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Recruitment dynamics of the grove-dominant tree *Microberlinia bisulcata* in African rain forest: extending the light response versus adult longevity trade-off concept

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Abstract In groves of ectomycorrhizal caesalpinia-ceous species in the Atlantic coastal forest of Central Africa the dominant tree *Microberlinia bisulcata*, which is shade-intolerant as a seedling but highly light-responding as a sapling, shows very limited regeneration. *M. bisulcata* saplings were mapped in an 82.5-ha plot at Korup and found to be located significantly far (>40 m) away from adults, a result

confirmed by direct testing in a second 56-ha plot. Sapling growth over 6 years, the distribution of newly emerging seedlings around adults, recruitment of saplings in a large opening and the outward extent of seedlings at the grove edge were also investigated. Two processes appear to have been operating: (1) a very strong and consistent restriction of the very numerous seedlings establishing after masting close to adults, and (2) a strong but highly spatially variable promotion of distant survivors by increased light from the deaths of large trees of species other than *M. bisulcata* (which itself has very low mortality rate). This leads to an apparent escape-from-adults effect. To maintain saplings in the shade between multiple short periods of release ectomycorrhizal connections to other co-occurring caesalp species may enable a ratchet-type mechanism. The recorded sapling dynamics currently contribute an essential part of the long-term cycling of the groves. *M. bisulcata* is an interesting example of an important group of tropical trees, particularly in Africa, which are both highly light-demanding when young yet capable also of forming very large forest emergents. To more comprehensively explain tropical tree responses, the case is made for adding a new dimension to the trade-off concept of early tree light-response versus adult longevity.

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Introduction

Attempts to categorize the responses of tropical rain forest saplings to different levels of light within a simple framework has until now proved difficult. Increasing knowledge over the last 50 years has shown that species are perhaps at best ranked along a continuum ranging from very shade-tolerant to very light-demanding (Rollet 1974; Canham 1989; Clark and Clark 1992; Wright et al. 2003). These limits are determined by the evolution of plants in terms of their physiology, growth and life-history strategies, recognizing also that a species' position along this axis will likely change with its ontogeny. The existence of distinct functional classes is debatable given the continually changing local environment that any tree encounters over its life-time, particularly the ever-shifting and fluctuating light levels within the understorey. One single axis in trade-offs, under which light-demanding fast growing species are short-lived and shade-tolerant slower growing ones have the opposite tendency (e.g. Poorter and Aerts 2003), is probably too restrictive. Combined with the notion of classification of types it is likely to be also of limited heuristic value (Richards 1996).

An exception to this continuum approach is the case of pioneer species. Their characteristics can be more readily distinguished than those of other rain forest trees because natural selection has positioned them at an extreme, even though they vary considerably among themselves in growth rate, light responsiveness, wood density and longevity (e.g. Dalling et al. 2001; Davies 2001). Likewise, persistence in deep shade requires certain physiological adaptations, growth and life-history forms, which can be of various grades such that some species with these traits reach the centre of the continuum where a mix of intermediate characteristics prevails. Removing the unnecessary restrictions of 'groups of species' and 'categories of response' might allow for a more informative, individualistic and pluralistic understanding of tree species in the forest (McIntosh 1987).

Across the three main tropical regions, namely Africa, C. and S. America and S. E. Asia, there exist many differences in evolutionary history, phytogeography, climate and soils and anthropogenic influences, to make every rain forest within them unique, at scales of 1–10³ km². Each area is indeed contingent on its past. Africa especially has been noted as

having forest of different structure and dynamics from the other regions, with a relatively lower frequency of middle-sized trees and higher frequencies of small and large ones, than the other continents (Richards 1996). Several ideas have been advanced by way of explanation: repeated regimes of natural disturbance at intervals of perhaps 60–180 years or more (Aubréville 1938; Newbery et al. 2004); recent anthropogenic effects through forest clearance which when abandoned led to the present late secondary forest (Letouzey 1968; White 2001); or a dynamics which permits many species to move fast through the intermediate tree size classes (Jones 1956; Clark and Clark 1987; Jans et al. 1993), possibly as a result of biotic factors putting a temporary 'brake' on early recruitment and this later being released on older trees. This accelerated transition implies an ontogenetic shift between small trees <10 cm dbh and pre-adult trees ≥10 cm dbh.

For many decades, it was thought that most canopy and emergent tree species in rain forests were shade-tolerant for the long-periods (*c.* 10–30 years) of slow juvenile growth, until an opportunity was afforded by locally increased light levels to allow them to grow faster and move up into the canopy (Whitmore 1984). Exceptions were known but generally disregarded as being unimportant and not fitting to a broad scheme, or interesting cases explained away as historical accidents, due to special habitats or a result of sampling problems. Even so, evidence has slowly mounted up, especially for African rain forests, that a substantial proportion of tree species of the canopy/emergent strata are only slightly or moderately shade-tolerant, and many are very light-responsive from a very young age (Rollet 1974; Hawthorne 1996; Newbery and Gartlan 1996; Richards 1996). They can sometimes reach very large sizes as adults, though not necessarily becoming the oldest trees in the region. Some are characteristically rare and widely spaced as individuals on the landscape (Foggie 1960; Hallé et al. 1978; Richards 1996), but others form clusters or groves (Letouzey 1968, 1985; Newbery and Gartlan 1996; Newbery et al. 1998, 2004). In between them are the many less obvious intermediately scaled species (van Steenis 1958; Jones 1956). The simple light and growth versus longevity trade-off idea does not seem to fit here: the species are light-responsive and fast growing when young, but they still reach great sizes and

ages. Any trade-offs existing—in a narrow sense defined for seedlings and saplings (e.g. Gilbert et al. 2006)—are likely better represented within a framework of more than two dimensions when considering larger saplings, and juvenile and adult trees.

The main line of reasoning behind the light-responding/fast growth and short life versus shade-tolerant/slow growth and long life has been that the fast height growth necessary to outpace neighbours was built on light-weight ('low-cost') stems (structures of low wood density) as opposed to slower growth in the understorey leading to heavier and stronger ('high-cost') stems (high wood density; Chave et al. 2006; King et al. 2006). The former would not be substantial enough for the load of large, long-lived forest trees, compared with the latter (Muller-Landau 2004). In the intermediate situation, a relatively light-responsive species in early life (not as fast as a pioneer proper), which then need to build wood strong enough to support a large tree later, would need either continuous above-average light levels or repeated and substantially elevated periods at intervals to realize this strategy. This could come about from several local disturbances around saplings and young trees over time, or it might be achieved by tidying over periods of insufficient light through access to necessary carbon-based resources for growth from elsewhere or both.

This additional carbon source could be other large and better illuminated neighbours linked via a network of ectomycorrhizal hyphae (Newbery et al. 1988, 2000; Simard et al. 1997, 2002; McGuire 2007; Teste and Simard 2008). Not all large-emergent species in Africa are ectomycorrhizal, however. Those forming large scattered emergents mostly are not. They do often have wind-dispersed seeds though, which helps them reach establishment sites far further away than non-wind-dispersed species. Their rareness is testament to the presumably very high losses of seeds and seedlings in the understorey with only very few seedlings and saplings, by chance, having the several putative releases of growth (Alexandre 1989). The alternative life-history is shown by the ectomycorrhizal caesalps, which have a strong propensity to form dense non-persistent patches (Letouzey 1968, 1985; Newbery et al. 1997, 1998), in which the mycorrhizas would be of likely great benefit to maintaining some growth during crucial periods of low-light intensity in the understorey. For African

tropical forests at least, the simple axis discussed at the start needs at least one major branch or second dimension within its non-pioneer part. By contrast, persistent monodominance among tropical trees (Connell and Lowman 1989; Hart et al. 1989; Torti et al. 2001) involves high and sustained tolerance of low light levels in the understorey with gradual replacement of adults over time (e.g. Gérard 1960; Hart 1995).

Support for the ecological importance of long-lived light-demanding trees species in African forests, and the hypothesized role of ectomycorrhizas, is presented here through a study of the sapling dynamics of *Microberlinia bisulcata* A. Chev. (Caesalpinioideae, Leguminosae = Fabaceae) in Korup National Park, Cameroon. This species reaches ages of typically 200–300 years in Korup, occasionally >350 years (unpubl. data). Following from the above arguments, it is not possible to categorize this species in a satisfactory manner (nor its co-subfamilial associates *Tetraberlinia bifoliolata* (Harms) Hauman and *T. korupensis* Wieringa (formerly, *T. moreliana* Aubr. in Korup). *M. bisulcata* appears not to be a 'non-pioneer light demander' as defined by Hawthorne (1996), because '...of the[ir] assumed tolerance of or requirement for shade as seedlings...'. The scheme of Poorter et al. (2006) included a long-lived pioneer category but the age threshold to short-lived pioneers was only 30 years and wood density 0.47 g cm^{-3} , both set too low for really large and long-lived tree species. Being a 'non-pioneer' in the classification of Swaine and Whitmore (1988) and Whitmore (1989) is in any case not so informative: likewise *M. bisulcata* is not a nomad in the classification of van Steenis (1958) as it is often locally highly abundant. Oldeman and van Dijk (1991) proposed a scheme of 'strugglers' and 'gamblers' which, whilst acknowledging mixed or intermediate strategies, did not allow for a full flexibility of response with ontogeny. Hallé et al. (1978) and Richards (1996) were both aware of a wide range in traits that could lead to the large-emergent tree life-style, though they did not suggest any common scheme.

At the end of a discussion about pioneer versus non-pioneer trees, Turner (2001, p. 246) wrote: 'The relative abundance of giant invaders in the rain forests of West Africa (...) has tantalized many ecologists into seeking an explanation'. Whilst some of these species may be invasive—as opposed to

being a regular feature of the natural long-term forest dynamics (*sensu van Steenis 1958*), the observation highlights an intriguing problem, the solution to which can surely lead to a deeper and more realistic understanding of the wide range of traits shown by tropical rain forest trees.

The specific aims for this article concerning *M. bisulcata* were thus (1) to quantify the very low survival of seedlings to the sapling stage (recruitment problem), (2) to estimate the density and growth of saplings with respect to distance to conspecific adult trees (restriction problem), (3) to assess the replacement potential with respect to stand dynamics (maintenance problem) and (4) to place this species in the context of other African forest trees' life-history strategies (classification problem). From the outset, the intention was not to test the hypothesis of Janzen (1970) and Connell (1971) *per se*, but to tackle the wider phenomenon of establishment near to versus away from parent trees, of which the hypothesis could be a part. Two central points will emerge from the findings: (1) even where parents are ectomycorrhizal preferential establishment away from them may be an *apparent* Janzen–Connell effect caused by differential rates in adult tree mortality and increases of light level in gaps, and (2) survival of seedlings to saplings in subsequent periods of low light levels might depend on support through long-distance ectomycorrhizal links to these parents.

