Seedling survival and growth of three ectomycorrhizal caesalpiniaceous tree species in a Central African rain forest

D. M. Newbery*[1], G. B. Chuyong†, L. Zimmermann* and C. Praz*[2]

* Institute of Plant Sciences, University of Bern, Altenbergrain 21, CH-3013 Bern, Switzerland
† Department of Life Sciences, University of Buea, P.O. Box 63, Buea, S.W. Province, Cameroon
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Abstract: Tree recruitment is determined in part by the survivorship and growth of seedlings. Two seedling cohorts of the three most abundant caesalpiniaceous species forming groves at Korup, Cameroon, were followed from 1995/1997 to 2002, to investigate why *Microberlinia bisulcata*, the most abundant species, currently has very few recruits compared with *Tetraberlinia korupensis* and *T. bifoliolata*. Numbers of seedlings dying, and the heights and leaf numbers of survivors, were recorded on 30 occasions. Survivorship after 2.5 y was 30% for *M. bisulcata* and 59% for the similar *Tetraberlinia* spp. together. After 7 y the corresponding values were 4 and 21%. Growth of all species was slow for the first 4 y; but survivors of *T. korupensis* became 63% taller, as the other species stagnated, by 7 y. The poor recruitment of *M. bisulcata* was the result of its very low seedling survival. Within species, the tallest seedlings of *M. bisulcata* and *T. bifoliolata*, but medium-height ones of *T. korupensis*, survived longest. This was likely due to higher root allocation in *T. korupensis*. Seedling dynamics of *M. bisulcata* and *T. korupensis* over 7 y accorded well with relative abundances of adult trees; *T. bifoliolata* is predicted to recruit later.

Key Words: Africa, grove dynamics, growth, *Microberlinia*, rain forest, seedlings, survivorship, *Tetraberlinia*

INTRODUCTION

Survival through the first few years of establishment is an important component of fitness for tropical trees (Swaine 1996, Turner 2001). Temporarily better-than-average survival may lead to an overall population increase, less-than-average survival may lead to a population decline (Botkin 1993, Shugart 1998). As a result, forest structure and composition, in terms of the relative abundances of different species in different size or age classes, is a complex compilation of recruitment and mortality over several decades (DeAngelis & Gross 1992, Vanclay 1994). Population changes can be transient, part of a cycle or a successional sere, or even a long-term directional trend (Connell & Slatyer 1977, Horn 1974). Cases where species clearly lack sufficient numbers of small trees, and failure to recruit has happened repeatedly, point to one or more factors keeping the population low, and leading to a possible decline or even local extinction of the species (Condit *et al.* 1998, Newbery & Gartlan 1996). Conversely, a relatively high abundance of small trees might suggest a wave of recruitment resulting in local dominance (Harper 1977, Jones 1950). The apparent imbalance in the numbers of trees of the different size classes necessary for continuous replacement (Connell *et al.* 1984, Hubbell & Foster 1990) becomes particularly obvious when it concerns a dominant species in a species-poor forest (Connell & Lowman 1989, Richards 1996).

Where a species has very low recruitment within the patches of adult trees, it must find new locations away from adults in order to maintain the population. This could be either at the edge of existing patches if seed dispersal is poor, or further away as new patches if seed dispersal is good. The first process leads to a locally expanding patch periphery, perhaps followed later by fragmentation and decay at the centre (Newman 1982, Watt 1947). The second process allows for a mosaic in which old stands are dying and new ones are establishing elsewhere within the forest on a larger landscape scale. Whether a species is perceived to be persisting or not is clearly dependent on the scale of field measurements (DeAngelis & Gross 1992, Shugart 1998). On a scale that is too small the dynamics may appear erratic and

unpredictable; on a large scale encompassing several patches changes may even out at an equilibrium density. Further, the inability of a tree species to replace itself *in situ* might appear to be selectively disadvantageous. However, if the conditions under which the species came to establish were different from those that it created later as a dominant tree there would be selective advantages in dispersing (Connell & Slatyer 1977, Huston & Smith 1987).

Adult trees of some tropical trees, when they reach a certain density or threshold biomass, can be hypothesized to affect the environment so as to curtail severely their own recruitment. This could be brought about by changes to the physical environment to which their seedlings are not well adapted: e.g. decreasing light and nutrient availability (Longman & Jenik 1987) or to biological changes such as the build up of species- or guild-specific predators or pathogens (Connell 1971, Janzen 1970). The basis to this process is the concept of cyclical dynamics, of establishment, growth, dominance, and then dispersal and re-establishment elsewhere paralleled with decay of old stands (Richards 1996, Swaine & Hall 1988, Watt 1947, Whitmore 1984). In such dynamics the (lack of) establishment of seedlings probably plays an important role. Key questions to be asked are: (1) what is the recruitment potential of each species; (2) which factors determine the rate of decline in survivorship; (3) do co-occurring species regenerate better, and why; and (4) what are the consequences of the relative survivorship rates for the species composition of the tree population?

A suitable ecosystem in which to follow these ideas is offered by groves of large tree species in the rain forests of western Central Africa, particularly in the Atlantic Coastal forests of Cameroon (Letouzey 1968, 1985; Schnell 1976–77, White 1983). In this region a 200-km-wide arc inland of the Bay of Biafra is characterized by several abundant, closely related species in the family Caesalpiniaceae (Leguminosae). Their distributions vary in spatial extent and composition from large almost monodominant tracts of forest through to patches of differing sizes with a few to several species of closely related taxa. Some have more-or-less good *in situ* regeneration whilst others appear to be decaying because of the evident lack of recruits (Condit *et al.* 1998, Letouzey 1968). A low density of juvenile trees may, however, not be reason alone for population decline if the few small trees have very high rates of survivorship to adulthood and high growth rates (Clark & Clark 1987, Jones 1956, Poorter *et al.* 1996).

This mosaic form of dynamics in African forests, necessarily understood on large spatial and temporal scales, was first recognized by Aubréville (1938), and elaborated by Letouzey (1968, 1985). Newbery & Gartlan (1996) evaluated the idea by analysing two large data sets from Cameroon. The process was highlighted by Richards (1996) as being one of the intrinsically differentiating features of African, as opposed to South and Central American and South-East Asian rain forests, and as being an example of the 'pattern and process' concept formulated by Watt (1947). This so-called 'Aubréville phenomenon' (Newbery *et al.* 1998, 2004) still remains largely unexplained in terms of a set of general working mechanisms. An essential component of this type of forest dynamics may lie with recruitment from seed to seedlings and saplings, which is the subject of the present paper.

Given their importance in explaining subsequent forest composition, reports of demographic studies in the tropical rain forests which followed the survivorship of defined seedling cohorts ≥ 5 y are surprisingly rare. Important cases are *Dipteryx panamensis* (Papilionaceae, Leguminosae) in Costa Rica over 5 y (Clark & Clark 1987), *Vouacapoua americana* (Papilion.) in French Guiana over 10 y (Forget 1997), and *Chrysophyllum* sp. nov. (Sapotaceae) in Queensland, Australia over 27 y (Connell & Green 2000). Survival percentages were 3, 11 and 6% for the three cases respectively. Other studies which have followed survivorship of populations present in the seedling bank from a particular starting time for ≥ 5 y (e.g. Delissio *et al.* 2002, Hart 1995) had the disadvantage that ages and cohort structure were unknown. Many more attempts have been made to record short-term survival, typically for 1–3 y, which may give misleading indications of the longer term dynamics and recruitment of the species concerned.

