

## Recruitment limitation after mast-seeding in two African rain forest trees

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**Abstract.** Seed and establishment limitation can have a major role in determining plant species' abundances and distributions in communities. Their relative importance, however, remains uncertain and controversial, especially for trees in forests where density-dependent mortality of seeds and seedlings may be common. In a primary African rain forest, we directly tested the strength of each limitation by using seeds of the tree species *Microberlinia bisulcata* and *Tetraberlinia bifoliolata* at eight addition levels and by following establishment over six weeks. Local background seed rain was also measured. Seedling recruitment was higher in seed-addition quadrats than in control quadrats, indicating seed limitation in both species. However, fitting the Beverton-Holt model indicated that establishment limitation was consistently 2–4 times stronger than seed limitation for *Microberlinia*, whereas seed limitation greatly exceeded establishment limitation for *Tetraberlinia*. Strong density dependence was operating in the short seed-to-seedling transition for *Microberlinia*, whereas it was almost negligible for *Tetraberlinia*. Although early postdispersal mortality was very high for both species (>80%), they may achieve local codominance as a result of differing strengths of seed limitation vs. establishment limitation. Assessing the importance of seed limitation for tree populations requires a knowledge of species-specific seed rain as well as a reliable recruitment function. The outcome of early establishment processes also needs to be seen in the context of later stages of tree dynamics.

**Key words:** Beverton-Holt function; Caesalpiniaceae; density dependence; establishment limitation; Korup National Park, Cameroon; *Microberlinia bisulcata*; postdispersal mortality; seed limitation; seedling recruitment; *Tetraberlinia bifoliolata*; tropical lowland rain forest.

### INTRODUCTION

Seed limitation can leave plant populations “seed limited,” i.e., with fewer individuals than possible, because too few seeds arrive to recruit at all potential regeneration sites suitable for establishment (Nathan and Muller-Landau 2000, Turnbull et al. 2000). This factor can have profound consequences for neighborhood interactions because sites are not occupied by adults of the locally most competitive species, but instead by inferior ones. The outcome may reduce competitive exclusion, determine species' distributions, and perhaps promote diversity (Horn and MacArthur 1972, Tilman 1994, Hurr and Pacala 1995), processes that are important especially in the more species-rich forests of the tropics (Eriksson and Ehrlen 1992, Muller-Landau and Hardesty 2005, Svenning and Wright 2005). Another form of limitation concerns the availability of suitable microsites. It could be a more critical and powerful determinant of many communities (Kobe and Vriesendorp 2009). This factor, termed “establishment limitation” (Nathan and Muller-Landau 2000), can be

due to both abiotic and biotic interactions, acting in either a density-dependent or a density-independent manner. However, density-independent mortality alone in the absence of niche differentiation is unlikely to promote species coexistence, whereas negative density dependence can substantially enhance it (e.g., Harms et al. 2000). The brief transition from seed to established seedling is often when individuals are both most abundant and vulnerable to death (Swaine 1996), and, accordingly, it is seen as a critical stage in a tree's life history. Knowing the relative importance of seed limitation and then establishment limitation for different species' recruitment patterns (sensu Eriksson and Ehrlen 1992) appears to be essential to understanding local coexistence within plant communities.

The relative roles of seed and establishment limitation in tree communities may be determined by experimental manipulation. Indirect evidence gained from comparing seed or seedling spatial distributions and species richness with those of surrounding adults in a Panamanian rain forest supported a pivotal role for seed limitation (Dalling et al. 1998, 2002, Hubbell et al. 1999). The same conclusion, however, was not reached for another species-rich forest in Borneo (Webb and Peart 2001). Direct evidence is made possible, however, when propagules of given tree species are added to plots and counts of emerging seedlings (early recruitment) are

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compared to those in paired control plots with no seeds added (Turnbull et al. 2000). If adding seeds leads to a statistically significant increase in population recruitment, the species' local population is considered seed limited. This approach of just added vs. control has been pursued widely in temperate vegetation where ~50% of experiments, mostly focused on short-lived plants in grasslands, detected evidence of seed limitation (Turnbull et al. 2000). In central Africa, where Makana and Thomas (2004) conducted the first such direct test on tropical trees, seedling recruitment of the light-demanding *Entandrophragma utile* and *Khaya anthotheca* in canopy gaps and the understory was ~22 times greater in seed-addition treatments than in controls. Seed limitation was shown experimentally to be a major factor in the Panamanian site mentioned, in the seedling recruitment of 31 of 32 plant species in its understory community (Svenning and Wright 2005).

However, the importance of seed limitation has been recently critiqued and questioned by Clark et al. (2007) and Poulsen et al. (2007). These authors convincingly argue that the traditional framework used to evaluate evidence for seed limitation in plant communities remains too simplistic. Taking variable establishment into account is crucial to detecting the relative strengths of the two limitations. In their recent meta-analysis of seed-addition studies, three points emerged. (1) Because most studies used too few levels of seed additions ( $\leq 3$ ), they were incapable of estimating a complete recruitment function. (2) Although most species were seed limited, the effect on seedling recruitment was weak because most seeds did not live to become seedlings. (3) Tree studies were considerably underrepresented, those from tropics being particularly sparse.

Three considerations lead to improved seed-addition experiments: (1) local seed rain needs to be estimated; (2) the levels added ( $\geq 5$ ) should cover the range of natural seed densities at the site, with sufficient replication; and (3) a biologically grounded mathematical framework should describe the two nonmutually exclusive limitations. Poulsen et al. (2007) suggested such a framework for plants, modified from research on reef fish recruitment (Schmitt et al. 1999). The aim is to quantify both the extent of seed limitation ( $L_S$ ) and establishment limitation ( $L_E$ ) and, contributing to the latter, limitations arising from both density-dependent ( $L_{DD}$ ) and density-independent mortality ( $L_{DI}$ ). Note that  $L_E \neq L_{DD} + L_{DI}$  because of interactive effects. There are two key aspects to this quantification. (1) The recruitment function that relates seed arrival to seedling establishment is the asymptotic Beverton-Holt function  $R = P_0S / \{1 + [P_0S/R_{max}]\}$ ; see *Data analysis*. (2) Seed limitation is treated as a continuous variable defined as the difference between maximum potential recruitment ( $R_{max}$ ) and recruitment arising from seed rain ( $R_{amb}$ ). Apart from special cases of single-species forests, it would be surprising if any tree species were not seed limited at some spatial scale (Clark et al. 1998, McEuen and

Curran 2004, Kobe and Vriesendorp 2009). The framework based on the Beverton-Holt function has the advantage that it allows one to determine the contribution of both seed and establishment limitation to recruitment limitation.

