



# Tree size and fecundity influence ballistic seed dispersal of two dominant mast-fruiting 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

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

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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  $\geq 50$  cm, and 41.7% of the basal area of trees  $\geq 10$  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<sup>-1</sup>), 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 ( $\leq 2.3$  m) than *T.*

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