Methods

Field data collection

Forest plot

Within an 82.5-ha permanent plot, the 'P-plot' in the southern part of Korup National Park, Cameroon (Gartlan et al. 1986; Newbery et al. 1988), all trees ≥ 50 cm stem diameter ('large' trees) had been mapped, measured, tagged and identified in 1991 (Newbery et al. 1998). Mapping of surrounding large *M. bisulcata* trees in the grove, of which the plot was a central and large part, had been completed in 2000 (Newbery et al. 2004). However, stem diameter measurements were only partial at the time of this sapling study and they were done later in 2005 using

a relascope, when the plot was re-enumerated. Of the 1651 large trees in the P-plot in 1991, *M. bisulcata* numbered 294 (17.8%), *T. korupensis* 279 (16.9%), *T. bifoliolata* 195 (11.8%), *Didelotia africana* 61 (3.7%), *Berlinia bracteosa* 42 (2.5%) and *Anthonotha fragrans* 25 (1.5%). The count of *M. bisulcata* became 292 in 2005 (nine deaths, seven recruits). Additionally, 42 large trees of this species occurred in the area caused by extending the plot 50 m on all sides (105 ha). For *M. bisulcata*, practically all large trees so defined would have been adults (Newbery et al. 2004). Mean nearest-neighbour large tree distance for *M. bisulcata* was 22.0 m ($n = 294$, range 1.4–72.8 m, median 18.8 m). Between 1991 and 2005, the rate of annualized mortality of all large trees was 1.42%, for *M. bisulcata* it was 0.22% and for other species 1.71% (D. M. Newbery and X. M. van der Burgt, unpubl. data).

Sampling of saplings

Of the 330 subplots (50 m \times 50 m), 42 in permanently wet areas (swamps, large streams and edges of rivers) and 35 bordering unmapped areas outside were excluded. The remaining subplots were ranked into eight classes based on the basal area of large trees of *M. bisulcata* and 64 of them were chosen, in a stratified random manner to achieve an even spread of sampling. Finally, within each chosen subplot a half-subplot (25 m \times 50 m) was selected at random from the four orientations possible. Eight of these last were replaced in the field on finding they had largish areas with streams, a river or open and low-swamp vegetation, though one half-plot did have a large tree fall. The status of these excluded half-subplots was double-checked in November 2008. The plot area sampled was 8 ha or 9.7% (see *Supplementary Electronic Materials* for P-plot map and sample layout). The advantage of using randomly placed (half-) subplots at distances 2- to 3-fold greater than tree–tree distances for *M. bisulcata*, compared with a fully enumerated grid, was that adjustment for spatial autocorrelation was obviated.

Inspection of the grove map showed that 15 of the half-subplots lay in the outermost border of subplots, and seven of these were at, or within 50 m of, the edge of the grove (defined by trees of *M. bisulcata* ≥ 50 cm stem diameter). To minimize the confounding effect of grove edge, these half-subplots were not

used in the main analysis that follows, only in a supporting role. The 49 half-subplots within the 62 ha so-defined may be viewed as being fully inside of the grove. Relating to the grove complex mapped in Newbery et al. (2004), 18 half-subplots fell in sub-grove II (western part of the P-plot) and 31 fell in sub-grove III (eastern part), these separated by a river and a swampy area. Adding the border samples, the sub-groves II and III had 19 (one more since this part was largely precluded in the setting up) and 35 half-subplots, respectively.

In one of the areas of highest densities of saplings of *M. bisulcata* in the P-plot, a 4-ha block (200 m × 200 m) was demarcated inside of and abutting the eastern border. All saplings were mapped and measured as in the half-subplot sampling. The survey half-plots constituted 9/32 of this block (28%).

Sapling measurement

Fifty-five small saplings ≥ 1 m relaxed height, but < 1 cm dbh (diameter at a breast height of 1.3 m) and 32 large saplings 1– < 10 cm dbh of *M. bisulcata* (exceptionally one sapling of 0.9 cm dbh) were censused 5–30 January 2003 (mean 17 January). Height (ht) and number of leaves (nlv) were recorded for small saplings, and dbh (callipers or a thin tape), with a subsample of heights for large ones. Survivors were remeasured around 16 March 2004 (interval = 1.16 years).

The tagged populations were remeasured on two further occasions, on 4 December 2005 and 29 October 2007 (median of 17 October and 9 November) for nlv in addition to ht for small saplings, and dbh again for large saplings. Times of measurement from the start were thus 0.0, 2.88 and 4.78 years. Annualized mortality (m_a) was calculated for saplings, and absolute (agr) and relative growth rates (rgr) in ht and nlv for small saplings and in dbh for large saplings. Four-ha block subplots were remeasured only in 2007 (dbh on a few block saplings was measured at 1.0 m), and a subsample had ht recorded.

New seedling shadow

For an estimate of the seedling shadow soon after establishment, new seedlings resulting from the previous 2004 mast fruiting had been counted in a 15°-segment away from the centre of each of three

large *M. bisulcata* trees in August–September 2004. Segments needed to have sufficient seedlings, and again free of seed input from other trees—a condition hard to find. Each segment was divided into three smaller ones of 5°, and then divided from tree centre to periphery, into 1-m wide radial intervals; counting was extended until no further individuals were found for 10 m. Position of crown edge was also recorded. Two of the trees were from within the P-plot and one outside of it, but within the grove. Their mean stem diameters (above buttress) and corresponding heights were 131 cm (range 125–142 cm) and 43.7 m (41.3–47.1 m), which were very close to those of a sample of 15 canopy individuals in a recent architectural study, 137 ± 9 and 44.3 ± 1.4 m (Newbery et al. 2009), although the mean diameter was little larger than the mean of the 2005-enumerated trees ≥ 50 cm stem diameter (117 ± 2 cm). The seedling shadow trees can be reasonably taken as being representative of the larger *M. bisulcata* trees in the plot despite the small sample size.

Seedlings at the grove edge

All of the nine trees of *M. bisulcata* (diameter ≥ 130 cm) on the eastern and north-eastern edges of the main grove were selected. The aim was to determine how far away from adults seedlings could establish. Grove edge was defined by trees being not > 200 m apart and other trees inside of them making a concavity. In a perpendicular-to-edge transect to each tree, of width 10 m and extending outwards by 100 m, all seedlings of *M. bisulcata* were recorded (8–22 December 2002) in 1-m intervals, and their relaxed ht and nlv recorded.

Seedlings and saplings in a large gap

In the wet season of 1999 (July–October) an area of c. 1.5 ha 500 m south of the P-plot within the grove experienced a wind-throw which brought down c. 30 trees with stem diameters ≥ 50 cm, but none were *M. bisulcata* which were left surrounding the gap. The fallen trees had a fan pattern indicating a gust coming with a thunderstorm. Seven well-separated quadrats of c. 4 m × 5 m in and around the perimeter of the gap area were demarcated in places where the density of *M. bisulcata* seedlings was highest. Most seedlings almost certainly originated from the most recent

masting in 1998. This small opportunistic study provided the possibility to follow a rare event (once in *c.* 20 years to our knowledge). Seedlings were tagged and measured for ht and nlv around 15 March 2000. Recording of alive/dead status and remeasurement of ht and nlv were made on 16 June 2000, mid-October 2001 and 2 April 2008. In and around the gap, 12 saplings of *M. bisulcata* *c.* ≥ 0.8 cm dbh were tagged in March 2000. Their dbh and ht were recorded then and in March 2003. Final dbh was measured on 15 May 2008.

Data analysis

Sapling neighbourhood

Distances from saplings to large trees, and their basal areas in the neighbourhoods, were compared with random locations from Monte-Carlo simulation in two principal ways. The first was to consider only saplings which were inside of the bordering subplots, so that the distance of any sapling was at least 50 m from the plot edge ($n = 63$). This permitted for every sapling a neighbourhood area of ≤ 50 m radius to be found, in which all large trees were identified. The second was to use the complete plot and sapling sample with the *M. bisulcata* trees mapped up to 50 m outside of it ($n = 87$).

Minimum distances to the nearest large trees of all species, *M. bisulcata*, *T. bifoliolata* and *T. korupensis*, of the two *Tetraberlinia* spp., or of any ectomycorrhizal spp., were found. Basal areas of these species, two *Tetraberlinia* species combined, and all ectomycorrhizal species were computed for areas of radius 10–50 m in 10-m intervals around each sapling. The maximum distance of 50 m, besides being the subplot dimension giving an average density of *M. bisulcata* of one large tree per subplot, was intermediate between the average *M. bisulcata* tree–tree distance (30 m) and the main maximum extent of dispersal (70 m).

The same variables were calculated for points randomly located across all subplots and half-subplots, which were not excluded or replaced in the setting up of the sampling. A further condition was that a random location could not be within 1.0 m of the centre of a large tree. As many random points as saplings ($n = 87$) were chosen: the procedure was repeated 199 times using a FORTRAN77 program.

When means of sapling values lay outside the ranges of the first 19, 49, 99 and 199 simulated values (inference procedure based on order statistics) the null hypothesis of no neighbourhood effect was rejected at $P = 0.05$, 0.02, 0.01 and 0.005, respectively. (The central limit theorem in statistics assures that the means of these approximately Poisson-shaped distributions will themselves follow a Gaussian distribution.) Analyses were repeated using small saplings, i.e. those with stem dbh < 2 cm ($n = 72$, and of which 54 were inside of the bordering subplots). Standard statistical techniques for spatial data were not applicable because saplings were not fully mapped.

Extension and grouping

In similar randomization tests using the later-completed grove maps of large *M. bisulcata* trees, either the large trees of 1991 or of 2005 within the main plot could be combined with those recorded outside in 2005. Further, the large trees of 2005 inside of the 50-m bordering subplots, could also be utilized as an alternative to the first approach. Records of mortality in 2005, for the period since 1991, allowed tests of distance to and neighbourhood basal area of alive and dead 1991-enumerated trees separately. Analyses were again repeated for small saplings.

The frequency distribution of the number of saplings in the 64 half-subplots differed significantly from that expected of a Poisson distribution with a mean of 1.25 ($P < 0.001$). To remove the effect of aggregation, and thus spatial non-independence, all saplings were classified by their *x*- and *y*-coordinates using a centroid sorting agglomerative algorithm based on Euclidean distance (Greig-Smith 1983). Saplings, which were ≤ 40 m apart (the *y*-axis ‘distance’ value of the dendrogram), were grouped and their average coordinates found. The distance 40 m is close to the mean of half-subplot length and breadth (37.5 m). This led to 30 sapling groups with the following compositions: 10 (of 1 sapling), five (2), five (3), three (4), six (5) and one (of 10 saplings). Repeated randomization tests used, first, the 21 groups located inside of the 50 m bordering subplots and all spp. of large tree, and second, all groups using the 1991-, or 2005-recorded, large trees of *M. bisulcata* in the whole plot and recorded in 2005 in the extended area. Mean number of

saplings per half sub-plot within the border was 1.29.