In this paper a long-term study of the seedling demography of three large caesalpiniaceous tree species exemplifying Aubréville dynamics is reported for a site in Central Africa. The results are related to what is known of the species' current sapling and tree densities.

STUDY SITE AND SPECIES

In the southern part of Korup National Park, in South West Cameroon, three large caesalpiniaceous tree species, *Microberlinia bisulcata* A. Chev., *Tetraberlinia bifoliolata* (Harms) Hauman and *T. korupensis* Wieringa (previously identified in Korup as *T. moreliana* Aubrév.), form large groves (Newbery *et al.* 1988, 1997, 1998, 2004). These canopy-emergent trees are fully intermixed with one another across the main grove of *c.* 1.5 km × 1.0 km in area, forming close to 50% of all trees ≥ 50 cm stem diameter (Newbery *et al.* 1998) and up to *c.* 70% of the basal area in 0.64-ha plots (Gartlan *et al.* 1986, Newbery *et al.* 1997). There are several other species of the subfamily within and outside of the groves (Newbery *et al.* 1988) but the most significant characteristic is that almost all of the caesalpiniaceous species are in the tribe Amherstieae and are ectomycorrhizal (Alexander 1989a,

Alexander & Högberg 1986, Newbery *et al.* 1988). The groves (of which two others are now been studied in Korup: Newbery *et al.* 2004 and X. M. van der Burgt and D. M. Newbery, unpubl. data) are established on phosphorus-poor, sandy, acidic and strongly leached soils where ectomycorrhizal status is likely to be the principal reason for their selection and codominance (Newbery & Gartlan 1996, Newbery *et al.* 1997).

An interesting feature of this forest is that despite its dominance *M. bisulcata* clearly lacks many small stems: recruitment is apparently very poor. There are very few small trees and hardly any saplings in comparison to the numbers of adults, as would be expected if some form of continuous replacement was in progress to achieve a stable size (or age) distribution over time. Furthermore, sizes of the large trees have a unimodal distribution, the most frequent trees having stem diameters of *c.* 1.1 m (maximum 2.5 m). By comparison, *T. bifoliolata* and *T. korupensis* are well stocked in the intermediate and small-size stem classes (maximum 1.5 m), with *T. korupensis* having more trees 10–<50 cm diameter than *T. bifoliolata* (Newbery *et al.* 1988, 1998). Together these distributions lead to the suggestion that *M. bisulcata*, in at least the main grove on transect P (see Gartlan *et al.* 1986) may die out in time and be replaced either by *T. bifoliolata* and then *T. korupensis* in succession or by a mixture of them both simultaneously (Newbery *et al.* 1998). One recently discovered grove of *M. bisulcata* in Korup in 2004 (X. M. van der Burgt and D. M. Newbery, unpubl. data) was shown to have a higher proportion of juvenile trees, however, and this demonstrates a likely continuation of the species.

The three caesalpiniaceous species share a similar floral and pollination biology, means of seed dispersal, germination and establishment strategy. Mast fruiting occurs every 2–3 y (Green & Newbery 2002, Newbery *et al.* 1998, 2006) which means that distinct cohorts are regularly established. Pods mature in May–October, and then split and explosively throw out their seeds up to 50–70 m away from the canopy. Epigeal germination produces two fleshy cotyledons within 1 wk of seed fall (Green & Newbery 2001a, 2002). In this way, seedling banks of the three species are started within *c.* 3 wk of one another (Newbery *et al.* 1998, 2006) and comparative survivorship can then be followed knowing the exact ages of the plants. Mast fruiting leads to very large numbers of seedlings, e.g. *M. bisulcata* adults (trees with stem diameters ≥ 50 cm) produced on average 83 500 seeds ha^{-1} in 1995, of which 12 960 ha^{-1} (16%) germinated and established as new seedlings (Green & Newbery 2002). *Microberlinia bisulcata* and *T. korupensis* have similarly sized microphyllous pinnate leaves (8–16 pairs, leaflets *c.* 8 mm × 20 mm) but *T. bifoliolata* has fewer mesophyllous, pinnate, leaves (two large leaflets *c.* 2 cm × 5 cm) (Aubréville 1970).

METHODS

In the eastern 25 ha of the main 82.5-ha plot in Korup (on transect 'P' of Gartlan *et al.* 1986), one 4-m × 4-m quadrat was established at random close to every 50-m grid-line intersection internal to this 500-m × 500-m area, plus 10 further quadrats selectively in the remaining part of the plot (n = 91). In November 1995, directly after seed fall and germination of the new cohort, 26 quadrats with sufficient numbers of seedlings (n $\geq$ 8) of *M. bisulcata*, *T. korupensis* and *T. bifoliolata* were selected. Each seedling received a numbered aluminium tag. Counts of seedlings were first made on 14 December 1995 (t_0). On 27 further occasions (t_1–t_{27}: 26 January 1996 to 25 June 1998) the alive/dead status of each seedling was recorded, together with the height (cm) and number of leaves of each survivor. Each census took 3–4 d to complete and the median dates have been used. The mean ($\pm$ SE) interval length was 34 ± 2 d (n = 27). Number of days (nd) from t_0 was very closely linearly related to interval number (int) (nd $= -3 + 32.4$ int, $r^2 = 0.998$, P $\ll 0.001$). The quadrats were later inspected on 16 December 1999 (t_{28}), 14 March 2000 (t_{29}) and 4 February 2003 (t_{30}). The time spans between t_0 and t_{27}, mid t_{28}/t_{29} and t_{30} were 2.53, 4.13 and 7.14 y respectively.

From t_{21} (30 September 1997, 1.79 y from t_0) a second cohort of seedlings was recorded in the same quadrats. These were tagged and recorded in the same way as for the first cohort, until t_{30}. The total number of seedlings followed was 1519, consisting of 994 in cohort 1 (at t_0) and 525 in cohort 2 (t_{21}–t_{22}). Thirty-four seedlings (almost all in one quadrat) were cut at ground level (presumably by rodents or ungulates) at t_7 (33 *M. bisulcata* and one *T. bifoliolata*). These were removed from the data set to leave 1485 seedlings in total and 960 in cohort 1. The numbers of starting seedlings in cohort 1 were therefore 391, 209, 360 for *M. bisulcata*, *T. korupensis* and *T. bifoliolata* respectively, and in cohort 2 correspondingly 200, 201 and 124. Appendix 1 shows the starting numbers of seedlings per quadrat.

Photosynthetically active radiation (PAR) and the ratio of red to far-red light (R:FR) were recorded on 28–31 May 1998, in each of the quadrats with the focus species, following the method of Green & Newbery (2001b). Climate data were available from the Bulu Station, Ndian, bordering the National Park. Dry seasons within the first 2.5 y of intensive sampling occurred when the 30-d running totals of daily rainfall fell below 100 mm (Newbery *et al.* 2006). They were 11 January 1996–29 February 1996 (50 d), 24 December 1996–21 March 1997 (88 d) and 28 December 1997–14 March 1998 (77 d).