We report here on a test of the relative importance of local-scale seed vs. establishment limitation of two mast-seeding, codominant African trees, *Microberlinia bisulcata* A. Chev. and *Tetraberlinia bifoliolata* (Harms) Hauman (Leguminosae). Their proximity to one another in the forest, combined with the fact that they often mast together, suggests that they are potential competitors for sites where they can establish as seedlings. Specifically, we asked the following questions. (1) Is early recruitment (defined as when seedlings have established) of *Microberlinia bisulcata* and *Tetraberlinia bifoliolata* limited by the availability of seeds? (2) What is the magnitude of seed limitation relative to establishment limitation? (3) How do different estimates of ambient seed rain change interpretations of (1) and (2)? (4) Is there evidence for conspecific adult neighborhood effects on recruitment? This work is the first direct test of seed limitation that combines many levels of seed addition with in situ estimates of ambient seed rain.

## METHODS

### *Study site and species*

The study area is in a lowland tropical rain forest in the southern part of Korup National Park, southwestern Cameroon (5°10' N, 8°70' E). It lies at 40–120 m above sea level on well-drained but acidic, nutrient-poor sandy soils (Gartlan et al. 1986). The climate is strongly seasonal, with a wet period between March and November and a distinctly dry one between December and February (rainfall ~5100 mm/yr; Newbery et al. 1998, 2006a).

*Microberlinia bisulcata*, *Tetraberlinia bifoliolata*, and a third species *Tetraberlinia korupensis* Wieringa, locally codominate to form large, distinct patches called groves (Newbery and Gartlan 1996, Newbery et al. 2004). Together they constitute ~70% of tree basal area (~50% and 85% of numbers of trees  $\geq 50$  and  $\geq 100$  cm stem diameter [measured at 1.3 m or higher to avoid buttresses and irregularities], respectively; Newbery et al. 1998). Although ranked first in both respects, *Microberlinia bisulcata*, however, is scarce in the <50 cm (especially 1–25 cm) diameter classes compared to the far more abundant *T. bifoliolata* and *T. korupensis* (Newbery et al. 1998; D. M. Newbery and X. M. van der Burgt, *unpublished data*). These ectomycorrhizal caesalpinaceous species share a mast-fruitletting cycle of 2–3 years, although not all three take part in every event (Newbery et al. 1998, 2006a). In 2007, the year of the present study, only *Microberlinia bisulcata* and *Tetraberlinia bifoliolata* masted. As the two species of interest, they will be referred to, henceforth, simply by their generic names (see Plate 1).

*Microberlinia* and *Tetraberlinia* produce discoid seeds that are ballistically dispersed from twisting pods on intermittent sunny days in August to October. Fallen pod valves persist on the ground for at least 6 months due to their tough, fibrous nature. Although similar in area, seeds of *Tetraberlinia* are thicker and heavier (1.57 g dry mass) than those of *Microberlinia* (0.64 g). Seeds of both species germinate very quickly under humid conditions (3–5 days) and neither species produces a seed bank.

#### Measuring local seed rain

To determine the range of seed-addition levels used in the experiment, on 28–29 August 2007 we set up 2–4 belts, each 1 m wide, on cardinal directions away from three trees each of *Microberlinia* and *Tetraberlinia* that had pods in their crowns and were relatively isolated from conspecifics. This was performed on a day following a major dispersal event. In 2-m intervals, belts were carefully searched for seeds by sifting through the litter. They extended until no seeds were found for 16–20 m. We found a maximum density of 33.5 and 22.5 seeds/m<sup>2</sup> for *Microberlinia* and *Tetraberlinia*, respectively. Moreover, in parallel sampling under a pair of adjacent *Microberlinia* trees, we found 95 seeds in one of 30 1.2-m<sup>2</sup> ground plots coming from a single dispersal event (equivalent to 79 seeds/m<sup>2</sup>). For this reason we included a high-density treatment of 96 seeds/m<sup>2</sup> to generate a complete recruitment function for this species. Seed densities were thus 96, 72, 50, 32, 18, 8, 4, and 2 seeds/m<sup>2</sup> for *Microberlinia* and 72, 50, 32, 18, 8, 6, 4, and 2 seeds/m<sup>2</sup> for *Tetraberlinia*.

#### Experimental seed additions

We added the variable densities of *Microberlinia* and *Tetraberlinia* seeds to square 0.49-m<sup>2</sup> quadrats between 15 and 20 September 2007. This timing corresponded to an overlap in the dispersal of both species. The *Microberlinia* population, however, was approaching completion whereas *Tetraberlinia* was at its peak in terms of the dispersal process. We installed the experiment in the eastern 25 ha of the main “P-plot” (82.5 ha) (Newbery et al. 1998). The 100 subplots (each 50 × 50 m) were divided into 10 blocks, 250 × 100 m each (N–S vs. E–W, respectively). Within each block two subplots were randomly selected to give 20 subplots for the experiment. Three subplots proved unsuitable because of very rocky and steep terrain or swampy conditions, and these were replaced with the nearest suitable subplot (one not adjacent to the others already chosen).

