Reproductive investment and seedling survival of the mast-fruiting rain forest tree, *Microberlinia bisulcata* A. chev.

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Abstract

In the southern part of Korup National Park, Cameroon, the mast fruiting tree *Microberlinia bisulcata* occurs as a codominant in groves of ectomycorrhizal Caesalpiniaceae within a mosaic of otherwise species-rich lowland rain forest. To estimate the amount of carbon and nutrients invested in reproduction during a mast fruiting event, and the consequential seed and seedling survival, three related field studies were made in 1995. These provided a complete seed and seedling budget for the cohort. Seed production was estimated by counting woody pods on the forest floor. Trees produced on average 26,000 (range 0–92,000) seeds/tree, with a dry mass of 16.6 kg/tree. Seeds were contained in woody pods of mass 307 kg/tree. Dry mass production of pods and seeds was 1034 kg ha^{-1}, equivalent to over half (55%) of annual leaf litterfall for this species, and contained 13% of the nitrogen and 21% of the phosphorus in annual leaf litterfall. Seed and young-seedling mortality was investigated with open quadrats and cages to exclude vertebrate predators, at two distances from the parent tree. The proportion of seeds on the forest floor which disappeared in the first 6 wk after dispersal was 84%, of which 26.5% was due to likely vertebrate removal, 36% to rotting, and 21.5% to other causes. Vertebrate predation was greater close to the stem than 5 m beyond the crown (41 vs 12% of seeds disappearing) where the seed shadow was less dense. Previous studies have demonstrated an association between mast years at Korup and high dry-season radiation before flowering, and have shown lower leaf-litterfall phosphorus concentrations following mast fruiting. The emerging hypothesis is that mast fruiting is primarily imposed by energy limitation for fruit production, but phosphorus supply and vertebrate predation are regulating factors. Recording the survival of naturally-regenerating *M. bisulcata* seedlings (6-wk stage) showed that 21% of seedlings survived to 31 mo. A simple three-stage recruitment model was constructed. Mortality rates were initially high and peaked again in each of the next two dry seasons, with smaller peaks in the two intervening wet seasons, these latter coinciding with annual troughs in radiation. The very poor recruitment of *M. bisulcata* trees in Korup, demonstrated in previous investigations, appears not to be due to a limitation in seed or young-seedling supply, but rather by factors operating at the established-seedling stage.

Introduction

Mast fruiting, the synchronous heavy fruiting of trees at intervals longer than a year, is shown by species in a wide range of temperate and tropical forest ecosystems. In tropical rain forests mast fruiting is best documented for the dipterocarp forests in South East Asia

(e.g. Janzen (1978) and Curran et al. (1999)), but the phenomenon also occurs to a more limited extent in rain forest in Africa and the neotropics (e.g. Hart (1995) and Forget (1992), Wheelwright (1986), Newbery et al. (1998)). A number of ideas have been put forward to explain mast fruiting. These may be summarized as two main non-exclusive hypotheses: (i)

the intermast period allows the build-up of resources (carbohydrates and mineral nutrients) necessary for the next fruiting event (Fenner 1991 Van Schaik et al. 1993) and (ii) mast fruiting may be an evolved predator (or pathogen) avoidance strategy, with seed/seedling predators or pathogens periodically satiated yet unable to maintain viable populations in the intermast interval (Silvertown 1980 Sork 1993 Wright et al. 1999). A wide variety of patterns of mast fruiting in terms of extent and timing have been recorded (Herrera et al. 1998), and it is likely that several causes operate interactively at different sites for different species.

Microberlinia bisulcata A. Chev. has a suite of characteristics which make it an interesting rain forest species in which to investigate the mechanisms controlling mast fruiting. It is among the very largest of African trees in terms of stature and biomass (Richards 1996), is strongly ectomycorrhizal (Newbery et al. 1988), and is seasonally deciduous (Chuyong et al. 2000). In the southern part of Korup National Park, Cameroon, *M. bisulcata* is restricted to groves scattered within a mosaic of otherwise species-rich lowland rain forest. Korup has a distinctive unimodal pattern of rainfall (mean of 5190 mm yr^{-1} for 1973–1995), with a single wet season peak (June-October) and a clearly-defined dry season (December-February) which varies slightly from year-to-year in intensity, start-date and duration. Within the groves *M. bisulcata* is codominant in the upper canopy with two other closely related ectomycorrhizal species, *Tetraberlinia bifoliolata* (Harms) Hauman and *Tetraberlinia moreliana* Aubrév. These three species locally form up to 70% of the basal area of all trees $\geqslant$ 30 cm gbh (girth at breast height). *M. bisulcata* has been the focus of long-term studies on forest structure, phenology, nutrient cycling and seedling dynamics in Korup (Newbery et al. (1988, 1997, 1998, 2000)).

Mast fruiting in Korup is a forest-wide phenomenon, occurring in the middle to late wet season, which includes several species within and outside the high-ectomycorrhizal (HEM-forest) groves (Newbery et al. 1998). Over a 9-yr period at Korup (1988–1997) there were three mast fruitings of *M. bisulcata* (1989, 1992, 1995), and since the time of the study reported here, there have been two more mastings (1997, 2000) (L. Zimmermann & D.M. Newbery, unpubl. data). *M. bisulcata* also flowered heavily in some inter-mast years (e.g. 1991, 1994), but did not go on to produce a measurable seed crop. Newbery et al. (1997) showed that the dry-season peak in radiation

was higher than average before each of the masting events (i.e. 1988–89, 1991–92, 1994–95). This suggested, by association, that the large trees at Korup required an intermast period of 2-3 yr to replenish their carbohydrate reserves and allow an effective fruiting.

The groves at Korup occur on sandy, well-drained, acidic soils with low phosphorus availability (Gartlan et al. 1986 Newbery et al. (1988, 1997)). Newbery et al. (1998) have demonstrated that the grove ectomycorrhizal species increase phosphorus concentrations in the surface fine-root layer of the soil. Following the 1989 masting of *M. bisulcata*, labile soil phosphorus concentrations declined in the inter-mast period much more steeply within the grove studied than outside of it (Newbery et al. 1997). A tentative hypothesis is that during mast fruiting, tree phosphorus reserves are also depleted, phosphorus return to the forest floor in leaf litter declines (as shown by Newbery et al. (1997)), and as a result soil phosphorus concentrations are temporarily lower than in years prior to masting. If a supra-annual phosphorus cycle is entrained with a climate-driven carbon one, ectomycorrhizas may be assisting in restocking the tree phosphorus for the next masting. The first of the three aims of the present work was therefore to estimate the investment of carbon and phosphorus involved in a masting of *M. bisulcata* by building a budget for the 1995 fruiting and comparing this investment in reproduction with that in leaves using litterfall data.

M. bisulcata has very poor regeneration within the high-ectomycorrhizal groves and, as far is known from extensive searching, none outside of them. Forests which have predominantly large individuals of species, and lack or have very few recruits, are a distinctive feature of the Central and West African lowland tropics (Aubréville (1938, 1971) Newbery and Gartlan 1996 Richards 1996). Large quantities of viable *M. bisulcata* seed are produced in mast years in Korup, and large numbers of young seedlings establish on the forest floor. These seedlings gradually die off over the next 2–5 yr such that, in terms of the relative numbers of germinants to survivors, recruitment into the sapling stages is extremely low compared with most other species (Newbery et al. (1998); unpubl. data). On average, only 5.0 ha^{-1} pole-sized (1–<10 cm dbh; diameter at breast height) individuals of *M. bisulcata* and 1.1 ha^{-1} small trees (10–<50 cm dbh) occurred within the main grove sampled by the 82.5-ha plot, for a corresponding 3.6 ha^{-1} large

trees ($\geqslant$ 50 cm dbh: upper range 225 cm, median *c.* 100 cm) (Newbery et al. 1998).

One possible reason for the apparently low recruitment of *M. bisulcata* within the grove may be density-dependant seed/seedling predation, herbivory, or pathogenic factors (*sensu* Janzen (1970) and Connell (1971)). Density-dependant mortality may reinforce selection for mast fruiting (Janzen 1978). The second aim, accordingly, was to estimate the proportion of seeds lost to likely vertebrate predation and pathogenic fungi in a mast year, and to measure their survival to the autotrophic seedling stage. An alternative reason for the lack of small stems to be borne in mind is the possibility that the pole-sized trees grow very fast with very high survival to compensate for their low densities, as has been suggested in related cases by Clark and Clark (1987) and Poorter et al. (1996). Results on this aspect (dealing with the later stage of sapling and pole growth) will be published elsewhere.