To examine the trends from t_0 to t_{27} all time intervals were considered. From t_0 to t_{30}, because the intervals

were much longer between t_{27} and t_{28} and t_{29} and t_{30} than within t_1–t_{27}, sets of times at intervals > 0.5 y were taken as follows: start numbers at t_0 (cohort 1) or t_{21} (cohort 2), and then mean numbers surviving, height or leaf number for: t_1–t_3, t_9–t_{11}, t_{17}–t_{19}, t_{25}–t_{27}, t_{28}–t_{29} and t_{30} (cohort 1); and t_{25}–t_{27}, t_{28}–t_{29} and t_{30} (cohort 2). The mean dates of these points in time were found. Data analysis was accomplished using FORTRAN_77 programs, followed by statistical testing with GenStat 7/8, S-Plus 6.1 and MiniTab 14 software. Survival analysis was guided principally by Kleinbaum (1996) and Lee (1992).

RESULTS

Survivorship

In cohort 1 for the first 2.5 y, *Microberlinia bisulcata* declined in proportion close to half that of *Tetraberlinia bifoliolata* and *T. korupensis*, to 29.9% and a mean of 58.8% respectively (Figure 1a). After 7.1 y the corresponding survival was 3.6% and 21.2% (Figure 1b). *Tetraberlinia korupensis* survived slightly better than *T. bifoliolata* at 2.5 and 7.1 y. For cohort 2 the differences were less clear at 2.5 y (Figure 1a) but by 7.1 y *T. bifoliolata* survived almost equally as poorly as *M. bisulcata* (mean 7.6%) compared with *T. korupensis* (34.8%) (Figure 1b). Thus whilst *M. bisulcata* and *T. korupensis* showed similar results in both cohorts, *T. bifoliolata* survived less well in cohort 2 than 1. Percentage survival (%S, points in Figure 1a) declined exponentially with time (t) for all species (*M. bisulcata*: $ln(\%S) = 4.58 - 0.466t$, F = 3771; *T. korupensis*: $ln(\%S) = 4.61 - 0.213t$, F = 1826; *T. bifoliolata*: $ln(\%S) = 4.58 - 0.226t$, F = 1328; df = 1,5 and $P \ll 0.001$ in all cases). This implies that the hazard rates were close to constant: S_t was 62.3, 80.8 and 79.7% of S_{t-1} for *M. bisulcata*, *T. korupensis* and *T. bifoliolata* respectively. The corresponding half-lives of the populations ($t_{1/2}$), found from the equations, were 1.43, 3.28 and 2.96 y. For cohort 2 (Figure 1b), with fewer points, %S also declined exponentially (*M. bisulcata*: $ln(\%S) = 5.29 - 0.449t$; F = 142; *T. korupensis*: $ln(\%S) = 4.81 - 0.182t$, F = 34.4; *T. bifoliolata*: $ln(\%S) = 5.17 - 0.460t$, F = 53.9; df = 1,2; $P < 0.03$ in all cases), and S_t was correspondingly 63.8, 83.4 and 63.1% of S_{t-1}. In cohort 2 the time series was too short to estimate $t_{1/2}$ reliably.

Differences in survival in cohort 1 between *M. bisulcata* and *T. korupensis* and between *M. bisulcata* and *T. bifoliolata*, based on Kaplan–Meier curves, were highly significant ($\chi^2 = 35.4$, df = 1, $P < 0.001$, both cases), but not between *T. korupensis* and *T. bifoliolata* ($\chi^2 = 0.08$, df = 1, P = 0.362). Cox proportional-hazards ratios
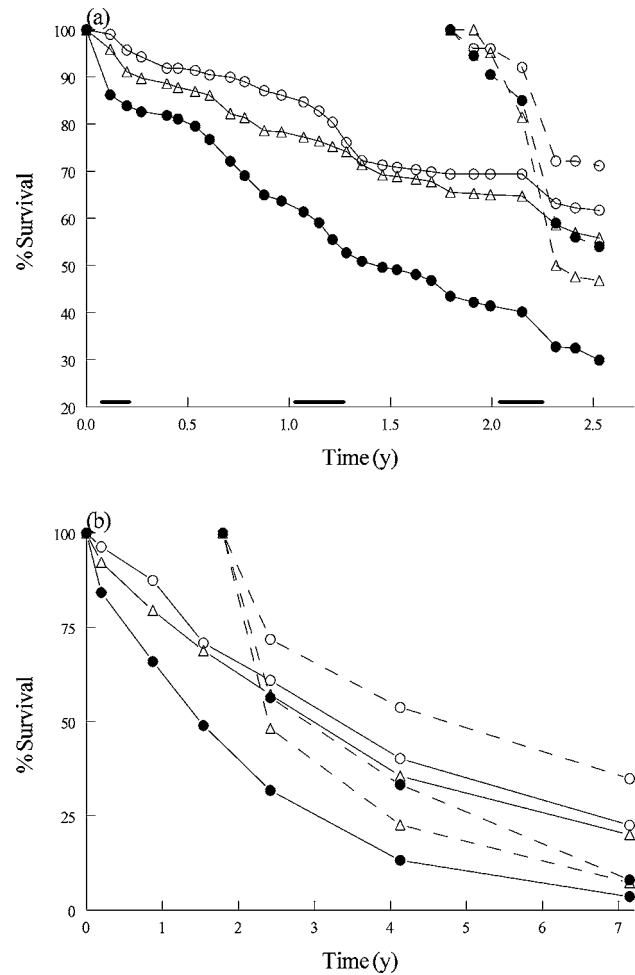
Figure 1. Percentage survival of seedlings of *Microberlinia bisulcata* (closed circles), *Tetraberlinia korupensis* (open circles) and *T. bifoliolata* (open triangles) in cohort 1 (1995, solid lines), and cohort 2 (1997, dashed lines) from recording times (a) t_0 to t_{27} and t_{21} to t_{27} at short intervals, and (b) t_0 to t_{30} and t_{21} to t_{30} at long intervals. The starting dates were 14 December 1995 (t_0) for cohort 1 and 30 September 1997 (t_{21}) for cohort 2. In (b), apart from t_{30}, points are means of two (t_{28-29} both cohorts, t_{21-22} cohort 2), otherwise three successive counts. Bars along the time axis indicate the dry seasons.

were 0.465 for *M. bisulcata*/*T. korupensis*, 0.730 for *M. bisulcata*/*T. bifoliolata*, and 1.137 for *T. korupensis*/ *T. bifoliolata* (with likelihood ratio and log-rank tests giving statistical values very close to the χ^2 ones).

For each species, those of the 26 quadrats which had ≥ 10 individuals at t_0 were found. For *M. bisulcata*, *T. korupensis* and *T. bifoliolata* there were 10, 5 and 10 such quadrats respectively (Appendix 1). Survival differences (with the Kaplan–Meier model) showed that for each species there were significant differences between quadrats (*M. bisulcata*: $\chi^2 = 48.7$, df = 9, $P < 0.0001$, *T. korupensis*: $\chi^2 = 10.5$, df = 4, P = 0.0327; *T. bifoliolata*: $\chi^2 = 50.4$, df = 9, $P < 0.0001$). Proportions of seedlings

surviving to t_{27} were not significantly related to either mean PAR or mean R:FR ($P \geq 0.1$).

