

Effects of Light Gaps and Litter Removal on the Seedling Performance of Six African Timber Species¹

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ABSTRACT

Valuable timber tree species frequently show poor regeneration after selective logging in tropical forests. Small size of logging gaps, lack of soil disturbance, and limited seed availability have each been blamed for observed regeneration failures. We investigated seed germination and seedling performance using a split-plot factorial design involving light availability and litter removal for six Central African timber tree species, hypothesizing that canopy gaps and litter removal would improve seedling establishment, and that less shade-tolerant species would show stronger responses to both factors. Contrary to our expectations, significantly more germinants established on intact litter than on exposed mineral soil 3 mo after seeding. After 18 mo, seedling survival, height and diameter growth, leaf area, and rooting depth were all much higher in gap plots than in the understory for all species, with the exception of *Gilbertiodendron dewevrei*, a highly shade-tolerant species whose survival was higher in the understory. Leaf production was negatively influenced by litter removal in the least shade-tolerant species, *Nauclea diderrichii*, with weak or positive effects in other species. *G. dewevrei*, while displaying a low-light threshold for growth, exhibited a surprisingly high growth response to increasing light comparable to more shade-intolerant species, a response that may help explain its local competitive dominance in the region. Due to the rapid closure of small gaps, we suggest that shade-intolerant species such as *N. diderrichii*, *Khaya anthotheca*, and *Entandrophragma utile* might benefit from more intensive silvicultural practices that create larger canopy gaps.

Key words: Central Africa; light gaps; litter removal; seedling establishment and growth; timber species; tropical moist forest.

A SOUND UNDERSTANDING OF FACTORS INFLUENCING THE REGENERATION of timber tree species is an important first step toward the sustainable management of tropical forests. Processes controlling the regeneration of tropical trees are strongly influenced by disturbance resulting from gaps generated by natural treefalls or harvesting operations (Brokaw 1985, Denslow 1987, Ashton *et al.* 1995, Hubbell *et al.* 1999). The effects of light availability on the growth of tropical tree seedlings have been frequently studied in the field and experimentally (Welden *et al.* 1985, Kwesiga *et al.* 1986, Moad 1992, Ashton 1995, Veenendaal *et al.* 1996, Agyeman *et al.* 1999, Hubbell *et al.* 1999). In general, seedling survival and growth increases with increasing light availability, but species vary largely in this response. Since timber harvesting creates canopy gaps, and thus increases light availability, it has often been assumed that selective logging would positively influence both residual tree growth and the establishment of new seedlings (Hartshorn 1989, Stanley & Gretzinger 1996, Dupuy *et al.* 1998). However, regeneration failure of important timber trees after logging is common in tropical forests (Rodan *et al.* 1992, Gullison *et al.* 1996, Struhsaker 1997, Fredericksen 1998, Kammesheidt 1998, Mwima *et al.* 2001).

Several factors may account for regeneration failure of tropical timber species after selective logging. Logging can remove a significant proportion of the advanced regeneration (Kuusipalo *et al.* 1996, Gardingen *et al.* 1998), leaving establishment from seeds to play a major role in the regeneration of logged stands. The removal of most large reproductive trees, however, can considerably reduce seed production in logged areas (Plumptre 1995). Low seed production, in conjunction with strong dispersal limitation (Dalling *et al.* 1998, Hubbell *et al.* 1999, Makana & Thomas 2004), has the potential to decouple the effects of canopy

opening on the regeneration of timber species. It also has been argued that many light-demanding timber species require larger canopy openings than that provided by the removal of single trees during “selective” logging (Boot & Gullison 1995, Fredericksen 1998).

Poor regeneration of tropical timber trees in logged forests can also result from increased seed and seedling predation (Basuta & Kasenene 1987, Struhsaker 1997, Guariguata & Pinard 1998) and competition with lianas and noncommercial pioneer trees (Putz 1984, Struhsaker 1997, Schnitzer *et al.* 2000, Gerwing 2001). In addition, recent studies in temperate and tropical forests suggest that seeds of many early-, as well as late-successional tree species require litter-free mineral soil, *i.e.*, treefall pits and mounds created by the uprooting of trees, to germinate and establish successfully (Snook 1996, Feller 1998, Kammesheidt 1998, Fredericksen *et al.* 2000).

Although the functional ecology of tropical tree seedlings has received considerable research attention (Swaine 1996), environmental influences on the seed germination and early establishment, even of valuable timber species, remain poorly characterized (Vázquez-Yanes & Orozco-Segovia 1984, Vázquez-Yanes *et al.* 1990, Kyereh *et al.* 1999). Kyereh *et al.* (1999) have argued that the lack of interest in seed germination ecology of tropical tree species is partly due to the fact that most of them have “recalcitrant” seeds with short viability and no dormancy. The main environmental factors controlling the germination of recalcitrant seeds include moisture availability and the quality of the seedbed. Mineral soil is generally considered a good seedbed because of its high water infiltration capacity, favorable aeration, and good hydraulic contact between soil particles and seeds. Litter is usually less suitable because it impedes penetration of radicles, thereby preventing contact with mineral soil (Smith 1995, Kozłowski 2002).

In this study we investigate the effects of litter removal and light availability on seed germination, seedling establishment, and growth of six valuable timber tree species in northeastern Congo basin, Democratic

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Republic of Congo. Three main hypotheses were tested: (1) removal of litter and organic matter improves seed germination and seedling establishment; (2) canopy gaps positively influence seedling establishment and growth, and therefore, (3) the simultaneous occurrence of exposed mineral soil and canopy gaps would offer the best conditions for tree regeneration. All three patterns were predicted to be most pronounced in less shade-tolerant species.

METHODS

STUDY SITE.—The research project was conducted at two different sites in northeastern Congo basin forest block. The main site (Mandumbi) was a logging concession located at 25 km northwest of the town of Beni (0°45'N, 29°15'E) in northeastern Democratic Republic of Congo. The elevation in the region is ~950 m above sea level. Mean annual rainfall is 1639 mm. Over a 22-yr period (1978–1999), the lowest annual rainfall was 934 mm (1979) and the highest was 2096 mm (1985). A dry season occurs from December to February, during which monthly average rainfall is less than 100 mm. May and October are the wettest months of the year, with average precipitations of 186 mm and 200 mm, respectively. Annual average daily temperature is 23.5°C and varies little during the year. With an average daily temperature of 24.4°C, March is the hottest month of the year, whereas August (22.9°C) is the coolest month (J.-R. Makana, pers. comm.).