Within each subplot a primary 35-m line was centered on a random bearing (Fig. 1), under relatively shaded conditions (by not crossing any large gaps). At 5-m intervals, eight secondary 10-m lines bisected perpendicularly. At each of these secondary lines, two quadrats of area 0.49 m<sup>2</sup> (separated by 50 cm) were demarcated with wire flags. Freshly fallen seeds of each species had

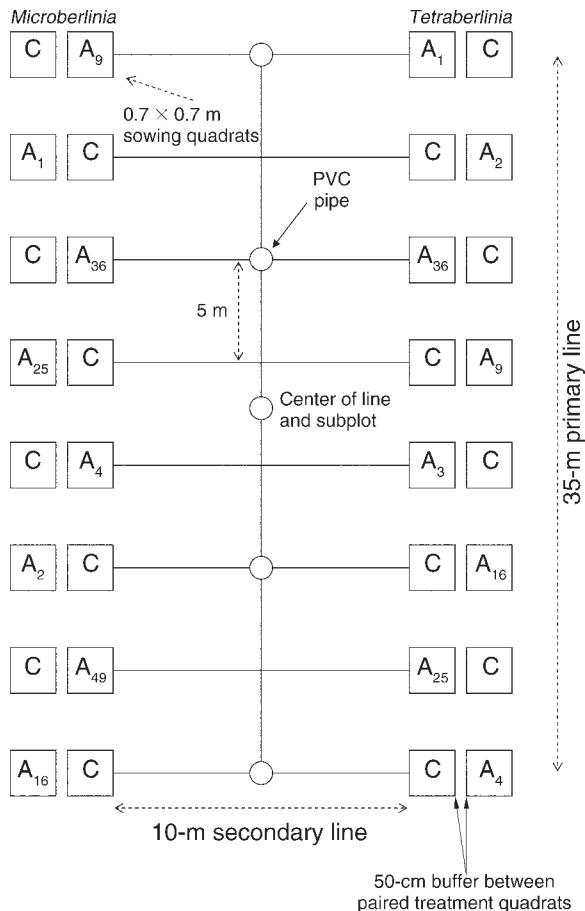


FIG. 1. Schematic of the experimental design used to test the relative strength of seed limitation vs. establishment limitation of *Microberlinia bisulcata* and *Tetraberlinia bifoliolata* trees at Korup, Cameroon. Seeds of each species were added to quadrats (A<sub>*i*</sub>, where *i* was the number of seeds added) paired with controls (no seeds added, C). The design was replicated across 20 subplots (each 50 × 50 m) at the study site, with seed density (A<sub>*i*</sub>) randomized separately for each subplot. Components shown are not all to scale.

been collected locally within the preceding 15 days, kept dry, and well mixed. Unusually small seeds were avoided, and seeds were screened twice for viability prior to sowing. To each addition quadrat, seeds of just one species were added, while its paired quadrat was designated a control (no seeds added). Each species was assigned a side of the primary line at random, and the density treatments were then randomized across the eight positions for each subplot (Fig. 1). To maximize interspersed, seeds were spread uniformly within quadrats in a grid-like fashion, or in a square for four, a triangle for three, diagonally for two, and at the center for one seed(s) added. The addition levels were accordingly 49, 36, 25, 16, 9, 4, 2, and 1 seeds for *Microberlinia* and 36, 25, 16, 9, 4, 3, 2, and 1 seeds for *Tetraberlinia*. Within each side of the primary line the paired control and density quadrats were alternated.

This safeguarded against possible losses of flags to foraging large mammals (mainly drills, duiker, and bush-pigs). Overall, in the 320 pairs of quadrats, we added 142 *Microberlinia* and 96 *Tetraberlinia* seeds to each transect. Replicated across the 20 subplots, this amounted to 4760 seeds added (2840 *Microberlinia* and 1920 *Tetraberlinia* seeds).

#### Ambient seed rain estimation

Estimation of the natural ambient seed rain density ( $S_{\text{amb}}$ ) in the forest is critical for the correct derivation of other parameters from recruitment models. To achieve that we used data from three sources: seed traps, individual tree fecundity, and seedling recruitment data. The last was an indirect estimate of the third parameter of the Beverton-Holt model (Poulsen et al. [2007]; see *Data analysis*), made for comparative purposes. Empirical data were collected from 476 seed traps (each 0.81 m<sup>2</sup>) at 68 locations (clusters were of seven traps each, 50 m apart in four separate blocks), as well as from the estimated individual fecundities for all 114 *Microberlinia* and 76 *Tetraberlinia* trees that reproduced within the 25-ha study area and in a surrounding 50-m buffer strip of 11 ha. This work was part of a concurrent study of seed dispersal in the same 25 ha (J. M. Norghauer and D. M. Newbery, *unpublished data*). For seed traps, summed seed counts per cluster over the 8-week monitoring period were used (15 August to 10 October 2007). For individual tree-level fecundities, at each reproductive tree we counted fallen pod valves (two valves form one pod) and their seed scars in four 3.14-m<sup>2</sup> ground plots situated on the four cardinal directions; we multiplied their density by the tree crown's horizontal area (using a conservative polygon area summation based on lateral crown extensions on six bearings). Dehisced pods under *Microberlinia* and *Tetraberlinia* trees were sampled 28 January–2 February and 12–17 March 2008, respectively.

Local ambient seed rain ( $S_{\text{amb-L}}$ ) specific to each of the 20 subplots was estimated for each tree species from their tree fecundity data, and was calculated as total seed produced per 1 m<sup>2</sup> within a subplot plus buffer (effective area 1.25 ha; see Appendix A). For the purposes of modeling the recruitment functions, these values were then halved and added to the manipulated densities, because the latter were made to 0.49-m<sup>2</sup> quadrats. A single, forest-wide ambient seed rain ( $S_{\text{amb-F}}$ ) for each species was calculated by dividing summed seed production of trees in the 25-ha study area and its 50-m buffer strip by the total area sampled (36 ha). A second forest-wide estimate of seed rain, this time made from seed trap data ( $S_{\text{amb-T}}$ ), was calculated for each species as the mean of the summed seed counts per cluster. In trapping, however, we probably underestimated the absolute seed rain of *Microberlinia*, but not *Tetraberlinia*, because of a short, unusual dry spell in late July–early August (S. Njibile, *personal communica-*

*tion*). Therefore,  $S_{\text{amb-T}}$  for *Microberlinia* could have been slightly higher.

