



Tree size and fecundity influence ballistic seed dispersal of two dominant mast-fruited species in a tropical rain forest



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ABSTRACT

Seed production, seed dispersal, and seedling recruitment are integral to forest dynamics, especially in masting species. Often these are studied separately, yet scarcely ever for species with ballistic dispersal even though this mode of dispersal is common in legume trees of tropical African rain forests. Here, we studied two dominant main-canopy tree species, *Microberlinia bisulcata* and *Tetraberlinia bifoliolata* (Caesalpinioideae), in 25 ha of primary rain forest at Korup, Cameroon, during two successive masting events (2007/2010). In the vicinity of c. 100 and 130 trees of each species, 476/580 traps caught dispersed seeds and beneath their crowns c. 57,000 pod valves per species were inspected to estimate tree-level fecundity.

Seed production of trees increased non-linearly and asymptotically with increasing stem diameters. It was unequal within the two species' populations, and differed strongly between years to foster both spatial and temporal patchiness in seed rain. The *M. bisulcata* trees could begin seeding at 42–44 cm diameter: at a much larger size than could *T. bifoliolata* (25 cm). Nevertheless, per capita life-time reproductive capacity was c. five times greater in *M. bisulcata* than *T. bifoliolata* owing to former's larger adult stature, lower mortality rate (despite a shorter life-time) and smaller seed mass.

The two species displayed strong differences in their dispersal capabilities. Inverse modelling (IM) revealed that dispersal of *M. bisulcata* was best described by a lognormal kernel. Most seeds landed at 10–15 m from stems, with 1% of them going beyond 80 m (<100 m). The *direct* estimates of fecundity significantly improved the models fitted. The lognormal also described well the seedling recruitment distribution of this species in 121 ground plots. By contrast, the lower intensity of masting and more limited dispersal of the heavier-seeded *T. bifoliolata* prevented reliable IM. For this species, seed density as function of distance to traps suggested a maximum dispersal distance of 40–50 m, and a correspondingly more aggregated seedling recruitment pattern ensued than for *M. bisulcata*.

From this integrated field study, we conclude that the reproductive traits of *M. bisulcata* give it a considerable advantage over *T. bifoliolata* by better dispersing more seeds per capita to reach more suitable establishment sites, and combined with other key traits they explain its local dominance in the forest. Understanding the linkages between size at onset of maturity, individual fecundity, and dispersal capability can better inform the life-history strategies, and hence management, of co-occurring tree species in tropical forests.

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1. Introduction

Plants on land have evolved an impressive array of reproductive features and morphological adaptations to move their offspring away from them (Ridley, 1930; Salisbury, 1942). This process of propagule dispersal, though brief in the life-cycle of trees, can have profound implications for later ecological processes affecting the

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fates of their seeds and juveniles, which in turn can have important, long-lasting consequences for the dynamics, composition and structure of plant populations and communities (Howe and Smallwood, 1982; Levin et al., 2003; Cousens et al., 2008). Recently, there has been increasing interest in both empirical and theoretical studies on animals that disperse seeds (Vander Wall, 2010; Schupp et al., 2010), especially in the zoologically-rich tropics where such vertebrates are increasingly threatened by hunting, habitat degradation, and forest fragmentation (Chapman and Onderdonk, 1998; Cordeiro and Howe, 2001). By contrast, those tree species with primarily wind, water, or ballistic mechanisms

remain remarkably understudied relative to their occurrence in tropical forests (Muller-Landau and Hardesty, 2005).

Although well-described for small, short-lived plants (Stamp and Lucas, 1983; Thiede and Augspurger, 1996), ballistic dispersal relying on the explosive ejection of seeds has been poorly studied for trees. This is surprising given its prevalence in several major flowering families such as the Euphorbiaceae and Leguminosae (=Fabaceae) (Ridley, 1930; Swaine and Beer, 1977). Detailed field studies are few and far between: we could not find more than four published papers that quantified the ‘seed shadow’ – the distribution of seeds around parental source(s) – of a ballistically-dispersed tree species (Swaine and Beer, 1977; Forget, 1989; Henkel et al., 2005; van der Burgt, 1997). Our ignorance of the basic patterns in ballistic dispersal of forest trees may also reflect a geographical (and taxonomical) bias caused by where research is conducted within the tropics. In African rain forests, however, it has been noted for a long time that many legume species are pod-bearing and rely primarily on explosive seed dispersal (Aubréville, 1968, 1970; Letouzey, 1968; Torti et al., 2001; Newbery and Gartlan, 1996; van der Burgt, 1997). For example, at Korup, Cameroon, the proportion of caesalpiniaceous species – these being the very large majority of those ballistically-dispersed – was recorded at 62.1% the density of trees ≥ 50 cm, and 41.7% of the basal area of trees ≥ 10 cm, in stem diameter (1991–2005; Newbery et al., 2013). This testifies to the very considerable importance of ballistic dispersal for trees in this *Caesalpiniaceae*-rich Atlantic coastal forest type (Letouzey, 1968, 1985). It also makes the *Caesalpinoideae* an excellent group of tree species for field study.

There are several practical challenges to studying ballistic dispersal in one or more closely related tree species in a forest. First, there is the matter of spatial clumping of adults that inevitably arises from reduced dispersal ability. For example, in Malaysian forest, the degree of clustering was shown to be greater in tree species with ballistic seed dispersal than in those relying primarily on wind or animal vectors (Seidler and Plotkin, 2006). In some tropical forests, many of the canopy trees that attain unusually high local dominance, or even monodominance – essentially forming ‘groves’ or pronounced patches of adults on the scale of several hectares – are in fact pod-bearing, ectomycorrhizal caesalp species (Connell and Lowman, 1989; Newbery and Gartlan, 1996; Torti et al., 2001; Peh et al., 2011; Newbery et al., 2013). Clumping of adult trees might also lead to positive density-dependent production of flowers and fruits through increased local pollination (Ghazoul, 2005), which could override negative effects of intraspecific resource competition and inbreeding (e.g., Jones and Comita, 2008).

Second, strong clumping of adults also means that overlapping seed shadows are likely to occur within a dense local population. Instead of sampling around spatially isolated fruiting trees or “known sources”, an inverse modelling (IM) framework is needed to quantify seed shadows that relies upon maximum likelihood methods to find the dispersal parameters that best fit the empirical data (Ribbens et al., 1994; Clark et al., 1999; Cousens et al., 2008). Recording of new seedlings may help refine seed shadows and detect maximum dispersal distances (e.g., Greene et al., 2004; Martin and Canham, 2010), and is essential for investigating to what extent seed and seedling distributions may differ due to non-random mortality arising from niche differences or natural enemies (Howe and Smallwood, 1982; Sagnard et al., 2007; Schupp et al., 2010; Moran and Clark, 2012).

Third, many tropical tree species display population-wide synchronized fruiting that happens on a supra-annual schedule, likely tracking environmental cues (van Schaik et al., 1993; Newbery et al., 2006a; Norden et al., 2007). These “masting” events produce copious seed crops that are thought to satiate predators (Janzen,

1974; Kelly and Sork, 2002), to yield greater gains in plant fitness than would an annual fruiting schedule (Silvertown, 1980; Hulme and Benkman, 2002; Visser et al., 2011). For this reason, empirical data from successive masting events are needed to show how dispersal varies temporally at the level of the individual and the population, and also between co-occurring species in a community.

Over 35 years ago, Janzen (1978) wrote that “. . . to understand the adaptive value of seeding patterns, it is imperative that we obtain information about individuals and thereupon build a population view”, a view echoed by Herrera et al. (1998). And yet, many IM studies of dispersal have rested on unverified, simplistic assumptions about the reproductive status and absolute numbers of seeds (or fruits) produced per individual tree. Specifically, that all trees produce offspring and these numbers scale up proportionally with parent stem diameter or basal area (Ribbens et al., 1994; Clark et al., 1999; Greene et al., 2004; Muller-Landau et al., 2008). Whether this tree-size fecundity relationship is constant across several years or masting events is also debatable given the few reliable datasets comprising *individual* tree records of numbers of seeds and fruits (Thomas, 2011; Weiner et al., 2009). Such records are also essential to quantify an important life-history parameter for a given population of trees: the stem diameter at onset of maturity, or ‘SOM’ (Thomas, 1996a; Wright et al., 2005). This, too, is overlooked in many IM studies, largely because it is unknown or assumed, even though it surely varies among species (Uriarte et al., 2005; Martin and Canham, 2010; Canham et al., 2014). How SOM for tree species is related to their per capita fecundity, seed mass, dispersal abilities, and reproductive capacity remains almost entirely unexplored.

Here, we report on a comprehensive field study of ballistic dispersal in primary lowland African rain forest at Korup (Cameroon). The general aim was to quantify the seed dispersal and seedling recruitment patterns of two codominant *Caesalpinoideae* (Fabaceae) main-canopy trees: *Microberlinia bisulcata* A. Chev. and *Tetraberlinia bifoliolata* (Harms) Hauman, which both masted in 2007 and 2010. Specifically, we wanted to answer these five questions: (1) How is tree crown area and fecundity related to stem diameters in each species? (2) How variable are seed and pod numbers for the two species within and between mastings? (3) What is the pattern of seed dispersal, and is it discordant with that of seedling recruitment in spite of masting? (4) Does including direct estimates of tree-level fecundity improve the IM approach? (5) What are the implications of the dispersal process for tree population dynamics and life-history strategies at Korup?

2. Materials and methods

2.1. Study site

The study was conducted in the southern part of Korup National Park (5°10 8'50 SW Cameroon, 50–150 m a.s.l.) in the 82.5-ha permanent “P-plot” (for a detailed description, see Newbery et al., 1998, 2013). This plot is situated within a large grove of *M. bisulcata* trees (Newbery et al., 2004) which is co-dominated by *T. bifoliolata* and *Tetraberlinia korupensis* Wieringa (Newbery et al., 2013). The climate here is generally very wet (>5000 mm of rain yr⁻¹), apart from the dry season (December through February; <100 mm per month; Newbery et al., 2006a).

2.2. Study species

The two species we studied are ectomycorrhizal, monocious, canopy-emergent trees (Newbery et al., 1998). The adults of *M. bisulcata* can attain greater maximum diameters (≤ 2.3 m) than *T.*

bifoliolata (≤ 1.3 m) and they can achieve average tree-top heights of 44 and 48 m respectively (Newbery et al., 2013). Prior observations suggested that the onset of reproduction occurs at larger diameters in *M. bisulcata* (c. 50 cm) than *T. bifoliolata* (c. 25–35 cm), and that both species flower annually but reproduction does not appear to be limited by pollinators. The *M. bisulcata* trees will generally mast every 2–3 yr (Newbery et al., 2006a) whereas the masting frequency for *T. bifoliolata* has not been so well studied: two mastings, in 1992 and 1995, were confirmed in a 6-yr period (1989–1995; Newbery et al., 1998), and four mastings in 2007, 2010, 2011, and 2013 were noted in the inclusive 8-yr period of 2006–2013 (Norghauer, unpubl. data).

