga, D.; Deleporte, P. Croissance de 13 essences de bois d'œuvre plantées en forêt gabonaise. *Bois For. Trop.* **1998**, *256*, 21–33.
28. Ndongo, P.-A.O.; Peltier, R.; Linjouom, I.; Louppe, D.; Smektala, G.; Beligné, V.; Njoukam, R.; Tieche, B.; Temgoua, L. Plantations de bois d'oeuvre en zone équatoriale africaine: Cas de l'arboretum de l'Enef de Mbalmayo au sud du Cameroun. *Bois For. Trop.* **2009**, *299*, 37–48.
29. Bourland, N.; Kouadio, Y.L.; Fétéké, F.; Lejeune, P.; Doucet, J.-L. Ecology and management of *Pericopsis elata* (Harms) Meeuwen (Fabaceae) populations: A review. *Biotechnol. Agron. Société Environ. Biotechnol. Agron. Soc. Environ. BASE* **2012**, *16*, 486–498.
30. Bourland, N.; Kouadio, L.; Lejeune, P.; Sonké, B.; Philippart, J.; Daïnou, K.; Fétéké, R.F.; Doucet, J.L. Ecology of *Pericopsis elata* (Fabaceae), an Endangered Timber Species in Southeastern Cameroon. *Biotropica* **2012**, *44*, 840–847.
31. Baraloto, C.; Goldberg, D.E.; Bonal, D. Performance trade-offs among tropical tree seedlings in contrasting microhabitats. *Ecology* **2005**, *86*, 2461–2472.
32. Kobe, R.K.; Pacala, S.W.; Silander J.A., Jr.; Canham, C.D. Juvenile tree survivorship as a component of shade tolerance. *Ecol. Appl.* **1995**, *5*, 517–532.

33. Walters, M.B.; Reich, P.B. Are shade tolerance, survival, and growth linked? Low light and nitrogen effects on hardwood seedlings. *Ecology* **1996**, *77*, 841–853.
34. Goodale, U.M.; Berlyn, G.P.; Gregoire, T.G.; Tennakoon, K.U.; Ashton, M.S. Differences in Survival and Growth among Tropical Rain Forest Pioneer Tree Seedlings in Relation to Canopy Openness and Herbivory. *Biotropica* **2014**, *46*, 183–193.
35. Coomes, D.A.; Grubb, P.J. A comparison of 12 tree species of Amazonian caatinga using growth rates in gaps and understorey, and allometric relationships. *Funct. Ecol.* **1998**, *12*, 426–435.
36. Hijmans, R.J.; Cameron, S.E.; Parra, J.L.; Jones, P.G.; Jarvis, A. Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* **2005**, *25*, 1965–1978.
37. Jones, A.; Breuning-Madsen, H.; Brossard, M.; Dampha, A.; Deckers, J.; Dewitte, O.; Gallali, T.; Hallett, S.; Jones, R.; Kilasara, M.; *et al.* *Soil Atlas of Africa*; Publications Office of the European Union: Luxembourg, Luxembourg, 2013.
38. De Namur, C. Aperçu sur la végétation de l’Afrique centrale atlantique. *Paysages Quat. L’Afrique Cent. Atl. ORSTOM Paris* **1990**, 60–67.
39. Letouzey, R. *Notice de la Carte Phytogéographique du Cameroun au 1/500,000*; Institut de la carte internationale de la végétation: Toulouse, France, 1985.
40. Royal Botanic Gardens Seed Information Database (SID). Version 7.1. Available online: <http://data.kew.org/sid/> (accessed on 15 December 2014).
41. Daïnou, K.; Laurenty, E.; Mahy, G.; Hardy, O.J.; Brostaux, Y.; Tagg, N.; Doucet, J.-L. Phenological patterns in a natural population of a tropical timber tree species, *Milicia excelsa* (Moraceae): Evidence of isolation by time and its interaction with feeding strategies of dispersers. *Am. J. Bot.* **2012**, *99*, 1453–1463.
42. Zanne, A.E.; Lopez-Gonzalez, G.; Coomes, D.A.; Ilic, J.; Jansen, S.; Lewis, S.L.; Miller, R.B.; Swenson, N.G.; Wiemann, M.C.; Chave, J. Data from: Towards a worldwide wood economics spectrum. Dryad Digital Repository. Available online: <http://datadryad.org/resource/doi:10.5061/dryad.234> (accessed on 15 December 2014).
43. Ouédraogo, D.-Y.; Fayolle, A.; Daïnou, K.; Demaret, C.; Bourland, N.; Lagoute, P.; Doucet, J.-L. Enrichment of Logging Gaps with a High Conservation Value Species (*Pericopsis elata*) in a Central African Moist Forest. *Forests* **2014**, *5*, 3031–3047.
44. Harrell, F.E. *Regression Modeling Strategies: With Applications to Linear Models, Logistic Regression, and Survival Analysis*; Springer-Verlag: New York, NY, USA, 2001.
45. Therneau, T.M. A Package for Survival Analysis in S. Available online: <http://CRAN.R-project.org/package=survival> (accessed on 15 December 2014).
46. Agyeman, V.K.; Swaine, M.D.; Thompson, J. Responses of tropical forest tree seedlings to irradiance and the derivation of a light response index. *J. Ecol.* **1999**, *87*, 815–827.
47. Kyereh, B.; Swaine, M.D.; Thompson, J. Effect of light on the germination of forest trees in Ghana. *J. Ecol.* **1999**, *87*, 772–783.
48. Poorter, L. Growth responses of 15 rain-forest tree species to a light gradient: The relative importance of morphological and physiological traits. *Funct. Ecol.* **1999**, *13*, 396–410.
49. Denslow, J.S. Gap partitioning among tropical rainforest trees. *Biotropica* **1980**, *12*, 47–55.
50. Wagner, M.R.; Cobbinah, J.R.; Bosu, P.P. *Forest Entomology in West Tropical Africa: Forest Insects of Ghana*; Springer: Dordrecht, The Netherlands, 2008.

51. Bosu, P.P.; Cobbinah, J.R.; Nichols, J.D.; Nkrumah, E.E.; Wagner, M.R. Survival and growth of mixed plantations of *Milicia excelsa* and *Terminalia superba* 9 years after planting in Ghana. *For. Ecol. Manag.* **2006**, *233*, 352–357.
52. Nichols, J.D.; Ofori, D.A.; Wagner, M.R.; Bosu, P.; Cobbinah, J.R. Survival, growth and gall formation by *Phytolyma lata* on *Milicia excelsa* established in mixed-species tropical plantations in Ghana. *Agric. For. Entomol.* **1999**, *1*, 137–141.
53. King, D.A. Allometry of Saplings and Understorey Trees of a Panamanian Forest. *Funct. Ecol.* **1990**, *4*, 27–31.
54. Vanclay, J.K. Assessing site productivity in tropical moist forests: A review. *For. Ecol. Manag.* **1992**, *54*, 257–287.
55. Midgley, J.J. Do mixed-species mixed-size indigenous forests also follow the self-thinning line? *Trends Ecol. Evol.* **2001**, *16*, 661–662.
56. Parrotta, J.A.; Turnbull, J.W.; Jones, N. Catalyzing native forest regeneration on degraded tropical lands. *For. Ecol. Manag.* **1997**, *99*, 1–7.

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