

Mast fruiting of large ectomycorrhizal African rain forest trees: importance of dry season intensity, and the resource-limitation hypothesis

David M. Newbery¹, George B. Chuyong² and Lukas Zimmermann¹

¹Institute of Plant Sciences, University of Bern, Altenbergrain 21, CH-3013 Bern, Switzerland; ²Department of Life Sciences, University of Buea, PO Box 63, Buea, S.W. Province, Cameroon

Summary

Author for correspondence:

D. M. Newbery

Tel: +44 31 631 8815

Fax: +44 31 631 4942

Email: david.newbery@ips.unibe.ch

Received: 16 December 2005

Accepted: 12 January 2006

- Mast fruiting is a distinctive reproductive trait in trees. This rain forest study, at a nutrient-poor site with a seasonal climate in tropical Africa, provides new insights into the causes of this mode of phenological patterning.
- At Korup, Cameroon, 150 trees of the large, ectomycorrhizal caesalp, *Microberlinia bisulcata*, were recorded almost monthly for leafing, flowering and fruiting during 1995–2000. The series was extended to 1988–2004 with less detailed data. Individual transitions in phenology were analysed.
- Masting occurred when the dry season before fruiting was drier, and the one before that was wetter, than average. Intervals between events were usually 2 or 3 yr. Masting was associated with early leaf exchange, followed by mass flowering, and was highly synchronous in the population. Trees at higher elevation showed more fruiting. Output declined between 1995 and 2000.
- Mast fruiting in *M. bisulcata* appears to be driven by climate variation and is regulated by internal tree processes. The resource-limitation hypothesis was supported. An 'alternative bearing' system seems to underlie masting. That ectomycorrhizal habit facilitates masting in trees is strongly implied.

Key words: dry season, ectomycorrhizas, mast fruiting, phenology, rain forest, trees, tropical Africa, *Microberlinia bisulcata*.

New Phytologist (2006) **170**: 561–579

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doi: 10.1111/j.1469-8137.2006.01691.x

Introduction

When and how much organisms allocate resources to reproduction is a central aspect of evolutionary ecology. Biological traits interact with environmental variables to result in various life-history strategies (Stearns, 1992). However, resources allocated to reproduction by an organism cannot be simultaneously allocated to growth, and this intrinsic trade-off determines many aspects of form and function, particularly in the case of plants (Harper, 1977).

Trees are almost entirely iteroparous but vary in their patterns of reproduction. In adult life there are essentially two alternatives: more or less continuous reproduction, usually on an annual or subannual cycle; or intermittent reproduction,

usually supra-annually. In the former, resources are regularly allocated to flowers and fruits, whilst in the latter there are intervals of one to many years with no or very low reproduction and then a year of high output. The pattern may be regular on an n -year cycle, or it can be sporadic. Clear supra-annual reproduction in trees is generally referred to as mast flowering and fruiting (Janzen, 1974; Silvertown, 1980; Kelly & Sork, 2002). In between, there are species which vary in reproductive output from year-to-year, and deciding when this becomes masting is usually made clear by the almost all-or-nothing situation of so-called 'on' and 'off' years (Norton & Kelly, 1988; Herrera *et al.*, 1998).

Understanding the proximate and ultimate causes of mast fruiting has led to a synthesis which recognizes that long-term

demographic and evolutionary processes interplay with short-term physiological ones (Waller, 1979, 1993; Lalonde & Roitberg, 1992; Isagi *et al.*, 1997; Fenner, 1998). A plausible evolutionary mechanism is predator satiation. The two are inseparable because how the tree functions physiologically affects its timing and intensity of allocation to reproduction, and survival is a result of the most successful life-history strategy that will determine the physiological mechanisms selected. In environments where mast flowering and fruiting are advantageous, tree species will be expected to have special mechanisms of phenological control.

Environmental resources are rarely constant in availability, and frequently trees grow in habitats where they are near the maxima of stature, growth rate and productivity, inevitably limited by one or a few factors (Kozlowski *et al.*, 1991). Allocation of resources to reproduction in mast years may be considerable and this can mean temporary deficits for other parts of the tree (Fenner, 1991). Furthermore, when resource input is low owing to environmental fluctuations, over-allocation to reproduction might severely affect competition and survival. In years where conditions are above the average, there may be surplus resources, but the timing may be inappropriate for reproduction. The storage component therefore becomes important (Yamauchi, 1996).

Large trees carry high maintenance costs, such as a high respiration load, owing to the decreasing proportion of total biomass in leaves and active roots, loss of dying parts (which may reduce resource uptake capabilities), susceptibility to damage from pathogens and large associated symbiont sinks (Wardlaw, 1990; Cannell & Dewar, 1994). Thus, as trees age, the cost of reproduction can be expected to become of greater consequence, and mechanisms that prevent over-allocation, or inappropriately timed allocation, are likely to be selected.

Whilst mast-fruiting has been well studied in the temperate zone (e.g. Matthews, 1955; Wenger, 1957; Eis *et al.*, 1965; Hilton & Packham, 1986; Norton & Kelly, 1988; Sork *et al.*, 1993; Sork, 1993; Koenig *et al.*, 1994; Crawley & Long, 1995; Tapper, 1996; Shibata *et al.*, 1998; Piovesan & Adams, 2001; Abrahamson & Layne, 2003), there is now an accumulating literature on tropical cases. Prominent among these are species in the Dipterocarpaceae in south-east Asia (Burgess, 1972; Janzen, 1974; Appanah, 1985; Ashton *et al.*, 1988; Ashton, 1989; Curran & Leighton, 2000), and in the Caesalpiniaceae in Central Africa (Newbery *et al.*, 1998; Green & Newbery, 2002) and northern South America (Forget, 1992; Zagt, 1997; Forget *et al.*, 1999; Henkel *et al.*, 2005).

Tree species that have mast fruiting are very frequently ectomycorrhizal (Curran, 1994; Newbery *et al.*, 1998; Henkel *et al.*, 2005) and this has led recently to an emerging hypothesis that ectomycorrhizas enable mast fruiting when the climate is variable (Newbery, 2005). The field is presently moving away from descriptive and correlative studies towards ideas of physiological mechanism and a better understanding of the controls on tree phenology. In this article, the results of a long-

term study on the phenology of a large Central African tree, *Microberlinia bisulcata* A. Chev. (tribe, Amherstieae; subfamily, Caesalpiniaceae; family, Leguminosae), are presented, which lead to a more advanced hypothesis of masting and open the way for further tests.

Study site and species

Site

The study was conducted in the southern part of Korup National Park, south-western Cameroon (5°10' N, 8°70' E). This lowland tropical rain forest stands on strongly weathered, well-draining, nutrient-poor, sandy soils at an elevation of 50–150 m above sea level (asl). Korup lies within the Guinea–Congolese refugium, one of the last large and intact remnants of the Atlantic Coastal Forest of western Central Africa (Letouzey, 1968, 1985; Gartlan, 1992). The forest composition and environment has been reported in detail by Gartlan *et al.* (1986), Newbery *et al.* (1988), Newbery & Gartlan (1996) and Newbery *et al.* (1997).

Daily rainfall, radiation, and maximum and minimum temperature records for 1 January 1988 to 31 December 2004, were available from the PAMOL Bulu Station, Ndian, 12 km southeast of the study site. Radiation was recorded using a Gunn-Bellani radiation integrator, and values (in ml) evaporated per day (V) were converted to radiation (R ; $W\ m^{-2}$) using the calibration $R = 63.0 + 17.69V$ (Pereira, 1959). Data missing for the periods 15–20 March and 28 March to 9 May 1993 were interpolated. Over the 17 yr of the study, mean daily rainfall reached a maximum in July to August and a minimum in January to February, and mean daily radiation was minimal in July to August and maximal in December to April (Fig. 1).

Species

M. bisulcata is a very large, buttressed, canopy-emergent tree species which characteristically forms large groves of approx. 0.5–1 km² in area (Newbery *et al.*, 2004). It is codominant with two other, less-abundant, ectomycorrhizal caesalps, *Tetraberlinia bifoliolata* (Harms) Hauman and *T. korupensis* Wieringa (formerly *T. moreliana* Aubr.) in southern Korup, and occurs occasionally in the surrounding region. *M. bisulcata* is a leaf-exchanging species (see Borchert, 1980), the newly flushing (pinnate) leaves in the dry season pushing off the old ones, which leads to a pronounced annual peak in litter fall (Chuyong *et al.*, 2000).

Shoot growth is pleonanthic and indeterminate (Hallé *et al.*, 1978; Borchert, 1980). Flowers of *M. bisulcata* are formed in panicles at the ends of the new shoots (Aubréville, 1970; Tucker, 1987, 2002, 2003), arising usually from the two last axillary buds. Species in the Amherstieae have their flowers characteristically enclosed in valvate bracteoles before anthesis (Cowan & Polhill, 1981). After pollination (by insects including mainly bees) one or two fibrous pods (= legumes, 10–15 cm

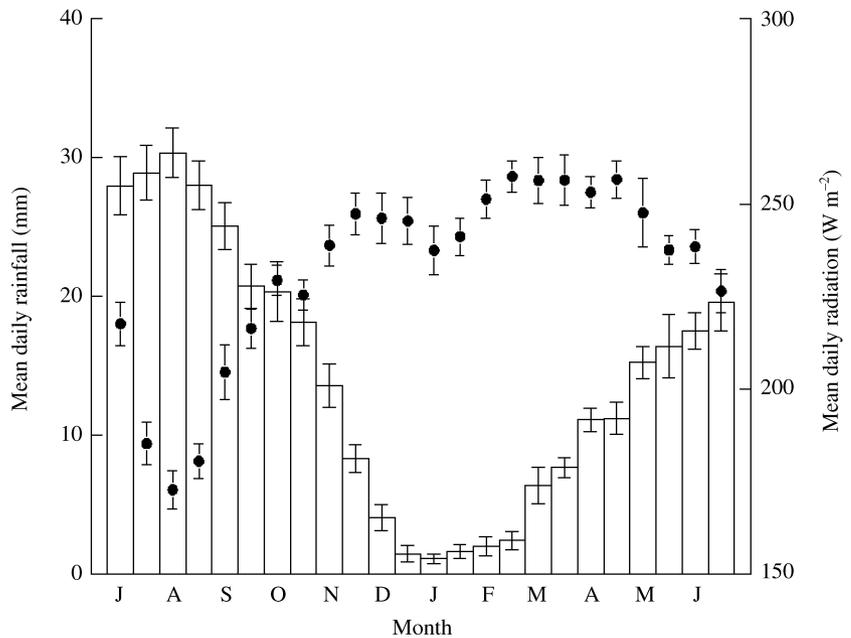


Fig. 1 Half-monthly means (\pm standard error) of (a) rainfall (open bars) and (b) radiation (closed circles) throughout the year at Bulu, close to Korup, Cameroon, averaged over 1988–2004.

long) form per shoot. On dry days, these split and twist to release the seeds explosively, and then fall with the now leafless shoot and panicle axis (cladopsis: Addicott, 1991; Chuyong, 1994).

