
Early regeneration of commercial timber species in a logged-over forest of southern Cameroon

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Summary

Natural regeneration of commercial timber species was investigated in 75 felling gaps demarcated in a tropical rainforest concession of Southern Cameroon. These gaps belonged to 5 forest blocks or age classes (1, 3, 6, 9, 12) and each class was composed of small, medium, and large-sized gaps. Species and seedling densities (numbers per unit area) were highest in 1 year-old gaps, whereas the most important sapling density was observed in 9 year-old openings. Medium-sized gaps exhibited species, seedling and sapling densities that were higher than those recorded for other size classes. Compared with contiguous undisturbed forest understorey (control), gap floor yielded significantly lower seedling density, although species and sapling densities did not vary with these environmental conditions. Most species could be found as saplings in gap and understorey respectively. Results suggest that gap areas of more than 1 300 m² considerably hamper the process of forest recovery in terms of recruitment and species diversity. They also indicate that species regeneration and conservation in felled-tree gaps not only depend on light conditions, but also on the control of weed development.

Résumé

L'étude de la régénération naturelle des essences commerciales a été menée dans 75 trouées d'abattage délimitées dans une concession localisée dans la forêt tropicale humide du Sud Cameroun. Ces trouées sont comprises dans 5 compartiments ou classes d'âge différentes (1, 3, 6, 9, 12 ans) et chacune des classes présentant les 3 types de trouées à savoir les trouées de petites, moyennes, et grandes dimensions. Les densités des essences et des semis (nombres par unité de surface) les plus élevées ont été trouvées dans les trouées d'un an d'âge tandis que la densité de gaulis la plus importante a été observée dans les ouvertures de 9 ans d'âge. Les trouées de taille moyenne ont montré des densités de semis et de gaulis les plus élevées par rapport à celles obtenues pour d'autres classes de taille. Par comparaison avec la forêt adjacente, au sous-bois non perturbé (témoin), le plancher de la trouée a produit une densité de semis plus faible, même si les autres paramètres n'ont pas varié en fonction de ces conditions environnementales. La plupart des essences sous forme de gaulis se trouvaient en même temps dans les trouées et sous-bois adjacents. Ces résultats suggèrent que les superficies des trouées situées au-delà de 1 300 m² gênent considérablement le processus de recouvrement de la forêt en fonction du recrutement et de la richesse floristique des essences. Ils montrent aussi que la régénération et la préservation des essences dans les trouées d'abattage ne dépendent pas seulement des conditions lumineuses, mais aussi du contrôle du développement des herbes.

Introduction

Background and justification

Canopy gaps, whether natural or felled-tree, are crucial to the regeneration of the tropical rainforest. For example, approximately 75% of the canopy tree species at La Selva (Costa Rica) are dependent on light gaps for successful regeneration (Hartshorn, 1978). It has even been stated that the regeneration of many commercial tree species depend on large-scale disturbances (Poorter *et al.*, 1996). Commercial timber trees are essentially primary or late secondary climax species known to exhibit important but varying levels of tolerance to shade in their establishment and growing habits.

The importance of treefall gaps lies in the fact that they provide the stimulus (following increased insolation) for tree regrowth from dormant or newly arrived seed as well as for growth resumption of previously overshadowed individuals of many canopy tree species. Exposure to sunshine was crucial in breaking the dormancy of commercial tree species both primary and secondary resulting in their germination (Hall, Swaine, 1980).

Although the importance of canopy gaps in determining tropical forest structure and dynamics has been widely emphasised (Kadambi, 1941 ; Richards, 1952 ; White, 1979 ; Picket, 1983) and studies on the regeneration pattern of seedlings are limited to natural gaps only (Strong, 1977 ; Denslow, 1980 ; Brokaw, 1985 ; Raich, Christensen, 1989) cited by Chandrashakara and Ramakrishnan (1994). Unfortunately, the occurrence of natural gaps is unpredictable, making it difficult and tedious to determine their ages. Consequently, it is not often easy to relate natural regeneration patterns to time elapsed since treefalls.