M. bisulcata flowers at the end of the dry season (January–March) and seed pods are mature by the mid-wet season (August–September). The hard, fibrous pods (typically *c.* 15 cm × 5 cm) are borne on the upper crown surface. Each pod contains 2–4 seeds. Pods are explosively dehiscent and this ballistic type of dispersal means that most seeds fall beneath the crown or close by. Some seeds may reach up to 60 m away if the data from Van der Burgt (1997) for *T. moreliana* (pods slightly smaller, seeds slightly heavier) are applied. Timing and extent of dispersal therefore play a major role in grove dynamics (Newbery et al. 1998).

To make a simple demographic model of seed and young seedlings of the 1995 *M. bisulcata* cohort, the third aim was to undertake a nursery germination trial and a field study of longer-term seedling survival. The model could then be tested by comparing the density of *M. bisulcata* seedlings in the field with that predicted from the stage-defined estimates.

Methods

Site

The study area was the eastern 25 ha (500 m × 500 m) of an 82.5-ha permanent enumeration plot which was established in 1991-93 on 'transect P' in Korup National Park, south-west Cameroon (5°1′ N, 8°52′ E). The plot was sited within a large grove of *M. bisulcata*, *T. bifoliolata* and *T. moreliana*, the three species forming 48.4% of the total basal area of trees with $\geqslant$ 50 cm dbh or diameter at breast height; (Newbery et al. 1998). Since almost all *M. bisulcata* trees in this size class were strongly buttressed, diameters were mostly measured with a relascope above the buttresses. The study area was divided into 10 subplots each of 100 m × 250 m. Further site details can be found in Gartlan et al. (1986) and Newbery et al. (1997, 1988).

Seed production

The woody pods of *M. bisulcata* allowed seed production to be measured indirectly, but reliably and relatively easily. At dehiscence, the woody valves fall beneath the tree. Unlike seeds, they are not consumed or removed by any animal and are resistant to decay for several months. The outlines of mature seeds are clearly visible in the fallen valves, so it is known how many mature seeds a pod contained. The valves were sampled with a tree-centred approach, as opposed to random positions within the forest plot. There was a total of 80 *M. bisulcata* trees ($\geqslant$ 50 cm dbh) in the 25-ha plot, with a minimum of three trees per subplot. Three trees were therefore selected at random within each subplot, which represented a 37.5% sample of all of the *M. bisulcata* trees. At each tree, three belt-transects 1 m in width were demarcated along strings radiating at random angles from the stem, and each transect was divided into 1-m² quadrats. Old valves from previous years were removed from the transects (18-21 July 1995), before any *M. bisulcata* seed fell in the year studied (1995). Every third 1-m² quadrat was selected outwards along these transects, beginning with the first, second and third quadrat from the stem in each of the three transects respectively. The transects extended beyond the edge of the crown, until no further pods were found. Where one crown of *M. bisulcata* abutted another, the transect was terminated where the crowns joined. In these cases, the assumption was made in calculations that any pods falling into quadrats from the adjacent tree were equivalent in number to those missed by not extending the quadrats under the crown of that neighbour.

The arrangement was such that each 1-m-wide annulus (concentric ring) around the tree was sampled by a quadrat. The median number of productive annuli per tree was 20 (range 8–27, excluding two trees which did not produce seed in 1995). The total number of valves falling into each quadrat was counted

and the number of mature seed positions in each valve was recorded. To calculate a total seed production for every tree, the total number of seed positions in each 1-m^2 quadrat was divided by two — since there were two valves for each pod — and multiplied by the area of the annulus it sampled. The annuli were summed to give a total seed production for each tree. Seed began to fall in mid-August 1995, and two counts of the pods were made on 4–6 September and again on 25–27 October 1995 after all the seed had fallen.

To measure the mean dry mass of seeds, one *M. bisulcata* tree was selected at random within each subplot and the nearest 10 seeds to a random point beneath the crown collected at the time of maximum seed fall. Seeds were dried at 80 °C and weighed to ± 0.01 g. The valves from one random quadrat at each tree were collected and their dry mass measured. Per-tree seed production estimates were converted to an area basis by multiplying by the number of trees in the 25-ha plot.

The nutrient concentrations of seed coat, endosperm, and valve were measured. Two samples of bulked seed coat, the endosperms of 10 seeds, and subsamples from 10 valves were analysed. Samples were milled in a steel ball-mill, and subsamples wet-ashed in a mix of H_2SO_4 and H_2O_2 with a Se catalyst (endosperm, 300 mg; valve, 600 mg; coat, 1.5 g). Nitrogen was analysed by the modified Bertholet reaction (dialysis) and phosphorus by the molybdenum blue reaction, both colorimetrically with an auto-analyser (Skalar Analytical B.V., Breda, Netherlands). Nutrient concentrations were multiplied by dry mass to give the nutrient content of *M. bisulcata* seeds and pods produced.

Post-dispersal seed predation experiment

There were two treatments in the seed predation experiment, each with two levels, in a factorial arrangement; distance to parent tree (near and far), and cages (open and caged to exclude vertebrate seed predators). Treatments were replicated once at a randomly selected *M. bisulcata* tree (≥ 50 cm dbh) within each of the 10 subplots. Trees already selected for the seed production study were excluded. This was equivalent to a randomised block design where *M. bisulcata* trees were 'blocks' and the 2 × 2 factorial arrangement was randomised within each block. Near quadrats were 5 m from the stem and far quadrats 5 m beyond the edge of the crown, at random angles from the stem. Positioning of far quadrats under neighbour-

ing *M. bisulcata* crowns was avoided. Open quadrats were each covered with a square (1.25 m × 1.25 m) of nursery shade netting raised 1.5 m from the ground to prevent seed falling into the quadrats during the experiment. Cages (40-cm cubic) to exclude vertebrate predators were constructed of 4-mm galvanised wire mesh. A 20-cm flap at the bottom edge of each cage was turned outwards and buried to prevent animals burrowing under the wire. Care was taken not to disturb the forest floor within cages.

At the peak of seed fall of *M. bisulcata* (28 August 1995), 10 sound seeds (i.e. those with no obvious external defects) were placed directly onto the undisturbed forest floor in each of the quadrats, arranged in a circle of radius 10 cm. This density (64.1 × 10^3 seeds ha^{-1}) was in the same order of magnitude as the natural seed fall density (83.5 × 10^3 seeds ha^{-1}; Table 1). The seeds were observed on three subsequent occasions (7 and 20 September, and 19 October 1995) and scored as present or absent for the following non-exclusive categories: germinated, rotten, evidence of white fungus, seedling (true leaves present). The data were proportions and therefore analysed by general linear modelling (binomial error distribution: GENSTAT 5.32, Payne (1993)). Before testing effects of the fixed treatments, deviance due to plots was first removed in each analysis.

Seed germination

The germination rate of *M. bisulcata* seed was tested under controlled conditions outside the forest. Seed from a randomly located *M. bisulcata* tree in each of the 10 subplots was tested. At the height of seed fall (late-August 1995), the closest 20 seeds to a random point beneath the crown were collected. (These seeds would not necessarily all have come from the nearest parent as ballistic dispersal could have brought seed from several neighbours to the sampled location.) The seeds were laid on moist soil, under neutral shade at 12% transmission of PAR, and germination was recorded at weekly intervals for 1 mo. From nursery experiments at Mana Bridge, near Korup (Green and Newbery 2001a) it was shown that light spectral quality was only very slightly altered by the black nylon mesh used for shading.

