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Dispersal limits natural recruitment of African mahoganies

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The abundance of forest tree species may be locally limited by the inability of species to disperse to all sites suitable for germination and establishment. This phenomenon of "dispersal limitation" has been suggested to promote the maintenance of high species diversity in tropical forests by slowing down competitive exclusion. We present the first direct experimental evaluation of dispersal limitation in tropical forests, and of its importance relative to other factors affecting recruitment. Seed addition, litter removal and light availability effects on seedling establishment were evaluated in a full factorial experiment on two African mahogany species, *Entandrophragma utile* and *Khaya anthotheca*. Seedling recruitment after 18 months, was ~22 times greater in seed addition treatments (with addition rates corresponding to the tail of seed shadows of large reproductive trees) compared to controls. This seed addition effect was an order of magnitude greater than either gap or litter removal effects, with similar results observed in both logged and primary forest locations. We conclude that dispersal limitation strongly limits seedling establishment for the two species studied. An important "applied corollary" of this result is that seed supplementation may substantially increase local abundance of valuable or rare species in disturbed or managed tropical forests.

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Dispersal limitation, or the failure for a given species to recruit in all sites suitable for its establishment, has been hypothesized to play an important role in structuring plant communities. The failure of propagules to reach all available sites may promote the maintenance of high species diversity by slowing down competitive exclusion (Tilman 1994, Hurtt and Pacala 1995, Hubbell 2001). Under dispersal limitation, many regeneration sites are won by default by species that are not necessarily the best competitors because superior competitors simply fail to disperse to those locations (Hubbell et al. 1999, Hubbell 2001). In tropical forest communities, several field studies have provided indirect support for dispersal limitation by showing that the composition of seedlings in canopy gaps closely reflected that of the adult communities around them (Dalling et al. 1998, Hubbell et al. 1999). However, contrasting results have been reported from an investigation in a faunally intact rain forest in Borneo, where local species richness of seedlings was not limited by the local species richness of adult trees (Webb and Peart 2001). The existence of evidence both for and against dispersal limitation in tropical forest trees calls for direct experimental investigations, comparable to studies in temperate forest and grassland communities (Primack and Miao 1992, Turnbull et al. 2000). A recent review by Turnbull et al. (2000) reported that approximately 50% of all plant species investigated in various seed addition experiments showed increased seedling recruitment in response to seed addition. However, species used in those studies were nearly all temperate herbaceous plants with relatively small seeds (Moles and Westoby 2002).

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Although dispersal limitation has attracted much interest because of its theoretical implications to plant community structure, composition and diversity (Tilman 1994, Hurtt and Pacala 1995, Hubbell 2001), it may also have practical management implications. It has been suggested that the regeneration failure of tropical timber trees is partly due to the limited availability of propagules, resulting from the removal of nearly all the large reproductive trees by logging (Plumptre 1995, Guariguata and Pinard 1998). Moreover, seed mortality can be very high in tropical forests as a result of seed predation by mammals, particularly rodents (Kasenene 1984, Basuta and Kasenene 1987, Guariguata and Pinard 1998), and attacks by seed-borers (Eggeling and Harris 1939, Hart 1995) or fungal diseases (Augspurger 1984).

In this paper, we present results from an experimental seed addition study on two important African timber tree species: *Entandrophragma utile* (Dawe & Sprague) Sprague and *Khaya anthotheca* (Welw.) C. DC. We hypothesized that seedling establishment of both species is hindered by limited seed dispersal (Medjibe and Hall 2002) and that seed addition would thus increase seedling establishment. Along with seed availability, the availability of suitable recruitment sites is believed to be responsible for poor regeneration of valuable timber trees in logged tropical forests. Studies in the neotropics suggest that mahogany (*Swietenia* spp.) primarily regenerates after severe disturbances, such as hurricanes, fires or flooding, that create large canopy openings and remove most of the existing vegetation and litter on the forest floor, exposing bare mineral soil (Lamb 1966, Boot and Gullison 1996, Gullison et al. 1996, Snook 1996). To assess the importance of site characteristics on the establishment of African mahogany, we also incorporated light availability and litter removal treatments in the present study.