Mean proportions of survivors of *M. bisulcata* in cohort 1 at t_1–t_3, t_9–t_{11}, t_{17}–t_{19}, t_{25}–t_{27}, t_{28}–t_{29} and t_{30} were not significantly dependent upon seedling numbers at t_0, (GLM logit regression; $n = 12$ quadrats with range 5–53 seedlings; $P > 0.05$). The other species had too few quadrats to test for density-dependence.

Mean PAR and R:FR ($\pm$ SE, range, median, $n = 26$) over the study quadrats (at $t = 2.45$ y in Figure 1) were 1.23% (± 0.15, 0.43–3.25, 1.14) and 0.357 (± 0.019, 0.16–0.54, 0.340) respectively. Quadrats were classified according to whether, in cohort 1, either *M. bisulcata* ($n = 8$), *T. korupensis* (4) or *T. bifoliolata* (10) were dominant (n at $t_0 \geq 50\%$ of all three species). Species' quadrats did not differ in mean PAR ($F = 0.67$, df $= 2,19$; $P = 0.525$), but they did in mean R:FR ($F = 8.45$, df $= 2,19$; $P = 0.002$) with *M. bisulcata* occurring at the highest (0.435 ± 0.016, SE), *T. korupensis* at the intermediate (0.349 ± 0.031), and *T. bifoliolata* at the lowest (0.240 ± 0.035) levels.

Growth

Seedlings of *M. bisulcata* in cohort 1 were smaller than those of *T. bifoliolata* and *T. korupensis* at t_0 (Figure 2; judging from the SEs) and by t_4 the order in height was *T. bifoliolata* > *T. korupensis* > *M. bisulcata*, and this was maintained to t_{27}. In cohort 2 the three species started at t_{21}–t_{22} with very similar heights (Figure 2a), but by t_{27} they had the same ordering as in cohort 1. Growth rates, however, were in the order *T. bifoliolata* > *M. bisulcata* $\geq$ *T. korupensis* for cohort 1 and *M. bisulcata* > *T. korupensis* > *T. bifoliolata* for cohort 2 (Table 1). Height increased almost linearly with time (Figure 2a) although second-order polynomials gave better fits (Mb, ht $= 18.5 + 2.97t - 0.285t^2$, $r^2 = 0.991$; Tk, ht $= 20.4 + 2.58t - 0.138t^2$, $r^2 = 0.989$; Tb, ht $= 20.3 + 4.12t - 0.506t^2$, $r^2 = 0.994$; for all, df $= 25$, $P \ll 0.001$).

Seedlings of *M. bisulcata* in cohort 1 had more leaves than either *T. korupensis* or *T. bifoliolata* at t_0 (Figure 3a), and the order of *M. bisulcata* > *T. bifoliolata* > *T. korupensis* was maintained to t_{24} (*T. korupensis* having half the number of *M. bisulcata* and *T. bifoliolata*) and from then on *M. bisulcata* and *T. bifoliolata* switched ranks. Although the trends were roughly linear for leaf number overall (Figure 3a), they were less easily fitted by polynomial equations. The curves for *M. bisulcata* and *T. korupensis* showed steps (these indicating leaf flushes) at t_{10} and t_{15}. Cohort 2 had the same ordering as cohort 1 (Figure 3a). Rates of increase in leaf number were in the order *T. korupensis* $\geq$ *T. bifoliolata* > *M. bisulcata* in cohort 1, but *T. korupensis* > *M. bisulcata* > *T. bifoliolata* in cohort 2 (Table 1). Points in Figures 2 and 3 are the mean heights,
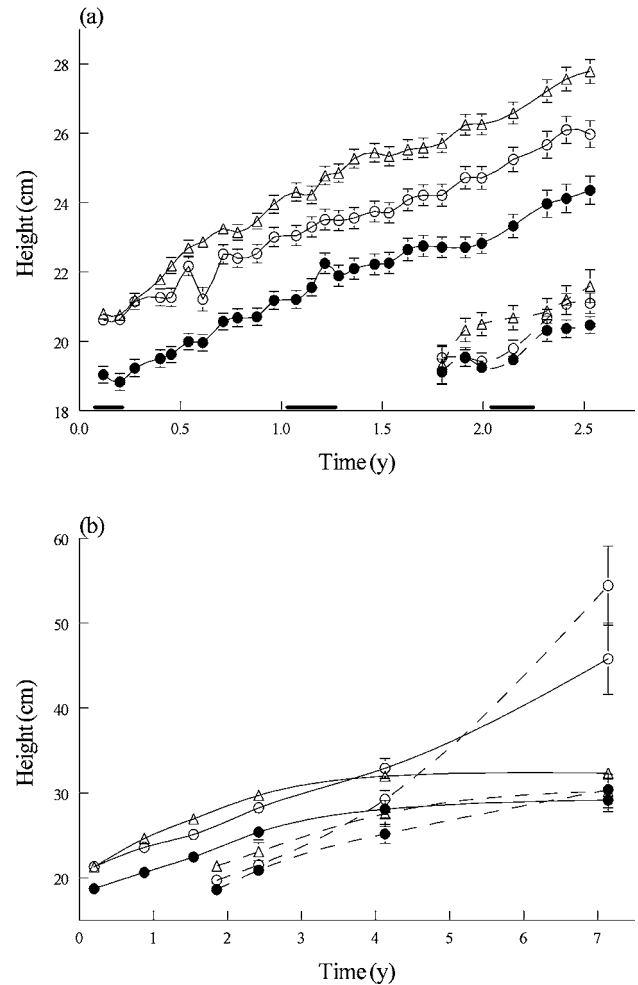
Figure 2. Change in height of seedlings of *Microberlinia bisulcata* (closed circles), *Tetraberlinia korupensis* (open circles) and *T. bifoliolata* (open triangles) in cohort 1 (1995, solid lines) and cohort 2 (1997, dashed lines) from recording times (a) t_0 to t_{27} and t_{21} to t_{27}, and (b) t_0 to t_{30} and t_{21} to t_{30}. The starting dates were as in Figure 1. In (a) the first points for cohort 2 are means of values at t_{21} and t_{22}. In (b) the same comments apply as in Figure 1. Bars on points show ± 1 SE. Horizontal bars along the time axis indicate the dry seasons.

and leaf numbers, of seedlings alive at those times, but the rates calculated in Table 1 are for seedlings which survived until either t_{27} or t_{30}.

At t_{27}–t_{28} height approached a maximum for *M. bisulcata* and *T. bifoliolata* so that by t_{30} cohorts 1 and 2 had similar values (Figure 2b). By contrast, *T. korupensis* increased considerably from t_{28}–t_{29} to t_{30} by 39 and 86% in cohorts 1 and 2 respectively. Whilst growth rates of t_{30}-survivors were more similar up to t_{27} in cohort 1 (Table 1), by t_{30} rates of *T. korupensis* were 2–3-fold those of *M. bisulcata* and *T. bifoliolata* in cohorts 1 and 2 (Table 1). Leaf numbers increased in a similar manner to height up to t_{30} for t_{30}-survivors (Figure 3b), though with small decreases in mean number between t_{28}–t_{29} and t_{30} for *M. bisulcata* and *T. bifoliolata* (Table 1), but increasing by 61 and 139% for

Table 1. Growth rates (agr, absolute; rgr, relative) in seedling height and leaf number of *Microberlinia bisulcata, Tetraberlinia korupensis* and *T. bifoliolata* in Korup, for cohorts 1 (1995) and 2 (1997) in the first 2.5 y (to t_{27}) and 7.1 y (to t_{30}).