Corroborative testing

A second permanent plot, the ‘NW-plot’ of 56.25 ha (750 m × 750 m) set up in 2003 (see Newbery et al. 2004), afforded the possibility of an independent test of the sapling frequency-with-distance hypothesis arising from the P-plot analysis. Inside of the 50-m border of subplots, and ignoring those areas with rivers, streams, permanently wet (swampy) ground (based on a fine-scale map of 2003), all half-subplots (both E–W and N–S orientations) were selected in turn across the whole of the NW-plot. The 25-m × 50-m area of each covered a 5 m grid of 6 × 11 points. For each point distance to the nearest large tree of *M. bisulcata* (mapped 2003) was determined, and the 66 values categorized into (1) <20, (2) 20 to <40, (3) 40 to <60, (4) 60 to <80, and (5) ≥80 m, to give a frequency table for each half-subplot. All potentially suitable half-subplots were then ranked in two ways: first using the frequencies in class 1 (=‘near’ to *M. bisulcata*), and then second using those in class 3 (=‘far’ from *M. bisulcata*). (Classes 4 and 5 had very low frequencies.) The first 14 half-subplots (not sharing a border or overlapping with a previously chosen one) had frequencies of 66 down to 62 (0–4 in class 2, none in higher ones). Likewise, 13 half-subplots could be found with maximally 51 down to 41 points in class 3 (none in class 1, 3–19 in 2 and 1–20 in 4, none in 5). Here an additional selection rule was applied that once the stepping reached 43/66 points in class 3, further half-subplots had to have a frequency in class 4 greater than that in class 2.

Between 4 and 6 November 2008, the half-subplots were completely searched for saplings of *M. bisulcata* of minimum ht 1 m or 1 cm dbh (maximum 10 cm dbh), and each was tagged and measured for ht and/or dbh. In just once case was the half-subplot overlapping a previously unnoticed small area of swamp, and it was accordingly moved east by 30 m. Recalculation of its grid neighbourhood distances showed that it had only 29 points in class 3, 35 in class 2 and 2 in class 1 (making the test more conservative). One selected half-subplot in part had evidence of an old gap. The total area sampled was 3.375 ha.

Results

Sapling distribution

Sapling sizes

From surviving large saplings, plus a supplementary sample of those recorded in 2007, the relationship $ht \text{ (cm)} = 85.6 + 151 \text{ dbh (cm)}$ was derived ($n = 21$, $F = 68.3$, $P < 0.001$, $r^2 = 0.77$); and this was used to convert the 2003 dbh measurements to ht. Decline in frequency with height class was very steep (Fig. 1a): it could not be linearized by either single or double-logarithmic transformation. An approximate height threshold for saplings below and above

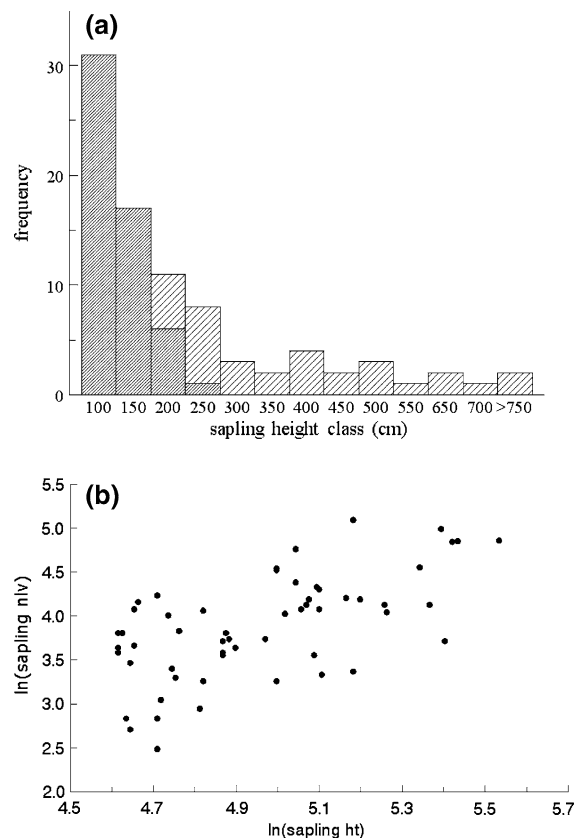


Fig. 1 Size and foliage distributions of sampled saplings of *M. bisulcata* in Korup in 2003. (a) Frequency of heights ($n = 87$): fine hatching represents the small saplings for which height was measured directly, coarse hatching the large saplings for which dbh was measured and converted to height. (b) The relationship between number of leaves and height for small saplings ($n = 55$)

1 cm dbh is 250 cm. Those of 5 cm dbh reached over 8 m. Mean (\pm SE) ht for small saplings in 2003 and 2004 were 145 ± 5 and 154 ± 6 cm ($n = 51$; two deaths, two missing data) and mean dbh correspondingly 2.31 ± 0.26 and 2.40 ± 0.27 cm ($n = 31$, one death), respectively. Values for the samples within the bordering subplots were very similar. Height and nlv (logarithmically transformed) were significantly positively correlated ($r = 0.625$, $df = 53$, $P < 0.001$). The spread in nlv remains constant across the ht range at a considerable $c. 1.5$ log-units, or a 4.5-fold change (Fig. 1b). Sample representation is analysed in the *Supplementary Electronic Materials* appended to this article.

Sapling neighbourhood

Saplings of *M. bisulcata* were not significantly further from any tree (i.e. all spp., Fig. 2a), but the basal areas of all tree species around them was marginally significantly lower than around random locations (Fig. 3a). Saplings were located highly significantly further away, however, from conspecific large trees ($P < 0.005$, Fig. 2b), and highly significantly closer to those of *T. korupensis*, than to random locations ($P < 0.005$, Fig. 2d). There was no significant difference for *T. bifoliolata* (Fig. 2c). Correspondingly, basal areas of large trees of *M. bisulcata* within radii of 10–50 m of saplings were

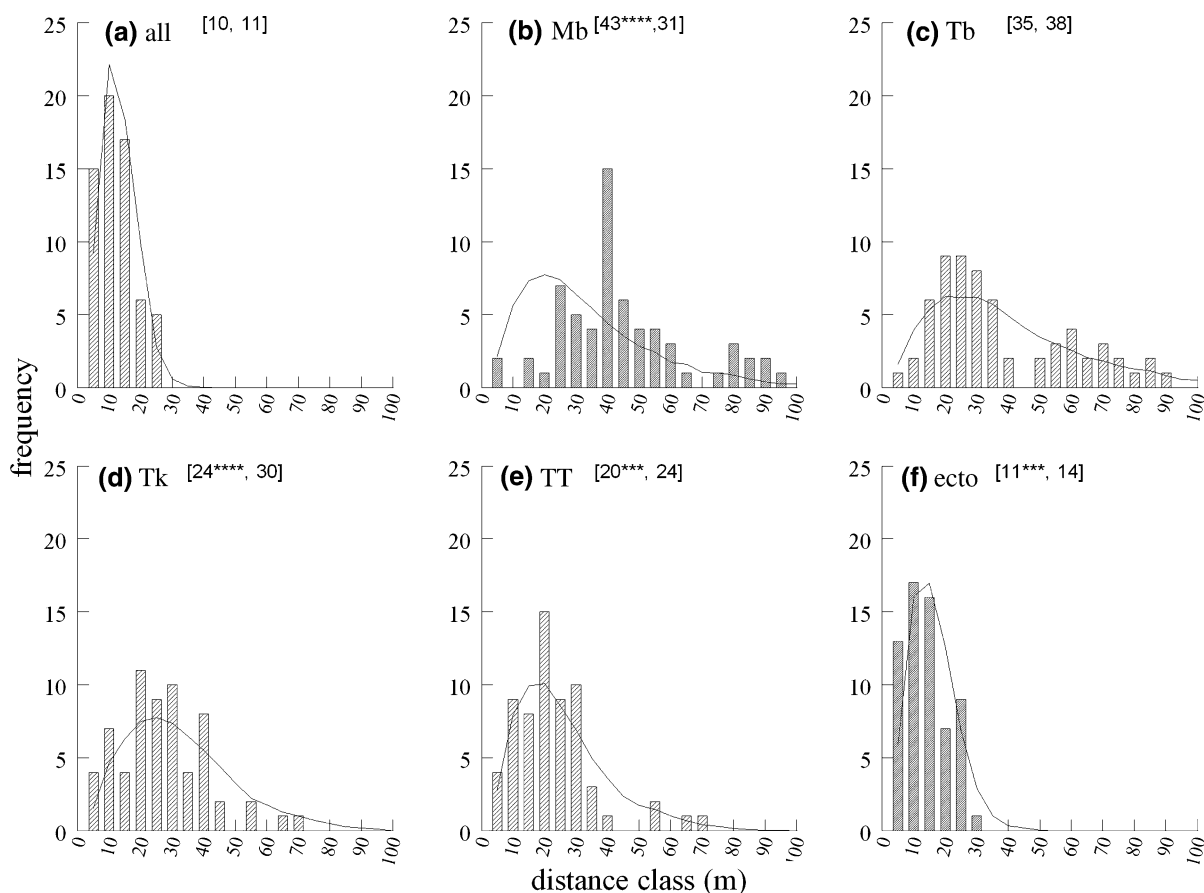


Fig. 2 Frequency distributions of distances (bars) from saplings (inside of the 50-m border) in P-plot ($n = 63$), to the nearest large tree (≥ 50 cm stem diameter) of (a) all trees (i.e. any sp.), and those of (b) *M. bisulcata* (Mb), (c) *T. bifoliolata* (Tb), (d) *T. korupensis* (Tk), (e) the two *Tetraberlinia* spp. together (TT), and (f) all (i.e. any of the) ectomycorrhizal spp.

(ecto); together with Monte-Carlo-simulated sets of locations (lines), proportionally rescaled to sum to the observed sample size ($n = 199$). In *square brackets* in each panel: mean distances for saplings and simulated locations, respectively, and the significance of the difference (***) $P < 0.01$, **** $P < 0.005$ and otherwise not significant $P > 0.05$

highly significantly lower ($P < 0.005$) than those around random locations, by a factor of *c.* 4-fold at 10 m, nearly 7-fold at 20 m, and 2- to 3-fold at 30–50 m distance (Fig. 3b). Basal area differences for *T. korupensis* were significantly higher at 20–50 m around saplings than around random locations ($P = 0.02$ – 0.005 , Fig. 3d), but they were weak and insignificant for *T. bifoliolata* (Fig. 3c). Accordingly, the (minimum) distance from saplings to either of the *Tetraberlinia* spp. (Fig. 2e) was shorter than to random locations ($P < 0.002$) and basal area differences of the *Tetraberlinia* species together were intermediate and significant at 20–40 m ($P = 0.02$ – 0.005 ; Fig. 3e). Ectomycorrhizal trees showed a similar non-significant pattern to all trees (Fig. 3f), yet distance to any ectomycorrhizal tree was shorter

for saplings than for random locations (Fig. 2f, $P < 0.01$).