Methods

Phenology

One-hundred and fifty trees of *M. bisulcata* (≥ 50 cm stem diameter) were randomly selected, in 1995, from a population of 294 trees enumerated in the 82.5-ha plot (Fig. 2) on transect P in 1991 (Gartlan *et al.*, 1986; Newbery *et al.*, 1998). No trees died during the study period. The diameter of the stem from each tree was known from the first enumeration in 1991.

Each tree was scored for intensity of leaf fall, leaf flush, flowering, immature (green) pod (= 'pods') and mature (brown) pod (= 'seeds') activity on 61 occasions (i.e. almost monthly), from January 1995 to December 2000. Recording lasted 2–3 d, and the median date was taken for each occasion. Three sides of a tree were each assessed as having: 0, none; 1, *c.* 25%; 2, *c.* 50%; and 3, up to 100% of the maximum cover possible,

and these values were combined to give integer tree scores on the scale 0–3. Assessment of flowering and seeding included observation of flowers and mature pods on the forest floor. Full cover, in the case of pods, meant that all branch ends had pods. Recording was repeated in a similar manner, between December 2003 and December 2004, at fortnightly intervals on those 71 trees of the eastern 32.5 ha of the plot (Fig. 2). The term 'masting' will be used generally for high synchronous activity of either flowering or fruiting (immature and mature pods).

Elevation of each tree and distance to the nearest permanent stream (or permanent swamp edge) were taken from a 1-m contour map of the plot (D. M. Newbery *et al.*, unpublished). These variables will be referred to simply as elevation and distance. High elevation and long distance imply less water availability, or access to it, in the dry season; low elevation and short distance, the converse.

Climate

For the years 1987–1988 to 2003–2004, mean daily rainfall and radiation, and minimum and maximum temperatures,

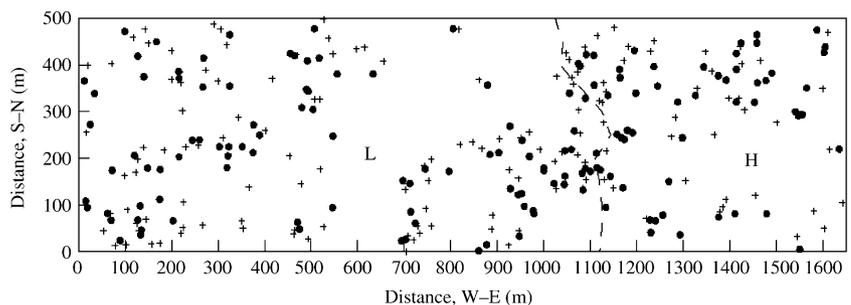


Fig. 2 Map of the 82.5-ha plot on transect P (Korup, Cameroon), showing the positions of the 150 *Microberlinia bisulcata* trees used (filled circles) and not used (crosses) in the phenology study of stem diameter ≥ 50 cm. The 113-m contour (dashed line) divides the plot into high (H) and low (L) elevation parts. S–N, south to north; W–E, west to east.

were calculated for the four quarters of each 12-month period starting on 1 December. Quarter 1 was the median-positioned dry-season period of December to February (Newbery *et al.*, 1998), and quarters 2, 3 and 4 were, respectively, the early, mid and late wet-season periods. The values for quarter 1 are referred to as the '3-month dry-season' means. A phenological year, as defined here, overlapped two calendar years (e.g. '1988–1989' ran from 1 December 1988 to 30 November 1989).

Running 30-d rainfall totals were calculated for the period 1 October to 30 April in the years 1995–1996 to 1999–2004. Where these totals fell below 100 mm, the dry season occurred (see Walsh, 1996, for definitions). Start and end dates, and thus duration of each dry season, were found together with total rainfall and average daily rainfall across the season. Values of these variables were also found for the previous 7 yr (i.e. 1987–1988 to 1993–1994) and the later 4 yr (2000–2001 to 2003–2004). These are referred to as the 'drought-defined dry-season' values.

Statistical analysis

Basic calculations were made with FORTRAN77 programs and statistical tests with GENSTAT 7.1 (Payne, 2000) and MINITAB 10. Logistic regressions of presence/absence of masting on independent variables were made with general linear models (GLM) using logit link function and binomial error distribution. Dispersion was estimated and the deviance ratio was taken as an approximate (*quasi*-) *F*-statistic. These regressions assumed independence of the successive dry seasons' climate data, which is reasonable given the intervening 8–9-month wet season each year. Where numbers of degrees of freedom were similar in a set of related tests they are given once at the start of a section in the Results.

Results

Tree size and topography

Trees of *M. bisulcata* were spread across the whole plot (Fig. 2). The size distribution was unimodal, with a mean [\pm standard error (SE)] stem diameter of 105.8 ± 2.3 cm (range 53.0–228.0 cm; $n = 150$). Diameters were allocated to three classes: 1, 50–79.9 ($n = 22$); 2, 80–119.9 ($n = 88$); and 3, ≥ 120 cm ($n = 40$). Elevation was bimodally distributed, reflecting the difference between the higher (drier) ground in the eastern part of the plot and the lower (wetter) part in the west. Trees could therefore be divided readily into two classes, namely 1, those occurring < 15 m ($n = 92$), and 2, those occurring ≥ 15 m ($n = 58$), above a reference elevation of 98 m asl. Mean relative elevations of the classes were 4.60 and 22.16 m, respectively. Distances to permanent streams and swamps (mean, 62 m; median, 50 m; range, 0–207 m) followed a Poisson-shaped distribution. These were allocated to four classes: 0 to < 20 ; 20 to < 40 ; 40 to < 60 ; and ≥ 60 m ($n = 21, 37, 32, 60$, respectively).

Climate trends 1985–2004

Mean annual daily radiation (average of the four 3-month periods, 1987–1988 to 2003–2004) increased over the period of study by 35 W m^{-2} or 15% ($F_{1,15} = 36.1$, $P < 0.001$; assuming independence of years in the regression), and minimum daily temperatures increased by 0.56°C or 2.5% ($F = 6.31$; $P = 0.024$). Mean annual daily rainfall and maximum daily temperatures changed insignificantly ($P = 0.72$ and 0.38 , respectively). The four 3-monthly radiation values (dry, early, mid- and late-wet seasons) increased by 47 W m^{-2} or 21% ($F = 23.1$, $P < 0.001$), 23 W m^{-2} or 9% ($F = 2.97$, $P = 0.11$), 33 W m^{-2} or 20% ($F = 9.87$, $P = 0.007$), and 35 W m^{-2} or 18% ($F = 23.2$, $P < 0.001$), respectively (Fig. 3).

Analysis of the dry-season rainfall and radiation trends between 1974 and 2004 at Bulu, showed a significant linear increase in radiation ($P < 0.001$), but none for rainfall (see the Supplementary Material). Thus, the step-up in radiation seen around 1997 in Fig. 3 was a local deviation in a longer trend. Rainfall in the dry season was only marginally negatively correlated ($P = 0.072$) with the El Niño Southern Oscillation (ENSO) region-3 sea surface temperature (SST) index, and radiation not at all ($P = 0.81$; Supplementary Material). Radiation at Bulu was strongly and positively correlated with the Southern Atlantic SST index in the mid-wet season ($P < 0.001$), and only marginally so in the dry season ($P = 0.049$): rainfall was significantly negatively correlated with the Southern Atlantic (SATL) SST index in the mid-wet season ($P < 0.001$) and not in the dry season ($P = 0.91$; supplementary material).

Rainfall in the dry season

The dry season was entire for 5 of the 6 yr (1995–1996 to 1998–1999) but in 1999–2000 it was divided into two parts (Table 1, Fig. 4). There was a similar frequency of cases in the previous 6 yr (where 1989–1990 was divided) but, in the later 4 yr, divided dry seasons were more frequent (2001–2002 and 2002–2003). For these divided years, duration of the dry season was defined in two ways: (i) from the start of the first part to the end of the last part, with dry-season means of the variables being found for the whole period (termed 'overall'); or (ii) as a sum of the parts, for which dry-season means were the averages of the part means weighted by their durations (termed 'combined'). Variations in starting time (7–43 d from 1 December), duration (29–122 d) and mean daily rainfall (0.81 – 3.59 mm d^{-1}) were high (Table 1).