Species	n	Height		Leaf number	
		agr (cm y^{-1})	rgr (cm cm^{-1} y^{-1})	agr (N y^{-1})	rgr (N N^{-1} y^{-1})
Cohort 1					
Survivors to t_{27},					
Growth t_{1-3}–t_{25-27}					
M. bisulcata	113	2.30	0.107	0.73	0.142
T. korupensis	129	2.30	0.099	1.07	0.352
T. bifoliolata	198	2.97	0.123	1.16	0.230
Survivors to t_{30}					
Growth t_{1-3}–t_{25-27}					
M. bisulcata	14	3.00	0.137	1.47	0.253
T. korupensis	47	3.12	0.127	1.56	0.442
T. bifoliolata	72[a]	3.80	0.151	1.88	0.326
Survivors to t_{30}					
Growth t_{1-3}–t_{30}					
M. bisulcata	14	1.50	0.064	0.50	0.084
T. korupensis	47	3.53	0.110	1.60	0.267
T. bifoliolata	72[a]	1.59	0.060	0.18	0.039
Cohort 2					
Survivors to t_{27}					
Growth t_{21-22}–t_{25-27}					
M. bisulcata	108 (82)[b]	4.04	0.205	2.58	0.570
T. korupensis	142 (103)[b]	3.19	0.155	1.02	0.450
T. bifoliolata	56 (49)[b]	3.00	0.135	0.26	0.064
Survivors to t_{30}					
Growth t_{21-22}–t_{30}					
M. bisulcata	16 (9)[b]	2.23	0.093	0.69	0.127
T. korupensis	70 (46)[b]	6.59	0.192	2.58	0.390
T. bifoliolata	9 (8)[b]	1.67	0.065	0.38	0.077

[a]: n = 71 for t_{25-27}; [b]: n in parenthesis for t_{21} and t_{22} averaged.

cohorts 1 and 2 for *T. korupensis* (Figure 3b). In summary, irrespective of the starting differences, *M. bisulcata* and *T. bifoliolata* stagnated in height and leaf number, whilst *T. korupensis* increased on average by 63% in height over the later 3 y.

The frequency distributions of heights and leaf numbers of seedlings of *T. korupensis* reaching t_{30} in cohorts 1 and 2 were positively skewed (Figure 4). In cohort 1, 38% of seedlings had heights ≥ 40 cm (21% ≥ 60 cm, 6.4% ≥ 120 cm) whilst in cohort 2 the corresponding values were 57% (31, 4.3). Similarly, 23.4% of seedlings had ≥ 20 leaves (4.3% ≥ 50); in cohort 2 the values were 28.6% (4.3%). Back-transforming from *ln*-transformed data gave mean heights (with 95% confidence limits) of 40.2 cm (35.0–46.2) for cohort 1 and 44.5 cm (38.3–51.7) for cohort 2. Likewise, means and limits of leaf numbers were 8.63 (6.56–11.4) and 10.0 (7.89–12.7) for cohorts 1 and 2 respectively. Thus, accounting for the non-normality of the data, mean height and leaf number of *T. korupensis* still remained above those of *M. bisulcata* and *T. bifoliolata* at t_{30} (cf. Figure 2b and 3b, displaying SE). The shapes of the distributions were similar between cohorts for leaf number (Figure 4b), but that for height in cohort 2 had a clear peak at *c.* 50 cm which was absent in cohort 1 (Figure 4a). Height and leaf number

(*ln*-transformed) were strongly correlated in cohort 1 (r = 0.828, df = 45, P < 0.001) and cohort 2 (r = 0.847, df = 68, P < 0.001). There were too few quadrats (n = 5) to permit a test of whether height of *T. korupensis* was related to PAR.

There were no clear associations between survivorship, height and leaf number growth of the three species with dry season, except for an increase in leaf number of longest surviving seedlings of *M. bisulcata* and *T. bifoliolata* in the second dry season of 1996–97 (Figure 3a and 5b,f). However, another similar increase occurred in the following wet season of the same year, yet none in the next dry season (1997–98).
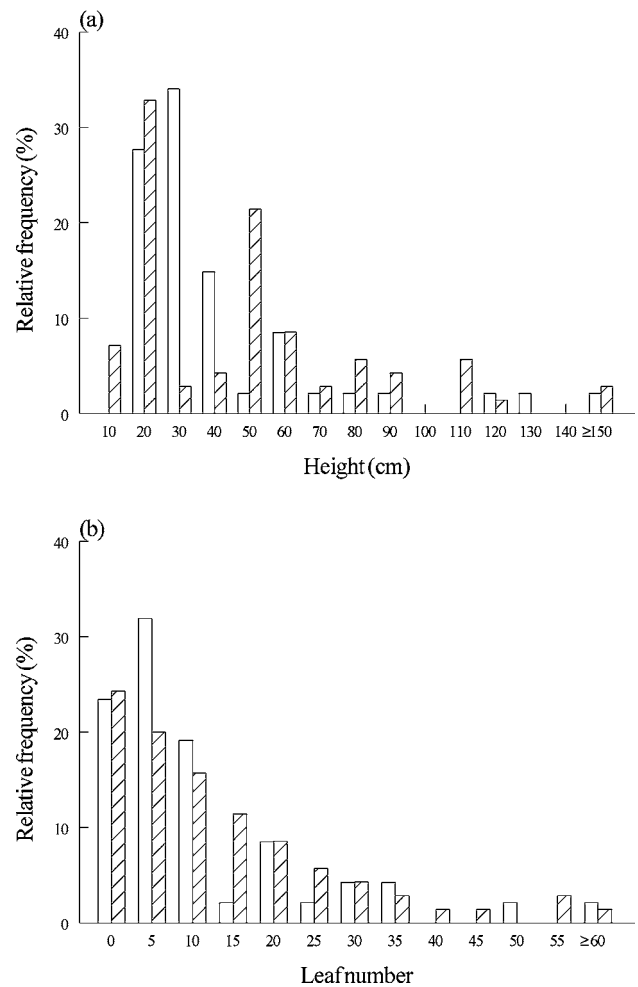
Survival and earlier growth