The two species produce smooth disc-shaped seeds housed in dehiscent pods that are shot out from the outer surfaces of crowns on sunny days (Appendix S1). Seeds lack any evident structural adaptations to encourage secondary dispersal by animals on the ground (e.g., arils or hooks). Dry seed mass (mean \pm SE) was determined at 0.64 ± 0.02 g for *M. bisulcata* and 1.57 ± 0.02 g for *T. bifoliolata* (from Green and Newbery, 2001a, 2001b). Earlier phenological surveys also indicated that seed dispersal occurred later in the wet season, mainly from August to October in years when one or both species mast fruited (Newbery et al., 1998). Fast germination precludes any seed banks from forming in both species, and their new, recently established seedlings are easily identified by their non-lignified stems. Seedlings of *T. bifoliolata* can persist much longer under deeply shaded conditions than those of *M. bisulcata* (Newbery et al., 2002, 2006a, 2006b; Norghauer and Newbery, 2011).

2.3. Tree-level estimates of fruit and seed numbers

The stems of the two species ≥ 10 -cm diameter in the P-plot were last enumerated in 2005. In the easternmost 25-ha (500 m \times 500 m) of the P-plot, these trees were evaluated as to whether they fruited or not, and for those fruiting four circular quadrats of 1-m radius (3.14 m²) were set up on the four cardinal bearings approximately midway between stem and crown edge. These quadrats were carefully searched among the litter for the recently fallen pod valves (two valves = one fruit pod). Valves were counted, with every 5th one cleaned and its visible seed indentations also counted (range: 0–7): valves lying more than 50% outside the plot's edge were not included in the final counts. Because of their distinct morphology and durable fibrous nature, new pods could be distinguished among species and within species from old ones which had mostly decayed since the previous masting. No plots were searched in directions lacking overhead crown projection. Because adults have separated, non-overlapping crowns, and their pod valves drop vertically after abscission beneath them, the probability of valves coming from neighbours other than the one counted was extremely small, and would not have biased individual fecundity estimates.

For the 2007 masting, *M. bisulcata* was sampled in this way on 28 January – 3 February 2008, and for *T. bifoliolata* later on 16–20 March 2008. In 2007, because 11 trap clusters were on the P-plot boundary (see Appendix S1), trees of *M. bisulcata* and *T. bifoliolata* in a 50-m buffer strip around the 25-ha forest area were also sampled for reproduction, and mapped, in March 2008. After the 2010 masting, trees of *M. bisulcata* and *T. bifoliolata* were sampled in the 25-ha area only, on 27 October 2010 – 8 January 2011. In total, the population size of *M. bisulcata* and *T. bifoliolata* trees surveyed for reproduction was >100 in 2007, though slightly smaller in 2010 (Table 1).

Lateral crown extensions, perpendicular to the ground along six bearings (0°, 60°, ..., 300°), were measured for all trees >30 -cm diameter whether they fruited in the masting years or not (excepting 1 and 3 trees of *M. bisulcata* and *T. bifoliolata*, respectively, all

non-fruited). A right-angle prism helped confirm each point (Husch et al., 2003) and the distance back to the stem was recorded (with 0.5-m accuracy). Each tree's projected horizontal (cross-sectional) crown area was found by connecting the end-points of the crown extensions with straight lines to form a hexagon, and the areas of the six constituent triangles summed to give crown area (m²). Sampling was opportunistically extended to several small non-fruited trees that were most likely still juveniles (<30 cm and <50 cm diameter for *T. bifoliolata* species and *M. bisulcata*, respectively).

To obtain total fecundity per individual tree, the average number of seed scars per valve was multiplied by total pod count (i.e. valve count/2) over the four quadrats (total area = 12.56 m² per tree), and this seed count scaled up to the tree's crown area. This calculation assumed that pods were distributed evenly on both crowns and on the ground beneath them. Crowns of *M. bisulcata* and *T. bifoliolata* were measured for the 25-ha area in April 2008 (post 2007 masting), but not re-measured after the 2010 masting.

The projected life-time reproductive capacity for each species was calculated in four steps: (1) A tree on the inflection of D_{crit} ('adulthood') was 'grown' in stem diameter on a 2.5-yr masting interval using mean absolute growth rates (*agr*) for three diameter-classes (10 – <50 , 50 – <100 and ≥ 100 cm); (2) For each time-step, the tree's seed output was then calculated using the 2007 polynomial regressions (see Fig. 1b and d in Results). (3) Each output was then corrected downward by percent adult mortality calculated over the $t = 2.5$ -yr period, m_{int} – mean annualized mortality rates per diameter-class (m_a) in the equation: $m_{int} = 1 - (1 - m_a)^t$; (4) Finally, seed outputs per time-steps until the tree reached its maximum size were summed to yield a cumulative life-time seed output. A caveat to this exercise is that the demographic and stem growth rates from Newbery et al. (2013) used in these projections span only a 20-yr period of forest dynamics (1991–2011). While this could have been done using tree ages (on the x-axis), age-size relationships were highly variable in both species (especially *M. bisulcata*). Note that in the approach above tree survivorship across intermast intervals has been incorporated.

2.4. Seed trapping

In both the 2007 and 2010 masting events, seed dispersal was studied in the easternmost 25-ha (500 m \times 500 m) of the P-plot (Appendix S1). A single seed trap consisted of a hessian sack, cut open on two sides, and hung from four posts of carried-in bamboo, at a height of 75–80 cm (to prevent seed loss to small terrestrial mammals). Hessian material was secured by threading nylon cord along sack edges to give concave-shaped traps of c. 0.89 m² (≈ 0.85 cm \times 105 cm) horizontal catch area at installation. To let rainwater pass through, 5–7 slits <1 cm wide were made to the lower part of the sacking. These traps needed to be in clusters to achieve sufficient catch area yet fit in among the smaller understory trees, and to cater for canopy variation around each location. Clusters also insured against single-trap losses to damage from large mammals (e.g., elephants) and were logistically more feasible to check upon regularly over such a large forest area. All seeds found in traps – intact, germinated and/or predated – were easily distinguished for *M. bisulcata* and *T. bifoliolata*. They were counted, and then discarded under or around the traps. In our censuses we were careful to avoid trampling any seedlings of each species at the trap-cluster locations. On these census visits, traps were checked, cleaned, and repaired if they had been damaged by branch falls or large mammals (bush-pigs, forest elephants, drills).

2.4.1. The 2007 masting event

Traps were grouped into 68 clusters of seven each and split almost equally among four randomly-situated blocks in the

Table 1

Measures of individual tree (*n*) sizes and fecundity for the two ballistically-dispersed rain forest species, studied in two masting years at Korup, Cameroon. Medians (Med.) with different letters are significantly different ($P < 0.001$) based on Mann-Whitney-*U* tests.[§]

	<i>Microberlinia bisulcata</i>				<i>Tetraberlinia bifoliolata</i>			
	Mean (\pm SE)	Med.	Range	<i>n</i>	Mean (SE)	Med.	Range	<i>n</i>
<i>All tree sizes</i> [*]								
Stem diameter (cm)	107.0 \pm 3.78	113.0 ^a	13.7–220.0	130	54.1 \pm 2.83	45.7 ^b	10.5–125.6	135
Crown area (m ²)	501.8 \pm 30.8	433.7 ^a	509–1498	125	123.9 \pm 11.7	68.9 ^b	1.3–471	115
<i>'Adult' tree sizes</i> [†]								
Stem diameter (cm)	116.7 \pm 3.20	116.2	47–220.0	116	67.1 \pm 2.91	68.1	25.5–125.6	99
Crown area (m ²)	541.4 \pm 30.8	475.9	70–1498	115	148.5 \pm 13.4	100.7	5.2–471	92
<i>2007 Masting</i> [‡]								
Seeds per pod	2.49 \pm 0.044	2.46 ^a	1.00–3.44	114	1.60 \pm 0.026	1.63 ^b	1.00–2.07	78
Pods per tree	6756 \pm 652	4335 ^a	3–30,333	114	3105 \pm 496	897 ^b	1–16,986	78
Seeds per tree	17,275 \pm 1644	11 260 ^a	12–72,329	114	5266 \pm 829	2079 ^b	6–29,263	78
<i>2010 Masting</i> ^{‡,§}								
Seeds per pod	2.60 \pm 0.073	2.58 ^a	1.00–3.92	73	1.81 \pm 0.040	1.81 ^b	1.36–3.00	41
Pods per tree	4507 \pm 578	2827 ^a	16–21 890	73	3999 \pm 683	2435 ^a	136–16,190	41
Seeds per tree	12,595 \pm 1716	6908 ^a	16–61 775	73	7249 \pm 1265	4158 ^a	233–30,526	41

Notes:

^{*} Stems ≥ 10 -cm diameter, not including any dead ones; this sample included those live stems in the 50-m buffer surrounding the eastern 25-ha section of the P-plot (see Appendix S1).

[†] Size-onset of reproduction for each species was determined using the modified logistic regression of Thomas (1996a) that was applied to the 2007 data (see Fig. 2a and c).

[‡] Sample of fruiting trees only; non-fruiters were excluded.

[§] Trees in this sample were restricted to inside the eastern 25-ha section of P-plot because of the altered seed trap design used in 2010 (see Appendix S1).

[§] *U*-statistic values for each variable tested, from top to bottom, were respectively: 2981.0, 1972.0, 356.5, 2573.5, 2032.0, 331.5, 1412.5, and 1197.0.

25-ha (see Table 1, Appendix S1). Because saplings or vines could not be cut away at Korup, the array of seven traps varied somewhat from location to location; however, in all cases they were positioned > 1 -m apart, and all but 12 traps were within 7 m of each NE-post (mean \pm SE distance of trap-edge to posts: 3.72 \pm 0.06 m, $n = 469$; one cluster was missed). Traps were installed on 15–22 August 2007 and censused again five times – on 25–27 August; 3–4, 14–15, 29–30 of September; and 11 October 2007 – until dispersal in both species had finished (i.e., no more *M. bisulcata* or *T. bifoliolata* seeds were being caught). Because of wear and heavy rains, trap dimensions were remeasured ($L \times W$ midway along each side) near the end of sampling on 12–13 October 2007. The traps had a mean (\pm SE) catch area of 0.830 \pm 0.003 m² (median = 0.828 m²), which was the value used in dispersal calculations for 2007. Preliminary observations in the field early in August 2007 indicated some seed fall had already occurred for *M. bisulcata*, but less for *T. bifoliolata*.