Seasons starting later tended to be shorter than those starting earlier (overall: $r_{16} = -0.695$, $P = 0.003$; combined: $r = -0.499$, $P = 0.049$): shorter seasons, however, tended to have higher mean daily rainfall than longer seasons in the combined ($r = -0.652$, $P = 0.06$), but not in the overall ($r = -0.250$, $P = 0.351$) case. The correlation between starting date and mean daily rainfall was weak and nonsignificant (overall: $r = 0.071$, $P = 0.793$; combined: $r = 0.161$, $P = 0.552$). Mean daily

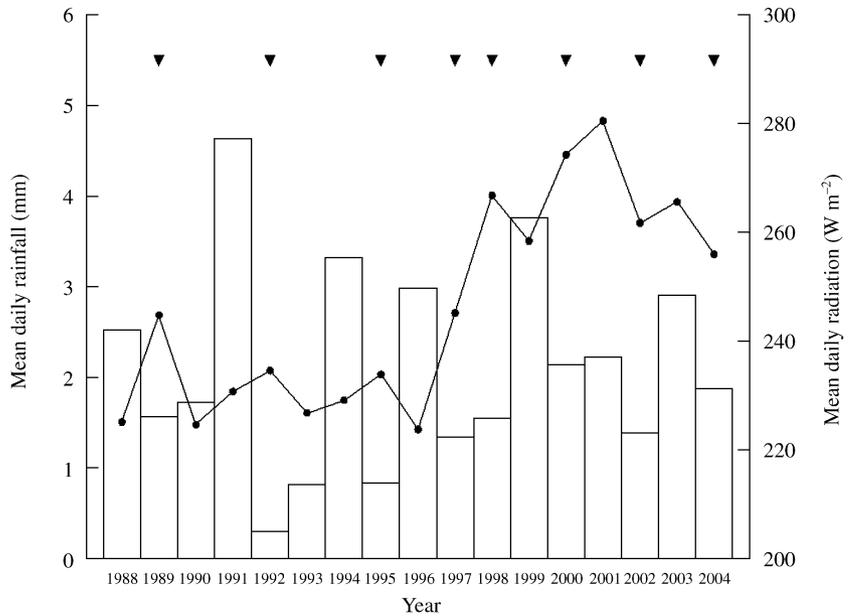


Fig. 3 Mean 3-month dry season (a) daily rainfall (open bars) and (b) radiation (closed circles) at Bulu, close to Korup (Cameroon), and for 1988–2004. Mast fruiting years are indicated by inverted triangles.

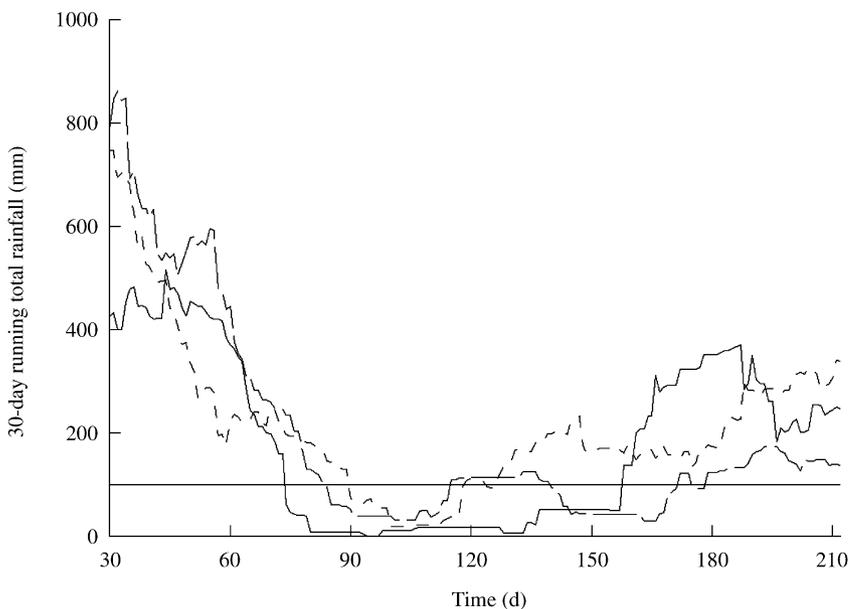


Fig. 4 Thirty-day running totals of rainfall over the dry season at Bulu, close to Korup (Cameroon), for a relatively dry (1994–1995; solid line), a relatively wet (1998–1999; short-dashed line), and a divided (1999–2000; long-dashed line) season. The horizontal line at 100 mm is the threshold below which drought occurred. The x-axis is the number of days since 1 October.

rainfall was positively and significantly correlated with minimum temperature in the overall ($r = 0.570$, $P = 0.021$), but not in the combined ($r = 0.396$, $P = 0.128$) case. Mean daily rainfall and radiation were significantly positively correlated in the overall ($r = 0.567$, $P = 0.022$), but not in the combined ($r = 0.021$, $P = 0.938$) case. Mean daily radiation and minimum temperature showed no significant correlations with either start date or duration ($P > 0.20$). These positive correlations originated because of the overall increases in radiation and temperature with time.

Mean daily rainfall values, as defined by the exact duration of the dry seasons (as in Table 1), were broadly correlated across

years with those based on the fixed December to February 3-month periods ($r_{15} = 0.654$, $P = 0.004$). However, in three of the years, differences were relatively large: in 1988 and 2001 the exact-duration rainfall was much higher, and in 1991 much lower, than the 3-month-duration rainfall.

Phenological events

Dates of recording were converted to times (in years) since 1 January 1995. Five leaf fall and flush events were recorded, and there were four flowering, fruiting and seedling events (Fig. 5; Appendix 1). Leaf fall in the dry season 1994–1995

Table 1 Summary of climatic variables for dry seasons 1989–2004 at Korup, Cameroon

Yr	Mast	Part yr	Number of days from 1.12	Duration (d)	Mean daily rainfall (mm)	Mean daily radiation (W m ⁻²)	Minimum temperature (°C)
(a)							
1988–89	M		36	74	1.22	246	18
1989–90			7	122	2.00	231	20
1990–91			40	43	2.30	235	20
1991–92	M		27	84	1.26	232	16
1992–93			20	76	1.49	226	18
1993–94			34	66	2.31	233	18
1994–95	M		13	84	0.81	234	16
1995–96			42	50	2.25	233	21
1996–97	M		24	88	1.48	239	20
1997–98	M		28	77	1.84	264	20
1998–99			29	29	3.42	268	20
1999–00	M		23	88	2.47	267	20
2000–01			12	83	3.59	280	20
2001–02	M		28	70	1.36	259	17
2002–03			26	95	2.80	281	20
2003–04	M		43	66	1.42	265	21
(b)							
1989–90		A,B	7, 64	44, 65; 109	1.96	233	
1999–00		A,B	23, 79	31, 32; 63	2.53	271	
2000–01		A,B	12, 52	8, 43; 51	1.91	288	
2002–03		A,B,C	26, 90, 117	61, 19, 4; 84	0.26	281	

(a) The start and end dates, mean rainfall and radiation, and minimum temperatures, for 'overall' periods. Mast fruiting/seeding years for *Microberlinia bisulcata* are indicated by a 'M'. (b) Data are given for the 4 yr in which the season was divided into parts, giving weighted means for the 'combined' periods. Minimum temperatures were the same as in (a).

was already mostly past by the start of recording and only a few trees were still flushing in January 1995. In 1996 there was no flowering, and therefore no fruiting and seeding; whilst in 1999 there was very little flowering and also no fruiting and seeding (Fig. 5). For each event the time of start and end of each activity was found for each active tree and from these the weighted mean start and end dates for the event were calculated. Leaf fall, leaf flush, flowering and seeding all occurred within relatively short periods of 1–2 months, but fruiting (i.e. pod formation) took several months (Fig. 5, Appendix 1). Leaf fall, leaf flush and flowering occurred in quarters 1–2, pods in quarters 2–3 and seed in quarters 3–4. For mast fruiting in any one defined 12-month period, the 'current' dry season was quarter 1 of that period, the previous dry season being that of the 12-month period before.

Detailed phenological data recorded at the fortnightly scale in the year 2003–2004 are shown in Fig. 6. Flowering lasted from April to August (5 months), and pod formation and ripening lasted from June to November (6 months). Phenology, in this year, showed good representation of the sequence of events found in the other years at the coarser monthly timescale (Fig. 5).

Frequency of masting

During the 6-yr period of continuous monitoring, *M. bisulcata* masted in 1995, 1997, 1998 and 2000 (Fig. 5). This was

unequivocally shown by the very high amounts of flowers, pods and seeds. There was correspondingly no masting in 1996 and 1999. Masting consists of three stages: the (mass) production of flowers, then fruits, and finally seeds. Each stage did not always follow completely from the one before on every tree. Flowers are a necessary precursor of fruiting, but pods can be small and abort without maturing into the 'seed' stage. In the following results mast years will be sometimes referred to in the abbreviated '95–97–98–00' form.

Considering, first, flower production, most trees produced flowers in all four mast years (78%) and nearly all (91%) in three or four of these years (Table 2). Of the 3- and 2-yr combinations, 95–97–00 and 95–00 were relatively the most frequent (7 and 5%, respectively). Taking pod production, 52% of trees masted in all 4 yr, 35.3% in three of the 4 yr (of which 95–97–98 was the most frequent combination at 28%), and 12.7% masted in either one or two of the 4 yr (Table 2). No tree failed to produce some flowers and pods in at least one of the four mast years, indicating that all trees were fertile. For seed production the pattern changed, with 30% of trees masting in each of the 4 yr (Table 2), 44.7% in three of the 4 yr (of which the combinations 95–97–98 and 95–97–00 were the most frequent, both 20.0%), 15.3% in 2 yr (of which the combination 95–97 was the most frequent, 6.7%), and 8.7% in just one of the 4 yr. Over the period 1995–2000, lack of seeding was recorded for only two trees (1.3%).