Wild seedling cohort

To monitor the survival of wild *M. bisulcata* seedlings of the 1995 cohort, four 2-m x 2-m quadrats were de-

Table 1. Seed production estimates for *M. bisulcata* in the mast year of 1995 on transect P, Korup National Park, Cameroon. The number with standard error in parenthesis, dry mass, nutrient concentration and content of seeds and woody pods produced per tree and per hectare within the study plot are shown. Leaf litter data for *M. bisulcata* are from Chuyong (1994), and are for collections from July 1990 to June 1992 (see text). Seed and pod mass and nutrient contents are expressed relative to *M. bisulcata* leaf litter.

| | | Plant part | | | | | Ratios | |
| | | Seed | | Pod | | Leaf | Seed/leaf | Pod/leaf |
		(/tree)	(ha^{-1})	(/tree)	(ha^{-1})	(ha^{-1} yr^{-1})		
Number	(×10^3)	26.1	83.5	12.2	38.9	–	–	–
		(4.4)	(14.0)	(1.8)	(5.9)			
Mass	(kg)	16.6	53.1	306.6	981.1	1880	0.028	0.522
Concentration	N (mg g^{-1})	14.5	–	3.8	–	18.5	–	–
	P (mg g^{-1})	1.80	–	0.24	–	0.79	–	–
Content	N (kg)	0.24	0.77	1.19	3.80	34.7	0.022	0.109
	P (kg)	0.030	0.095	0.072	0.232	1.48	0.064	0.156

marcated within each subplot, prior to the 1995 mast fruiting. Quadrats were positioned in areas where *M. bisulcata* seedlings grew, with the aim of sampling enough young individuals overall, and including several more quadrats with higher densities. These new recruits of the 1995 cohort were tagged, using uniquely-numbered aluminium tags, on 19 October 1995, this being the last day of sampling for the seed predation experiment. Thus this cohort was a sample of seedlings of similar age and stage of development as seedlings surviving in the experiment. Seedling height, number of leaves and deaths were recorded at monthly intervals until December 1997 and then on a final occasion in April 1998. Daily mortality rates (Dq_x) were calculated by $Dq_x = (l_x - l_{x+1})/(D_{x, x+1})$ (Silvertown 1987), where l_x is the proportion surviving to day x and $D_{x, x+1}$ is the length of the interval in days.

Light levels in the seedling quadrats were measured in April 1996 and April 1998. PAR (photosynthetic active radiation) and R:FR (660–730 nm red–far red ratio) measurements were taken on the forest floor concurrently with an above-canopy PAR sensor 0.5 km to the east. Three PAR and one R:FR sensors (Skye Instruments, Wales) were mounted on a rotating beam (radius 1.2 m) at a height of 70 cm and 16 sets of spot readings taken in each full rotation of the beam Green and Newbery (2001a, 2001b) give more details of this method.). The mean of spot readings over the quadrat was expressed as a percentage of the above-canopy PAR for the recording period. Quadrats were visited in random order and each was measured in morning, midday and afternoon periods over 3 days.

Rainfall and global radiation data were obtained from the Bulu Station of Pamol Plantations, 10 km to the SE of transect P. Radiation was measured there using a Gunn-Bellani evaporimeter and the volume of water evaporated was converted to J m^{-2} using the calibration of Pereira (1959). Rainfall and radiation data were expressed as monthly (30-day) running totals, such that each daily value is the total of that day and the previous 29 days.

Seed and seedling budget of 1995 cohort

The seed production, seed predation and wild seedling survival data were combined to produce a seed and seedling population estimate for the 1995 *M. bisulcata* cohort. The seed production estimate provides the input of propagules in the 1995 cohort (August/September 1995). The uncaged treatment in the seed predation experiment (mean of near and far quadrats) estimates the proportion of these propagules which survived to produce young seedlings with true leaves (19 October 1995). The wild *M. bisulcata* quadrats provide a sample of seedlings at this age and stage of development, for which survival and growth were monitored from 19 October 1995 to 27 April 1998. The proportion of seeds and seedlings surviving in each sample was calculated as the mean number of the original cohort surviving in each quadrat. That is, each quadrat was given an equal weighting in the calculation of the average, rather than each seed or seedling, as the quadrat is the appropriate area unit. Combining the three estimates in this way, a population estimate for seeds and seedlings of the 1995 mast cohort was produced, from August 1995 to April 1998.

Results

Seed production

The mean seed production estimate (± SE) for *M. bisulcata* trees in the 1995 mast year (n = 30) was 26,100 ± 4,400 seeds/tree (Table 1). Two trees of the sample of 30 did not fruit during this mast; the range in seed production for fruiting trees was 3,000 – 92,000 seeds/tree. There were 80 *M. bisulcata* trees ⩾ 50 cm dbh in the 25-ha study plot and thus seed production, on an areal basis, was estimated to be 83,500 seeds ha^{-1}. The average number of seeds in each pod was 2.04 ± 0.08 (SE, n = 28 trees; range 0–6). There were no significant correlations between tree dbh (⩾ 50 cm; range 52.5–160.5, median 96.2 cm) and seed production (r = 0.25, df = 26, P > 0.05), or between dbh and the number of seeds per pod (r = 0.34, df = 26, P > 0.05). There was, however, a significant positive correlation (r = 0.50, df = 26, P = 0.007) between total seed production of trees and the number of seeds per pod, suggesting that trees achieving higher production did so in part by increasing the number of seeds in each pod.

The mean (± SE) mass of *M. bisulcata* seeds (n = 110) was 0.64 ± 0.02 g dry weight, of which, on average, 79% was endosperm and 21% was seed coat. The mean mass of valves (half-pods) was 12.6 ± 0.2 g (n = 188). The average mass of a pod at dehiscence, given two valves and the average of 2.04 seeds/pod, was thus 26.5 g, of which 25.2 g was pod and 1.3 g was seed.

Seed and pod nitrogen and phosphorus concentrations are given in Table 1. Seed and pod production were compared with annual leaf litterfall of *M. bisulcata* within the same grove, estimated before the present study (July 1990 – June 1992; Chuyong (1994) and Chuyong et al. (2000)). Litterfall nutrient concentrations were available for bulked wet (April to November) and dry (December to March) season samples. Yearly mean nutrient concentrations were calculated by weighting for the mass of litterfall in each month. The total mass of seeds produced was relatively small when compared with leaf litterfall (Table 1), equivalent to less than 3% in terms of mass (0.028). The total mass of pods produced in this mast year, however, was equivalent to a little more than half of the dry mass of annual leaf litterfall (0.52).

The nitrogen concentration in seeds was lower than that in *M. bisulcata* leaf litter, but of the same order of magnitude (seed:leaf = 0.78). Whereas, the phosphorus concentration in seeds was considerably higher than in leaf litter (seed:leaf = 2.28). The total amount of nitrogen in seeds in the mast year was relatively small compared with the annual nitrogen content of leaf litterfall (0.022). Taken together, seeds and pods were equivalent to 55% of annual leaf litterfall mass, and contained an equivalent of 13% of the nitrogen and 21% of the phosphorus in annual leaf litterfall.

Germination rates

M. bisulcata seed germination rates were obtained in the forest from the caged treatment of the seed predation experiment, and also outside the forest under neutral shade. Only this caged treatment was used for the germination test since it was not affected by vertebrate removal of seeds. Germination rates in the forest test were high (mean 97%, range 90–100%) and germination was rapid with 98% of the germination that occurred during the experiment having begun within 10 days (by 7 September 1995) and 100% within 23 days (by 20 September 1995). Near and far treatments had no significant effect on the proportion of seeds germinating in the cages (Table 2, GLM, deviance change = 0.73, df = 1, P > 0.05). Rates for near and far caged treatments were therefore combined for each *M. bisulcata* tree to allow a comparison with germination outside the forest. This showed no difference between germination rates on the forest floor and outside the forest on moist soil under neutral shade (97.0 and 94.5% respectively, change in deviance = 1.56, df = 1, P > 0.05).

Seed predation

By the final date of observation in the seed predation experiment (19 October 1995), all remaining *M. bisulcata* seeds which had failed to germinate were dead and had rotted, and all surviving germinated seeds had developed as seedlings with the first true leaves expanded. The seed predation experiment was thus deemed to have finished because the fate of all seeds was known.

The proportion of seeds surviving to produce young seedlings (after 42 days) was not significantly affected by distance to the parent tree (GLM, deviance change = 1.06, df = 1, P > 0.05; Table 2). The effect of enclosure had a highly significant effect on the number of seeds surviving to young seedling age (GLM, deviance change = 37.9, df = 1, P < 0.001).

Table 2. The post-dispersal fate of seeds of *M. bisulcata* on the forest floor of lowland tropical rain forest at Korup National Park, Cameroon. The mean proportion (and range, n = 10 trees) of 10 seeds germinating, surviving to produce seedlings, rotting, and other deaths over 42 days. All surviving propagules had produced seedlings with fully expanded leaves by this time. Near quadrats were 5 m from the stem and far quadrats were 5 m beyond the edge of the crown. Cages were of 4-mm mesh and excluded vertebrate seed predators.

