Structure and inferred dynamics of a large grove of Microberlinia bisulcata trees in central African rain forest: the possible role of periods of multiple disturbance events

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Structure and inferred dynamics of a large grove of *Microberlinia bisulcata* trees in central African rain forest: the possible role of periods of multiple disturbance events

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(*Accepted 15 February 2003*)

Abstract: A 272-ha grove of dominant *Microberlinia bisulcata* (Caesalpinioideae) adult trees $\geq$ 50 cm stem diameter was mapped in its entirety in the southern part of Korup National Park, Cameroon. The approach used an earlier-established 82.5-ha permanent plot with a new surrounding 50-m grid of transect lines. Tree diameters were available from the plot but trees on the grid were recorded as being $\geq$ 50 cm. The grove consisted of 1028 trees in 2000. Other species occurred within the grove, including the associated subdominants *Tetraberlinia bifoliolata* and *T. korupensis*. *Microberlinia bisulcata* becomes adult at a stem diameter of *c.* 50 cm and at an estimated age of 50 y. Three oval-shaped subgroves with dimensions *c.* 850 m × 1350 m (90 ha) were defined. For two of them (within the plot) tree diameters were available. Subgroves differed in their scales and intensities of spatial tree patterns, and in their size frequency distributions, these suggesting differing past dynamics. The modal scale of clumping was 40–50 m. Seed dispersal by pod ejection (to *c.* 50 m) was evident from the semi-circles of trees at the grove's edge and from the many internal circles (100–200 m diameter). The grove has the capacity, therefore, to increase at *c.* 100 m per century. To form its present extent and structure, it is inferred that it expanded and infilled from a possibly smaller area of lower adult-tree density. This possibly happened in three waves of recruitment, each one determined by a period of several intense disturbances. Climate records for Africa show that 1740–50 and 1820–30 were periods of drought, and that 1870–1895 was also regionally very dry. Canopy openings allow the light-demanding and fast-growing ectomycorrhizal *M. bisulcata* to establish, but successive releases are thought to be required to achieve effective recruitment. Nevertheless, in the last 50 y there were no major events and recruitment in the grove was very poor. This present study leads to a new hypothesis of the role of periods of multiple extreme events being the driving factor for the population dynamics of many large African tree species such as *M. bisulcata*.

Key Words: grove formation, multiple disturbances, seed dispersal, size distribution, spatial pattern, tropical rain forest

INTRODUCTION

In the Atlantic coastal forests of western Central Africa, several tree species in the subfamily Caesalpinioideae (Fabaceae; alternatively Leguminosae) tend to grow in patches or clusters of a few ha to some km^2 in area (Aubréville 1968, de Saint-Aubin 1961, Letouzey 1968, 1985, White 1983). Where these aggregations are well defined by one or a few related species which are structurally dominant, the trees may be said to grow in 'groves'. In Korup National Park there is a fine example of such a caesalp grove which is dominated by *Microberlinia bisulcata* A. Chev. together with two other large caesalps, *Tetraberlinia bifoliolata* (Harms) Hauman and *T. moreliana* Aubr. (now = *T. korupensis* Wieringa 1999 in Cameroon) (Gartlan *et al.* 1986, Newbery & Gartlan 1996, Newbery *et al.* 1988, 1997, 1998*a*). The grove is precisely defined by the presence of *M. bisulcata*. Whilst the two *Tetraberlinia* species are strongly associated with it, they are found more widely at the local scale. Other tree species of much lower abundance are interspersed throughout the grove. The three caesalps are ectomycorrhizal species (Alexander 1989, Moyersoen *et al.* 1998, Newbery *et al.* 1988).

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An interesting problem at Korup, which has wider relevance to thinking on tropical rain-forest dynamics especially in Africa, is why *M. bisulcata* is presently so extremely poorly represented as saplings and small trees (Newbery *et al.* 1998*a*, 2000). Every 2–3 y mast fruiting leads to copious seed production and a large seedling bank (Green & Newbery 2002). This poor recruitment appears to be largely a result of the very slow growth, high levels of leaflet loss and very low survival of seedlings of *M. bisulcata* in the predominantly densely shaded conditions at the forest floor (Green & Newbery 2001*a*). The seeds of *M. bisulcata* are relatively small, despite the large investment in heavy pods (Green & Newbery 2001*b*, 2002). At high light levels of *c.* 40% PAR in the nursery *M. bisulcata* grows fast and survives well (Green & Newbery 2001*b*). It also grows and survives well when planted out at 2 y in completely open conditions (unpubl. data; D. M. Newbery & G. B. Chuyong).

These characteristics do not allow *M. bisulcata* to be readily classified within the conventionally recognized guilds of pioneer and climax species (Swaine & Whitmore 1988, Turner 2001, Whitmore 1990). It responds to light as a 'quasi-pioneer' species in its early years but it has high longevity (> 200 y) and it attains huge sizes as a canopy/emergent tree. Far from being an exception, it is one of a large group of common and important tropical African tree species (Forni 1997, Hawthorne 1996, Newbery & Gartlan 1996, Pierlot 1966, Poorter *et al.* 1996, Richards 1996). That much of the thinking on tropical ecology in general has been determined by studies in South-East Asia and the South and Central Americas, and not in Africa, is a reflection of the fact that rain forests in Africa have received much less attention. Richards (1996) championed the view that the dynamics of African tropical forests are fundamentally different from those of other regions.

In his seminal study of forest dynamics of Côte d'Ivoire, Aubréville (1938) highlighted the case of *Piptadeniastrum africana* (Hook. f.) Brenan (formerly *Piptadenia africana* Hook. f.). In an 80-ha patch at Banco, 315 trees ≥ 5 cm stem diameter were recorded, of which 199 (63%) were ≥ 50 cm diameter. In the classes 5–10 and 10–20 cm there were just 3 and 16 trees respectively. Aubréville (1938) argued that for this species to remain in an equilibrial abundance on the landscape it must be regenerating elsewhere, perhaps in patches. Direct evidence (i.e. data) for this happening for *P. africana* was not presented, however. Devred (1958) reported a similar situation for *Cynometra alexandri* C. H. Wright in the Belgian Congo (Zaïre), and Letouzey (1968) drew attention to further examples in *Baillonella toxisperma* Pierre and *Lecomptedoxa klaineana* (Pierre ex Engl.) Dubard in south-eastern Cameroon. In each case gregariousness could be associated with poor seed dispersal, although isolated individuals could also be found occasionally.

The light-demanding requirements of *M. bisulcata* and its poor recruitment beneath adults is in strong contrast to those of another widespread ectomycorrhizal caesalp, *Gilbertiodendron dewevrei* (De Wild.) J. Léon. (Connell & Lowman 1989, Gérard 1960). This species dominates huge tracts of the Congo basin, forms large patches, and has mast fruiting. However, its seedlings are very shade-tolerant and all size classes of tree are to be found within the forest (Hart 1995, Hart *et al.* 1989). One important character explaining the difference in ecologies may be seed size: the mass of a seed of *G. dewevrei* is 30 g (Hart 1995) whilst that of *M. bisulcata* is 0.64 g (Green & Newbery 2001*b*).

