Primary forest dynamics in lowland dipterocarp forest at Danum Valley, Sabah, Malaysia, and the role of the understorey

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Primary forest dynamics in lowland dipterocarp forest at Danum Valley, Sabah, Malaysia, and the role of the understorey

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Changes in species composition in two 4-ha plots of lowland dipterocarp rainforest at Danum, Sabah, were measured over ten years (1986–1996) for trees $\geqslant$10 cm girth at breast height (gbh). Each included a lower-slope to ridge gradient. The period lay between two drought events of moderate intensity but the forest showed no large lasting responses, suggesting that its species were well adapted to this regime. Mortality and recruitment rates were not unusual in global or regional comparisons. The forest continued to aggrade from its relatively (for Sabah) low basal area in 1986 and, together with the very open upper canopy structure and an abundance of lianas, this suggests a forest in a late stage of recovery from a major disturbance, yet one continually affected by smaller recent setbacks.

Mortality and recruitment rates were not related to population size in 1986, but across subplots recruitment was positively correlated with the density and basal area of small trees (10–< 50 cm gbh) forming the dense understorey. Neither rate was related to topography. While species with larger mean gbh had greater relative growth rates (rgr) than smaller ones, subplot mean recruitment rates were correlated with rgr among small trees. Separating understorey species (typically the Euphorbiaceae) from the overstorey (Dipterocarpaceae) showed marked differences in change in mortality with increasing gbh: in the former it increased, in the latter it decreased. Forest processes are centred on this understorey quasi-stratum.

The two replicate plots showed a high correspondence in the mortality, recruitment, population changes and growth rates of small trees for the 49 most abundant species in common to both. Overstorey species had higher rgrs than understorey ones, but both showed considerable ranges in mortality and recruitment rates. The supposed trade-off in traits, viz slower rgr, shade tolerance and lower population turnover in the understorey group versus faster potential growth rate, high light responsiveness and high turnover in the overstorey group, was only partly met, as some understorey species were also very dynamic.

The forest at Danum, under such a disturbance–recovery regime, can be viewed as having a dynamic equilibrium in functional and structural terms. A second trade-off in shade-tolerance versus drought-tolerance is suggested for among the understorey species. A two-storey (or vertical component) model is proposed where the understorey–overstorey species' ratio of small stems (currently 2:1) is maintained by a major feedback process. The understorey appears to be an important part of this forest, giving resilience against drought and protecting the overstorey saplings in the long term. This view could be valuable for understanding forest responses to climate change where drought frequency in Borneo is predicted to intensify in the coming decades.

Keywords: Borneo; dipterocarp forest; drought disturbance; ecosystem feedback; rainforest dynamics; understorey

1. INTRODUCTION

Over the time-scales of decades to centuries, species-rich tropical forest tree communities are unlikely to be constant in their species composition, or to show stable equilibria in their dynamics. How well the principal factors controlling their dynamics are understood lies in the statistical strength of predictions made about future forest composition. The present ability to make reliable projections remains, however, very low. Three main reasons for this observation are (i) the time-span of observations needed to model such a community type is large, possibly greater than 500 years; (ii) spatial variation in species composition within it is very considerable (hectares to kilometres squared in scale); and (iii) the environment, especially the climate, affecting it also changes with the centuries (and decadal fluctuations), selecting some species over others. To this almost ubiquitous state of non-equilibrium dynamics at the species level, must be added an important historical component,

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that of large stochastic events which can determine to a considerable degree the long-term dynamics of a forest (see Newbery *et al*. 1998). In these species-rich tropical forests, many species are necessarily rare and populations of all species may fluctuate considerably over decades. Therefore, apart from very species-poor forests (sometimes monodominant), usually growing at edaphic and climatic extremes, it is not feasible (at least currently) to attempt to relate the composition and dynamics of all or even most species individually to the ecosystem. There exists a large component of indeterminism. Nevertheless, the need now to have predictive models to estimate tropical forest cover in the coming decades, under a range of conditions and scenarios, calls for simpler, more robust methods in which small numbers of general, well-defined variables are used—ones which are not too sensitive to the vagaries of every individual species' dynamics. This means searching for dynamic equilibrium models at the ecosystem level.

Frequent disturbances of low to moderate intensity, occurring largely at random, continually affect forest growth and composition on many sites, perhaps even to the extent that in some areas the forest does not completely regain a steady-state biomass (or does so just for short periods) before being again disturbed. This situation was summarized well by a general model of community dynamics proposed by Huston (1979), and combined with the earlier seminal ideas of Watt (1947), it seems particularly applicable to tropical forests (Huston 1994; Shugart 1998). Several important theoretical consequences follow, which relate frequency and intensity of disturbance, competition intensity and tolerance mechanisms, and ecosystem structure and functioning to dynamics (either equilibrium or non-equilibrium) and species diversity. Combining pragmatic sampling considerations with the need for a robust testable model, two approaches thus appear feasible for tropical rainforest. Either species-based community models can be constructed that are highly site-specific (several hectares) and consider probably only small time steps of five to ten years ahead (Botkin 1993), or more widely usable ecosystem models could be built in which the variables are based on more stable structural and/or functional groupings of species, ones that can be applied over larger spatial and temporal scales (e.g. Bossel & Krieger 1991, 1994). An additional essential requirement for reliable prediction is that vegetation change be related to physical site conditions and climatic variables in physical terms (Woodward 1987).

The interface between forest tree community and forest ecosystem (*sensu* Whittaker 1975) can be achieved by adopting ecophysiological and structural groups of tree species (Longman & Jeník 1987; Hallé *et al*. 1978; Orians *et al*. 1996; Smith *et al*. 1997), either as a few classes or as a major component, which determine how similarly functioning species vary together in absolute and relative abundance from site to site and with time (O'Neill *et al*. 1986; Huston 1994). Species determinations are still necessary to allocate trees to groups. The suggestion, based on the dynamics data presented here from Danum, is that primary forest under a regime of disturbance and varying states of recovery can be understood in terms of understorey and overstorey groups of species, and that the most important deterministic interactions between trees should occur in the small-tree size class, which contains nearly all of the individuals of the understorey species and the smaller individuals of the overstorey ones. If site and climate do select species then it can be proposed that competition is likely to be strongest in this size class or quasi-stratum. This simplification leads to some interesting questions in ecosystems analysis, theoretical dynamics and perhaps a useful practical application. To qualify this approach, how special Danum is compared with the rest of north-east Borneo must also be discussed.

Very few sample plots in the tropics can, however, address this issue because practical forestry has been almost entirely driven by harvesting and that has meant measuring the large trees, assessing the growth of the next potential coupe, or counting, the seedling bank as a predictor of future (overstorey) regeneration. To date there has been a great lack of ecological interest in the small sapling, pole and understorey trees because these, in the main, form uncommercial small stems and as a result their taxonomy is generally poorly known compared with timber species. Yet clearly these species' small stems are very abundant numerically and are densely occupying some forests like Danum (Newbery *et al*. 1992, 1996). For many decades silvicultural practice has been to remove these 'useless' trees (Nicholson 1965*a*, e.g. for Sabah). Most textbooks on tropical forest ecology barely mention understorey species, concentrating on the canopy trees and pioneers in direct contrast, but notable exceptions are Hallé *et al*. (1978) and Richards (1996), whose treatment of forest structure and architecture recognizes the potential role of these small-stemmed species. Richards (1996, pp. 47–48) wrote 'Although a division of the forest into storeys is useful for some purposes, it is becoming increasingly clear that ecologically the most important horizontal boundary is that separating the lower layer of closely packed tree crowns, which are often interwoven with lianes, from the much more open layer above where the crowns are broader and more widely spaced.'

The two 4-ha Danum plots were set up in 1985 with this idea in mind by including trees down to 10 cm gbh, not measuring the smaller seedlings and saplings, and appreciating that very large trees were not going to be sampled in detail either. The basic hypothesis was that the understorey is a functionally integral part of the dipterocarp forest ecosystem, important in recovery processes following disturbance, essential for regeneration of the overstorey, and in its structural and floristic composition is an indicator of forest history. The understorey may be a key component of ecosystem resilience and stability, and this needs to be demonstrated against the null model that the understorey simply fills an empty niche left by the growing stand of overstorey (canopy and emergent) species.

The forest at Danum appears to have been strongly disturbed in the recent past, most probably by drought, and is presently recovering (Newbery *et al*. 1992). Vegetation analyses have shown that a subset of the understorey species has been selected on small ridges—a proposed drought-tolerant guild (Newbery *et al*. 1996). Increasing evidence from the analysis of climate records by Walsh (1996*a*,*b*) and Walsh & Newbery (1999) supports the notion that the Danum forest (and possibly much of

Sabah's lowland rainforest) is continually drought-disturbed and recovers. (Occasionally at other sites fire also has followed.) That Bornean rainforest has an equitable aseasonal climate was contested by Brünig (1969, 1971), in explaining the heath forest formation in north-west Borneo, and this thesis is now being extended to the whole island. Intermittent very dry periods are part of the decadal–century-scale environmental fluctuations across this landscape.

In this paper, the changes over a background drought-free, ten-year period (1986–1996; being serendipitously between the drought events of 1982–1983 and 1997–1998) in this lowland dipterocarp forest of Sabah are reported at the species and subplot levels, and with particular attention directed toward under- and overstorey species' small trees. One aim is to establish a basic approach to quantifying and predicting further changes under drought and non-drought conditions. Such a model is needed to answer pressing questions about the future management of the lowland rainforest if global and regional climate change lead to increased frequency and intensity of droughts (Hulme & Viner 1998; Walsh & Newbery, this issue). Two principal questions are: How adapted are the tree species at Danum to this regime? What limits to drought stress can they tolerate before the ecosystem collapses functionally and then structurally?

2. METHODS

(a) *The original enumeration*

The two 4-ha permanent plots were originally set up at Danum in 1985–1986. Each is 100 m wide (W–E) and 400 m long (S–N), and they lie parallel to one another at *ca.* 300 m apart. Fuller details are to be found in Newbery *et al.* (1992, 1996). Each plot was subdivided into 100 subplots of 20 m × 20 m. In the first enumeration every living tree $\geqslant 10$ cm girth at breast height (gbh) (1.3 m) was mapped to the nearest 0.1 m, numbered with an aluminium tag, and measured for gbh (to the nearest 0.1 cm) at a paint mark. Each tree was identified to a distinct taxon, 71% to the species level and 23% to the genus. Gbh measurements were made between mid-September 1985 and mid-March 1986 for plot 1 and mid-November to mid-December 1986 for plot 2.