	Open		Caged	
	Near	Far	Near	Far
Germination	0.94 (0.6–1.0)	0.89 (0.4–1.0)	0.96 (0.8–1.0)	0.98 (0.9–1.0)
Post-germination				
Survival to seedling	0.11 (0–0.4)	0.21 (0–0.5)	0.52 (0–1.0)	0.33 (0.1–0.6)
Rotten	0.42 (0–0.8)	0.30 (0–1.0)	0.23 (0–0.8)	0.27 (0–0.9)
Other causes	0.47 (0.1–1.0)	0.49 (0–1.0)	0.25 (0–0.5)	0.40 (0–0.8)

That is, vertebrate predation (or predation by animals unable to pass through a 4-mm mesh) did have a significant effect on the survival of *M. bisulcata* seeds in this mast year. There was also a significant interaction between distance and cage (GLM, deviance change = 11.13, df = 1, P < 0.001), such that the difference between caged and open treatments was much greater near to the stem (0.41), than far away (0.12, Table 2). Therefore, vertebrate predation was greater close to the stem, than beyond the edge of the crown. The mean difference in the proportion of surviving propagules between caged and uncaged treatments at the 20 positions is that component of mortality which can be attributed to vertebrates, and this was 26.5% (range 0 to 100%). One *M. bisulcata* tree of the 10 selected in the predation experiment did not produce seed in 1995 and all uncaged seeds placed at this location were removed by the first observation, 10 days later.

A large proportion of seeds of *M. bisulcata* rotted after germination and as young seedlings. White coralloid fruiting bodies of an unidentified (probably pathogenic) fungus were frequently observed on seeds and young seedlings of *M. bisulcata*, and also on the seeds and seedlings of *T. bifoliolata* and *T. moreliana*. Overall, this fungus was recorded on 74.5% of seeds and seedlings recorded as rotten (Table 2), although this may have been an underestimate because the fruiting bodies were delicate and easily destroyed by the frequent heavy rains at that time of year (August–October).

The caged treatments were used to test for effects of plot and distance on the number of seeds rotting (and those rotting with white fungus), as these treatments were not influenced by seed removal. (In the open treatment seeds may have been removed before they rotted). There were no significant effects of distance to parent tree for either variable (GLM, rotten: deviance change = 0.52; with white fungus: deviance change = 1.10; df = 1, P > 0.05, in both cases). The open treatment provided a combined measure of the relative proportions of seeds removed by vertebrates, those rotting, and those due to unaccountable deaths in the wild population. The mean percentage of mortality in the 20 open quadrats was 84.0% (range 50 to 100%), of which it was estimated that 26.5% was due to vertebrate removal, 36.0% (range 0 to 100%) was recorded as rotting and 21.5% (range 0 to 80%) consisted of unaccounted deaths. The unaccounted deaths may have included non-viable (non-germinating) seed, insect attack and other factors not specifically recorded.

Although PAR readings were not taken in the field, from the size of the wire mesh an estimated 66% PAR was transmitted in the cage treatment, and from nursery experiments (Green and Newbery 2001a), the plastic shading mesh transmitted 60% PAR in the open treatment. Since the latter had open sides the two treatments thus had very similar light regimes. In the 52 days of the predation experiment seedlings would not have reached the fully autotrophic stage to be yet totally reliant on PAR.

Wild seedling survival

There were 267 new recruits in total (mean 6.7 per quadrat, median 4; but only five quadrats with ⩾ 20 seedlings and seven with ⩾ 10) of *M. bisulcata* in the cohort tagged on 19 October 1995. These recruits had all established since the previous census of quadrats on 7 September 1995. Two quadrats of the 40 had no new recruits. Of these 267 seedlings, 57 (21.3%) were still alive at the last measurement, i.e. after 31 mo (27 April 1998). On a per-quadrat basis the mean
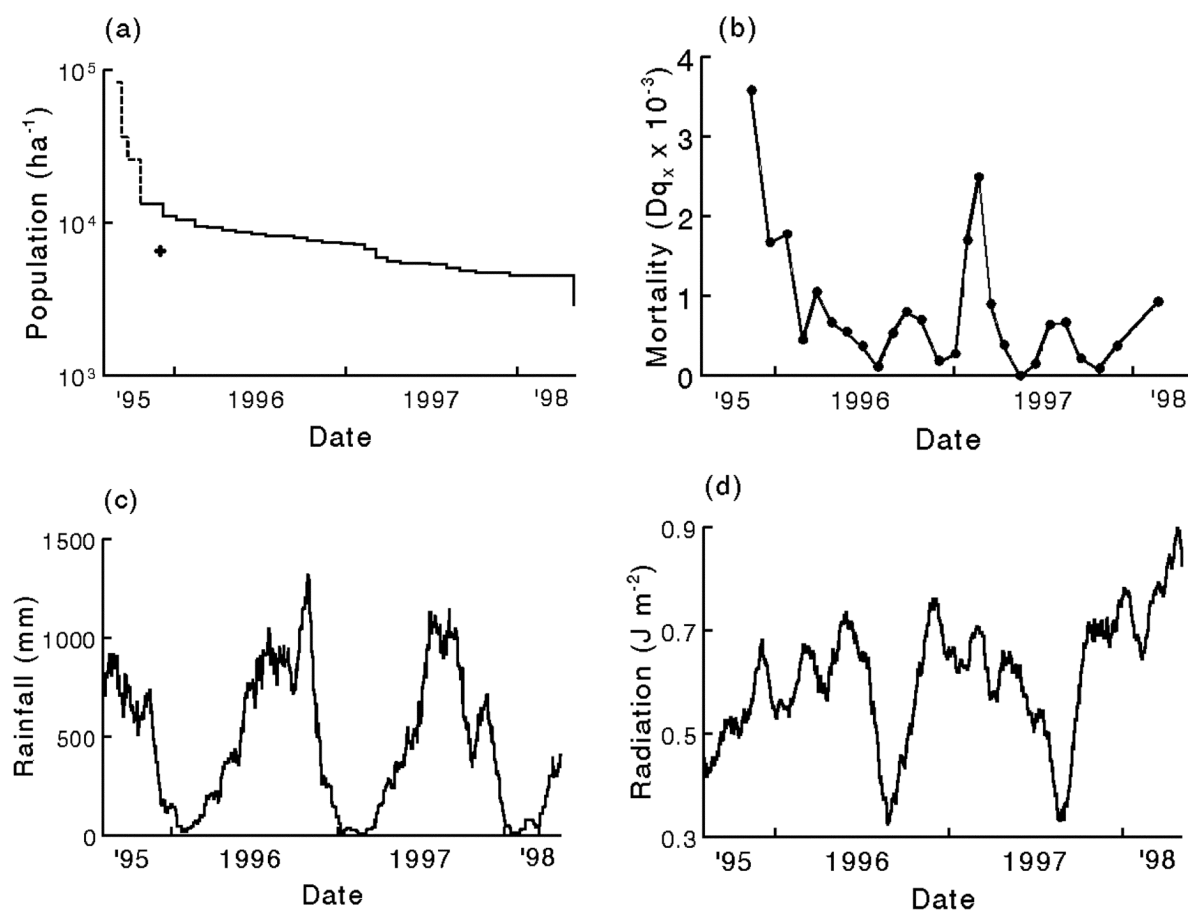
Figure 1. Survivorship of the 1995 mast year seed and seedling cohort of *M. bisulcata* and associated climatic variables. (a) Change in the population of seeds and seedlings. The estimate of seed production provided the starting point, survival of seeds to seedlings in open quadrats are shown by the dotted line, and survival of wild seedlings onwards by the solid line. **+** indicates an independent measure of the density of seedlings of the cohort in the study plot by Newbery et al. (1998); (b) daily mortality rates for the seedling cohort (Dq_x, Silvertown (1987), see text); (c) monthly (30-day) running totals of rainfall; (d) monthly running totals of global radiation.

survival was 22.3%. Seven seedlings (2.6%) were recorded as being cut at ground level by animals. Mortality rates of *M. bisulcata* were initially high, remained high during the first dry season, and peaked again in the subsequent two dry seasons (Figure 1). Smaller peaks in mortality occurred during the two wet seasons, coinciding with the troughs in radiation.

