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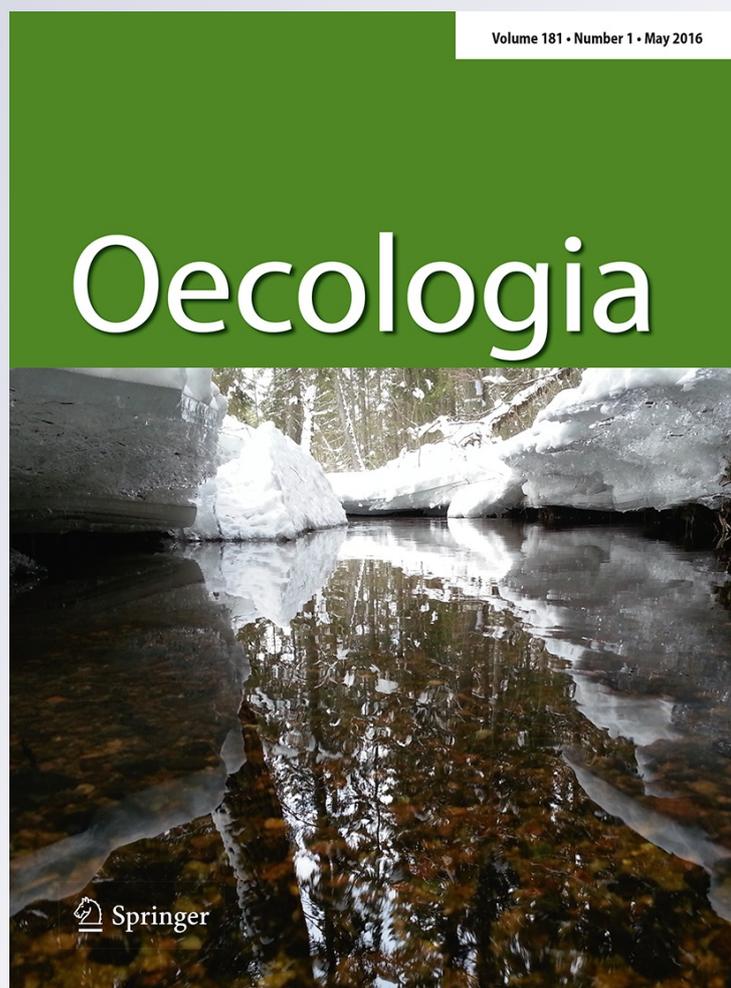
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Density-dependent dynamics of a dominant rain forest tree change with juvenile stage and time of masting

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Abstract Although negative density dependence (NDD) can facilitate tree species coexistence in forests, the underlying mechanisms can differ, and rarely are the dynamics of seedlings and saplings studied together. Herein we present and discuss a novel mechanism based on our investigation of NDD predictions for the large, grove-forming ectomycorrhizal mast fruiting tree, *Microberlinia bisulcata* (Caesalpinaceae), in an 82.5-ha plot at Korup, Cameroon. We tested whether juvenile density, size, growth and survival decreases with increasing conspecific adult basal area for 3245 ‘new’ seedlings and 540 ‘old’ seedlings (< 75-cm tall) during an approximately 4-year study period (2008–2012) and for 234 ‘saplings’ (≥ 75-cm tall) during an approximately 6-year study period (2008–2014). We found that the respective densities of new seedlings, old seedlings and saplings were positively, not and negatively related to increasing BA. Maximum leaf numbers and heights of old seedlings were negatively correlated with increasing basal areas, as were sapling heights and stem diameters. Whereas survivorship of new seedlings decreased by more than one-half with increasing basal area over its range in 2010–2012, that of old seedlings decreased by almost two-thirds, but

only in 2008–2010, and was generally unrelated to conspecific seedling density. In 2010–2012 relative growth rates in new seedlings’ heights decreased with increasing basal area, as well as with increasing seedling density, together with increasing leaf numbers, whereas old seedlings’ growth was unrelated to either conspecific density or basal area. Saplings of below-average height had reduced survivorship with increasing basal area (probability decreasing from approx. 0.4 to 0.05 over the basal area range tested), but only sapling growth in terms of leaf numbers decreased with increasing basal area. These static and dynamic results indicate that NDD is operating within this system, possibly stabilizing the *M. bisulcata* population. However, these NDD patterns are unlikely to be caused by symmetric competition or by consumers. Instead, an alternative mechanism for conspecific adult–juvenile negative feedback is proposed, one which involves the interaction between tree phenology and ectomycorrhizal linkages.

Keywords Density dependence · Lowland tropical forest · Mast fruiting · Negative feedback · Seedling growth and mortality

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Introduction

Because ecology is concerned with interactions that determine the sizes of populations and distributions of species, questions of how populations persist, fluctuate and are limited at different spatial and temporal scales, as brought about by changes in their density, have attracted much interest. This useful, yet elusive concept of “density dependence” remains a cornerstone of thinking in population dynamics and community ecology. Density dependence occurs when changes in population density affect one

or more of the demographic rates of a population (birth, death, immigration or emigration) to limit population growth rates at high density or, conversely, to release them at low density, via the various interactions between individuals (Harper 1977; Hixon et al. 2002; Krebs 2002; Vandermeer and Goldberg 2003; Herrando-Perez et al. 2012).

Typically, density dependence is explored statistically in the form of a so-called “density-dependent relationship”, where a demographic response variable, or sometimes an estimate of the population growth rate, is plotted against population density (number or biomass per unit area; Watkinson 1986; Sibly and Hone 2002; Herrando-Perez et al. 2012). Although density dependence by definition is closely related to the regulation of population size *sensu stricto* (i.e. number of adults), since at least one demographic variable must be under density-dependent control for regulation to be even possible, these tests alone cannot be proof of population regulation *per se* (Watkinson 1986; Krebs 2002; Newbery and Stoll 2013). Indeed, much controversy and confusion about the prevalence of density dependence in community dynamics has been due to the weak use of language and badly defined terms which have often been applied in a muddled fashion across sub-disciplines (reviewed by Herrando-Perez et al. 2012).

It is a widely accepted principle that density dependence can affect the dynamics of animal and short-lived plant populations (see examples in Harper 1977; Watkinson 1986; Sibly and Hone 2002; Krebs 2002; Maron and Crone 2006). Much less clear is its role in the population dynamics of trees, especially in tropical rain forests that support a mix of rare and common species (Letouzey 1968; Aubréville 1970; Janzen 1970; Turner 2001). These long-lived organisms will produce many offspring—especially during mast fruiting events (Silvertown 1980; Kelly and Sork 2002; Newbery et al. 2006a)—which could be subject to density-dependent mechanisms in combination with density-independent ones acting on early survival, growth and recruitment. As the monitoring of overstorey tree species beyond one generation (20–50 years) is considered an infeasible option in scientific studies, it is also near-impossible to perform density-dependence analyses using time-series data (but see Newbery and Stoll 2013; Chisholm et al. 2014). An alternative approach is one that looks at shifts in tree species composition and spatial dispersion through life-stages (ontogeny) to detect density dependence since this should have a spatial or neighborhood component due to dispersal limitations and/or local edaphic conditions (e.g. Wills et al. 2006; Lan et al. 2009; Bagchi et al. 2011). Nevertheless, because density dependence features prominently in theories which explain prevention of canopy (mono)dominance and the maintenance of species richness, it needs to be rigorously investigated (Connell and Lowman 1989; Chesson 2000; Turner 2001; Wright 2002; Bagchi et al. 2011).

If a population is sampled across a sufficiently large area, immigration and emigration will be negligible and likely equivalent (Watkinson 1986; Berryman 2002; Hixon et al. 2002). This balance simplifies tests of density dependence, so that studies which satisfy this criterion become reasonable on short ecological time-scales, specially for species with limited dispersal capabilities (e.g., those with ballistic means; Seidler and Plotkin 2006; Norghauer and Newbery 2015). In searching for density-dependent relationships in tropical forests, in contrast to reproduction and recruitment processes (e.g. Wills and Condit 1999; Jones and Comita 2010), researchers have paid more attention to mortality, especially that of seeds, seedlings and saplings (Turner 2001; Zimmerman et al. 2008; Comita et al. 2014). Although competitive ability and mortality risks are linked to the juvenile growth of overstorey tropical tree species, how their growing juveniles are affected by density dependence has received little attention from researchers. A few notable examples where it has been studied are the investigations of Newbery and Stoll (2013) on small trees, of Blundell and Peart (2004) on saplings, and of Mangan et al. (2010) on seedlings in a reciprocal-transplant experiment. Explicit consideration of juvenile growth dynamics becomes very important if fast-growers make a disproportionately high contribution to the population size of adults (Zuidema et al. 2009). If negative density dependence decreases juvenile growth rates, this should lead to changes in not only size but also survival rates: for this reason, not only height, but also leaf number is an important trait to consider in such studies, especially in studies on weakly shade-tolerant species since foliar condition should increase carbon gain (Blundell and Peart 2004).