The four principal characteristics of (1) poor dispersal of seeds, (2) strong positive response to light as seedlings and saplings, (3) gregariousness of adults and (4) very poor regeneration below adults are all evident for *M. bisulcata*. The situation is even more acute for this species because, apart from some remnant adults outside of Korup, isolated individuals or patches of recruits have not been found in the areas around the groves within the Park. The key questions, therefore, are how were the groves of *M. bisulcata* formed and how are they maintained?

Theories about the ecology of rain forests have been built frequently upon the idea of equilibrium dynamics (Huston 1994). In the medium term (10^2–10^3 y) forest composition is seen as being broadly constant and turning over regularly and continuously with some spatial variation in local space as gaps from fallen trees are filled by recruits (Whitmore 1984). Tree populations might drift slowly with time in a quasi-random manner (Hubbell 2001). In recent years (see Newbery *et al.* 1998*b*) an alternative view has emerged that forest dynamics could be strongly punctuated in some tropical regions, that extreme and occasionally rare climatic events may play a very significant role. This view leads to the idea of non-equilibrium dynamics, one that is historical and that, additionally, may involve long-term directional change. The key postulate emerging from Korup, and which is supported by other sites, is that non-equilibrium dynamics characterize the African tropics whilst the equilibrium model fits better the forests in South-East Asia and the Americas.

The hypothesis, here developed further from Newbery & Gartlan (1996) and Newbery *et al.* (1998*a*) for Korup, is that *periods of multiple extreme events*, not single separated ones, have the most important effects on forest composition, patterns and dynamics. These determining periods account for many of the distinctive features of the primary African tropical forest such as its relative species-poorness, broad niches with respect to edaphic factors, local or regional dominance of some species or families, the Aubréville–Letouzey phenomenon of gregariousness and lack of *in situ* replacement, and tree size distributions with many small and very large

trees but relatively few medium-sized ones (Richards 1996).

With these points in mind, the present paper reports on the shape and composition of a large entire grove of *M. bisulcata* trees in Korup and examines its internal spatial and tree-size structure. Static contemporaneous observations on forest structure can often give valuable insights into past dynamics. This in turn leads to a refinement of the working hypothesis which can be applied and tested in other sites, and to a re-evaluation of theories of how rain forest changes with time in different tropical regions.

STUDY SITE AND SPECIES

Korup National Park, in south-west Cameroon (5°10′N, 8°70′E), is composed entirely of tropical rain forest. Lying within the ancient Guinea–Congolean refugium (White 1983), it is one of the last western remnants of Atlantic coastal forest, *la forêt biafriéene* (Letouzey 1968, 1985). It has a very high conservation value among African primary forests (Gartlan 1986, 1992). The study site itself in the southern part of Korup receives an average of 5040 mm of rainfall annually (1984–2001) and the climate is strongly seasonal with one distinct dry season for the months of December to February. The soils are derived from highly weathered quartzite, very sandy and low in phosphorus and potassium content. The site is located *c*. 50 km NNE of the coast at an elevation of 65–100 m asl. Further details of the environment and the floristic composition can be found in Gartlan *et al.* (1986), Newbery *et al.* (1988, 1997, 1998*a*), Newbery & Gartlan (1996) and Chuyong *et al.* (2000).

Microberlinia bisulcata is the largest tree in Korup in terms of median (*c*. 1.1 m) and maximum diameters (2.85 m): in 1991 it formed 60% of all trees ≥ 100 cm in diameter (D. M. Newbery *et al.*, unpubl. data). It reaches heights of *c*. 45 m, crown diameters of *c*. 70 m, and may develop large buttresses of up to *c*. 2 m high at over 10 m from the stem. The strongly seasonal rainfall leads to *M. bisulcata*, and the other large canopy-emergent species, being deciduous. Newbery *et al.* (1997, 1998*a*) and Chuyong *et al.* (2000) give further details on patterns of phenology and nutrient cycling.

The realization in the mid-1980s that the grove existed came from a detailed analysis by Gartlan *et al.* (1986) of earlier forest plot data collected in 1975–77 and the subsequent studies of Newbery *et al.* (1988). At intervals along four parallel 5-km (E–W) transect lines in the southern part of the Park, 135 0.64-ha plots had been marked and trees with stem diameters ≥ 30 cm gbh (girth at breast height) recorded. Part of the grove was crossed by the southernmost line 'P' (see also Newbery & Gartlan 1996). It was later more intensively sampled by means of

an 82.5-ha plot (1650 m E–W by 500 m N–S, divided into 330 subplots of 50 m × 50 m) set up in 1991 (Newbery *et al.* 1998*a*). The mid E–W line of this plot lay on transect 'P'. All trees ≥ 50 cm stem diameter (at breast height (dbh) or above buttresses) were mapped, tagged, measured (for diameter) and identified. Of a total of 1315 trees ≥ 50 cm diameter, 295 were *M. bisulcata* (Newbery *et al.* 1998*a*).

Species names follow Aubréville (1970), Keay (1989) and Lebrun & Stork (1991).

METHODS

Mapping the grove

A map was made of all *Microberlinia bisulcata* trees ≥ 50 cm diameter, that grow in the grove, inside and around the 82.5-ha plot of Newbery *et al.* (1998*a*). Enlarging this plot was not possible given the resources and time available in the workable dry-season months. The following approach was therefore taken: (1) *M. bisulcata* trees ≥ 50 cm diameter were mapped; (2) the co-ordinates of the trees were estimated but not measured; (3) stem diameters were not recorded unless close to the 50-cm limit (except in the eastern part); (4) trees were not tagged; and (5) the corners of the subplots were not permanently marked. The fieldwork took place in the period January to June 2000.

Microberlinia bisulcata trees outside the plot of Newbery *et al.* (1998*a*) were mapped by walking a series of parallel lines away from the plot, at right angles of its edge using a compass. The terrain was mostly flat with a general W-to-E increase of 30 m elevation over 3 km. These lines started or ended at the corners of each 50 m × 50-m subplot forming the plot's edge, and were thus 50 m apart. Lines were interrupted every 50 m (measured with a 50-m tape); and from these points the four adjacent 50 m × 50-m subplots were surveyed. If a *M. bisulcata* tree ≥ 50 cm diameter (measured when close to this limit) was found its position was mapped with an estimated maximum error of ± 5 m. The coordinates of the trees were later read from the map.