Methods

The species

Both *E. utile* and *K. anthotheca* are large deciduous trees belonging to the family Meliaceae, to which also belong the more widely known new world mahoganies in the genus *Swietenia*. *E. utile* and *K. anthotheca* occur throughout west and central Africa to western Uganda (Eggeling and Harris 1939). *Khaya anthotheca* produces erect woody capsules that dehisce from the apex into 4 valves. Seeds are generally dispersed from December to March. The pendulous capsules of *E. utile* dehisce into 5 valves and disperse seeds from January to March when trees are leafless. Seeds of both species are commonly attacked by seed-boring beetles or eaten by small rodents. On average seeds of *E. utile* are ~9.5 cm long and 2 cm wide and weigh ~350 mg (including the long papery wing); those of *K. anthotheca* are 4 cm long and 2.5 cm wide and they weigh ~250 mg.

Although both species have been proposed for inclusion in CITES appendix I or II, neither of them has actually been listed in CITES appendices due to insufficient information on regeneration, extent of plantations, and sustainability under current management regimes (WCMC 2002)

Study sites

The study was conducted in a 17-year old logging concession located 25 km northwest of the town of Beni (0°45″N latitude, 29°15″E longitude) and in primary forest in the Epulu sector of the Ituri Forest (1°25″N and 28°38E) in northeastern Democratic Republic of Congo. The elevation in the region varies from 750 m to ~1000 m above sea level. Mean annual rainfall in Beni is 1639 mm and 1725 mm in Epulu. 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 at both sites is 23–25°C and varies little through the year.

The vegetation in the region is a mixture of evergreen forest, including extensive areas of "mbau forest" dominated by *Gilbertiodendron dewevrei* (De Wild.) Léonard, and "mixed forests" in which no species is predominant, but other Caesalpinoid legumes, such as *Julbernardia seretii* (De Wild.) Troupin and *Cynometra alexandri* C. H. Wright, are abundant (Makana et al. 1998). At the eastern edge of the region, evergreen forests grade into a semi-deciduous forest whose canopy is dominated by light-demanding tree species that include *Entandrophragma* spp. (Meliaceae), *K. anthotheca* (Meliaceae), *Albizia* spp. (Mimosaceae) and *Canarium schweinfurthii* Engl. (Burseraceae). Evergreen mixed forest is the main vegetation type in Epulu, while semi-deciduous forest prevails at the Beni site.

Data collection and analysis

The overall study design involved a replicated, factorial combination of seed addition (seeds added vs no seeds), litter removal (intact litter vs mineral soil), and gap environment (gap vs understory locations). Four 2 × 2 m quadrats separated by a 0.5 m buffer constituted a plot. Within each plot, all litter and organic matter were removed on two randomly selected quadrats, exposing mineral soil. The other two quadrats were left untouched. Twelve locally collected seeds of each species were uniformly dispersed on one of each litter treatment quadrat. The whole experimental unit was replicated 10 times in gaps and paired closed-canopy understory locations to evaluate the effects of light availability on seedling establishment. Plot locations were thus dependent on the presence of a gap in mature forest, but were otherwise situated uniformly through the study areas and did not systematically avoid potential parent trees of either study species. Only two plots were closer than 50 m of reproductive trees of *K. anthotheca*. Eighteen months after seeding we counted the number of surviving seedlings in each quadrat.

To estimate seed dispersal distances from parent trees, *K. anthotheca* seeds were counted in 2.5 × 1 m quadrats along 50 × 1 m transects departing from the base of three isolated seed trees in the four cardinal compass directions. To quantitatively describe the seed shadow, we fit an exponential decay model for points ≥ 8 m from the base of the tree (beyond the tree crown).

Seedling survival rates were calculated in two different ways. First, we calculated absolute survival rates as the proportion of surviving seedlings with respect to the initial population size for two time intervals: from seeds to 11-week old seedlings, and from 11-week old seedlings to 18-month old seedlings. Second, to better enable comparisons with other studies we estimated the rate of population decline for the latter interval using the exponential mortality coefficient γ as $\ln(N_0/N_1)/t$, where N_0 and N_1 are population counts at the beginning and the end of the measurement interval t (Sheil et al. 1995).

Because there were seldom any seedlings in quadrats that received no seeds, we used logistic regression to statistically evaluate the effects of seed addition and other treatment factors on seedling establishment. For this purpose, seedling abundance was tallied into three categories: 0 for no seedling, 1 for quadrat with 1 to 6 seedlings, and 2 for quadrats with more than 6 seedlings. Statistical analyses were conducted using SAS v. 8.1.