#### Establishment and light availability

Relaxed plant height (height measured from the ground perpendicular to the tallest live part of the plant, irrespective of tissue type, i.e., stem, leaf, leaf petiole) and leaf number for all survivors were recorded 6 weeks later (27–28 October 2007; see Plate 1). Counts of the “other” species in each quadrat were noted. On 25–27 November, light available to seedlings was estimated using a hemispherical lens, one photograph centered on each quadrat pair and taken at a height of 75 cm (Fig. 1). Photographs were analyzed with Gap-Light Analyzer software (Frazer et al. 1999).

Percentage canopy openness (mean  $\pm$  SE) was 4.26%  $\pm$  0.05% when averaged over pairs of control–addition quadrats ( $n = 320$ ). It was similar across addition levels and for species (ANOVA, full model:  $F_{15,304} = 0.61$ ,  $P = 0.86$ ). Addition levels were therefore not confounded by chance differences in light environment.

#### Data analysis

For comparative purposes we first carried out the analysis typically done in nearly all seed-addition studies to date. For seedling counts of each species, addition levels were pooled as one treatment and compared with the paired controls. The sign test was used because distributions of counts were highly skewed, with many values of zero or one (Svenning and Wright 2005).

We estimated five recruitment functions for the *Microberlinia* and *Tetraberlinia* tree species. Following the conceptual framework and notation of Poulsen et al. (2007), we fitted the curvilinear power ( $R = aS^b$ ), Ricker hump-shaped ( $R = aSe^{-bS}$ ), and asymptotic Beverton-Holt ( $R = P_0S/\{1 + [P_0S/R_{\text{max}}]\}$ ) functions, where  $a$  and  $b$  are curve coefficients and  $e$  is the base of the natural logarithm. The Beverton-Holt (BH) model is our prime focus and of most general use because it incorporates both density-dependent (DD) and density-independent (DI) mortality; where  $R$  is seedling density at 6 weeks,  $P_0$  is the proportional recruitment under DI mortality only (between 0 and 1), and  $R_{\text{max}}$  is the maximum recruit density if the system were saturated with seeds (i.e., density dependence only). We also fitted two reduced versions of the BH function: one that simplified to a linear form ( $R = P_0S$ ) and lacked limitation due to DD mortality ( $L_{\text{DD}}$ ) on recruitment; and one that was nonlinear, ( $R = S/\{1 + [S/R_{\text{max}}]\}$ ) and instead lacked limitation due to DI mortality ( $L_{\text{DI}}$ ). In all analyses,  $S$  refers to seed density inputs, i.e., the number of seeds experimentally added to the quadrats plus an estimate of the subplot-specific ambient seed rain ( $S_{\text{amb-L}}$ ).

As previously described, we directly measured each species' overall  $S_{\text{amb}}$  at our site in two ways:  $S_{\text{amb-F}}$  and  $S_{\text{amb-T}}$ . We also halved their values to obtain densities on a 0.5-m<sup>2</sup> basis (very close to the quadrat area), and these two measures, along with the null, indirect,



PLATE 1. Recently established tree seedlings (~6–7 weeks after seed germination) of (a) *Microberlinia bisulcata* and (b) *Tetraberlinia bifoliolata*, two dominant forest canopy species at Korup, Cameroon. Depending on its seed mass, *Microberlinia* will produce 3–6 pinnate leaves, each 5–10 cm in length, whereas *Tetraberlinia* always produces two opposite compound leaves, each with two large leaflets similar in length (these latter were counted as leaves in the present study). Photo credits: J. M. Norghauer.

estimate ( $S_{\text{amb-N}}$ ) fitted from recruitment data alone, were used to calculate three sets of values for  $R_{\text{amb}}$ ,  $L_E$  and  $L_S$ ,  $L_{\text{DD}}$  and  $L_{\text{DI}}$ , for each species, using parameter values from the BH model (Poulsen et al. 2007). Under this framework,  $R_{\text{amb}}$  is seedling recruitment under ambient conditions ( $=P_0S_{\text{amb}}/[1 + (P_0S_{\text{amb}}/R_{\text{max}})]$ );  $L_E$  is establishment limitation ( $L_E = S_{\text{amb}} - R_{\text{amb}}$ ), and  $L_S$  is seed limitation ( $L_S = R_{\text{max}} - R_{\text{amb}}$ ). Limitations due to DD and DI mortality are defined as the increase in recruit density when each process is removed ( $R_{\text{DD}}$  and  $R_{\text{DI}}$ , respectively) compared to their recruitment under ambient conditions. Therefore,  $L_{\text{DD}} = R_{\text{DD}} - R_{\text{amb}}$ , where  $R_{\text{DD}} = P_0S_{\text{amb}}$ ; and  $L_{\text{DI}} = R_{\text{DI}} - R_{\text{amb}}$ , where  $R_{\text{DI}} = S_{\text{amb}}/(1 + (S_{\text{amb}}/R_{\text{max}}))$ .

For each of the eight addition levels, we fitted models to raw data for 20 replicate quadrats ( $n = 160$  per species) using PROC NL MIXED in the SAS package, Release 8.2 (SAS Institute, Cary, North Carolina, USA). The procedure minimizes the negative log-likelihood; we used the default quasi-Newton algorithm and assumed a Poisson error distribution to our seedling count data. A mixed model, based on the REML (restricted maximum likelihood) method, was used to test whether plant size was affected by species and treatment (addition vs. control); with percentage canopy openness included as a quantitative variable. In this statistical model, subplot was designated the main random factor and was crossed with each of the species and treatments in the model (Quinn and Keough 2002). Height and leaf number were square-root transformed. To avoid pseudoreplication,

quadrat-level means were used. Individuals with zero leaves or heights <10 cm were excluded from analyses.

## RESULTS

Six weeks after seeding, 199 *Microberlinia* seedlings established from the 2840 seeds sown (7.0%). For *Tetraberlinia*, more than twice as many seedlings established, 362 from the 1920 sown (18.8%). An additional 25 and 34 seedlings of *Microberlinia* and *Tetraberlinia*, respectively, established successfully but were uprooted or had their stems clipped by animals (probably rodents and large grasshoppers). In the control treatment, at least four times more *Microberlinia* than *Tetraberlinia* established (129 vs. 26), with 6 and 4 seedlings, respectively, uprooted or clipped. In this analysis, and the one following, we assumed that germination rates were constant across addition levels. In a separate seed-marking trial that used 37 and 23 seeds, respectively, of *Microberlinia* and *Tetraberlinia*, germination rates were correspondingly 92% and 100% after 7 days (30 August 2007) for seeds not completely eaten or removed (J. M. Norghauer, unpublished data). These results are in line with the mean of 97% for *Microberlinia* reported by Green and Newbery (2002).