To our knowledge, only four field-based studies have robustly tested density dependence in tropical tree species by using both static and dynamic measurements across multiple juvenile stages (i.e. seeds or new seedlings through to at least the large sapling stage; Pinero et al. 1984; Alvarez-Buylla 1994; Matos et al. 1999; Blundell and Peart 2004). No such in-depth investigation has yet been conducted in the African rain forest, despite it being known that the many large tree species in this system dominate the canopy in patches—a phenomenon which is especially true for the legume subfamily Caesalpinioideae that is characterized by ectomycorrhizal root mutualisms, ballistic seed dispersal and a masting reproductive behavior (Letouzey 1968; Aubréville 1970; Newbery and Gartlan 1996).

The term “negative density dependence” (NDD) refers conceptually to negative feedbacks between tree parents and their progeny (Herrando-Perez et al. 2012). When the survivorship and growth responses of juveniles are tested as a function of their conspecific density or that of adult

basal area abundance, the sign of the slope is predicted to be “negative”. Herein we defined a “juvenile” as any immature subcanopy stem which is no longer dependent on its seed reserves and which has a stem diameter of < 10 cm. Nonetheless, whether it is intraspecific competition or predation that drives NDD, for even a single species it is one thing to detect NDD and still another to identify the plausible mechanisms for it. Indeed, to quote Comita et al. (2014), “Future studies should assess mechanisms underlying distance- and density-dependent mortality in order to determine whether Janzen (1970) and Connell (1971) were correct in their focus on natural enemies”.

We investigated juvenile sizes and densities of *Microberlinia bisulcata* (Caesalpiniaceae) and their dynamics after a mast fruiting event of *M. bisulcata* at Korup, southwestern (SW) Cameroon. Seed mortality and NDD in the seed-to-seedling phase of this tree species has been reported (Norghauer and Newbery 2010, 2011). The objective of our field study was to determine whether juvenile size structure and the dynamics of *M. bisulcata* show evidence of NDD. Our approach was to examine several predictions consistent with a link between NDD and these parameters: (1) that the density and ratios of differently sized *M. bisulcata* juveniles change across areas varying in abundance of *M. bisulcata* adults; (2) that the size of *M. bisulcata* juveniles, in terms of leaf numbers and/or height, is reduced where *M. bisulcata* adults are more abundant; (3) that juvenile performance, in terms of survivorship or individual growth rate, is reduced where *M. bisulcata* adults are more abundant; (4) that the performance of smaller *M. bisulcata* juveniles is also reduced at higher local densities of similarly sized conspecifics; and (5) that because masting is temporal, NDD dynamics might also change over time.

Materials and methods

Study system

Microberlinia bisulcata is a large canopy-emergent tree that is capable of attaining stem diameters of > 2 m and crown diameters of > 40 m (Norghauer and Newbery 2015), as well as of forming extensive buttresses when growing on nutrient-poor soils (Newbery et al. 2009), where adult trees form high-density groves and can also dominate patches within a grove to varying degrees (Newbery et al. 1998, 2013). The species is ectomycorrhizal and endemic to the Cameroon/Nigerian coastal rain forest (Newbery et al. 1988; Newbery and Gartlan 1996). Trees are monoecious, and reproduction does not begin until individuals attain a stem diameter of 45–50 cm; fruiting occurs every 2–3 years in masting events (Newbery et al. 2006a; Norghauer and

Newbery 2015). The seeds are dispersed ballistically from pods situated atop dome-shaped tree crowns in the latter half of the wet season. They are discoid-shaped, with a mass of *c.* 0.64 g, and they rapidly germinate on the ground (Newbery et al. 1998; Green and Newbery 2001a). Newly established seedlings have 3–6 pinnate leaves, depending on the seed mass (Norghauer and Newbery 2011). Being weakly shade-tolerant, the persistence of *M. bisulcata* seedlings in the forest understory decreases quickly after a few years unless they receive above-average light levels (Green and Newbery 2001a, b; Newbery et al. 2006b), whereas seedlings in and around gaps formed by tree- and branch-falls respond very well to the increased light availability, albeit at greater risk of herbivory and seed predation (Norghauer and Newbery 2011, 2013). The population of *M. bisulcata* trees masted more strongly in 2007 than in 2010 (Norghauer and Newbery 2015).

The survival and growth dynamics of natural *M. bisulcata* juveniles was monitored for 4–6 years in primary lowland rain forest of Korup National Park, in Cameroon (5°10'N, 8°70'E). In the southern part of the Park is a large grove of mapped *M. bisulcata* adult trees (stem diameter \geq 50 cm) that spans several square kilometers (Newbery et al. 2004). In the eastern part of this grove is situated the permanent 82.5-ha ‘P-plot’ that was established in 1991 and re-censused in 2005 (with a few trees re-censused in 2007). Although *M. bisulcata* is one of 113 species recorded in the plot with a stem diameter of \geq 50 cm, this species dominates the canopy, ranking first in density (3.54 stems ha⁻¹) and in basal area (4.09 m² ha⁻¹) (Newbery et al. 2013). This forest region is very wet, even by tropical standards: in the period of 1988–2004, it annually received on average *c.* 5100 mm of rain, with most precipitation falling over a 9-month period (March to December; Newbery et al. 2006a). The soils are sandy and well-drained and are very deficient in phosphate and potassium (Newbery et al. 1997). The fauna at Korup is largely intact because illegal hunting is minimal and well controlled.

The gradient of adult sampling areas

When studying the population of large, long-lived tree species, it is important that their adult neighborhoods be considered at an appropriate spatial scale which sufficiently captures the natural variation in the tree sizes and densities (Watkinson 1986; Berryman 2002), since these together will influence the local conspecific seed rain and ensuing seedling bank structure at finer spatial scales. For these reasons, we first chose a 1-ha “core area” (100 m \times 100 m) as the unit of replication for the conspecific adult neighborhoods to test the various lines of evidence for density dependence, and then selected a final set of *n* = 20 core

sampling areas (CSAs; see Electronic Supplementary Material [ESM] 1 for layout) in a non-biased way using a priori criteria to minimize “edge” effects from surrounding conspecific adult-sized trees (full details in ESM 2). Key features of these CSAs are summarized in Table 1. Noteworthy is that the basal area of the two codominant *Tetraberlinia* tree species in the forest neither increased nor decreased with adult basal area of *M. bisulcata*. Second, and perhaps to be expected, the combined basal area of the remaining tree species with large individuals in the CSA was negatively correlated, but not significantly so, with increasing basal area of *M. bisulcata*.

Sampling of tree juveniles

In each CSA three classes of *M. bisulcata* juveniles were the focus of intensive sampling. These were (1) “new” seedlings, which had established from the 2007 masting; (2) “old” seedlings, which had established prior to 2007 but were < 75 cm tall; (3) “saplings”, those individuals ≥ 75 cm tall and with a stem diameter of up to *c.* 100 mm measured at 1.3 m along the stem. New seedlings of *M. bisulcata*, with their non-woody stems, are easily distinguished from the old ones, but could conceivably be of similar size to the latter, whereas saplings are undoubtedly older than either seedling class given their low shade-tolerance ability.

We used a stratified-random sampling approach to ensure an adequate interspersion of new and old seedlings and to control for habitat heterogeneity within CSAs. Specifically, for new seedlings, in each of the four 50 × 50-m subplots that made up a CSA, the center of a “quadrat” was located randomly from 81 sample points (9 × 9 array, inter-sample distance 5 m). The term “quadrat” is a misnomer, strictly speaking, as it had a circular shape to minimize the perimeter-to-area ratio (hereafter, referred to just as “quadrat”). Its radius was increased from 3, to 4, 5 or 7 m to identify more seedlings (the aim was to have at least $n = 25$ per subplot, for $n = 100$ per CSA). All quadrat edges were > 7 m from the trunk-stem of the nearest *M. bisulcata* adult. Up to three quadrats per subplot, as needed, and hence up to 12 quadrats per CSA were set up in this way and searched for new seedlings, which were counted for their leaf numbers and marked with plastic forks or spoons pushed deep into the ground. Some subplots had a dearth of seedlings and consequently, to obtain a sufficient number for performance monitoring, we took one or more 25-m × 25-m subplot quarters closest to an *M. bisulcata* adult. All quadrats were searched for old seedlings—along a fixed 7-m radius from the center of the quadrat—and the old seedlings identified were labeled with numbered aluminum tags. Relaxed plant height was measured to the nearest 0.5 cm and leaf number was counted.

By contrast, the saplings, which are sparse in the forest (Newbery et al. 2010), were searched for in 10-m strips by two to three persons across the entire CSA, given numbered aluminum tags and then measured for their height and/or diameter at 1.3 m along the stem (if tall enough): if possible, their leaves were also counted (to a maximum of approx. 265 leaves). Initial diameters were measured twice, perpendicularly, using dial calipers, and subsequent measurements were made with electronic calipers to achieve greater precision and sampling efficiency in the follow-up censuses. For some large stems, a fine metal tape had to be used to measure girth, which was then converted to diameter.