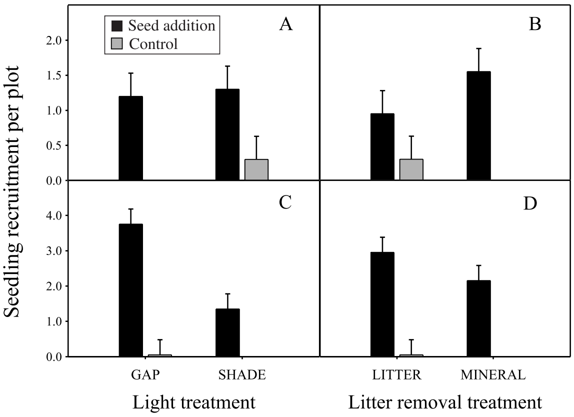

Fig. 1. Mean numbers of seedlings per quadrat for two African mahogany tree species (A, B *Khaya anthoteca*; C, D *Entandrophragma utile*) in an experiment involving seed addition, litter removal and canopy cover in northeastern Congo Basin. Values plotted are least squares means + 1 SE. A set of four 2 × 2 m quadrats separated by 0.5 m buffers were located in gaps and nearby closed canopy understory. All litter and organic matter were removed from two randomly selected quadrats while it was left intact in the remaining ones. Twelve seeds of each of two African mahogany species were uniformly dispersed in one of each litter removal treatment quadrat.

Results

At 18 months after seeding, the total pooled establishment rate across treatments was 15.8% or 152 seedlings out of 960 seeds sown. Preliminary analyses showed that similar experimental results were obtained for both the primary forest and logging concession sites (data not shown), so further analyses pooled all data across sites. Seed addition had a highly significant effect on seedling establishment ($\chi^2 = 28.3$, $p < 0.0001$), with seedling densities in seed addition plots averaging ~22 times those in controls (Fig. 1). The gap vs understory main effect term was also significant ($\chi^2 = 5.14$, $P = 0.0234$), with seedling densities 69% higher in gaps than understory locations. There were more seedlings on gap plots than on plots under closed canopy, mainly due to the response of *E. utile* (Fig. 1). The litter removal main effect term was not significant ($\chi^2 = 0.09$, $P = 0.3480$). However, the interaction between the species and the litter removal treatment was almost significant ($P = 0.070$), due to the contrasting behavior of the two species with respect to this treatment. *K. anthoteca* showed higher establishment rates on mineral soil whereas *E. utile* did better on litter (Fig. 1). Seeds of *E. utile* are larger than *K. anthoteca* seeds, and they were probably more preyed on by rodents on mineral soil quadrats where they were more conspicuous.

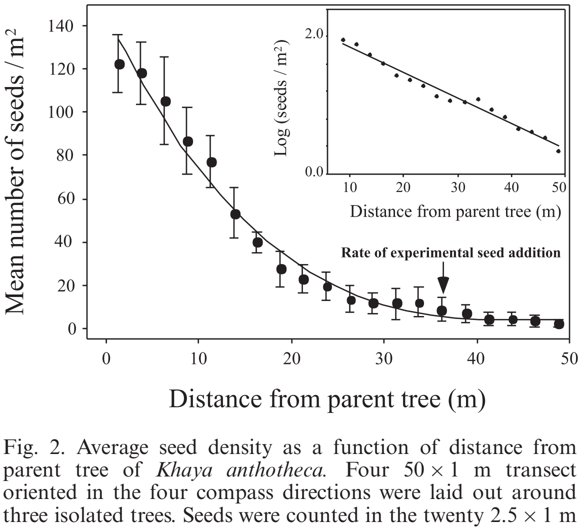

Fig. 2. Average seed density as a function of distance from parent tree of *Khaya anthotheca.* Four 50 × 1 m transect oriented in the four compass directions were laid out around three isolated trees. Seeds were counted in the twenty 2.5 × 1 m quadrats of each transect. The insert represents the decrease of seed density with distance from the tree beyond tree canopy (≥ 8 m from tree base). The regression equation is $y = 2.22 - 0.037x$ and $r^2 = 0.981$.