The vegetation in the Mandumbi region is a semideciduous moist forest dominated by light-demanding tree species such as *Alstonia boonei* De Wild., *Entandrophragma* spp., *Khaya anthotheca* (Welw.) C. DC., *Albizia* spp. and *Canarium schweinfurthii* Engl. Two shade-tolerant species, *Gilbertiodendron dewevrei* (De Wild.) Léonard and *Julbernardia seretii* (De Wild.) Troupin, form pure stands along streams and swamps. Active crop fields and secondary vegetation of various ages reflect large-scale human activities in the region.

A second site was located at Epulu, in the 1,350,000-ha Okapi Wildlife Reserve. Field investigation at this site was carried out within the 5-km² Lenda study area (LSA, 1°19'N and 28°38'E) established by the Centre de Formation et de Recherche en Conservation Forestière (CEFRECOP). Elevation at LSA is about 770 m above sea level. Mean annual rainfall is 1725 mm. Three months (December–February) generally have mean rainfall below 100 mm. Mean daily average temperature is 23°C under closed canopy (Hart & Carrick 1996).

The vegetation at LSA is mainly composed of the single-dominant evergreen forest, dominated by *G. dewevrei*, a Caesalpinoid legume. This species forms extensive areas of closed-canopy forest across most of the Congo basin rainforest block, and may comprise up to 90 percent of the canopy trees in some stands (Gérard 1960, Hart *et al.* 1989, Makana *et al.* 1998). There is also an old secondary forest created by shifting agriculture during the 1960s in this study area.

EXPERIMENTAL DESIGN.—The experiment was set up using a split-plot full factorial design, involving light availability and soil disturbance. For soil disturbance treatments, all litter and organic matter was removed from the soil surface, exposing mineral soil. The effects of light availability were assessed by replicating the experiment in gaps and under nearby closed canopy. Four 2 × 2 m quadrats, separated by 0.5 m buffer zones,

constituted a plot, which is the experimental unit for the whole-plot treatment, while the 2 × 2 m quadrats form the experimental units for the subplot treatment. For this study, light availability (gap vs understory) constitutes the whole-plot treatment, whereas soil disturbance (litter vs mineral soil) makes up the subplot treatment. Ten plots were established at each site, half of which were in gaps and half under closed canopy. Each gap was paired with an understory plot; the two plots constituted a block and were located within 50 m of each other. In gaps, the plots were oriented in a north–south direction, so that all quadrats were exposed to direct sunlight for approximately the same duration daily. Both logging gaps and natural treefall gaps were used in the experiment. Average gap size was 106 ± 25 m², but logging gaps (228 ± 31 m², *N* = 4) were much larger than natural treefall gaps (61 ± 5 m², *N* = 6). The litter and organic matter layer was relatively thick at the end of the dry season, averaging 3.6 ± 0.3 cm. Litter was made up of nondecomposed leaves that covered a layer of humus mixed with secondary and fine roots of living vegetation. In two quadrats all litter and organic matter was removed by hand, while the other two were left untouched in each replicate.

Tree species included in the study were chosen to represent a range of shade-tolerance classes from among the most heavily exploited and valuable timber species in the Eastern Congo basin (Table 1). Nursery-grown seedlings *ca* 6 mo in age of three timber trees (*Entandrophragma cylindricum* (Sprague) Sprague, *Nauclea diderichii* (de Wild.) Merr., and *Autranella congolensis* (de Wild.) A.Chev. and natural seedlings (wildings) of *G. dewevrei* from the most recent fruiting event were planted on one of each soil treatment quadrats. Each quadrat received a total of 18 seedlings: 5 seedlings of *E. cylindricum* and *G. dewevrei*, and 4 seedlings of each of the other two species. Wildings of *G. dewevrei* were taken from locations no more than 500 m away from the plots where they were transplanted. In addition, 24 seeds of two species of African mahogany (*K. anthotheca* and *Entandrophragma utile* (Dawe & Sprague) Sprague) were collected at the Mandumbi site, and uniformly dispersed on the remaining subplots. The whole experiment was replicated at two sites, Mandumbi and Epulu.

TABLE 1. Some ecological characteristics of the species used in the experiment. Guild and foliage information from Pieters (1977) and Agyeman *et al.* (1999).

Species name	Family	Guild	Adult foliage
<i>Nauclea diderichii</i> (De Wild.) Merr.	Rubiaceae	Pioneer	Evergreen
<i>Khaya anthotheca</i> (Welw.) C. DC.	Meliaceae	Light demander	Evergreen
<i>Entandrophragma utile</i> (Dawe & Sprague) Sprague	Meliaceae	Light demander	Deciduous
<i>Autranella congolana</i> (De Wild.) A. Chev.	Sapotaceae	Light demander	Deciduous
<i>Entandrophragma cylindricum</i> (Sprague) Sprague	Meliaceae	Light demander	Deciduous
<i>Gilbertiodendron dewevrei</i> (De Wild.) J. Léonard	Caesalpinaceae	Shade tolerant	Evergreen

The experiment commenced at the beginning of the rainy season, which occurs at the end of February or the beginning of March. This timing was particularly appropriate because it corresponds to the seasonal pattern of seed dispersal and germination of African mahogany species. Most of these species disperse their seeds from November to March, but seed germination generally occurs at the beginning of the rainy season. After seeding, plots were revisited to monitor seed germination. At Epulu seeds were sown in late February, whereas sowing occurred a month later at Mandumbi. The number of germinants/seedlings was recorded at each visit to the plots. As for the planted seedlings, three variables were measured at the beginning of the experiment: total aboveground height after planting, the number of leaves, and stem diameter at 10-cm height. The three variables were measured again at the end of the experiment for all surviving seedlings. A subset of seedlings of *K. anthotheca* and *E. utile* were harvested in each treatment combination to measure total biomass.

LEAF AREA.—To estimate leaf area, leaf length and width were measured for all the fully expanded leaves of randomly selected seedlings of each studied species. For species with compound leaves, leaflets were individually measured instead of the whole leaf. Leaf length was measured from the tip of the acumen to the point where the leaf margin joined the petiole; width was measured at the widest point perpendicular to the midrib (Thomas & Ickes 1995). All leaves were measured to the nearest millimeter. For a sample of *ca* 90 randomly chosen leaves, we determined leaf area by drawing the shapes of the leaves on paper. The leaf images were scanned and then analyzed using an image-analysis program (Scion Image 4.2: Scion Corporation, Frederick, M.D.). Using the calculated areas and the original leaf lengths and widths, we fitted a regression equation to estimate leaf area for all the seedlings whose leaves were measured. The relationship between individual leaf area and the product of leaf length and width was linear and explained 99.5 percent of the variation in leaf area. Although there were significant differences among species in this relationship (ANCOVA *F*-tests for differences in intercepts and slopes with $P < 0.05$), these differences accounted for only 0.23 percent of the total variation in leaf area. Therefore, we used a single equation for all species combined to calculate leaf area: $LA = 0.696(L \times W)$, where *LA* is the area of individual leaf, *L* is leaf length and *W* is leaf width. The relationship found here is very similar to that observed by Thomas and Ickes (1995) for Malaysian species.