For the whole plot area (with border subplots, $n = 87$ saplings), the large *M. bisulcata* trees outside of it were used as neighbours. Results strongly confirmed the greater distance to (42 vs. 32 m, $P < 0.005$), and lower basal area around (Fig. 4a), *M. bisulcata* saplings compared with the random locations (mostly at $P < 0.005$). Replacement of these 1991-recorded large trees by 2005 ones led to a smaller difference in distance (36 vs. 31 m, $P < 0.01$, $n = 87$), although basal area differences for radii of 10–50 m remained very much the same ($P < 0.002$). Further, when 2005-trees were used as neighbours to saplings within the border ($n = 63$), the difference in distance (34 vs. 30 m) became non-significant, yet

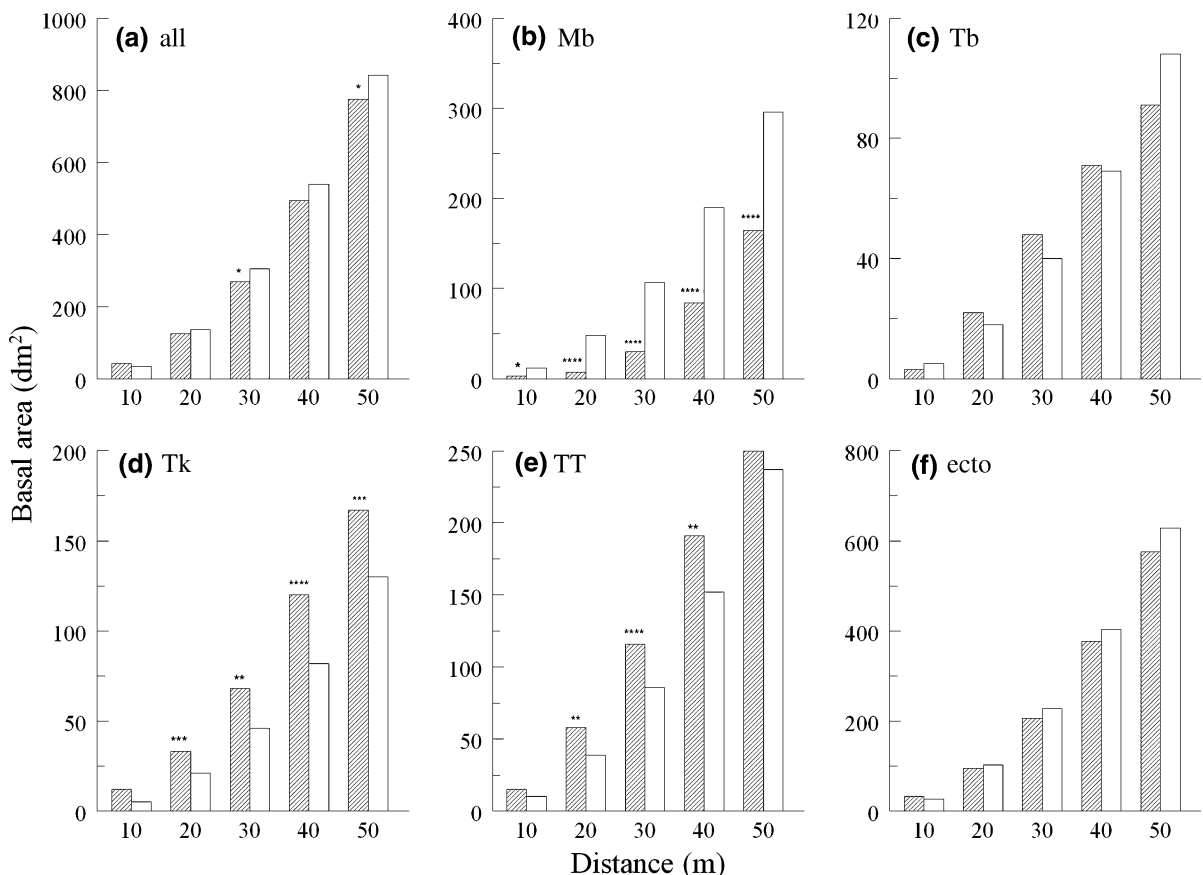


Fig. 3 Mean basal areas of large trees (≥ 50 cm stem diameter) in 10-m radial increments between 10 and 50 m around saplings ($n = 63$, inside of the 50 m border) in P-plot (hatched bars) and the same for Monte-Carlo-simulated sets of locations ($m = 199$, open bars): (a) all tree spp., (b) *M. bisulcata* (Mb), (c) *T. bifoliolata* (Tb), (d) *T. korupensis* (Tk),

(e) the two *Tetraberlinia* spp. together (TT), and (f) all ectomycorrhizal spp. (ecto). Asterisks indicate the level of significance of the difference between observed and simulated neighbourhoods (* $P < 0.05$, ** $P < 0.02$, *** $P < 0.01$ and **** $P < 0.005$)

basal area differences remained large and significant ($P = 0.01$ – 0.005). The likely reason in the last two cases was that 11 saplings gained, as their new nearer-neighbours, trees which had recruited into the ≥ 50 cm size class by 2005. And, since these recruits had minimal basal areas compared with larger trees in the rest of the stand, differences in basal areas changed very little between 1991 and 2005.

Neighbourhood of grouped saplings

Using average locations of the groups of saplings inside of the border subplots, the central result for *M. bisulcata* large trees was maintained, although the difference in distance (40 vs. 32 m) was

non-significant—probably due to the smaller sample size ($ng = 21$). Differences in basal area were significant at 20–30 m ($P < 0.002$), but were less pronounced and less significant at radii 10 and 40–50 m (Fig. 4b). The same difference in distance to nearest *M. bisulcata* was more significant when all cluster points (40 vs. 32 m, $P < 0.02$, $ng = 30$) were considered although this lessened when 2005 tree data replaced 1991 ones for saplings within the border subplots (37 vs. 31 m, $P < 0.02$, $ng = 21$). In all three tests using grouped sapling locations, basal area differences between sapling and random locations were very similar, and consistently highly significant ($P < 0.002$) for radii of 20–30 m ($P < 0.002$ also for 40 m in cases involving all

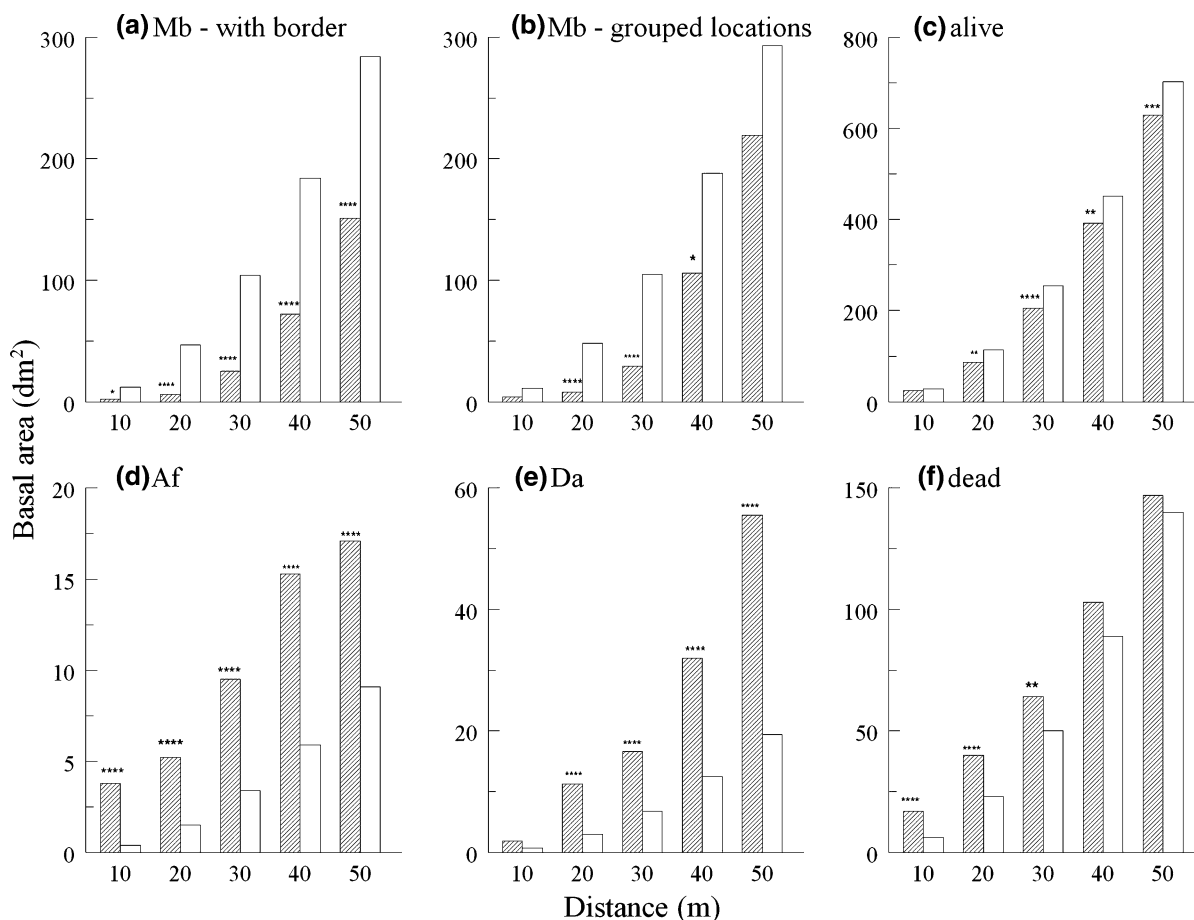


Fig. 4 Mean basal areas of large trees (≥ 50 cm stem diameter) in 10-m radial increments between 10 and 50 m around saplings in P-plot ($n = 63$, hatched bars) and the same for Monte-Carlo-simulated sets of locations ($m = 199$, open bars): (a) *M. bisulcata* (Mb) with the 50-m border ($n = 87$), (b) *M. bisulcata* in grouped locations within the border

($ng = 21$), and within the 50-m border ($n = 63$) for (c, f) alive and dead trees of all spp., (d) *A. fragrans* (Af) and (e) *D. africana* (Da). Asterisks indicate the level of significance of the difference between observed and simulated neighbourhoods (* $P < 0.05$, ** $P < 0.02$, *** $P < 0.01$ and **** $P < 0.005$)

sapling groups and the 2005 data within the bordering subplots; cf. Fig. 4b). The effect declined from *c.* 8-fold, through 4-fold, to 2-fold, and finally 1- to 2-fold at 50 m (same cases at $P < 0.005$). The large trees recruited in 2005 had much less influence than they did for individual saplings, since these trees were mostly close to clusters of saplings that became single locations. The zone of influence of large *M. bisulcata* trees appeared then to lie within a circle of radius *c.* 30 m.