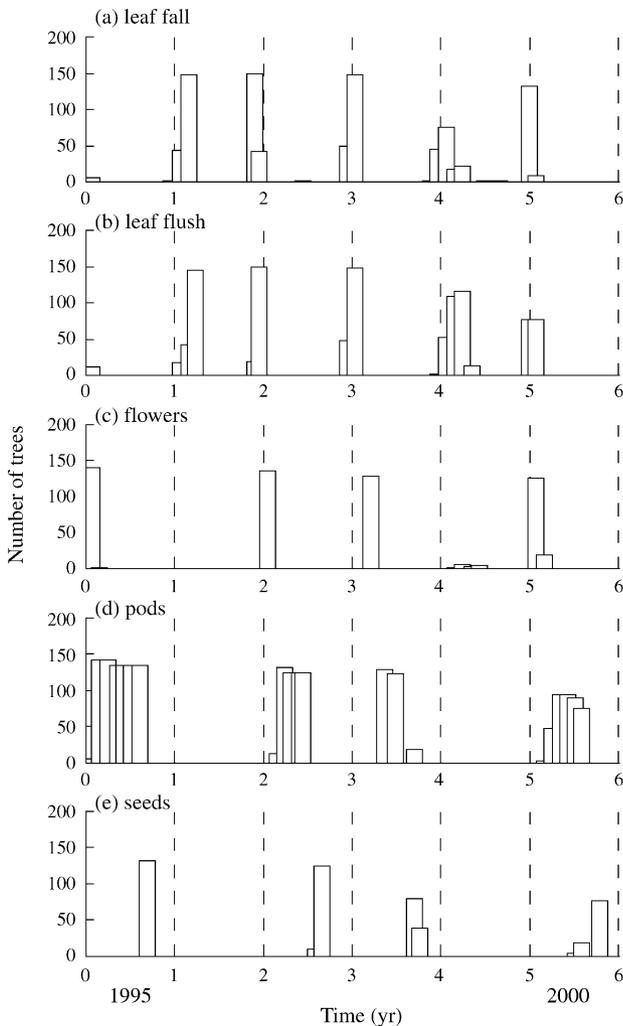


Fig. 5 Frequency of trees of *Microberlinia bisulcata* in Korup (Cameroon), which had (a) leaf fall, (b) leaf flush, (c) flowering, (d) pods and (e) seeds, in 1995–2000. The x-axis is time since 1 January 1995. Each bar refers to a census.

Transitions within mast years

In 1995, 1997 and 1998, the intensity of flowers was mostly high (scores of 2 and 3), but in 2000 it was much lower (scores of 0 or 1; Table 3). Intensities of pods in these years followed a similar pattern except that the number of trees with no pods in 2000 markedly increased, also shown by the number of trees that flowered and failed to have pods (Table 4). Intensity of seed production followed the same patterns as pods for 1995, 1997 and 2000 but in 1998 there was a clear change to lower scores for seeds than pods (Table 3). (In 1998 many immature pods were shed early.) Accordingly, in 1998 the numbers of trees with pods, but no seeds, was substantially higher than in the other years (Table 4). Three trees in 1998 had seeds where pods had been overlooked, probably because they were few in number or of small size. A further indication of transition was that over the years 1995, 1997 and 1998,

the number of trees with seed scores lower than pod scores increased (from 5.3 to 20.7%), although in 2000 this was very low because the overall pod and seed scores were low (Table 3). Nevertheless, in 1998 and 2000, there were, respectively, 12.0 and 10.6% of trees whose seed scores were higher than pod scores.

These results indicate that each masting event was different and that there was a regression over time: those of 1995 and 1997 were quite similar, with high scores for nearly all trees, but in 1998 pod intensity began to decrease and this was followed by low seed intensity. In 2000, flower production was lowest, with many trees failing to have pods and consequently had low seed intensities. Masting thus declined from 1997 to 2000 in two steps with, first, the failure of some trees to seed in 1998 and, second, failure of some trees to form pods in 2000.

Association of masting with tree size, elevation and distance to streams

The frequency with which trees masted as flowers (\leq three or four times) was not significantly associated with tree diameter ($\chi^2_2 = 3.42$, $P = 0.198$), elevation ($\chi^2_1 = 0.82$, $P = 0.365$) or distance ($\chi^2_3 = 1.87$, $P = 0.601$). However, the frequency with which trees masted as pods (\leq two, or three or four times) was significantly associated with elevation ($\chi^2_2 = 7.06$, $P = 0.029$), but not with either tree diameter ($\chi^2_4 = 7.46$, $P = 0.113$) or distance ($\chi^2_6 = 5.46$, $P = 0.487$). In the low- and high-elevation classes, the relative percentages of trees masting twice or less, or three or four times were 14, 42 and 44%, and 10, 24 and 66%, respectively. This means that at higher elevation, more trees had a fourth year of pods (in 2000). A similar, but weaker, pattern was found when masting as seed was considered: for elevation, the association was only marginally significant ($\chi^2 = 5.09$, $P = 0.079$) and for diameter and distance it was nonsignificant ($\chi^2 = 2.92$, $P = 0.571$; $\chi^2 = 2.29$, $P = 0.892$; respectively).

The association between frequency of masting and elevation became stronger when only trees in the middle diameter class were analysed ($\chi^2_2 = 11.1$, $P = 0.004$ for pods, and $\chi^2_2 = 5.74$, $P = 0.057$ for seed). This indicates that in this tree size class, proportionally more trees had the fourth year of pod masting in the higher-elevation class (low: 16, 52, 32%; high: 6, 25, 69%; two, three or four times, respectively), but also that more trees had a third or fourth year of seed masting (low: 34, 43, 23%; high: 13, 47, 40%). Total masting intensity over 6 yr was significantly positively correlated with tree size (flowers: $r_{s,148} = 0.196$, $P = 0.016$; pods: $r_s = 0.193$, $P = 0.018$; seed: $r_{s,146} = 0.186$, two cases of zero omitted; $P = 0.024$).

Comparisons between trees

Comparisons between trees that did or did not mast, with pods or seeds, in a particular mast year, were restricted because most trees masted (Fig. 5, Appendix 1). The only reasonable

Table 2 Numbers of masting trees of *Microberlinia bisulcata* in Korup, Cameroon, for different sequences of years 1995–2000

Frequency	Sequence of years	Flowers		Pods		Seeds	
		No. of trees	Totals	No. of trees	Totals	No. of trees	Totals
4	1995–1997–1998–2000	117	117	78	78	45	45
3	1995–1997–1998	3		42		30	
	1995–1997–2000	11		6		30	
	1995–1998–2000	2		4		6	
	1997–1998–2000	3	19	1	53	1	67
2	1995–1997	0		3		10	
	1995–1998	0		3		3	
	1995–2000	7		2		2	
	1997–1998	0		1		2	
	1997–2000	1		1		5	
	1998–2000	2	10	1	11	1	23
1	1995	1		4		6	
	1997	0		0		1	
	1998	1		2		2	
	2000	2	4	2	8	4	13
0		0	0	0	0	2	
Total			150		150		150

Table 3 Changes in the phenology of trees of *Microberlinia bisulcata* in Korup, Cameroon 1995–2000: maximum intensities of masting

Event	Yr	Number of trees with maximum score for											
		Flowers				Pods				Seed			
		0	1	2	3	0	1	2	3	0	1	2	3
1	1995	9	4	50	87	8	8	50	84	18	8	43	81
2	1997	15	5	70	60	18	16	77	39	26	8	92	24
3	1998	22	3	113	12	18	22	108	2	60	38	43	9
4	2000	5	128	9	8	55	91	4	0	56	77	16	1

Table 4 Changes in the phenology of trees of *Microberlinia bisulcata* in Korup, Cameroon 1995–2000: transitions between phenological stages

Event	Yr	Flowers → pods				Pods → seeds			
		Number of trees with				Number of trees with			
		Flowers but no pods	No flowers but pods	Flowers but pods of lower score	Flowers with pods of higher score	Pods but no seeds	No pods but seeds	Pods but seed of lower score	Pods with seed of higher score
1	1995	1	2	12	5	10	0	8	1
2	1997	4	1	32	3	8	0	16	1
3	1998	0	4	25	0	45	3	31	18
4	2000	53	3	12	3	1	0	3	16

possibilities of achieving this were for pods in 2000 ($n = 95$ vs 55 trees) and for seeds in 1998 ($n = 90$ vs 60 trees) and 2000 ($n = 94$ vs 56 trees). The possibilities of comparing trees with or without masting in 1998 and 2000 with a common history of having masted in both 1995–1997 and/or 1998 were limited

slightly further by the sample sizes. A majority of trees masted in both 1995 and 1997: 129 trees for pods and 115 trees for seeds. A further 16 trees had pods in either 1995 or 1997, and a further 27 had seeds in either 1995 or 1997. One-hundred and twenty trees masted with pods in 1995, 1997 and 1998,

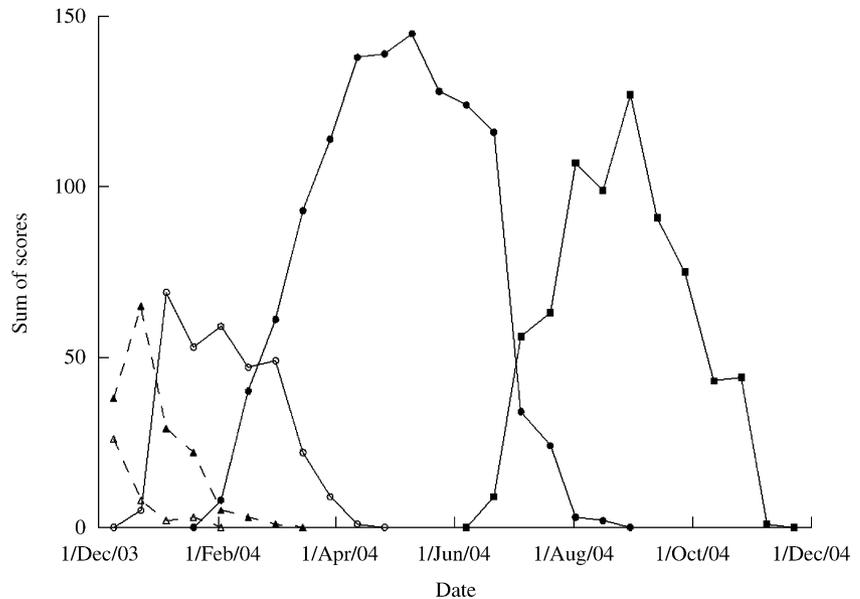


Fig. 6 The pattern of leaf flush (closed triangles) and fall (open triangles), and of flowering (open circles), fruiting (closed circles) and seeding (closed squares), of 71 trees of *Microberlinia bisulcata* in Korup (Cameroon) during 2003–2004 (score maximum = 213).

with or without 2000, allowing comparisons between those that did and those that did not mast in 2000. One-hundred and fifteen trees masted with seeds in both 1995 and 1997, and variously seeded in either 1998 and/or 2000, allowing comparisons between trees with and without masting in 1998, and those with and without masting in 2000, to be made.