ROOTING DEPTH.—At the final harvest a hole was dug around a subset of randomly selected seedlings of two species (*K. anthotheca* and *E. utile*) until we reached the tip of the main root. The length of the taproot was then measured to the nearest centimeter.

LIGHT MEASUREMENTS.—To evaluate relationships between seedling performance and light availability, the light environments of randomly selected seedlings were assessed using hemispherical canopy photography. This technique estimates light availability on the basis of canopy architecture, thus having the advantage of estimating light availability over a long period of time (Rich *et al.* 1993). Hemispherical canopy photography has been widely used in ecological studies in temperate and tropical forests (Rich *et al.* 1993, Clearwater *et al.* 1999, Robinson & McCarthy 1999, Beaudet & Messier 2002). Photographs were taken using a digital camera

(Coolpix 950, Nikon Corporation, Japan) mounted with a fisheye lens (LC-ER1, Nikon Corporation, Japan). The camera was carefully leveled on a tripod and aligned with north before each use. Photos were taken directly over the top of individual seedlings or at a height of *ca* 60 cm (the minimum height of the camera plus the tripod) for smaller seedlings. For seedlings ≥ 150 cm, the stem was moved away and the photograph was taken at the stem position. Photographs were preferentially taken during overcast sky conditions in August and September 2002 at the end of the growing period. For gap plots, one photograph was also taken at the center of each 2×2 m quadrat at the beginning of the experiment in March 2001 before the gaps were invaded by pioneer vegetation. All photos were directly downloaded onto a computer and analyzed using WinSCANOPY 2001a (Régent Instruments, Inc., Quebec, Canada), assuming standard overcast sky conditions with 50 percent diffuse and 50 percent direct radiation. Average yearly value of total photosynthetic photon flux density (PPFD, mol/m²/d) was used to assess relationships between light availability and seedling height growth.

DATA ANALYSIS.—Seedling growth rate analyses were undertaken for height, diameter, and the number of leaves. Relative growth rates (RGR) were calculated for height and diameter increment as follows:

$$RGR = \frac{\ln W_2 - \ln W_1}{t_2 - t_1},$$

where W_1 and W_2 represent height or diameter at time t_1 and t_2 , respectively. Treatment effects on seed germination and seedling performance attributes were evaluated using ANOVA with a split-plot design. Site was treated as a blocking factor. Seedling height and diameter, and the number of seedlings per plot were log transformed to equalize variances and produce nearly normal distributions (Sokal & Rohlf 1981). We employed censored regression to assess the relationships between light levels and seedling height growth. Censored regression was more appropriate in this case because we hypothesized that most seedling death was due to inadequate light levels. In a censoring model, all points below (or above) a certain threshold (censored points) are observed only by the value of the threshold (Schmid *et al.* 1994). For this study the threshold was zero, and all dead seedlings (censored points) were given the value of zero growth. This allowed the use of all the available data, which substantially improved the estimation of the relationship between light availability and seedling height growth relative to other regression models (model I or model II linear regressions).

RESULTS

SEED GERMINATION.—Germination was studied for two species, *K. anthotheca* and *E. utile*. Overall germination rate was 31 percent (299 germinants out of 960 seeds sown). The germination of *K. anthotheca* seeds began 2 weeks after seeding, but *E. utile* seeds did not emerge before 3 full weeks. Seed germination extended over more than 10 weeks, but by the end of the 13th week all seeds were believed to have either germinated or died. Germination occurred earlier and seeds germinated faster in the forest understory than in gaps ($\chi^2 = 6.7$, $P = 0.035$). In the forest understory, 70 percent of germination occurred within the first 9 weeks compared to only *ca* 40 percent in gap

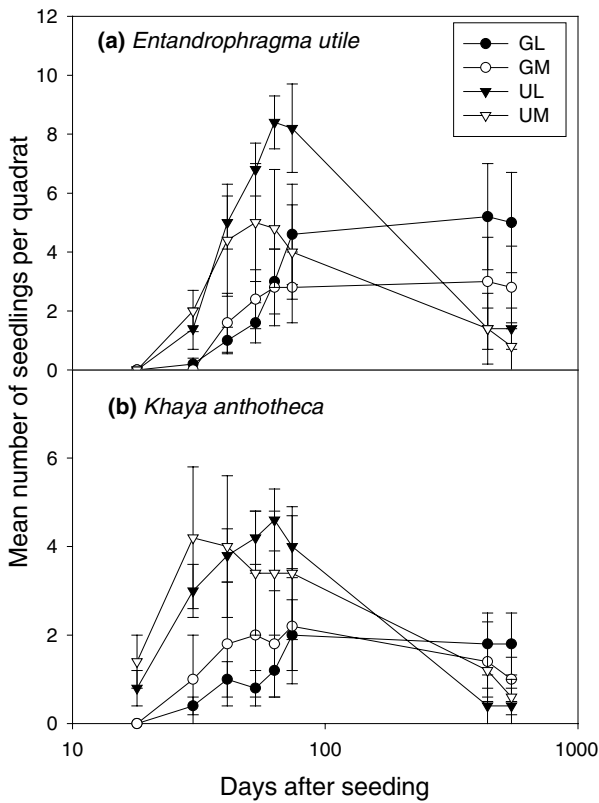


FIGURE 1. Temporal patterns of germination and seedling population decline of four treatment combinations at the Epulu study site. Triangles represent understory plots; circles gap plots. Open symbols represent exposed mineral soil, while filled symbols are for undisturbed forest floor. Thus GL: intact litter quadrats in gap plots; GM: exposed mineral soil quadrats in gap plots, UL and UM: intact litter and exposed mineral soil in understory plots.

plots. Germination rates were higher under closed canopy than in gaps (Fig. 1), but the difference in the ultimate number of germinants between gap and understory plots was not statistically significant ($F = 1.48$, $P = 0.255$). Contrary to our predictions, the total number of germinants was significantly greater on intact litter than on mineral soil 13 weeks after seeding ($F = 3.71$, $P = 0.020$), despite the fact that germination started earlier in the litter-removal treatment (Fig. 1).

In general, *K. anthotheca* seeds germinated earlier and faster than those of *E. utile* ($\chi^2 = 9.6$, $P = 0.008$), but the latter species had a higher number of germinants than the former, especially on gap plots. *K. anthotheca* had a much higher germination success on understory plots than in gaps ($F = 5.98$, $P = 0.037$), while *E. utile* showed significant differences in germination rate with regard to soil treatments ($F = 5.47$, $P = 0.031$), performing better on litter than on exposed mineral soil.