2.4.2. The 2010 masting event

This number of traps was increased by almost 20% (Table 1) to cover a single 16-ha block, still within the P plot (see Appendix S1). Each cluster consisted of four traps positioned 1.5 m away from its centre, on the four cardinal bearings. Based on the 2007 between-trap variation, it appeared that a minimum of four traps per cluster sufficed, and traps were better employed in 2010 by putting them under more adults. These centres were positioned at the NE-corner-posts (as in 2007), and in the middle of each subplot (Appendix S1). This time they were installed earlier in the wet season (27 June – 10 July 2010) to avoid missing any first-dispersing trees. Traps were censused 10 times, beginning on 16 July 2010 and weekly thereafter through 27 August; then again on 23 September and 2 October, and finally on 14 October 2010. Trap dimensions ($L \times W$) were measured on 15–16 October 2010, and had a mean (\pm SE) catch area of 0.855 \pm 0.002 m² (median = 0.860 m², $n = 578$ with two badly damaged traps omitted).

2.5. Maximum dispersal distances of *M. bisulcata* seeds

On the eastern edge of the *M. bisulcata* grove, three large fruiting trees were found for which far dispersal events (> 50 m) to one

side were unlikely to be confounded by seed inputs from conspecifics. Stem diameters of these trees were 162.5, 182.5 and 220.0 cm when last measured in 2005 (Newbery et al., 2013). At each tree, two transects were run c. 45° apart that started at 50 m from the tree stem. On each transect 25 traps in a wedge-shaped formation were set up, so that there were 1, 3, 5, 7 and 9 traps in a “zig-zag” formation in the increasing annuli of 50 – < 60 , 60 – < 70 , 70 – < 80 , 80 – < 90 , and 90 – < 100 m distance intervals, respectively. These traps ($n = 50$ per tree) were installed on 26–29 July 2010 and censused six times: on 6, 13 and 27 August; on 23 September; and on 2 and 14 October 2010. The dimensions ($L \times W$) of all 150 traps were measured on 13 October 2010 and gave a mean (\pm SE) trap area of 0.911 \pm 0.005 m² (median = 0.916 m²). Unlike those within the P-plot, these traps were made of 1-mm \times 4-mm hole-sized nylon mesh, and suspended from small tree stems.

2.6. Seedling recruitment patterns

The 25-ha of the P-plot in which seeds were trapped had 11 \times 11 NE-corner posts (121 in total). After the 2007 and 2010 mast-fruiting events, ‘new seedlings’, those establishing from the most recent event, were counted within a 5-m radius of each post. For each circular plot (78.54 m²), the portion of its area under water was estimated (to nearest 1/8th), and categorized as being swampy or not. This yielded a total of 121 locations and 9503 m² of ground sampled (Appendix S1). In the 2007 masting year, *M. bisulcata* and *T. bifoliolata* were sampled in this way on 10–12 and 21–23 November 2007; in the 2010 masting year, on 17–22 October 2010.

2.7. Inverse modelling (IM) of seeds in traps

Parameter estimates were found by inverse modelling using the method of maximum likelihood (function mle2 in R-package ‘bbmle’; R Core Team, 2013). The probability density function, $f(r)$, of the model was divided by $2\pi r$ (where r is the radial distance of a trap from the source tree centre, in units of metres) to give the 2D function, $g(r)$, the probability of a seed falling in 1 m² of trapped area (following the notation of Cousens et al., 2008). The expected

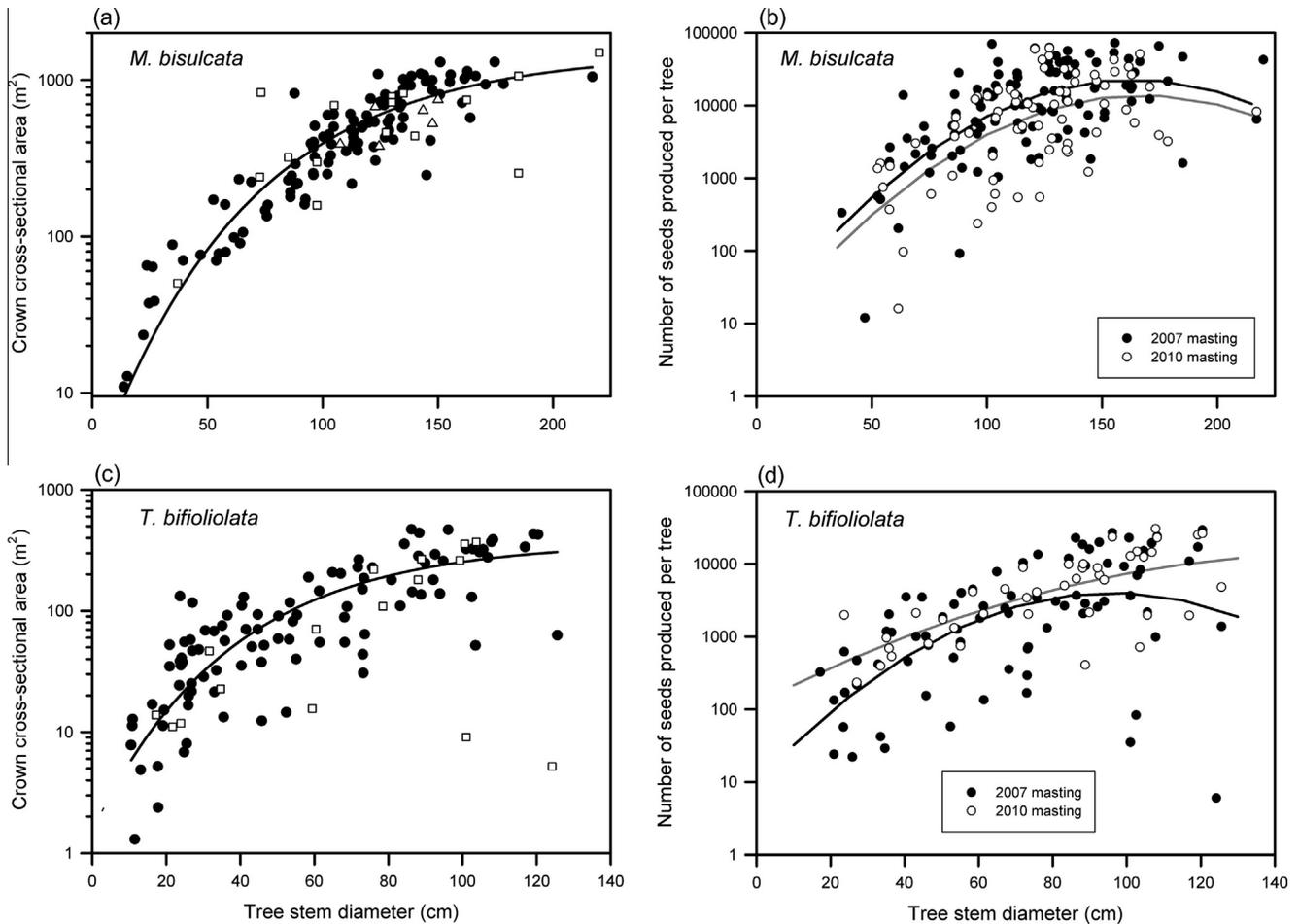


Fig. 1. Individual tree (a and c) crown area projections and (b and d) seed production plotted against their stem diameters for *Microberlinia bisulcata* and *Tetraberlinia bifoliolata* populations studied in two successive masting events at Korup, Cameroon. Each symbol is a single tree. Solid lines are functions fitted to the data: (a) Gompertz, $y = 1506.9 \cdot \exp(-\exp(-(x-119.2)/64.9))$, $\text{adj. } r^2 = 0.68$; (c) lognormal, $y = 5508022 \cdot \exp(-0.5 \cdot (\ln(x/178.8)/0.34)^2/x)$, $\text{adj. } r^2 = 0.20$. Note the different range in values for the x-axes between the two species. In (a) and (c), the open square symbols are trees sampled outside the P-plot; the open triangles in (a) are additional trees that were measured in the 2009 intermast year. In (b) and (d), the polynomial equations were tested separately for each 2007 (black lines) and 2010 (gray lines) masting year, omitting individual trees with zero seed production (non-fruiterers). The fitted equations were: Mb-2007, $\log(y) = 0.985 + 0.0413x - 0.0001264x^2$; Tb-2007, $\log(y) = 0.988 + 0.0545x - 0.000284x^2$; Mb-2010, $\log(y) = 0.793 + 0.0400x - 0.0001195x^2$; Tb-2010, linear, $\log(y) = 2.462 + 0.01393x$. Note that the y-axis in all four panels is on a logarithmic scale.

number of seeds within a particular trap that came from one source tree was therefore $g(r) \times Q \times \text{trap area}$, where Q was the tree's fecundity. Up to several trees would have contributed seeds to any one trap, so the total expected seed count per trap was the sum of all source inputs at their corresponding distances. Minimization of the negative sum of log-likelihoods was arrived at using the "BFGS" algorithm (in 'optimx', within mle2), and checked in many cases using simulated annealing ("SANN"). The fitted model could be returned to $f(r)$, the probability of a seed being dispersed r metres from an 'average' source tree (Cousens et al., 2008). The essential IM functions in R are given in Appendix S2: Bolker (2008) and Schurr et al. (2008) provided important programming guidance.

Dispersal models considered were restricted to the generalized exponential, gamma, lognormal, Wald and Weibull forms. Theoretically there can be no seeds (S) at zero distance because this point is within the tree stem, nor realistically within the stem radius (typically ≤ 1 m), or where buttresses extend outwards from the stem: traps were located at minimum 1 m from tree centres (for the two species \times years), so this was effectively the minimum distance that could be modelled. A maximum distance of 100 m was used since this was known to be well beyond what the species could achieve solely by ballistic means of dispersal.

The observed data were clearly best described by a negative binomial (range in deviance, 0.96–4.27, $\text{df} = 2-7$) rather than the Poisson distribution (442–886, $\text{df} = 3-8$), for both species and years (Appendix S3), and this was taken as the likelihood function (Hilbe, 2011). The frequency distributions of observed counts (S) are shown in Appendix S3. Particularly noteworthy are the 'flat' distributions for counts > 0 for *T. bifoliolata* in both 2007 and 2010. Those for *M. bisulcata* were more continuous. Dispersal was assumed to be isotropic in both species because pods generally form on all parts of their crowns.