Censuses for juvenile mortality and growth

The sample of new seedlings was initially located and marked between 18 and 28 January 2008 and amounted to 3245 individuals. They were incompletely re-censused for deaths between 5 and 9 May 2008, but a complete re-census was carried out between 20 and 24 November 2008. A third census was performed between 9 and 13 April 2010: these survivors ($n = 898$) were labeled with a blue ribbon, and those which were still alive 1 month later, between 7 and 12 May 2010, were marked with numbered aluminum tags ($n = 865$) and height measured and leaf number counted. A fourth and final census was performed between 22 and 28 February 2012. Some new recruits from intermittent reproduction between the masting events of 2007 and 2010 were noted, counted and added to the sample in May 2008, and also again in April 2010.

The sample of old seedlings was initially located and marked between 16 and 24 May 2008 and amounted to 465 individuals. These seedlings were re-censused between 12 and 16 April 2010 and in a last re-census between 22 and 28 February 2012. The total sample increased to $n = 540$ when a number of initially-overlooked seedlings, mostly from inside the very large 25-m × 25-m quadrats, were added to the sample in November 2008 ($n = 21$) and in April 2010 ($n = 54$) (time intervals for these latter individual growth rates were corrected for in the analyses).

The sample of saplings were initially located and marked over a 3-week period (between 15 February and 8 March 2008) and amounted to 198 individuals. This number increased to 234 when 36 more saplings that had been initially overlooked were included (time intervals for these latter growth rates were corrected for in the analyses.) The saplings were re-censused three more times: between 17 and 23 April 2010, between 4 and 10 March 2012 and, finally, between 26 and 30 January 2014. Sixteen of the original 40 saplings at a single CSA in that final re-census were censused later, on 23 May 2014; for six of these 16

Table 1 Main characteristics of the twenty 1-ha core sampling areas (CSAs) used to investigate density-dependent relationships in the juvenile dynamics of the dominant canopy tree, *Microberlinia bisulcata* (Mb), at Korup, Cameroon

| CSA | Core BA of Mb ^e | Core BA of Tb and Tk ^d | Core BA of MTT ^a | Core BA of all tree species taken together ^a | Core BA of AZ species ^a | Mean percent-age total transmission (March 2008) ^b | Mean percent-age canopy openness (March 2008) ^b | Mean percent-age canopy openness (March 2012) ^b | No. of quadrats sampled | Total area sampled for new seedlings (m ²) ^c | Total area sampled for old seedlings (m ²) ^c |
|-----|----------------------------|-----------------------------------|-----------------------------|---|------------------------------------|---|--|--|-------------------------|---|---|
| 1 | 1.36 | 3.07 | 4.43 | 7.60 | 3.17 | 2.41 | 4.87 | 4.90 | 6 | 1790 | 1866 |
| 2 | 1.60 | 0.76 | 2.36 | 6.54 | 4.17 | 1.59 | 3.96 | 1.67 | 4 | 2029 | 2029 |
| 3 | 2.29 | 0.00 | 2.29 | 5.27 | 2.98 | 1.67 | 3.84 | – ^d | 4 | 2500 | 2500 |
| 4 | 2.92 | 2.57 | 5.49 | 12.23 | 6.74 | 2.22 | 4.89 | 1.72 | 8 | 833 | 1232 |
| 5 | 3.22 | 3.69 | 6.91 | 10.73 | 3.82 | 2.38 | 4.81 | 0.42 | 4 | 1482 | 1558 |
| 6 | 3.32 | 5.46 | 8.78 | 11.17 | 2.39 | 1.02 | 3.57 | 1.67 | 6 | 2387 | 2491 |
| 7 | 3.54 | 0.22 | 3.76 | 6.85 | 3.08 | 1.81 | 4.32 | 1.17 | 6 | 1216 | 1395 |
| 8 | 3.87 | 2.04 | 5.92 | 11.19 | 5.27 | 2.05 | 4.54 | 0.92 | 6 | 1216 | 1395 |
| 9 | 3.93 | 3.76 | 7.68 | 12.56 | 4.87 | 1.64 | 4.09 | 1.25 | 6 | 1093 | 1395 |
| 10 | 4.66 | 2.67 | 7.33 | 9.84 | 2.51 | 0.79 | 3.86 | 0.84 | 4 | 1482 | 1558 |
| 11 | 5.60 | 1.72 | 7.33 | 14.12 | 6.79 | 1.39 | 3.82 | 2.42 | 5 | 770 | 770 |
| 12 | 5.61 | 0.41 | 6.02 | 9.19 | 3.17 | 2.27 | 4.85 | 1.56 | 4 | 179 | 616 |
| 13 | 6.31 | 4.56 | 10.87 | 15.36 | 4.48 | 1.89 | 4.45 | 1.67 | 9 | 933 | 1385 |
| 14 | 6.91 | 1.14 | 8.06 | 12.44 | 4.38 | 1.47 | 3.95 | 1.56 | 5 | 1090 | 1241 |
| 15 | 7.58 | 1.36 | 8.93 | 13.98 | 5.05 | 1.69 | 4.34 | 0.95 | 7 | 650 | 1078 |
| 16 | 7.92 | 6.40 | 14.31 | 17.93 | 3.62 | 1.36 | 3.93 | 2.29 | 4 | 408 | 616 |
| 17 | 8.10 | 0.00 | 8.10 | 11.42 | 3.32 | 2.79 | 5.08 | 1.15 | 4 | 283 | 616 |
| 18 | 9.90 | 3.26 | 13.16 | 14.90 | 1.74 | 1.59 | 3.99 | 1.60 | 6 | 544 | 924 |
| 19 | 12.14 | 1.69 | 13.82 | 15.40 | 1.57 | 2.05 | 4.74 | 4.69 | 4 | 201 | 616 |
| 20 | 13.98 | 0.58 | 14.57 | 16.20 | 1.63 | 1.99 | 4.44 | 0.83 | 4 | 305 | 616 |
| | | | | | Pearson's <i>r</i> | Slope | Slope | Slope | Sum | Sum | Sum |
| | vs. Mb-BA | –0.092 | | | –0.426 | 0.005 | 0.004 | –0.002 ^e | 106 | 21,391 | 25,897 |
| | <i>P</i> -value | 0.699 | | | 0.061 | 0.65 | 0.80 | 0.75 | | | |

^a Data are presented as the basal area (BA; m² ha^{–1}) abundance of the dominant canopy tree *Microberlinia bisulcata* (Mb), of the two co-dominant tree species *Tetraberlinia bifoliolata* (Tb) and *T. korupensis* (Tk) and of the summed abundance of these three tree species (MTT; where MTT = [Mb + Tb + Tk]), as well as of all other tree species with a stem diameter of ≥ 50 cm (AZ; all non-MTT tree species)

^b Measures of forest canopy openness, transmitted light and sampling effort are provided for each core sampled area (CSA). Mean values per CSA do not include any 25-m × 25-m quadrats (see “Materials and methods”)

^c Total area sampled for seedlings (new and old) differed among CSAs and is reported here to the nearest m²; for saplings, the entire area was surveyed (20 ha)

^d No quadrats had been established in this CSA, so no measurements were available (only 25-m × 25-m quadrats were used)

^e Canopy openness values were log-transformed to meet assumptions for regression because of two very high values (new gaps).

individuals the stem diameters were measured with dial calipers (to the nearest millimeter).

In sum, population data on *M. bisulcata* juvenile dynamics were collected for both new and old seedlings over a (+/−) 4-year period (2008–2012), whereas for saplings the sampling period spanned almost 6 years (2008–2014). The reasoning behind the use of unequal time periods is that density-dependent processes likely operate faster in the new and old seedlings, which are more abundant, smaller and more vulnerable to mortality than in the sparser but larger saplings, for which a longer period might better reveal accrued change or temporal variation in any density-dependent processes acting on their individual performances.

Forest canopy

On two consecutive days of overcast sky conditions (30/31 March 2008), we used hemispherical photography to quantify the variation in percentage canopy openness and associated total light transmission within and among the 20 CSAs. A digital color photograph was taken at the center of each quadrat using a Nikon Coolpix 950/5 camera (Nikon Corp., Tokyo, Japan) held level at 1 m above the ground and oriented north (“fish-eye”; auto-settings). For the very large 25-m × 25-m quadrats, a photograph was taken at each corner ($n = 4$, later averaged per quadrat). The photographs were analyzed following standard protocols outlined in previous publications (see Norghauer and Newbery 2013) using Gap-Light Analyzer v. 2.0 software (Frazer et al. 1999).

It was not possible to take hemispherical photographs again *c.* 48 months later, during the final census of new and old seedlings. Instead, under overcast conditions (7–8 March 2012) we took four canopy openness readings (facing N, S, E, W) at the centers of the quadrats using a rectangular convex mirror (60 etched intersections, recording the counts of those unambiguously falling on ‘open sky’). The mirror was mounted in a level horizontal position on a tripod at 1 m ground (the 25-m × 25-m quadrats were omitted). These readings were averaged per quadrat to yield a percentage measure. The range of vision (out of 180°) for this mirror was determined outside the forest using a clinometer: it was found to be 48°–50° when used in the field and thus smaller and less precise than the reading provided by the hemispherical photography (180°), but it was still useful for evaluating canopy cover across the CSAs.

Performance metrics of juveniles

To avoid pseudo-replication we used the proportions of new and old seedlings surviving per quadrat (i.e.