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. These forests need to be managed in order to mitigate the effects of damage and ensure the sustainability of timber supplies and other goods and services. The ecological responses of many canopy tree species, at varying levels of development, to felling gaps of various sizes may provide a clue to appropriate silvicultural interventions favouring the attainment of the canopy by selected species. This is particularly important for species displaying fluctuating patterns, sparseness or absence of regeneration as described by Poorter *et al.* (1996). Yet very little or no experimental consideration has been given to the effects of felling gap size and age on the recovery of the forest vegetation.

The theory of gap-phase regeneration dynamics proposes that different species of trees partition canopy gaps because they are preferentially adapted to a particular gap size class (Denslow, 1980). According to Orians (1982) cited by Brown (1993), such gap size specialisation could constitute an important axis for niche differentiation thereby acting as a mechanism for maintaining the extraordinarily high species diversity of tropical rain forest.

The following objectives will be achieved during this study :

- assess natural regeneration of essentially commercial timber species in terms of seedling/sapling densities and species richness in various-sized gaps and their bordering understoreys over a range of age classes,
- determine the relative site preferences of individual or groups of species based on sapling distributions with respect to gap size and light conditions.

Study site

The Tropenbos-Cameroon Programme (TCP) site lies approximately 80 km east of Kribi in the southern region of Cameroon between latitudes 2°47'-3°14'N and longitudes 10°24'-10°51'E. It covers about 1 700 km² and much of this area is under commercial logging. The humid seasons come up from September to November, and from April to May, interrupted by relatively dry seasons spanning the periods between December to march and June to august. The climate is humid tropical with an average annual temperature of around 25°C. Mean annual rainfall is estimated at 1 900 mm. The rocks of the TCP site are part of the pre-cambrian complex while soils resulting from the weathering of this parent material are predominantly poor, acid and ferrallitic sandy clay. The forest belongs to the Guineo-Congolian domain made up of dense humid evergreen forests dominated by Caesalpinaceae. Much of the vegetation has been degraded by shifting cultivation and logging activities.

Sample plots used in this study are located in felled-tree gaps occurring on spatially distinct and topographically varied sites (represented by corresponding villages), which have each in turn been subjected to logging once during the past 12 years. From the oldest to the most recent exploitation sites with altitudes above sea level indicated in brackets, the forests units or blocks involved are : Ebimimbang (110 m), Assok II (200 m), Minkan (500 m), Nyangong (700 - 900 m) and Nkoutou (250 m). Their top and sub-soil structures are distinguished by varying levels of clay content.

Materials and methods

Gap size measurements

One hundred and twenty randomly selected felled-tree gaps, almost equally represented in numbers over 5 logged-over sites, were determined using Runkle's definition (Van der Meer, 1995) which estimates gap size at the forest floor. Evaluated gap sizes ranged from 450 m² to 5 005 m², averaging 1 225 m². 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 (1989). Based on mean gap size and range common to all blocks, gap size classes were sub-divided as follows : small (700-1 000 m²), medium (1 000-1 300 m²), large (1 300-1 700 m²).

Experimental design

The experimental lay-out is 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. 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. In each forest block, five 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.

Experimental procedure

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 felled tree. Five equidistant belt transects, each measuring 5 m wide, were disposed perpendicularly on either side of these axes. 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 every gap, enumeration surveys proceeded in every other plot (measuring 5x1 m) within each transect. It consisted of identifying and recording seedlings (<1m tall) and saplings (either >1 m tall or diameter at breast height -dbh- from 2-20 cm) according to species, size, transect location and light condition. Samples of inventoried species were harvested for later comparative studies with nursery-raised control seedlings in order to ascertain accuracy of the tree identification process.

Data analysis

Multi-way analysis of variance (with replications) were conducted, following log (1+x) transformations of the dependent variables, viz : seedling and sapling densities (number of individuals per m²) and species richness (number of species per m²) in order to establish the level of significance or non-significance of means with respect to the following factors and associated statistical levels in brackets :

- gap age (1, 3, 6, 9, 12 years)
- gap type (small, medium, large)
- random gap location (5 replicates)
- light condition (gap, understorey)

Results and Discussions

A list of about 40 species recorded during the survey is indicated in table 1. It also shows the frequency of juvenile occurrence of these species in order of importance for the 75 gaps investigated. Other results are discussed below as follows.