2.8. IM of seedlings in quadrats

To reach an inverse model for seedlings, using seed source data, required an extra term in the model and thus a fourth parameter to be estimated (Greene et al., 2004; Martin and Canham, 2010; Canham et al., 2014). This term scaled the mean number of seeds/tree down to mean number of seedlings/tree (see Appendix S3 for empirical estimates). The expected number of seeds within a particular trap was now $g(r) \times f(Q, g) \times \text{trap area}$. Two alternative forms were considered: $f(Q, g) = Q/g$ or Q^g where Q was individual tree fecundity as used in IMs for seeds.

2.9. Relating seed to seedling 'shadows'

The fitted $f(r)$ curves for seeds and seedlings of *M. bisulcata* in each year – back-calculated from their respective lognormal $g(r)$ fits (i.e. $\times 2\pi r$) – were multiplied by their corresponding mean numbers of seeds per fecund tree or by mean numbers of seedlings per fecund tree (Appendix S3). Mean seeds/tree could be found using either of two methods: (1) simply averaging Q estimates per fecund tree, or (2) taking the total numbers of seeds in the total area trapped, scaling up to the expected numbers per 25 ha, and then dividing by numbers of fecund trees. The first was used here, although it was recognized that not all seeds produced fell into traps (some being caught in branches and foliage), and that some *M. bisulcata* seeds were missed in 2007 due to the late start of trapping. The second method, however, was the only one that could be applied to scale up seedling counts to 25 ha, again dividing by the corresponding numbers of fecund trees to get mean seedlings/tree. On this basis, in 2007 the ratio of numbers of seeds to seedlings was 11, and in 2010 it was 21. From the IM seedling fits with $f(Q, g) = Q/g$, g was 6.0 in 2007 and 13.4 in 2010, the differences in scaling between simple averaging and modelling can be largely explained by the non-uniform distribution of seeds and seedlings with distance from trees.

3. Results

3.1. Tree size and fecundity

The size allometry of *M. bisulcata* and *T. bifoliolata* trees was noticeably different in several respects (Fig. 1a and c). First, *M. bisulcata* can exceed stem diameters of 150 cm, and sometimes even 200 cm, whereas the *T. bifoliolata* trees cannot – in fact, they rarely exceeded 110 cm in diameter. Second, *M. bisulcata* could support much broader crowns, on average 3–4 times the size of *T. bifoliolata* (Table 1). Third, crown area appears to accumulate faster in *T. bifoliolata* than *M. bisulcata* but then is reversed: at a 50-cm diameter they were c. 90 m² and 70 m², respectively, but at a 100-cm diameter, the *M. bisulcata* had crowns of c. 400 m² compared to c. 250 m² for *T. bifoliolata* (Fig. 1a and c). The size-class distributions of the two species are obviously different at the site (see Newbery et al., 2013): the many more stems in the 10–50 cm diameter category for *T. bifoliolata* compared to *M. bisulcata* translates into significant disparities in their mean and median stem diameters (Table 1).

A total of c. 32,000 and 26,000 pod valves from the 2007 mastings were found for *M. bisulcata* and *T. bifoliolata* respectively (see Plates in Appendix S1). And likewise c. 25,000 and 31,000 valves were counted from the 2010 mastings. Pods of *T. bifoliolata* never held more than three seeds, more often just one or two seeds, whereas those of *M. bisulcata* could hold between one to seven seeds (Appendix S1). *M. bisulcata* consistently produced a higher mean number of seeds per pod than *T. bifoliolata* in both mastings events (Table 1). For fruiters of both species, in both mastings, fruit production was highly skewed, with a minority of individuals in the population having very many pods in their crowns (Appendix S3). For each species, there was considerable variation in seed production for a given tree diameter in the 2007 masting, which ranged from 10- to 100-fold differences depending on the size-class considered (Fig. 1b and d). In the 2010 masting, this high variation was again evident in the *M. bisulcata* population, whereas that of *T. bifoliolata* showed lower variation. Common to both species in 2007, however, was a trend in asymptotic seed production which apparently peaked at c. 125–150 cm diameter for *M. bisulcata* but at much lower size for *T. bifoliolata* (c. 80–100 cm diam). In 2010, while the polynomial again gave an

improved fit (over linear regression) for *M. bisulcata* it did not for *T. bifoliolata* (Fig. 1b and d).

M. bisulcata median fruit production per tree in 2007 was almost 5-fold greater than *T. bifoliolata*, translating into a 3-to-4-fold greater number of seeds available for dispersal. In 2010, *M. bisulcata* again produced more fruits and seeds per tree on average than *T. bifoliolata*, but their median outputs were not significantly different (Table 1). Across both mastings events, however, the maximum number of pods on any tree of *M. bisulcata* was almost 2-fold higher than any of *T. bifoliolata* (respectively, 30,333 and 16,986), while the corresponding maximum number of seeds was more than 2-fold (72,329 and 30,526).

For comparative purposes, considering just those fruiting trees sampled in the 25-ha of the P plot, the total inputs into the forest summed over all individuals by *M. bisulcata* and *T. bifoliolata* populations were 1,470,950 and 344,007 seeds in 2007 – in the 2010 mastings, these totals were lower in each species by 37% and 14% respectively, at 919,434 and 297,203 seeds. Overall, more seeds were produced by both *M. bisulcata* and *T. bifoliolata* in 2007, when also a greater proportion of individuals fruited in each population than in 2010 (Fig. 2). Although per-capita fruit production showed considerable variation, it was generally higher in 2007 than in 2010 for both species, and it was positively correlated between mastings events across individuals (Fig. 3).

The static inter-individual allometric relationship between a tree's reproductive output (R) and its size in diameter (V) can be expressed linearly using logarithms of the power equation $Y = bX^K$; where the slope value, K , represents a ratio of these two important life-history traits (R/V , Thomas, 1996b; Weiner et al., 2009). Using numbers of pods leads to a conservative assessment since more than one seed can arise from one pod (from a single ovary), especially for *M. bisulcata* (Table 1). Excluding "zero-fruited" trees, the 2007 values (\pm SE) for K were 3.17 ± 0.35 and 2.36 ± 0.41 for *M. bisulcata* and *T. bifoliolata* respectively ($F_{1,112} = 83.5$, $P < 0.0001$, $r^2 = 0.43$; $F_{1,76} = 32.5$, $P < 0.0001$, $r^2 = 0.30$). For the latter species, when three large outlying trees – possibly senescent (see Fig. 1d) – were removed, the fit was much improved ($K = 2.94 \pm 0.31$, $F_{1,73} = 91.7$, $P < 0.0001$, $r^2 = 0.56$). While the ranking stayed the same between species in 2010, the K -values were slightly lower at 2.95 ± 0.44 for *M. bisulcata* and 2.16 ± 0.30 for *T. bifoliolata* ($F_{1,71} = 44.4$, $P < 0.0001$, $r^2 = 0.39$; one outlier removed, $F_{1,38} = 51.5$, $P < 0.0001$, $r^2 = 0.58$).

3.2. Size at onset of seed production

Standard logistic regression curves always gave a larger size at onset of maturity, SOM, as defined by the inflection point in Fig. 2, than did the modified fitting of Thomas (1996a). Based on the more robust sample of 2007, stems of *M. bisulcata* needed to be c. 50% larger in diameter than those of *T. bifoliolata* to begin seeding (Fig. 2a and c). An assumption in this estimation, that individuals consistently produce seed beyond the onset-size of fruiting (Thomas, 1996a), was poorly met with the 2010 data, however, especially for *T. bifoliolata* (Fig. 2b and d). Consequently, for 2010 a much larger diameter was estimated for the onset-size of fruiting in this species (c. 45 cm). Using SOM estimates from 2007, of those individuals in each population with reproductive potential, *M. bisulcata* had a greater proportion of seeders in 2007 and 2010 (97% and 87% respectively) than did *T. bifoliolata* (76% and 54%; Table 1).

The life-time fecundity projections revealed two important species differences (Fig. 4). First, up to a 125-cm diameter, a *M. bisulcata* tree will not have produced as many seeds as a similar-sized *T. bifoliolata*, which, growing much more slowly, participates in more mastings events in spite of a life-time maximum size which