Seed additions, when pooled across the eight levels, had a highly significant positive effect on seedling establishment for both tree species (sign tests,  $n = 160$ : *Microberlinia*,  $P = 0.003$ ; *Tetraberlinia*,  $P < 0.0001$ ). However, more *Microberlinia* than *Tetraberlinia* seedlings established in the control quadrats, and, on average, adding seeds increased seedling recruitment

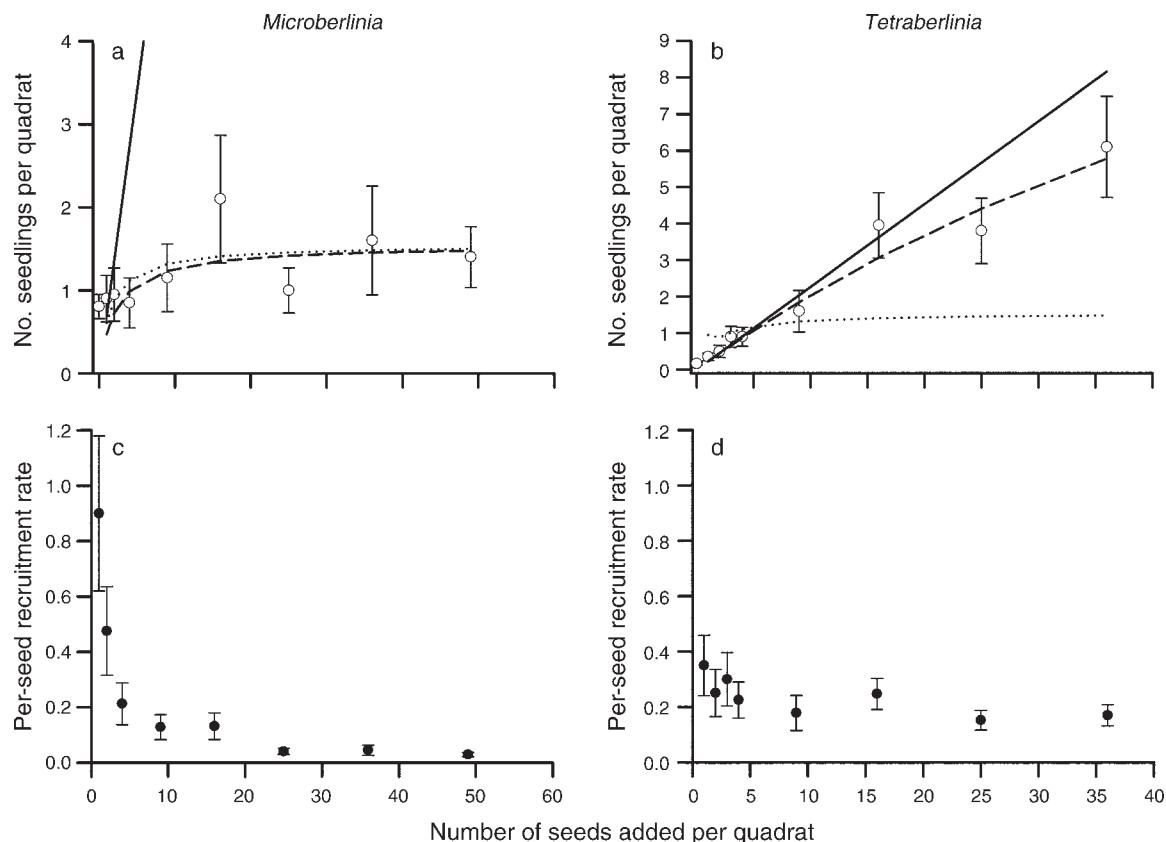


FIG. 2. The relationship between experimental seed density and (a, b) density of seedlings established  $\sim 6$  weeks later, and (c, d) per-seed recruitment rate for *Microberlinia bisulcata* and *Tetraberlinia bifoliolata* trees at Korup, Cameroon. Panels (a) and (b) illustrate three forms of recruitment based on  $P_0$  (density-independent survival) and  $R_{\max}$  (maximum seedling density) parameter values from the full Beverton-Holt (BH) function (Table 1 and Appendix B): solid line, no limitation from density-dependent (DD) mortality (using  $P_0$  only); dotted line, no limitation from density-independent (DI) mortality (using  $R_{\max}$  only); and dashed line, full BH model (using both  $P_0$  and  $R_{\max}$ ). Recruitment values (mean  $\pm$  SE) are shown for the 20 subplots at each addition level. Fits of the two reduced BH functions to the raw data ("No DD-mortality" and "No DI-mortality"; see Table 1) based on their respective parameter values are shown in Appendix B. Panels (a) and (b) do not share the same y-axis scale but do include the "zero" augmentation level (i.e., control) on the x-axis.

by 50% in *Microberlinia* (means  $\pm$  SE:  $1.244 \pm 0.161$  seedlings vs.  $0.806 \pm 0.146$  seedlings) and 1400% in *Tetraberlinia* ( $2.262 \pm 0.291$  seedlings vs.  $0.163 \pm 0.040$  seedlings), 6 weeks after quadrats were seeded. When addition levels were pooled at the subplot level, again significantly more seedlings were found in seed-addition than in control quadrats for *Microberlinia*, and especially more for *Tetraberlinia* (Mann-Whitney  $U$  test,  $n = 20$ ,  $P = 0.037$  and  $P < 0.001$ , respectively). Averaged across addition levels (following Clark et al. 2007), *Microberlinia* and *Tetraberlinia* had similar per-seed recruitment rates, however ( $t$  test,  $n = 318$ ; means 0.25 vs. 0.23, respectively,  $P = 0.24$ ; Fig. 2c, d).