Causes of part-masting in 1998 and 2000

Using all 150 trees, the presence of pods in 2000 was strongly positively dependent on elevation ($F_{1,148} = 9.15$, $P = 0.003$). In the lower- and higher-elevation classes, 51 and 83%, respectively, of trees had pods. (Ordinal regression using the intensity values gave very similar results at $P < 0.001$.) Neither diameter of tree ($P = 0.91$) nor distance to streams ($P = 0.78$) had any significant effect on the presence of pods. For presence of seeds in 2000, the relationship with elevation was again strongly positive ($F = 9.61$, $P = 0.002$), with 50 and 83% of trees having seeds in the low- and high-elevation classes, respectively. Relationships with diameter and distance to streams were again very weak ($P = 0.98$ and 0.90 , respectively). In 1998, the presence of seeds did not depend on diameter, elevation or distance to streams ($P = 0.16$, 0.28 and 0.69 , respectively). Furthermore, adding the term presence of seeds in 1998 to the regression of seeds in 2000 on elevation made no significant improvement to the model (P of deviance change = 0.45): the association of presence of seeds in 1998 and in 2000 was also very weak ($\chi^2_1 = 1.37$, $P = 0.24$) and likewise for pods ($\chi^2 = 0.043$, $P = 0.84$). The relationship between intensity and elevation (judged by the size of F) decreased slightly when considering pods and then seeds (pods: $F_{1,148} = 7.33$, $P = 0.008$; seed: $F = 6.27$, $P = 0.013$).

For no phenological variable and year did the addition of the interaction (elevation \times size) result in significance ($P > 0.05$ and > 0.80 for the pods and seeds in 2000, respectively).

The presence of pods in 2000, on trees with a common history of having pods in 1995, 1997 and 1998, was similarly strongly positively dependent on elevation ($F_{1,118} = 6.56$, $P = 0.012$) but it was not dependent on diameter or distance ($P = 0.83$ and 0.96). In low- and high-elevation classes, 54 and 83% of trees had pods, respectively. In 1998, the presence of seeds showed a lack of relationship with diameter, elevation and distance ($P = 0.26$, 0.22 and 0.92 , respectively). By contrast, in 2000, the presence of seeds was strongly positively dependent on elevation ($F = 6.37$, $P = 0.013$), with 53 and 83% of trees with seeds in low- and high-elevation classes, respectively, although again this was not dependent on diameter and distance ($P = 0.80$ and 0.86).

The one strong (positive) relationship was therefore the dependence of presence of pods and seeds in 2000 on elevation, irrespective of whether individual trees had masted before in 1995, 1997 or 1998. This suggests that history of activity before the last event played little role in masting.

Pods and seeds in relation to dry-season climate

Considering first the years of detailed recording (1994–1995 to 1999–2000), start date alone was not consistently different for mast and nonmast years: 1996–1997 to 1999–2000 were very similar (number of days since 1 December = 23–29) but in 1994–95 and 1995–96 they were much earlier and later, respectively (Table 1). Considering duration of the dry season, masting occurred in years with long seasons (> 63 d) and nonmasting in years with short seasons (50 d), although the value for 1996–1997 at 50 d is not much different from

the lower end of the range for masting years. Taken together, failure to mast occurred in years that had either a dry season that started very late (1995–1996) or one that was very short in duration (1998–1999). The partial masting in 1999–2000 could have been because the dry season was broken and its first part was short (31 d).

The two nonmasting years (1996, 1999) and the less strong masting year (2000) had higher-than-average daily rainfall (2.735 mm, $n = 3$) than the three masting years (1.376 mm, $n = 3$) in their corresponding dry seasons – a twofold difference. It therefore seems that early, more-intense dry seasons led to masting whereas late, less-intense ones did not.

How is this conclusion supported by data from the previous 6 yr? In 1988–1989 and 1991–1992 there was definitely considerable masting. The dry season in 1988–1989, however, started relatively late but had a typical duration, whilst that in 1991–1992 started much earlier (Table 1). What these two seasons had in common, compared with the other four nonmasting seasons, was their lower mean daily rainfall (1.244 mm, $n = 2$; vs 2.009, $n = 4$). The year that does not fit the pattern was 1992–1993: the dry season daily rainfall intensity was 1.486 mm and that season started relatively early: 1989–1990 started the earliest but led to no masting, possibly because the average daily rainfall was quite high and the season was also divided.

Masting in years before and after 1995–2000

The main patterns were supported by forest-wide general observations referred to in Newbery *et al.* (1997), Chuyong *et al.* (2000) and Green & Newbery (2002). Although Newbery *et al.* (1998) recorded flowering of *M. bisulcata* in 1991 on a smaller sample of trees ($n = 10$), this was not borne out by the concurrent 1991–1993 litterfall trapping of Chuyong (1994) – and there were scarcely any pods and seeds that year. By contrast, the mass flowering of 1992 resulted in a very pronounced peak of floral-parts litter (Chuyong, 1994).

In the course of a leaf-phenology study in early 2003, Schwan (2003) scored the density of fallen pods around 73 of the *M. bisulcata* trees used in 1995–2000, in a 300-m wide

east to west central strip (49.5 ha) of the P-plot. Thirteen trees had very high numbers of pods, 29 low–moderate numbers, and 31 a few or none. Judging from their state of decomposition, these pods were very likely to have fallen in 2002. From other on-site observations there was no masting in 2001 and 2003. Therefore, these phenology data can be safely incorporated into a wider analysis over 17 yr (1988–2004), the mast years being 1989, 1992, 1995, 1997, 1998, 2000, 2002 and 2004.

Pod density around the trees scored in 2003 was significantly associated with elevation class: 51, 38 and 11% of trees in the lower-elevation class ($n = 47$), and 29, 38 and 33% in the higher class ($n = 24$) had pods in classes 1, 2 and 3 ($\chi^2_2 = 6.22$, $P = 0.045$). This supports the results from 2000 with heavier fruiting at the higher elevations.

Dependence of masting on dry season rainfall

The occurrence of masting in each of the 16 yr 1988–1989 to 2003–2004 was regressed on mean daily rainfall and radiation in each of the quarters of the year and the same variables for the year before (i.e. with a 1-yr time lag). (Independence between years was necessarily assumed.) Only two cases were statistically significant, masting was strongly negatively dependent on mean daily rainfall in (dry season) quarter 1 ($F_{1,14} = 8.00$, $P = 0.013$; Fig. 7a), and strongly positively dependent on mean daily rainfall in quarter 1 of the year before ($F = 18.42$, $P < 0.001$; Fig. 7b). Therefore, as quarter 1 of the year of masting (i.e. the current year) became drier (more intense), and quarter 1 of the previous year became wetter (relatively much less intense), the probability of masting strongly increased. Neither the inclusion of radiation nor the use of combinations of rainfall and radiation led to significantly improved regressions. Mean daily rainfall in quarter 1 in current and previous years were, however, only marginally correlated ($r_{14} = -0.457$, $P = 0.075$).

Using the ‘overall’ definition of dry season (Table 1, section a), masting was significantly negatively dependent on mean daily rainfall ($F_{1,14} = 10.44$; $P = 0.006$), but not dependent on duration, starting date, mean daily radiation, total rainfall or

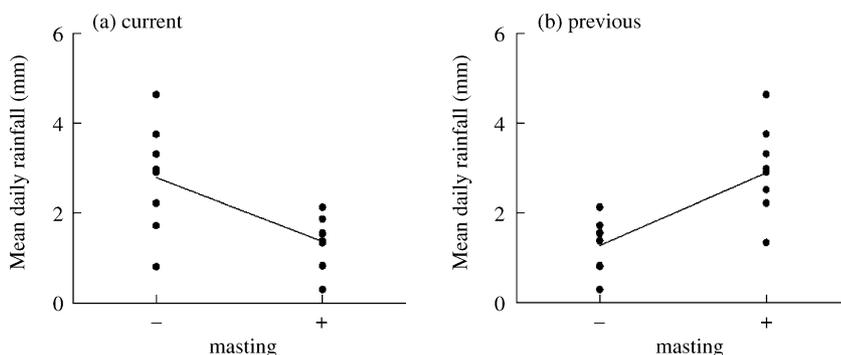


Fig. 7 Mean daily rainfall in (a) the dry season before fruiting (i.e. of the current year) and (b) that of the previous year, for years without (–) and with (+) masting of the *Microberlinia bisulcata* population in Korup (Cameroon) during 1988–2004. Lines join the means of the two classes.

minimum temperature ($P > 0.25$). Years with masting had almost half the mean daily rainfall as those without (1.482 vs 2.520 mm, $t_{\text{adj.12}} = 3.39$, $P = 0.005$). Adding any of the other variables into the model with mean daily rainfall did not lead to an improved fit. Regressing masting on mean daily rainfall in the previous dry season led to a significant positive dependence ($F = 10.90$, $P = 0.005$): years with masting had almost twice the mean daily rainfall in the previous year than those without (2.712 vs 1.555 mm, $t_{\text{adj.12}} = 3.55$, $P = 0.004$). Again, starting date, mean daily radiation and total rainfall were not significant ($P > 0.18$) but masting was marginally negatively dependent on duration of the previous dry season ($F = 3.57$, $P = 0.080$), and positively dependent on minimum temperature in the previous dry season ($F = 5.26$, $P = 0.038$). Using the 'combined' definition of dry season (Table 1, section b), the regressions of masting on current and previous dry season daily rainfall became insignificant ($P > 0.20$) and the only significant ones were those using duration and minimum temperature in the previous season (both cases, $P = 0.038$). The most striking contrast between mast and nonmast years was in the difference between the current and previous years' mean daily rainfall, -1.230 and 0.964 mm, respectively; $t_{\text{adj.11}} = 6.19$, $P < 0.001$).