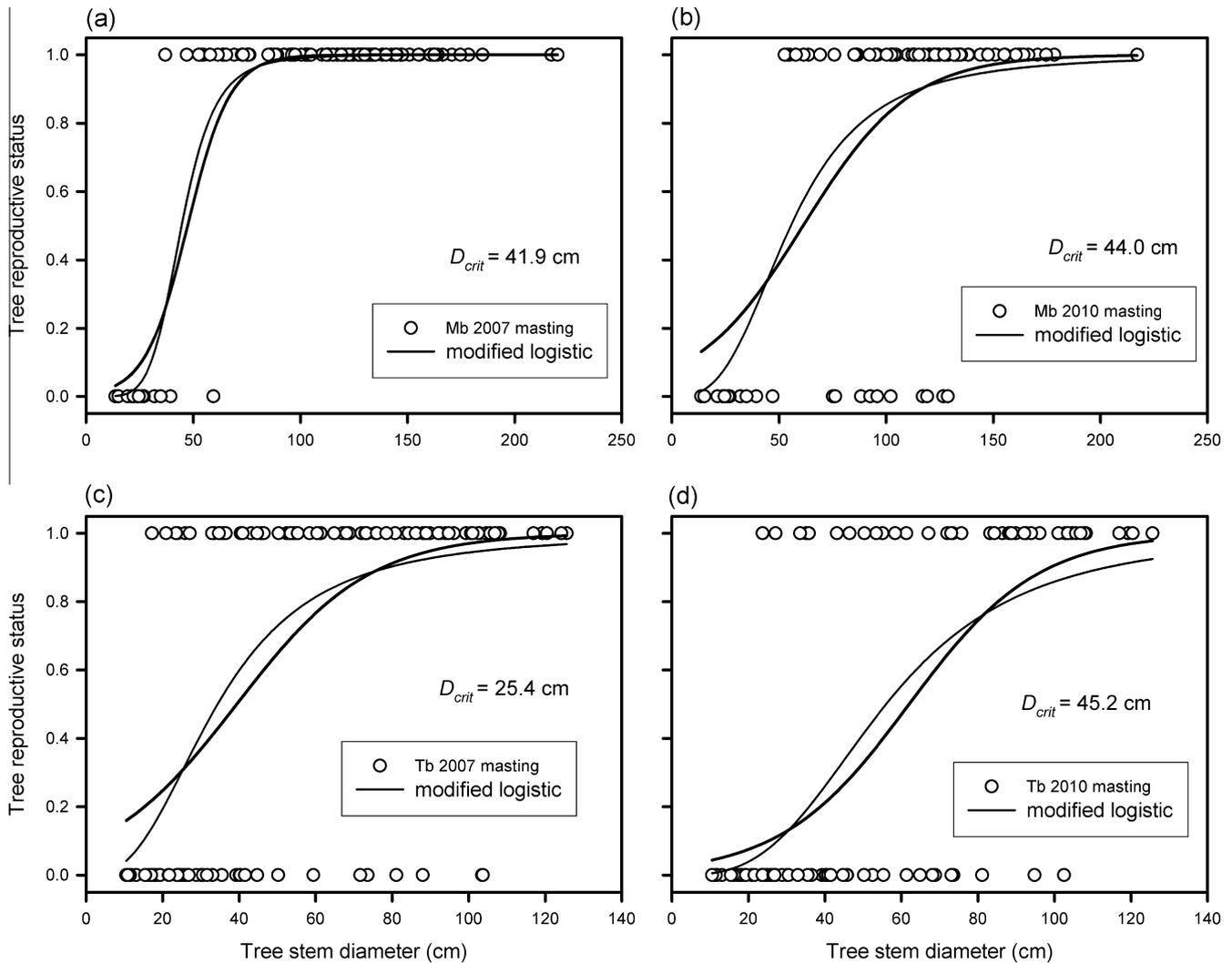


Fig. 2. Reproductive status of stems ≥ 10 -cm diameter surveyed for fruit production in the *Microberlinia bisulcata* (Mb) and *Tetraberlinia bifoliolata* (Tb) populations studied in two successive masting events at Korup, Cameroon. The thick, solid line is the standard logistic function fitted to the data for which 1 = fruited, and 0 = non-fruited state. The thinner line is a modified form of the logistic (Thomas, 1996a) taking the form $P = [e^{a+b(\ln S)}] / [1 + e^{a+b(\ln S)}]$, where P is the probability of reproduction, and S is a tree's diameter: the inflection point of this curve is the estimated size (D_{crit}) when individuals are capable of producing offspring (i.e., seeds). Parameter estimates for the modified regression are (a) $a = -21.64$, $b = 5.699$; (b) $a = -12.04$, $b = 2.998$; (c) $a = -9.34$, $b = 2.641$; and (d) $a = -12.51$, $b = 3.108$.

is half that of *M. bisulcata* (in relative terms, however, both species can begin seeding at near identical proportions of their maximum size [RSOM = 0.19–0.20]). Second, by having to “delay maturity”, in the sense of waiting until a comparatively large SOM is reached to begin seeding, *M. bisulcata* is able to produce just over 1 million seeds for dispersal, or 5.14 times as many than could a *T. bifoliolata* tree, before dying (see asterisks in Fig. 4).

3.3. Seed dispersal relative to source trees

3.3.1. Seed trapping success

In both masting years, approximately 80% of the trap clusters caught at least one seed of *M. bisulcata*, whereas a lower percentage of them caught *T. bifoliolata*, especially in 2010 (Table 2, Appendix S3). Nevertheless, the mean number of seeds caught for each species was comparable between masting years, but still about 3-fold greater in *M. bisulcata* than *T. bifoliolata*. Not unlike fruit production of individual trees (Appendix S3), seed counts in traps were highly skewed. In accord with the summed seed inputs from tree-level fecundity, more seeds were caught in 2007 than 2010 despite the latter's greater sampling effort (Table 2).

3.3.2. IM of *M. bisulcata* seeds in traps

For both 2007 and 2010, the lognormal model fitted best with lowest $-2LL$ -values (Table 3, Fig. 5; LL = log-likelihood). There were $p = 3$ parameters, scale (mean distance) ‘ a ’, shape ‘ b ’ and the negative binomial coefficient, ‘ k ’, so that AIC was equal to $-2LL + 2p$. Details of the model fitting and output criteria used are given in Appendix S2.

3.3.3. Tree fecundity effects

Replacing empirical estimates of tree fecundity (Q) by a power function of tree stem diameter, as diam^q , and estimating parameter ‘ q ’ also in the IM of *M. bisulcata* seed counts in traps (lognormal model), increased the AIC by 26.1 (log-likelihood ratio, $LR \sim \chi^2$, $P < 0.001$, $q = 2.01$) in 2007 and 62.6 ($P < 0.001$, $q = 1.90$) in 2010. This indicated that having individual tree fecundity data significantly improved model fitting for seeds.

3.3.4. Maximum dispersal distances of *M. bisulcata* seeds

For one of the three trees sampled on the grove edge no seeds were caught in the traps. However, at the other two trees, four and seven seeds were caught in total. At the largest tree, two seeds landed 90–100 m from it, while 1, 2, 2 and 0 seeds landed in the

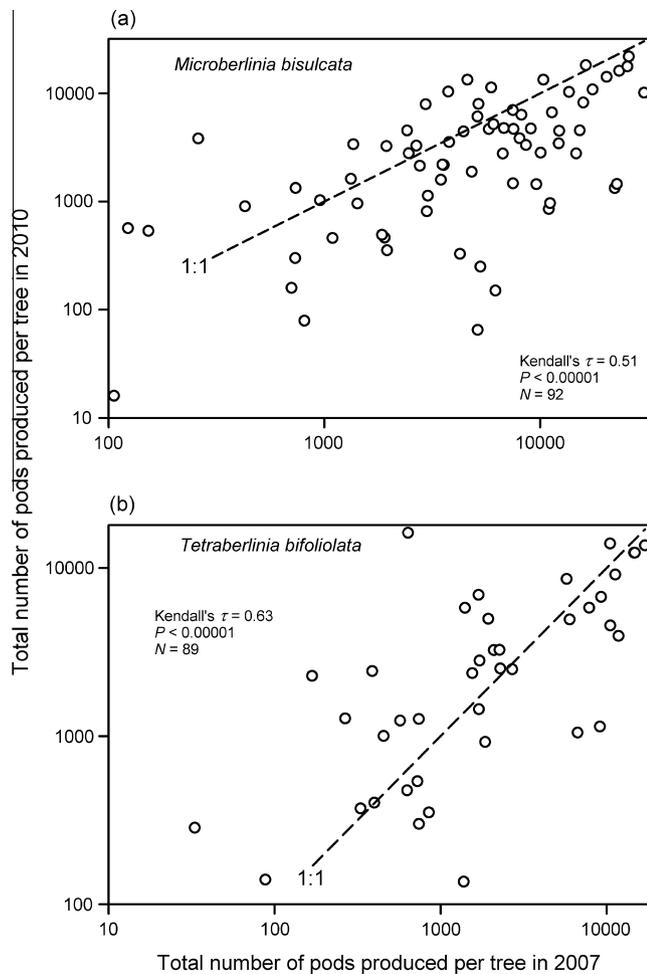


Fig. 3. Levels of fruit (pod) production of all individual trees ≥ 10 cm diameter inside the eastern 25-ha section of the P-plot in two successive mastings events at Korup, Cameroon. When those trees that did not fruit in both mastings years were excluded from the samples, the correlations for (a) and (b) respectively were $\tau = 0.43$ ($n = 83$) and $\tau = 0.43$ ($n = 62$). Note the logarithmic axis scales.

80 – <90, 70 – <80, 60 – <70, 50 – <60 distance intervals respectively. At the other tree, the furthest seed was caught in the 70 – <80 m interval (2 and 1 seeds, respectively, at 60 – <70 m and 50 – <60 m).

3.3.5. IM of *T. bifoliolata* seeds and alternative approach

Extensive model fitting was made for this species, for both 2007 and 2010, but with minimal success. No single or mixture model could be found that met the set of output criteria in the same way as for *M. bisulcata* (Appendix S2). An alternative ‘composite density’ approach was applied, details of which are given in Appendices S5. Seed density declined more steeply in the 2010 than 2007 year, but in both years seed densities rapidly approached zero at distances of c. 35–40 m (Fig. 6).

3.4. Seedling distributions relative to source trees

For *M. bisulcata*, the best fitting inverse model for ‘dispersed’ seedlings in quadrats, with respect to seed source trees, was again the lognormal (Table 3). It performed well with regard to all of the results criteria mentioned for seed modelling (Fig. 5; Appendix S4). For seedlings the $f(Q, g) = Q/g$ led to a better fit for the 2007 seedlings, while $f(Q, g) = Q^g$ was better for the 2010 ones. Seedling

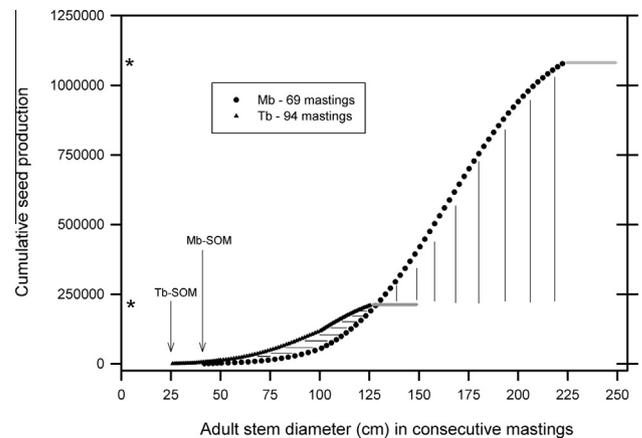


Fig. 4. The life-time reproductive capacity of *Microberlinia bisulcata* (Mb) compared to *Tetraberlinia bifoliolata* (Tb), expressed as cumulative life-time seed output. Mastings were assumed to occur at 2.5 yr intervals, or time-steps, for both species. An adult tree was ‘grown’ until it reached the maximum size observed in the present study (125.6 and 220 cm diameter for Tb and Mb respectively). Owing to its smaller size-onset of reproduction, SOM, (Fig. 2), and subsequent slower growth, *T. bifoliolata* can participate in more mastings events than *M. bisulcata* in its lifetime. For the three size-classes intervals of 10 – <50, 50 – <100, and ≥ 100 cm stem diameter, the corresponding absolute stem growth rates (agr) rates (see Appendix S6) of Mb exceed those of Tb whereas the m_a rates for Mb are very much lower than for Tb (0%, 0.12%, and 0.30% yr^{-1} vs 1.82%, 1.83%, and 3.05% yr^{-1} – from Newbery et al., 2013). The gray bars indicate extreme but infrequent larger diameters attainable by each species at the site. Asterisks are total numbers of offspring produced at maximum sizes.

distributions for *T. bifoliolata* again allowed no reliable and sensible inverse model fitting and no modelling results are presented.

3.5. Relating seed to seedling ‘shadows’

Cumulative $f(r)$ plots for *M. bisulcata* showed that dispersal-with-distance was very similar for seeds and seedlings within each year, indeed much closer in 2010 than in 2007 (Appendix S4). In 2007 there was a tendency for seedlings to be further from stems than seeds indicating slight adult-seedling repulsion that year. In 2007, 95% of seeds were within 40.8 m, while in 2010 they were within 76.7 m; and correspondingly for seedlings the distances were 53.5 and 84.6 m. In the lighter mast year (2010), seeds dispersed – and seedlings established – further away from adults than in the heavier one (2007).