“survivorship”)—and not the survival of individual seedlings—as the sample unit of replication, since it is questionable whether the survival of an individual seedling is truly independent from the survival of another seedling, especially at high densities within some quadrats. Proportions per quadrat were used because, in addition to testing for the influence of adult BA across the 20 CSAs, the influence of the density of conspecific new seedlings after mast fruiting was also to be tested within them (i.e. adding another variate in the models). For saplings, however, individual survivorship over the 1-ha CSAs was determined.

The survivorship of new seedlings was determined for three successive time intervals, namely, January–November 2008; November 2008 to May 2010; May 2010 to February 2012. The survivorship of old seedlings could only be determined for two time intervals, namely, May 2008 to April 2010; April 2010 to February 2012. The survivorship of individual saplings was determined for three time intervals, namely, February/March 2008 to April 2010; April 2010 to March 2012; March 2012 to January 2014. The formal analyses (using generalized linear mixed models [GLMMs]; see section “Analyses for testing for density-dependent relationships”) included the longest possible intervals for each of the three juvenile samples because density-dependent effects might accrue over time.

In addition to survivorship, because the growth rate of a juvenile tree may be influenced by its initial absolute size and partly determine recruitment rates and later risks to mortality, relative growth rates (RGR) were determined. For surviving juveniles, RGR was calculated for each individual as:

$$\text{RGR} = (\ln [S_{t_j}] - \ln [S_{t_i}]) / (t_{ij})$$

where S is the size response variable of interest (height in centimeters, or number of leaves, or stem diameter in millimeters); subscripts t_i and t_j denoted the start and end of given time interval respectively; t_{ij} denotes the duration of the interval in years.

The calculations for RGR were made for all three juvenile classes using the same corresponding time intervals as for survivorship, but median sample dates were used to define these (in years). For height and leaf number changes in the intervals January 2008 to November 2008 and November 2008 to May 2010, data for new seedlings were unavailable. For changes in leaf number, saplings with starting heights up to *c.* 325 cm were used; likewise, for height changes, those up to *c.* 465 cm could only be reliably measured; saplings with stem diameters of ≥ 10 mm or, alternatively, at least 200 cm tall were used for calculations of changes in diameter at breast height.

Analyses for testing for density-dependent relationships

Static measures for juveniles

For a given CSA, the densities of new and old seedlings in quadrats were first averaged separately and transformed to a per-hectare basis in order to compare their densities at this scale with those of saplings (given the unequal sampling among classes across CSAs; Table 1). For sizes, medians were used because the data were positively skewed, as were maxima since these show the best responding juveniles that are the most likely to become adults.

Juvenile survivorship

For new and old seedlings, we used GLMMs, with a binomial error structure and the logit link, to test the effects of light (percentage total transmission; Table 1), basal area abundance ($\text{m}^2 \text{ha}^{-1}$) and seedling density (N m^{-2}) upon survivorship. Hereafter, basal area abundance is referred to simply as basal area. In mixed models, as in standard multiple regression, the order in which main terms are entered may alter significance levels (although not of their highest order interaction; Galwey 2006). Models for seedling survivorship consisted then of four terms: light transmission was entered first (to allow for its influence), basal area was entered second (among-CSA; upper stratum), seedling density was then entered (within-CSA; lower stratum), followed last by the interaction between basal area and seedling density. Seedling densities for new and old seedling survival were their corresponding new and old starting ones (i.e. ages were not combined).

Models were fitted separately for each juvenile class and time interval. To check whether spatial trends across the plot might have confounded the effects of the variates, models were re-run using CSA x - and y -coordinates. Because so few of the saplings died, they were analyzed for just the one 6-year period, using simple logistic regression of survivorship on basal area. The dispersion parameter was estimated (i.e., not fixed at 1.0) in all GLMMs.

Juvenile growth rates

Linear mixed models (LMMs) were used to analyze the growth changes of new and old seedlings, with the same fitted terms and for the same classes and intervals (plus spatial checks) as for survivorship. New seedlings were sufficiently numerous to allow for individual-level growth rates: by contrast, old seedlings were sparse and their seedlings' rates needed to be averaged at the quadrat level. Saplings were treated individually in four (50-m \times 50-m) subplots

of each CSA in order to accommodate within-CSA variation in basal area and microsite conditions.

In both the GLMMs and LMMs, the predictor variables were mean-centered. Centering stabilizes variances of fitted estimates and minimizes the influence of possible collinearity between basal area and seedling density (Aiken and West 1991; Quinn and Keough 2002; Schielzeth 2010; Afshartous and Preston 2011). Fitting was achieved by restricted maximum likelihood in GenStat version 15.2 (VSN Int. Ltd, Hemel Hempstead, UK). Models were checked that they met statistical assumptions using composite diagnostic graphics.

Results

Light levels in the forest understory

As expected, the percentage total transmitted radiation (direct + diffuse light) had a close relationship that was both linear and positive with percentage canopy openness when estimated from the hemispherical photographs ($r^2 = 0.79$, $F_{1, 104} = 384.2$, $P < 0.001$). Moreover, the distributions of their residuals were normal, and the averaged values in 2008 did not change significantly across the gradient of adult *M. bisulcata* basal area (Table 1). Canopy openness ranged from 2.91 to 5.89 % across the 106 quadrats in March 2008 and from 0 to 15.0 % in the 87 quadrats assessed in April 2012, but almost all of these latter values were < 3 % (median 1.25 %) except for two CSAs where new gaps were present, and these values did not change significantly with the gradient of adult *M. bisulcata* basal area. With the caveat that canopy openness could not be measured in the same way in 2008 and 2012, their mean change was -2.57 %. Finally, across the 20 CSAs, the means of the three light-related metrics did not change significantly with the basal area of all species (Table 1) (three correlations: Pearson r -values -0.100 to 0.045 , P -values 0.68 – 0.95).

Initial abundance and sizes of juveniles

New seedlings

In 2008, at least 100 individuals were found and marked in quadrats in all 20 CSAs except two (for which adult basal area values were quite low (1.60 and $2.29 \text{ m}^2 \text{ha}^{-1}$, respectively). There was a positive significant correlation between seedling density at the quadrat level and basal area ($r = 0.39$, $P < 0.001$; $n = 106$ quadrats), which strengthened after removing two outlying quadrats with unusually high densities ($c. 4 \text{ m}^{-2}$) more than twofold higher the

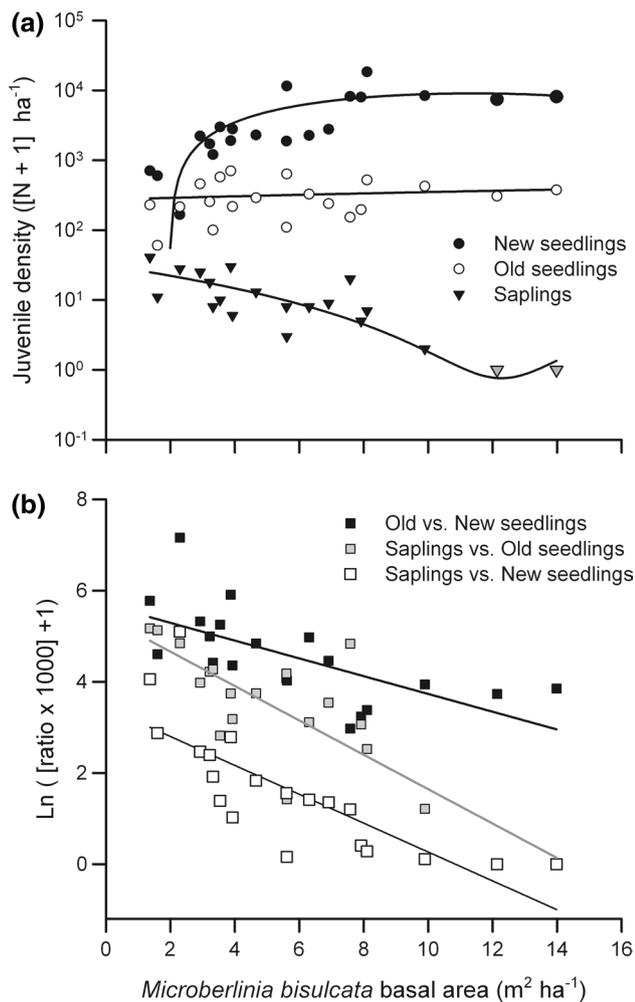


Fig. 1 The relationship between the basal area of *Microberlinia bisulcata* and density of three stage classes of juveniles of *M. bisulcata* (a) and ratios of density of these life stages (b) in twenty 1-ha core sampling areas (CSAs) of conspecific adult neighborhoods at Korup, Cameroon. **a** Regression equations (and r^2) are presented separately for the three life stages—new seedlings: $\log[\text{density}] = 2.27 + 0.318[\text{basal area}] - 0.0146[\text{basal area}]^2$, $r^2 = 0.66$, $F_{2, 17} = 19.4$, $P < 0.001$ and $P = 0.01$ for linear and quadratic terms, respectively; old seedlings: $\log[\text{density}] = 2.30 - 0.0214[\text{basal area}]$, $r^2 = 0.02$, $F_{1, 18} = 1.29$, $P = 0.27$; saplings: $\log[\text{density}] = 1.55 - 0.1104[\text{basal area}]$, $r^2 = 0.67$, $F_{1, 18} = 39.15$, $P < 0.001$). Two gray triangles indicate zero recruitment of saplings. **b** Regressions are: old/new seedlings, $y = 5.687 - 0.1951x$, $r^2 = 0.41$, $F_{1, 18} = 13.93$, $P = 0.002$; saplings/old seedlings, $y = 5.419 - 0.3773x$, $r^2 = 0.68$, $F_{1, 18} = 40.72$, $P < 0.001$; saplings/new seedlings, $y = 3.436 - 0.3169x$, $r^2 = 0.60$, $F_{1, 18} = 29.33$, $P < 0.001$. **a** The y-axis is on a log scale; **b** the ratios have been ln-transformed to facilitate visual comparisons

maximum recorded for the rest of the population (c. 2 m^{-2} ; ESM 3) ($r = 0.52$, $P < 0.001$; $n = 104$ quadrats). Scaled-up counts per hectare indicated that these seedling densities increased asymptotically with basal area (Fig. 1a). Most of these seedlings (53 %) had four leaves (range 1–8) and hence the same medians and similar maxima in leaf number across adult basal area (Fig. 2a).