The different recording methods did not allow comparative quantification of the intensity of masting across the whole period. Whilst intensity of flowering, fruiting and seeds was known accurately for 1995–2000, the same level of information was lacking for the periods before and after this period (except for 2004). Therefore, giving different various weights to the individual events in the regressions (2000 receiving a weight of 0.5, for instance) was not reliable: in all probability, 2002 also had not as strong a masting event. Regressions run with down-weighted masting in 2000 led, however, to only very slightly different values of the statistics. The most important information was whether a substantial event did or did not occur.

Change of rainfall threshold defining dry periods

The above results used a threshold of 100 mm for the 30-d sum of rainfall. Changing this to either 80 mm or 120 mm altered the regressions of masting on climate very little. With the 'overall' definition of dry season, masting remained significantly negatively dependent on mean daily rainfall in the current dry season (80 mm, $P = 0.015$; 120 mm, $P = 0.021$), but the positive dependence on mean daily rainfall in the previous dry season became a little less significant (80 mm, $P = 0.051$; 120 mm, $P = 0.037$). All other variables led to nonsignificance, except for duration in the previous year with the 80-mm threshold, where masting was again negatively dependent ($P = 0.006$). Daily rainfall means, defined by either the 120- or 80-mm thresholds, were strongly significantly correlated each with those defined by the 100-mm threshold ($r_{14} = 0.976$ and 0.753 , respectively, $P \leq 0.001$).

Connection between mast fruiting and timing of leaf fall and leaf flush

In those 12-month periods between 1994–1995 and 1999–2000, in which there was no masting, start of leaf fall and leaf flush in the dry season were delayed by 0.6–1.8 months (c. 2–8 weeks) compared with periods in which masting did occur (Fig. 5, Appendix 1). This pattern was fully consistent, although the small sample size of $n = 6$ obviated statistical testing. Those years with late leaf fall/flush were all those with late-starting, less-intense (relatively wetter) dry seasons. In the mast years, leaf fall/flush was relatively early, this being certainly so for 1996–1997, 1997–1998 and 1999–2000, and to be strongly inferred for 1994–1995 in which the peak in litter fall/flush was well past by January 1995 (Fig. 5). Trees that masted in 2000 did not, however, flush their leaves earlier at the higher than the lower elevations (5.04–5.05 yr, $n = 58$ vs 5.01–5.02 yr, $n = 92$, respectively).

Confirmatory data from the earlier years 1988–1989 to 1993–1994 are less complete but nevertheless useful. In plots dominated by *M. bisulcata* and which overlapped with the present area of study, Chuyong (1994) showed a late peak in leaf litter-fall in February to March 1991 (i.e. the 1990–1991 period), which was a nonmasting year, and an early peak in December 1991 where 1991–1992 was a masting year. Newbery *et al.* (1997) recorded a wide peak in litter fall in the same area from February to March 1990: 1989–1990 was not a masting year either. Thus for 3 of the 6 yr, for which there were additional data available, support for the pattern found for 1994–1995 to 1999–2000 is 100%. This strongly leads to the hypothesis that intensity of the dry-season (i.e. low rainfall) is the principal driving factor of masting in *M. bisulcata*.

Masting and minimum temperature and radiation in dry season

Variation and differences in mean daily minimum and maximum temperatures and radiation between 1 October and 31 April (including all dry seasons) gave no explanations of masting in the years 1994–1995 to 1999–2000 (Table 1). In these months of the year, temperatures ranged from 22.0–23.3°C and 31.3–32.2°C ($n = 212$), and radiation from 229–257 W m⁻². The years 1988–1989 to 1993–1994 showed very similar values. Had flower initiation taken place in the previous quarter of the year, minimum temperatures would have been also still too high (19–21°C: cf. the probable triggers of 16–18°C) and these, in any case, showed no association with mast years.

Within the period of detailed phenological recording, the only notably large drop in minimum temperature was to 16–18°C on 18–21 January 1995. In the other years, temperatures did not fall below 20°C. Outside this period, minimum temperature fell to 16–18°C throughout 1–11 January 1992, and to 18°C on 16–17 January 1989. Thus, for just three of the eight masting events was minimum temperature lowest,

suggesting that it was unlikely to have been a cue for flowering in *M. bisulcata*.

Discussion

Mast fruiting in a variable environment

The overall frequency of heavy fruiting was eight times in 16 yr (i.e. once every 2 yr on average), although the pattern did deviate from a repeated on-off sequence. Masting was strongly dependent on climate in the current and previous years, subject also to there usually being a minimum time interval of 1 yr between masting events. The reported results appear to support alternate bearing as the basis to mast fruiting in *M. bisulcata*, and the explanations put forward lead to a general reconsideration of the phenomenon in trees. Interestingly, the interval between mast fruitings events was 2 yr before 1997–98 but 1 yr afterwards.

Water stress in the dry season was probably the trigger for annual leaf exchange in *M. bisulcata* because the peak in leaf fall fits so closely to the pattern of declining rainfall (Newbery *et al.*, 1997; Chuyong *et al.*, 2000). No second peak occurred later in the dry season to suggest that there was severe water limitation to new leaf growth. Whilst most fine roots of *M. bisulcata* are in the surface 50 cm (Newbery *et al.*, 1997), some larger ones could allow access to water deeper in the soil profile and, together with water stored in the tree (in the stem, branches, roots and mycorrhizas), an adequate tree water balance was probably maintained. Evidence of stem shrinkage in the dry season suggests indeed that stored water played a role (Schwan, 2003). Soil moisture content data collected during the dry seasons of 2004 and 2005 indicated that soils became drier as the season progressed but they did not reach critically low levels (X. M. van der Burgt & D. M. Newbery, unpublished). From this it is assumed that low water potentials in old leaves would primarily occur because of increasing temperatures and lowered humidity of the air, combined with some lowering of soil water availability.

Reich & Borchert (1984) and Borchert (1994a,b) have shown, for Central American dry-forest trees, that exchange of leaves in the dry season was caused by the release from low stem water potentials after leaf loss, which allows a rehydration of branches (probably partly from stem storage) and this stimulates flushing. Of the three principal phenological patterns analysed by Borchert (1992), *viz.* I, flowering during leaf regrowth; II, flowering at the end of shoot growth and leaf maturity; and III, flowering from resting buds after leaf fall, *M. bisulcata* clearly follows pattern I. Borchert (1992) further remarked that this pattern is common among caesalps.

Mast fruiting years in *M. bisulcata* occurred when the dry season of the current year was drier than average (a 'dry' dry season, with a mean daily rainfall of < 2.12 mm, or 190 mm in 3 months), the preceding year's dry season was wetter than average (a 'wet' dry season, with a mean daily rainfall of

≥ 2.12 mm), and normally the preceding year was nonmasting. This rule fits the 16-yr sequence, with the exception of 1998 (Fig. 3). This particular year was relatively dry and *M. bisulcata* had masted in the previous year. The double-year of masting may be explained by its coincidence with the shift in radiation from lower to higher levels. Although ENSO conditions were reported across much of the tropics in 1998 (Curran *et al.*, 1999; Williamson & Ickes, 2002), Korup was little affected by them (Supplementary material), as shown by other studies of climate variation in west and central equatorial Africa (Nicholson & Kim, 1997; Nicholson *et al.*, 2000; Pocard *et al.*, 2000; Camberlin *et al.*, 2001). Other cases of two consecutive years of 'dry' dry seasons (*viz.* 1989–90 and 1992–93) did not lead to masting in the second year. The situation at Korup may be compared with that at Barro Colorado Island, Panama, where higher-than-average community-level fruiting was associated with ENSO events, putatively as a result of raised radiation levels in those years (Wright *et al.*, 1999; Wright & Calderon, 2006).

The dry season is the one period of the year when trees can potentially accumulate much of their new carbon resources by photosynthesis at a fast rate. Radiation levels are higher than in the wet season (Fig. 1), the former (aside from a slight fall when the Harmattan brings dusts in January) having very low daytime cloud cover, the latter with contrastingly high daytime cover. When the dry season starts, early trees exchange their leaves earlier than when the season starts later. The early flushing trees can correspondingly photosynthesize under conditions of maximal radiation for longer than late-flushing trees.

The higher radiation levels in 1998 probably led to higher evapo-transpiration levels compared with those before 1997: this would have meant that daily rainfall in the dry season did not parallel the water stress suffered by the trees. The 'dry' dry-season rainfall values for 2000, 2002 and 2004 were probably effectively lower, this bringing them more into line with the pre-1997 rainfall values. Closer inspection of the rainfall data in the dry season (1997–1998) revealed that this year was not exceptional in any way: it started around the median time, was of average length and was unbroken (Table 1). That the radiation levels rose in this season might suggest that instead of waiting a year for recovery, there were enough new internal carbon resources to allow for a next masting in 1998, immediately after that in 1997. This being the case, the proposed year normally necessary for resource restocking between 1997 and 1998 was missing. Table 4 shows that in 1998 the number of trees with pods but no seeds (as a result of the mentioned early pod abortion), and those with seed scores less than pod scores, was unusually high. This might suggest that the masting in 1998 was falsely triggered by extra carbon resources, yet it was not fully realized because, according to the hypothesis developed below, extra nutrients usually taken up in the intervening wetter year were lacking.

When the dry season after a recovery year was again 'wet' (e.g. 1991 and 1994) then masting was delayed for one year and

a very high level of fruiting occurred in that ('dry') year (Table 3). From direct observations on pod and seed production (Green & Newbery, 2002) and seedling demographic work on the 1995 seedling cohort (D. M. Newbery *et al.* unpublished), it is reasonably certain that 1995 was the strongest mast fruiting of the series and, in comparison, 1998 and 2000 were the weakest. The time series contains no sequences of three consecutive 'dry' dry seasons, although from 1999–2000 to 2001–2002 there did occur a sequence of three relatively 'wet' seasons. That the dry season in 2000 was drier than the one in 1999 fits well with the model put forward, and it is interesting that in 2000 masting was relatively weak because the dry season was seemingly not intensive enough in that year to support a large event.