(b) *Second enumeration*

In the second enumeration the coordinates of the trees were used to produce maps (one per subplot) to assist in locating trees and distinguishing the recruits (i.e. those trees which reached $\geqslant 10$ cm gbh and survived to this enumeration date). The re-measurements began in November 1995 and were completed by December 1996, with the exception of a few very large trees measured in February 1997. Work started in plot 1 and alternated between plots as each successive S to N hectare was completed. In each subplot, each tree was first checked to determine whether its number tag was still attached. In the absence of a tag, the stem was inspected for a paint mark, the position of the tree was compared with those on the map, and observations on species and girth were compared with data on any trees previously recorded close to the relevant location. These measures nearly always resulted in an unequivocal identification of the tree as either one particularly numbered individual or a recruit. If the tree had been recorded in the original enumeration it was examined to determine whether it was still alive, using the criterion of living tissue above ground, and all trees recorded as dead or missing were subsequently double-checked to ensure that no coppice shoots had been overlooked. Having established the status of the tree the following procedures were followed.

(i) *Survivors*

Trees surviving from the original enumeration were measured at the previous point of measurement unless (i) the previous paint mark had been lost, in which case the gbh was measured at 1.3 m or as close to that height as possible, avoiding stem deformations, etc.; (ii) the development of buttresses or emergence of a large branch rendered the previous point of measurement unusable; or (iii) the stem was dead at the previous point of measurement. Occasionally gbh was also recorded at an alternative point because buttress growth was predicted to distort the girth at the existing one by the next enumeration. For each surviving tree, irrespective of whether the previously measured stem was alive or dead, any new stems were measured at 1.3 m and girths $\geqslant 5$ cm were recorded. Where a tree had multiple stems, the gbh of each was exactly measured separately. Gbhs were measured separately using either a thin 2 m long steel tape or, for larger trees, a 5 m one. After removal of loose bark and moss, the tape was aligned with the top of the paint mark and pulled tight around the stem, under any lianas. Rarely, it proved impossible to insert the tape beneath a constricting liana and calipers were used to measure the diameter instead, taking two measurements at right angles. Even with the aid of a ladder to reach above the buttresses, some trees could not be measured by the foregoing methods, and for these individuals diameters were estimated optically with a relascope, taking two readings at *ca.* 90° to one another. The condition of the stem at the point of measurement was recorded in one of 17 nominal classes, e.g. stem deformed, fluted, cracked, fused with a liana, bark stripped, etc., as a means of identifying those most accurate measurements for later analysis. The point of measurement was freshly marked on all trees, either as a new band of yellow paint or, for larger trees only, with a nail hammered into the stem 10 cm above the point of measurement. Finally, if the previous tag had been lost, the relevant number was embossed on a plain tag and replaced. Notes were made on the condition of live trees: AA, apparently undamaged; AB, broken above and old stem measured below break; AC, broken and coppicing, old stem dead and new stem measured if it was large enough; AD, old stem dead standing to ± base, new one measured if it was large enough; AH, half-broken below but old stem alive at point of measurement, or one of two old stems broken; AL, leafless; and AU, alive (partially) uprooted tree ± prone.

(ii) *Non-survivors*

For every tree that had died since the first enumeration, and which could be located, the mode of death was recorded as uprooted (DU), broken above (DA) or at (DB) the base, or dead standing (DS), if enough of the tree remained. If the tree was too badly decomposed, or if only its tag was left, the mode of death was recorded as unknown (DN). If a thorough search around the expected position revealed neither suitable debris nor tag, the tree was recorded as missing (DM).

(iii) *Recruits*

All unmarked, unlabelled trees were rapidly screened, stems $\geqslant 9$ cm gbh at *ca.* 1.3 m height being selected for closer inspection. A steel tape was used to measure the height up the stem starting from ground on the up-slope side of the tree where relevant, and the point of measurement marked at 1.3 m, unless stem deformation or a liana made a different point necessary. The gbh was measured to the nearest millimetre using a thin steel tape, each stem of multiple-stemmed individuals measured separately, and any tree $\geqslant 10$ cm gbh was recorded as a recruit. If a constricting liana prevented measurement with the tape, calipers were used to measure diameter (taking two readings at 90° where possible), and any tree $\geqslant 3.04$ cm dbh was recorded. (A few gbhs on later calculation were found to be just <10 cm and excluded.) Recruits were yellow-paint marked at the upper edge of the point of measurement and the new tree labelled with a uniquely numbered tag. The position of each recruit was determined with reference to one or two of the nearest previously enumerated trees, from which a compass bearing and distance were recorded.

(iv) *Taxonomy*

Subsequently, a specimen of the foliage (rarely fertile) was collected from each recruit, dried and identified at the Herbarium of the Sabah Forest Department and the Rijksherbarium, Leiden, where all previous collections from the plots have been collated. It was particularly important to have this reference collection from 1985–1989 (Newbery *et al.* 1992) so that sterile material could be matched as exactly as possible, especially for those taxa still known only to the genus. The completed data set with all taxonomic checks and revisions was ready for analysis in March 1998.

(c) *Preliminary data analysis*

In general, the two enumerations will be simply referred to as '1986' and '1996'. The data files, one per plot, for the 1986 enumeration were expanded with the new 1996 data. These first contained the tree numbers, species codes (cross-referencing to a dictionary), X- and Y-coordinates and 1986 gbh. Added to these were principally the recruited trees and their measurements in 1996, the gbhs of 1986 survivors, the dead tree category of non-survivors and alive tree category of survivors, precise date of re-enumeration, point and method of remeasurement, and stem condition at the point. By definition a recruit in 1996 had 0.0 cm gbh in 1986 and a 1986 tree that died 0.0 cm gbh in 1996, but importantly, some trees that were still alive in 1996 had regressed in gbh below 10 cm, compared with their 1986 values. This was because of either (i) categories AC, AD or AH pertained, (ii) slight negative remeasurement errors of trees close to 10 cm; or (iii) shrinkage, or bark–moss loss. Thus a census summary of trees $\geqslant 10$ cm gbh in 1996 would exclude these. The data files were checked for internal consistency of species codes, categories, and measurements both within and across plots using a suite of FORTRAN programs. On revisiting trees in 1996, it was discovered that a few small individuals recorded as trees of one particular species were in fact lianas and thus the total number of trees in 1986 changed from 9002 to 8973 (-26, -3 as missing) in plot 1 and 8983 to 8971 (-12, none missing) in plot 2 after their removal.

Since both enumerations were spread over intervals of some months, the time differences were found for each subplot within each plot and hence for each individual. In 1985–1986 the dates of measurements were recorded to approximately the nearest week or fortnight (24 August 1985 to 15 March 1986) in plot 1, and for plot 2 the middle date of 30 November 1986 was used. For 1996 the dates were more precisely known (to the day). Mean time intervals were 10.40 yr (range 10.01–11.48, $n = 10\,280$) for plot 1, and 9.60 yr (range 9.05–10.23, $n = 10\,063$) for plot 2.

(d) *Wider basal area estimates*

In January 1998, using thirteen 500-m N–S lines, 100 m apart, six each within the two 25-ha blocks (starting *ca.* 250 m west of plot 2) and one *ca.* 150 m west of plot 2 within its block, a relascope sweep was made at each 100-m interval. These 72 values may be taken as quasi-independent replicates of the forest adjacent to and west of the main plots.

(e) *Storeys*

In a previous analysis of the 1986 data, Newbery *et al.* (1992, 1996) adopted a structural classification based on tree density and basal area (ba) in two size classes, and this was used here: overstorey, with a ba ratio of >0.8 and density ratio of 0.2 for trees $\geqslant 30$ cm:$\geqslant 10$ cm gbh; understorey, with ratios of <0.6 and <0.2 and intermediate, 0.6–0.8 and 0–0.4 respectively. This classification is dependent on the tree size distributions recorded in the plots in 1986.

3. RESULTS

(a) *Taxonomic revisions and change in species richness*

The number of taxa in the 8 ha at Danum was revised from 511 (Newbery *et al.* 1992) to 492 after taxonomic revisions; 18 taxa were gained from splitting, one liana was omitted and 36 taxa were removed by 'lumping'. In 1996, the number of taxa (including regressors) had increased to 591 because 20 taxa were lost (through mortality over ten years) and 119 were new in 1996 as recruits. If only 1996 trees $\geqslant 10$ cm gbh are considered the new count was 587 (115 recruiting species). This imbalance between species gained and those lost from dying is almost certainly largely due to the conservative allocation of vegetative juvenile specimens to new taxa. (Out of the 115 recruiting, new taxa, 94 (82%) had one or two stems only, and only eight taxa (7%) had five or more stems.) A more reliable estimate of change in species number (see Newbery *et al.* 1992) is to consider those species with frequency $f \geqslant 5$ in both plots: this gives 250 in 1986 (revised from 247), and 253 in 1996 for trees $\geqslant 10$ cm gbh (255 with regressors), which indicates negligible change.

Thirty-five taxa had complete name revisions, some simply to earlier-noted synonyms. Among the taxonomic 'splits', the most important changes were *Scorodocarpus borneensis* dividing into this species (95 trees) and *Dysoxylon alliaceum* (97) (both in the 1986 list); *Pternandra coerulescens* (46) splitting to *Strychnos* sp. (37)—the liana now omitted—with seven trees left of this tree species and two of other taxa; and *Vatica dulitensis* (80) dividing into this taxon (65) and a new taxon *Vatica vinosa* (15). All other changes of the 1986 identifications were more minor.

(b) *Change in forest structure*

Densities of trees $\geqslant 10$ cm gbh decreased by 4.7% in plot 1 and 2.8% in plot 2 between 1986 and 1996 (table 1). Trees $\geqslant 30$ cm gbh increased slightly in density in plot 1 by 0.6% but much more in plot 2 by 7.4%. Densities of large trees $\geqslant 100$ cm gbh rose slightly in both plots. Small trees (defined as 10–<50 cm gbh) constituted 89.8 and 90.0% of all trees in 1996 in plots 1 and 2, respectively. These latter decreased slightly in the interval (table 1).

Table 1. *Changes in density and basal area abundances of trees in different size classes between 1986 and 1996 at Danum, showing also the losses and gains, with inferred growth, in basal area in the interval*

	density (ha^{-1})				basal area ($m^2 ha^{-1}$)			
gbh (cm)	1		2		1		2	
	1986	1996	1986	1996	1986	1996	1986	1996
$\geqslant 10$	2243	2138	2243	2180	30.5	32.1	31.0	34.6
$\geqslant 30$	484	487	455	489	26.3	28.2	26.8	30.6
$\geqslant 100$	61	63	66	68	17.3	18.9	18.6	21.5
$10-<50$	2028	1919	2039	1962	7.20	7.05	7.03	7.11
$\geqslant 50$	215	219	204	218	23.3	25.0	24.0	27.5
$\geqslant 31.4$	448	455	421	451	26.1	28.0	26.5	30.3

Basal area increased by 5.2% in plot 1 and 11.6% in plot 2 over the ten years for trees $\geqslant 10$ cm gbh, this being largely accounted for by increases in the basal area of trees $\geqslant 100$ cm gbh (table 1). Loss in basal area through trees dying was 4.65 and 3.27 $m^2 ha^{-1}$, and that gained as recruits, 0.47 and 0.33 $m^2 ha^{-1}$, respectively, for plots 1 and 2. Using the formula $ba_{96} - ba_{86} = ba_{grown} - ba_{lost} + ba_{recr}$, the trees surviving in plot 1 grew less than those in plot 2, 5.83 versus 6.58 $m^2 ha^{-1}$, respectively. These whole-stand growth increments were 19.1 and 21.0% of the 1986 basal area measures. Trees that grew in girth but died before the end of the census interval were of course unaccountable. The small trees formed 22.0 and 20.5% of the 1996 basal areas of plots 1 and 2, respectively.