Our data indicate that maximum dispersal distance for *K. anthotheca* is over 50 m, with an average seed input of 2 seeds m^{-2} at this distance (Fig. 2). An exponential decay model produced a very good fit of the decrease of seed density with distance from parent tree beyond tree crown ($r^2 = 0.981$, $P < 0.0001$). Using this model, we estimated that average seed density falls below 1 seed m^{-2} at 60 m from parent tree, and that ~75% of all the seeds were dispersed within 30 m of the parent tree for *K. anthotheca*. The rate of seed addition used in the experiments (6 seeds m^{-2}), thus corresponds to a distance of ~36 m from parent trees, or roughly 4.5 times the crown radius of the largest trees surveyed. Seeds of both *K. anthotheca* and *E. utile* were observed more than 100 m away from any seed-producing tree.

Table 1 shows seedling performance parameters in gap and understory conditions. Seedling height growth was higher in gaps than in the forest understory for both species. On average, the 10 tallest of the seedling population in gaps were two and half times taller than those of the understory population. Survivorship significantly increased from seeds to 11-week old seedlings (Table 2), especially in gap plots. Under gap conditions, seed survival and initial seedling establishment of *E. utile* (to 11 weeks) was reduced by litter removal. In contrast, later seedling survival in *E. utile* was improved by the litter removal. The opposite patterns were observed for *K. anthoteca* (i.e. litter removal resulted in decreased seed survivorship, but increased seedling survivorship). In understory plots, litter removal had a negative effect on seed survival in both species, a positive effect on post-germination seedling survival in *E. utile*, but a negative effect on post-germination seedling survival in *K. anthoteca*.

Discussion

Although dispersal limitation has been experimentally demonstrated in numerous short-lived herbaceous plants (Turnbull et al. 2000), this study is the first experimental demonstration of its existence in tropical forest trees. Seedling recruitment after 18 months was ~22 times higher in seed addition than control plots, an effect that was an order of magnitude larger than that of either the presence of treefall gaps, or of mineral soil exposure. The smaller effects of gap and litter removal effects on recruitment also showed complex interactive effects that varied with species and ontogenetic state. Our findings thus support theoretical models that suggest that local distribution and abundance of tropical tree species is strongly limited because species are unable to disperse to unoccupied sites that otherwise would be suitable for their establishment (Tilman 1994, Hurtt and Pacala 1995, Hubbell 2001). The rate of seed addition used in this study is equivalent to 6 seeds m^{-2}, or the rate of addition at roughly 35–40 m from the parent tree, well into the tail of the seed shadow (Fig. 2). This is thus not an excessive rate of seed supplementation, but rather similar to the average rate that would naturally occur if the trees were relatively evenly dispersed and made up 1–2% of the canopy tree population.

Although seed addition effects were dominant, this study also confirms earlier observations that African mahogany species are strongly light-demanding during seedling establishment stages (Eggeling and Harris 1939, Pieters 1977, Swaine and Whitmore 1988). First, seedlings of the both species survived better in gaps than under closed canopy (86.7% vs 24.5% and 59.0% vs 36.9% for *E. utile* and *K. anthoteca*, respectively). Second, despite the presence of many surviving seedlings under closed canopy, only seedlings located in gaps that were not completely overtopped by herbaceous and pioneer vegetation showed substantial height growth. Most seedlings in the forest understory were stunted and many were showing clear signs of negative growth (leaf and/or leader loss). Thus if one intends to use seed supplementation as a means to promote seedling recruitment for African mahogany species, care must be taken

Table 1. Mean seedling height of two species of African mahogany in a seed addition experiment in northeastern Congo basin. Figures are least square means (standard errors).

Species name	Mean height (cm)		Mean height of the 10 tallest seedlings (cm)	
	Gap	Understory	Gap	Understory
Entandrophragma utile	29.5 (1.2)	16.5 (2.2)	48.5 (2.7)	18.6 (2.9)
Khaya anthotheca	34.7 (2.0)	16.4 (2.1)	48.9 (2.9)	18.6 (2.7)
Gap plots	Litter	Mineral soil	Litter	Mineral soil
Entandrophragma utile	26.7 (1.5)	32.0 (1.8)	44.8 (4.3)	52.3 (3.5)
Khaya anthotheca	32.0 (3.0)	37.4 (2.6)	52.0 (4.9)	45.9 (3.2)
Understory plots	Litter	Mineral soil	Litter	Mineral soil
Entandrophragma utile	16.9 (2.7)	16.0 (3.4)	19.1 (3.2)	18.0 (4.9)
Khaya anthotheca	16.8 (2.3)	16.0 (2.7)	19.0 (4.3)	18.2 (3.5)

Table 2. Seed and seedling survival of two African mahogany species in northeastern Congo Basin. Seed survival rate was calculated as the proportion live seedlings 11 weeks after seed addition to the number of seeds added; and seedling survival as the proportion of the number of seeds at 18 months to the number of seedlings 11 weeks after seed addition.