All *M. bisulcata* trees were therefore observed at least twice, the second time being when the next parallel line was walked. A line ended when no more *M. bisulcata* trees were found within 150–200 m. Then, after walking 50 m to the left or right, a new line was followed back to the edge of the plot, 50 m away from the starting point. Every 400 m the distance to the previous line was checked. At the four corners of the plot, an E–W or N–S baseline was made, running away from the plot, with temporary markings at 50-m intervals. These baselines were used to continue the mapping lines. In this way, the whole grove outside of the plot was mapped. The inside of the plot of Newbery *et al.* (1998*a*) was checked with the same
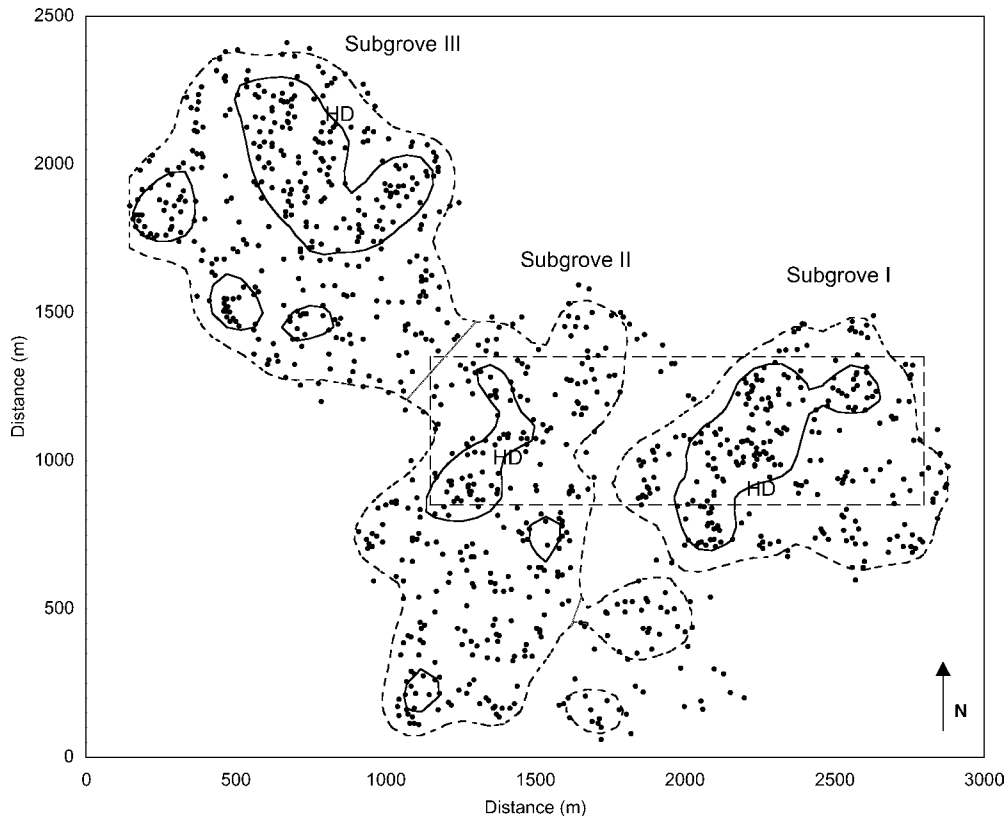
Figure 1. Mapped positions of 1028 *Microberlinia bisulcata* trees ≥ 50 cm stem diameter (closed circles) forming a large grove in the southern part of Korup National Park, Cameroon. Contours of tree density at 2 and 4 trees ha^{-1} (small-dashed and solid lines respectively) define the low (LD, 2–4 trees ha^{-1}) and high (HD, > 4 trees ha^{-1}) areas, the delimitation the three subgroves with thicker straight lines to NW and SE of subgrove II, and perimeter of the 82.5-ha permanent plot (large-dashed line). Those HD areas used in the analysis are indicated.

procedure, recording in addition dead *M. bisulcata* and those smaller trees that had grown to a size of ≥ 50 cm diameter since the plot was established in 1990–1991.

A *M. bisulcata* tree of ≥ 50 cm in diameter was usually visible from a distance of up to 30–40 m. Besides the recognizable form of the crown and the pinnate leaf structure, it has a characteristic appearance to the bark. Its seedlings are easy to recognize and they are often present up to *c.* 50 m, but never further than *c.* 70 m, from the stem of the nearest parent tree. It is therefore unlikely that any *M. bisulcata* trees ≥ 50 cm diameter would have been overlooked using this method.

The threshold of change from juvenile to adult status in terms of stem diameter was determined by examining all *M. bisulcata* trees encountered with diameters of 40–70 cm and checking with binoculars whether they had pods: year 2000 was a moderately large mast year. Sometimes immature pods were found below the crowns.

The data were used to make a map of the whole grove, showing all trees of *M. bisulcata* ≥ 50 cm diameter. The absence of *M. bisulcata* further than 150–200 m from the edge of the grove, within the area of Figure 1, was confirmed by walking a series of parallel lines spaced 250 m apart. This means that, further out from the edge

of the grove, an individual *M. bisulcata* tree or a group of such trees less than *c.* 100–150 m diameter, may have been overlooked. After the map had been completed, two aeroplane flights (by X. M. van der Burgt) were made over the grove and surrounding forest to further confirm the absence of the distinctive *M. bisulcata* crowns outside of the grove.

In the eastern 32.5-ha part of the 82.5-ha plot (Figure 1), the stem diameters of the *M. bisulcata* trees were measured with a relascope, at 1.30 m or higher if the presence of buttresses made this necessary. Trees just outside of the plot and east of X = 2100 m (Figure 1) were similarly measured. Trees within the plot had been measured first in 1990–91.

Density analysis

A contour map of the local density of *M. bisulcata* trees in the grove was constructed using a Gaussian 75-m-bandwidth smoothing technique (S-Plus 2000) applied to the 50 m × 50-m gridded data. From this map, three subgroves (I to III) were defined and these analysed separately. To reduce the large heterogeneity in local tree

density, two relatively more homogeneous areas were selected within each subgrove for further analysis.

For each area, the spatial structure was analysed using second-order neighbourhood analysis (Ripley 1977, 1981). It was important to stratify the analysis into low-density (LD) and high-density (HD) areas because neighbourhood analysis is strongly affected by larger-scale heterogeneity (trends in density and anisotropy; Ripley 1988). The square-root of the cumulative frequency distribution of other trees at a distance $\leq d$ to each tree taken in turn gives the function L(d). The Poisson expectation of a random distribution is given by $L(d) - d = 0$. Departure from this indicates the degree of aggregation (positive) or regularity (negative). For analysis of the Korup data, d in the range 100–200 m (interval of 10 m) was used. Monte Carlo simulations (n = 1000 runs for each analysis) provided confidence intervals under the null hypothesis of spatial randomness ($\alpha = 0.05$ and 0.01). The spatial pattern analyses were carried out with the Spatial Stats module of S-Plus (2000) (see Kaluzny *et al.* 1998), and because the different areas had irregular shapes (following the contour lines), the method and program of Goreaud & Pélissier (1999) and Pélissier & Goreaud (2001) were also used.

Parts of subgroves I and II were within the original 82.5-ha plot (Newbery *et al.* 1998a) for which stem diameters of trees (≥ 50 cm dbh or diameter above buttresses) were available. The chi-squared statistic was used to compare the frequency distributions of the diameters of *M. bisulcata* trees between subgroves for the LD and HD areas, and the Kolmogorov–Smirnov (KS) test was used to compare diameters themselves. These tests were repeated for the non-*M. bisulcata* trees. Moran's index, I_M (Cliff & Ord 1981, Haining 1990), tested for the presence of autocorrelation in the spatial distribution of the diameters in subgroves I and II (program of Sawada 1999).