Conditional and other neighbourhoods

Using only saplings and random locations ≥ 30 m from a large *M. bisulcata* tree, showed two main results: first, apart from three isolated and scattered cases of significance, *M. bisulcata* saplings did not differ significantly from random locations for all, *M. bisulcata*, *T. bifoliolata*, *T. korupensis* and both *Tetraberlinia* spp. ($P > 0.05$), although distance from saplings to ectomycorrhizal trees was significantly less than to random locations (11 vs. 16 m, $P < 0.002$) and basal areas of them were significantly greater at radial distances of 10, 20 and 30 m (35 vs. 17, $P < 0.01$; 96 vs. 65, $P < 0.01$, and 179 vs. 143, $P < 0.02$, respectively). Other components of the non-*M. bisulcata* ectomycorrhizal neighbourhood, beside *T. bifoliolata* and *T. korupensis*, appeared to be affecting *M. bisulcata* saplings.

Following the last indications, analysis with the three next most abundant ectomycorrhizal species, showed that saplings of *M. bisulcata*, were also significantly closer to large trees of *D. africana* than they were to random locations (51 vs. 69 m, $P < 0.005$), but this was not the case for *A. fragrans* (102 vs. 97 m) and *B. bracteosa* (110 vs. 99 m). More clearly shown was that the basal areas of *A. fragrans* and *D. africana* around saplings were *c.* 2.5- to 3-fold greater than random locations for radii of 20–50 m (Fig. 4d, e; $P < 0.002$). Basal areas of *B. bracteosa* did not differ significantly across the range 10–50 m ($P > 0.05$).

Irrespective of species identity, differences in distances between saplings and random locations to 1991-trees, still alive in 2005, were quite small even though they were significant (14 vs. 12 m, $P < 0.02$). Likewise, the distances to trees dead by 2005 differed little (25 vs. 28 m, $P < 0.02$). The corresponding basal areas were more strongly differing, however

($P = 0.02$ – 0.002), more in the lower part of the range in radii for dead trees (10–30 m, Fig. 4c), more in the upper part of it for alive trees (30–50 m, Fig. 4d). Basal area of dead trees around saplings at radius 10 m was almost 3-fold greater than that around random locations, and at 20 and 30 m it was 74 and 28% more. Numbers of trees dying per species were unfortunately far too few to allow tests of whether the effect of dead trees was species-specific.

Using only saplings < 2 cm dbh ($n = 52$ within border subplots) altered the overall results only very slightly and they are not reported here in any detail. They often involved just small changes in significance level, whilst differences stayed very largely in the same direction as the complete sample. This suggests that, if sapling size was generally positively correlated with age, distance and basal area relationships were holding over many years, at least for period 1991–2005. There were far too few saplings between 2 and 10 cm dbh to perform a sensible analysis.

Growth in relation to neighbourhood

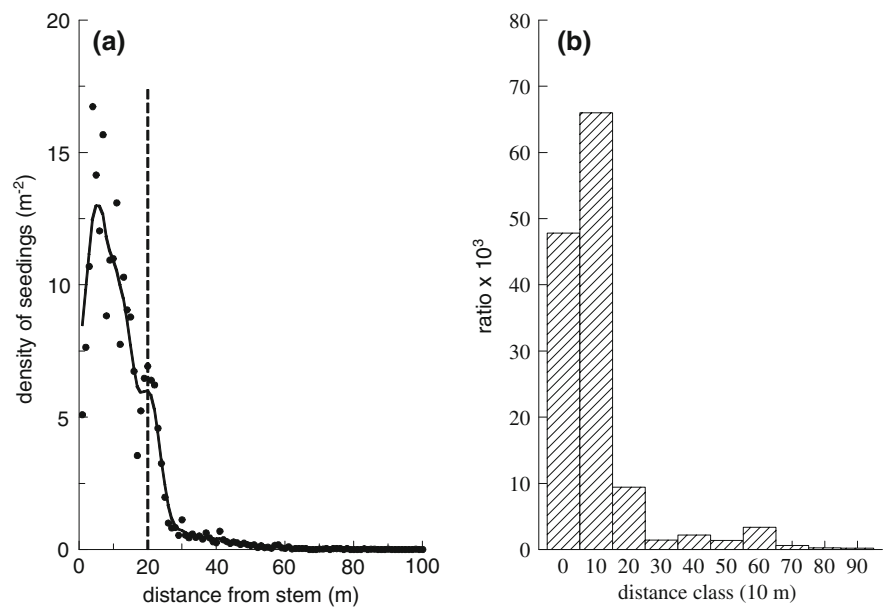
Mean (\pm SE) relative growth rates (*rgr*) in ht of small saplings (4.13 ± 0.90 cm m⁻¹ year⁻¹, $n = 51$) and dbh of large saplings (1.38 ± 1.09 cm m⁻¹ year⁻¹, $n = 31$) in 2003–2004 were only significantly correlated with distance to all trees in the case of heights of small saplings within the bordering subplots ($r = 0.464$, $df = 37$, $P = 0.003$, applying a Bonferroni α of 0.05/6). In particular, among the other five distance categories, correlations with distance to *M. bisulcata* were very weak ($P > 0.48$). Using the full sample of saplings (i.e. those within the bordering subplots too), correlations of *rgr* remained insignificant both for the 1991 and 2005 data sets ($P > 0.20$). Whilst *rgr* for ht and dbh, and for distances, were sufficiently close to normally distributed (indeed for *M. bisulcata*), those for BA were largely not (because often, and especially for *M. bisulcata*, values were zero at distances < 30 m) and this prevented involving them in correlations.

Recruitment processes

New seedling shadow

The mean number of seedlings per tree in 2004 was 607.3, and the total density 217.3/100 m². Seedling

Fig. 5 Change in (a) density of newly emerged seedlings of *M. bisulcata* (vertical dashed line is average distance to edge of canopy) and (b) the ratio of seedlings to saplings (as found in the survey), with distance from three conspecific adult trees free of influences of other adults' seed input



counts per tree segment were averaged for each radial interval from the tree's centre, converted to densities using segment interval areas (Fig. 5a) and smoothed curves fitted by a kernel method (triangular estimation, band width = 5 m; S-Plus). In the segments, 63.2 and 85.8% of the counts lay up to 20 and 30 m from the tree centres, respectively, and correspondingly 84.1 and 95.6% of seedlings on a density basis. Canopy edge coincided with the outer peak in counts and the sill in densities (Fig. 5a). Seedlings between 40 and 45 m accounted for 2.9% in terms of counts, and 0.8% of density. The density-weighted mean distance of seedlings to the tree centre was 12.4 m.

Neighbourhood restriction

The sampling recorded 63 saplings in 6.125 ha, leading to a mean density of 10.285 saplings ha⁻¹ (close to one sapling every 1/10 ha or 1.0285 × 10⁻³ m⁻²). The area suitable for *M. bisulcata* within the bordering subplots (i.e. disregarding 39 swamp and stream subplots) was 62 – 9.75 = 52.25 ha. Scaling up, the estimated total number of saplings is 537. Within this same area, there were 230 large trees of *M. bisulcata*, suggesting then an average of 2.335 saplings per large tree. Assuming these saplings occurred ≤100 m from stems (see Fig. 2b) they can be distributed across successive 10-m intervals away

from them in proportion to the counts found with distance in the original sampling (Fig. 2b again). Therefore, as distance-to-tree is a radial measure to find the expected density of saplings with increasing distance from stems, counts per 10-m distance interval were divided by corresponding annulus areas. The ratio of seedling density to sapling density is a measure of the intensity of restriction of the tree on recruitment. The effect is very large in the range 0–30 m from the stem and then drops by approximately one order of magnitude between 30 and 70 m (Fig. 5b). Plotted on a logarithmic scale, the ratio suggests a 'plateau' for this last referred-to distance range.

Edge-of-grove seedlings

Mean density of seedlings per 1-m interval (total $n = 1188$) decreased with distance from the tree (Fig. 6a). An exponential regression explained 93% of the variance ($y = 1.17 (0.88^x) + 0.046$, $P < 0.001$). There is a small peak at *c.* 48 m from the trees. For the nine trees, mean ± SE crown radius was 23.6 ± 4.8 m (range 17–31 m), mean maximum distance from stem 66.8 ± 8.8 m (55.9–82.9 m) and from crown edge 43.2 ± 5.8 m (37.0–54.9 m).

Mean ht was 18.94 and 32.3 cm beneath and outside the crown, respectively (Mann–Whitney *U*-test on medians 19 and 22 cm, $P < 0.0001$; 22.1 cm

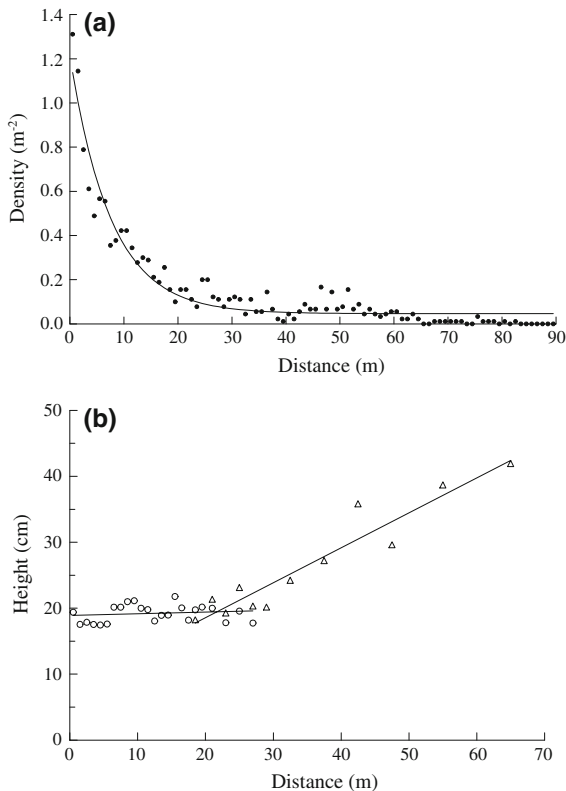


Fig. 6 Change in (a) density of the established bank of seedlings of *M. bisulcata* in 2002, and (b) their mean heights, with distance from nine conspecific adult trees on the eastern and north-eastern edges of the grove: in (b) *open circles*, below crowns; *open triangles*, outside of crowns (note: crowns varied in diameter hence overlap in symbols at 20–30 m)

overall). Mean ht of the seedlings (in cm) were then found for 38 distance classes (dist; 1 m for 0–30 m, 5 m for 30–70 m, and >70 m combined). Figure 6b shows a two-step function with an almost horizontal line below the crown ($ht = 18.9 + 0.0258 \text{ dist}$, $F = 0.52$, $df = 1,22$; $r^2 < 0.1$) and an increasing line outside ($ht = 7.97 + 0.530 \text{ dist}$, $F = 95.7$, $df = 1,10$; $r^2 = 0.896$, omitting >70 m value). Number of leaves (median = 4, range 1–112) was significantly positively correlated with ht ($r_s = 0.52$, $df = 1185$, $t = 20.92$, $P < 0.001$).