Growth curves of seedlings surviving to set time intervals (t_7–t_{12}, t_{13}–t_{18}, t_{19}–t_{24}, t_{25}–t_{30}) show different patterns for the species; seedlings of greater height and more leaves at the start did not always survive the longest (Figure 5). *Microberlinia bisulcata* and *T. bifoliolata* behaved very similarly but differently from *T. korupensis*. From t_1 to *c.* t_{10}, *M. bisulcata* and *T. bifoliolata* increased in height generally in parallel, with the early-dying seedlings
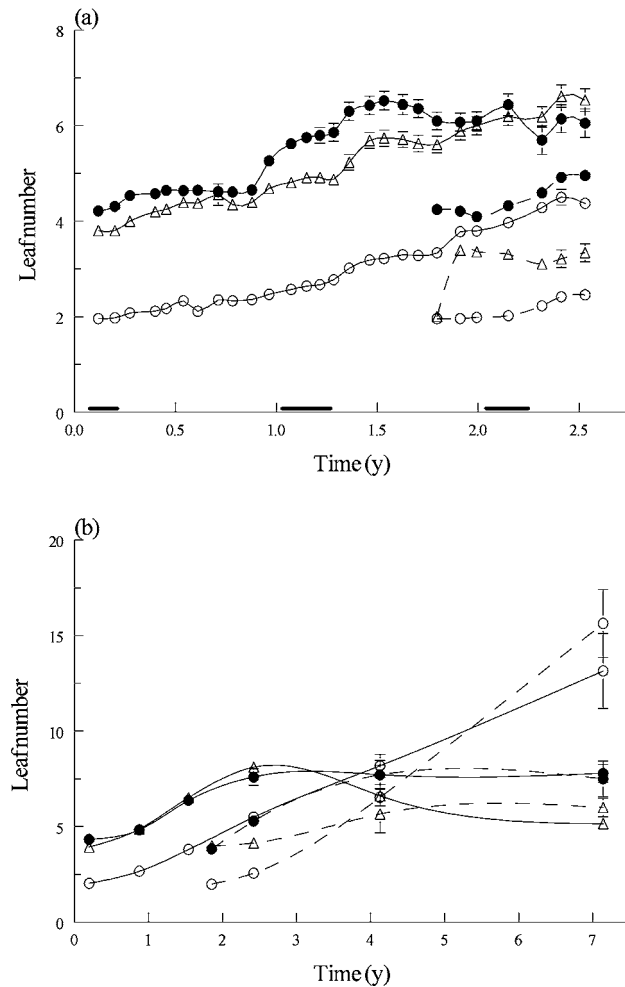
Figure 3. Change in leaf number of seedlings of *Microberlinia bisulcata* (closed circles), *Tetraberlinia korupensis* (open circles) and *T. bifoliolata* (open triangles) in cohort 1 (1995, solid lines) and cohort 2 (1997, dashed lines) from recording times (a) t_0 to t_{27} and t_{21} to t_{27}, and (b) t_0 to t_{30} and t_{21} to t_{30}. The starting dates were as in Figure 1, and comments about points and averaging in Figure 2 also apply here. Bars on points show ± 1 SE. Horizontal bars along the time axis indicate the dry seasons.

Figure 4. The frequency distribution of (a) heights, and (b) leaf numbers, of *Tetraberlinia korupensis* seedlings at recording time t_{30} in cohorts 1 (open bars) and 2 (hatched bars). Maximum heights and leaf numbers were 150 cm and 60 for cohort 1, and 240 cm and 74 for cohort 2, respectively.

having lower heights and less leaves than the late-dying ones. From t_{11} only the late survivors (time interval 4, i.e. to t_{25}–t_{30}) showed marked increases in height and leaf number whilst for time intervals 1 to 3 height and leaf number stagnated (Figure 5a,b,e,f). By contrast seedlings of *T. korupensis* were more widely separated in height at t_1–t_5 but the order of time intervals was 1, 2, 4 and then 3 (Figure 5c): that is seedlings in interval 3 had the greatest heights, and from t_1–t_{18} intervals 3 and 4 (longest survivors) had parallel increases in height. For leaf number (Figure 5d) differences between time intervals were less clear, all following a common rise in increasing leaf number, although again interval 3 had the highest mean number of leaves at least until t_{12}. The data show that relationships between starting height and

leaf number and growth rates were not linearly related to survivorship in a simple way.

The positive dependence of length of survival time between t_{13} and t_{27} on the size and growth of seedlings in the starting period t_1–t_{12}, was strongly significant for leaf number and rates of height and leaf number growth for *M. bisulcata* and *T. bifoliolata* (Table 2) on applying the Cox proportional-hazards model. As the size or rate variable increased the risk of dying decreased: the hazard rate became < 1.0. Except for height growth rate, the relationships for *T. korupensis* were not significant. In none of the tree species was survival dependent on height *per se*. Regressions using initial intervals of t_1 to either t_3, t_6, t_9 or t_{15}, and survival in the periods thereafter to t_{27}, gave similar but mostly less pronounced results. The lack of dependence in *T. korupensis* corresponds to the lack of order in the growth curves in Figures 5c,d. The
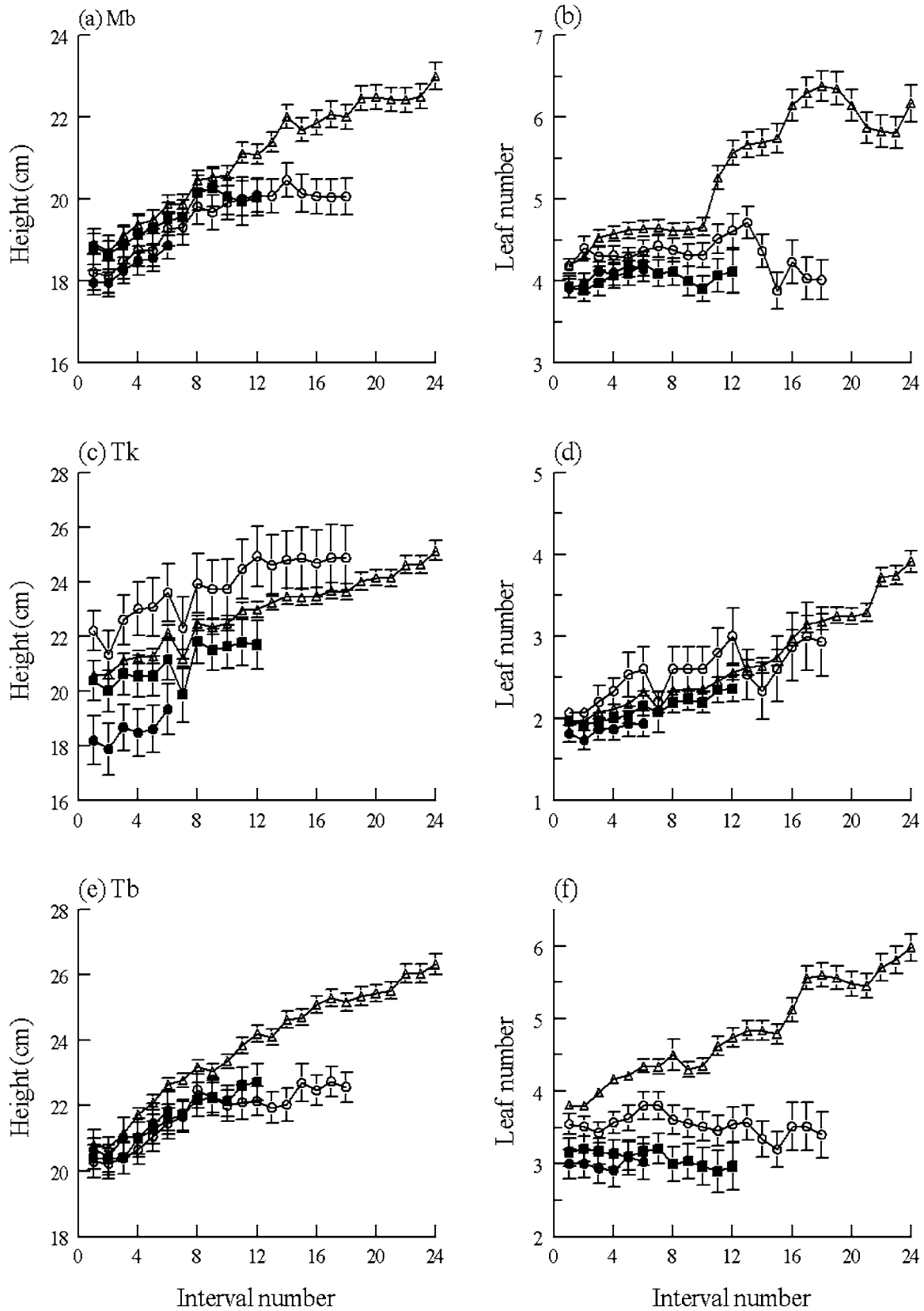
Figure 5. Changes in mean height and leaf number with time (interval number) of survivors of (a,b) *Microberlinia bisulcata* (Mb), (c,d) *Tetraberlinia korupensis* (Tk), and (e,f) *T. bifoliolata* (Tb), to four time intervals: recording times t_{7-12} (closed circles), t_{13-18} (closed squares), t_{19-24} (open circles) and t_{25-30} (open triangles). Bars on points show $\pm$ 1 SE.