Plotting counts-with-distance curves for *M. bisulcata* seeds and seedlings in the two years (Fig. 7) revealed several interesting similarities and differences. Peak (modal) seed production in 2007 ($882 m^{-1}$) was close to double that in 2010 ($436 m^{-1}$), although in the latter dispersal was on average further than the former. By contrast, peak seedling density in 2007 ($67.8 m^{-1}$) was ~ 3.5 -fold that in 2010 ($19.4 m^{-1}$). These estimated densities from the IMs gave seed/seedling peak ratios of 13.0 and 22.5, slightly higher than those from the average-over-25 ha empirical counts. Within years, however, modal and mean distances for seeds and seedlings were very similar. Comparing fits with $f_n(Q, g) = Q^g$ across years, the mean (\pm SE) g -values were 0.815 ± 0.012 in 2007 and 0.717 ± 0.014 in 2010 (Table 3), implying density-dependent losses (g being < 1.0) in the seed-to-seedling transition in both years, and the process being stronger in the year with fewer seeds (2010) than the one with more (2007). Again, no comparable analysis could be made for *T. bifoliolata* because of the inadequate IMs of its seed dispersal pattern.

Both species could, however, be compared for their spatial extent of seedling recruitment in the forest. In 2007 at least one *T. bifoliolata* seedling was found alive in 45% of the ground quadrats

Table 2
Description of trap design and counts of ballistically-dispersed seeds caught in them for *Microberlinia bisulcata* (Mb) and *Tetraberlinia bifoliolata* (Tb) rain forest trees in two masting years at Korup, Cameroon.

	2007 Masting event		2010 Masting event	
	Mb	Tb	Mb	Tb
Number of trap-cluster locations	68		145	
Number of traps per cluster	7		4	
Total trap area per cluster (m ²)	5.81		3.42	
Total area sampled for seeds (m ²)	395.1		495.9	
Proportion of clusters with seed	0.84	0.53	0.76	0.39
Mean number of seeds per cluster	30.9 ± 6.1	28.1 ± 7.3	11.3 ± 2.0	10.8 ± 2.8
Median number of seeds per cluster	8	1	4	0
Mean seed density over clusters (no./m ²)	5.32	4.84	3.30	3.16
Mean seed density over all traps (no./m ²)	4.42 ± 0.36	4.02 ± 0.42	2.83 ± 0.26	2.71 ± 0.36
Total number of seeds caught in all traps	2103	1913	1643	1571

Table 3
Statistics of the fit of the log-normal model to counts (*S*) of (a) seeds dispersed to traps, and (b) seedlings in quadrats, for *Microberlinia bisulcata* in two masting years (*a* = scale, *b* = shape), with *g* as the seed source-to-seedling dependence parameter in (b). The 95% confidence limits are given in parenthesis below means and standard errors of estimates; MA is major axis regression.

Statistics and estimates	Mb 2007		Mb 2010	
(a) Seeds		<i>z</i>		<i>z</i>
AIC	467.7		771.2	
<i>a</i> ± SE	19.25 ± 1.06 (17.01, 21.35)	18.14***	27.63 ± 1.89 (24.44, 32.19)	14.64***
<i>b</i> ± SE	0.548 ± 0.052 (0.473, 0.693)	10.52***	0.830 ± 0.060 (0.729, 0.975)	13.91***
<i>r</i> _(obs-exp; S>0)	0.885		0.858	
MA α ; β _(obs-exp; S>0)	-0.08, 1.09		-0.06, 1.04	
Mean distance (m)	19.3		27.6	
Mode (m)	12.3		9.8	
(b) Seedlings				
Dependence model	<i>Q/g</i>		<i>Q^g</i>	
AIC	1019.7		509.5	
<i>a</i> ± SE	21.73 ± 1.53 (18.60, 24.92)	14.20***	29.94 ± 3.98 (23.50, 41.81)	7.52***
<i>b</i> ± SE	0.694 ± 0.058 (0.590, 0.835)	11.94***	0.853 ± 0.100 (0.697, 1.151)	8.50***
<i>g</i> ± SE	5.956 ± 0.715 (4.601, 7.444)	8.33***	0.7167 ± 0.0143 (0.6901, 0.7485)	50.03***
<i>r</i> _(obs-exp; S>0)	0.871		0.824	
MA α ; β _(obs-exp; S>0)	0.365, 0.973		0.090, 1.011	
Mean distance (m)	21.7		29.9	
Mode (m)	10.6		10.1	

*** *P* < 0.001.

surveyed, which was half that for *M. bisulcata* (91%). But in 2010 fewer quadrats had new seedlings of either species (35% and 79% respectively).

4. Discussion

4.1. Seed production

The masting event in 2007 was stronger than the one in 2010 for *M. bisulcata*, evidenced by a larger proportion of individuals fruiting, fewer pods aborting, and a greater per capita fecundity (seeds and pods). For *T. bifoliolata* per capita fecundity was greater in 2010 than 2007, mainly because only the most fecund (usually the largest) trees in 2007 also produced seeds in 2010. Within-population variation in seed production in a masting year was very high for each species, ranging over four orders of magnitude. This, coupled with high individual variation across events, indicated that trees were rarely either consistently heavy-fruiterers or non-fruiterers. The 2007/2010 results extend the series of previous eight mast fruiting events for *M. bisulcata* (1989–2004) at Korup documented in Newbery et al. (2006a). Importantly, including estimated

individual tree fecundities in each year, including ‘zero-fruiterers’, rather than relying upon allometric scalings of fecundity on stem diameter, significantly improved the IM fitting for *M. bisulcata*.

That fecundity must increase in proportion to tree diameter in IM-dispersal studies has been questioned before. Martin and Canham (2010) found that while two temperate species (*F. grandifolia* and *Q. rubra*) did increase in fecundity once large enough to reproduce, five others showed no trends. Similarly, five tropical tree species had flat relationships while four more had curvi-linear relationships in Puerto Rican forest (Uriarte et al., 2005) – not unlike the asymptotic patterns found for *M. bisulcata* and *T. bifoliolata*. Nevertheless, larger-sized tropical (and extra-tropical) trees are probably more likely to flower and seed than smaller-sized ones (Thomas, 2011). At Korup, the clumped distributions of the source trees generated coarse-scale patchiness in the seed rain, which became patchier at finer-scales because of high intraspecific variation in fecundity across diameter-classes that was largely driven by subsets of heavy fruiterers in each population. Highly unequal fruiting also characterized red oak regeneration (Moran and Clark, 2012), suggesting this may not be an uncommon feature in masting trees. Neglecting to properly consider *individuality*, i.e., tree-level fecundity and cases of ‘zero-fruitering’ trees, may introduce

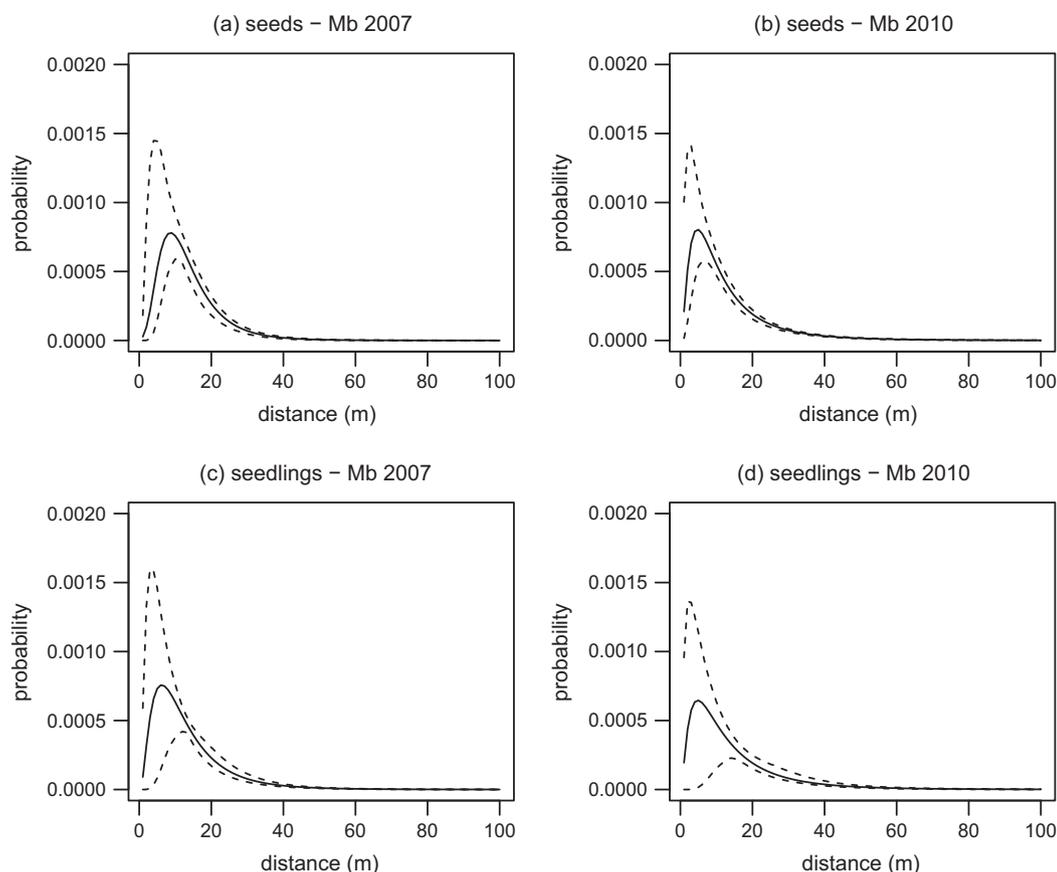


Fig. 5. Fitted lognormal dispersal kernels ($g[r]$) derived by inverse modelling (solid line) and their 95% bootstrapped confidence envelopes (dashed lines) for seeds and seedlings of *Microberlinia bisulcata* in 2007 and 2010. Probability is the expected relative frequency that a seed falls into a trap (a and b), or a seedling establishes in a quadrat (c and d), of 1 m^2 within the circular area around an average source tree, whose radius (r) is the distance shown.

spatial biases in modelling, as was shown for *Abies alba* and *Pinus halpensis* (Sagnard et al., 2007 and Schurr et al., 2008 respectively; also see Clark et al., 2004; Canham et al., 2014). Hence, as further shown by our study, IM studies of the dispersal process could be more robust and make better predictions if seed production is quantified *directly* for individual ‘source’ trees.