The highest mean daily rainfall in the dry-seasons of masting years occurred in 2000 (Fig. 3) and in this year masting was more frequent in trees on higher than lower elevations. Both parts of the plot would have received the same amounts of radiation, so the difference was probably caused by water availability (i.e. the lower part probably remained relatively wetter for longer than the upper part). The wetter soils would have encouraged continuing or renewed root and mycorrhizal growth, this creating an increasingly stronger sink to divert resources away from pods and seeds. Itoh *et al.* (2003) also found that mast fruiting of the dipterocarp *Dryobalanops aromatica* Gaertn. f. in Borneo was aggregated on topographically drier sites.

Mast fruiting and ectomycorrhizas

The occurrence of a 'wet' dry season before the masting 'dry' one has two possible effects. First, the year of nonfruiting would enable a tree to restock its resources (i.e. replace reserves that were used by the last masting) (Kozłowski, 1971; Janzen, 1978). Green and Newbery (2002) showed that, as with other large mast-fruiting trees, the investment in carbon and nutrients in a reproductive event was considerable: the equivalent of 55% of the annual dry weight production of leaves was used for *M. bisulcata* pods and seeds in 1995; and the corresponding relative amounts of N and P were 13 and 21%. Henkel *et al.* (2005) recorded an even higher reproductive dry weight allocation, of 3.0 t ha⁻¹, for the ectomycorrhizal caesalp, *Dicymbe corymbosa* Spruce ex Benth, in Guyana, with correspondingly high allocations of N and P. In the main, *M. bisulcata* trees in Korup are very large and presumably have high respiration rates associated with the maintenance of a considerable biomass of wood (Schwan, 2003), roots and ectomycorrhizas (Newbery *et al.*, 2000). It is to be expected that mast fruiting temporarily creates another major sink for resources. Several authors (e.g. Wycherley, 1973; Wright & van Schaik, 1994; Wright *et al.*, 1999) have argued that many tropical forests are, in fact, radiation-limited because of the prolonged periods of cloud cover in wetter parts of the year. Moreover, in the nonmast year, the main sinks – the roots and mycorrhizas – will have more opportunity of access to internal carbon resources,

and together with the relatively moister soil conditions in a 'wet' dry season they are (i) likely to have better survival and growth rates, and (ii) take up more nutrients, than in a 'dry' dry season. In large ectomycorrhizal trees, then, the reproductive parts of a tree and the root–mycorrhizal system may be seen as being in competition for resources, aside, that is, from stem and root storage sinks, which are continually having a background influence (Kozłowski, 1971). In short, resource balance (especially carbon) is likely to be precarious in such huge trees, and under these conditions heavy fruiting each year is probably not 'affordable'.

The same process appears to operate for other ectomycorrhizal tree species. Piovesan & Adams (2001) have shown that masting in beech, *Fagus sylvatica* L., in Europe is associated with a very dry summer the year before (the time of floral initiation) but in addition there had to be a wet summer before that triggering one. The tree needed somehow to be primed. The association of high shoot carbohydrate levels in dry summers and masting was recognized much earlier by Büsgen & Münch (1929), although the internal causes (controls) to which they referred have eluded explanation even today and that beech also needed a wet year for seed maturation further enforces the basic idea of a process of alternation determined by the internal tree physiology interacting with climate. However, it should not be thought that a pattern of alternation is strictly adhered to: the interval between masting may be relaxed for reasons discussed later. Koenig & Knops (2000) also showed significant negative autocorrelations between tree fruit and seed crops in any one year and those 1–2 yr before in several temperate-masting and ectomycorrhizal tree species.

That most mast tree species are ectomycorrhizal is very significant (Curran, 1994; Newbery *et al.*, 1998; Henkel *et al.*, 2005; Newbery, 2005). Curran (1994) specifically elucidated this connection first for dipterocarps in south-east Asia. It is the cycling of nutrients which appears to link the activity of mycorrhizas to mast fruiting. Newbery *et al.* (1997), in their phenology and climate ectomycorrhizal response (PACER) hypothesis, showed that leaves shed in a year following mast fruiting had lower P concentrations than those in other years. At Korup, with its very low soil P concentrations, it is likely that in the year of masting less P was taken up and some P in reserve was allocated to fruits and seeds. Furthermore, percentage withdrawal of P on leaf fall in ectomycorrhizal species was found to be approximately half that of nonectomycorrhizal species in this forest (Chuyong *et al.*, 2000), and P availability appeared to limit P mineralization during decomposition on the forest floor (Chuyong *et al.*, 2002). Therefore, if P levels were lower, the extra activity of roots and ectomycorrhizas in the 'wet' dry season might conceivably allow the balance of P in the tree to be adjusted. So argued, the activities of ectomycorrhizas appear to complement and support mast fruiting when alternate bearing operates. Another role of ectomycorrhizas is their ability to store nutrients, especially P

(Smith & Read, 1997), which could help the tree build up resources for a next mast fruiting. Also possible is that the rate at which leaves flush (i.e. new leaves grow) is, in part, dependent on nutrient reserves within the tree from the previous year. Greater and faster leaf expansion would enable the capturing of more radiation early, before any slowing in photosynthesis had occurred, as a result of possible limitations in leaf water later in a long 'dry' dry season.

At a site, such as Korup, where rainfall fluctuates annually, there is a higher probability of alternating 'wet' and 'dry' dry seasons than of two similarly 'wet', or similarly 'dry', dry seasons following one another. To deal with the nonalternating situation requires a flexible and dynamic system in which an internal threshold must be crossed to achieve flowering. The obvious candidate is carbohydrate concentration. If the concentration is not high enough in one year to allow mast fruiting, then other sinks will become alternative sinks for the carbon reserves (inferring from Kozłowski, 1971; Kozłowski *et al.*, 1991). A corollary to this is that there may be a propensity towards a system of alternate bearing, one which behaves as a form of stabilizing 'attractor', using self-adjusting physiological mechanisms. Delay in reproduction also means that resource acquisition must more than compensate those resources permanently allocated elsewhere in the tree in order to achieve the threshold required in the subsequent year, or even the year beyond that one.

Within the detailed 6-yr study, masting only occurred when there was mass flowering (Fig. 5) (flowering failed in 1996 and 1999). Whilst no masting of fruits can occur without the presence of flowers first, there was only one tentative case of flowering followed by fruiting failure – in 1991 (Chuyong, 1994). Here, the sample size was small, however ($n = 10$ trees). It is significant that the dry season of 1990–1991 started late and was short (Table 1). Heavy early rains may have washed pollen away and rendered fertilization ineffective. In the same way, many more trees flowered than produced fruits in 2000 (Table 3). Conversely, it would be expected that in 'dry' dry seasons, pollination is more efficacious. This leads to the idea of mast fruiting being controlled in two stages: a first threshold in resources is crossed, which initiates flowers, and then a second threshold determines anthesis. Pollination success and carbon gain may positively reinforce each other to bring about masting.

Some interesting tropical examples hint in a similar direction. Schulz (1960) mentioned '... that the majority of the canopy species of the primary forest [in Suriname] fruit *every second year*.' (his italics). That some of these trees were probably ectomycorrhizal caesalps was later illustrated by Zagt (1997) for the synchronously biennial-flowering (and fruiting) *Dicymbe alstonii*. By contrast, Janzen (1978) describing the phenology of two Costa Rican tree species in the Leguminosae, *Cassia grandis* L. f and *Hymenaea courbaril* L., showed their fruiting patterns to resemble closely alternate bearing, but the fruiting of individuals was not synchronous. The tree species were

neither caesalps nor ectomycorrhizal. Furthermore, in Sri Lanka, some dipterocarps tend towards flowering more heavily approximately every second year, others flowering annually (Ashton, 1989); and in Thailand (at the northern limit of dipterocarp distribution) half of a stand reportedly flowered heavily one year with little flowering the next (Ashton, 1982).

Flowering and temperature

Mast fruiting was not correlated with minimum temperatures in the dry season of leaf-flush and flowering, in the previous dry season, or in the wet season preceding a flush. Newbery *et al.* (1998) saw some indication of minimum temperatures playing a role, but this was not borne out by the present longer time series. Variation in minimum temperatures across the years was, in any case, generally very small, and on the occasions when temperatures did fall below 18°C this was fleeting and erratic. In the context of the resource model proposed above, minimum temperature would presumably be an unreliable cue for flowering in this environment. Mass flowering of dipterocarps in south-east Asia has been convincingly related to minimum night-time temperatures in ENSO years at intervals of 5–13 yr (Ashton *et al.*, 1988). However, these events in Asia are much more prominent features set against the background of an otherwise relatively equable annual climate: in western Central Africa, ENSOs add only slightly to the repeated and dominant influence of the strong annual dry season. At Korup, the 1998 ENSO did not have any noticeable effect on minimum temperature.

Floral initiation

At which stage, and in which season, flowers of *M. bisulcata* are initiated unfortunately remains uncertain because too little is known of the floral biology and pollination ecology. Information on floral initiation is indeed still lacking generally for tropical trees (Borchert, 1983; Longman & Jenik, 1987; Owens, 1995). From what is known of anatomical floral development in legumes (Tucker, 1987, 2003), and the genus *Microberlinia*, in particular (Tucker, 2002), initiation is probably during bud formation at the end of the previous wet season because flowers form after leaf exchange in the following dry season. Either the new shoot is entirely programmed so that the last axillary buds are already initialized to become flowers, or axillary buds are initialized during shoot growth (Borchert, 1980, 1983). This might be solved in the future by direct observations of bud anatomy over the complete phenological cycle, in both mast and nonmast years (R. Borchert and S. Tucker, pers. comm.). Borchert (1983) recounted exactly the same problem for *Erythrina poeppigiana* O. F. Cook (Leg.); in the intervening 20 yr there has been surprisingly little progress in the understanding of floral initiation in tropical trees.

