Understorey Regeneration of *Lophira alata* as Affected by Seed Tree Size and Growing Conditions

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Summary

Demographic pressure and slash and burn practices are two factors which reduce the number of Lophira alata *plants in its natural range where it is more represented by young plants. The hypothesis that its understorey regeneration may be affected by seed tree size and growing conditions was investigated in the tropical moist forest in southern Cameroon using mature trees of various diameter classes for a sustainable management of the species. Biomass partitioning was also examined in regenerating seedlings growing in loading bays and forest understorey. Seedling density was highest when seed tree diameter at breast height (dbh) was 100 cm or more. A strong positive correlation was found between seed tree diameter dbh and crown size expressed as mean diameter of projected crown area, but crown size correlated much better with seedling density. Compared with their counterparts of the same height growing in loading bays in full sunlight but devoid of litter and topsoil, seedlings found in understorey exhibited lower root: shoot ratio, indicating that soil-derived resources were more limiting in loading bays than on undisturbed forest floor. Leaf weight per area (leaf dry weight/leaf area) (LWA) and leaf packing (leaf number/cm shoot height) were almost 2-fold greater in loading bays than in understorey. As seedlings seldom grew taller than 50 cm in the latter environment, it may be inferred that root: shoot ratio, LWA, and leaf packing can be used to assess the sustainability of growth and development of this pioneer species at the seedling stage.*

Résumé

Régénération de *Lophira alata* en sous-bois sous l'influence de la taille du semencier et des conditions de croissance

La pression démographique et l'agriculture itinérante sur brûlis sont deux facteurs qui réduisent le nombre de plants de Lophira alata *dans sa répartition naturelle où il est représenté par les jeunes plantules. L'hypothèse selon laquelle la régénération en sous-bois de* Lophira alata *pouvait être influencée par la taille des semenciers et les conditions de croissance était étudiée dans la forêt tropicale humide du sud Cameroun en considérant les grands arbres de différentes classes de diamètre pour un aménagement soutenu de cette essence. La répartition du feuillage était aussi examinée sur les jeunes plantules poussant en clairière et en sous-bois. La densité des plantules était élevée quand le diamètre à hauteur de poitrine des semenciers était de 100 cm ou plus. Une forte corrélation était trouvée entre le diamètre à hauteur de poitrine des semenciers et la dimension de la couronne comme diamètre moyen de la surface de projection de la couronne mais seulement, la dimension de la couronne était mieux correlée avec la densité des plantules. Comparées aux plantules de même hauteur poussant en clairière exposées au soleil mais dépourvues de la litière et du sol de surface, les plantules du sous-bois ont exhibé un bas ratio racine: pousse, indiquant que les ressources dérivées du sol étaient plus limitées en clairière qu'en surface du sol du sous-bois. Le poids des feuilles par unité de surface (Poids de feuille sèche/surface des feuilles) (PFS) et le pacquage des feuilles (nombre des feuilles/hauteur des pousses en cm) étaient presque deux fois plus grand en litière qu'en sous-bois. Comme les plantules du sous-bois ont difficilement dépassé 50 cm de haut, il peut être déduit que le ratio racine:pousse, PFS et le pacquage des feuilles peuvent être utilisés pour évaluer la croissance et le développement soutenu de cette essence pionnière en stade de plantules.*

Introduction

The tropical moist forests of Cameroon are complex, heterogeneous, and have stratified ecosystems with a mixture of plant species each requiring specific conditions for establishment, survival, and growth to maturity (2). Due to economic and population pressure, these forests are increasingly being exploited, either for commercial purposes or for subsistence farming. This has resulted in the degradation and rapid

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disappearance of important timber species of the country. Already, lack of forest cover in many parts of the country is not only causing acute timber shortage but also serious soil erosion and environmental degradation in general.

Commercial timber trees are essentially primary or late secondary species known to tolerate varying levels of shade during their establishment and growth habits. The apparent absence of juveniles from several species in the mature forests has been reported for African forests in particular. It has been also remarked that for several species which are dominant in the canopy, seedlings, saplings and treelets are virtually absent in the understorey (14). In the shaded understorey of a closed-canopy forest, survival is, among others, an important factor determining the abundance and distribution of tree species of rain forest prior to gap creation.