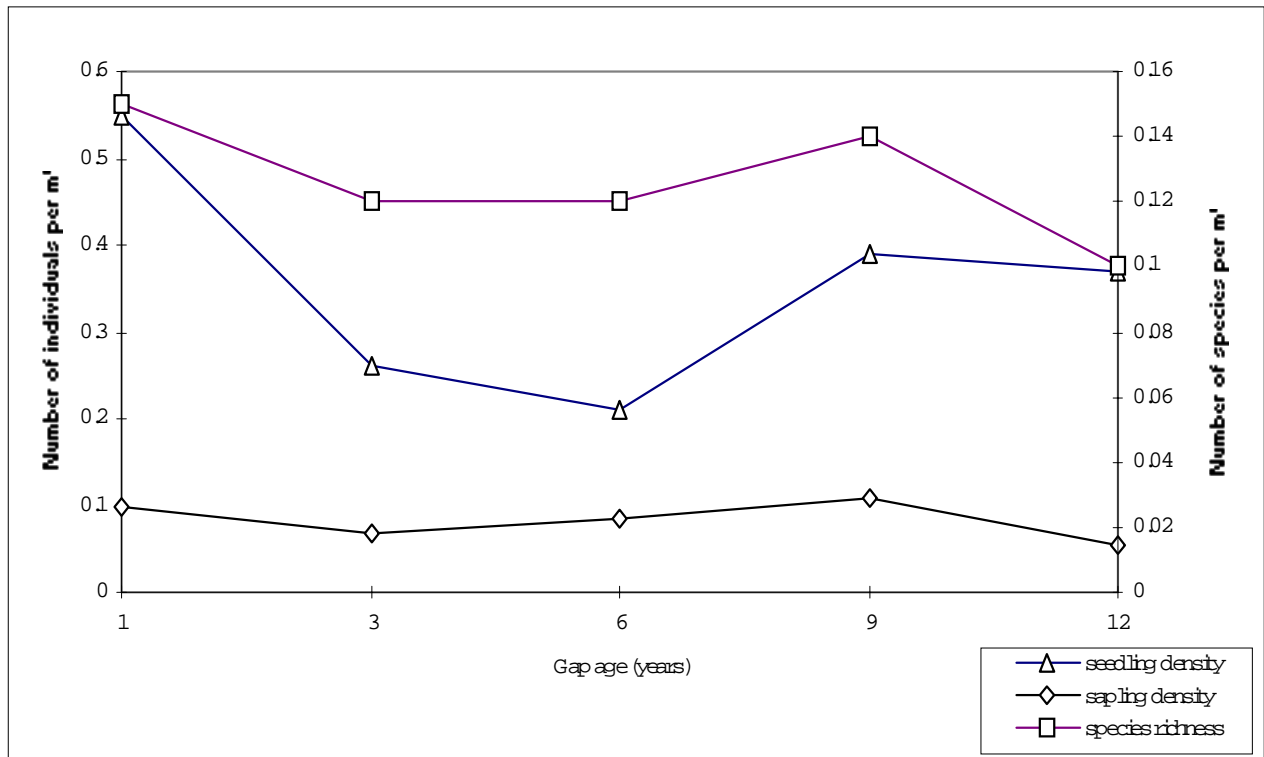
Table 1: frequency of occurrence of juveniles of various species in 75 felling gaps

<p>Group I : species present in >50 gaps</p> <p><i>Staudtia kamerunensis, Pycnanthus angolensis, Lophira alata, Canarium schweinfurthii</i></p>
<p>Group II : species present in >25 gaps</p> <p><i>Desbordesia glaucescens, Diospyros spp., Afzelia pachyloba, Pterocarpus soyauxii, Piptadenastrium africanum, Erythrophleum ivorense, Pterygota macrocarpa, Zanthoxylum heutzii, Eribroma oblonga, Distemonanthus banthamianus, Guarea cedrata, Mammea africana, Funtumia sp.</i></p>
<p>Group III : species present in <25 gaps</p> <p><i>Lovoa trichilioides, Alstonia spp., Poga oleosa, Milicia excelsa, Terminalia superba, Antrocaryon klaineinum, Didelotia letouzeyi, Guarea thompsonii, Tetraberlinia bifoliolata, Berlinia bracteosa, G. dewevrei, Guibourtia tessmanii, Nauclea diderrichii, Zanthoxylum gillettii, Paraberlinia bifoliolata, Petersianthus macrocarpum, Entandrophragma candollei, Mitragyna ciliata, Khaya ivorensis, Ongokea gore, Plagiosiphon multijugus, Ceiba pentandra</i></p>