Growth of saplings

Among the 55 small saplings, three died between 2003 and 2005 ($m_a = 1.93\%$) and a further seven between 2005 and 2007 (7.33%): between 2003 and 2007 m_a was 4.11%. Of the large saplings none died

between 2003 and 2005 (0%) and only two by 2007 (3.34%), giving an overall rate of 1.34%. In 2007, five small and two large sapling survivors had top die-back, or their stems snapped, to become less than 1 m in ht. In the block, 10 of the 48 small saplings died between 2003 and 2007 (4.77%) and two of the 27 large saplings (1.60%). Reduced height from top die-back and damage affected three small saplings in the block, but no large ones. Averaging, the estimates of m_a for small and large saplings were *c.* 4.1 and 1.5%, respectively.

Changes in ht, nlv and dbh were found for the survivors in 2007, i.e. for 45 small and 24 large saplings, in the survey. In the case of large saplings, aside from losses, six other individuals lacked dbh estimates at either 2005 or 2007 mainly due to top die-back and loss of the point of measurement at 1.3 m. When changes were calculated for the survivors at the end of each interval different samples, with several inconsistencies, were being compared over time.

Height of surviving small saplings increased relatively rapidly between 2003 and 2005, but then fell slightly to 2007 (Fig. 7a). By contrast, nlv declined more slowly at first and then more rapidly (Fig. 7b). Large saplings, continued to grow in dbh with time, however (Fig. 7c). The *agr*- and *rgr*-values for 2003–2005 and 2005–2007 reflect these trends, the difference between periods being more pronounced in *rgr* (Fig. 7d–f) than *agr* (not shown) for nlv, less so for ht, and little for dbh.

The SEs on the growth variables were generally considerable (Fig. 7): doubling them gives approximate 95% confidence limits. Histograms of ht and nlv at the different dates, and their *agr* and *rgr* estimates, were approximately normally distributed. Those of dbh, however, were moderately positively skewed; and this resulted in skew in *agr*, but not *rgr*, estimates. Attempts to remove the skew (square and fourth-root transformations, using medians and quantiles, or omitting the two largest saplings ≥ 5 cm dbh) led to very little change in the relative differences across time and between periods for *agr* and *rgr*. Six saplings had particularly high *agr* (1.86–3.65 mm year^{-1}) and *rgr* (3.69–1.17 $\text{cm m}^{-1} \text{ year}^{-1}$) values, enhancing the skew and thereby contributing to the faster rise in dbh in that period compared to 2003–2005 (Fig. 7c).

The 4-ha block sample (38 survivors) supported the trends seen in the larger survey except that the large

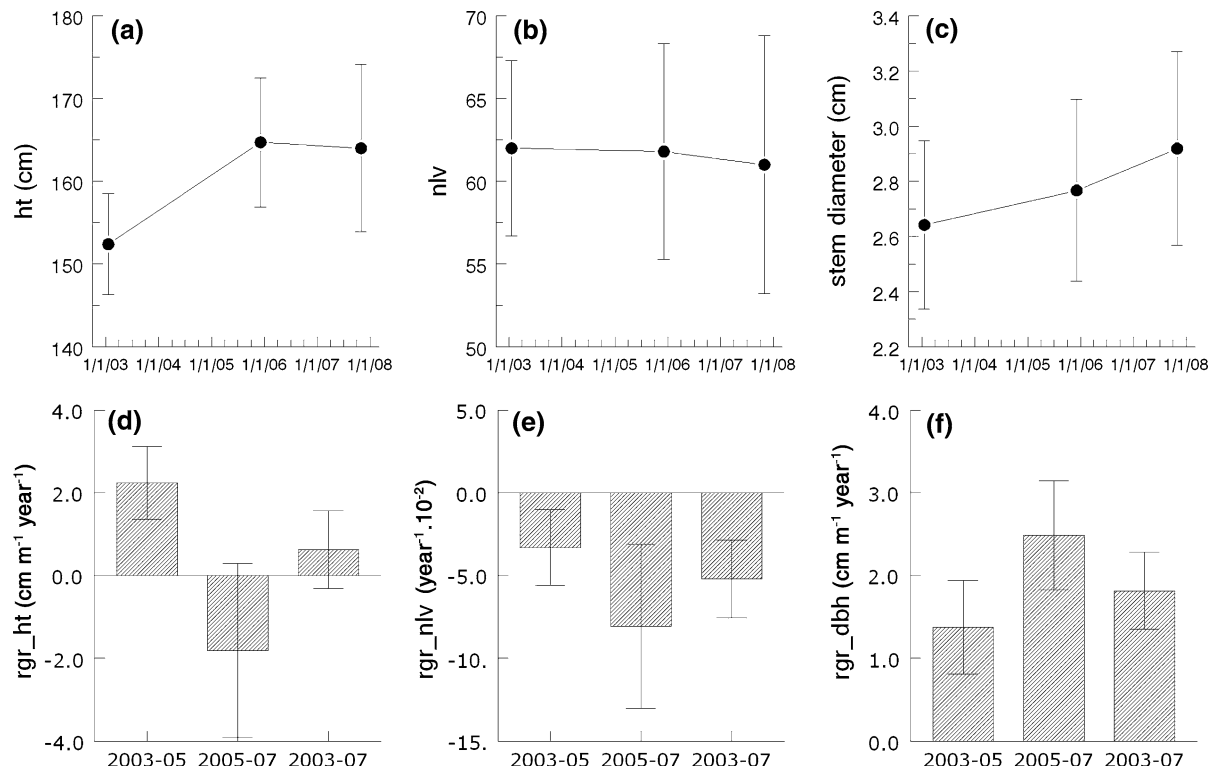


Fig. 7 Changes in the means (\pm SE) of (a) height (ht) and (b) number of leaves (nlv) of small saplings ($n = 45$), and of (c) stem diameter (dbh) of large saplings ($n = 24$), of *M.*

bisulcata, which survived from 2003 to 2007 and (d–f) the corresponding relative rates (*rgr*) in the three intervals 2003–2005, 2005–2007 and 2003–2007

saplings were smaller (2.12 ± 0.19 cm dbh in 2003, 2.37 ± 0.24 cm in 2007), the *agr* correspondingly lower (0.517 ± 0.196 mm year⁻¹), but the *rgr* similar (2.09 ± 0.72 cm m⁻¹ year⁻¹). Height increased from 150.3 to 166.9 cm (*agr* 3.47 ± 1.21 cm year⁻¹, *rgr* 1.67 ± 0.83 cm m⁻¹ year⁻¹) and mean nlv was almost constant again between 66.0 ± 5.2 and 66.6 ± 7.2 although by 2007 the frequency distribution of *rgr*-values had become strongly negatively skewed due to several damaged and sparsely leaved individuals (*agr* 0.121 ± 1.27 year⁻¹, *rgr* -3.64 ± 2.36 year⁻¹ · 10⁻²).

Among the small saplings in the survey, ht growth rates were significantly dependent on nlv in 2003: $agr_{ht03-07} = -6.57 + 0.145 \text{ nlv}_{03}$ ($F = 15.81$, $df = 1,43$, $P < 0.01$, $r = 0.519$) and $rgr_{ht03-07} = -3.65 + 0.069 \text{ nlv}_{03}$ ($F = 7.64$, $df = 1,43$, $P = 0.008$, $r = 0.388$). This result was supported by the block small saplings although less strongly with corresponding values of $r = 0.342$ ($P = 0.036$) and $r = 0.226$ ($P = 0.173$). In 2003, mean ht:dbh ratio

(cm/cm) for large saplings was 200 ± 7 ($n = 51$ in survey and block; mean dbh and ht 2.18 and 401 cm, respectively). In the block in 2007, the ratio was 215 ± 9 ($n = 20$; 1.60 and 333 cm).

Correlation analysis between these saplings' various growth variables (*agr* or *rgr* of ht, nlv and dbh with distances to nearest adult neighbours (six classes) or BA of them around the saplings (also six classes), and the three time intervals for 2003–2005–2007, within the border led to very few significant, and largely inconsistent, cases (14/216 cases = 3.2% at $P < 0.05$: ns with Bonferroni adjustment; 3 of these 14 were *rgr* mirroring *agr* for the same variable). Using the *M. bisulcata* data, which included the border subplots (growth variables the same but with distance to just large *M. bisulcata* trees and BA of *M. bisulcata* around saplings, for either 1991 or 2005), no case was significant (0/72, $P < 0.05$). These results are accordingly not reported in any detail here. The important conclusion, nevertheless, is that growth of survivors to 2007 was

unrelated to tree neighbourhood especially where it involved *M. bisulcata*.

Gap seedlings and saplings

From 2000 to 2008, seedlings of *M. bisulcata* declined exponentially with 10% survival. Average ht of survivors increased slowly, approximately doubling to *c.* 70 cm over 8 years, and after a short faster increase in the first year leaf number rose only very slightly with time (Fig. 8). For the large saplings, taking those eight within an initial dbh range of 1–6 cm (since they had the most complete records and are comparable with the main sapling survey), mean (\pm SE) dbh increased from 2.78 ± 0.52 in March 2000, to 3.96 ± 0.72 in March 2003, and 4.99 ± 1.05 cm in May 2008. Heights at the first two dates were 424 ± 32 and 535 ± 58 cm, respectively, and ht:dbh ratios correspondingly 153 and 135. For 2000–2003 and 2003–2008 estimates of dbh *agr* were 0.39 and 0.20 cm year⁻¹ and the corresponding *rgr* estimates were 11.79 and 4.47 cm m⁻¹ year⁻¹, respectively. Compared with sapling rates from the survey (0.0578 cm year⁻¹ and 1.818 cm m⁻¹ year⁻¹; Fig. 7c, f) these were 15 and 3.5-fold higher for *agr* and 6.5- and 2.5-fold higher for *rgr*.