SEEDLING SURVIVAL.—Patterns of seedling survivorship were strongly influenced by species shade tolerance status (Table 2). The difference in survivorship with respect to light treatment (gap vs closed canopy) was very dramatic for the pioneer tree *N. diderichii*. Only 12.5 percent of the

TABLE 2. Seedling survival (%) of six timber tree species in northeastern Congo basin. Numbers in parentheses are standard errors of the means. Seedlings of *K. anthotheca* and *E. utile* germinated directly from seeds sown on the experimental plots and their survival rates were calculated as the proportion of the number of seedlings at 18 mo to the number of seedlings 11 weeks after seeding.

Species name	All plots			Species effects†
	Gap	Understory	Cover	
<i>Nauclea diderichii</i>	95.0 (3.3)	12.5 (4.2)	***	a
<i>Khaya anthotheca</i>	59.0 (12.3)	27.1 (10.2)	**	a
<i>Entandrophragma utile</i>	87.3 (5.4)	28.7 (11.7)	***	a
<i>Austranella congolana</i>	97.5 (2.5)	92.5 (5.3)	ns	b
<i>Entandrophragma cylindricum</i>	92.0 (4.4)	86.0 (6.7)	ns	bc
<i>Gilbertiodendron dewevrei</i>	79.0 (5.0)	88.0 (3.3)	ns	ac
Gap Plots				
	Litter	Mineral soil	Litter effects	Species effects
<i>Nauclea diderichii</i>	100.0 (0)	90.0 (6.1)	ns	a
<i>Khaya anthotheca</i>	47.2 (18.5)	58.8 (15.6)	ns	bc
<i>Entandrophragma utile</i>	80.2 (10.5)	93.1 (6.9)	ns	ac
<i>Austranella congolana</i>	100.0 (0)	95.0 (5.0)	ns	a
<i>Entandrophragma cylindricum</i>	92.0 (4.9)	92.0 (8.0)	ns	ac
<i>Gilbertiodendron dewevrei</i>	78.0 (6.6)	80.0 (8.4)	ns	ac
Understory Plots				
<i>Nauclea diderichii</i>	15.0 (6.1)	10.0 (6.1)	ns	a
<i>Khaya anthotheca</i>	22.5 (14.9)	45.0 (14.7)	ns	ad
<i>Entandrophragma utile</i>	39.5 (15.0)	35.5 (15.0)	ns	bd
<i>Austranella congolana</i>	95.0 (5.0)	90.0 (10.0)	ns	c
<i>Entandrophragma cylindricum</i>	88.0 (8.0)	84.0 (11.7)	ns	c
<i>Gilbertiodendron dewevrei</i>	88.0 (5.8)	88.0 (3.7)	ns	c

Significance level: ns $P > 0.05$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

† Survival rates of species with the same letter are not statistically different. Significance levels were adjusted for multiple comparisons using the Tukey–Kramer procedure.

seedlings of this species survived under canopy shade, whereas survival rate was very high in gaps (Table 2). Two other species, the nonpioneer light demanders *K. anthotheca* and *E. utile*, showed significantly greater survival rates in gaps. The very shade-tolerant *G. dewevrei* was the only species that showed a trend toward higher survival rates under forest canopy than in gaps. Seedling mortality of that species occurred mostly immediately after seedlings were transplanted from the forest understory into gaps. The effects of litter removal on postgermination seedling survival were not significant (Table 2).

SEEDLING GROWTH.—The growth of the two African mahogany species for which seeds were directly sown on the experimental plots was analyzed separately. For these species (*K. anthotheca* and *E. utile*) there was

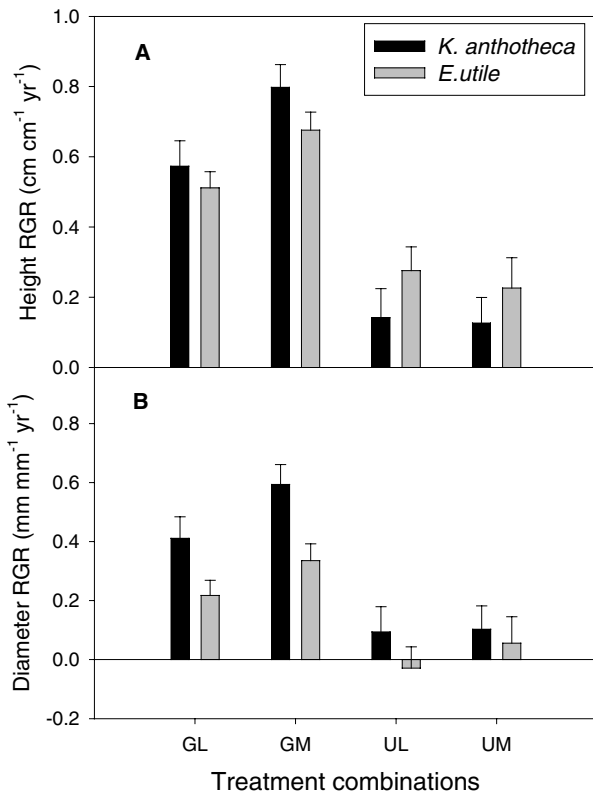


FIGURE 2. Seedling relative growth rates of two African mahogany species as a function of treatment combination. Errors bars are one standard error of the means. GL: intact litter quadrats in gap plots; GM: exposed mineral soil quadrats in gap plots, UL and UM: intact litter and exposed mineral soil in understory plots.

a significant effect of light availability on height relative growth rates (HRGR, $F = 71.8$, $P < 0.0004$). Litter removal increased HRGR, but its effects were only marginally significant ($F = 4.42$, $P = 0.074$). The interaction between light and litter was not significant ($F = 2.4$, $P = 0.12$), though the two species showed apparently different responses to light availability. *K. anthotheca* had higher HRGR than *E. utile* in gaps, whereas the latter had higher HRGR than the former under closed canopy (Fig. 2). Diameter relative growth rates (DRGR) showed similar patterns as HRGR with respect to light availability, and the three-way interaction (Light \times Litter \times Species) was significant ($F = 6.4$, $P = 0.014$). For both species, the best conditions for growth occurred on mineral soil under gap environments (Fig. 2).

The growth of planted seedlings exhibited the expected trend of higher performance in gaps than in the forest understory (Table 3). For both HRGR and DRGR there was significant variation among the four species, and the interaction between light treatment and species was also significant. In gaps, HRGR was the lowest for *E. cylindricum*, but this species had the highest HRGR in the forest understory. The pioneer *N. diderichii* had the highest DRGR of all the species in gaps, but it showed a negative and second lowest DRGR under closed canopy. *G. dewevrei* and *E. cylindricum* appeared to be more shade tolerant than the other

TABLE 3. Relative growth rates and leaf production of six African timber tree seedlings in gaps and under closed canopy in northeastern Congo basin. Numbers in parentheses are standard errors of the means.