There were no significant relationships between percent survival in each quadrat and the mean percent PAR transmission and R:FR in the quadrats (P = 0.63 and 0.80 respectively). To test whether, mortality of very young seedlings obscured a relationship between survival and PAR or R:FR; the number of final survivors was expressed as a percentage of those in each sample, and these percentages tested. There were still no significant relationships between seedling survival

and light level (all P > 0.05). It is important, though, to consider the range of light levels in these quadrats (Figure 2). Few quadrats were in the more lighted conditions, with only three having > 3% above-canopy PAR (based on means of April 1996 and April 1998 light measurements). An independent survey of general forest floor light levels within the grove was conducted (J.J. Green & D.M. Newbery; unpubl. data). Light levels were measured in the same manner as in the present study: in five (4-m^2) quadrats along each of five randomly-positioned and orientated 10-m transects within each subplot (n = 250 quadrats, Figure 2). The mean PAR in the seedling quadrats (1.86%) was significantly different from the mean PAR in the general forest survey (1.14%, t = −2.74, df = 63, P = 0.008; χ^2 = 43.6, df = 2, P < 0.001). The
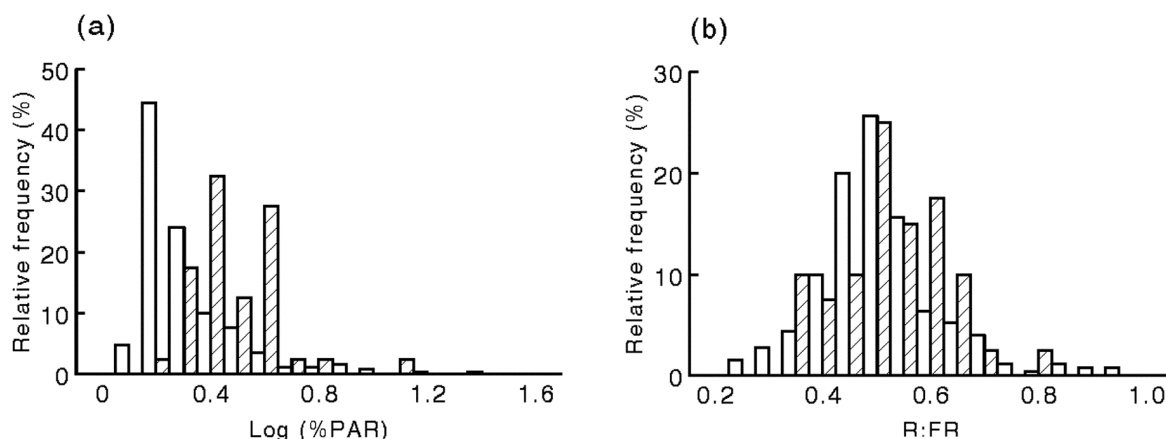
Figure 2. Frequency distributions of: (a) per cent transmission of above-canopy photosynthetically active radiation (PAR), and (b) ratio of red (660 nm) to far-red (730 nm) light in 4-m^2 quadrats on the forest floor in rain forest in Korup National Park, Cameroon. Hollow bars are a survey of general forest floor light levels (n = 250 quadrats, from Green and Newbery (2001b)) and shaded bars are quadrats in which *M. bisulcata* seedling survival was monitored in this study (n = 40 quadrats).

corresponding mean R:FR ratios were very similar, however (0.49 vs. 0.48).

The proportion of the seedling cohort (as of 19 October 1995), surviving to 27 April 1998, was weakly negatively, but not significantly, dependent on either the number in the quadrat (range 0–29), the number of older existing seedlings (0–10), nor these two counts combined (0–33) per quadrat (GLM with binomial error and logit transformation, n = 40; change in deviance 2.40, 1.39 and 1.42 respectively, df = 1, P > 0.10). This indicated that survival was not density-dependent, and that the per-quadrat mean survival value would not have been unduely weighted by the fates of isolated seedlings.

M. bisulcata *seed and seedling population*

The seed production, seed predation and wild seedling survival data were combined to produce a population estimate for the 1995 mast year cohort until April 1998 (Figure 1). It was estimated that of 83,500 seeds produced per hectare, 12,960 (16%) would survive to produce young seedlings with true leaves. And of these, 2,890 ha^{-1} (22.3%) would have survived the subsequent two dry seasons (reaching April 1998). The population was 3.5% of the seeds produced.

Discussion

Investment in fruiting in mast years

The two years recording of leaf litterfall by Chuyong et al. (2000) were in an intermast interval (1990–1991). In an earlier study, Newbery et al. (1997) also recorded leaf litterfall from end 1988 to early 1991, but for all species together in the same 'HEM forest' (forest with high abundances of ectomycorrhizal trees) (Fig. 10, *loc. cit.*). The collection procedures differed so the two data sets are not exactly comparable. However, the ratio of leaf litterfall in the known 1989 mast year to that in the following 1990 non-mast year was calculated to be 0.74:1.0. Since *M. bisulcata* constituted 39% of the total litterfall in HEM forest (at least in 1990 and 1991 from Chuyong et al. (2000)), and it can be assumed that *M. bisulcata* litterfall followed the same year-to-year pattern as the whole bulked sample, the estimate of 1880 kg ha^{-1} yr^{-1} in Table 1 might be tentatively corrected as a proportion to 1392 kg ha^{-1} yr^{-1}. In which case the ratio of reproductive investment to leafing in the mast year rises *c.* 74%.

In absolute and relative terms in relation to leaf litterfall, the allocation to mast fruiting in *M. bisulcata* is high for trees. Proctor (1984) provides data for flower/fruit fall and for leaf litterfall for 13 different sites in Africa, S. America and SE Asia with a mean of 0.583 t ha^{-1} yr^{-1} and 5.96 t ha^{-1} yr^{-1} respectively. (In most litterfall studies all reproductive parts have been recorded together and reported as one fraction.)

In none of these studies was masting specifically mentioned. In addition, Lugo and Frangi (1993) reported 0.6 t ha^{-1} yr^{-1} fruitfall for a leaf litterfall of 5.5 t ha^{-1} yr^{-1} taken from Proctor (1984) tables, and Dunham (1990) for a drier African woodland had a fruit fall of 0.25 t ha^{-1} yr^{-1} for which Proctor (1984) has an estimated matching leaf fall of 2.7 t ha^{-1} yr^{-1}. Taking these 15 pairs of estimates together gives a pantropical baseline annual fruit and flower fall which is *c.* 9.8% of leaf litterfall. Fruitfall alone would be slightly less. As Chapman et al. (1994) have pointed out though, the mass of fruit trapped underestimates fruit production as no account is made of removal by animals in the tree. Nevertheless, the investment in fruiting in a mast year by *M. bisulcata* is minimally *c.* 5.6-fold greater than an 'average baseline' tropical forest, and correcting for likely leaf litterfall in a mast year it is *c.* 7.6-fold higher. If the mast-year fruit production estimate for *M. bisulcata* is divided by the mean intermast interval of 2.75 yr then the 55% minimum (upward 74%) in the 1995 mast year becomes 20.0% (resp. 27%) on an annual basis, still 2–3 fold higher than the baseline value.

Estimates of seed and fruit production in mast-fruiting species are infrequent in the literature. For *Fagus sylvatica* in Denmark, Nielsen (1977) recorded 121 and 196 g m^{-2} yr^{-1} (nuts plus cupules) in two mast years (1969 and 1974), which was 12 and 21% respectively of the leaf litterfall. In three other sources cited by Nielsen (1977), beech fruit fall ranged from 143 to 200 g m^{-2} yr^{-1} in 'good' years.

Sork et al. (1993) estimated that black and white oaks (*Quercus velutina* and *Q. alba*) produced maximally 3200 and 2150 acorns per tree respectively in mast years. With corresponding mean acorn weights of 1.75 and 3.28 g (Sork 1993), this leads to 5.60 and 7.05 kg of acorns per tree (our calculations). If it is assumed, maximally, that tree crowns covered the ground completely then using mean projected canopy area values of Sork et al. (1993), acorn production translates to 1057 and 1175 kg ha^{-1} yr^{-1}, or on average 1.12 t ha^{-1} yr^{-1}. For the Himalayan oaks *(Q. leucotrichophora* and *Q. floribunda*), Singh et al. (1990) reported 3.5 t ha^{-1} yr^{-1} in an exceptionally good mast year compared with a 'normal' mast year of 2.5 t ha^{-1} yr^{-1}. Leaf litter fall on average over several intermast and mast years was 4.34 t ha^{-1} yr^{-1} which leads, for normal mast years, to fruit allocation being 57% of leaf production, a value comparable to *M. bisulcata*.