For the $10-<50$ cm class, trees advancing beyond 50 cm gbh (ba_{adv}) formed an additional loss from the 1986 abundances: 1.281 and 0.924 $m^2 ha^{-1}$ in plots 1 and 2. Gains from recruits, 0.440 and 0.330 $m^2 ha^{-1}$, and losses from mortality, 0.626 and 0.534 $m^2 ha^{-1}$, meant that net growth of survivors was 1.315 $m^2 ha^{-1}$ in plot 1 and 1.208 $m^2 ha^{-1}$ in plot 2. These increments formed 18.3 and 17.2% of the 1986 basal area (table 1), and correcting to a ten-year basis this averaged 17.8%. The growth in this size class was thus very similar for the plots.

Mean basal area from the relascope survey was 29.8 $m^2 ha^{-1}$ (s.e. = 1.34, $n = 72$; 98% confidence limits 26.6 and 33.0). This estimate is slightly below the means of the two 4-ha plots (table 1).

The Danum forest thus continued to aggrade with the growth of larger trees yet little decrease in density of the smaller ones.

(c) *Mortality and recruitment at the plot level*

Two forms of mortality and recruitment, periodic and annual, were found. Periodic rates were calculated by expressing numbers of deaths (n_d), or recruits (n_r), as percentages of the 1986 population sizes (n_{86}), ($m_p = (n_d/n_{86}) \times 100$; $r_p = (n_r/n_{86}) \times 100$), corrected linearly to a ten-year basis. Annualized rates were found from the equations

$$m_a = 1 - (1 - (n_d/n_{86}))^{1/t},$$

and

$$r_a = (1 + (n_r/n_{86}))^{1/t} - 1,$$

where t was the relevant time interval (Alder 1995; Sheil *et al.* 1995; Sheil & May 1996).

Alternatively, recruitment can be expressed as a percentage of the n_{96} populations, i.e. the rate at which the number of survivors, n_s, increased to reach n_{96}, where $n_{96} = n_s + n_r$, and n_{96} and n_s are corrected for loss of regressors and, in the case of small trees, those advancing to $\geqslant 50$ cm gbh. The relevant periodic rate is $rr_p = (n_r/n_{96}) \times 100$ and the annualized rate is

$$rr_a = (n_{96}/n_s)^{1/t} - 1.$$

Plots 1 and 2 had very similar starting populations (table 2) but changed at different rates. Periodic mortality was significantly greater in plot 1 than plot 2, while recruitment was only slightly greater in plot 1 than 2. Recruitment rates were lower than mortality rates in both plots. These recruitment estimates do not account for the trees that recruited and then died within the census interval, and thus went unrecorded. Annual recruitment rates could be approximately adjusted by correcting with the mortality rate of trees in the 10–14.9 cm gbh class (m_{a10}): $r_a' = 100 \times r_a/(100 - m_{a10})$ (following Phillips *et al.* 1994). As a result recruitment rates increased slightly.

When surviving small trees which had gbhs $\geqslant 50$ cm in 1996, and regressors were excluded (so that n_s and n_{96} lay strictly within $10-<50$ cm gbh), rr_p and rr_a for this class increased slightly (table 2). Three trees in plot 1 (but none in plot 2) recruited (from <10 cm gbh) to $\geqslant 50$ cm gbh in ten years; thus almost all recruits lay in the $10-<50$ cm range.

Considering all trees that survived to be the 1996 population, i.e. including those whose gbhs fell below 10 cm, then plot 1's density decreased by 2.52% from 1986 to 1996 and plot 2's by 0.80%. If the regressors were excluded then the decreases became 4.68 and 2.81%, respectively.

For the small trees ($10-<50$ cm gbh), mortality rates were similar to those for all trees, but because numbers of recruits remained nearly the same (these almost all being within the 10–50 cm class), recruitment rates were higher and the percentage changes in the populations were less—a 0.73% decrease in plot 1 and a 0.20% increase in plot 2 with regressors included, and 3.08 and 1.96% decreases with regressors excluded. (If trees which grew to $\geqslant 50$ cm gbh were excluded, but regressors included, these changes became -3.12 and -1.69%, respectively.) Adjusted recruitment rates were *ca.* 2% higher than mortality rates.

For trees $\geqslant 10$ cm dbh (i.e. $\geqslant 31.4$ cm gbh, the pantropical limit used in many studies), m_p was 18.8 and

Table 2. *Basic population parameters for all* ($\geqslant$ *10 cm gbh*) *and small* (*10–*$<$ *50 cm gbh*) *trees in the two 4-ha plots at Danum in 1986–1996 and the periodic and annualized mortality* (m_p, m_a) *and recruitment* (r_p, r_a) *rates based on 1986 populations, with recruitment based on 1996 populations* (rr_p, rr_a) *and annual recruitment rate* (r'_a) *adjusted for the unaccounted dead recruits* ($m_{a\text{-adj}}$)

(For small trees, in (*a*), the values in parentheses are recalculated changes when survivors $\geqslant$50 cm gbh were excluded.[c] Rates rr_p and rr_a are based on n_{96} and n_s corrected for regressors (all) and for regressors and those advancing (small).)

parameter	all		small	
	plot 1	plot 2	plot 1	plot 2
(*a*) number of trees				
in 1986, n_{86}	8973	8971	8111	8156
surviving, n_s	7466	7819	6771	7092
			(6580)	(6938)
dying, n_d	1507	1152	1340	1064
recruiting, n_r	1281	1080	1281	1080
			(1278)	(1080)
in 1996, n_{96}	8747	8899	8052	8172
			(7858)	(8018)
difference, n_{diff}	-226	-72	-59	$+16$
			(-253)	(-138)
regressing, n_{sx}	194	180	191	176
in all, n_{all}	10 254	10 051	9392	9236
(*b*) mortality				
m_p (% 10 yr^{-1})[a]	16.15	13.38	15.89	13.59
m_a (% yr^{-1})	1.752	1.421	1.722	1.446
recruitment				
r_p (% 10 yr^{-1})	13.73	12.54	15.19	13.79
r_a (% yr^{-1})	1.291	1.191	1.420	1.304
r'_a (% yr^{-1})[b]	1.312	1.208	1.443	1.323
rr_p (% 10 yr^{-1})	14.39	12.90	16.03	14.35
rr_a (% yr^{-1})	1.572	1.387	1.769	1.555

[a] 98% confidence limits: all: plot 1, 15.36–16.96; plot 2, 12.65–14.13; small: plot 1, 15.05–16.73; plot 2, 12.81–14.38.

[b] $m_{a(10-15)}$ for plot 1, 1.570; plot 2, 1.420; used to adjust r_a.

[c] n of trees 10–$<$ 50 cm gbh in 1986 which survived to $\geqslant$50 cm gbh in 1996: plot 1, 191; plot 2, 154; plus 3 and 0 advancing from $<$ 10 to $\geqslant$50 cm gbh.

13.1% for plots 1 and 2, respectively, and the corresponding m_a was 2.07 and 1.30%. In plot 1 there were proportionally more trees $\geqslant$10 cm dbh dying than overall (table 2) but little size effect for plot 2.

Individuals of pioneer species (following Newbery *et al.* (1992), with taxonomic revisions) numbered 279 and 247 in plots 1 and 2 in 1986, and 253 and 248 (corrected for regressors) in 1996. The corresponding rates of m_p were 21.0 and 13.1%, and r_p were 13.1 and 14.3%, respectively. Population changes ($\ln(n_{96}) - \ln(n_{86})$; ten-year corrected, see also later use) were -0.094 and 0.004. The combined pioneer population thus stayed low and virtually constant.

(d) *Mortality and recruitment across species*

Two types of analysis were followed: one based on species, one based on subplots. For each species with $n_{86} \geqslant 10$, the periodic and annual mortality and recruitment rates were calculated, first for all trees, $\geqslant$10 cm gbh, and second for small trees, 10–$<$ 50 cm gbh. Analysis with all trees involved 135 and 136 species in plots 1 and 2, respectively (not exactly the same list of species for each plot), and analysis of small trees 128 and 126 species, respectively. In the first instance, species with more than ten individuals were considered to have unreliable estimates of mortality and recruitment rates, and a large majority of the incompletely known taxa (to genus largely) fell in this abundance class of one to nine trees per plot. Furthermore, in this class only four out of 241 species in plot 1 and three out of 238 species in plot 2 had five or more recruits. Of those taxa newly recruiting by 1996, only five had five or more individuals (maximum of ten). Thus, ignoring these very few rarer and mostly poorly identifiable taxa from the start and end of the census is likely to have had little effect on the main patterns.

Across species within each plot, m_p was not significantly correlated with $\ln(n_{86})$ for both all and small trees (table 3). Mortality showed a characteristic wedge-shaped pattern (figure 1*a*) with greater spread in mortality rates among the species with the smaller population sizes (typically 10–30 trees per plot). This effect is in keeping with the expected confidence limits if all species had a mortality rate equal to the whole plot mean; smaller samples (approximately ten) are naturally more likely to have occasionally large mortalities on a simple chance sampling basis. In contrast, r_p was significantly and positively correlated with $\ln(n_{86})$ in both plots (table 3) when all trees were involved but the relationship was much weaker with small trees. Thus common species had greater rates of recruitment than rarer ones, and when the trees $\geqslant$50 cm gbh were excluded the r_p among the rarer species increased, i.e. the recruitment became a larger proportion of the smaller trees of rare canopy species. Recruitment and mortality were correlated positively across species but only when small trees were considered (table 3); species with higher proportions dying also had generally higher proportions recruiting.

To demonstrate further the important effect of small sample size on mortality, more abundant species—those with $n_{86} \geqslant 30$ individuals per plot—were subsampled by selecting at random ten individuals 20 times and pooling the values of all the resulting counts of mortalities. This involved 71 species from plot 1 and 68 from plot 2 (1420 and 1360 values). In plot 1, 11.3% of outcomes had four or more mortalities and in plot 2 this was 7.2%. The observed frequency distributions were significantly different ($\chi^2 = 186$ and 245, respectively, d.f. $= 5$, $p \ll 0.001$) to those expected based on the mean m_p for the species and plots used; there were relatively many more cases of zero and four or more mortalities. This is what was found for species with small sample sizes (10–20) in figure 1*a*.