Species	Height growth (cm/cm/yr)			Species [†]
	Gap	Understory	Cover	
<i>Nauclea diderichii</i>	1.24 (0.06)	0.1 (0.10)	***	a
<i>Khaya anthotheca</i>	0.69 (0.06)	0.12 (0.02)	***	b
<i>Entandrophragma utile</i>	0.60 (0.03)	0.25 (0.03)	**	ab
<i>Autranella congolana</i>	0.46 (0.04)	0.05 (0.01)	***	c
<i>Entandrophragma cylindricum</i>	0.29 (0.03)	0.14 (0.01)	***	c
<i>Gilbertiodendron dewevrei</i>	0.34 (0.03)	0.10 (0.01)	***	c
Diameter growth (mm/mm/yr)				
<i>Nauclea diderichii</i>	0.86 (0.06)	-0.002 (0.1)	***	a
<i>Khaya anthotheca</i>	0.49 (0.05)	0.09 (0.03)	***	ac
<i>Entandrophragma utile</i>	0.28 (0.03)	-0.02 (0.03)	**	b
<i>Autranella congolana</i>	0.21 (0.02)	0.07 (0.01)	***	bc
<i>Entandrophragma cylindricum</i>	0.25 (0.03)	0.13 (0.01)	**	a
<i>Gilbertiodendron dewevrei</i>	0.26 (0.02)	0.14 (0.01)	**	a
Change in the number of leaves				
<i>Nauclea diderichii</i>	10.5 (2.7)	-0.1 (1.1)	***	a
<i>Khaya anthotheca</i>	4.5 (0.5)	3.5 (0.7)	ns	a
<i>Entandrophragma utile</i>	5.2 (0.3)	5.7 (0.7)	ns	a
<i>Autranella congolana</i>	4.8 (0.6)	1.0 (0.3)	***	a
<i>Entandrophragma cylindricum</i>	0.7 (0.2)	0.9 (0.3)	ns	b
<i>Gilbertiodendron dewevrei</i>	2.0 (0.2)	0.4 (0.06)	**	b

Significance levels: ns $P > 0.05$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

[†]Growth rates of species with the same letter in each growth attribute are not statistically different (adjusted for pairwise comparisons using the Tukey–Kramer procedure).

species, exhibiting higher growth rates than the other species in the forest understory.

Leaf production was generally greater in gaps than in the forest understory and varied significantly among species (Tables 3 and 4). The two species of *Entandrophragma* showed a trend toward higher leaf production under closed canopy. The seedlings of these species produced many small and simple leaves in the understory, but fewer larger and/or compound leaves in gaps. There was a significant interaction between species and litter-removal treatment (Table 4). On average, *N. diderichii* produced more leaves on litter quadrats than on exposed mineral soil, whereas three other species (*A. congolana*, *K. anthotheca*, and *G. dewevrei*) produced more leaves on mineral soil than on litter quadrats. Leaf area production was strongly influenced by light availability and varied among species (Fig. 3). Leaf area had a strong positive correlation with seedling height growth regardless of species (Pearson's $r = 0.922$, $P < 0.0001$). Under gap conditions, the highest leaf area was observed in *N. diderichii*, which also showed the greatest HRGR, whereas *E. cylindricum* had the lowest values for both leaf area and height growth.

Aboveground biomass and the length of the taproot were measured for the two species whose seedling germinated directly from seeds

TABLE 4. ANOVA table of the treatment effects on seedling growth attributes. All six species were included in the analysis. Cover type (gap vs understory) was the whole plot treatment, whereas litter removal was the subplot treatment. "Species" was treated as a treatment factor.

Effects	Height growth		Diameter growth		Leaf production	
	F	P-value	F	P-value	F	P-value
Cover	257.7	<0.0001	77.7	0.0009	24.9	0.0075
Litter	0.1	0.7613	1.6	0.2802	2.9	0.1616
Species	19.5	<0.0001	11.3	<0.0001	30.3	<0.0001
Cover × species	12.5	<0.0001	17.6	<0.0001	13.7	<0.0001
Cover × litter	1.5	0.2169	0.3	0.611	0.1	0.7507
Litter × species	2.0	0.0731	0.6	0.389	3.1	0.0096
Cover × litter × species	1.9	0.0921	0.9	0.4605	0.8	0.5566

(*K. anthotheca* and *E. utile*). Both growth attributes showed similar patterns, the two species performing better in gaps than in the understory and *K. anthotheca* doing relatively better than *E. utile* (Fig. 4a,b). The difference in biomass and rooting depth between gap and understory plots was more pronounced for *K. anthotheca* than for *E. utile*. Leaf area ratio (LAR) was greater for understory seedlings than for gap seedlings, but the difference was significant only for *K. anthotheca*, for which LAR was more than twice as high in understory as in gap seedlings (Fig. 4c).

SEEDLING LIGHT RESPONSE.—Seedling light environment was highly variable both between and within canopy cover type (Table 5). Estimated

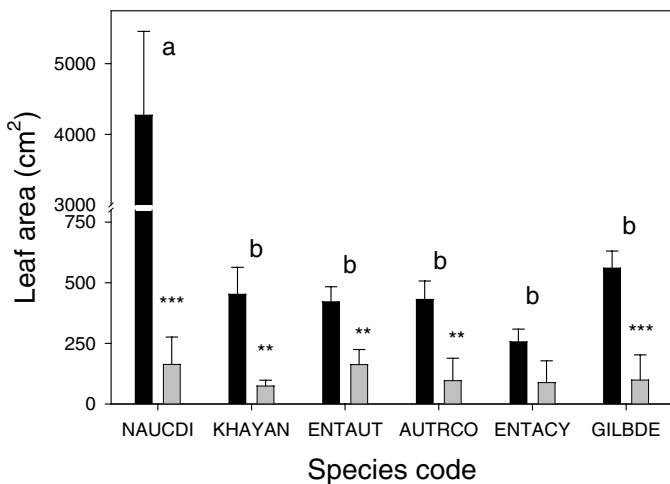


FIGURE 3. Leaf area of the seedlings of African timber trees grown in gaps and in the forest understory for 18 mo. Species codes as follows, NAUCDI: *Nauclea diderichii*, KHAYAN: *Khaya anthotheca*, ENTAUT: *Entandrophragma utile*, AURCO: *Austranella congolensis*, ENTACY: *E. cylindricum*, GILBDE: *Gilbertiodendron dewevrei*. Significance levels for cover effects (gap vs understory): * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Species with the same letter are not significantly different.