RESULTS

Extent, composition and form of the grove

A map of the *Microberlinia bisulcata* grove in the south of Korup National Park, Cameroon, with a total of 1028 *M. bisulcata* trees of stem diameter ≥ 50 cm as of June 2000, is shown in Figure 1. The centre of the grove is at 5°01′N, 8°48′E. Its area was estimated to be *c.* 272 ha or 2.72 km^2 by drawing an outline along the 50-m grid which enclosed all trees and included the area of forest without *M. bisulcata* trees running NNE between X, Y = 1500, 250 and 2000, 1300 (Figure 1). The mean density of trees ≥ 50 cm diameter was 3.78 ha^{-1} (range of 0–15 ha^{-1}). Data from the 82.5-ha plot of Newbery *et al.* (1998a), lying inside the grove (see Figure 1), are

incorporated here with some updating and corrections since 1991 and 1997. Of the 295 *M. bisulcata* trees that Newbery *et al.* (1998a) found in 1990–1991, six had died and six new ones had grown to ≥ 50 cm diameter.

At the eastern end of the grove (X > 2750 m; Figure 1) there was a concentration of some of the largest trees of *M. bisulcata* with no smaller trees further eastwards of them. The edge of the grove elsewhere, and especially in the north-west, showed several cases of overlapping near semi-circles of trees (e.g. at X, Y = 200, 1800; 900, 2200; 1200, 2000; Figure 1). Within the grove several (near) circles of trees were found (e.g. at X, Y = 1050, 750; 1150, 650; 1400, 700; 2000, 950; and 2650, 800; Figure 1). These circles are inferred by the presence of round or slightly oval areas without *M. bisulcata* trees. The diameters of these semi-circles and circles were *c.* 100–200 m (Figure 1).

Microberlinia bisulcata trees produce fruits for the first time at diameters of 46–55 cm so that a mean diameter of 50 cm can be taken as the threshold for defining an adult.

Distributions of tree densities and sizes in the grove

The local density of *M. bisulcata* trees inside the grove (Figure 1) showed no directional gradient. The grove, however, has several dense areas of various shapes and sizes. The contour lines at 2 trees ha^{-1} delimited two large areas which lacked *M. bisulcata* trees between them (Figure 1). The absence of trees is not associated with a river, or with seasonally inundated forest – a habitat in which *M. bisulcata* trees do not grow.

Three subgroves could be identified. Subgrove I formed the eastern unit and was delimited entirely by the contour line of 2 trees ha^{-1}. Subgroves II (central) and III (north-west) were separated by an isthmus of relatively low tree density (Figure 1). A small south-eastern part of subgrove II was excluded to avoid spatial analysis involving a non-convex hull. Areas of low-density stands of trees within each subgrove (LD) were defined as lying between contour lines of 2 and 4 trees ha^{-1}, and areas of high density (HD) were each of the largest units per subgrove defined by the contour lines ≥ 4 trees ha^{-1}. Each area (LD or HD per subgrove) had sufficiently large sample sizes for further analysis ($\geq$ *c.* 50 trees each; Table 1). The groves were elliptical in shape with the following approximate dimensions: I, 800 m × 1100 m; II, 800 m × 1600 m; and III, 1000 m × 1300 m; leading to an average dimension of 850 m × 1350 m (90 ha).

Diameter distributions of *M. bisulcata* in the LD and HD areas of subgroves I and II (Table 1, Figure 2) showed significant differences ($\chi^2 = 19.6$, df = 9, P = 0.021). Within these subgroves – no diameters were available for subgrove III – areas did not differ (KS statistic = 0.158, P = 0.131 and KS statistic = 0.105, P = 0.868, for subgroves

Table 1. Densities of *Microberlinia bisulcata* trees (≥ 50 cm diameter) in three subgroves of the main grove at Korup, with their stem diameters and those of other species in subgroves I and II. Low- (LD) and high- (HD) density areas within subgroves were defined by the contour lines in Figure 1 as 2–4 and > 4 trees ha^{-1} respectively.

	Subgrove I		Subgrove II		Subgrove III	
	LD	HD	LD	HD	LD	HD
Grove density						
Area sampled	46.7	18.5	71.6	8.0	63.0	21.9
Number of *M. bisulcata* trees	123	132	236	47	176	130
Mean density (trees ha^{-1})	2.64	7.13	3.29	5.89	2.79	5.95
Diameter (cm) of trees in the plot						
Trees of *M. bisulcata*						
Mean ± SE (n)	98 ± 3.3 (58)	101.7 ± 2.3 (113)	112.8 ± 3.3 (65)	111.6 ± 4.2 (44)	–	–
Median (range)	99 (53–161)	104 (53–168)	108 (62–219)	105 (59–177)	–	–
Trees of other spp.						
Mean ± SE (n)	72.3 ± 1.0 (436)	71.6 ± 1.3 (208)	70.0 ± 1.0 (344)	70.1 ± 1.8 (99)	–	–
Median (range)	60 (50–177)	66 (50–167)	65 (50–139)	63 (50–127)	–	–

–, no data collected.

I and II respectively). On pooling the data for LD and HD areas, subgroves I and II were highly significantly different (KS statistic = 0.217, P = 0.0028). This difference was largely due to fewer smaller trees (50–70 cm diameter) in subgrove II compared to subgrove I (Figure 2). A similar subgrove × area comparison for the other (non-*M. bisulcata*) trees was not significant ($\chi^2 = 4.46$, df = 9, P = 0.879).

Spatial structure of trees within subgroves

The spatial structure was more marked in the LD than HD areas (Figure 3; confidence limits for 95% and 99%). Subgroves II and III showed clear dips of regularity at 10 m in the LD areas. This 10-m structure was absent in subgrove I which, by contrast, showed a strong just-significant aggregation at the scale of 20–80 m (Figure 3). A peak in aggregation was also evident in subgrove II at 40 m. Considering distances < 100 m in the LD areas, there was a clear trend in disappearance of regularity at short distances, and appearance of aggregation at intermediate distances, when moving from subgroves III to I. For distances ≥ 100 m (LD), there was a tendency towards regularity at the scale of 130–190 m for subgrove III, at 120 m for subgrove II and at 170 m for subgrove I. This suggests a repeated structure consisting of small groups of trees separated at distances of 120–200 m. In the HD areas the same trends as those for the LD areas were found but they were less marked. At distances < 100 m, subgrove III showed regularity at 10 m whereas subgrove I showed aggregation at the scale of 40–90 m (Figure 3). At distances ≥ 100 m, trends towards regularity were found only in subgroves II and III at the scale of 160–200 m. When LD and HD trees were pooled for each subgrove and the analyses repeated (results not shown), the patterns in the LD areas were masked and undetectable.

The highly significant peak (P < 0.001) of aggregation at 40 m in the LD area of subgrove II indicates that the trees were forming small patches. Inside these patches the local density around the trees was higher than expected from randomness under the Poisson distribution. Trees had a neighbourhood density at 40 m that was higher than that expected. In subgrove II, the small patches are clearly distinguishable in Figure 4. The distance between two patches was *c.* 120 m, which corresponds to the peak of regularity. In subgroves I and III, some small isolated patches are also evident but most of the trees with high densities within 40 m formed larger patches: these large patches probably resulted from the coalescence or superposition of smaller patches (Figure 4).