Table 2. Dependence of survival time between t_{13} and t_{27} of cohort 1 (1995) seedlings of *Microberlinia bisulcata*, *Tetraberlinia korupensis* and *T. bifoliolata* on their mean heights and leaf numbers (and absolute growth rates of these) between t_1 and t_{12}, using the Cox proportional hazards model. The exponent of the regression coefficient (b) is the hazard rate (*HR*). Significance was tested by Wald's statistic (z).

Species	n	Height	Height growth rate	Leaf number	Leaf number rate
M. bisulcata	237				
b		-0.502	-0.172	-0.459	-0.465
HR		0.951	0.842	0.632	0.628
z		-1.54	-3.73	-4.58	-6.71
P		0.124	<0.001	<0.001	<0.001
T. korupensis	175				
b		-0.034	-0.188	-0.135	-0.252
HR		0.967	0.828	0.874	0.777
z		-0.68	-2.39	-0.45	-1.45
P		0.499	0.017	0.650	0.146
T. bifoliolata	242				
b		-0.114	-0.210	-0.704	-0.569
HR		0.892	0.810	0.495	0.566
z		-2.69	-3.54	-6.24	-5.20
P		0.007	<0.001	<0.001	<0.001

patterns in survivorship with height were confirmed by making separate Kaplan–Meier survival plots for each of six height classes (mean heights t_{1-12}) and finding the survival closest to t_{24}. For *T. korupensis* survival was optimal at height classes 3–4 (20–24 cm).

DISCUSSION

Differential species' responses

Microberlinia bisulcata survived the least well of the three species, with approximately half of the numbers of seedlings of the *Tetraberlinia* spp. alive at 2.5 y and only a quarter of them at 7.1 y. Although early establishment losses were significant, so also was the survival over the longer period in distinguishing the species. Seedling cohorts were not obviously influenced by the dry season although a consistent pattern might be difficult to find when each of the first three seasons likely had a different effect on the seedlings as their ontogeny advanced. In the second year, the strongest and fastest growing individuals might have been able to benefit from the temporarily elevated PAR levels and achieve new flushes of leaves. Coincidentally, the first dry season of this study was shorter and less extreme than the two that followed. There was no evidence of density-dependent survivorship for *M. bisulcata*, this confirming the result of Green & Newbery (2002).

In the first 2.5 y, *T. bifoliolata* was nearly always taller than *M. bisulcata* and *T. korupensis*. Relative leaf number was more difficult to compare across species, especially when considered in terms of represented leaf areas. The remarkable trend after 4.1 y was the much better growth of survivors of *T. korupensis*, compared with the other two species in terms of height and leaf number (Figures 2b and 3b), although decline in survivorship was almost the same for all three species in this interval (Figure 1b). Variance of survivors to 7.1 y was considerable for *T. korupensis*, some seedlings becoming very tall. What was more surprising was that seedlings of *T. korupensis* in cohort 2 reached larger sizes than those in cohort 1 although they began growing 2 y later, suggesting that they both experienced a common 'release' between 4.1 and 7.1 y.

Start of recording

The recording of the *M. bisulcata* cohort 1 seedlings in 1995 started on 14 December (t_0), which was 3–5 wk after most of the seeds had germinated and the cotyledons had expanded. Already most of them had their first two leaves. Recording of the second cohort in 1997 was earlier in the life-history on 30 September (t_{21}). This second cohort showed a much steeper early decline in seedling numbers than the first cohort (Figure 1), doubtless because losses were fastest earlier on. The nearest calendar date of recording in 1997 to that first one in 1995 was 11 December (t_{24}), the fourth point on the curve for cohort 2 in Figure 1a. Phenological recordings on parent trees (Newbery *et al.* 2006) showed that in 1995 the period of seed fall was short and intense in September, whilst in 1997 seed fall was spread less intensely over the months of July and August, i.e. it occurred *c.* 1 mo earlier in 1997 than in 1995. Thus, if germination and early seedling growth rates can be taken as having the same modus in both years, the equivalent start date (to t_0 of cohort 1) for cohort 2 would be t_{25}. By this date 59, 72 and 50% of *M. bisulcata*, *T. korupensis* and *T. bifoliolata* respectively had survived (Figure 1a). If cohort 2 were to be set at 100% at t_{25}, the decline in numbers to t_{27} would closely mimic that of cohort 1 between t_1 and t_3. Alternatively, the numbers at the second data point (date) for cohort 2 in Figure 1b (average of t_{25}–t_{27}) could be reset to 100% and the result would again confirm that *M. bisulcata* declined faster over the longer time period than *T. korupensis* and *T. bifoliolata*.

Seedling survival and forest structure

The similarly better survival of *T. korupensis* and *T. bifoliolata* than *M. bisulcata* in cohort 1 was in the inverse of the basal area abundances of the species as adult trees in the plot (stem basal areas of trees $\geq$ 30 gbh: *M. bisulcata* 10.55, *T. korupensis* 2.21, and *T. bifoliolata* 2.61 m^2 ha^{-1}, Newbery *et al.* 1997; corresponding numbers of trees $\geq$ 100 cm stem diameter: 2.06, 0.52 and 0.45 ha^{-1}, Newbery *et al.* 1998). This same result was found with the transplant trials of Green & Newbery (2001b) after just

1 y. This suggests a density-dependent process: the greater the adult tree biomass, the lower the species' seedling survival and recruitment.