Species name	Seed survival (%)		Seedling survival (%)		Exponential mortality coefficient (y^{-1})	
	Gap	Understory	Gap	Understory	Gap	Understory
Entandrophramga utile	33.3	31.7	85.0	36.8	0.125	0.768
Khaya anthotheca	16.7	30.4	57.5	39.7	0.426	0.710
Gap plots	Litter	Mineral soil	Litter	Mineral soil	Litter	Mineral soil
Entandrophramga utile	39.2	27.5	74.5	100.0	0.227	0.000
Khaya anthotheca	12.5	20.8	60.0	56.0	0.393	0.446
Understory plots	Litter	Mineral soil	Litter	Mineral soil	Litter	Mineral soil
Entandrophramga utile	41.7	21.7	40.0	30.8	0.705	0.907
Khaya anthotheca	35.0	25.8	31.0	51.6	0.902	0.509

to increase the likelihood of seeds landing onto sites suitable for seedling establishment. Suitable sites comprise areas with an appropriate substrate for seed germination and sufficient amount of solar radiation to allow young seedlings to maintain high levels of photosynthesis (Kozlowski 2002). For African mahogany trees such sites may include logging gaps and abandoned farmlands.

The potential application of seed addition to forest management and biodiversity conservation however requires that we ask what the likelihood is that the increase in seedling recruitment would lead to any change in the density of adult trees given the high seedling mortality in tropical forests (De Steven and Putz 1984, Struhsaker 1997). One cannot follow the entire life history of long-lived trees in this kind of experiment. However, it is reasonable to argue that, other things being equal, an increase in seedling recruitment will result in an increase in adult tree density. Seedling survival of the species involved in this study was quite high in gap environments during the early stages of establishment and should be expected to increase as seedlings grow larger (Silvertown and Lovett Doust 1993). Survival of mahogany saplings (1–4.9 cm dbh) in four 10-ha plots of undisturbed mature forest in the region was ~90% for a 6-year period, which is equivalent to an exponential mortality coefficient of 0.018 (J.-R. Makana, unpubl.). Given this mortality estimate, for every 1000 seeds added in gaps it is expected that 1.3 individuals of *K. anthoteca* and 47.7 individuals of *E. utile* would be alive after 10 years.

Because of frequent regeneration failure of important timber species after logging (Struhsaker 1997, Kammesheidt 1998, Mostacedo and Fredericksen 1999), many studies on the sustainable management of tropical forests for timber production recommend that a substantial number of seed trees should be left after logging to ensure natural regeneration, and that those trees should be evenly dispersed in the forest stand (Plumptre 1995, Guariguata and Pinard 1998). This recommendation is clearly unrealistic for African mahogany tree species because the densities of adult trees of these species are already very low (less than 2 trees per ha) in most undisturbed forest areas (J.-R. Makana, unpubl.). Our results suggest that while seed availability can limit seedling establishment, seed addition has the potential to reverse the situation, in spite of high seed and seedling predation. In the absence of natural regeneration of important timber trees, enrichment planting is the usual alternative. However, this technique generally involves high costs in nursery maintenance and field labor that can be too expensive for forest managers in tropical forests (Appanah and Weinland 1993, Guariguata and Pinard 1998). Moreover success is not completely guaranteed as planted seedlings may be out-competed by herbaceous vegetation and lianas (Struhsaker et al. 1996) in the absence of sustained tending.

We suggest that a much more efficient alternative to natural regeneration and/or enrichment planting may be the addition of seeds at favorable sites over the targeted area. Seeds can easily be collected annually for most African mahogany species in the region, including *K. anthoteca* and most species of *Entandrophragma*. Further research on these species' reproduction, seed biology, and demography in post-logged forests is needed to fully evaluate such an approach. More broadly, if dispersal limitation is indeed of primary importance in structuring tropical tree communities, then targeted additions of seeds and other propagules may generally offer an effective tool for improving sustainability and mitigating anthropogenic impacts in these most diverse ecological systems.

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