4.2. Reproductive traits and capacities

Timing of reproduction during the ontogeny of a tree is a key component in determining fitness. In tree species, reproduction and dispersal of offspring starts after a relatively long juvenile stage compared with other plant life forms, and for those that mast fruit it continues intermittently until old age. Besides fecundity schedule, tree size at onset of maturity (SOM) is a life-history trait that links growth rate and tree allometry to population dynamics. It determines too, in part, how resources are allocated to achieve an optimal strategy in a given environment (Bell, 1980; Stearns, 1992; Charnov, 1993). However, to fully understand tree life history schedules SOM must be linked to mean age at maturity and longevity.

Fecundity in both study species showed strong departures from unity for the fitted b -parameter in R - V scalings. These departures are consistent with life-history theory on optimal allocation of resources and do not support a simple biomechanics interpretation for size-dependent fecundity in trees (Thomas, 1996b; Weiner et al., 2009). The SOM for *M. bisulcata*, at 42(–44) cm, is among the highest reported for any tropical forest tree species; and it accords with earlier approximate estimates of 46–55 cm by

Newbery et al. (2004). The value is, *prima facie*, comparable to *Prioria copaifera* (Fabaceae, Caesalpinioideae) at 47 cm and *Alchornea costaricensis* (Euphorbiaceae) at 43 cm in Panamanian forest (Wright et al., 2005); and to *Diospyros maingayi* (Ebenaceae) at 51 cm in Malaysian forest (Thomas, 1996a). The SOM for *T. bifoliolata*, at 25 cm, was more typical of many other tropical tree species.

Different tree species will, however, grow at different rates of stem diameter increment until the onset of maturity, so similar SOM-values will likely imply very different ages at onset. For instance, the average age when *M. bisulcata* matures was close to 65 years (estimated from D_{crit} and the stem growth rates compiled in Appendix S6), which is a little higher than the estimate of 51 years obtained by dendrochronology (Newbery et al., 2013), while for *T. bifoliolata* it was 84 years (Appendix S6). Trees of *M. bisulcata* and *T. bifoliolata* very rarely exceeded stem diameters of 2.3 and 1.3 m in recent decades at Korup, with likely maximal ages of 240 and 333 years respectively (again see calculations in Appendix S6). Thus while *T. bifoliolata* reaches just over half the maximum size of *M. bisulcata*, due to its one-third to one-half slower growth rates (varying with ontogeny), it becomes much older and so may participate – albeit less intensively – in more masting events than *M. bisulcata* in which to disperse its seeds (see Fig. 4).

4.3. Seed dispersal

The greater variation in crown area as a function of stem diameter (range 20–120 cm) in *T. bifoliolata* than *M. bisulcata* may have been due to asymmetric competition and differing liana loads.

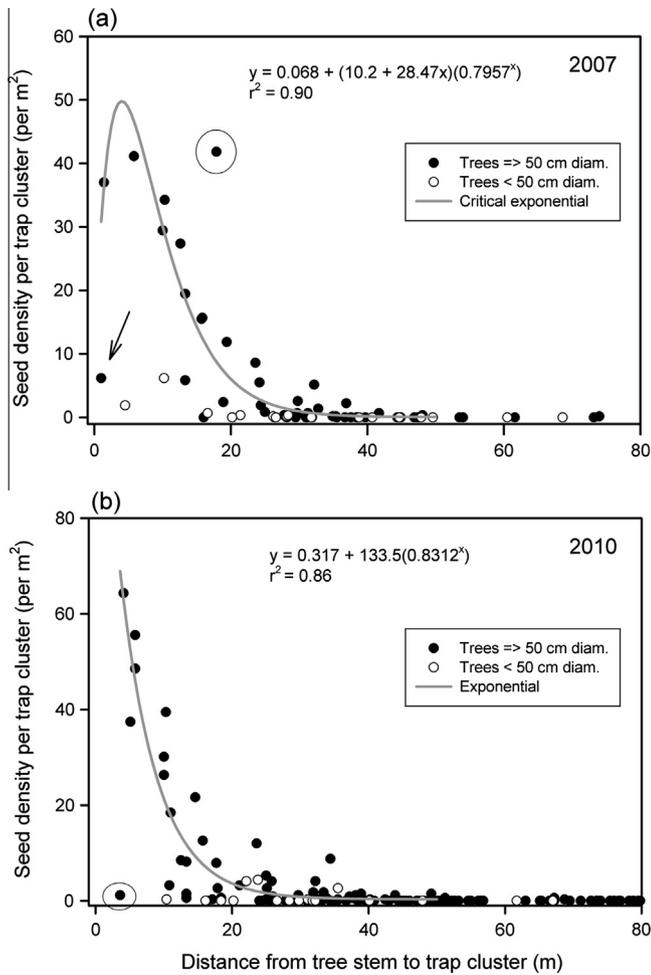


Fig. 6. Seed density as a function of distance to the nearest and/or most fecund *Tetraberlinia bifoliolata* trees for the masting population in 2007 and 2010. In both years, functions were fitted using least squares regression to the subset of data consisting of 'large' trees (*sensu* Newbery et al., 2013) up to 50 m distance from seed traps. In (a), the circled tree had produced c. 10,600 seeds and was 14.7 m further away from the nearest tree to that trap-cluster, which itself was 8.9 m away from the cluster and had produced 2087 seeds; the arrow points to a 53.2-cm-diameter tree smothered with vines, which had produced only 512 seeds. With these two outliers included, the model fitting was lower ($r^2 = 0.69$) than when the former outlier was corrected and the latter one omitted ($F_{3,41} = 133.67$; $P < 0.001$). In (b), the circled tree had a 103.5-cm diameter, but its only 'half-crown' extended in the opposite direction of the trap-cluster. With this outlier included the model fitting was lower ($r^2 = 0.63$) than with it omitted ($F_{2,79} = 249.6$; $P < 0.001$).

Trees of *T. bifoliolata* approaching the canopy need to adjust their crown shapes to fit in closely among the broader more symmetrical crowns of their larger *M. bisulcata* neighbours (Newbery et al., 2013). Liana loads and resulting partial crown breakages were also noticeably higher on *T. bifoliolata* than *M. bisulcata* (J.M. Norghauer, pers. obs.). Besides causing crown asymmetry, liana loads may result in reduced tree fecundity on heavily infested trees (Wright et al., 2005; Kainer et al., 2006). Crown asymmetry would have led to irregular patterns of seed dispersal (i.e., anisotropy) and seedling recruitment around adult trees. This too may partly explain the inability to obtain significantly robust IM fits of any dispersal kernel for *T. bifoliolata*, in contrast to *M. bisulcata*.

The best-fitting dispersal kernel ($g[r]$ and $f[r]$) for *M. bisulcata* in both masting years was the lognormal pdf. The probability of a seed landing on the ground was therefore not highest at the tree stem but beneath the crown, in this case at a distance of 10–15 m from the stem. Tree architecture should play a determining role in the shape of a dispersal kernel (Thiede and Augspurger,

1996; Cousens et al., 2008). *M. bisulcata* has a domed umbrella-shaped crown, which is unusually deep and spreading, on which its pods mature at the ends of panicles as extensions to the almost leafless twigs, and are thus well exposed, much like small 'flags', above the canopy foliage (Plates in Appendix S1; Newbery et al., 2006a; Newbery et al., 2013). These adult traits should optimize the ballistic trajectory of ejected seeds. From pods held higher than the maximum point of foliage on the crown surface, seeds will likely be thrown either beyond the crown or back over it. However, when pods are positioned lower, seeds not ejected away from stem will often collide with higher parts of the tree's crown and then fall vertically. This is not to preclude that some seeds will travel through gaps in the canopy and into branches below. Since the outer crown annuli have the most pods, the latter trajectory will be the more common, dropping proportionally more seeds beneath the parent canopy, as the lognormal pdf describes. The dispersal tail will consist of those seeds more freely ejected over the crowns of both the *M. bisulcata* tree and its immediate neighbours.

Another factor helps to explain the lognormal distribution and its model peak beneath the canopy. Seeds thrown back into the crown that collide with branches could be deflected in almost any direction, whereas collisions with the stem will mostly deflect seeds away from it. Greene et al. (2004) drew attention to this factor in their study of dispersal of several temperate – albeit largely wind-dispersed – tree species, and for which the lognormal was also the best fitting kernel by IM. Thus while the lognormal 'description' for *M. bisulcata* is understandable, a mechanistic explanation modelling all of the factors is highly complex. For *T. bifoliolata* the effects of neighbours, especially the larger-crowned *M. bisulcata*, are even more acute. This explains the almost complete absence of a tail for *T. bifoliolata* and the failure to fit a pdf with IM. Analyses of seed paths (Schurr et al., 2008; Herrera et al., 2011) was not possible since crown dimensions of the other trees besides the two studied were lacking.

The shape and scale parameters of the dispersal kernel of *M. bisulcata* changed between masting years. The c. 50% greater mean distance that seeds of *M. bisulcata* dispersed in 2010 than 2007 might have resulted from a lessening trajectory curtailment by neighbouring foliage in 2010 compared to 2007. Interestingly, *T. bifoliolata* (for which neighbours' foliage was putatively a major factor) also dispersed further in 2010 than 2007. Less interference, and hence greater clearance for seeds, is plausible too if trees that fruited were larger in 2010 than 2007. For *M. bisulcata*, median crown area was slightly larger in 2010 than 2007 (512 vs 478 m²), while the relative difference between years was much greater for *T. bifoliolata* (186 vs 124 m²). Temporal changes in IM-derived kernels have been reported but usually ascribed to changing fruit production and animal disperser behaviour (e.g., Martínez and Gonzalez-Taboada, 2009). Although a particular kernel type may prevail as a species' primary mode of dispersal (Cousens et al., 2008) – like the lognormal for *M. bisulcata* – it is often modified by other abiotic and biotic factors. Furthermore, a kernel might be expected to change when strong environmental perturbations result in temporarily high leaf loss (such as dry periods; Newbery et al., 2004) and some deaths among non-*M. bisulcata* species. Under such a scenario, the reduced interference from other neighbouring species' foliage would allow for the larger seed shadow required for grove infilling and expansion by *M. bisulcata*.