Two ecological species groups have been distinguished and defined (16) among tropical rain forest tree species: the pioneer and climax species (extremes of evolutionary specialisation). The climax species are able to germinate, establish and grow in the deep shade of a closed-canopy forest understorey, whilst the pioneer species only establish and grow in gaps in the forest canopy in which full sunlight penetrates to the forest floor for at least part of the day. This definition focuses on the early stages of a tree's life-cycle, that of germination and seedling establishment. In general spatial distribution of seeds is entirely determined by the distribution of reproducing adults and their seed dispersal strategy. After dispersal, environmental factors start having an impact on the germinating seeds. The spatial distribution of many of those, like light, proximity to sources of pathogens and herbivores and secondary dispersers is heterogeneous, which causes the original spatial distribution of the seeds to be modified (5). It is likely that after a number of years the surviving seedlings are distributed according to the occurrence of gaps in the area.

With the advent of logging for commercial uses, recovery of the forest following man-made disturbances may have become less certain, especially considering the extensive damage that is being inflicted on young trees, constituting future harvest generations. There is a fear that these rain forests will disappear as a result of the expansion of agriculture and of commercial logging (20). Opinions differ as to the relative weight of the various factors involved. Despite this, there is a widespread consensus that sustainable management is important in preventing further degradation and deforestation (17).

More attention has been devoted to studies on mature tropical trees than on seedlings demography (20). Moreover, experiments on early regeneration are limited to a number of species and largely focused on the neotropical lowland forest too. Seemingly, therefore, African forests are lagging behind in research efforts whose outcome could reveal important similarities and differences with those of the neotropics. In fact, Smith and Bariteau (15) stated that natural regeneration should be referred to as a result of many processes including flowering, fruiting, germination and post-germinative development.

There is a need, therefore, to design forest management systems for sustained *Lophira* production in the moist forest of Cameroon. Hence, the main objective of the present study is to establish trends in regeneration dynamic of *Lophira alata* (seedlings and sampling densities) in relation to the seed tree dbh and mean crown diameter. Since understorey conditions are known to be unfavourable to sustainable development of this pioneer species, we predicted that seedlings growing in low light (understorey) and high light (loading bays) environments would exhibit differences based on biotic and abiotic factors and morphological characteristics.

Material and methods

Site description

The study was carried out from April to December 1999 in the Tropenbos-Cameroon Programme (TCP) research area located in the evergreen moist tropical forest zone of southern Cameroon, between 2° 45' and 3° 15' N and 10° 15' and 11° E at about

Table 1
Location, elevation, rainfall, soil types, and soil characteristics of experimental areas

Locality	Ebimimbang	Ebom	Nyangong
Location	3°03'N, 10°28'E	3°05'N,10°41'E	2°58'N,10°45'E
Elevation (m.a.s.l)	100	440	550
Rainfall (mm)*	1707	2019	1780
Soil types	Ultisols	Ultisols, Oxisols	Oxisols
Clay (%)**	10-40	40-60	60-80
PH (water)	6.1	4.7	4.3
Carbon (%)	1.69	2.26	2.21
Nitrogen (%)	0.15	0.18	0.19
Available P in H_2O (µg/ml soil)	0.01	0.005	0.002

* Annual means of rainfall from 1995 to 1998
** Data derived from (26)

80 km east of Kribi. The site covers a total land area of about 200 000 hectares (18) and coincides to a large extent with former concessions of the Dutch logging company of WIJMA-Douala S.A.R.L (GWZ). The climate is humid tropical with average annual temperatures of about 25 °C and a mean annual precipitation of 2000 mm. Soils are moderately heavy clayey, generally strongly acid, deep and well drained, with low to medium organic matter content (Table 1).

They are classified in the FAO system as xanthic ferralsol (18). The forest belongs to the Guineo-Congolian domain made up of dense humid evergreen forests dominated by Caesalpiniaceae. Much of the vegetation has been degraded by shifting cultivation and logging activities.