Dipterocarps in West Kalimantan produced 156–196 kg ha^{-1} wk^{-1} of fruits over the 5–6-wk mast fruiting periods of 1987 and 1991, respectively (Curran et al. 1999) Curran and Leighton (2000). These data translate to 25–30 kg ha^{-1} wk^{-1} over the year, or 1.30–1.56 t ha^{-1} yr^{-1} (mean 1.43 t ha^{-1} yr^{-1}). Drawing again on the data in Proctor (1984) leaf litter fall in SE Asian dipterocarp forests is on average 6.05 t ha^{-1} yr^{-1}, giving a relative investment in mast fruiting of 23.6%.

Altogether these estimates suggest that strongly masting species invest dry mass in the order of 20–60% of that allocated to leaves. This must have a substantial effect on tree internal carbon balance. It is remarkable to note again from Newbery et al. (1998) that these strongly masting species are all ectomycorrhizal.

Carbon limitation to masting and role of nutrients

The dry mass of seeds and pods produced by *M. bisulcata* in the mast year was equivalent to over half the annual dry mass of leaf litterfall produced in two non-mast years (July 1990 – June 1992). This large photosynthate demand supports the suggestion put forward by Newbery et al. (1998) that the large caesalp trees require an intermast period to replenish their carbohydrate reserves for effective fruiting. It is important to recognise that the fruiting *M. bisulcata* trees are very large (the mode of nearly-symmetrical dbh distribution of trees >50 cm was 90–100 cm, Newbery et al. (1998)) and large trees suffer the greatest respiratory loads (Kozlowski et al. 1991). In addition, *M. bisulcata* is expected to support a large mass of ectomycorrhizal fungi (Newbery et al. 1988).

There is increasing evidence that the growth of rain forest canopy trees may be limited by radiation in some parts of the tropics (Van Schaik et al. 1993 Wright and van Schaik 1994). For example, photosynthetic measurements show that canopy leaves generally operate below saturation (Doley et al. 1987 Oberbauer and Strain 1986) and productivity can be higher during sunny periods than under cloudy (wet season) conditions (Longino 1986 Van Schaik 1986). At Korup, there was a correspondence between the three recorded mast years and dry-season radiation (Newbery et al. 1998). Similarly it has been suggested that accumulation of sunshine hours was the underlying cause of mast fruiting in SE Asian dipterocarps (Wycherley 1973 Ng 1976). Further evidence, from a different ecosystem, of mast fruiting being energy

limited comes from Sork (1993) who found a positive correlation between intermast interval and seed size in 18 temperate oak species. This suggests that large-seeded species require an intermast period to build up reserves (Fenner 1991). In the dry season, *M. bisulcata* releafs soon after the old leaves are shed and this is when radiation levels are still high (Newbery et al. 1998).

The nitrogen and phosphorus content of the fruit produced by *M. bisulcata* in the mast year was equivalent to 13% and 21% of the annual leaf litter loss in two non-mast years (July 1990 – June 1992). Leaf loss is only one nutrient sink to the tree, and there may be losses of equivalent magnitude below-ground through fine-root turnover (Vitousek and Sanford 1986 Vogt et al. 1986 Green 1992). The nutrient demands of fruit production are not insignificant, but without a complete internal and external nutrient budget of *M. bisulcata* trees it is not possible to conclude whether nitrogen or phosphorus availability are limiting factors in fruiting frequency. Unfortunately, we do not have an estimate of the mineral nutrient cost of flowering in 1995. Chuyong (1994) recorded a large peak in phosphorus content of reproductive litter within the grove in the 1992 mast flowering, but did not separate flowers of *M. bisulcata* from those of other species. In Guyana, Zagt (1997) recorded 0.7 kg ha^{-1} yr^{-1} phosphorus input in flower fall for the mass-flowering *Dicymbe altonii* (Caesalpiniaceae) compared with 0.5 kg ha^{-1} yr^{-1} returned in the leaf litter of this species, indicating that floral parts can, exceptionally, have a significant effect on phosphorus cycling. However, *M. bisulcata* flowered in some intermast years (e.g. 1991 and 1994), and then aborted fruiting, which suggests that it is not flowering which limits the frequency of mast fruiting.

Newbery et al. (1997) found that phosphorus concentrations and phosphorus inputs in litterfall in the ectomycorrhizal grove were lower following mast fruiting in 1990, than in either 1989 or 1991. They suggested that the phosphorus reserves of the large caesalps may have been depleted by the nutrient demands for fruit production and hence the litterfall phosphorus concentration was reduced. However, litterfall data specifically for *M. bisulcata* that span a mast year do not exist and therefore it is not possible to say quantitatively whether the phosphorus contained in fruits accounted for a measured reduction in litter concentration. That trees have to find *c.* 21% of phosphorus annually lost in litterfall, it seems reasonable that a portion of this may be met by internal cy-

cling within the tree and that it may have a cummulative effect on litterfall concentrations in intermast years (and hence on soil phosphorus labile pools). In summary, our findings support the postulated pattern put forward by Newbery et al. (1998) that fruiting is primarily limited by carbohydrate availability, with phosphorus as a secondary and possibly regulating factor.

Germination and pathogens

Germination of *M. bisulcata* seed produced in the mast year was uniformly high, occurred rapidly after seed fall, and showed no difference between caged areas on the forest floor (97%) and controlled conditions outside the forest (94.5%). Few dispersed seeds were damaged or non-viable and it appeared that predispersal insect predation was low. Pathogenic fungal attack (damping-off), however, was evident after germination in over a third (36%) of the seeds and young seedlings and was the most common cause of mortality recorded. High rates of young seedling mortality from pathogenic fungi have been recorded in other tropical rain forests, for example, in the neotropical caesalp *Dicymbe altsonii*, Zagt (1997) recorded a level of 83%; and in some cases distance-dependence from parent trees has been shown (e.g. Augspurger (1983, 1984)).

The pathogenic attack on *M. bisulcata* is important because it occurred rapidly after dispersal on germinating seeds and appeared to spread to adjacent young seedlings. That seeds and young seedlings of *T. moreliana* and *T. bifoliolata* were also attacked by the white fungus suggests that the sequence of seed fall amongst the codominant tree species (see Newbery et al. (1998)) may be important for escape from fungal attack. This aspect of the seed ecology of *M. bisulcata* deserves further study.

Effect of predation (seed removal)

Since small tight clumps of emerging seedlings have not been observed it is assumed that there was little or no caching of seeds and that seed disappearance was largely due to predation (i.e. loss from the population). Furthermore, it would seem *a priori* unlikely that burial in rodent caches is important for *M. bisulcata* dispersal since germination is epigeal (fleshy cotyledons raised above-ground), and moistened seeds have no dormancy, germinating within a few days. Vertebrate predation accounted for a quarter of

all seeds produced in this mast year and a greater proportion of seeds were removed close to the stem, where the seed shadow was denser (Green and Newbery 2001b). This suggests that a seed is more likely to escape vertebrate predation in a mast year, if it is thrown (dispersed) further from the tree, although overall, when other factors were included, survival to the seedling stage was not significantly higher further from the tree.

A large body of research has been dedicated to testing the predictions of the Janzen-Connell model of density/distance-dependant attack on seeds and seedlings (Lieberman 1996). No consensus has been reached, although invertebrate predation conforms more frequently to the model than vertebrate predation (Hammond and Brown 1998). This may be because vertebrate feeding patterns tend to be influenced by the relative abundance of a wider range of resources than invertebrates (Schupp 1990 Forget 1993) and it is perhaps also not surprising that density-dependence has not been universally found given the diversity of phenologies, adult densities, seed crops and predator communities tested. At Korup, supra-annual synchronous fruiting, a high density of adults, a large seed crop and limited dispersal all occurred. If trees had fruited asynchronously, vertebrate losses would probably have been higher than those recorded in 1995 (Janzen 1978 Hart 1995), but this cannot be tested. Given that vertebrate predation of *M. bisulcata* seed was relatively high in a mast year, vertebrates may select against asynchronously fruiting trees once a supra-annual pattern has been initiated (Harper 1977 Waller 1993).