When recruitment was calculated on the n_{96} basis (all trees), numbers of recruits can also be viewed as a binomial variable. For the 129 and 135 calculable values based on just recruitment and 1996 population sizes (regressors not removed in this case), figure 1*b* shows that again most points fell within the 98% confidence limits expected by chance sampling about the mean recruitment. The main difference from mortality is that many species had zero recruitment, these falling below the lower confidence line. To compare the two forms of recruitment rate the 123 and

Table 3. *Correlations for all* ($\geqslant 10$ *cm gbh*) *and small* (10–< 50 *cm gbh*) *trees in each plot at Danum across species with* $\geqslant 10$ *individuals per plot in 1986, and/or* $\geqslant 10$ *valid–reliable growth estimates, for periodic mortality* (m_p) *and recruitment* (r_p) *and 1986 population size* (n_{86}), *mean girth* (*gbh*), *and absolute* (*agr*) *and relative* (*rgr*) *growth rates*

(Correlation coefficients: r, Pearson's; r_s, Spearman's.)

		all		small	
		plot 1	plot 2	plot 1	plot 2
r_s	n	[135,136]		[128,126]	
$\ln(n_{86})$	m_p	0.008	0.026	0.126	0.079
	r_p	0.271^{**}	0.321^{***}	0.186^{*}	0.120
m_p	r_p	0.162	0.133	0.292^{***}	0.298^{***}
r_s	n	[111,124]		[105,116]	
ln(gbh)	m_p	0.091	0.030	0.070	−0.003
	r_p	0.093	0.073	0.002	−0.034
ln(agr)	m_p	0.155	0.145	0.126	0.181
	r_p	−0.004	0.148	0.106	0.250^{**}
ln(rgr)	m_p	0.161	0.169	0.131	0.180
	r_p	0.105	0.250^{**}	0.184	0.283^{**}
r	n	[113,126]		[107,118]	
ln(gbh)	ln(agr)	0.726^{***}	0.644^{***}	0.613^{***}	0.581^{***}
	ln(rgr)	0.519^{***}	0.429^{***}	0.486^{***}	0.474^{***}

$^{*}p \leqslant 0.05$, $^{**}p \leqslant 0.01$, $^{***}p \leqslant 0.001$.

131 species in plots 1 and 2 with calculable rates (and also valid growth rates) in common were taken, and of these 94 and 93, respectively, were non-zero recruitment values. Both r_p and rr_p (uncorrected) were very strongly correlated ($r_s = 0.987$ and 0.988, $p << 0.001$, for plots 1 and 2). Above *ca.* $r_p = 30\%$ the scatter between the estimates increased due to the extent by which mortality reduced n_{86} to n_s in the interval, especially in those species with smaller populations sizes. Therefore, apart from the top nine recruiting species in each plot, r_p and rr_p differed little, but only for rr_p are the binomial limits valid.

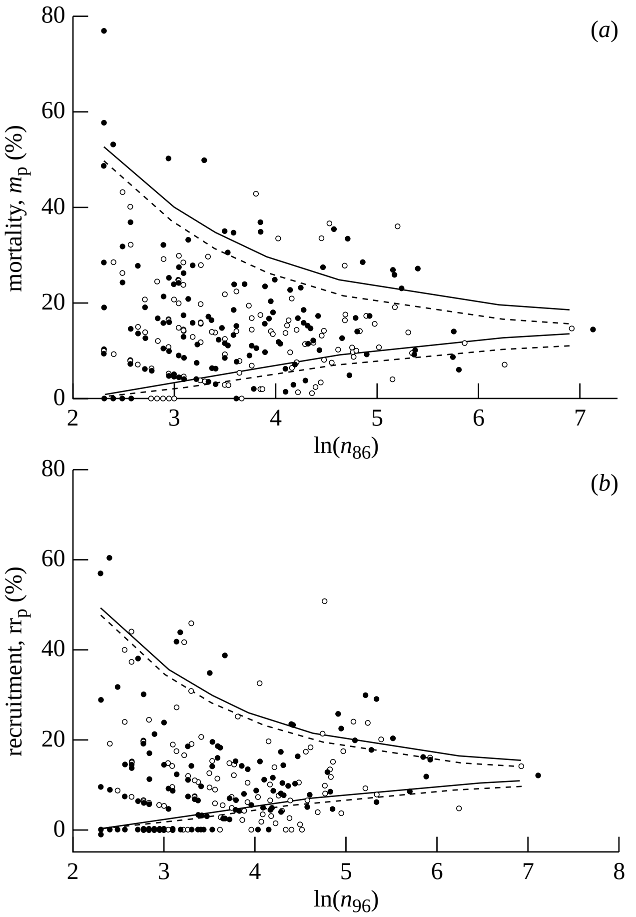

Figure 1. Relationships between (*a*) periodic (ten-year) mortality (m_p) and population sizes in 1986 (n_{86}), and (*b*) periodic recruitment (rr_p) and population size in 1996 (n_{96}), for all trees $\geqslant 10$ cm gbh of the 135 and 136 species with $n_{86} \geqslant 10$, and of the 129 and 135 species with $n_{96} \geqslant 10$, in plots 1 (filled circles) and 2 (open circles), respectively, at Danum. The 98% confidence limits to the binomial distribution, based on the pooled estimates of m_p and rr_p for these species, are shown for plots 1 (solid line) and 2 (dashed line).

(e) *Growth*

Girth (gbh) increment rates (absolute and relative) were found for those species with $\geqslant$ten reliable measurements. All data were censored to remove tree girths based on the relascope measurements: these latter had large and variable absolute growth rates of 22 ± 6 (s.e.) and 59 ± 10 mm yr^{-1} in plots 1 and 2, respectively ($n = 29$ and 23). Only trees for which the paint mark persisted were used. From the alive categories those regrowing or coppicing from below a break lower than the mark (AC, AD, AH) were excluded. Furthermore, those trees remeasured over buttresses, deformed by excrescences, fluted stems, stilt or adventitious roots; where lianas were deforming, embedded or fused; or the bark was stripped, delaminated or split were also excluded.

Some trees showed negative growth: 722 out of the 7044 uncensored valid trees (i.e. excluding those without certain remeasurement but including the relascope records) in plot 1, and 940 out of the 7407 equivalent trees in plot 2. Plotting logit-transformed proportions in increasingly negative growth class intervals showed a clear negative linear decline (very closely matching in both plots) down to -0.4 mm yr^{-1} and then an increase and flattening of the distribution. This hiatus marked an operational threshold: trees with $\leqslant -0.4$ mm yr^{-1} (74 in plot 1 and 54 in plot 2) were taken to be due to mistakes or gross (relascope or reading) errors, while those > -0.4 mm yr^{-1} were accepted as part of the population. These slight negative values, forming part of a logistic distribution, were due to 'normal' remeasurement errors and natural reasons such as shrinkage (sometimes prior to death), unapparent bark loss, etc. Using a steel tape on both enumerations in exactly the same way should have avoided bias but use of calipers instead of tape for some trees may have led to a small influence on remeasurements. These negative growth rates applied to all size classes not just the 10–< 15 cm one. In summary, taking censored, validly remeasured trees with growth rates above this threshold led to 6537 and 6890 growth rate values for plots 1 and 2, respectively, these being 87.6 and 88.1 of the survivors.

Mean absolute (agr) and relative growth (rgr) rates were strongly and significantly correlated with mean gbh across species (the variables logarithmically transformed),

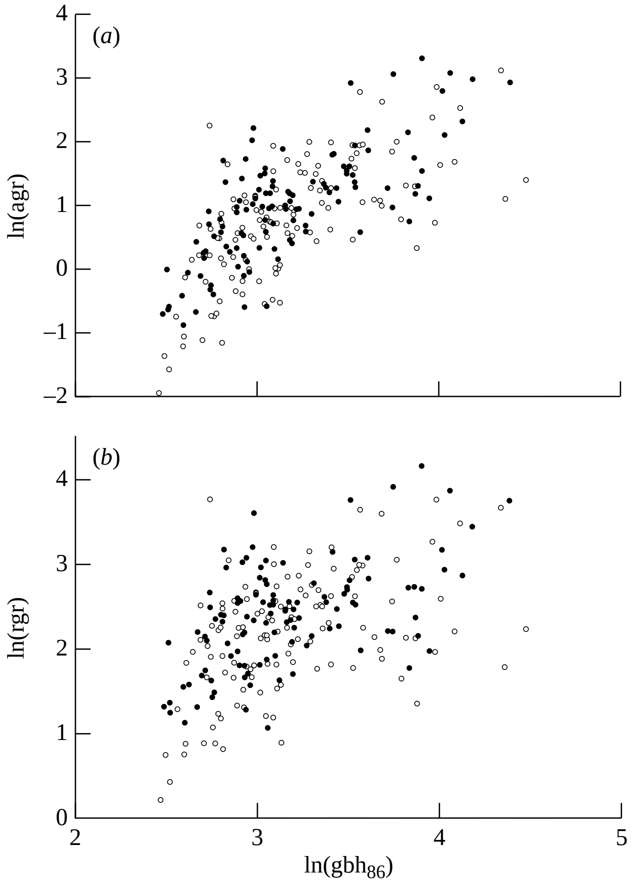

Figure 2. Relationships between (*a*) absolute (agr), and (*b*) relative (rgr) mean growth rates over the period 1986–1996 and tree girth in 1986 (gbh_{86}), for all trees ⩾10 cm gbh in 1986 of the 111 and 124 species with $n_{96} \geqslant 10$ trees and reliable remeasurements (see text) in plots 1 (filled circles) and 2 (open circles), respectively, at Danum. The untransformed units for agr were mm gbh yr^{-1} and for rgr mm mm^{-1} gbh $yr^{-1} \times 10^3$.

both for all and small trees (table 3, figure 2). Because within-species individual growth rates and gbhs were not always normally distributed, correlations were made using the means of the logarithms of individual values, and also using the medians per species, but the results were similar to those using the logarithms of the means per species. Thus trees with on-average larger stems tended to have larger growth rates. There was more variation between species in relative than absolute growth rates for species of given mean gbh (figure 2). Relationships between m_p and r_p and gbh, agr and rgr were not strong (table 3). In plot 2 alone rgr was significantly positively correlated with r_p for all and small trees, i.e. those species recruiting faster also grew faster especially for the smaller trees.