Test in NW-plot

Of the 17 individuals recorded, 10 were small (≥ 1 m ht but < 1 cm dbh) and seven were large saplings

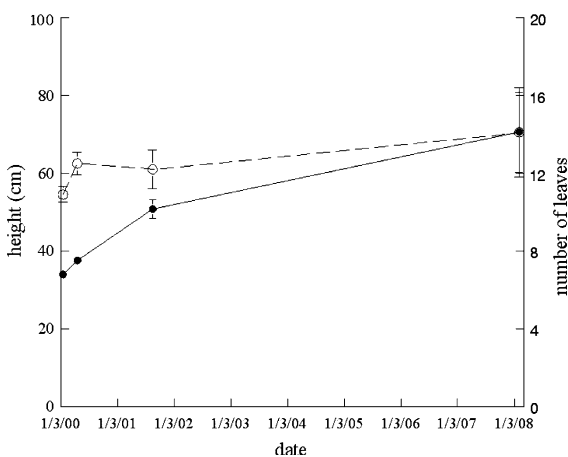


Fig. 8 Sapling recruitment of *M. bisulcata* in a large natural gap in Korup National Park, south of the main P-plot, 2000–2008: closed circles, height; open circles, number of leaves

(≥ 1 cm dbh), giving a combined density of 5.037 ha⁻¹. Frequency of occurrence was significantly lower in the near than far half-subplots (1 of 14 vs. 6 of 13; Fisher's exact probability test, one-tailed $P = 0.029$). Numbers of seedlings and saplings in near and far half-subplots were 2 and 15, respectively, and applying a log-linear model for Poisson counts, the near distance class was significantly lower in density than the far one (deviance ratio = 7.64, $df = 1,25$, P of approx. $F = 0.011$). Where recorded, mean (\pm SE) ht was 151 ± 12 cm ($n = 12$) and dbh 1.38 ± 0.27 cm ($n = 12$).

Discussion

Sapling distribution: the recruitment problem

If large *M. bisulcata* trees were distributed evenly in the forest each would occupy $82.5 \text{ ha}/294 = 2810 \text{ m}^2$, i.e. an area of 53 m square. Mean distance to the eight surrounding trees would be 64 m, and thus maximum nearest-neighbour distance for any point 32 m. (An equivalent circular area would have a radius of 30 m.) These estimates of maximum distance are very close to what was found on average for randomness under MC simulation (31 m). Saplings of *M. bisulcata* were found at an average distance of 43 m from adults, however. The situation is akin to the frequency-at-distance model of Becker et al. (1985). The statistical pattern found in P-plot was well corroborated by the independent test of the hypothesis in the NW-plot where saplings were found significantly more frequently away (40–60 m) from adult trees than close to them (< 20 m).

Mean nearest-neighbour distance for large trees of *M. bisulcata* was 22 m, implying a random to slightly clustered distribution. If saplings were occurring mostly in between adult trees than nearest adult distances for saplings would be 11 m—making a distance of 43 m extremely unlikely. That occurrence was at distances 12 m further than expected (31 m) indicates that saplings were being displaced away from clusters of adults (in the simplest situation away from pairs of large trees), whether by pure chance or some aggregation process, into the spaces where *M. bisulcata* trees were not occurring. This suggests both selection against seedlings close to adults and selection for saplings away from them.

Since the crown radius of *M. bisulcata* is close to a mean of 20 m the saplings are occurring at 23 m beyond that albeit within the typical dispersal range of up to 70–90 m from the stem. The *M. bisulcata* trees are not so densely packed in the groves that crowns often touch (sometimes occasional pairs do). When a seed is thrown far from a tree of *M. bisulcata*, and the resulting seedling is somehow restricted from being close to the same or another *M. bisulcata*, then this seedling must be closer to trees of other species, especially ones of the two *Tetraberlinia* spp. Since the number of trees of *T. korupensis* (279) was higher than that of *T. bifoliolata* (195) in the P-plot it could be explainable on a chance basis alone that saplings on average occurred closer to the former than the latter. Rarely considered in such recruitment-with-distance studies is how tree neighbourhood changes with time, as was shown for *M. bisulcata* in 1991 and 2005.

The mean distance away from ‘all’ trees was only very slightly different from randomness (1 m closer), yet, for ectomycorrhizal spp. it was 3 m closer, because this latter was the net outcome of being closer to non-*M. bisulcata* trees and further away from *M. bisulcata* ones. These non-*M. bisulcata* trees were not on average as large in size as the *M. bisulcata*, but they were collectively more abundant and closer to one another. The distance results are mirrored more strongly in the BA neighbourhoods, confirmed with a larger sample of *M. bisulcata* out to the plot boundary and even by analysis of grouped saplings. Two points: (1) the alive tree BA would have included *M. bisulcata* (cf. Figs. 4c and 3b) and (2) among the dead trees there were very few of *M. bisulcata* compared with other species. Accordingly, it would be more likely that saplings ended up near to dead-tree locations.

Does tree death simply mean new gaps with more light? And since other species of large trees are dying at rates much higher than do *M. bisulcata* then better-lit conditions must on average occur elsewhere than around *M. bisulcata* trees. However, the recorded dead-tree influence does not appear large enough to explain the inhibition of *M. bisulcata* saplings close to conspecific adults although it doubtless contributed to sapling survival. (The influence of trees that died before 1991 is largely unknown.) If gaps did occur around the perimeter of *M. bisulcata* trees (as in the model of Moravie et al. 1997) and this was selective, then to achieve an average distance away from the

adults of 43 m would mean that they survived at the far side of these opened areas, i.e. 20 m of *M. bisulcata* crown radius plus *c.* 25 m across a *Tetraberlinia* crown, not close to the *M. bisulcata*, which would continue to give some shade due to its height and immense crown size. This might also explain the peak in seedling density 45–50 m from the grove edge.

A surprising aspect of the results was that the small saplings did not show a different distance or BA neighbourhood relationship compared to all saplings which could have implied that survival (translated to age and increasing size) was happening at sequentially increasing distances away from the *M. bisulcata* adults. The complete lack of distance/BA effects on growth of established saplings suggests that if some form of restriction operated it did so at an earlier stage, most likely on the newly established seedlings, and was being registered in the seedling bank several years later. After that saplings grew and survived, or died, free of any distance or density effects. That the saplings measured were extremely variable in growth rates (Fig. 7), and in terms of leaf number even negative overall, indicates a hugely varying fortune for each sapling, reflected too in the very large range in nlv in any sapling ht class (Fig. 1b). A few saplings were able to grow on (perhaps temporarily and then stop), whilst most others either stagnated or declined. Many saplings had obviously been damaged and broken in the past, probably reflecting long-term accumulated effects of branch fall, and this being the cause of the many negative growth rates in height and leaf number and near-zero rates in dbh. To its advantage, however, the microphyllous form of *M. bisulcata* may well lessen the impact of woody debris by letting just some of the leaflets to be displaced from the whole leaf. Considerable damage to saplings of *Dipteryx panamensis* caused by falling litter was reported by Clark and Clark (1991).

Recruitment processes: the restriction problem

The pattern of recruitment found may be seen as a result of two processes acting over time. First, from early establishment to large seedling, there is a strong set of negative effects on growth and survival close to the adult tree. Second, for those seedlings surviving away from the adults, there is a strong positive effect

promoting onward growth and survival as saplings. After that it is a question of tolerating the understorey conditions until the sapling can grow into a subcanopy tree, and then its survival and onward growth seems almost completely assured. The two processes might be seen as operating over phases lasting for the first and second 10-year period of the tree's life, judging from demographic studies on seedlings (Newbery et al. 2006b), seedling and sapling bank sizes (Newbery et al. 1998) and sapling/small tree growth rates (this paper).

The restriction of seedling survival and sapling growth within significant distances from large conspecific trees seems unlikely to be due to any inhibition by the adult tree alone although this might play a contributing role. Survival and growth is going to be mostly poor anywhere in the forest due to the low PAR levels and small seed reserves of *M. bisulcata* (Green and Newbery 2001a, b). Various biotic agents could, singly or collectively, prevent seedlings growing close to parents, e.g. intense intraspecific root competition, allelopathy, species-specific pathogens or herbivores (Janzen 1970; Connell 1971; Clark and Clark 1984; Carson et al. 2008 for a recent review), reversed carbon flow towards large adults via ectomycorrhizas (Newbery et al. 1998), or even heavy pod-fall damage after masting. So far there is no strong experimental or field correlative evidence for any of them, but tests are currently under way.

Lower light levels below the crowns of *M. bisulcata* than below those of the other main canopy and emergent species can be ruled out with high confidence on several grounds: (1) the extensive survey of light levels by Green and Newbery (2001b) did not find a pattern, (2) direct comparison at the edge of the grove, under and away from *M. bisulcata*, showed no significant difference (Praz 2003), (3) the mostly emergent crowns of *M. bisulcata* (Newbery et al. 2009) are very high and therefore lateral light to the seedlings is necessarily higher than beneath lower coverage and (4) *M. bisulcata* is a semi-deciduous leaf exchanger with much reduced leaf area in the dry season, when old leaves fall and the new pale-green leaflets are expanding (Newbery et al. 2006a).

A simpler explanation for the second process, to explain the distribution of larger seedlings and saplings away from adults, is that saplings are selected in locations as a result of the spatial and temporal dynamics of the forest operating for the

present stage of grove development. As trees of other species die in and around the much better surviving dominant *M. bisulcata* (annualized mortality rate 1991–2005 of *M. bisulcata* was 1/7.7 or about an eighth that of the other tree species) they create the possibilities for recruitment of *M. bisulcata*, by enhancing light conditions for its seedlings and saplings. Such possibilities must be very rare within or very close to *M. bisulcata* trees (i.e. <20 m). The nursery and transplant experiments of Green and Newbery (2001a, b) showed very clearly that seedlings of the small-seeded *M. bisulcata* were on the one hand very shade-intolerant but on the other hand very light-responsive to increases in light level (up to 36% PAR).

Supporting evidence for the outstanding ability of *M. bisulcata* to grow from saplings into small trees in completely open conditions comes from a nursery trial close to Korup. Forty seedlings germinated from the 1995 masting (Green and Newbery 2001a, b) were planted out in 1999 into a cleared area and the 24 survivors by 2001 remeasured in 2002, 2006 and 2008 for growth (D. M. Newbery and G. B. Chuyong, unpubl. data). Seven healthy (2006-defined) green-leaved sapling trees, allowing remeasurement at 130 cm ht (i.e. for dbh) in 2006–2008, attained very high mean growth rates by 2006: estimated *agr* 1.95 cm year⁻¹ and *rgr* 55.4 cm m⁻¹ year⁻¹ (mean start dbh = 0.96 cm). Between 2006 and 2008 these rates decreased to 1.30 cm year⁻¹ and 23.0 cm m⁻¹ year⁻¹ (mean dbh in 2006 = 6.42 cm). The rates are very much higher than those found in the forest for saplings in the present study of likely similar age and size class. Values of *agr* and *rgr* were 34- and 31-fold higher in the nursery than forest for 1999–2006, and 23- and 13-fold higher for 2006–2008. Average ht:dbh ratios were at least 3-fold higher in the forest than in the nursery (208 vs. 62), largely because dbh in the forest was 30% that in the nursery (1.9 vs. 6.4 cm) compared with the just 1.3-fold greater ht (370 vs. 290 cm).