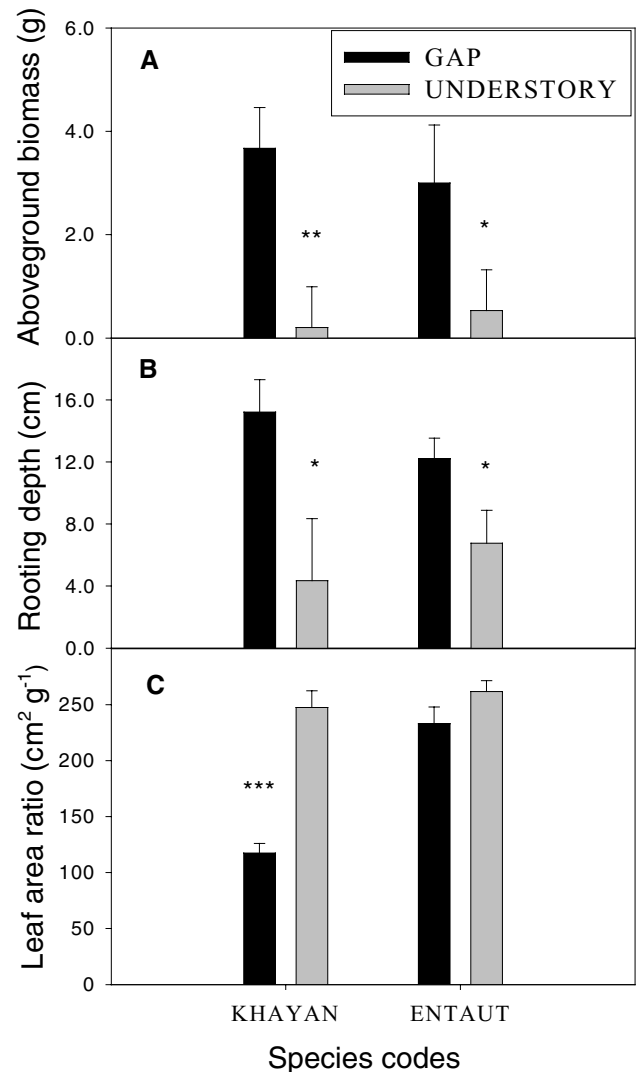


FIGURE 4. Aboveground biomass (a), rooting depth (b) and leaf area ratio (c) as a function of light treatment in the seedlings of two species of African mahogany. Labels on the horizontal axis as follows, KHAYAN: *Khaya anthotheca*; ENTAUT: *Entandrophragma utile*. Significance levels for cover effects: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

light availability ranged from 1.94 mol/m²/d (or 3.7% of full sunlight) to 27.74 mol/m²/d (53% of full sunlight). The average potential light availability observed for the clearings was more than twice that of gap sites and three times the average potential light availability of understory sites. For gap sites, estimated light availability changed considerably during the duration of the experiment. Average potential light availability of gap sites decreased from 15.96 mol/m²/d in March 2001 to 8.25 mol/m²/d in September 2002. This decrease in light availability in most part is due to the invasion of gaps by pioneer vegetation that overtopped seedlings of all species, with the exception of *N. diderichii*.

All the six species examined showed the expected trend of increased growth with increasing light availability (Fig. 5). The relationship was tight for *K. anthotheca* ($R^2 = 0.81$), *N. diderichii* ($R^2 = 0.78$), and

TABLE 5. Seedling light environment in gaps and under closed canopy in northeastern Congo basin. Light measures were also taken in two small clearings where seeds of *K. anthotheca* and *E. utile* were planted. All figures are estimated photosynthetic photon flux density (PPFD, mol/m²/d).

Cover type	Mean (SE)	Minimum	Maximum
Clearing	17.52 (0.72)	5.93	27.74
Gap-2001	15.96 (1.97)	11.72	23.30
Gap-2002	8.25 (0.28)	2.14	20.67
Understory	5.85 (0.18)	1.94	8.79

E. utile ($R^2 = 0.70$). The remaining species showed relatively lower R^2 values (0.27–0.57). The slope of the regression of seedling height increment on light availability varied among species. The regression coefficient was the lowest for *E. cylindricum* (1.6 cm/yr/mol/m²/d), indicating a lower increase in seedling height growth with increasing light availability, and intermediate for *K. anthotheca* (7.0), *Autranella* (4.3), *E. utile* (4.4), and *G. dewevrei* (3.3). The regression slope for the pioneer *N. diderichii* (26.5) was 16 times higher than that of *E. cylindricum*, indicating a much stronger response to increased light availability in *N. diderichii*. In general, the more light demanding a species, the higher its regression slope, with the notable exception