Trees that formed patches in subgrove II (i.e. those areas with high neighbourhood density at 40 m) showed a sharper unimodal frequency distribution in their diameters than those not forming patches (areas with low neighbourhood density, Figure 5). Correspondingly, the trees in the high-neighbourhood-density areas had a smaller variance in tree diameters than those in low-neighbourhood-density ones ($F_{\text{one-tailed}} = 0.511$, df = 73, 34; P = 0.0084). Most of the trees in the patches had a diameter between 90 and 130 cm. In subgrove I, there was a pronounced lack of small trees (50–70 cm diameter) in the low-neighbourhood-density areas compared to the high-neighbourhood-density ones ($\chi^2_{\text{one-tailed}} = 3.27$, df = 1, P = 0.035; Figure 5). Comparison of the overall diameter distributions with the KS test, however, showed no significant differences for either subgrove I (KS
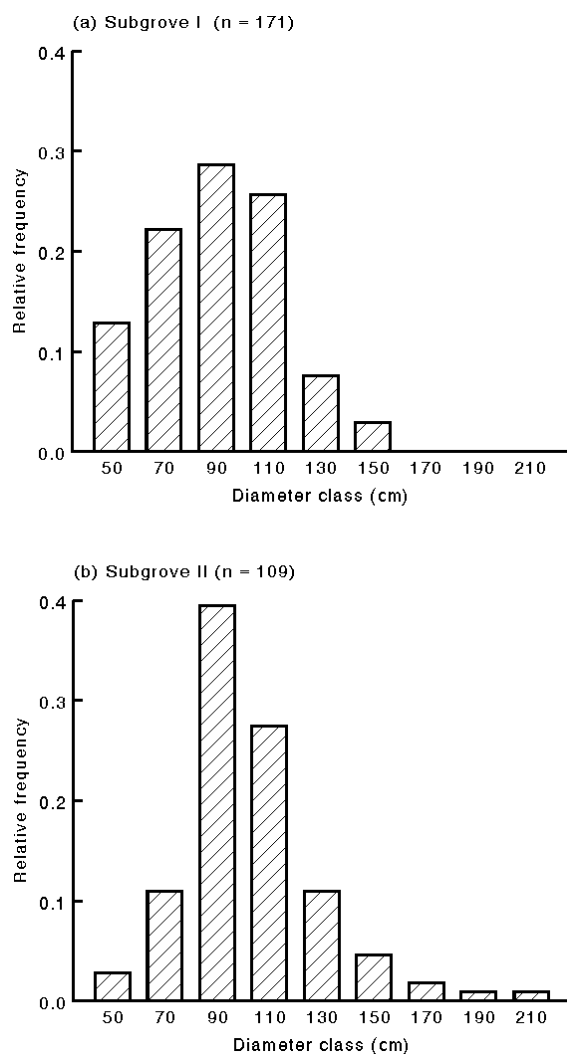
(a) Subgrove I (n = 171)

(b) Subgrove II (n = 109)

Figure 2. Relative frequency distributions of the diameters of *Microberlinia bisulcata* trees (n = sample size) from within (a) subgrove I and (b) subgrove II, at Korup. The x-axis values are the lower limits of the classes (i.e. 50 means 50–69.9).

statistic = 0.137, P = 0.525) or subgrove II (KS statistic = 0.166, P = 0.442).

A positive autocorrelation of diameters at short distances of < 10 m (Moran's $I_M = 0.516$, P = 0.007), and negative autocorrelations for the distance lags of 110–120 m ($I_M = -0.140$, P = 0.022) and 180–190 m ($I_M = -0.193$, P < 0.001), were found in subgrove I. There were no significant autocorrelations for subgrove II (P > 0.05). In subgrove I, trees within 10 m of one another were smaller than trees separated from each other at greater distances (Wilcoxon ranked sign-test, P = 0.0006; Table 2). The observed positive autocorrelation in diameters was mainly a result of the smallest trees being closest together. In subgrove II, the trees within 10 m of one another were also smaller than

those at greater distances (P = 0.033; Table 2) but they were larger and fewer in subgrove II than in subgrove I.

Data for the map of the grove came from using two approaches: the enumerated plot of 82.5 ha, and the extended mapping with grid lines (Figure 1). Trees were possibly more accurately located by the former than the latter approach, with measurement errors least in subgrove I, and most in subgrove III, and intermediate in subgrove II. Freeman & Ford (2002) have shown with simulated data that as measurement error in location increases patterns become less significant and are detected at larger scales, whilst inhibition processes become less distinct. In the Korup data the pattern was more significant in subgrove I than subgroves II and III but the scale did not change (Figure 3). Freeman & Ford (2002) calculated that the SD of measurement error needs to be at least twice the cluster size to have an effect; and this was very unlikely to be the case for the Korup since the trees could be double-checked from the next parallel 50-m line (i.e. a tree was at maximum 25 m from a line). Furthermore, inhibition processes were more significant in subgrove III than I, the opposite of what might be expected if measurement errors were having a confounding effect. The differences between groves, therefore, seem not to be due to the different methodologies: the likely small increase in error was probably unimportant compared with the scales of inhibition and pattern found.

DISCUSSION

Shape and extent of the grove

The grove of *Microberlinia bisulcata* trees in Korup has a well-defined edge (Figure 1). There are no other important differences in tree species composition between the inside and outside of the grove (Gartlan *et al.* 1986, Newbery & Gartlan 1996, Newbery *et al.* 1997), though at a larger scale (within the southern part of Korup) *M. bisulcata* was found to be strongly associated with its codominants *Tetraberlinia bifoliolata* and *T. korupensis*. There are no significant changes in soil type or in topography (Gartlan *et al.* 1986, Newbery *et al.* 1988). Rivers and patches of seasonally inundated forest occur both inside and outside of the grove, and to varying extent along its edges. The absence of *M. bisulcata* outside of the grove cannot, therefore, be readily explained by differences in known environmental factors. Other groves of *M. bisulcata* do occur in the surroundings of Korup; the nearest ones found to date are 12 km to the south (Newbery *et al.* 2002), and 13 km to the SSE and 16 km to the SE (X. M. van der Burgt, *pers. obs.*).