The results of fitting the different recruitment functions are summarized in Table 1 (see Appendix B). All models successfully converged on a solution; recruitment at each seed-addition level is presented in Fig. 2a, b. Generally, both measures of fit indicated only minor differences between some of the alternative models (Table 1 and Appendix B). However, based on

the deviance statistic ( $-2 \log$ -likelihood) the recruitment function for *Microberlinia* was best described by the Beverton-Holt model, which included both DD and DI mortality (Fig. 2a). The DD mortality-only model provided a comparable fit when the number of parameters was taken into account (lowest AIC; Table 1). For *Tetraberlinia* the BH model provided an improved fit over both the DD and DI mortality-only versions (Table 1, Fig. 2b), but was comparable to the Ricker hump function, which gave a good fit to *Tetraberlinia* recruitment too (see Appendix B). Noticeably different between the two species was the maximum recruit density ( $R_{\max}$ ) estimated from the BH model, which was more than 10-fold higher for *Tetraberlinia* than *Microberlinia* (Table 1). These seemingly conflicting results led us to visually inspect both the *Microberlinia* and *Tetraberlinia* data more closely on a per-subplot basis (Appendix C). For *Microberlinia* the form of the relationship between recruit density and seed density was, as suspected, generally consistent among

TABLE 1. Parameter estimates and statistics of five seedling recruitment functions for *Microberlinia bisulcata* and *Tetraberlinia bifoliolata* trees at Korup, Cameroon.

Recruitment model	<i>Microberlinia</i>						<i>Tetraberlinia</i>					
	Parameter				Statistics		Parameter				Statistics	
	$P_0$	$R_{max}$	$a$	$b$	-2LL	AIC	$P_0$	$R_{max}$	$a$	$b$	-2LL	AIC
No DD limitation	0.06223				690.7	692.7	0.1801				718	720
No DI limitation		1.4590			584.2	<b>586.2</b>		4.232			810.9	812.9
Full BH model (DD + DI)	0.6784	1.5453			<b>583.7</b>	587.7	0.2267	19.780			<b>713.5</b>	<b>717.5</b>
Ricker function			0.2197	0.0451	591.2	595.2			0.2240	0.0094	713.4	717.4
Curvilinear power function			0.7522	0.1900	583.9	587.9			0.2591	0.8755	714.2	718.2

Notes: Model abbreviations are BH, Beverton-Holt function; DD, density-dependent, and DI, density-independent, mortality.  $P_0$  is density-independent survival and  $R_{max}$  is maximum seedling density for BH;  $a$  and  $b$  are curve coefficients. Deviance is given as  $-2 \times \log$ -likelihood ( $-2LL$ ); AIC is Akaike's information criterion. Best fits among models are shown in boldface.

subplots (except 7-D). By contrast, *Tetraberlinia* showed more variation among subplots, with a mix of strong to negligible linear responses in recruitment (slope minimum, maximum:  $-0.15, 0.49$ ), as well as a few that appeared clearly hump-shaped.

We next quantified the relative strengths of seed ( $L_S$ ) and establishment ( $L_E$ ) limitation for each species using the pair of parameter estimates  $P_0$  and  $R_{max}$  from the BH model (Table 1) and our two empirical estimates of forest-wide ambient seed rain ( $S_{amb-F}$  and  $S_{amb-T}$ ). These latter estimates were more disparate for *Tetraberlinia* than for *Microberlinia*, although, taken together,  $S_{amb-N}$  was within 20% of the  $S_{amb-F}$  estimate. First, the effect of  $L_E$  on seedling recruitment was 2–4 times stronger than  $L_S$  for *Microberlinia*, whereas for *Tetraberlinia* the  $L_S$  was 15–40 times stronger than  $L_E$ , depending on how  $S_{amb}$  was derived (Table 2). The values of  $L_E$  and  $L_S$  generally showed less variation for *Microberlinia* than for *Tetraberlinia* because the latter's estimate of average  $S_{amb-T}$  was  $\sim 3.5$  times greater than for either the  $S_{amb-F}$  or the null estimate,  $S_{amb-N}$ . Second, limitation on

*Microberlinia* recruitment due to DD mortality ( $L_{DD}$ ) varied twofold depending on how  $S_{amb}$  was measured in the field. Moreover, the strength of  $L_{DD}$  relative to limitation from DI mortality ( $L_{DI}$ ) ranged from being 12 times (using  $S_{amb-F}$ ) down to two times greater (using  $S_{amb-N}$ ; Table 2). These discrepancies were less pronounced for *Tetraberlinia*, for which  $L_{DI}$  greatly exceeded  $L_{DD}$  in all cases.

An alternative way to gauge the relative importance of different forms of limitation on seedling recruitment is to use the elasticity of the density dependence parameter ( $e_{R_{max}} = R_{amb}/R_{max}$ ) in the BH model. This  $e_{R_{max}}$  indicates how far from saturation a species is, depending on the shape of its recruitment function. It allows for a better comparison among life-forms than using  $L$  values alone (Poulsen et al. 2007). In our forest, *Microberlinia* was approaching saturation over a twofold range:  $e_{R_{max}}$  derived using  $S_{amb-F}$  exceeded 50% (the asymptote) and this was twice as strong as that estimated using  $S_{amb-T}$ . By contrast, *Tetraberlinia* was clearly far from satura-

TABLE 2. Recruitment limitations and elasticities for *Microberlinia bisulcata* and *Tetraberlinia bifoliolata* trees at Korup forest, Cameroon, derived from the Beverton-Holt (BH) model (see Table 1) using three estimates of seed rain ( $S_{amb}$ ).