(f) *Mortality, recruitment and growth across subplots*

At the subplot level, combining all species per subplot, sample size was not so much of a limitation. Numbers of trees in 1986 varied between 55 and 118 (mean 89.7) in plot 1, and 58 and 126 (mean 89.7) in plot 2. Since contiguous 20 m × 20 m subplots are not likely to be statistically independent, 25 out of the 100 subplots per plot were subsampled at random 1000 times and the mean correlation coefficients found for the pairs of variables of interest (table 4). (These coefficients were generally slightly smaller than those based on those using all 100 values.) Mortality, m_p, was very weakly correlated with $\ln(n_{86})$, but r_p was significantly negatively correlated in both plots (table 4*a*, figure 3*a*). Neither rate was correlated with mean gbh per subplot, though both were moderately correlated, positively, with agr (table 4*a*), and just significantly so for r_p in plot 2. Rgr was more strongly and consistently correlated with r_p (figure 3*b*), but not m_p, in both plots.

Table 4. *Correlations between mortality and recruitment (periodic, and* r_p*; and counts per plot* n_d *and* n_r*) across 100 subplots (20 m × 20 m) within each plot at Danum, with the 1986 population densities (*n_{86}*) and basal area abundance (*m^2 *subplot,* ba_{86}*) and mean subplot girth (gbh), absolute (agr) and relative (rgr) growth rates for all (⩾10 cm gbh) trees and partly for small (10–< 50 cm gbh) trees using Pearson's r (and Spearman's* r_s *in brackets) from 1000 sets of n = 25 random subplots*

	plot 1		plot 2	
(*a*) rates	m_p	r_p	m_p	r_p
all trees				
$\ln(n_{86})$	−0.051	-0.502° $[-0.414^{(*)}]$	0.069	-0.505^{**} $[-0.486^{\circ}]$
$\ln(ba_{86})$	0.082	0.038	0.003	−0.051
ln (gbh)	0.064	−0.042	0.087	−0.063
ln (agr)	0.250	0.428 $[0.461^{*}]$	0.302	0.467° $[0.452^{*}]$
ln (rgr)	0.157	0.547^{**} $[0.562^{**}]$	0.267	0.589^{**} $[0.589^{**}]$
small trees				
$\ln(n_{86})$	−0.105	-0.511^{**} $[-0.427^{*}]$	−0.113	-0.503° $[-0.477^{*}]$
$\ln(ba_{86})$	0.074	-0.404^{*} [−0.352]	−0.028	-0.463° $[-0.483^{*}]$
(*b*) counts	n_d	n_r	n_d	n_r
all trees				
$\ln(n_{86})$	$0.395^{(*)}$	−0.287	0.347	−0.262
$\ln(ba_{86})$	0.080	0.037	0.023	−0.039
small trees				
$\ln(n_{86})$	0.361	−0.248	0.248	−0.233
$\ln(ba_{86})$	0.405^{*}	−0.202	0.241	−0.298

$^{*}p \leqslant 0.05$, $^{(*)}$ just < 0.05, $^{\circ}p \leqslant 0.02$, $^{**}p \leqslant 0.01$, $^{***}p \leqslant 0.001$.

In marked contrast to density of stems, the basal area per subplot of all trees showed no correlation with either m_p or r_p (table 4*a*). These correlations (with $n = 100$) were very similar when small trees were used, except that in the case of ba_{86}, r_p was negatively and significantly correlated in both plots. This indicates that density of small trees per subplot (and their ba) was much more important, especially in relation to recruitment patterns, than the highly variable basal areas of all trees, this strongly influenced by the less frequent large (and taller) trees > 50 cm gbh. (Densities of small trees were only slightly less than those of all trees: 45–110 (mean 81.1) and 51–118 (mean 81.6) in plots 1 and 2, respectively.) Because of the slight non-normality in the data, some correlations of interest were rerun with a Spearman's non-parametric test, these showing supporting strong correlations (table 4*a*).

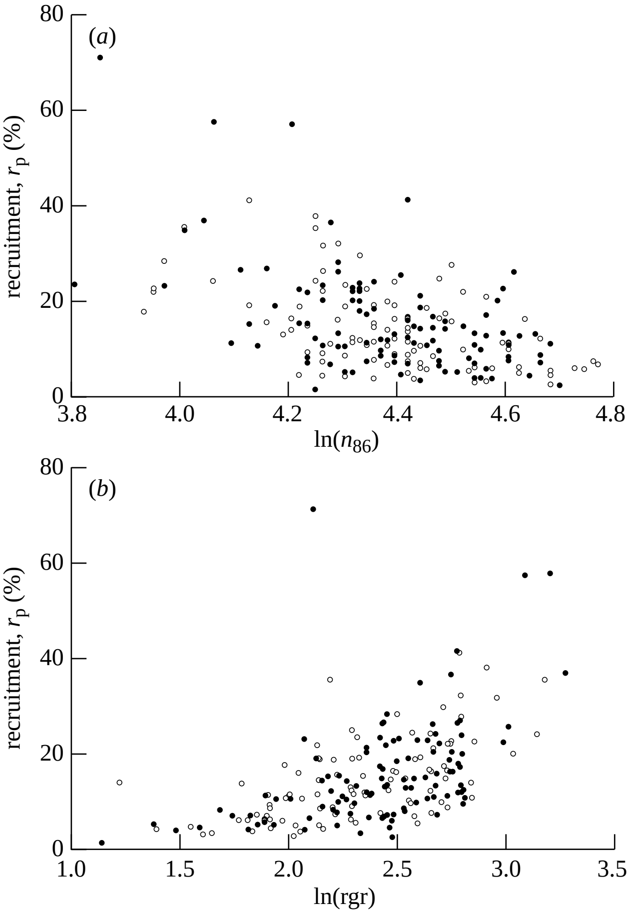

Figure 3. Relationships between periodic (ten-year) recruitment (r_p) per subplot and (*a*) population sizes in 1986 (n_{86}), and (*b*) mean relative growth rate (rgr), based on reliable remeasurements (see text), for all trees $\geqslant 10$ cm gbh in 1986 in the 100 subplots of plots 1 (filled circles) and 2 (open circles) at Danum. Original units for rgr as figure 2.

When numbers of recruits (n_r) per subplot were correlated with $\ln(n_{86})$ the significance fell compared with r_p, indicating that this latter negative correlation was in part due to the proportions involved; n_r was likewise unrelated to $\ln(\text{ba}_{86})$, both for all and small trees (table 4*b*). But n_d was positively correlated with $\ln(n_{86})$, although just not significantly for small trees. Hence as n_r decreased with $\ln(n_{86})$ (and ba_{86}, small) and was strengthened when expressed as a percentage r_p, the positive trend for n_d was compensated for when expressed as a percentage m_p. Thus, while subplots with low numbers of small trees (and small-tree ba_{86}) had more recruits and faster rates of recruitment, they had fewer deaths, yet the rate of mortality evened out across the range of subplot densities. Subplots with greater recruitment also had faster (largely small-stemmed) tree growth rates.

(g) *Mortality, recruitment and topography*

Using again the randomization procedure (1000 runs of 25 subplots), neither mean elevation nor slope per subplot (as calculated in Newbery *et al.* (1996)) were significantly correlated ($p > 0.05$) with any of m_p, r_p, n_d and n_r, for all or small trees. The only consistent pattern was a negative relationship between m_p and elevation for both all and small trees $r = -0.248$ to -0.265, $p = 0.05$–0.10), suggesting less mortality on ridges than on lower slopes.

(h) *Mortality in relation to tree size*

Six classes of increasing gbh were created by successively doubling the lowest 5 cm class (10–< 15 cm) (figure 4), which ensured that the large-gbh classes had sufficient trees. Numbers were corrected to a ten-year basis by linear interpolation (i.e. from 10.4 yr for plot 1 and 9.6 yr for plot 2). For all trees (figure 4*a*), the proportion dying increased in plot 1 to the intermediate size classes and then declined, while in plot 2 it declined overall. Understorey and intermediate tree species (figure 4*b*,*c*) had increasing mortalities over the first four classes (to *ca.* 85 cm gbh), there being almost no trees beyond this girth class. In marked contrast, overstorey tree species had the highest rates of mortality in the smallest size classes (figure 4*d*), the lowest ones in the fourth class and then this rising again for very big trees. These patterns were matched by the Euphorbiaceae (typical understorey trees, figure 4*e*) and Dipterocarpaceae (typical overstorey trees, figure 4*f*), and with an even more pronounced drop in mortality in the 45–< 85 cm gbh class for the dipterocarps. If 98% confidence limits are an approximate guide to likely significant differences, mortality was significantly greater (by *ca.* threefold) in the dipterocarps than euphorbs in the 10–< 15 and 15–< 25 cm gbh classes. The low and significant dip for dipterocarps suggests the subcanopy trees with high survivorship were rapidly growing on into the main canopy. The two storeys showed opposite and compensating trends in mortality with size.

(i) *Comparisons between the plots*

From the foregoing results the more interesting and reliable size class appears to be the small one (10–< 50 cm gbh) and comparisons between plots, summaries of species and modelled predictions are better focused on these trees. This conclusion was also reached from floristic analysis relating species patterns to topography (Newbery *et al.* 1996). Table 5 therefore shows the dynamics of the first 50 most abundant species in each plot, these forming a joint list of 64 species but from which the problematic *Scorodocarpus borneensis* has been separated. These 64 are the same used in Newbery *et al.* (1996). The 53 and 59 species with $n_{86} \geqslant 10$ in plots 1 and 2 formed 73.9 and 74.8% of the small trees in total, respectively.

Population sizes of the most abundant 49 species which were common to the two plots (table 5) were similar in both plots ($r_s = 0.722$, d.f. $= 47$, $p < 0.001$) and lay closely about the 1:1 line (figure 5*a*). These 49 species constituted 71.0 and 66.6% of the small trees in total in plots 1 and 2. Population changes ($\ln(n_{96} - \ln(n_{86}))$, corrected for advanced growth and regressors, to a ten-year basis, were also strongly correlated ($r_s = 0.608$, $p < 0.001$) with the storeys well intermixed (figure 5*b*).