Seedling mortality

The rate of mortality of seeds and young seedlings of *M. bisulcata* was initially high (Figure 1), and only 16% of propagules survived to produce a seedling aged 6 wk. High rates of early seedling mortality have been recorded in a number of studies, for example Garwood (1982) recorded a loss of 67% of newly germinated seedlings (species pooled) during the first 2 mo. Given the very high mortality during and immediately after germination (Lieberman 1996), the age at which rain forest tree seedlings are first censused will have a large influence on estimates of percentage mortality, and on seedling half-life where survivorship is not log-linear (e.g. Li et al. (1996)).

Mortality of young *M. bisulcata* seedlings remained high through the first dry season, which they

entered aged *c*. 5 mo (Figure 1), and peaked again in the subsequent two dry seasons. In addition, two smaller peaks in seedling mortality coincided with periods of low radiation in the two wet seasons. This pattern of seedling mortality is different to that found for a mixed-species cohort within the grove from the 1992 mast year (Newbery et al. 1998), where there was no peak of seedling mortality in the second dry season. The 1993/94 dry season at Korup, however, was not particularly dry (Newbery et al. 1998), unlike that in 1996/97 (Figure 1), which may explain the absence of a second peak in mortality in the earlier study. An alternative explanation is that *M. bisulcata* seedlings (of the 1995 cohort), were more susceptible to subsequent dry seasons after their first year than a mixed species cohort from the same forest. This suggests that drought intolerance could be a factor in the lack of recruitment of *M. bisulcata* beyond seedling stages within the ectomycorrhizal grove. The lack of density-dependence in seedling survival indicates that the sample mean survival was representative of the population, and the selection of the additional high-density quadrats did not bias the results.

Seedling survival and light

The pattern of *M. bisulcata* seedling mortality suggests that mortality is also related to wet season light availability (Figure 1). While a relationship between the mean light level of seedling quadrats and mortality was not found, all quadrats were relatively shaded and mean levels of light were not greatly different from a random selection of positions on the forest floor. Green and Newbery (2001a) tested the survival of *M. bisulcata* seedlings in very low PAR conditions in controlled conditions outside the forest. Under 0.22 and 0.50% of external PAR (with neutral shade cloth), mortality of *M. bisulcata* within 1 yr was high (97% and 78%, respectively). Raising the light level to 1.1 or 1.3% PAR, however, was sufficient to ensure the survival of the majority of the seedlings for 1 yr (corresponding mortalities of 11 and 8%). This suggests that the light compensation point for *M. bisulcata* seedlings lies somewhere between 0.50 and 1.1% PAR. The majority of the wild seedling quadrats in the present study were near this level of PAR (Figure 2). Given other potential factors present in the forest environment, such as herbivory, pathogenic attack or root competition, the typical light levels of the seedling quadrats during wet seasons were low enough to induce seedling mortality.

Seed and seedling survival estimates

A test of the seed production and seed predation estimates is available by an independent count of the 1995 cohort of *M. bisulcata* by Newbery et al. (1998). They used a series of eighty-one 4-m × 4-m quadrats systematically arranged, plus 10 quadrats stratified between subplots, in the same 25-ha plot used in the presently-reported study. They recorded the seedling density of the 1995 cohort in November 1995 as 6,590 ha^{-1}, which has to be compared with the early-December estimate of 11,120 ha^{-1} from this study – a 1.7-fold difference. The model involved the multiplication of three separate estimates, each with its errors. The conversion from the mean number of seeds per tree to a plot-hectare basis may have been particularly inaccurate. There are several other reasons for the difference: (i) The seed production did not account for pre-predated seed loss within pods, although this was thought to be very small (J.J. Green, *pers. obs.*); (ii) Vertebrate predation may have been underestimated as the higher vertebrate predation near the tree stem was not weighted for the greater density of seed close to the tree. This was because the radial distribution of seed around the tree was not known, only the distribution of pods. If the survival value for seeds close to the tree (0.11) is used, however, the seedling density estimate falls to 7650 ha^{-1}. (iii) Seed predation was density dependent, higher densities attracting proportionally greater removal compared with the fixed design in the experiment. (iv) The 40 quadrats did not randomly sample the light regime across the whole forest, and their tendancy to being in slightly higher PAR locations (Fig. 2a) may have increased survivorship marginally. Weighed against these factors are two further ones which when corrected for would make the modelled estimate even higher: (i) The plastic mesh in the open treatment reduced the PAR and arguably could also have reduced survival. (ii) If a larger random sample of wilding quadrats had been used and density-dependent seedling survival operated, even if weakly negative, the survival on average would have been higher since the denser quadrats would have been relatively much less frequent. Population densities and model predictions are nevertheless in the same order of magnitude but clearly more aspects need to be recorded and experimented with to gain a closer agreement.

Control of mast fruiting and seedling survival

The results here concur with the hypothesis put forward by Newbery et al. (1998) that mast fruiting is probably primarily imposed by energy limitation for fruit production, but that phosphorus limitation and vertebrate predation are likely to be co-regulating (contributing) factors. The lack of recruitment of *M. bisulcata* within the ectomycorrhizal grove is not limited by seed or seedling supply, but rather a result of factors operating on seeds and seedlings, such that very few manage to develop beyond the seedling stage. This may be due to a low tolerance of dry season conditions after their first year of emergence and a low tolerance to shade in the following wet seasons. The role of pathogens and their interaction with seedling ecophysiology in *M. bisulcata* requires more detailed investigation as this seems the strongest pointer. For a better understanding of reproductive allocation in *M. bisulcata*, precise estimates of carbon and nutrient allocation would be needed to all parts of the tree, most essentially to roots and mycorrhizas, wood growth and internal storage as well leaf production in the year of masting.

Acknowledgements

References

Aubréville A. 1938. La forêt coloniale: les forêts de l'Afrique occidentale. Annales de l'Academie des Sciences Coloniales, Paris.

Aubréville A. 1971. Regeneration patterns in the closed forest of Ivory Coast. In: Eyre S.R. (ed.), World vegetation types. Columbia University Press, New York, pp. 41–55.

Augspurger C.K. 1983. Seed dispersal of the tropical tree, *Platypodium elegans*, and the escape of its seedlings from fungal pathogens. Journal of Ecology 71: 759–771.

Augspurger C.K. 1984. Seedling survival of tropical tree species – interactions of dispersal distance, light-gaps, and pathogens. Ecology 65: 1705–1712.

Chapman C.A., Wrangham R. and Chapman L.J. 1994. Indices of habitat-wide fruit abundance in tropical forests. Biotropica 26: 160–171.

Chuyong G.B. 1994. *Nutrient cycling in ectomycorrhizal legume-dominated forest in Korup National Park, Cameroon*. PhD Dissertation, University of Stirling, UK.

Chuyong G.B., Newbery D.M. and Songwe N.C. 2000. Litter nutrients and translocation in a central African rain forest dominated by ectomycorrhizal trees. New Phytologist 148: 493–510.

Clark D.B. and Clark D.A. 1987. Population ecology and microhabitat distribution of *Dipteryx panamensis*, a neotropical rain forest emergent tree. Biotropica 19: 236–244.

Connell J.H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine mammals and in train forest trees. In: den Boer P.J. and Gradwell G.R. (eds), Dynamics of populations. Centre for Agricultural Publishing and Documentation, Wageningen, pp. 298–310.

Curran L.M. and Leighton M. 2000. Vertebrate responses to spatiotemporal variation in seed production of mast-fruiting Dipterocarpaceae. Ecological Monographs 70: 101–128.

Curran L.M., Caniago I., Paoli G.D., Astianti D., Kusneti M., Leighton M. et al. 1999. Impact of El Nino and logging on canopy tree recruitment in Borneo. Science 286: 2184–2188.

Doley D., Yates D.J. and Unwin G.L. 1987. Photosynthesis in an Australian rainforest tree, *Argyrodendron peralatum*, during the rapid development and relief of water deficits in the dry season. Oecologia 74: 441–449.

Dunham K.M. 1990. Fruit production by *Acacia albida* trees in Zambezi riverine woodlands. Journal of Tropical Ecology 6: 445–457.

Fenner M. 1991. Irregular seed crops in forest trees. Quarterly Journal of Forestry 85: 166–172.

Forget P.M. 1992. Regeneration ecology of *Eperua grandiflora* (Caesalpiniaceae), a large-seeded tree in French Guiana. Biotropica 24: 146–156.

Forget P.M. 1993. Post-dispersal predation and scatterhoading of *Dipteryx panamensis* (Papilionaceae) seeds by rodents in Panama. Oecologia 94: 255–261.