In a 1989–91 transplant experiment, seedling survival for *M. bisulcata, T. korupensis* and *T. bifoliolata* was 33, 76 and 65% respectively (Newbery *et al.* 2000), which closely matches values in the present study of 47, 70 and 68% (at 1.66 y, Figure 1). Green & Newbery (2002) found 67% survivorship of *M. bisulcata*, corresponding (at 1.01 y) to 63% in the present study. In the transplant study, *T. korupensis* achieved much larger shoot mass than either *M. bisulcata* or *T. bifoliolata* (1.05 vs 0.34 and 0.61 g), and it was the only species to achieve positive growth.

In a survey of 880 quadrats (each 2-m × 2-m) in November 1995 (i.e. sooner after the masting of 1995 than the 14 December start date in this study) the densities of seedlings in the new cohort were 6593, 927 and 3729 ha^{-1} for *M. bisulcata, T. korupensis* and *T. bifoliolata*, respectively (Newbery *et al.* 1998). There was a strong dominance by *M. bisulcata* seedlings with the three species in the relative proportions 59: 8: 33%. However, seedlings ≤ 30 cm in height in the bank of March 1995 (i.e. *before* the masting) had densities of 844, 960 and 977 ha^{-1} (30: 35: 35), and those ≥ 30 in height but < 1 cm stem diameter occurred at 608, 1116 and 1722 ha^{-1} (18: 32: 50). Finally, small trees in the stem diameter class 1–< 10 cm dbh occurred at 5, 92 and 177 ha^{-1} (2: 34: 64).

The past dynamics may be inferred as follows: *M. bisulcata* started out being relatively very abundant but declined considerably to having very few small trees; *T. korupensis* rose rapidly from being relatively uncommon as small seedlings but being more common as larger ones, and then stabilized its contribution; and finally *T. bifoliolata* started at an intermediate position but increased only much later. Whilst it would be too inaccurate (and too convenient) to match the 2.5- and 7.1-y data in the present study with the ≤ 30-cm height class and ≥ 30-cm height to 1-cm diameter class (and assume stability in population dynamics with time over several mastings), the degree of correspondence is nevertheless very good. In the course of the present *c.* 7-y study *M. bisulcata* did decline, *T. korupensis* did increase at this stage around 4–7 y, and *T. bifoliolata* had not by then shown any marked differential growth or survival. If demography were followed for 20 y, *T. bifoliolata* would probably be shown to be released some years after *T. korupensis*.

Due to the way that their seeds are dispersed, seedlings of the three species were rarely found in balanced mixtures: they tended to occur in patches dominated by one species (Appendix, Table 1). This is an integral aspect of the spatial dynamics in the field and it means that intraspecific interactions are likely to be more important than interspecific ones at the local-quadrat scale in the first years of growth. The demography studied was therefore largely concerned with near single-species populations.

Possible differential mechanism

Part of the explanation for the better survival of *T. korupensis* and *T. bifoliolata* compared with *M. bisulcata* may lie with their seed sizes. Seeds of the former were found to be 2.1- to 2.5-fold greater in mass than the latter (1.36 and 1.57 g vs. 0.64 g; Green & Newbery 2001a), and nursery experiments, especially the treatments with low irradiance comparable to those over the quadrats in this study, showed that the heavier-seeded species had better survival and growth in the first year (Green & Newbery 2001a,b). Small seed size at the start of establishment, combined with subsequently slow growth (and possible susceptibility to pathogens) under low light conditions remains the best explanation for the currently very low recruitment of *M. bisulcata* in Korup (Augspurger 1983, 1984; Green & Newbery 2001b, Newbery *et al.* 1998, 2004). However, seed size does not explain the much better growth of *T. korupensis* than *T. bifoliolata* seedlings between 4.1 and 7.1 y found in this study.

In contrast to *M. bisulcata* and *T. bifoliolata*, the largest seedlings (judged by height above ground and number of leaves) of *T. korupensis* in the first year were not the ones that survived the longest (Figure 5). To speculate, *T. korupensis* was probably investing relatively more resources below-ground, to enlarging its root system, than the other species. This strategy may have led to the later growth success of its survivors. Newbery *et al.* (2000) found root-shoot ratios of *M. bisulcata, T. korupensis* and *T. bifoliolata* to be 0.44, 0.50 and 0.37 respectively, suggesting relatively most investment in roots by *T. korupensis*. Further, *T. korupensis*, became more heavily colonized by ectomycorrhizas than *M. bisulcata* and *T. bifoliolata* (Newbery *et al.* 2000).

In the current study quadrats with *T. korupensis* seedlings did not have higher mean PAR than those of *M. bisulcata* and *T. bifoliolata*, whilst their mean R:FR ratio lay between the other two species' values. This suggests that light was not the primary cause of the differences in growth. These light measurements, furthermore, were made close to t_{26}, the time when *T. korupensis* continued its rise in height whilst *M. bisulcata* and *T. bifoliolata* started to level off (Figure 2b).

Drawing on results from other field and experimental studies of these three tree species at Korup, the following hypothesis for *T. korupensis* is offered. This species grew better than the other two later on because it had better P-nutrition, either through a slightly larger and/or better colonized root system (which may have led to more effective mycorrhizal network connections) or a more efficacious mechanism of P-uptake (Smith & Read 1997). This would have enabled it to respond faster

than the other species to local increases in PAR, and hence achieve stronger onward growth and recruitment. The exact nature of interactions between these three species' seedlings and their adult trees, via perhaps the putative ectomycorrhizal hyphal network (Alexander 1989b, Simard *et al.* 1997, 2002), remains unknown, however.

Conclusion

The central question posed was to what degree the demography of a seedling cohort over *c.* 7 y could explain the current structure and dynamics of the caesalpiniaceous groves in Korup. Results over the first 3 y indicated the future replacement of *M. bisulcata* by *Tetraberlinia* spp. as far as survivorship was concerned, but further recording at 4–7 y highlighted how the *Tetraberlinia* spp. differed from one another in their subsequent growth rates. The present results make an important contribution towards modelling the Aubréville phenomenon in Central African rain forests.

ACKNOWLEDGEMENTS

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Appendix 1. Numbers of seedlings of three species at the start of recording (14 December 1995) in two cohorts 1 (1995) and 2 (1997) in 26 quadrats in Korup National Park: Mb, *Microberlinia bisulcata*; Tk, *Tetraberlinia korupensis*; and Tb, *T. bifoliolata*.

quad	cohort 1			cohort 2		
	Mb	Tk	Tb	Mb	Tk	Tb
1	32	0	0	11	0	0
2	4	1	0	7	19	1
3	0	0	30	0	0	11
4	21	0	0	3	0	0
5	8	0	0	1	1	1
6	15	0	54	0	0	3
7	20	0	0	10	5	0
8	3	0	24	2	8	22
9	3	0	32	0	7	22
10	22	0	0	7	3	0
11	26	0	4	20	0	0
12	0	0	45	3	9	25
13	53	0	4	32	0	2
14	0	0	30	0	3	4
15	13	0	0	7	0	0
16	126	0	0	22	0	0
17	5	3	0	11	5	3
18	1	0	31	9	0	4
19	1	0	18	3	29	1
20	3	0	16	6	0	0
21	0	0	69	0	9	21
22	3	35	3	13	19	1
23	23	29	0	19	3	3
24	1	51	0	4	3	0
25	0	47	0	0	67	0
26	8	43	0	10	11	0
All	391	209	360	200	201	124