For these 49 spp. 91 trees in plot 1 and 81 in plot 2 grew to $\geqslant 50$ cm gbh and were excluded from the 10–< 50 cm gbh n_{96} populations, of which 22 and 13, respectively, were *Shorea parvifolia*—32.5 and 21.9% of this species' stems, the most for any single species in the two plots taken together. In plots 1 and 2, 191 and 176 trees respectively regressed below 10 cm gbh by 1996 (table 2). Expressed as a

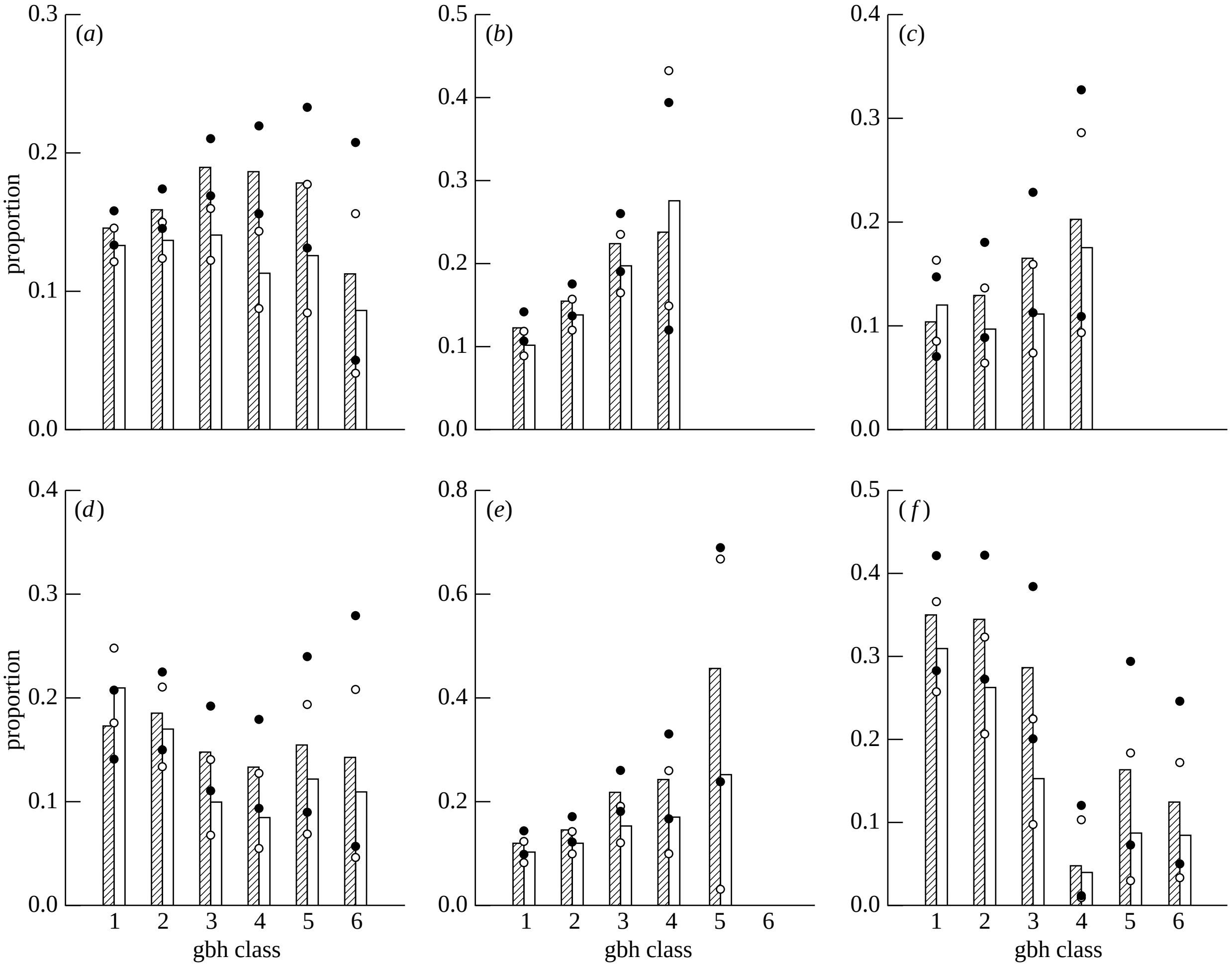

Figure 4. Proportions of trees dying in successively doubled size class intervals $\geqslant 10$ cm gbh for species (*a*) of all trees in the plots; (*b*) from the understorey, (*c*) from the intermediate storey, and (*d*) from the overstorey, pooled from the 50 commonest species in each plot, i.e those 64 defined in table 5 for trees 10–< 50 cm gbh; and (*e*) from the family Euphorbiaceae and (*f*) from the family Dipterocarpaceae (all species in plots) at Danum. Hatched bars, plot 1; open bars, plot 2. The 98% binomial confidence limits are shown for each class in plots 1 (filled circles) and 2 (open circles). For a size class with no bar there were no trees occurring. Size classes: 1, 10–14.9; 2, 15–24.9; 3, 25–44.9; 4, 45–84.9, 5, 85–164.9; 6, $\geqslant 165$ cm gbh.

percentage of the n_{86} population sizes, the following species had prominently high occurrences: *Pentace laxiflora* (plot 1, 15.1%; plot 2, 11.4%), *Dillenia sumatrana* (plot 1 only, 16.1%), *Litsea caulocarpa* (10.1 and 6.1%) and *Syzygium castaneum* (17.8 but 2.1%). These species appear to coppice well when damaged by wood fall.

Periodic mortality and recruitment were significantly correlated across plots ($r_s = 0.638$ and 0.658, $p < 0.001$) and, apart from two species with very high mortalities, storeys were again not scattered similarily about, or separated along, the central 1:1 line (figure 5*c*,*d*). Thus species appeared to have characteristic rates of mortality and recruitment which were replicated across plots. Chi-squared tests on ten-year-corrected m_p values showed (for 33 testable cases—numbers of dead trees being too low otherwise) only two species with significant ($p < 0.05$) differences: *Dimorphocalyx muricatus* and *Mallotus penangensis* had greater m_p values for plot 1 than plot 2. For recruitment only one out of 26 valid cases was significant with a greater r_p for *Reinwartiodendron humile* in plot 2 than plot 1.

Absolute and relative growth rates showed even closer agreement than m_p and r_p between plots ($r = 0.881$ and 0.860, $p < 0.001$), with two to three clearly very high values (figure 5*e*,*f*); rgr values were generally less in plot 2 than plot 1, and a curvature indicating that slow growers tended to be even more slow growing in plot 2 than 1. The storeys formed a sequence along the 1:1 line, with generally faster growth rates for the overstorey than understorey species, recalling that these graphs show comparisons for small trees (10–< 50 cm gbh) only within and under the subcanopy.

Taking the means of mortality, recruitment, population change and growth in the two plots for each species, for rgr versus r_p (figure 6*a*) two separate curves are just discernable where rgr increases more steeply with r_p for the overstorey than for the understorey, but with some notable exceptions. *Shorea fallax* (overstorey) follows the understorey trend whereas *Cleistanthus glaber*, *Buchanania insignis* and *Polyalthia rumphii* behave more like overstorey species. Among the intermediate-storeyed species, *Mallotus penangensis* is strikingly different from the rest of its group in its relatively high recruitment but moderate rgr. Two understorey species with low rgr were *Antidesma neurocarpum* and *Hydnocarpus borneensis* (see table 5).

Adding six other overstorey dipterocarps that were abundant in only one plot (table 5) to figure 6*a*

Table 5. *Periodic mortality* (m_p) *and recruitment* (r_p) *rates* (*decrease or increase over 1986 population sizes*, n_{86} *% 10 yr*$^{-1}$) *and relative growth rates in stem girth* (*rgr; mm mm*$^{-1}$ *yr*$^{-1}$ $\times 10^3$) *for small trees* (*10–< 50 cm gbh*) *in plots 1 and 2 at Danum for the 50 most abundant species in 1986*[a] *in each plot as listed in Newbery* et al. (*1996: table 5*)[b] *with their storeys* (*St*)[c]

(— indicates that in one plot there were insufficient trees to estimate the parameters, and those species marked # are not included in the plot–plot comparisons. The 49 species in common between the plots are classified as four-character codes (Cl)[f].)

species	St	plot 1				plot 2				Cl
		n_{86}	m_p (%)	r_p (%)	rgr (yr^{-1} × 10^3)	n_{86}	m_p (%)	r_p (%)	rgr (yr^{-1} × 10^3)	
Mallotus wrayi	1	1246	14.5	11.7	9.0	1010	14.6	14.2	9.5	M—
Dimorphocalyx muricatus	1	315	14.0	8.2	7.2	523	7.3	4.7	4.6	-rg-
Ardisia colorata	1	214	9.4	23.3	10.2	354	11.8	16.8	11.9	-R–
Fordia splendidissima	1	315	8.9	17.7	11.0	201	14.0	21.8	9.2	-R-D
Madhuca korthalsii	3	283	5.4	14.9	11.8	149	1.4	11.3	11.2	mR-D
Maschalocorymbus corymbosus[d1]	1	222	27.3	15.6	8.5	182	36.1	13.7	8.2	MR-d
Shorea fallax	3	175	23.4	34.3	16.6	151	20.5	29.4	20.1	MRGD
Polyalthia cauliflora	1	215	10.3	5.8	5.3	108	16.5	5.8	4.4	-rgd
Litsea caulocarpa	1	172	26.8	31.8	17.3	145	15.8	26.6	15.4	MRG-
Cleistanthus glaber	1	75	15.4	0.0	8.2	210	9.7	7.8	6.8	-r-d
Reinwartiodendron humile[d2]	1	127	28.3	3.8	5.9	127	18.2	11.6	6.4	M-gd
Baccaurea stipulata	2	125	9.3	4.6	7.9	107	9.9	4.0	8.7	mr-d
Polyalthia xanthopetala	1	170	25.3	19.1	8.8	61	18.8	20.5	11.2	MR–
Lophopetalum beccarianum	1	112	5.1	28.3	19.4	116	8.8	16.8	11.6	mRGD
Aporosa falcifera[d3]	3	106	14.5	10.0	12.4	98	11.8	9.7	13.8	–Gd
Mallotus penangensis	2	117	15.7	29.8	12.7	82	3.7	22.4	10.7	mR-D
Pentace laxiflora	3	93	16.6	16.6	23.9	90	10.5	12.8	22.0	-RGd
Polyalthia sumatrana	3	78	8.6	9.9	17.5	100	8.4	16.7	17.6	mRG-
Litsea ochracea	2	66	18.9	11.6	16.6	83	13.8	0.0	11.9	MrGd
Koilodepas laevigatum#	(2)	0	—	—	—	144	10.1	3.6	6.4	
Dacryodes rostrata	2	57	6.8	5.1	9.9	86	7.3	1.2	7.2	mr–
Knema latericia	1	60	1.6	20.8	12.1	81	2.6	20.5	12.4	mRGD
Dysoxylon cyrtobotryum	3	62	14.0	9.4	17.2	78	13.3	6.7	20.8	–Gd
Polyalthia rumphii	1	75	11.6	7.7	12.4	64	6.6	6.6	11.6	m—
Xanthophyllum vittelinum	2	33	0.0	2.9	5.8	97	10.8	0.0	2.5	mrgd
Syzygium elopurae	2	66	17.5	0.0	6.9	63	9.8	1.6	4.8	-rgd
Shorea johorensis	3	67	45.8	21.5	59.7	62	45.4	15.1	38.5	MRGd
Chisocheton sarawakanus	3	69	11.2	12.6	15.1	58	9.1	9.1	11.1	m-Gd
Shorea parvifolia	3	65	42.8	29.5	67.4	62	45.6	15.2	55.6	MRGd
Antidesma neurocarpum	1	63	22.9	13.8	3.1	56	33.6	9.3	2.9	M-gd
Buchanania insignis	1	30	9.6	3.2	13.4	87	8.4	0.0	5.8	mr-d
Hydnocarpus borneensis	1	44	2.2	15.4	6.0	63	9.9	3.3	2.3	m-g-
Mallotus stipularis	2	69	12.4	11.0	9.9	36	5.7	17.0	9.8	mR–
Parashorea melaanonan	3	50	26.9	13.4	14.3	52	18.3	6.1	13.1	M-Gd
Dehaasia gigantocarpa	1	65	7.4	4.4	6.1	38	0.0	8.2	5.3	mrg-
Alangium javanicum[d4]	2	44	8.8	8.8	6.3	50	14.7	10.5	8.6	–gd
Syzygium chrysanthum	3	66	16.0	8.7	8.5	25	12.6	8.4	5.8	–gd
Gonystylus keithii	3	54	1.8	19.7	14.5	37	14.1	5.6	7.7	m—
Lithocarpus niewenhuizii	3	40	14.4	7.2	13.7	50	8.3	6.3	19.3	–Gd
Barringtonia lanceolata	3	50	3.8	15.4	9.5	36	0.0	2.9	5.6	m–D
Hopea nervosa#	(3)	(4)	—	—	—	82	40.3	72.8	25.8	
Diospyros elliptifolia	2	47	16.5	4.1	5.3	27	3.9	0.0	5.3	-rgd
Ryparosa hullettii#	(1)	78	11.2	3.7	2.9	(6)	—	—	—	
Magnolia gigantifolia[d5]	1	22	13.1	8.8	6.8	60	15.8	0.0	3.5	-rgd
Popowia pisocarpa	1	52	20.5	5.6	5.7	30	14.0	0.0	2.4	Mrgd
Popowia odoardoi	1	54	25.0	12.5	4.8	28	29.9	7.5	6.3	M-gd
Shorea pilosa#	(3)	(6)	—	—	—	75	19.1	32.8	30.1	
Hydnocarpus polypetala#	(1)	(1)	—	—	—	77	1.3	2.7	8.9	
Polyalthia congesta	2	38	7.6	2.5	11.4	39	13.4	5.4	12.4	-r-d
Magnolia candollei var. singapurensis[d6]	1	35	13.8	2.8	4.9	58	14.3	0.0	3.7	-rgd
Syzygium tawaense	3	40	12.0	12.0	13.8	33	16.0	19.2	15.6	-RG-
Pternandra galeata[d7]	2	38	22.9	17.8	8.0	32	19.4	6.5	12.3	M–d
Shorea pauciflora#	(3)	70	27.5	27.5	17.6	(0)	—	—	—	
Dillenia sumatrana#	(1)	(0)	—	—	—	67	14.5	9.7	7.1	
Aglaia silvestris[d8]	3	43	20.2	4.5	10.5	25	12.5	12.5	15.9	M-gd
Valica dulitensis#	(3)	(1)	—	—	—	46	15.6	8.9	10.2	