Seedling density

Seedling density varied significantly with gap age ($P < 0.0001$), gap type ($P < 0.030$), and light condition ($P < 0.030$) (Tables 2, 3 and 4). The highest value (0.55 stems/m²) was recorded one year after gap creation. This was followed by a steep decline by year 6 (0.21 stems/m²) after which it increased abruptly and attained 0.39 stems/m² at 9 years (Figure 1). 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 (Chandrashakara, Ramakrishnan, 1994). In that study, selection-felled gaps exhibited a tree seedling density of 7.2 stems/m² 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, 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.

Figure 1: trends in population densities and species richness with respect to gap age



Medium gaps exhibited a significantly higher seedling density (0.40 stems/m²) compared with large and small-sized ones in which 0.33 and 0.32 stems/m² were recorded respectively. Large openings (loading bays) have been reported to exhibit lower seedling densities than treefall gaps and skid trails and smaller openings in a study on forest regeneration after logging (Hawthorne, 1993). This could be attributed to high light intensity favourable 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 colonised 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 (Whitmore, 1984).

Seedling density observed in the adjacent understorey was significantly higher (0.39 stems/m²) than the one recorded in gaps (0.31 stems/m²). Hawthorne (1993) reported that seedlings of pioneer tree species were more abundant in gaps and “chablis” than in twilight whereas for non-pioneer species the contrary was observed. In our study, the significantly higher tree seedling density recorded in adjacent forests might be due to the relative abundance of non-pioneer tree species. Table 5 shows that a majority of species investigated can indifferently grow as saplings both in gaps and adjoining understoreys (non-pioneer species) (Brokaw, 1985).

Table 2 : multi-way analysis of variance : means of juvenile population parameters with respect to age

Parameter	Felling gap age					P-value
	1	3	6	9	12	
seedling density (stems/m ²)	0.55	0.26	0.21	0.39	0.37	0.000***
sapling density (stems/m ²)	0.098	0.068	0.085	0.11	0.055	0.000***
species richness (no. of species/m ²)	0.15	0.12	0.12	0.14	0.10	0.000***

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

Parameter	Gap type			P - value
	Large	Medium	Small	
seedling density (stems/m ²)	0.33	0.40	0.320	0.030*
sapling density (stems/m ²)	0.083	0.091	0.077	0.103NS
species richness (no. of species/m ²)	0.12	0.13	0.12	0.076NS

Sapling density

Sapling density varied significantly with age ($P < 0.0001$) (Table 2). The highest sapling density (0.11 stems/m²) was recorded 9 years after gap formation. This may have been due to recruitment of seedlings into the sapling class. The decline after 9 years may be imputed to high mortality of pioneer species as a result of canopy closure. Chandrashakara and Ramakrishnan (1994) reported large-scale mortality of herbs, shrubs, and secondary species in the 5-10 year period of gap closure.

The result obtained for species richness (Table 4) is consistent with the citation that there is no significant difference in species composition between gaps and understorey (Rollet, 1983). In a similar observation, Chandrashakara and Ramakrishnan (1994) found that tree seedlings and saplings either had lower values ($P < 0.05$) in canopy gaps, or showed no significant difference for the values between canopy gaps and the undisturbed adjacent site. Significant differences between 1 and 6 years (Table 2) may be due to high mortality of light-demanding species as a result of competition with shrubs and herbs (Chandrashakara and Ramakrishnan, 1994).