For *T. bifoliolata*, seeds were more strongly aggregated around source trees, because large spaced adults (>50 cm stem diameter) contributed predominantly to this species' pattern of dispersed seeds. Since the maximal dispersal distance was rarely as large as 50 m too, seeds of *T. bifoliolata* were strongly patchily distributed compared with the more homogeneous and broader spatial spread of seeds of *M. bisulcata*. This difference between the species was matched by their frequency distributions (counts histograms)

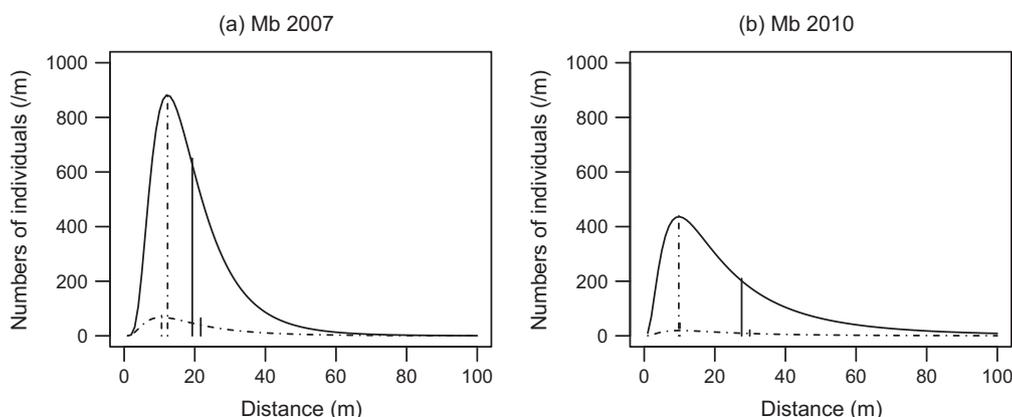


Fig. 7. Dispersal kernels for seeds and seedlings of *Microberlinia bisulcata* in (a) 2007, and (b) 2010, presented in terms of predicted counts per 1-m interval of radial distance (r) away from source trees. The numbers of individuals (seeds or seedlings) were derived by scaling up the $f(r)$ -kernels (fitted by inverse modelling) by average numbers of seeds produced by, or seedlings found around, fecund source trees in the respective years. The solid and dashed lines are the mean and modal distances of the fitted distributions respectively (as in Table 3).

of seeds in traps and seedlings in quadrats. The results accord further with an earlier seed-addition experiment at Korup (in the same 25 ha of forest) showing that seedling recruitment of *T. bifoliolata* was more seed-limited than that of *M. bisulcata* (Norghauer and Newbery, 2010).

Just three other field studies of ballistic seed dispersal in canopy trees have been published. For four trees of *T. moreliana* in Gabon, the maximum distance dispersed from the stem was 70 m, and with a mean pod release angle of 17.2° to the horizontal (van der Burgt, 1997). For two trees of another caesalpiniaceous species, *Eperua falcata*, in Guyana, the distance was only 30 m (Forget, 1989). Finally, for a single tree of *Hura crepitans* (Euphorbiaceae), in Ghana, seeds travelled up to 45 m, with a near-optimal pod angle to the horizontal of 34° (Swaine and Beer, 1977). The positioning of pods in the crowns of *M. bisulcata* and *T. bifoliolata* is very similar to that of *T. korupensis* in Korup, so seed release is quite likely to have ballistic dynamics similar to that described by van der Burgt (1997). In addition, Hart (1995) noted that the two ballistically-dispersed caesalp trees *Gilbertiodendron dewevrei* and *Julbernardia serrettii* at Ituri in Zaïre, with average seed masses of 30 and 4 g, dispersed respectively 5–10 and 30–40 m beyond tree crown edges. Prior studies on ballistic dispersal have involved very small sample sizes: the present study is the first to have used adequate statistical sampling for both tree population size and forest site.

4.4. Population dynamics

The discussion here focusses on the dynamics of *M. bisulcata* for two main reasons. Firstly, this species dominates the Korup groves and appears to drive the dynamics of its co-dominants *T. bifoliolata* and *T. korupensis*, as well as the other less abundant canopy species (Newbery et al., 2013). Secondly, the very poor recruitment of *M. bisulcata* has attracted much study of its different life stages and the factors controlling them at the site (Newbery et al., 1998, 2006b, 2010). The valuable data on the fecundity and dispersal of *T. bifoliolata* can be brought together with the same for *M. bisulcata* to help better understand the latter's dynamics. Implications for adult-juvenile repulsion in *M. bisulcata* (Newbery et al., 2010) and grove expansion (Newbery et al., 2004) will be addressed in the context of current modelling of grove dynamics (D.M. Newbery et al., unpublished).

4.4.1. Seed-to-seedling stage

There was indirect evidence of negative density dependence operating on *M. bisulcata* in the transition from seed to seedling

in 2007 but not in 2010, and this accords well with the results of two other studies at Korup. From a seed addition experiment during the 2007 masting, Norghauer and Newbery (2010) found that the new seedling recruitment function for *M. bisulcata* was also density-dependent. Earlier, during the 1995 masting, Green and Newbery (2002) showed that seed-to-seedling survival in control plots was almost twice as high further from (5 m beyond crowns) than close to fruiting trees.

4.4.2. Biotic interactions

Although seeds falling into tree-fall gaps have an increased risk of being predated by small mammals, the latter could be satiated there and simultaneously the risk of predation by invertebrates is lower too. This interaction reverses in the understorey however (i.e. under closed canopy conditions), and applies to both species (Norghauer and Newbery, 2011). Strongly localised seed dispersal should, therefore, be most effective in satiating the invertebrate predators. Acting counter to this last process, however, distance-dependent attack by leaf-eating insects of seedlings in gaps will tend to act in the direction of spatial repulsion of the surviving saplings by their parents, particularly for *M. bisulcata* (Norghauer et al., 2014).

4.4.3. Competition

Trees of *M. bisulcata* can disperse their seeds much further than can those of *T. bifoliolata*. And within the *M. bisulcata* population, larger individuals can disperse their seeds further than smaller ones because they are generally both taller and have wider crowns. *M. bisulcata* had approximately double the per capita seed output (averaging over the two years) than *T. bifoliolata*. Together, this affords *M. bisulcata* a considerable advantage over the smaller-crowned, less fecund, *T. bifoliolata* in local (within-grove) competition for space and resources.

4.5. Implications for life history strategies

By delaying reproduction until it has reached a stem diameter of 45–50 cm, *M. bisulcata* invests all resources until then to vegetative growth, to produce a tree that is near maximum height, with main branches, mature crown, and an extensive root and buttress system (Newbery et al., 2009). Above and below ground it is in a strong competitive position with *T. bifoliolata*, *T. korupensis* and the other less abundant large-tree species. Capturing space will allow *M. bisulcata* to attain high survivorship, grow faster, expand its crown and then reproduce effectively. The fast stem growth is in

part a result of its strong dependence on ectomycorrhizas for P uptake and recycling (Newbery et al., 1988, 1997). By contrast *T. bifoliolata* starts to produce seed as a smaller – although not necessarily younger – tree, when its form and height are moderate, and it will be subject to competitive dominance of *M. bisulcata* as a neighbour which leads to more limited reproductive output. This may explain why *T. bifoliolata* masts less intensely, and shows larger within-species differences, than *M. bisulcata*. Besides being able to satiate predators more effectively than *T. bifoliolata* (Norghauer and Newbery, 2011), *M. bisulcata* with its less shade-tolerant seedlings will have greater potential to reach lighted gaps and recruit and hence generally raise its fitness above that of *T. bifoliolata* (Newbery et al., 2010). Conversely, *T. bifoliolata* has more shade-tolerant seedlings, so a more limited dispersal than *M. bisulcata* is not so disadvantageous because its seedlings can also survive well away from gap areas.

A large SOM entails opportunity costs, however, as finite resources are invested into growth that could be used for reproductive structures. But in accord with optimal resource allocation models (Stearns, 1992; Kozlowski, 1992), this strategy in *M. bisulcata* would be selected because it has a near-zero risk of dying as an adult (0.12–0.30% yr⁻¹, Newbery et al., 2013), which when coupled to its stature and small seed size offsets these potential costs to fitness. Moreover, a comparatively very fast growth rate in *M. bisulcata* means that it can reach SOM faster – maturing sooner in age – and also become larger for the next masting opportunity to produce even more offspring (see Fig. 4).

These combined traits of *M. bisulcata* are rather unusual for rain forest tree species. It does not fit with a life-history view that fast growth incurs higher mortality risks across ontogeny and reduced longevity. A very important characteristic of *M. bisulcata* is its low tolerance of shade, yet high response to lighted conditions, as a seedling/sapling (Green and Newbery, 2001a, 2001b). It is not a pioneer species *per se*, attested also by it having no seed bank and a relatively inefficient means of dispersal compared to species using wind or animal vectors, but has been categorized as a long-lived light demanding tree species (Newbery et al., 2010, 2013). These converging life-history traits in *M. bisulcata* vis-à-vis those of smaller SOM, slower growth, higher adult mortality and better seedling shade-tolerance in *T. bifoliolata*, are compatible with some aspects of life-history theory and are consistent with well-known trade-offs (e.g., competition vs colonization, seed mass vs seed numbers; Salisbury, 1942), and perhaps especially that of a 'tolerance-fecundity' trade-off in forest trees (Muller-Landau, 2010).

Going beyond these considerations, however, the *M. bisulcata* trait-set instead further suggests a strategy that is adapted to an unstable environment, and consequently an unstable size/age population structure. Conceivably then, the larger SOM and competitive stature of *M. bisulcata*, in comparison to *T. bifoliolata*, not only ensures that enough seeds are produced and dispersed locally for grove in-filling and possible expansion, but that more essentially it can take optimal advantage of long-term temporal variation in the environment that creates opportunities for large waves of recruitment, i.e. transient dominance (Newbery et al., 2013). A wider consideration of life-history models applied to tropical rain forest trees may well confirm that other species like *M. bisulcata* have delayed trees SOM as a key trait for their regeneration and persistence.

4.6. Conclusions

Ballistic dispersal is the most common means of dispersal among the caesalpinoid Leguminosae (Fabaceae) of the Atlantic coastal forests of Central Africa. Moreover, all tree species which are within its tribe Amherstieae (i.e. most of those at Korup) are ectomycorrhizal (Letouzey, 1968; Aubréville, 1970; Newbery

et al., 1988, 2000), and these same species show a tendency towards spatial aggregation in the form of small patches up to large groves. In this context, the research presented here from Korup is a first step towards better linking their seed dispersal ability over space and time and its other associated reproductive traits to differing tree life histories and their attendant population structures and dynamics. Because ballistic dispersal does not permit effective escape of juveniles from their adults, biotic pressure from seed predators and pathogens would have further selected for mast fruiting. Gains in fitness achieved by successful local establishment on soils which afford competitive superiority and dominance, appear to have offset losses in fitness caused by natural enemies, and resulted in a multi-faceted evolutionary stable strategy.

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Appendices S1–S6

Supplementary material associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2014.11.005>.

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