Many central African rain forests have been influenced by agriculture in previous centuries and now have
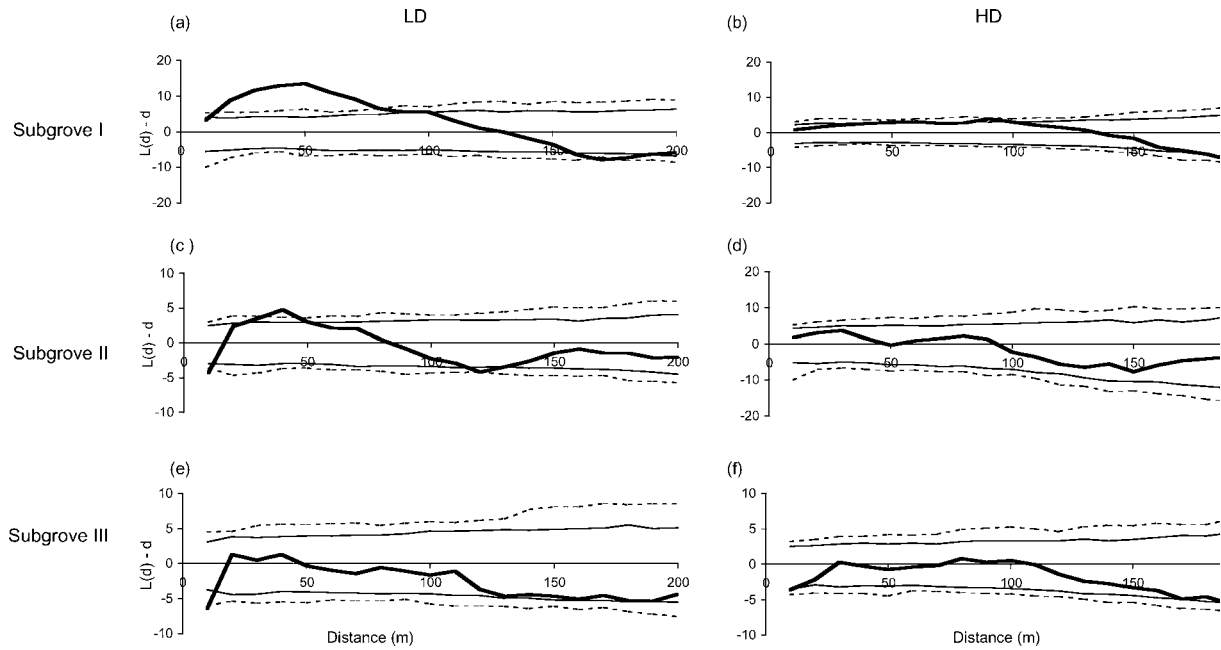
Figure 3. Second-order nearest-neighbour spatial analysis of *Microberlinia bisulcata* trees ($\geq$ 50 cm diameter) in each area (low (a,c,e) and high (b,d,f) density, LD and HD, 2–4 and > 4 trees ha^{-1}, respectively) within subgroves I–III at Korup. The bold line is the spatial statistic, L(d)-d, calculated from the data: thin and dashed lines are 95 and 99% confidence limits based on Monte Carlo simulations.
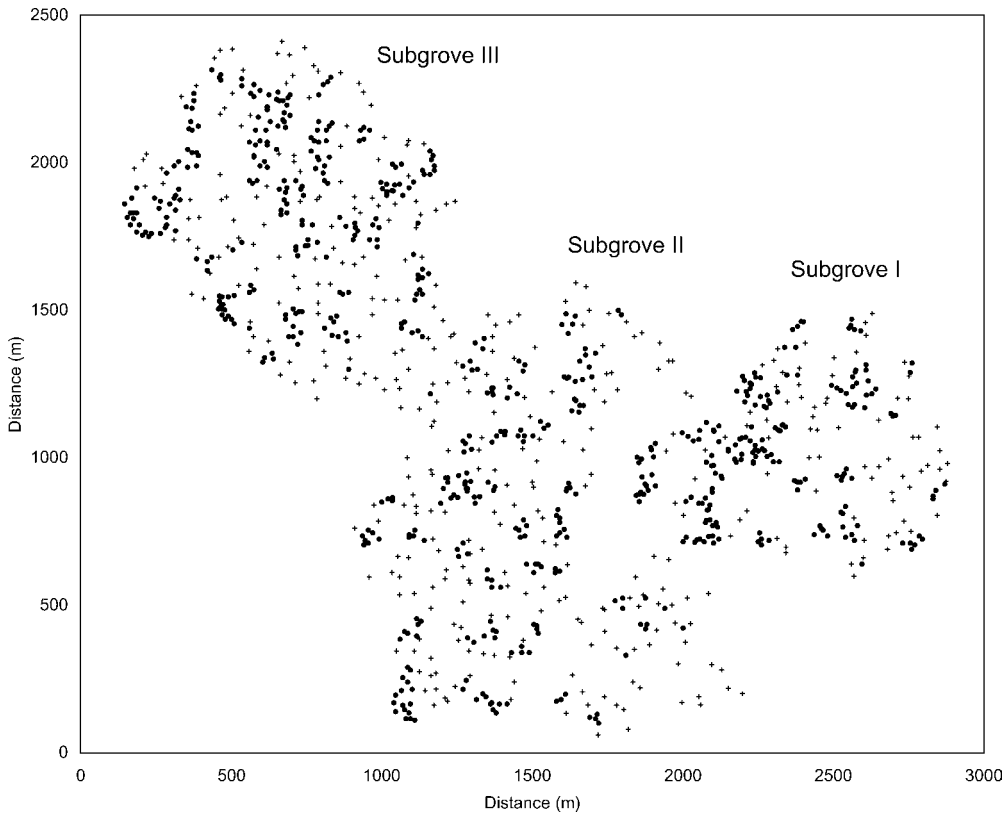

Figure 4. The grove of *Microberlinia bisulcata* trees at Korup showing those trees with neighbourhood densities (nden) at 40 m > (large dots) and $\leq$ (crosses) the mean density of 3.29 trees ha^{-1}.
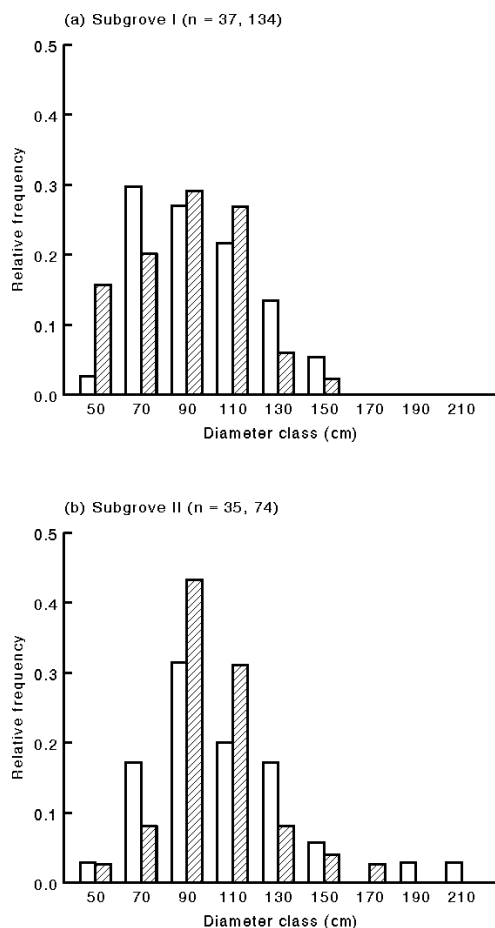
Figure 5. Relative frequency distributions of the diameters of *Microberlinia bisulcata* trees (n = sample size) in 40-m neighbourhoods (nden) with > (open bars) and ≤ (hatched bars) the mean density of 3.29 trees ha^{-1}, from within (a) subgrove I, and (b) subgrove II, at Korup.

Table 2. Stem diameters (cm) of *Microberlinia bisulcata* trees (≥ 50 cm diameter) in two of the subgroves of the main grove at Korup, with or without neighbours of this species within 10 m.