Species and estimate	$R_{amb}$	$L_S$	$L_{DI}$	$L_{DD}$	$L_E$	$e_{P_0S}$	$e_{R_{max}}$
<i>Microberlinia</i>							
$S_{amb-F}$ (6.57 seeds/m <sup>2</sup> )	0.914	0.631	0.136	1.316	2.371	0.41	0.59
$S_{amb-T}$ (5.45 seeds/m <sup>2</sup> )	0.841	0.704	0.145	1.007	1.884	0.69	0.31
$S_{amb-N}$ (5.61 seeds/m <sup>2</sup> )	0.716	0.920	0.317	0.559	2.089	0.56	0.44
Mean	0.823	0.752	0.200	1.083	2.115	0.55	0.45
<i>Tetraberlinia</i>							
$S_{amb-F}$ (1.36 seeds/m <sup>2</sup> )	0.153	19.63	0.504	0.001	0.527	0.99	0.01
$S_{amb-T}$ (4.96 seeds/m <sup>2</sup> )	0.547	19.23	1.657	0.015	1.933	0.97	0.03
$S_{amb-N}$ (1.08 seeds/m <sup>2</sup> )	0.120	20.80	0.406	0.001	0.420	0.99	0.01
Mean	0.273	19.89	0.856	0.0057	0.960	0.98	0.02

Notes:  $S_{amb-F}$  and  $S_{amb-T}$  are direct tree fecundity and seed trap estimates of seed rain, respectively;  $S_{amb-N}$  is an indirect estimate using the BH model (i.e.,  $S_i$  became  $A_i + S_{amb-N}$ , where  $A_i$  is addition at level  $i$ ). In this last case,  $P_0$  and  $R_{max}$  differed from values in Table 1 because a third parameter was fitted to the raw data (for *Microberlinia*,  $P_0 = 0.4547$  and  $R_{max} = 1.6362$ ; for *Tetraberlinia*,  $P_0 = 0.2242$  and  $R_{max} = 20.92$ ). All  $S_{amb}$  estimates shown in this table were halved for the analyses.  $R_{amb}$  is seedling recruitment under ambient conditions. Seed limitation ( $L_S$ ) is the difference between maximum potential recruitment ( $R_{max}$ ) and recruitment arising from seed rain ( $R_{amb}$ ).  $L_E$  is establishment limitation;  $L_{DD}$  and  $L_{DI}$  are limitations arising from density-dependent and density-independent mortality, respectively. Elasticities for the BH function range from 0 to 1, and quantify proportional changes in seedling recruit density per unit change in a given parameter. The  $e_{P_0S}$  is the joint elasticity of the parameters describing seed input,  $S$ , and density-independent mortality,  $P_0$ , and is calculated as  $1 - e_{R_{max}}$ , where  $e_{R_{max}}$  is the elasticity of the density-dependent parameter,  $R_{max}$ , and is calculated as  $R_{amb}/R_{max}$ .

tion, where DD mortality was not likely to be a major factor influencing recruitment (all  $e_{R_{\max}} < 0.04$ ; Table 2).

*Tetraberlinia* seedlings grew significantly larger than *Microberlinia* seedlings only in addition quadrats (mixed-model, species  $\times$  treatment term,  $F_{1,241} = 6.04$ ,  $P = 0.015$ ; no main effects were significant; Appendix D). Mean leaf number was similar for species and treatments ( $P > 0.20$ ). Neither variable was significantly affected by percentage canopy openness (for height,  $P = 0.56$ ; for leaf number,  $P = 0.25$ ).

In 21 addition and 21 control quadrats of *Microberlinia*, there was  $\geq 1$  naturally established *Tetraberlinia* seedling (maximum 2). Likewise in 37 addition and 35 control quadrats of *Tetraberlinia*,  $\geq 1$  naturally established *Microberlinia* seedlings were found (maximum 8). Total recruitment at the subplot scale (sum of established seedlings per species per primary line) was not significantly related to either conspecific adult neighborhood (density and basal area of adults) or total conspecific seed inputs summed for 1 ha centered on each subplot (three linear regressions per species, all  $P \geq 0.25$ ).

## DISCUSSION

### *Seed vs. establishment limitation*

*Microberlinia* and *Tetraberlinia* differed considerably in the relative strengths of seed vs. establishment limitation that affected them. The Beverton-Holt (BH) model showed that the recruitment of *Microberlinia* was limited least by the availability of seeds and most by postdispersal density-dependent (DD) mortality in the seed-to-seedling transition. Conversely, the recruitment of *Tetraberlinia* was constrained primarily by seed availability, followed by density-independent (DI) mortality, and least by DD mortality. The rates of postdispersal mortality found (82–93%) were consistent with those from recent meta-analyses (~85%, Clark et al. 2007; ~98%, Poulsen et al. 2007). The contrast between the  $e_{R_{\max}}$  values for *Microberlinia* (0.31–0.59) and those summarized by Poulsen et al. (2007) (mean  $e_{R_{\max}}$  of 0.06) reflects differences in detection abilities and plant life-form and community structure.

The much stronger seed limitation experienced by *Tetraberlinia* than *Microberlinia* is consistent with its 2.5-fold larger seed mass supporting a wider relationship that species with larger seeds tend to be more seed limited than those with smaller seeds (Moles and Westoby 2002, McEuen and Curran 2004; but see Svenning and Wright 2005). Differences in seed size, however, only translated into slight height differences, although above- and belowground biomass may have differed more between species (cf. Green and Newbery 2001a, b). The trade-off between seed size and seed number means that *Tetraberlinia* had lower per capita fecundity (J. M. Norghauer and D. M. Newbery, unpublished data), and thus fewer opportunities to reach sites suitable for establishment than did *Microberlinia*. This limitation was exacerbated by *Tetraberlinia* having

fewer reproducing adults than *Microberlinia* in the 25 ha during the 2007 masting (76 vs. 114 trees with pods), and having crowns one-third the area of *Microberlinia*. Other less dominant trees in more diverse forests than ours could be even more seed limited than *Tetraberlinia*; but perhaps not temporally if they disperse seed annually, and less so spatially if via wind or animal vectors (Seidler and Plotkin 2006).