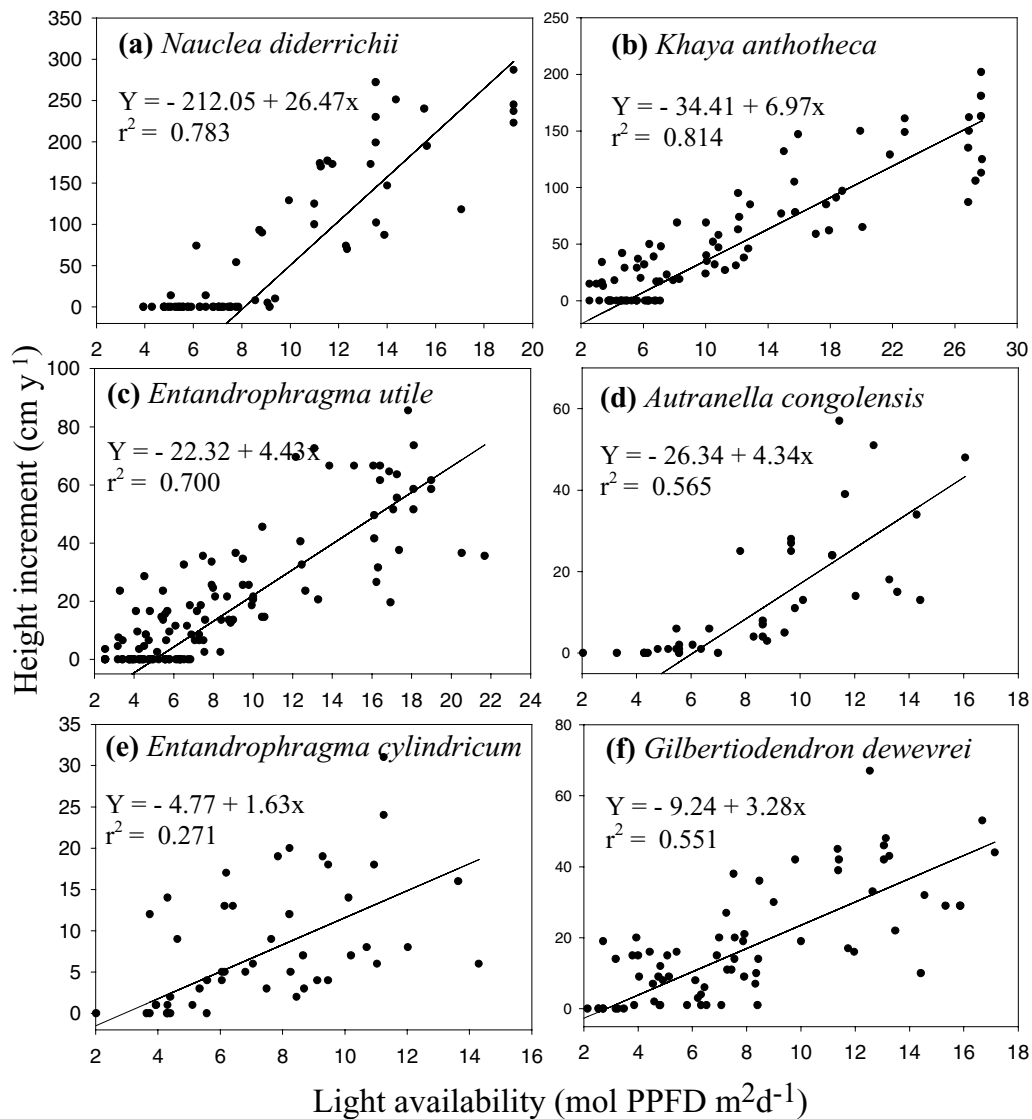


FIGURE 5. Relationships between height growth and light intensity for six species of African timber tree seedlings. Light measurements were made using hemispherical photography, and censored regression was utilized to model the relationship between seedling growth rates and irradiance.

of *G. dewevrei*, which exhibited higher light growth response than *E. cylindricum*, despite its high shade tolerance.

The value of light level at which seedling height increment was expected to be equal to zero (the x-intercept) was calculated for each species. This estimate of the minimum average daily light requirement for seedling maintenance may provide a useful measure of species shade tolerance in natural conditions, allowing quantitative comparisons among species. *Khaya anthotheca* and *E. utile*, the two species for which seeds were directly sown in the plots, were examined separately because their growth may still be dependent on seed reserves and, therefore, these species may exhibit lower values of the minimum light requirement compared to other species. Among the planted seedlings, *G. dewevrei* showed the lowest value of the minimum light requirement for seedling maintenance (2.8 mol/m²/d), indicating a higher shade tolerance than all the other species. The second lowest value was observed for *E. cylindricum* (2.9 mol/m²/d), whereas *N. diderichii* exhibited the highest value of minimum light requirement (8.0 mol/m²/d), indicating that the species is strongly light demanding. Seedlings of *N. diderichii* survived poorly under closed-canopy conditions and many of the surviving seedlings showed negative growth. Seedlings of *K. anthotheca* and *E. utile* generally showed lower values for minimum light requirement than *A. congolana* (6.1), despite the well-established light-demanding status of the former, suggesting that seedlings of *K. anthotheca* and *E. utile* were probably still benefiting from seed reserves. X-intercepts were 4.9 and 5.0 per mol/m²/d for *K. anthotheca* and *E. utile*, respectively.

DISCUSSION

LITTER REMOVAL AND SEEDLING ESTABLISHMENT.—One of the main hypotheses tested in this study was that litter removal improves seed germination and seedling establishment of tropical forest trees, particularly in shade-intolerant African mahoganies (*cf.* Snook 1996). The results of the litter-removal treatment did not support this hypothesis. Initial establishment was greater on intact forest floor than on exposed mineral soil, and seedling survival was only slightly higher on mineral soil as compared to intact litter. The observed improvement in seedling survival in response to litter removal was not strong enough to compensate for lower germination rates on mineral soil. Previous observational, as well as experimental studies on temperate and tropical trees have suggested that exposed mineral soil improves seed germination and seedling establishment (Pugnaire & Lozano 1997, Feller 1998, Sedláková & Chytrý 1999, Fredericksen *et al.* 2000, Karlsson & Örlander 2000, Harrington & Bluhm 2001). Exposed mineral soil is believed to be a better seedbed compared to litter because it provides good hydraulic contact between the seeds and soil particles, whereas litter impedes the penetration of radicles, thereby preventing contact with mineral soil (Kozłowski 2002). However, the requirement for exposed mineral soil may be more important for small-seeded tree species than for species with large seeds because the radicles of very small seeds may have difficulty penetrating even thin layers of leaf litter to reach mineral soil (Putz 1983, Molofsky & Augspurger 1992). The seed sizes of the two species used in the germination component of this study were relatively large (*ca* 250 mg for *K. anthotheca* and *ca* 350 mg for *E. utile*) compared to seeds of pioneer

species for which seedling establishment was improved by litter removal (*cf.* Molofsky & Augspurger 1992).

Although the ultimate results of the study did not support the hypothesis that litter removal positively affects seedling establishment, initial germination data were consistent with this hypothesis. Five weeks after seeds were sown the number of germinants was higher on mineral soil than on litter. We believe that the shift in the patterns of seedling abundance relative to the litter-removal treatment (Fig. 1) was mainly due to higher seed predation on mineral soil. Although we did not specifically quantify seed predation, seed counts during the first few weeks of the experiment revealed that the number of removed seeds was greater on exposed mineral soil than on litter (31% vs 26% of the total number of seeds) 4 weeks after seeding. The removal of all litter and organic matter could have made it easier for predators to locate seeds on mineral soil sites, resulting in lower germination success and establishment. The role of leaf litter in protecting seed and young seedling from mammalian seed predators has been experimentally demonstrated for two Amazonian tree species (Cintra 1997). These findings suggest that the potential positive effects of litter removal on seedling establishment of non-pioneer tropical trees may be offset by higher seed predation on exposed mineral soil. On the other hand, the effects of scarification on seed predation may be highly scale dependent: predators can destroy a large fraction of seeds in small experimental litter-removal plots such as those used in this study, whereas they may not have as large an impact if scarification is on an operational scale.

LIGHT GAP AND SEEDLING PERFORMANCE.—The effects of light on seed germination of nonpioneer tropical tree species are widely variable, but many species germinate better in shady environments and the germination of other species may be severely depressed at high light intensity (Baskin & Baskin 1998, Kyereh *et al.* 1999, Morris *et al.* 2000). The germination of the seeds of *K. anthotheca* and *E. utile* conformed to these observations. Although the germination rates of the two species were not statistically different between gaps and understory conditions, understory plots had over 40 percent more seedlings than gap plots 13 weeks after seed sowing. The germination of *K. anthotheca* was more negatively affected by high light than that of *E. utile*. Kyereh *et al.* (1999) observed that optimum irradiance level for the germination of *K. anthotheca* was ≤ 2 percent of full sunlight, while that of *E. utile* was between 30 percent and 50 percent of full sunlight. The flat seeds of *K. anthotheca* are likely more liable to desiccation than *E. utile* seeds.