From the work of Borchert (1980) and Borchert *et al.* (2002, 2004) the most likely mechanism behind flowering is declining

leaf-water potential at the end of the wet season (into the dry season). This causes the formation of buds which contain new shoots. When concentrations of carbohydrates are high enough, these new shoot's axillary buds will have flower initials. Precisely when and for how long these buds develop during the wet season is uncertain for *M. bisulcata*. The slowing of growth itself will also probably raise concentrations of carbohydrates at the shoot tips (see Bernier *et al.*, 1981). Flowers do not appear at the same time as the first new leaves, but *c.* 1 month later. Each raceme has many flowers, but only one, or sometimes two, terminal ones usually develop into pods. As a pod develops, the accompanying terminal leaf falls away – as do those below it on the supporting shoot later – so that at maturity the pod is left exposed at the end of the old raceme axis and twig. In this way, the pod is optimally positioned above the canopy for seed dispersal. The developmental process suggests that flower growth and pod formation are determined by endogenous factors in the current dry season – after initiation in the previous wet season.

Studies of alternate bearing in fruit and nut trees (Monselise & Goldschmidt, 1982), and particularly in apple (Davis, 1957; Jonkers, 1979) are revealing. Floral initials are laid down in the year before flowering (and fruiting). It is thought that in the current year of fruiting, the presence of fruit suppresses initiation so that in the next year there are no flowers (Sachs, 1977). This physiological mechanism is a possible basis to alternate bearing. It is likely that floral initiation is determined by two related processes: low concentrations of leaf carbohydrates (as the current allocation is shunted mostly to fruits) and thus low GA concentrations suppress initiation, whilst high carbohydrate concentrations and higher GA concentrations (in the rest year) cause initiation (Sachs, 1977; Bernier *et al.*, 1981; Goldschmidt & Golomb, 1982). Manipulative experiments have corroborated this basic hypothesis, although the exact link between tree carbohydrate and hormone concentrations still remains poorly understood. A further interesting example is the alternating high and low flowering in *Metrosideros excelsa* Soland. ex. Gaertn., determined by alternating floral initiation and suppression apparently in the buds of the year preceding flowering (Sreekantan *et al.*, 2001).

Resource allocation and nutrients

If carbohydrate levels are the internal means to triggering flowering in the next year, this could be expected to be moderated by the climatic conditions that determine the build-up of renewed resources within the tree. Even if flowers were initiated in the year before, the amount of resources gained in the current year will be crucial for pod filling, and also have a carry-on effect into the next year. If resources were too low in the rest year, then presumably the flower initiation would be delayed for a year: if there were exceptionally higher resources in the year following a fruiting one then perhaps, as in 1997–1998, a double year could occur. The hypothesis allows for the

widely recognized fact that masting in some species is not a completely on/off response; some trees might have better resources than others, some may have parts of their crowns able to flower and fruit, yet others not, and also in rather more equable climates with no overlain signal in the weather, at every 2–3 yr not all trees must be in synchrony. This synchronization is a necessary feature of the predator satiation hypothesis (Janzen, 1974) but is not required for the resource limitation one *per se* (Norton & Kelly, 1988; Kelly & Sork, 2002). An example of very variable and overlapping fruiting cycles is seen in neighbouring populations of *Gilbertiodendron deweveri* (De Wild.) Léonard in the Congo basin (Hart, 1995) and among co-occurring *Quercus* species in North America (Sork *et al.*, 1993). It may also be the reason why, at a metalevel of data compilation, Herrera *et al.* (1998) doubted the general feature of bimodality associated with masting. From the arguments give above, ectomycorrhizal species might be expected to have stronger bimodality than nonectomycorrhizal tree species.

Ectomycorrhizas probably play an important role in building up root carbohydrate concentrations. In an analogous way, Goldschmidt & Golomb (1982) showed that roots of mandarin (*Citrus reticulato* Blanco) trees had 17-fold higher carbohydrate concentrations in 'off' than 'on' years. Stevenson & Schackel (1998) went a step further by recognizing alternate bearing in pistachio (*Pistachio vera* L.) as a masting phenomenon, and that carbohydrates for reproduction in the 'on' years were allocated to wood and to roots in 'off' years, which implies a switching mechanism and not a storage effect. Rosecrance *et al.* (1996, 1998) reported how alternate bearing in pistachio in the 'on' year depended upon both N, P and K uptake and storage in 'off' years; trees being more storage-dependent for N and P, but more dependent on uptake from the soil for K in the 'on' year (Brown *et al.*, 1995). Neilsen *et al.* (1990) further showed for apple that addition of P in the 'off' year considerably increased flowering and fruit set in the 'on' year. Similarly, the data for Korup point to not only carbohydrates but possibly also the site-limiting element P playing a role in application of Sach's nutrient diversion hypothesis (Sach, 1977). That extra K uptake from the soil might be needed in mast years remains untested for *M. bisulcata*.

Concluding ideas

Masting seems to be strongest in very large trees of *M. bisulcata*, and parsimony leads to the hypothesis that this is because of a critical internal carbohydrate balance. Over time, natural selection has led to the iteroparous reproductive trait of alternate bearing or biennial fruit production. The prevention of flowers being initialized for the next year in the same year as fruiting ensures that there is enough energy for successful reproduction. The larger the investment in seeds and their enclosing and supporting tissues, such as the pods in *M. bisulcata*, the stronger the requirement for alternation (or masting).

Pods of *M. bisulcata* are borne like flags above the canopy leaves. The supporting 'stalk' is made up of last year's woody twig, the current shoot and the raceme axis. Neighbouring senescent leaves also presumably support the maturing pod through local nutrient retranslocation. When a pod splits and twists, its seeds are shot far out across the canopy. This mechanism ensures a maximal dispersal distance of 50–70 m per generation. When trees are mast fruiting, their upper branches will have many pods and the vegetation immediately below them will therefore be largely leafless. This would appear to allow for more effective dispersal than if there were only a few pods in an otherwise well-foliated intermingled canopy. Here then is a further possible selective advantage of masting: the more pods per tree the greater the potential mean fitness per seed through enhanced dispersal.

Flowering and fruiting was highly synchronous in *M. bisulcata*. In the nonmasting years there were none or extremely few trees flowering. If the resource hypothesis was the sole explanation, then some trees that were growing very well might have masted a year earlier than the others, or some that were in poor situations might have needed an extra year than the norm. This did not appear to happen. If, however, trees are connected to one another in groves via hyphal networks, in a 'wet' dry season the levels of carbohydrates may become equilibrated and trees achieve similar concentrations in their shoots to have the same potential to initiate flowers. Likewise, in the fruiting year, a mediating signal might be sent to the buds to achieve common suppression. This may be a further way in which the evolution of masting is linked with the ectomycorrhizal habit in dominant tree species.

Acknowledgements

We thank the Institute of Agronomic Research (IRAD), Ekona Centre, Buea for hosting our project over many years (Head, Dr S. Zok); the Ministries of Forests and Environment (MINEF) and Education, Scientific and Technical Research (MINREST) for permission to research in Cameroon; Korup National Park (Conservator, A. Kembou) for access to the site; Plantations PAMOL du Cameroun for continued use of the Bulu weather records; the European Commission (DG XII-contract TS3-CT93-0233, 1994–98) and the Swiss National Science Foundation (Grant 3100–066655, 2002–05) for financial support; University of Bern for investment of a project vehicle; E. Abeto, M. Ekawe, the late J. J. Green and X. M. van der Burgt for field assistance; P. S. Ashton, R. Borchert, J. Maley and S. Tucker for correspondence; and T. W. Henkel, S. J. Wright and a third anonymous reviewer for their valuable comments.

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Supplementary Material

The following supplementary material is available for this article online:

Item S1 Longer-term trends in climate at Korup and their correlations with SST

This material is available as part of the online article from [http://www/blackwell-synergy.com](http://www.blackwell-synergy.com).

Appendix I

Events in phenological activity of 150 *Microberlinia bisulcata* trees in Korup, Cameroon

Event	Dates		Number of trees active in period	Sum of scores over period	Mean weighted start time since 01.01.95 (yr) ^a	Relative advance or delay in first time (yr)
	Start	End				
Leaf fall						
1	16.12.95	27.02.96	150	455	1.14	+0.12
2	24.11.96	12.12.96	150	493	1.90	-0.12
3	11.12.97	12.01.98	150	460	3.01	-0.01
4	17.12.98	30.03.99	135	163	4.07	+0.05
5	27.12.99	24.01.00	141	153	4.99	-0.03
Leaf flush						
1	23.01.96	25.03.96	150	459	1.22	+0.15
2	24.11.96	12.12.96	150	412	1.95	-0.12
3	11.12.97	05.02.98	150	456	3.02	-0.05
4	20.01.99	06.05.99	134	292	4.14	+0.07
5	27.12.99	24.01.00	143	156	5.02	-0.05
Flowering						
1	26.01.95	24.02.95	141	366	0.07	-0.03
2	19.10.97	19.10.97	135	325	2.05	-0.05
3	16.03.98	14.05.98	128	266	3.21	+0.11
4	24.01.00	29.02.00	145	170	5.08	-0.02
Fruiting						
1	26.01.95	10.08.95	142	2076	0.15	+0.07
2	27.02.97	11.06.97	132	1112	2.23	-0.09
3	14.05.98	11.09.98	132	406	3.37	-0.02
4	29.02.00	02.08.00	95	405	5.29	+0.03
Seeding						
1	11.09.95	11.09.95	132	337	0.70	+0.01
2	31.07.97	27.08.97	124	274	2.65	-0.06
3	11.09.98	06.10.98	90	180	3.71	+0.02
4	06.07.00	12.10.00	94	113	5.74	+0.03

The start and end dates of recording of the event are indicated. Number of trees active are the maximum of trees active across the period of the event, and the sum of scores are the total of all trees \times months in the period (thus the sums can be $> 150 \times 3 = 450$ if the event lasted over several months). A more accurate definition of the timing of the event is given by the weighted mean start and end times of the active trees, and the relative advance or delay with respect to the mean of the four or five events. There was no masting in 1996 and 1999.

^aMean weighted end dates were very close to those of the start except for fruiting. For events 1–4 these were 0.60, 2.44, 3.51 and 5.56 yr, respectively.

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