### *Density-dependent mortality in Microberlinia*

Indeed, local seed and establishment limitation would be expected to vary spatially and temporarily across the grove because seed density varies with masting year and distance from reproductive trees, and individual trees also vary in fecundity. Even so, for *Microberlinia*, but less so for *Tetraberlinia*, adults were so dense and reproductive output so high in mast years that some seeds probably reached most places in the grove. To assess how frequently seed density might reach levels high enough for DD mortality to happen, we reexamined the seed trap data for each species. We estimated the percentage of forest area receiving more than  $S_{\text{amb}}$  at which the DI-only and DD-included mortality curves estimated from the Beverton-Holt model began to diverge (Fig. 2a, b). Density-dependent mortality would have had an effect at 8 seeds/m<sup>2</sup> for *Microberlinia*, and at 18 seeds/m<sup>2</sup> for *Tetraberlinia*. Scaled up, density dependence could operate in 22% and 10% of the study area for the two species, respectively; in effect, very near parent trees. *Microberlinia*, more so than *Tetraberlinia*, staggers its seed fall over a 2–3 month period, so bulked trap counts would have been spread out, and effects of DD mortality perhaps ameliorated. Halving  $S_{\text{amb-F}}$  and  $S_{\text{amb-T}}$  for *Microberlinia* suggests that  $L_{\text{DD}}$  may be weakened by more than 50% (to 0.512 and 0.347); taking one-third of  $S_{\text{amb-F}}$  and  $S_{\text{amb-T}}$  would lead to an 80% weakening (to 0.242 and 0.176). From our study we gained two connected insights. (1) How  $S_{\text{amb}}$  was measured could change the quantitative estimates in limitation and elasticity analyses by more than 50%. (2) Using recruitment data alone gave the lowest estimates of seed rain ( $S_{\text{amb-N}}$ ), and thus of  $R_{\text{amb}}$ , which, in turn, inflated seed limitation ( $L_S$ ) for both species (Table 2). As trap layout by chance missed a portion of the 25 ha lacking adult *Tetraberlinia* trees, this may have led to a small overestimation of  $S_{\text{amb-T}}$ . An additional insight gained is that using a mean per-seed recruitment rate to gauge the extent of seed limitation is potentially misleading because it does not account for density-dependent effects on plant recruitment (Fig. 2c, d).

The causal mechanisms responsible for strong density dependence found in *Microberlinia* remain unknown. We are inclined to discount intraspecific competition because, at the maximum density added, a seedling would have occupied, on average,  $\geq 100$  cm<sup>2</sup> which, over 6 weeks, was probably too large a spacing for shoot (but perhaps not for root and ectomycorrhizal) interactions to operate strongly. From field observations, other work

in progress, and Green and Newbery (2001*b*), we suspect that pathogenic fungi or invertebrate predators may be driving this process (Janzen 1970, 1980, Bell et al. 2006).

#### *Implications for grove dynamics*

A major motivation for this investigation was to contribute to a plausible integrated set of explanations for the very low survival rate of *Microberlinia* seedlings (cf. *Tetraberlinia*) after masting in the Korup groves. Its subsequently very low recruitment rate into the sapling bank suggests a possible lack of tree replacement in the forest (Newbery and Gartlan 1996, Newbery et al. 2004, 2006*b*, 2009). The experimental results in this paper strongly support a DD process, in part, determining early recruitment of *Microberlinia*.

Yet it remains unclear whether density dependence is the only process operating, because  $R_{\max}$  estimated for *Microberlinia* ( $\sim 3$  seedlings/m<sup>2</sup>; Table 1) was still 4–5 times higher than the mean forest-wide seedling density in 1995 (close to our 6-week period for seedling establishment) of 0.66 seedlings/m<sup>2</sup> (Newbery et al. 1998), and close to double that of 1.67 seedlings/m<sup>2</sup> recorded for newly germinated seedlings in October 1995 by Green and Newbery (2002). In the 7-year demography study of Newbery et al. (2006*b*), the density of the 1995-cohort of *Microberlinia* seedlings at 3–5 weeks after germination was 0.94 seedlings/m<sup>2</sup> in quadrats even selected for relatively high starting densities. Density dependence may be operating in the densest patches of seedlings, and other processes continue to reduce the seedling density further, and elsewhere.

Earlier nursery and field transplant experiments showed that new *Microberlinia* seedlings are intolerant of deep shade (<1% PAR) for prolonged periods, but *Tetraberlinia* to a lesser degree (Green and Newbery 2001*a, b*). The seed mass of *Microberlinia* is  $\sim 40\%$  that of *Tetraberlinia*, which means that *Microberlinia* would probably exhaust its reserves sooner than *Tetraberlinia*. This interestingly matches the similar  $\sim 40\%$  lower survival in *Microberlinia* than in *Tetraberlinia* in the present study. Both species, however, need considerably raised light levels (typically afforded by canopy gaps) so that they can recruit further (Green and Newbery 2001*a, b*).

Our results suggest that strong DD mortality need not operate in both codominant species (as in *Tetraberlinia*) in order to promote local coexistence in the groves at Korup, provided that a lack of density dependence is accompanied by strong seed limitation (as defined here). *Microberlinia* is clearly limited by the availability of microsites for establishment of its seedlings, but only a subset of these sites may prove suitable for establishment of adults because of very high mortality in the post-seedling to sapling phase (Newbery et al. 2006*b*), but relatively better survival for saplings to juvenile trees (Newbery et al. 2010). Crucial shifts in mortality and recruitment rates of *Microberlinia* seem to occur once a sapling stem diameter of  $\sim 2$  cm is reached, although this

is happening at a spatial scale larger than that for newly germinating seedlings. Conversely, *Tetraberlinia* may escape the constraints on its recruitment imposed by strong seed limitation by building clusters of shade-tolerant seedlings in the understory. The differing strengths and outcomes of seed limitation and establishment limitation for *Microberlinia* and *Tetraberlinia* inevitably preset, in a fundamental way, their tree replacement rates in the forest.

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#### APPENDIX A

Table of local ambient seed rain estimates and calculation note (*Ecological Archives* E091-164-A1).

#### APPENDIX B

Overall recruitment vs. seed density graphics (*Ecological Archives* E091-164-A2).

#### APPENDIX C

Subplot-level recruitment vs. seed density graphics (*Ecological Archives* E091-164-A3).

#### APPENDIX D

Summary table of seedling size analyses and statistics (*Ecological Archives* E091-164-A4).