The growth of tropical tree seedlings generally shows a strong positive relationship with light availability (*e.g.*, Oberbauer & Strain 1985, Ashton 1995, Agyeman *et al.* 1999), with pioneer trees having a much higher growth response to light intensity than shade-tolerant species (Veenendaal *et al.* 1996). Patterns of seedling survival and growth in this study were consistent with these previous findings, with greater seedling survival and growth in gaps than in the forest understory for all species. The magnitude of the difference in seedling performance between gap and understory sites varied widely among species, and was greater for shade-intolerant than for shade-tolerant species. The pioneer *N. diderichii* exhibited the highest growth response to light availability, having the highest height RGR in gaps and the lowest survival rate in the understory. In fact, this species showed negative growth in the forest

understory as expressed by a considerable loss of leaves as well as negative diameter RGR (see Table 3). *K. anthotheca* had the second greatest height growth rate of all species. Pieters (1977) classified this species as heliophytic (light loving), which is consistent with its requirement for full overhead light with side protection to grow to its full potential (Dupuy & Koua 1993). *Khaya anthotheca* is one of the first mature forest trees to colonize open areas such as abandoned farmlands (J.-R. Makana & S. C. Thomas, pers. comm.). Seedlings of *E. utile* also appeared to be light demanding: they had negative diameter growth and a much lower aboveground biomass under closed canopy compared to their performance in gaps. Earlier investigations on the growth of *E. utile* suggest that the species requires 50–90 percent of full sunlight for optimum development (Catinot 1965 in Lamprecht 1989). Canopy gaps rapidly close during the first year after creation due to the growth of lianas complementing lateral extension of trees bordering the gap (Yavitt *et al.* 1995, but see van der Meer & Bongers 1996). We observed that gap closure, after 1 yr, reduced light levels approximately to the threshold of light-demanding species, but not of shade-tolerant species. Our results thus suggest that the rapid closure of canopy gaps (*cf.* Table 5) is a silvicultural bottleneck for the successful establishment of light-demanding species in logged forests.

Gilbertiodendron dewevrei and *E. cylindricum* exhibited unexpected growth responses to light availability. The former is one of the most shade-tolerant canopy tree species in Central Africa (Gérard 1960, Richards 1996), but it showed a greater response to increased light availability than *E. cylindricum*, which showed the lowest growth rate under gap conditions as well as the poorest relationship with irradiance in spite of it being previously classified as light demanding (Hawthorne 1993, Kobe *et al.* 1995, Sheil *et al.* 2000). *E. cylindricum* is the most common *Entandrophragma* species in Central and West Africa (Sheil *et al.* 2000, Treue 2001, Hall 2002) and is well represented in the understory of the studied area. Thus, it appears that *E. cylindricum* is probably much more shade tolerant than previously thought (*cf.* Hall *et al.* 2003).

The unexpected strong light growth response observed for *G. dewevrei* may partly help to explain the striking dominance of this species in the rain forests of Central Africa. The leaf area response to light availability (Fig. 3) of *G. dewevrei* in canopy gaps was second only to that of the fast growing pioneer *N. diderichii*. A rapid growth in response to increased light availability due to canopy opening would confer a major advantage in interference competition for light to *G. dewevrei*. Given its prolific reproduction and its seedlings' tolerance to deep shade (Hart 1995, Richards 1996), which result in the formation of a considerable seedling bank in the understory, a rapid growth in response to increased light availability may allow *G. dewevrei* to outcompete all other late-successional tree species during gap recolonization, thus increasing or strengthening its dominance with the creation of each new gap.

INTERACTIVE EFFECTS OF LIGHT GAP AND LITTER REMOVAL ON SEEDLING PERFORMANCE.—The simultaneous occurrence of canopy gaps and soil disturbance (litter removal) positively influenced the early performance of seedlings of *K. anthotheca* and *E. utile*. In gaps, seedlings survived and grew better on mineral soil than on intact litter. The seedling height RGR of these two species was about 30 percent higher on mineral soil than on litter. This difference can likely be attributed to less competition on exposed mineral soil sites due to the removal of pre-existing vegetation, and therefore, greater availability of light and soil resources (water

and nutrients) for the newly established seedlings. When gap formation is accompanied by soil disturbance and the removal or destruction of existing understory vegetation, gaps are not only areas of increased light availability, but are also areas of reduced belowground competition (Gerhardt & Fredriksson 1995, Veenendaal *et al.* 1995, Fredericksen *et al.* 2000, Cahill & Casper 2002). This combination of environmental factors seems to have different effects on newly established seedlings than on seedlings established before gap formation (*cf.* Harrington & Bluhm 2001).

While the interactive effects of canopy gap and litter removal improved seedling survival and growth, they seemed to offer the least suitable conditions for the seed germination of *K. anthotheca* and *E. utile*. Seed germination of many nonpioneer timber trees is enhanced in shady and moist environments (Baskin & Baskin 1998, Morris *et al.* 2000). Germination may be severely suppressed in large gaps due to seed desiccation (Kyereh *et al.* 1999). The germination of *K. anthotheca*, which has flat seeds prone to desiccation, was severely depressed in gaps, but the germination of *E. utile* seeds was little affected. The removal of leaf litter from the soil surface, while offering better conditions for seedling establishment (Fredericksen *et al.* 2000), may also increase the probability of seeds being discovered by predators (Cintra 1997, Makana & Thomas 2004). As a silvicultural measure, litter removal or scarification will likely yield the best results if applied during or prior to a massive seed input, *i.e.*, mast fruiting, that satiates seed predators (see Karlsson & Örlander 2000).

In conclusion, the results of this study suggest that litter removal does not improve the seedling establishment of *K. anthotheca* and *E. utile* in the study region. We speculate that the poor seedling establishment observed after litter removal was primarily the consequence of higher seed predation on exposed mineral soil. An experiment involving predator exclusion is needed to test this hypothesis. As expected, the seedlings of all the species performed better in gaps than in the forest understory; however, we hypothesize that the growth of light-demanding species may be improved further by the creation of larger gaps, and that most of the studied species would benefit from weed control or liberation treatments.

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Queries

- Q1** Author: Please check the year in 'Welden *et al.* 1985.'
- Q2** Author: Please check table number here.
- Q3** Author: "Veenendaal *et al.* 1995" is not present in the list. Please check.
- Q4** Author: Please check if 'Dr. W. Junk' is the publisher.