	Subgrove I	Subgrove II
Trees with ≥ 1 neighbour at < 10 m distant		
Mean ± SE (n)	89.0 ± 3.3 (40)	99.0 ± 3.9 (17)
Median (range)	87 (53–125)	98 (59–129)
Trees with no neighbour at < 10 m distant		
Mean ± SE (n)	104.8 ± 2.1 (136)	114.1 ± 2.9 (94)
Median (range)	106 (56–168)	111 (57–219)

old secondary growth (Letouzey 1968). This raises the question as to whether the grove at Korup is a site of earlier habitation. Unlike Southern Bakundu Reserve, lying *c.* 90 km SE (Richards 1963) and the Okomu Forest Reserve in Nigeria, 400 km NW of Korup (Jones 1955, 1956), no traces of past human culture have been found from sampling along transect 'P' (18 soil pits of Newbery

et al. 1997). It seems unlikely that such a sandy, nutrient-poor soil would have been used for crops; and if *M. bisulcata* was associated with past habitation the grove would probably have a much less complete and less regular outline. Korup, at least in the southern part where the grove occurs, appears to be composed of primary forest (Gartlan 1986).

Along the E–W transect 'P' running through the grove (line Y = 1100 m in Figure 1), Newbery *et al.* (1988) recorded the two *Tetraberlinia* spp. extending well beyond the limits defined by the occurrence of *M. bisulcata*. *Tetraberlinia bifoliolata* was found 300 m further west and 1050 m further east, *T. korupensis* 900 m west and 450 m east. Sampling outside of the grove in the present study confirmed that the area in which the two *Tetraberlinia* spp. occurred was much larger than that of the *M. bisulcata* grove, and extended mostly beyond the limits of Figure 1. A number of other ectomycorrhizal, non-gregarious species (*Berlinia bracteosa* Benth., *Didelotia africana* Baill. and *Anthonotha fragrans* (Bak.f.) Exell & Hillcoat) are scattered within and outside of the grove (Gartlan *et al.* 1986, Newbery & Gartlan 1996, Newbery *et al.* 1988). The edge of the *M. bisulcata* grove is therefore not an edge between forests of high and low-to-nil basal-area abundance of ectomycorrhizal trees.

Several morphospecies of fungi are shared by *M. bisulcata*, the *Tetraberlinia* spp. and the other ectomycorrhizal tree species in Korup (Alexander 1989, Buyck *et al.* 1996, Moyersoen *et al.* 1998, Newbery *et al.* 1988, Onguene & Kuyper 2001; I. J. Alexander *pers. comm.*). Root-sterilized *M. bisulcata* seedlings transplanted into low- and high-abundance ectomycorrhizal forest plots became well inoculated with ectomycorrhizas (Newbery *et al.* 2000), thus demonstrating no limitation of inoculum for *M. bisulcata* to establish well away from existing adults. The shape of the *M. bisulcata* grove appears not to be determined by the occurrence of ectomycorrhizas specific to this tree species.

Internal form and seed dispersal

Microberlinia bisulcata has explosive seed dispersal. On sunny days during the mid-to-late wet season ripe pods twist open and eject their seeds. The pods have approximately the same shape, size and structure as those of *Julbernardia seretii* (De Wild.) Troupin and *T. moreliana*, for which maximum dispersal distances of 40 and 60 m from the crown edge respectively have been recorded (Hart 1995, van der Burgt 1997). From its pod and seed size, *M. bisulcata* would be expected to display a similar maximum dispersal distance, and this is confirmed by the fact that its seedlings at the edge of the grove occur only up to 40–50 m from the crowns of the adult trees. The restricted dispersal of *M. bisulcata* means that the next

generation establishes either inside the grove or within 40–50 m of its edge. The maximum potential rate of expansion of the grove can be taken accordingly as 50 m per generation. This limited dispersal capability explains almost certainly the complete absence of *M. bisulcata* from the surrounding forest outside of the grove ($\leq$ 3 km away).

Local distributions of other African caesalps show a similar dependence on explosive seed dispersal. Evrard (1968) reported that patches of *Brachystegia laurentii* (De Wild.) Louis, *Gilbertiodendron dewevrei*, *G. ogoouense* (Pellegr.) J. Léon. and *J. seretii* in the Congo (Zaïre) also expanded slowly as a result of the same limiting means of dispersal. The transition from *G. dewevrei*-dominated forest to mixed forest (where *G. dewevrei* is almost absent) is abrupt too and without associated changes in topography or soils (Hart *et al.* 1989). Gérard (1960) did not find seedlings of *G. dewevrei* more than 20 m from the edge of groves of adults when these occurred outside of main areas of *G. dewevrei*-dominated forest. No other means of dispersal for these caesalps is known.

Seed dispersal is therefore hypothesized to be the most fundamental factor determining the regular and isotropic radial expansion of trees around their adults. Unless other factors interfere (e.g. where periodically inundated areas occur), new recruits will be found in circles and the edge of an idealized grove could be a circle of ever-increasing radius. Nevertheless, older trees die and their offspring will infill such a grove with time. The internal patterns and outside shape of the mapped grove in Korup can, perhaps only partly, be explained by this simple process alone. The grove shows no obvious bands of trees of decreasing size and age radiating out from centres which suggests that counter-directional or overriding processes play a complicating role.

Trees $\geq$ 50 cm diameter growing in semi-circles of 100–200 m diameter were common at the edge of the grove, especially for subgrove III (Figure 1). Here parent trees had most likely died and left spaces in the centres of the semi-circles of what are now their offspring. Some semi-circles were much larger and these probably originated from either more than one parent tree or after two generations. The lower limit to the radius of the semi-circles is *c.* 50 m, a value which is similar to the smaller scale of pattern among trees $\geq$ 50 cm diameter (Figure 3). Green & Newbery (2002) found that vertebrate predation of seeds on the forest floor was 3.5-fold greater near to *M. bisulcata* tree stems ($\geq$ 50 cm diameter) than 5 m beyond their crowns, showing that the relative survival of seedlings is best at, or just beyond, the canopy edge. The inferred circular structures, like the dispersal ranges, suggest a radial expansion rate of *c.* 50 m per generation.

Semi-circles of trees on the edge of the grove, together with the circular shapes found within the grove, show that the grove had been expanding up to the time when the present adult trees established. The presence of only one semi-circle of juvenile trees (X, Y = 2200, 250; Figure 1), and just a few solitary juveniles (X. M. van der Burgt, *pers. obs.*), again indicates that the grove has not expanded further since the present *M. bisulcata* trees became adults. Even the exceptionally large, and therefore presumably very old, *M. bisulcata* trees standing at the eastern edge of subgrove I (Figure 1) have failed so far to produce a single tree of 10–50 cm diameter outside of the grove although a few trees < 10 cm diameter were indeed found. The grove stopped extending eastwards at this point.

Growth of trees in the grove

Preliminary estimates of stem diameter growth rates of juvenile *M. bisulcata* trees (10–50 cm diameter) in the Korup grove (1999–2000; X. M. van der Burgt, unpubl. data) and from a plantation of *M. bisulcata* in Southern Bakundu Forest Reserve established in 1986 (D. M. Newbery; unpubl. data) were 1.2 and 1.5 cm y^{-1} respectively. Growth in the first 10 y is probably between a third to a half of that in later years based on first measurements of nursery outplants (1997–2001) and a gap regeneration study in progress. Hence, a mature 50-cm-diameter tree would have an estimated age of nearly 50 y. With masting occurring every 2–3 y (Newbery *et al.* 1998a), recruitment could start close to the 50-y interval. The grove could expand, therefore, at a maximum rate of about 100 m per century. These various pieces of evidence on growth rates, estimated ages, dispersal distances and spatial patterns are in good agreement and provide a consistent first estimate of potential expansion rate.