Study species

Lophira alata (Banks ex-Gaertn) is a commercial timber species that has been classified as a pioneer species (7), given its ability to germinate and develop only under gaps in the forest canopy or in twilight zone that are influenced by nearby gaps. *Lophira alata* (Ochnaceae) is a native large tree species, which provides highly valued timber and which is among the most frequently harvested tree species nationwide. It ranked fourth in total national export in 1998. Locally the most abundant timber, *Lophira* constituted 60% of extracted wood volume. The species has a strategy of mass flowering and fruiting in certain years while in other years it hardly produces seeds. Its seeds are bulging and elongated, weighing about 1.0 g. It was selected on the basis of its commercial value, abundance and choosen to cover the spectrum of regeneration strategies from pioneer to small gap specialist to understorey species (8). To some extent the present situation may be considered a competition in which the exploited commercial species has a large competitive disadvantage compared to others. A change in relative abundance of the species would certainly affect the future commercial value of the forest to a large extent.

Site selection and sampling

The present study is based on old secondary forest site (non-gap region) and canopy gap formed through loading bays. A gap was defined as a vertical opening in the forest extending through all foliage level to about 2 m of the crown projection limit (3).

In canopy gaps, seventy-five randomly selected felled-tree gaps, almost equally represented in number over 5 logged-over sites were determined using Runhle's definition (18). These gaps were randomly located in 5 spatially distinct logged-over sites. Preferred gaps were of the 700-1700 m^2 size range averaging 1225 m^2. The frequency distribution of the obtained gap size values showed the existence of very many small gaps and very few large ones as observed elsewhere by Whitmore (21). Based on mean gap size and range to all blocks, gap size classes were subdivided as follows: small (700-1000 m^2), medium (1000-1300 m^2), and large (1300-1700 m^2). Gap ages were provided by corresponding stump marks for up to 6 year-old logged-over forest beyond which one had to rely on interviews in order to establish time elapsed since exploitation for older gaps.

The experimental lay-out was a split-plot with major plots represented by logged-over forest blocks of different ages (1, 3, 6, 9, and 12 years) and minor plots by gap types (small, medium, and large) nested within forest blocks. In each block, 5 replicates of each gap type were retained for sampling survey. Thus 3 gap types x 5 replicates x 5 forest blocks= 75 gaps were systematically surveyed.

A main axis was positioned along the line linking the crown to the stump of the felled tree. In case a gap had been occasioned by felling two or more trees, the main gap axis was laid along the direction of the biggest tree. Five equidistant belt transects, each measuring 5 m wide were disposed perpendicularly on either side of this axis. Transect outlines were marked by pickets whose positions had been predetermined with the aid of a compass. Each transect was extended on both sides of the main axis into the adjacent relatively undisturbed forest by 10 m. For each gap, enumeration surveys was proceeded in every other plot (measuring 5 x 1m) within each transect. It consisted of identifying and recording seedlings (< 1m tall) and samplings (either > 1m tall or diameter at breast height (dbh) from 2-20 cm) according to size, transect location, and light condition.

In the old secondary forest sites (non-gap regions) forty-nine parent trees belonging to four diameter classes were randomly selected for their isolation from other mature trees of the same species, and for their distribution among diameter classes. Seedling measurements by cross callipering were carried out in 5 m^2 (5 m x 1 m) plots under each sampled seed tree. For each seed tree, two plots were laid along a north-south line and two were laid along an east-west line. The lines intersected at the bottom of the seed tree so that plots of the same line were located 1 m apart on either side of the stem.

Sample preparation and analytical methods

Twelve seedlings of about 50 cm high growing in full light (loading bays) and 12 others developing in low light (understorey) were selected for assessment of leaf morphology at this critical height. From each seedling, two leaf fragments of about 12 to 20 cm^2 were sampled of which one originated from an upper position in the crown (recent leaf) and the other from a lower position (old leaf). Following removal, leaf fragments were treated according to previously described methods (10). Briefly, they were oven-dried at 70 °C for 48 h, cooled in a desicator then weighed to the nearest 0.1 mg. Leaf weight per area (LWA) of

each fragment was calculated by dividing leaf dry weight with surface area.
For plant measurement, the number of leaves per seedling was counted and seedling height was measured with a rigid tape. Leaf packing was then obtained by dividing leaf number by individual seedling height, as defined by Boyce (1). Root and shoot dry weight were measured after careful removal of the entire seedling from soil, and each root system was washed free of soil in water prior to drying. Root and stem tissue were oven-dried following the same procedure as leaf fragments.