(*Cont.*)

Table 5. (*Cont.*)

species	St	plot 1 n_{86}	plot 1 m_p (%)	plot 1 r_p (%)	plot 1 rgr (yr$^{-1}\times10^3$)	plot 2 n_{86}	plot 2 m_p (%)	plot 2 r_p (%)	plot 2 rgr (yr$^{-1}\times10^3$)	Cl
Aglaia odoratissima	2	36	18.7	2.7	3.5	19	27.7	5.5	4.9	Mrgd
Knema oblongata#	(1)	(7)	—	—	—	48	2.2	6.5	9.6	
Syzygium castaneum#	(1)	46	33.7	0.0	13.0	(6)	—	—	—	
Dipterocarpus kerrii#	(3)	(0)	—	—	—	51	4.0	4.0	13.8	
Cleistocalyx perspicuinervis#	(1)	(3)	—	—	—	42	7.3	4.9	6.0	
Chisocheton pentandrus#	(1)	37	7.9	0.0	7.9	(7)	—	—	—	
Shorea angustifolia#	(2)	(0)	—	—	—	38	21.7	29.8	8.0	
sum of species ($n_{86}\geqslant10$) (plot 1, 53; 2, 59)		5991				6099				
pooled estimates[e]			15.3	13.7			13.6	12.3		
sum of 49 species		5760				5429				
pooled estimates[e]			15.2	13.8			13.6	11.6		
[*Scorodocarpus borneensis–Dysoxylon alliaceum* mixture[e]		73	4.0	10.5		72	11.6	11.6	]	

[a] On taxonomic revision in 1996 one species entered and one species left the 50 first ranked lists for both plots.

[b] Of the 64 species listed in Newbery *et al.* (1996) one is omitted due to taxonomic confusion: *Scorodocarpus borneensis*.

[c] Storeys: 1 understorey (u and (u)), 2 intermediate (i), 3 overstorey (o), following Newbery *et al.* (1996).

Previous names as given in Newbery *et al.* (1996), synonyms now mostly adopted:

[d1] *Maschalocorymbus* sp. [d2] *Aglaia dubia*. [d3] *Aporusa acuminatissima*. [d4] *Alangium ebanaceum* (syn.). [d5] *Talauma gigantifolia* (syn.). [d6] *Talauma singapurensis* (syn.). [d7] *Kibessia galeata* (syn.). [d8] *Aglaia ganggo* (syn.)

[e] Using plot mean time period 1, 10.4 yr and 2, 9.6 yr to correct to ten-year basis.

[f] M,-,m; R,-,r; G,-,g; are the top, mid and lower third ranked values of mean plot m_p, r_p and rgr, respectively; and D,-,d, the high (> +5), medium and low (< −5) percentage changes. NB Two or three short dashes become a longer dash in places.

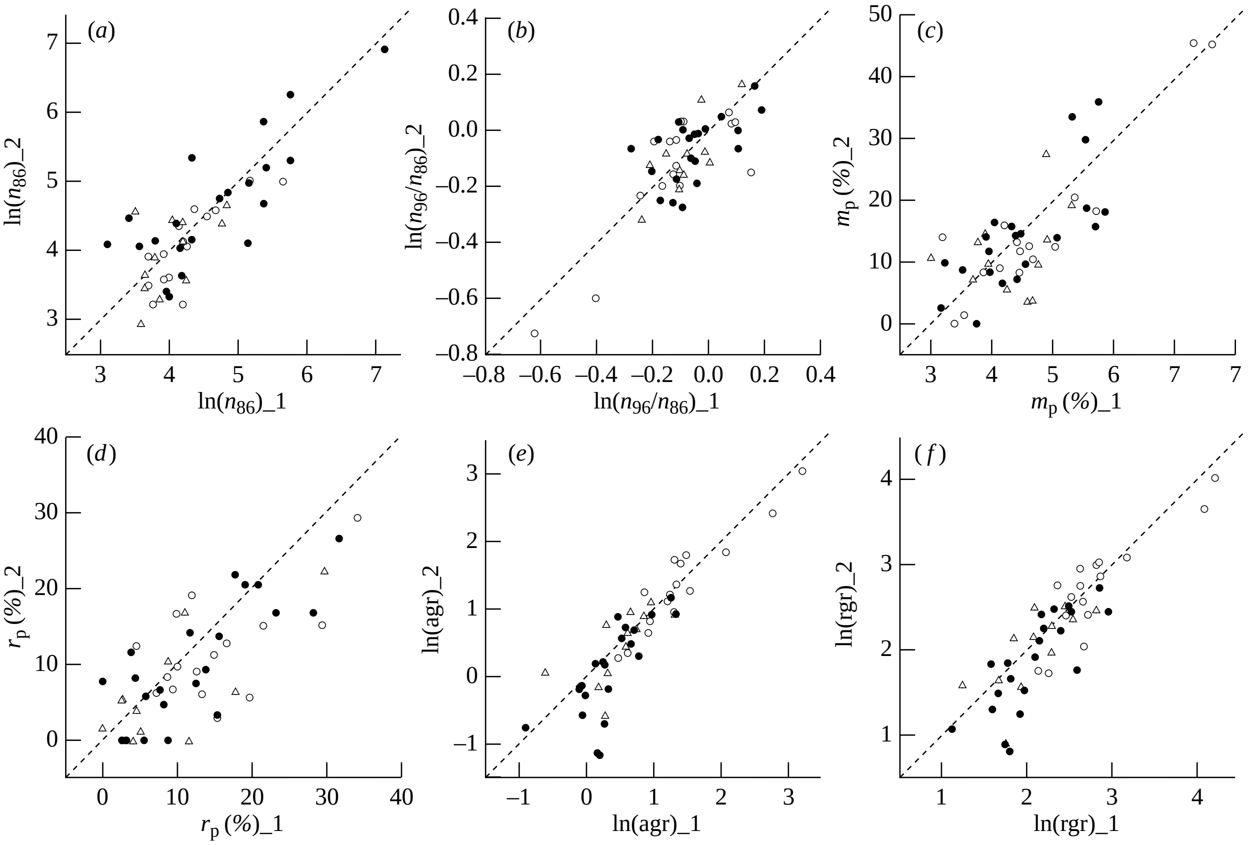

Figure 5. Comparisons between the two plots at Danum for the 49 small-sized (10 − < 50 cm gbh) tree species: (*a*) population sizes in 1986 (n_{86}); (*b*) population change (ln(n_{96})–ln(n_{86})), with advanced trees ⩾50 cm gbh and regressors removed, corrected to ten-year basis; (*c*) periodic (ten-year) mortality (m_p); (*d*) periodic recruitment (r_p); and (*e*) absolute (agr) and (*f*) relative growth (rgr) rates. Structural classes: filled circles, understorey ($n = 21$); open triangles, intermediate-storeyed ($n = 12$); and open circles, overstorey ($n = 16$). Units for agr and rgr are as in figure 2.

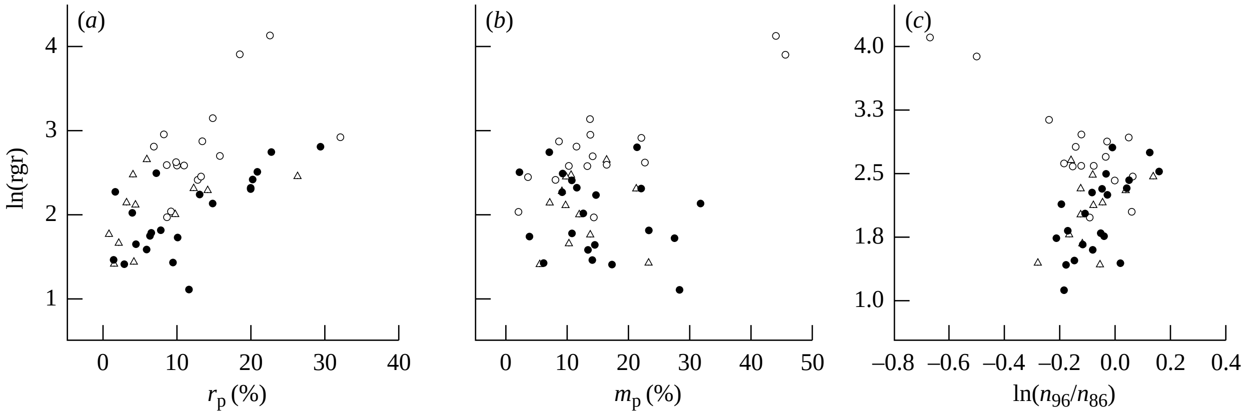

Figure 6. Relationships between relative growth rate (rgr) and (*a*) periodic recruitment (r_p), (*b*) periodic mortality (m_p), and (*c*) population change (as explained in figure 5*b*) using the means (prior to transformation for rgr) of the estimates for the two plots at Danum, for the 49 small-sized (10–< 50 cm gbh) tree species in the structural classes: filled circles, understorey; open triangles, intermediate-storeyed; and open circles, overstorey (group sizes as in figure 5).