Old seedlings

Of the 106 quadrats sampled, 32 did not have any seedlings in this juvenile class (ESM 3), leading to a sparse, imbalanced matrix for survivorship and growth analyses. Quadrat-level densities of old seedlings were not significantly correlated with basal area ($r = 0.05$, $P = 0.61$; $n = 106$ quadrats). When averaged at the latter 1-ha scale, their densities did not mirror that of new seedlings under an assumption of random mortality, showing instead no change with increasing basal area (Fig. 1a) (linear regression; 95 % confidence interval (CI) of slope -0.01806 , -0.06066). This differentiation through ontogeny was evidenced by a significant decline in the ratio between these two juvenile classes with increasing basal area (Fig. 1b). In terms of their sizes, however, the median and maximum heights showed negative relationships with basal area (Fig. 2b), as did their leaf numbers (Fig. 2c).

Saplings

No stems were found for this juvenile class in the two CSAs with the highest adult basal areas. In terms of their densities, there was a highly significant and negative relationship with increasing basal area (Fig. 1a) (linear regression; 95 % CI of slope -0.1475 , -0.07334). In turn, the ratios of saplings to old seedlings and to new seedlings declined significantly with basal area (Fig. 1b).

As expected, the initial sizes of saplings were skewed, with distributions that appeared to be log-normal for leaf numbers, stem diameters, and heights. Nevertheless, the counted leaf numbers increased predictably with their measured heights (regression: $\ln[\text{leaves}] = -3.43 + 1.465 \ln[\text{height}]$, 95 % CI of slope $[1.274, 1.656]$, $r^2 = 0.57$, $F_{1, 168} = 228.9$, $P < 0.001$; one outlying value removed because more than half of its stem was dead). In turn, for those individuals which had both their heights and stem diameters directly measured, the relationship was also positive ($\ln[\text{height}] = 3.90 + 0.688 \ln[\text{dbh}]$; 95 % CI of slope $[0.5816, 0.7952]$, $r^2 = 0.73$, $F_{1, 59} = 166.5$, $P < 0.001$). This result suggested that a sapling reaching a stem diameter of 1 cm would be, on average, c. 240 cm in height—a threshold closely matching that previously estimated from a smaller random sample of *M. bisulcata* measured by Newbery et al. (2010). Although the maximum heights and stem diameters decreased significantly with increasing basal area, the median values did not (Fig. 2d, f). The correlation for leaf numbers was non-significant for median values, while it was negative, although not quite significant, for maximum values (Fig. 2e). That seedling density and adult basal area did not interact hints that a typical mechanism may not be generating NDD (i.e., “sib-sib” symmetric competition, natural enemies). This will be discussed later in light of the results presented.

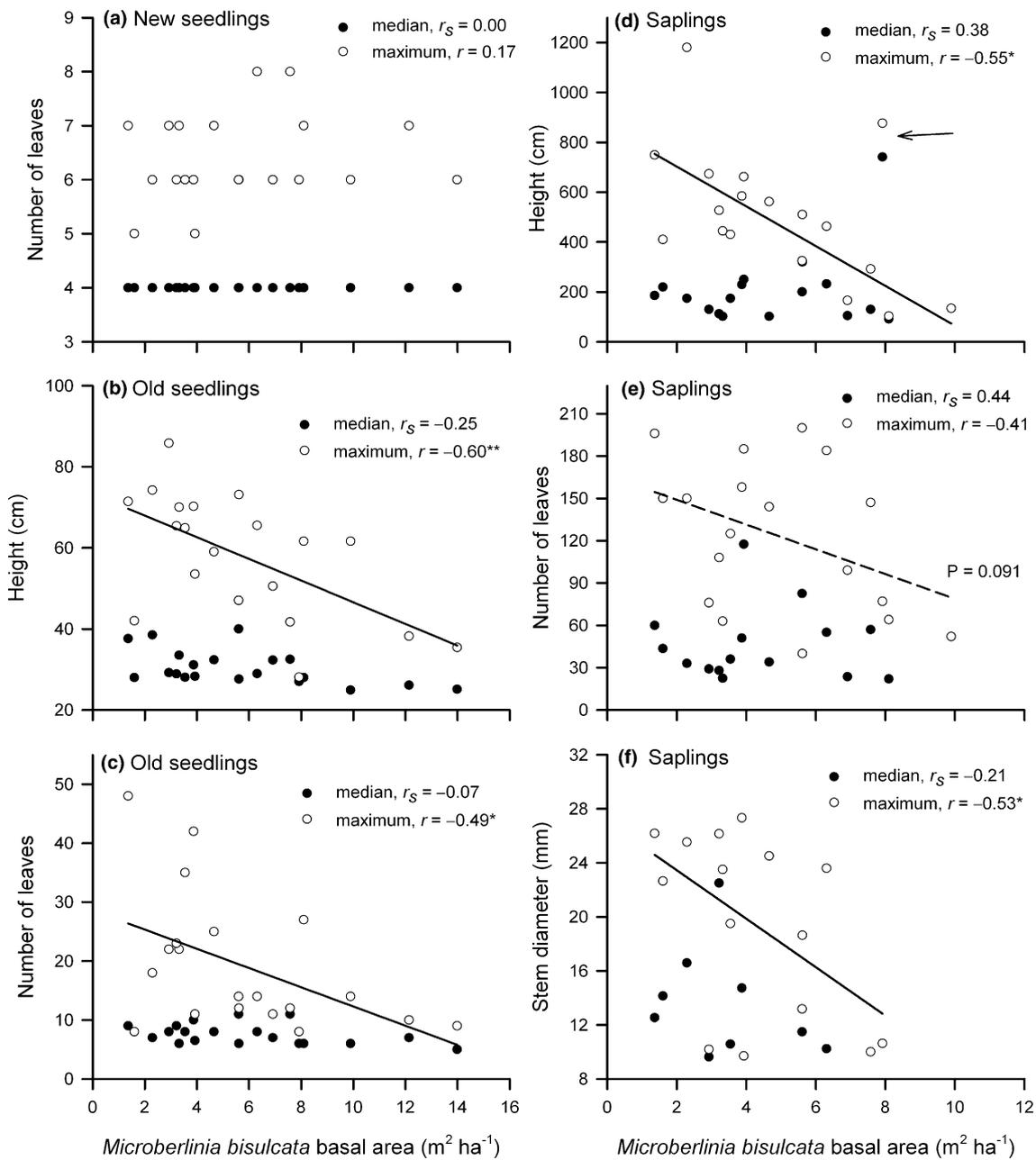


Fig. 2 The relationship between *M. bisulcata* basal area and median or maximum values of various measures of plant size for different life stages of juveniles sampled in the twenty 1-ha CSAs of conspecific adult neighborhoods at Korup, Cameroon. **a** New seedlings in 2008 for which only leaf number was measured. **b, c** Old seedlings for which both height (**b**) and leaf number (**c**) were measured. **d–f** Saplings for which stem height (**d**), leaf number (**e**) and stem diameter (**f**) were measured. For large stems, height was extrapolated using the regression of $\ln(\text{height}) = 3.86 + 0.698 \ln[\text{stem diameter}]$. **e** Leaf number is for stems with a height of < 325 cm. Diameter in **f** (in diameter at breast height, cm) is for stems with a height of

≥ 200 cm. Arrow in **d** points to a pair of three saplings growing far from a cluster of adults in CSA #16 (see ESM 1); when these values were omitted from the analysis the relationship became negative yet insignificant ($P = 0.563$)—but the negative relationship with maximum height was strengthened considerably ($r = -0.74$, $P < 0.001$). Significant coefficients for Spearman's (r_s , for median) and Pearson's (r , for maximum) correlations are indicated by asterisks ($*P \leq 0.05$, $**P \leq 0.01$). Solid lines fitted to maximum values are significant, dashed lines indicate near-significant ($P < 0.10$) relationships; no line is shown for the non-significant relationships