The high juvenile growth rate would likely not be sustainable in adult *M. bisulcata*, although these large trees in the last decade still grew at *c.* 1 cm y^{-1} (D. M. Newbery *et al.*, unpubl. data). Analysis of a stem section from a very large (182-cm diameter) *M. bisulcata* tree in what is now a farm at the edge of the Park by ^{14}C-dating (M. Worbes, unpubl. data) indicated an age of 220–250 y. Counts of 'rings' (stained bands) corresponded to this age estimate when it is assumed that rings are produced annually. (This last assumption is likely to be true given the strong seasonality of rainfall at Korup, the deciduousness of *M. bisulcata*, and the clearly defined period of new leaf expansion every dry season.) The average annual diameter increment was thus *c.* 0.80 cm y^{-1}. On this basis the typically largest trees now in the grove (*c.* 160 cm diameter) are 200 y old, whilst trees with the median (or modal) diameter of 104 cm (Table 1) are only 130 y. Some of the oldest trees could have been parents to the trees now 50–130 y old. The majority of the *M. bisulcata* trees in the grove (i.e. those of the broad modal size/age class) are estimated to have originated around 1870.

How did the grove reach its present form?

The hypothesis that disturbances from drought initiated the grove in recent history was first advanced by Newbery & Gartlan (1996). The data in the present paper allow a refinement of the idea in the following way. The extensive droughts in Africa of 1740–50 and 1820–30 (Nicholson 1981) may well have been the original events that established the grove from a few trees within its present extent. Each period of events led to a wave of release and recruitment of *M. bisulcata*. Evidence for the latter period being very dry is, however, stronger than for the former (Nicholson 1981). The markedly deciduous nature and strongly ectomycorrhizal status of *M. bisulcata* (Newbery *et al.* 1988, 1998*a*, 2000) suggest that it is highly drought-resistant. In nursery experiments, seedlings were tolerant of high light conditions (*c.* 40% PAR) during the dry season (Green & Newbery 2001*a,b*), and saplings grow well in completely open conditions (D. M. Newbery & G. B. Chuyong, unpubl. data).

The period *c.* 1870 to 1895 was generally a very wet one for Africa, according to Nicholson (1981), except for the Atlantic coastal region of western Central Africa which was apparently relatively dry. Although data sources are scant and Korup lies towards the border region of this wet–dry exchange, it is reasonable to suppose that this period was another one of dryness for Korup and it enabled further recruitment of *M. bisulcata*. The broken rainfall records from 1889–1902 and 1905–1914 for Douala on the Atlantic coast (Chadwick-Healey 1992) show that at least 1897–98 were unusually dry years. The present size (and implied age) structure of the grove today corresponds to this 1870–95 period. Recruitment from the 1870-originating trees appears to have been much poorer in the last century than before, and this implies, from the hypothesis, that large disturbance events were absent. Climate records exist for Korup only since 1973, but together with those for 1922–1972 at Douala there is no evidence of periods of very dry years between 1922 and 2001. Further dendrochronology in progress on samples from very large *M. bisulcata* trees may shed light on this problem.

The hypothesis fits with what is known about growth rates, age of maturity and seed dispersal of *M. bisulcata*. From 1740 to 1820 the 80-y interval would have been long enough for those seedlings originating in 1740 to have reached maturity, so that they, along with survivors of 1740-originating trees, could have contributed to a second wave of recruitment from 1820. These last recruited, in turn, would just have reached maturity by 1870 (50 y later) and contributed to the most recent and probably most substantial wave of recruitment as a result of the proposed 1870–95 events. Many of the trees of *M. bisulcata* originating from 1740 probably died by the early 1900–1920s, to leave the 'tell-tale' circular

areas which today lack large trees of this species. But some of the trees which originated in 1820 probably also survived to become the presently very large trees of the grove, notably those at its edges. They would have been *c.* 180 y old in 2000. Considering seed dispersal, trees in 1740 could have been up to 200 m apart so that with two steps of 50 m they would be 100 m apart in 1870. The filling in and expansion of the grove to its present density and extent would have been possible by one more dispersal step – a result of the proposed 1870–95 period of events. The question as to how trees originally might have been spaced at 200 m apart leads to the speculation that a now non-extant agent of dispersal had a role, or that the trees were scattered remnants of a previous forest dynamic cycle.

Differences in size distributions and spatial patterns (Figures 2, 3 and 5) between the three subgroves (Figures 1 and 4) suggest that they may have had different histories, i.e. they reacted differently to climatic factors. After the establishment of the grove, regeneration in subgrove II appears to have been reduced considerably as there are now relatively few small trees. By contrast, in subgrove I, if a similar (slightly smaller) median diameter is taken and thus a similarly typical age for the larger trees, there are more small trees which indicates that subsequent regeneration was better. One way in which this might have occurred is that in subgrove I further large non-*M. bisulcata* trees occasionally died to create gaps into which more *M. bisulcata* saplings recruited. The key difference between subgroves I and II lies with their topographies: I is higher, and the soils drier – especially in the dry season – than II and *M. bisulcata* would be expected to be more favourably selected in I than II. The less-dense understorey on the higher ground may have just allowed sufficient light for local recruitment.

Multiple disturbance events

In the context of recruitment of *M. bisulcata*, disturbance events need be regarded as being grouped, i.e. they occur multiply within certain periods of several years. Within a period, each disturbance subsequent to the first one would be expected to give a strong compounding effect. One dry year may be insufficient to release the seedlings and saplings because, after the death of trees, the vegetation in the understorey closes over rapidly. (Drought-killed trees generally remain standing.) Since *M. bisulcata* is very shade-intolerant (Green & Newbery 2001*a*), another one or two disturbances subsequent to the initiating one would be much to its selective advantage. Even a moderate drought may result in prolonged leaflessness which would probably enhance recruitment.

The refined hypothesis of grove formation envisages waves of recruitment resulting from periods in which there were repeated climatic disturbances – *periods of*

multiple extreme events. At each step a proportion of the stronger saplings would make major increments in height and stem growth towards the canopy. With only single events, or events too far apart, saplings would stagnate and die in the shade. The fastest consolidation of the grove appears to be possible when the periods of events are spaced in time to coincide with the minimum age of the next maturing cohort of trees. In this way *M. bisulcata* could maximize its competitiveness and population growth rate at the site in the early years of establishment, aided by the key traits of rapid growth in the light combined with ectomycorrhizal symbiosis for enhanced phosphorus acquisition (Green & Newbery 2001*a,b*; Newbery *et al.* 1997, 1998*a*).

The long-term dynamics of these African forests at the scale of 10^2–10^3 y appears to be highly contingent upon, and driven by, periods of strong climatic disturbances. At these time scales there may be a quasi-equilibrium. The short-term dynamics at the scale of several decades are consequently in a highly non-equilibrium state. Understanding more precisely how periods of multiple extreme events affect forest recruitment should provide a coherent model for the ecology of light-demanding, long-lived African tree species such as *M. bisulcata*.

ACKNOWLEDGEMENTS

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