Data analysis

The effect of seed tree size on seedling density, and that of growing conditions on leaf and plant morphology were evaluated using one-way and multiple-way analyses of variance. All statistical analyses were performed using SYSTAT, Inc., Evanton, Il, (U.S.A) after appropriate transformation of seedling density, root:shoot ratio, leaf packing, and LWA. Post-hoc tests were used for mean separation if significance was indicated at $p< 0.05$.

Results and discussion

Seedling density

In the gap sites, seedling density varied significantly with gap age ($P< 0.0001$), gap type ($P< 0.030$), and light condition ($P< 0.030$). The highest value (0.55 stem/m^2) was recorded 1 year after gap creation. This was followed by a steep decline by year 6 (0.21 stem/m^2) after which it increased abruptly and attained 0.39 stem/m^2 at 9 years. A non significant decrease in seedling density was observed between years 9 and 12. This pattern of variation is similar to the one recorded for selection-felled gaps in a humid tropical rainforest in India (4). In that study, selection-felled gaps exhibited a tree seedling density of 7.2 stem/m^2 at age 1, 3.1 at age 5 and 6.9 at age 10. The decline in seedling densities observed between 1 and 6 years may be accounted for by the detrimental effect of competing vegetation on seedling development (herbs and shrubs) after gap formation. The sudden increase noticed after 6 years may be due either to the adverse effects of canopy closure on weed development or to competition among herb and shrub species.
Medium gaps exhibited a significantly higher seedling density (0.40 stems/m^2) compared with large and small-sized ones in which 0.33 and 0.32 stems/m^2 were recorded respectively (Table 3).
Large openings (loading bays) have been reported to exhibit lower seedling densities than treefall gaps, skidtrails and smaller openings in a study on forest regeneration after logging (7). This could be attributed to high light intensity favorable to herb and shrub development. On the other hand, the decline observed in small gaps may be associated with root competition between tree seedlings and surrounding forest. Elsewhere, a strikingly similar result has been obtained before. In an early experiment on Gunung Gede in Java (Indonesia), which apparently has never been repeated or extended, artificial small gaps of 0.1 ha in primary forest were soon colonized by young individuals of primary forest species. By contrast, in larger gaps of 0.2-0.3 ha these persistent individuals were suppressed by a lush vegetation of invading tree species (20).
In the forest understorey, small trees and shrubs (< 15 m maximum height) make up 38.4% of individuals, which indicate a good regeneration in forest understorey.

Table 2
Effect of seed tree size (dbh) on seedling density in an understory environments

Class number	Diameter (D) range (cm)	Number of sampled seed trees (replicates)	Seedling density within the projected crown area (stem number/m^2)
I	$50< D\leq 80$	13	0.24 ± 0.09a
II	$80< D\leq 110$	11	0.28 ± 0.08a
III	$110< D< 140$	11	1.72 ± 0.17b
IV	$D\geq 140$	14	2.25 ± 0.19c

∗ Densities followed by the same letter are not significantly different by post-hoc test ($p= 0.05$).

Table 3
Multi-way analysis of variance: means of juvenile population parameters with respect to gap size

	Gap type			
Parameters	Small	Medium	Large	P-value
Seedling density (stem/m^2)	0.32	0.40	0.33	0.03*
Sampling density (stem/m^2)	0.077	0.091	0.083	0.103 ns

Table 4
Correlation coefficients between seedling density, seed tree diameter at breast height, and mean diameter of projected crown area

	Diameter at breast height (cm)	Mean diameter (cm) of projected crown area
Seedling density	0.46 (P= 0.001)	0.56 (P< 0.0001)
Mean diameter of Projected crown area	0.89 (P< 0.0001)	1