Table 2 The effects of light and conspecific neighborhoods on the survivorship of the *Microberlinia bisulcata* tree juveniles at Korup, Cameroon^a

| Juvenile class | Predictor variables | | |
|--|-------------------------|--------------------------------|----------------------------------|
| | Percentage light | Basal area ^b | Seedling density |
| New seedlings | | | |
| January 2008 to November 2008 | NS | NS | NS |
| November 2008 to May 2010 | NS | NS | NS |
| May 2010 to February 2012 | NS | −0.1033* (0.0448) | NS |
| Approximate 2-year period (January 2008–May 2010)—pooled | NS | NS | NS |
| Entire 4-year period | NS | −0.1138* (0.0584) ^c | NS |
| Old seedlings | | | |
| May 2008–April 2010 | 0.2696* (0.131) | −0.1307** (0.0445) | NS |
| April 2010–February 2012 | 0.6308** (0.186) | NS | 7.212 [¶] (3.976) |
| Entire 4-year period | 0.5531** (0.163) | NS | NS |
| Saplings | | | |
| February/March 2008–January 2014 | Basal area ^b | Stem height | Interaction: basal area × height |
| | NS | 0.0106*** (0.00239) | 0.00123*** (0.00195) |

* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$; [¶] $P \leq 0.10$; non-significant (NS), $P > 0.10$

For significant relationships, the slope parameter estimates (and standard error) are reported. Corresponding tables with complete statistics from the fitted models can be found in ESM 4

^a Estimates were obtained from GLMMs that centered the fixed variates and included random effects unless otherwise indicated (see "Materials and methods")

^b Adult-sized trees (≥ 50 -cm stem diameter; Norghauer and Newbery 2015)

^c A linear mixed model using arcsine square-root-transformed proportions of survivors yielded a non-significant P -value of 0.122, with a significant effect of percentage light transmission ($P = 0.042$)

Juvenile dynamics: interactions between seedling density and basal area

A total of 16 mixed models were fitted fully, i.e., with an interaction term, for the survivorship and growth of the new and old seedlings. However, in 13 of these models (81 %) the coefficient for the interaction term was non-significant ($P > 0.05$; range 0.07–0.99). Moreover, the three models which were significant were only marginally so (P -values of 0.011, 0.027 and 0.040, respectively). This result suggests that interactions between seedling density and basal area were having low effects and even then these were unreliable because variate sampling errors would have been part of this product term (Afshartous and Preston 2011). On this basis, all models were re-fitted without the interaction term (ESM 4 and 5), and these are the ones reported here.

Juvenile dynamics: new and old seedlings

Survivorship

The new seedlings survived equally well in the first two intervals of monitoring that spanned almost 2 years (2008–2010)—or when pooled for this period—irrespective of

seedling density or basal area (Table 2). However, in the third interval (2010–2012), which coincided with the next masting event of 2010, proportionally fewer new seedlings survived at higher basal areas than at lower basal areas (Fig. 3a). This significant relationship contributed to the negative influence of basal area on survivorship over the approximately 4-year complete study period of 2008–2010 (although residuals were skewed). Light levels were a poor predictor of new seedling survivorship in any interval (Table 2). Omitting from the above analyses those two quadrats with unusually high seedling densities (see ESM 3) did not yield qualitatively different results in any interval: the basal area effect in the third interval remained significant ($P = 0.013$).

Survivorship of old seedlings was negatively affected by basal area in the first 2-year interval (2008–2010), but not in the time interval of 2010–2012 (Table 2; Fig. 3b). For these juveniles, seedling density was also not a significant predictor of survivorship (like for new seedlings), although in all intervals their survivorship was strongly enhanced by increasing light levels (Table 2).

Overall, 4-year survivorship of new seedlings and old seedlings was 10.3 and 25.0 %, or as annualized mortality rates (m_a), 42.6 and 31.1 % year^{−1}, respectively. Full statistics for the above analyses of survivorship are given in ESM 4.

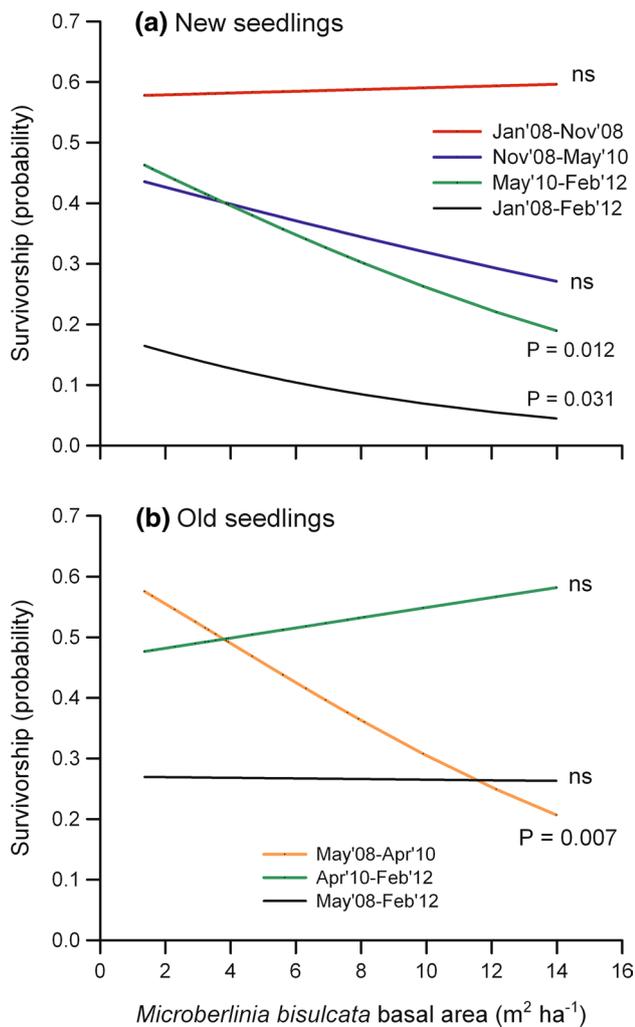


Fig. 3 Relationship between basal area of *M. bisulcata* and survival probability of new seedlings (a) and old seedlings (b) over a 4-year period (2008–2012) at Korup, Cameroon. Probability values were calculated from coefficients fitted by a GLMM in which light availability was held constant (at its mean); *ns* denotes a non-significant effect of basal area abundance (refer to Table 2 and ESM 4 for statistics)

Growth

For new seedlings in the one time interval measured, 2010–2012, RGR in height was significantly negatively related to both basal area and seedling density (Table 3; Fig. 4a, c). However, RGR in leaf number was only significantly affected by seedling density, albeit strongly (Fig. 4a). Variation in light had only a marginally positive effect (Table 3).

By contrast, in the same interval (2010–2012), RGR in height of old seedlings also decreased with increasing seedling density, but with only a near-significant correlation (Table 3; Fig. 4b). No significant effects of either basal area or seedling density were detected in the previous interval (2008–2010), or over the entire 4-year period. For old

seedlings, RGR in leaf number was not significantly influenced by either predictor, in any interval (Table 3; Fig. 4b, d). Full statistics for the above analyses of growth are given in ESM 5.

Juvenile dynamics: saplings

Survivorship

When analyzed simply as proportions over the 1-ha area per CSA ($n = 18$), sapling survivorship was unaffected by basal area (Table 2). However, when individual probabilities were examined—which is not unreasonable since saplings might experience very different microsites within a CSA—not only did taller saplings survive better than shorter ones, but survivorship of the latter declined with basal area in a significant interaction (Table 2; Fig. 5a; ESM 4). Overall 6-year survivorship was much higher for saplings than for seedlings, at 70.5 % ($m_a = 5.72$ % year⁻¹, one-sixth).

Growth

Surviving saplings in CSAs with high basal area had significantly lower RGR in terms of leaf number (but not diameter or height) than those with low basal area (Table 3; Fig. 5b). Using mean RGR values per CSA—i.e. not taking within-area variation into account—led to a loss of significance for basal area affecting leaf number ($P = 0.326$; for height and diameter the P -values were 0.739 and 0.749; ESM 5).