Table 4 : multi-way analysis of variance : Means of juvenile population parameters with respect to light condition

Parameter	Light condition		
	Gap	Under-storey	P-value
seedling density (stems/m ²)	0.31	0.39	0.030*
sapling density (stems/m ²)	0.087	0.081	0.476NS
species richness (no of species/m ²)	0.12	0.13	0.367NS

Sapling distributions

Among 26 species (including or groups of species) selected for individual multiple analysis of variance tests, some had their sapling densities approximated to zero following the analysis (Table 5). For individual or groups of species studied, *Diospyros spp.*, *Desbordesia glaucescens* and *Zanthoxylum heitzii* significantly preferred small ($P < 0.001$), small/medium ($P < 0.05$), and medium/large ($P < 0.05$) gaps respectively (Table 5). Apart from these exceptions, saplings of most species were indifferent in their distributions among gap types. Furthermore, with the exception of *Staudtia kamerunensis* and *Zanthoxylum heitzii* whose saplings exhibited predilections for the understorey ($P < 0.05$) and gap floor ($P < 0.001$) respectively, other species did not respond to any gap/understorey dichotomy (Table 5). Some of these results are consistent with classifications made by Hawthorne (1993) for *Zanthoxylum sp.* and *Guarea cedrata*.

Conclusions

Low recovery rate from injury inflicted by logging, competition from profuse non-tree light demanders and pre-existing shade bearers appear to be the main obstacles to tree seedling regeneration in felled-tree gaps. It has been demonstrated that high mortality of secondary tree species is associated with canopy closure leading to reduction in population size and species richness. On the other hand, medium gaps seem to be more suitable for regeneration processes and species diversification.

Most timber species featured in this investigation do not have any particular preference as to gap size and light condition although a good number of these species are poorly represented in the experimental plots. Future research should be geared towards determining the preference of such species with regard to light regime.

Table 5 : distributions of commercial timber species among gap types and between gap and understorey

Species	Sapling densities (stems/m ²)	Seedling densities (stems/m ²)	Gap type preference	Gap/non gap preference
<i>Tetraberlinia bifoliolata</i>	0.016	0.060	indifferent	indifferent
<i>Staudtia kamerunensis</i>	0.012	0.044	indifferent	understorey (p<0.005)
<i>Diospyros spp.</i>	0.009	0.018	small gaps (p<0.001)	indifferent
<i>Canarium schweinfurthii</i>	0.006	0.005	indifferent	indifferent
<i>Pycnanthus angolensis</i>	0.005	0.026	indifferent	indifferent
<i>Zanthoxylum heutzii</i>	0.005	0.005	medium/large gaps (p<0.05)	gaps (p<0.001)
<i>Funtumia spp.</i>	0.003	0.021	indifferent	indifferent
<i>Pterygota macrocarpa</i>	0.003	0.014	indifferent	indifferent
<i>Didelotia letouzeyi</i>	0.002	0.022	indifferent	indifferent
<i>Dismonanthus benthamianus</i>	0.002	0.016	indifferent	indifferent
<i>Lophira alata</i>	0.001	0.050	indifferent	indifferent
<i>Desbordesia glaucescens</i>	0.001	0.013	small/medium (p<0.05)	indifferent
<i>Piptadenastrium africanum</i>	0.001	0.012	indifferent	indifferent
<i>Mammea africana</i>	0.001	0.010	indifferent	indifferent
<i>Lovoa trichiliodes</i>	0.001	0.010	indifferent	indifferent
<i>Guarea cedrata</i>	0.001	0.006	indifferent	indifferent
<i>Plagiosiphon multijugus</i>	0.001	0.005	indifferent	indifferent
<i>Afzelia spp.</i>	0.001	0.003	indifferent	indifferent
<i>Alstonia boonei</i>	0.001	0.003	indifferent	indifferent
<i>Pterocarpus soyauxii</i>	0.001	0.002	indifferent	indifferent
<i>Eribroma oblonga</i>	0.000	0.009	indifferent	indifferent
<i>Erythrophleum ivorensis</i>	0.000	0.006	indifferent	indifferent
<i>Pentachlethra macrophylla</i>	0.000	0.002	indifferent	indifferent
<i>Dialum sp.</i>	0.000	0.001	indifferent	indifferent
<i>Paraberlinia bifoliolata</i>	0.000	0.001	indifferent	indifferent
<i>Nauclea diderichii</i>	0.000	0.000	indifferent	indifferent

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