Adult mortality and gaps: the maintenance problem

The possibility remains that if forest dynamics, and the mortality of *M. bisulcata* trees in particular, was higher it might have favoured a temporary increase in the establishment of *M. bisulcata* saplings, which

would have been older than 20 years in 2003. Comparing the records for large trees censused in 1977 in the earlier 0.64-ha plots of Gartlan et al. (1986), with those in the same locations nested within the main P-plot in 1991, revealed that only two of 29 trees of *M. bisulcata* died in the 14 years: an m_a of 0.51%. This rate is slightly above the 1991–2005 one but still appreciably lower than the forest on average and the other main species. Further indications of possibly raised disturbance levels before 1991 are difficult to glean retrospectively. Positions of large trees of *Musanga cecropioides*, a pioneer reaching on average 58 cm stem diameter in P-plot ($n = 15$), and of *Xylopia aethiopica* and *Zanthoxylum tessmannii*, early mid-secondary species of mean diameter 59 cm ($n = 13$) in 2005, did not at all coincide with the clusters of *M. bisulcata* saplings found, and may at *c.* 30 years old even predate them. Unfortunately, other measures for the window 20–30 years prior to 2003 are lacking.

The study of the seedlings in the 2000-gap showed too that the early advantage of increased light caused by tree falls was being lost by 2008 as the understorey vegetation closed in. From the demography of a 1995-cohort of *M. bisulcata* seedlings in undisturbed forest, Newbery et al. (2006b) reported a 3.6% survival after 7.1 years, which is about one-third the 10% in the large gap at 8 years. Further, in the former case surviving seedlings stagnated in ht growth after 4 years to reach just less than 30 cm height at 7.1 years, compared with the mean of 70 cm after 8 years in the gap. Sapling growth, in terms of *agr* and *rgr* in stem dbh, was also several fold higher in the gap area compared with that found in the sapling survey presented in this paper, although not as high as the rates achieved by the open-grown healthy saplings in the nursery. Increased light was of benefit to *M. bisulcata* recruitment, but it could not be optimally sustained in the forest.

Overall the results suggest that *M. bisulcata* needs increased light over several periods in order to recruit successfully. Light levels increase temporarily from place to place in the forest in a patchwork mosaic due to tree and branch fall. Tree fall is mostly happening at locations away from the large *M. bisulcata* trees; though sometimes *M. bisulcata* trees do lose large branches to create near gaps (pers. obs). The effect of the increased light might be relatively short, however, and the seedlings moving up to saplings then

have to wait for another opening nearby to grow on a little more. This process might operate like a ratchet. Many seedlings and saplings will not be fortunate to receive the light increases 2–4 times over the perhaps 20–30 years needed to build a small tree resistant enough to stand in the forest understorey, until eventually it can grow up into the canopy. After the poor survival of the first 7–10 years, this second and third local tree death is most likely to be away from the stable standing *M. bisulcata* adults: i.e. sapling survival is seen then as a set of multiplied probabilities. Unlike a typical pioneer species, *M. bisulcata* cannot achieve the very rapid height growth with which it could outpace its understorey neighbours because it builds relatively dense wood (0.70 g cm⁻³, M. Worbes pers. comm.) to form eventually a very large tree. The spreading plagiotrophic shoots of *M. bisulcata* in the understorey would aid capture of light from various lateral sources, a flexibility of architectural form proposed for another African legume *Piptadeniastrum africanum* by Oldeman (1989).

The probability of a large tree not of *M. bisulcata* dying in a 3-year period (p_{nMb}) was 0.050. Smaller sub-canopy trees falling might raise this estimate slightly, however. Supposing that a seedling or sapling requires three such events in their vicinity in order to sufficiently increase its light conditions (and thus growth and survival) over a 10-year period, the second event is within one grid-tree unit around the first ($p_{nMb} * 8$) and the third likewise is occurring among those not already affected ($p_{nMb} * 7$), then the ‘ratchet probability’ of this outcome is $p_{ratchet} = p_{nMb}^3 * 56 = 0.007$. Very approximately, and allowing a margin for rare multiple falls and falls of smaller trees nearby and the much less frequent falls of large *M. bisulcata*, the chance of this effect is ~1% at any location in the forest.

Approximately 1 month after the major mast fruiting in 1995, the density of *M. bisulcata* seedlings (≤ 30 cm tall) was 6593 ha⁻¹ (Newbery et al. 1998). This 30 cm was the stagnation ht found in the demographic study (Newbery et al. 2006b) and applying the *M. bisulcata* survival rate of 3.6% after 7.1 years would leave an upper estimate of 237 individuals ha⁻¹ (the bank would also have had a small proportion of seedlings surviving from earlier cohorts). If this density is multiplied by the ratchet 1%, the sapling density expected after 20–30 years

would be $<2.37 \text{ ha}^{-1}$. The sapling survey showed 10.875 ha^{-1} : a 4- to 5-fold higher value. Given that the start density was overestimated, the actual density was likely *c.* 5-fold higher than expected based on this simple model.

According to the above idea, a ratchet effect of 1% appears far too low then to maintain the already very low-density sapling population. The requirement to survive several years between pulses of increased radiation might possibly be achieved by the ectomycorrhizal symbiosis of *M. bisulcata*. The surface spreading roots which are characteristic of early tree growth allow effective exploration for, and acquisition of, nutrients especially phosphorus in the surface soil (Newbery et al. 1997, 2009). At the same time, they should increase the chances of linking into the mycorrhizal network. Whilst proximity to a large aging tree of its own species very early on was clearly a disadvantage, for unknown reasons, being now closer (as a larger individual too) to the more actively growing *Tetraberlinia* spp. could be of benefit. This idea could also explain how saplings are found significantly closer to *A. fragrans* and *D. africana*. For *M. bisulcata* to remain dominant in the groves would therefore require that it closely shared ectomycorrhizal species with the other caesalps which facilitated its *later* survival, which seems plausible and highly likely (Alexander 1989; Newbery et al. 1988, 2000).

Reconsideration of tropical tree responses to light: the classification problem

There are scattered examples of long-lived light-demanding species of large stature in the tropical literature. Gullison et al. (1996) found that the large-leafed mahogany, *Swietenia macrophylla* King, in primary forest in Bolivia needed major disturbances to recruit and form patches of emergent adults. These openings were largely due to landslides or flooding. This species is relatively shade-tolerant as a seedling and sapling, but responds very fast to light. In selectively logged forests in Brazil, however, Grogan et al. (2005) found that further tree falls could release recruits established in gaps and this was sufficient to allow scattered regrowth with stem *agr* of $>1 \text{ cm year}^{-1}$. In a similar way, the very large and light-responsive species *Vochysia ferruginea*, *Jacaranda copaia* and *Simarouba amara*, grew very well

in logged forest in Costa Rica with *agr* of *c.* 1.5 cm year^{-1} (Finegan et al. 1999). *Dipteryx panamensis*, another large scattered tree in rainforest in Costa Rica, with apparently low sapling recruitment like *M. bisulcata*, was found to maintain its population structure by relatively good survival in shade, but with an ability to respond to periods of light when opportunities allowed upward growth (stem *agr* of 0.8 cm year^{-1} ; Clark and Clark 1987). Since this species was rarely utilizing gaps it must have been optimizing its growth through surrounding smaller changes in the forest cover. Further, of six species of scattered and rare emergent tree species studied at La Selva one, *Pithecellobium elegans*, was similar to *M. bisulcata* in Korup by having a low *agr* in the 1–4 cm dbh class (0.4 mm year^{-1}) and a high *agr* in the 10–20 cm class (6.3 mm year^{-1}).

Species such as *Khaya ivorensis*, *Pycnanthus angolensis*, *Ceiba pentandra* and *Nauclea diderrichii* in Cote d'Ivoire all have in common their scattered rareness in the primary forest (Alexandre 1989), suggesting low recruitment success and a large chance component in experiencing multiple releases. Jones (1950) divided emergent tree species in Benin forests (S. E. Nigeria) into three groups: (1) soft-wooded and highly shade-intolerant (e.g. *Ceiba pentandra*, *Canarium schweinfurthii*), (2) hard-wooded, when young light-demanding and fast growing, less than 1 (e.g. *Piptadeniastrum africanum*, *Entandrophragma* spp.) and (3) hard-wooded and relatively shade-tolerant as saplings (e.g. *Khaya ivorensis*, *Lovoa klaineana*). The case for *Entandrophragma*, in particular, has been recently well-supported by Makana and Thomas (2005). None of these fit the conventional 'shade-tolerant' and 'light-demanding' categories in sapling physiology but are somewhere intermediate, each differing also in other life-history traits. Indeed, the notion of fixed definition of shade-tolerance with which to classify trees appears untenable (Carson et al. 2008). From Chile Lusk (1999) reported on a very long-lived (>750 years), very dense-wooded tree, *Weinmannia trichosperma*, which is wind-dispersed, rare and scattered, yet very intolerant of shade as a seedling and highly light responsive in later growth.

Microberlinia bisulcata and the other co-occurring caesalps in coastal Atlantic forests of western Central Africa are similar to these last mentioned species except that they (1) have very local seed dispersal by

mechanical means and (2) they form clusters and groves. Ballistic dispersal, compared with other syndromes, generally leads to the tightest clustering of trees (Seidler and Plotkin 2006); yet clearly the groves here are 10–20 times larger in extent than the dispersal range of *M. bisulcata*. If *M. bisulcata* had evolved to disperse further (e.g. by wind or animals) it would have been unable to fully utilize any physical connections to adults. This strongly suggests the ectomycorrhizal/masting/local dispersal traits are co-evolved, and the compact form of the groves is maintained by a sufficient but not-too-great distancing of saplings from adults to allow infilling and edge expansion. In this way, *M. bisulcata* has a strategy for maximizing its spread locally where it is edaphically well-adapted. What appears to be ‘escape’ from the parent trees is largely the result of contingent forest turnover. The large difference in mortality rates between *M. bisulcata* and other species simply means that because it dominates and outlives the other trees it can, albeit relatively poorly, recruit.

The situation in Korup, with apparently non-persistent groves locally dominated by *M. bisulcata*, contrasts strongly with that of monodominant forest of another caesalp species *Gilbertiodendron dewevrei* in the Congo Basin. Hart (1995) showed that *G. dewevrei* is highly persistent with high sapling survival in the understorey, and it performs better than *Julbernardia serrettii* (another caesalp), which is abundant in neighbouring mixed forest. Further comparisons of forest dynamics in Central Africa can be found in Newbery and Gartlan (1996): there are many interesting questions to be followed in understanding species differences among the Caesalpinioideae across the region.

To conclude, it need not be that the escape of the Janzen–Connell mechanism leads always to increased diversity in a forest (Connell et al. 1984): dependent on the turnover and species-specific mortality rates, the mechanism can also reduce diversity and promote local dominance. The dynamics of the system sets the rules at any given point in time. That nearly all tests have referenced seedling distribution and survival to *living* adult trees, often over quite short periods, means that if the seedlings do respond to light they must be growing better further away where other species’ trees, *ceteris paribus*, are dying. In general, the larger the variance in m_a among canopy-emergent species the more frequently establishment-at-distance

is expected to happen for those species with lower m_a . The study presented here for *M. bisulcata* illustrates well this non-equilibrium situation.

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