Spatial autocorrelation

In terms of patterns of survivorship, there was little evidence of directional, spatial autocorrelation across the 20 CSAs in the P-plot: in the GLMM re-runs, x - and y -covariates were mostly non-significant ($P > 0.05$). The exception was a marginal significant east–west spatial trend ($P = 0.048$) for new seedlings in their second time interval studied (i.e. during November 2008 to May 2010); a similar, near-significant trend was present in the third time interval ($P = 0.064$). In the re-analysis of RGR variables, no spatial trends were detected for new seedlings (range of P -values 0.16–0.87). However, the leaf numbers of old seedlings in their first time interval (2008–2010) decreased slightly from east to west (x -covariate, $P = 0.032$) and from north to south (y -covariate, $P = 0.010$), but these significant trends retained the non-significant effects originally found for basal area and seedling density (see Table 2). The re-runs of the other five growth-LMMs for this juvenile class yielded non-significant covariates (range of P -values 0.19–0.95). Likewise, for the sapling class, spatial trends

Table 3 Slope parameter estimates and their standard errors for effects of light and conspecific neighborhoods on relative growth rates of *Microberlinia bisulcata* juveniles at Korup, Cameroon^a

| Juvenile class | Height | | | Leaf numbers | | |
|--|------------------|-------------------------|------------------------------|-------------------------------|-------------------------|------------------------|
| | Percentage light | Basal area ^b | Seedling density | Percentage light | Basal area ^b | Seedling density |
| New seedlings ^c | | | | | | |
| May 2010– February 2012 | NS | −0.00365* (0.00165) | −0.01503* (0.00566) | 0.02639 [¶] (0.0135) | NS | −0.0678*** (0.0166) |
| Old seedlings ^d | | | | | | |
| May 2008– April 2010 | NS | NS | NS | NS | NS | NS |
| April 2010– February 2012 | NS | NS | −0.2821 [¶] (0.151) | NS | NS | NS |
| Entire 4-year period | NS | NS | NS | NS | NS | NS |
| Saplings (February 2008 to January 2014) | | | | | | |
| Simple regression on means | | NS | . | . | NS | . |
| With random effects (LMM) | | NS | . | . | −0.01621* (0.00508) | . |

* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$; [¶] $P \leq 0.10$; NS, $P > 0.10$

Not shown are the tests for effects on the saplings' stem diameter growth (non-significant). Corresponding tables of complete statistics from the fitted models can be found in ESM 5. In the table the '.' indicates not applicable to saplings (see Table 1)

^a Estimates were obtained from linear mixed models (LMMs) that centered the fixed variates and included random effects, unless otherwise indicated (see "Materials and methods")

^b Adult-sized trees (stem diameter of ≥ 50 cm; Norghauer and Newbery 2015)

^c For the height LMM, two outliers with confirmed severe stem-dieback had to be removed to satisfy model assumptions

^d For both height and leaf numbers, a single outlier stem with severe stem-dieback had to be removed from the 2008–2010 LMMs successfully fit them; similarly, a different, single outlier for height growth over the whole 4-year period had to be removed from that LMM (again, with confirmed severe die-back)

across the 20 CSAs were not apparent (range in P -values 0.25–0.88 for all RGR metrics).

Discussion

The NDD predictions tested here were supported in varying degrees. Taken together, the static and dynamic measurements of juveniles in three size classes revealed reasonably strong evidence of NDD in the *M. bisulcata* groves at Korup.

Seedling and sapling densities and their dynamics

The moderately positive correlation between densities of new seedlings and basal area suggests that mortality in the seed-to-seedling transition is insufficient to override localized higher seed inputs and seedling production from more, or larger, adults. Hence, while NDD is known to limit seedling establishment (Norghauer and Newbery 2010), this has little effect at the population level, being enhanced by a masting strategy. However, changes in juvenile densities in relation to increasing basal area—first positive for new

seedlings, then null for old ones and finally negative for saplings—together with their declining negative ratios strongly suggest that NDD reversed this trend through ontogeny.

Contrary to what might be generally expected at a time when they were most abundant and vulnerable, survival of new seedlings was unrelated to conspecific neighborhood, although a relationship was evident for these seedlings 3–4 years later. Remarkably, this ontogenic timing matches what was detected as NDD for old seedlings, since the NDD effect was significant in the period May 2010–April 2012 for new seedlings, but in the May 2008–April 2010 interval for old seedlings. These new and old seedlings would have very largely come from the 2007 and 2004 masting cohorts, respectively. NDD was therefore detected in those periods when (1) seedlings, new and old, were both a few years in age, and (2) the next mast fruiting year of 2010 coincided (Norghauer and Newbery 2015). Intriguingly, both periods lie within the 1-year over which resource accumulation and allocation probably occurs for a reproducing tree of this species (Newbery et al. 2006a). The absence of NDD in the survival of old seedlings in 2010–2012 could simply reflect that NDD had already generated insufficient numbers.

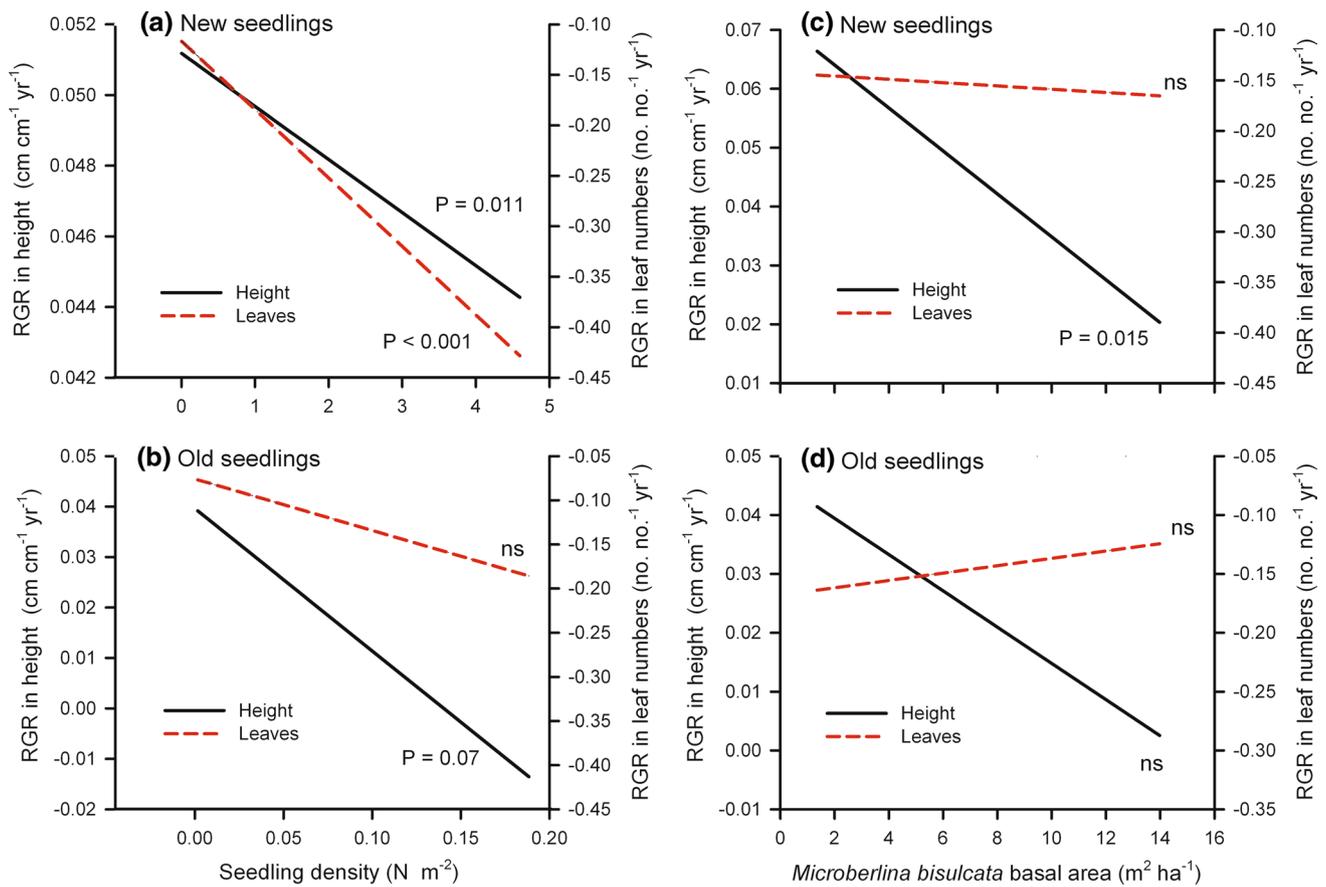


Fig. 4 The relative growth rates (*RGRs*) in height (*left y-axis*) and leaf number (*right y-axis*) of two classes of *M. bisulcata* tree juveniles as a function of conspecific seedling density (**a, b**) and conspecific basal area abundance (**c, d**), over a comparable 2-year period

(2010–2012) at Korup, Cameroon. *ns* denotes a non-significant effect of either seedling density or basal area, when the other conspecific variate, along with light availability, was held constant (at its mean), as tested in LMMs (refer to Table 3 and ESM 5 for statistics)

Unlike basal area, seedling density had negligible effects on survival, which points towards an adult-mediated mechanism behind NDD and away from a biotic mechanism among seedlings (i.e. competition or enemies). Moreover, symmetric competition was unlikely at such low densities of < 1 m⁻² for new seedlings and of < 0.15 m⁻² for old seedlings. Competition among seedlings in other tropical forest species has been shown to be negligible (Paine et al. 2008; Svenning et al. 2008) and is more likely to occur in canopy-disturbed areas (gaps; Denslow 1987). Leaf herbivory by mobile host-specific insects in areas of gaps that promote upward growth may be associated with basal area and distance to adult trees (see Norghauer et al. 2014), but *M. bisulcata* seedlings showed little, if any, signs of such herbivory, being mostly in the shaded understory where leaflets are primarily shed and not eaten (Norghauer and Newbery 2013). A parallel field experiment at a nearby forest site did not find support for pathogen-induced density-dependent mortality in seedlings of *M. bisulcata* following

establishment (Norghauer et al. 2010), in line with our 2008–2010 results. Furthermore, differential seedling survival due to varying light levels is untenable as these did not differ with basal area (Table 1), being similar in the understory below crowns of *M. bisulcata* and other canopy species (Green and Newbery 2001b). Similarly, by sampling 82.5 ha of forest, we conclude that it is also reasonable to exclude idiosyncratic interactions between *M. bisulcata* and neighboring rare species to explain NDD.