The highest seedling density (2.25 seedlings/m^2) (p < 0.0001) has been recorded under parent trees > 140 cm dbh (Class IV). This density was significantly greater than those observed under class I and II seed trees respectively (Table 2).
These observations are consistent with the idea that seed production and dispersal range may be greater for very large trees compared with trees below the minimum girth (7). Contrary, in studying forest regeneration after logging, the author (7) have considered overmaturity to be absolutely detrimental to seed production in forest tree species. The fact that in the present study, a 42% increase in seedling density was observed between the third and fourth diameter classes suggests that the maturity of seed producers is an important factor for seedling density, since all seed trees and their progenies (seeds and seedlings) were exposed to similar climatic conditions. Alternatively, the lack of natural regeneration under some parent trees could be attributed to variation in understorey conditions affecting germination and seedling establishment. For a tree species failing to regenerate the key factors to be considered were the quantity of viable seeds produced, the frequency of seed production, light conditions for germination and establishment, and the ability of seedling, to grow on to saplings and poles (9).
Correlation analyses showed that there were significant correlations between seedling density, seed tree dbh, and mean diameter of projected crown area (Table 4).
Although seed tree dbh was strongly and positively correlated with crown diameter (R= 0,89) (p< 0.0001), the latter variable was found to be better correlated with seedling density (R= 0,75) (p< 0.0001) compared with the former (R= 0.55) (p= 0.001). The correlation coefficients found between seed tree characteristics and seedling density indicated that those parameters account only for a very small portion of the total variation in seedling regeneration. Other factors may be involved as well.
Seedlings growing in full sunlight exhibited a LWA (67.6 g/m^2) that was 76% greater than the value recorded for seedlings developing in the understorey environment (38.5 g/m^2) (Table 5).
These values fall within the range found by Oldeman (12) for leaves of the shade-intolerant species *Betula pendula* growing under different light levels (34.9 to 86.1g/m^2). In his study, LWA was observed to increase with increasing irradiance, both in pioneer and in non-pioneer species (*Lonicera xylosteum* and *Corylus avellana*), although the relative variability in LWA was smaller for *Betula pendula* than in the other two species. In our study, the pattern of variation in LWA of *Lophira alata* with respect to light intensity is quite similar to that observed in *Betula pendula*, described as a typical pioneer species. Since leaf position did not have any significant effect on LWA, the increased LWA in light conditions may be mainly associated with the stimulatory effect of light on leaf tissue production as pointed out by Oren *et al.* (13).
Leaf packing was 2 times larger in full light (0.63 leaf/cm shoot height) (p< 0.0001) than in the understorey (0.30 leaf/cm shoot height) (Table 5). Likewise, the root-shoot ratio exhibited by seedlings growing in light were higher compared with the ratio recorded in understorey. This may be an indication of poorer nutrient status of loading'bays (bare soil) compared with understorey. Root-shoot ratio increased with decreasing soil-derived resources such as water and nutrient supply has been reported (6). In *Gmelina arborea,* Ogbonnaya and Kinako (11) observed that root-shoot ratio declined with increasing amounts of high supplied nitrogen because this increase resulted

Table 5
Effect of growing environment on leaf and seedling morphology

	Growing environment	
Leaf and seedling characteristics	Understory	Loading bays
Leaf weight per area (LWA) (g dry weight/m^2)	38.5b	67.6a
Leaf packing (leaf number/cm shoot height)	0.30b	0.63a

∗ Within rows, means with different letters are significantly different at p< 0.05.

in more nitrogen transported to the shoots where it enhanced the utilization of carbohydrates for protein synthesis and growth.

Conclusion

This study has shown that the degree of natural regeneration of *Lophira alata* in the forest depends on several factors including the presence and size class distribution of parent trees. We also demonstrated that the concept of overmaturity in this species can be assessed using seed tree characteristics such as diameter at breast height and mean diameter of projected crown area. In studying tropical forest regeneration after logging, Hawthorne (7) has classified *Lophira alata* as a pioneer species, according to Whitmore (21) definition of pioneer and non-pioneer tree species. In the present study, we have found this species as seedlings (<1 m in height) and saplings (between 1 and 5 m in height) in loading bays, but only as seedlings under complete forest shade, which prompt us to consider it as a non-pioneer light demander. Seedlings growing in full light developed morphological traits that were different from those displayed by completely shaded ones. It appeared that medium gaps seem to be more suitable for regeneration processes and that *Lophira* does not have any particular preference as to gap size and light condition although it is poorly represented in the experimental plots. Since only the former plants could develop into saplings, further research should be focused on refining biochemical traits associated with such morphological differences, that could be used as efficient indicators for sustainable growth and development of *Lophira alata* in disturbed or undisturbed forest ecosystems.

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