Gartlan J.S., Newbery D.M., Thomas D.W. and Waterman P.G. 1986. The influence of topography and soil phosphorus on the vegetation of Korup forest reserve, Cameroun. Vegetatio 65: 131–148.

Garwood N.C. 1982. Seasonal rhythm of seed germination in a semi-deciduous tropical forest. In: Leigh E.G., Rand A.T. and Windsor D.M. (eds), The ecology of a tropical forest, seasonal rhythms and long-term changes. Smithsonian Institution Press, Washington, DC, pp. 173–185.

Green J.J. 1992. Fine root dynamics in a Bornean rain forest. PhD Dissertation, University of Stirling, UK.

Green J.J. and Newbery D.M. 2001a. Light and seed size affect establishment of grove-forming ectomycorrhizal rain forest tree species. New Phytologist 151: 271–289.

Green J.J. and Newbery D.M. 2001b. Shade and leaf loss affect establishment of grove-forming ectomycorrhizal rain forest tree species. New Phytologist 151: 291–309.

Harper J.L. 1977. Population biology of plants. Academic Press, New York.

Hammond D.S. and Brown V.K. 1998. Disturbance, phenology and life-history characteristics: factors influencing distance/density-dependent attack on tropical seeds and seedlings. In: Newbery D.M., Prins H.H.T. and Brown N.D. (eds), Dynamics of tropical communities. Blackwell Science, Oxford, pp. 51–78.

Hart T.B. 1995. Seed, seedling and subcanopy survival in monodominant and mixed forests of the Ituri Forest, Africa. Journal of Tropical Ecology 11: 443–459.

Herrera C.M., Jordano P., Guitian J. and Traveset A. 1998. Annual variability in seed production by woody plants and the masting concept: reassessment of principles and relationship to pollination and seed dispersal. American Naturalist 152: 576–594.

Janzen D.H. 1970. Herbivores and the number of tree species in tropical forests. American Naturalist 104: 501–528.

Janzen D.H. 1978. Seeding patterns of tropical trees. In: Tomlinson P.B. and Zimmerman M.H. (eds), Tropical trees as living systems. Cambridge University Press, Cambridge, pp. 83–128.

Kozlowski T.T., Kramer P.J. and Pallardy S.G. 1991. The physiological ecology of woody plants. Academic Press, New York.

Li M., Lieberman M. and Lieberman D. 1996. Seedling demography in undisturbed tropical wet forest in Costa Rica. In: Swaine M.D. (ed.), The ecology of tropical forest tree seedlings. UNESCO/Parthenon, Paris and Carnforth, UK, pp. 285–314.

Lieberman D. 1996. Demography of tropical tree seedlings: a review. In: Swaine M.D. (ed.), The ecology of tropical forest tree seedlings. UNESCO/Parthenon, Paris and Carnforth, UK, pp. 131–138.

Longino J.T. 1986. A negative correlation between growth and rainfall in a tropical liana. Biotropica 18: 195–207.

Lugo A.E. and Frangi J.L. 1993. Fruit fall in the Luquillo Experimental Forest, Puerto Rico. Biotropica 25: 73–84.

Newbery D.M. and Gartlan J.S. 1996. A structural analysis of rain forest at Korup and Douala-Edea, Cameroon. Proceedings of the Royal Society of Edinburgh 104B: 177–224.

Newbery D.M., Alexander I.J., Thomas D.W. and Gartlan J.S. 1988. Ectomycorrhizal rain-forest legumes and soil-phosphorus in Korup-National-Park, Cameroon. New Phytologist 109: 433–450.

Newbery D.M., Alexander I.J. and Rother J.A. 1997. Phosphorus dynamics in a lowland African rain forest: the influence of ectomycorrhizal trees. Ecological Monographs 67: 367–409.

Newbery D.M., Alexander I.J. and Rother J.A. 2000. Does proximity to conspecific adults influence the establishment of ectomycorrhizal trees in rain forest. New Phytologist 147: 401–409.

Newbery D.M., Songwe N.C. and Chuyong G.B. 1998. Phenology and dynamics of an African rain forest at Korup, Cameroon.

In: Newbery D.M., Prins H.H.T. and Brown N.D. (eds), Dynamics of tropical communities. Blackwell Science, Oxford, pp. 267–308.

Nielsen B.O. 1977. Beech seeds as an ecosystem component. Oikos 29: 268–274.

Ng F.S.P. 1976. Gregarious flowering of dipterocarps in Kepong, 1976. Malaysian Forester 40: 126–137.

Oberbauer S.F. and Strain B.R. 1986. Effects of canopy position and irradiance on the leaf physiology and morphology of *Pentaclethra macroloba* (Mimosaceae). American Journal of Botany 73: 409–416.

Payne R.W.Genstat Committee 1993. Genstat 5.32. Reference Manual. Oxford Science Publications, Oxford.

Pereira H.C. 1959. Practical field instruments for estimation of radiation and evaporation. Quarterly Review of the Royal Meteorological Society 85: 253–261.

Poorter L., Bongers F., van Rompaey R.S.A.R. and de Klerk M. 1996. Regeneration of canopy tree species at five sites in West African moist forest. Forest Ecology and Management 84: 61–69.

Proctor J. 1984. Tropical forest litterfall II: the data set. In: Chadwick A.C. and Sutton S.L. (eds), Tropical rain forest: the Leeds symposium. Leeds Philosophical and Literary Society, Leeds, UK, pp. 83–113.

Richards P.W. 1996. The tropical rain forest. 2nd edn. Cambridge University Press, Cambridge.

Schupp E.W. 1990. Annual variation in seedfall, postdispersal predation, and recruitment of a neotropical tree. Ecology 71: 504–515.

Silvertown J.W. 1980. The evolutionary ecology of mast seeding in trees. Biological Journal of the Linnean Society 14: 235–250.

Silvertown J.W. 1987. Introduction to plant population ecology. 2nd edn. Longman, London.

Singh S.P., Rawat Y.S., Rana B.S. and Negi G.C.S. 1990. Effects of unusually large seed crop on litterfall and nitrogen retranslocation in Himalayan oaks. Forest Ecology and Management 32: 79–86.

Sork V.L. 1993. Evolutionary ecology of mast-seeding in temperate and tropical oaks (*Quercus* spp). Vegetatio 108: 133–147.

Sork V.L., Bramble J. and Sexton O. 1993. Ecology of mast-fruiting in three species of North American deciduous oaks. Ecology 74: 528–541.

Van der Burgt X.M. 1997. Explosive seed dispersal of the rainforest tree *Tetraberlinia moreliana* (Leguminosae-Caesalpinioideae) in Gabon. Journal of Tropical Ecology 13: 145–151.

Van Schaik C.P. 1986. Phenological changes in a Sumatran rain forest. Journal of Tropical Ecology 2: 327–347.

Van Schaik C.P., Terborgh J.W. and Wright S.J. 1993. The phenology of tropical forests – adaptive significance and consequences for primary consumers. Annual Review of Ecology and Systematics 24: 353–377.

Vitousek P.M. and Sanford R.L. 1986. Nutrient cycling in moist tropical forest. Annual Review of Ecology and Systematics 17: 137–167.

Vogt K.A., Grier C.C. and Vogt D.J. 1986. Production, turnover and nutrient dynamics of above- and below-ground detritus of world forests. Advances in Ecological Research 15: 303–376.

Waller D.M. 1993. How does mast fruiting get started? Trends in Ecology and Evolution 8: 122–123.

Wheelwright N.T. 1986. A seven-year study of individual variation in fruit production in tropical bird-dispersed tree species in the family Lauraceae. In: Estrada A. and Fleming T.H. (eds), Frugivores and seed dispersal. Junk, Dordrecht, Netherlands, pp. 19–35.

Wright S.J. and van Schaik C.P. 1994. Light and the phenology of tropical trees. American Naturalist 143: 192–199.

Wright S.J., Carrasco C., Calderon O. and Paton S. 1999. The El Nino Southern Oscillation, variable fruit production, and famine in a tropical forest. Ecology 80: 1632–1647.

Wycherley P.R. 1973. The phenology of plants in the humid tropics. Micronesia 9: 75–96.

Zagt R.J. 1997. Pre-dispersal and early post-dispersal demography, and reproductive litter production, in the tropical tree *Dicymbe altsonii* in Guyana. Journal of Tropical Ecology 13: 511–526.