With the exception of height in the 2010–2012 period, the growth of old seedlings was unrelated to their density, although growth of the cohort of new seedlings was clearly related to density (for both relative changes in height and leaf numbers). Because the latter established at such low densities, and with no signs of natural enemy attack, this may be an “apparent” effect of NDD since seedling density also reflects proximity to source trees and their fecundity. While larger-sized trees will produce more seeds on average than smaller ones (Norghauer and Newbery 2015), all

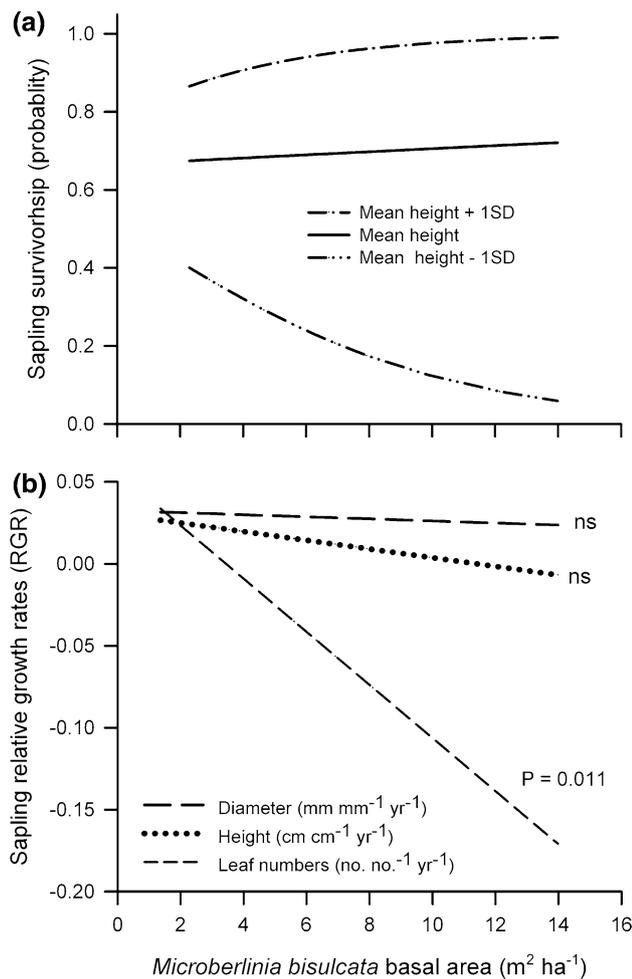


Fig. 5 Depiction of the significant interaction effects between the starting heights of saplings of *M. bisulcata* and conspecific basal area abundance upon sapling survivorship (a), and the effects of basal area alone on sapling growth rates (b), over approximately a 6-year period (2008–2014) at Korup, Cameroon. Survival probabilities were calculated from coefficients fitted by a GLMM (p. 284 in Galwey 2006; refer to Table 2 and to ESM 4 for statistics). *ns* in (b) denotes a non-significant effect of basal area abundance, as tested in a LMM for height (refer to Table 3 and ESM 5 for statistics)

else being equal, those trees attaining an above-average per-capita fecundity will have required more energy to produce more offspring. This also points to a negative feedback between adults and the seedlings growing beneath them, which is speculated upon in the following section ("A novel postulate for NDD").

The best predictor of sapling survival was undoubtedly initial size. However, the results further suggest that below-average-sized saplings in terms of height could also experience NDD. In addition, it was more difficult for saplings to maintain their leaf numbers at higher basal areas than at lower ones, which was not seen in the earlier 4-year sapling study of Newbery et al. (2010). Although insect herbivores

can cause reductions in leaf numbers of large seedlings and saplings with increasing basal area at Korup, this demonstrated Janzen–Connell effect was restricted to vigorously growing stems in gaps (Norghauer et al. 2014). In the present study, most of the saplings were not found in gaps, or if they were only temporarily in the 6-year period, suggesting again that a different underlying mechanism was operating for NDD.

The results of our study add to the information provided by the four previous studies that have investigated NDD in-depth for a tree population in primary tropical forest. Three of these were in the Neotropics, with two conducted in a 5-ha area in Mexico for a subcanopy palm (*Astrocaryum mexicanum*; Pinero et al. 1984) and a true pioneer (*Cercopia obtusifolia*; Alvarez-Buylla 1994), and one conducted in a 1-ha area in Brazil for another subcanopy palm (*Euterpe edulis*; Matos et al. 1999). The fourth study examined a common dipterocarp canopy tree in a 75-ha area in Borneo (*Shorea quadrinervis*; Blundell and Peart 2004). In all four cases the authors concluded that the studied populations were subject to stabilizing forces. Our data on congruent NDD juvenile dynamics at Korup in 82.5 ha of rain forest are in agreement with the static numbers and ratios presented in terms of increasing *M. bisulcata* basal area, thus suggesting a stabilizing force on its population size too—under current environmental conditions. However, a modeling approach would be needed to test whether this NDD can affect population dynamics on longer time scales.

A novel postulate for NDD

The results suggest ontogenic and temporal features of how NDD may be stabilizing the *M. bisulcata* population. Because these features do not subscribe to current standard theory, they point to a novel mechanism of negative feedback between adults and juveniles that may arise from an ectomycorrhizal (ECM) symbiosis and mast-fruiting life history. There is strong evidence that ECM networks connect roots of neighbors to facilitate the movement of carbon and nutrients between trees and seedlings (reviewed in Simard and Durall 2004; Selosse et al. 2006). Being strongly ectomycorrhizal, *M. bisulcata* is also distinctly mast fruiting in its phenology, which involves much investment of carbon and nutrients (Green and Newbery 2002; Newbery et al. 1988, 1997, 2006a; Norghauer and Newbery 2015). Newbery et al. (1998) were the first to suggest that the draining of resources away from seedlings towards adults could accelerate seedling mortality in the understory. Enhanced by the novel results of our study, we propose that a plausible mechanism underlying NDD in *M. bisulcata* is likely a carbon (and possibly nutrient) drain that peaks in years of mast fruiting. This temporal feedback could be viewed as a form of a “size-driven asymmetric”

competitive interaction (Weiner 1988), particularly given the limited ballistic dispersal of seeds establishing many seedlings within dense stands of large trees and their extensive, overlapping root systems and ECM networks (Newbery et al. 2004, 2009, 2013).

Indeed, the possible negative effects of ECM networks upon tree seedlings in a density-dependent context remain almost entirely unexplored. This is in contrast to their putative benefits for woody plant establishment and performance (Onguene and Kuyper 2002; Alexander and Lee 2005; McGuire 2007; Booth and Hoeksema 2010). Although a contentious topic (Selosse et al. 2006; Simard and Durall 2004), mutualistic feedbacks have been vaguely suggested (Johnson et al. 1997; Koide and Dickie 2002), and some conspecific plant–soil feedbacks might be mediating chemically and not pathogenically for tropical tree seedlings (McCarthy-Neumann and Kobe 2010). It is also plausible that the amount of carbon transfer to seedlings can be inversely related to the “donor” size of conspecific adults, as shown for another an ECM tree species (Teste et al. 2009). Also consistent with our postulated mechanism is that many temperate tree species in USA forests subject to NDD are ECM and mast-fruiting (Zhu et al. 2015; Johnson et al. 2012). Presently under way at Korup is an ECM exclusion experiment using planted *M. bisulcata* seedlings.

Could such a negative feedback mechanism also be plausible on an evolutionary basis? Because most *M. bisulcata* seeds fall below the crowns (Norghauer and Newbery 2015), NDD means that any survivors are those in the dispersal tail, furthest away from the adults under which surviving saplings would otherwise come into close competition when older. However, saplings positioned away from adults by NDD may still enter a common ECM network with other tree species, such as the closely related and codominant *Tetraberlinia bifoliolata* and *T. korupensis* (Newbery et al. 1988, 2000), perhaps to their benefit later in ontogeny. Alternatively, the “drain effect” might be a temporary negative consequence, an unavoidable cost of the continuing functioning of the common ECM network; and offset by disproportionately greater gains in fitness from the copious seed production and likely accelerated stand recovery of younger trees of *M. bisulcata* during long-term cycles of transient dominance (Newbery et al. 2013).

Conclusions

This field study represents the first in-depth investigation of negative density dependence in an African rain forest tree species. The complementary NDD patterns and dynamics detected for this species were, however, not likely generated by conventional mechanisms of intraspecific juvenile competition or natural enemies. Instead, we introduce the

idea of a negative feedback between adults and juveniles in the form of asymmetric carbon/nutrient drain through a shared ECM network. We speculate that our postulated intraspecific feedback functions as a temporarily fluctuating one with an ontogenic feature in that NDD mainly affects the survival of older seedlings and the leaf area and survival of smaller saplings, both size classes of juveniles being by then presumably well connected into the forest ECM network.

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Author contribution statement JMN and DMN conceived and designed the study. JMN conducted the field work to collect the data. JMN carried out the statistical analyses. JMN and DMN interpreted the analyses and wrote the manuscript.

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