Table 6. *Periodic mortality and recruitment rates, growth rates, population sizes and their changes for small trees (10–< 50 cm gbh) using the averages of the estimates for the two plots at Danum for the 49 species in common (cf. table 5), classified according to three storeys (u, understorey; i, intermediate; o, overstorey)*

(The means shown are the means of the species' means per class.)

	storey				
	u	i	o	all	t_{u-o}(d.f.)[b]
	$n = 21$	$n = 12$	$n = 16$	$n = 49$	
periodic					
mortality, m_p (%)	14.76	12.30	16.41	14.70	−0.46 (24)
recruitment, r_p (%)	11.33	7.29	13.33	11.00	−0.85 (34)
growth rates					
absolute, agr (mm yr^{-1})	1.49	1.83	5.38	2.84	−5.32# (26)***
relative, rgr					
(mm mm^{-1} yr^{-1} × 10^3)	8.12	8.47	19.38	11.88	−4.51# (28)***
population					
size per plot, n_{86}	174	61	77	114	2.16# (33)*
change[a], 1986–1996	−0.062	−0.088	−0.137	−0.093	1.38 (21)
percent change[c], ch_p	−5.39	−7.92	−11.18	−7.90	1.31 (24)
turnover[d], to_p	13.04	9.80	14.87	12.85	−0.75 (25)

\# Log-transformed test.

[a] Change $= \ln(n_{96}) - \ln(n_{86})$ in ten years, corrected for advancing (a_p) and regressing (b_p) trees.

[b] Adjusted d.f.

[c] $ch_p = r_p - m_p - a_p - b_p$.

[d] $to_p = (m_p + r_p)/2$.

suggested that *Shorea pilosa* lay on the upper overstorey curve, *S. angustifolia* and *S. pauciflora* joined *S. fallax* on the lower one, and *Dipterocarpus kerrii* and *Vatica dulitensis* lay with the intermediate-storeyed trees with their much lower r_p (in contrast with the four *Shorea*'s higher values). *Hopea nervosa* had an exceptionally high recruitment in plot 2 alone (table 5) and its rgr value would place it at the extreme of the lower curve. Extending the analysis further to include 12 species not in table 5 (these with ⩾30 trees in 1986 in both plots) brought little further insight to the pattern and process represented by figure 6*a* except for one unusual case. *S. argentifolia* had high rgr and mortality in both plots but an outstandingly large difference in r_p (the greatest discrepancy found) with 77% in plot 1 but only 6% in plot 2. This is probably an example of where small sample sizes with large errors place the analysis close to the edge of confidence.

For rgr versus m_p and population change, figure 6*b*,*c* separated out the two very fast-growing dipterocarps *Shorea johorensis* and *Shorea parvifolia* and left the rest as a large indivisible group.

(j) *Growth and dynamics in structural guilds*

The reasonably close agreement between plots suggests that species' data could be averaged in the knowledge that plot–plot replication gives some confidence in dynamics being species-specific. With regard to structure, the understorey and overstorey, forming the two most distinct classes, differed significantly in agr and rgr but not in m_p or r_p, and also not in population change (table 6). The effect of excluding trees advancing beyond 50 cm gbh was greatest for the overstorey.

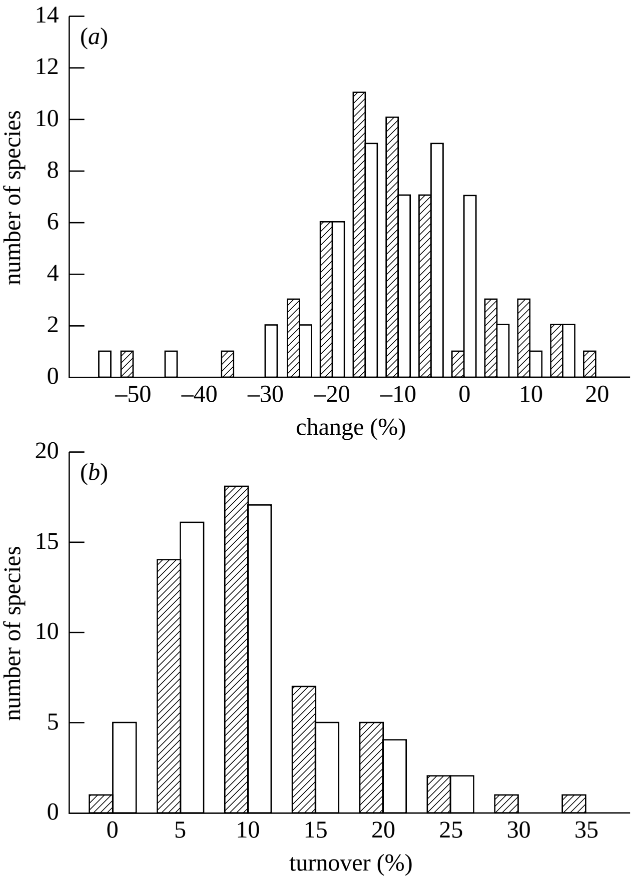

Figure 7. Frequency distributions of the 49 species common to the two plots at Danum (table 5) for (*a*) percentage change, ch_p $(=r_p - m_p - a_p - b_p)$, and (*b*) turnover, $to_p (=(m_p + r_p)/2)$, among the small trees (10–< 50 cm gbh). Plot 1, hatched bars; plot 2, open bars. For an explanation of the variables refer to the text.

Some caution is needed concerning the allocation of species to the three structural classes as this was based on the 1986 gbh frequency distributions. It is possible that an overstorey or intermediate-storeyed species was classified as understorey because it was then growing almost entirely as small trees. This might explain a little of the overlap of groups in figure 5 and also some misplacement in figure 6*a*. Of the 65 species given in table 5, records of maximum gbh could be found in local and regional floras for all but seven of them. Those species categorized in table 5 as understorey which had a gbh $\geqslant 100$ cm recorded elsewhere, and this being appreciably greater than the second largest measured gbh at Danum, were *Buchanania insignis*, *Dehaasia gigantocarpa*, *Lophopetalum becarianum*, *Magnolia candollii*, *M. gigantifolia* and *Polyalthia xanthopetala*. These might be candidates for larger-storeyed species, but without wider searches at Danum it is not known whether they would grow there as large as elsewhere. The other species appear to be assigned correctly. Four out of the seven unknowns, however, were understorey species so some additional uncertainty does remain.

(k) *Percentage change, turnover and projections*

For the ten-year interval the percentage changes to the 1986 populations were found by $ch_p = r_p - m_p - a_p - b_p$, in the 10 − < 50 cm gbh class (table 5). The term a_p is the percentage of trees in 1986 in this size class advancing beyond 50 cm by 1996 and b_p is the percentage of trees regressing (back) below 10 cm gbh by 1996. (This ch_p value is very close to the estimate of $(n_{96} - n_{86}) \times 100/n_{86}$.) For the 49 species in common to both plots, ch_p was slightly negatively skewed with a mean of $-7.44\% \pm 1.83$ (s.e.) (range −47.2 to 20.5, median −9.1%) for plot 1, and mean $-8.36\% \pm 1.88$ (range −51.4 to 17.5, median −7.6) for plot 2 (figure 7*a*).

In plot 1, eight species can be described as 'static' in their dynamics ($-5.0\% \leqslant ch_p < 5.0\%$), 32 were decreasing ($< -5\%$) and nine were increasing ($\geqslant 5\%$); corresponding values for plot 2 were 16 static, 28 decreasing and five increasing. This general trend, with decreasing population sizes of small trees and more so in plot 2 than 1, agrees with the overall plot summaries (table 2). The three storeys showed a trend of increasing ch_p with size as proportionally more trees moved up and out of the 10− < 50 cm class. Species with larger trees are also presumably less subject to damage from wood fall compared with ones with smaller trees. Differences between storeys in ch_p were not significant (table 6).

Turnover ($to_p = (m_p + r_p)/2$) is a measure of the dynamism of each species (Phillips *et al.* 1994). The two plots showed similarly slightly positively skewed distributions (figure 7*b*): the mean for plot 1, 13.7 ± 1.0 (s.e.) (range 1.5–36.2, median 11.7), was slightly greater than that for plot 2, 12.0 ± 1.0 (range 1.5–30.4, median 11.3). Again, within each storey there was a large range in values and no significance in the difference between under- and overstorey (table 6).

The ch_p values found for the 1986–1996 changes in densities for the 49 species in each plot were used to predict densities in 2006. The proportions of trees in the understorey, intermediate and overstorey classes remained, and are predicted to remain, quite constant, with *ca.* 66% stems of the 10–< 50 cm gbh class being understorey species, but this suggesting a slight increase (in plot 2 by 2%, but none in plot 1) between 1986 and 2006 (figure 8). Overstorey and intermediate-storey species correspondingly fall between 1986 and 2006 by *ca.* 2% in plot 2. The species' ch_p values within storeys appear to balance one another, leading to some form of structural stability under this scenario of continuing quasi-constant conditions.

(l) *Species' dynamics characteristics*

The 49 species considered in the two replicate plots form a continuum across the storeys and are, unsurprisingly, not readily divisible into groups according to their m_p, r_p and rgr characteristics (figure 5*b*). Codings in table 5 indicate high, medium and low rankings of m_p, r_p and rgr (lists split into thirds), and for ch_p the medium category was defined as 'static' (viz −5.0–< 5.0% change).

The distribution of points along the 1:1 line for m_p (figure 5*c*) suggests three disjunctions: m_p was very high for the two dipterocarps *Shorea johorensis* and *S. parvifolia* (44–46%), then followed a group of ten species with $m_p = 21$–32%, *Maschalocorymbus corymbosus*, *Antidesma neurocarpum*, *Popowia odoardoi*, *Reinwartiodendron humile*, *Aglaia odoratissima*, *Parashorea malaanonan*, *Polyalthia xanthopetala*, *Shorea fallax*, *Litsea caulocarpa* and *Pternandra galeata*. There is then a dense group of 33 species

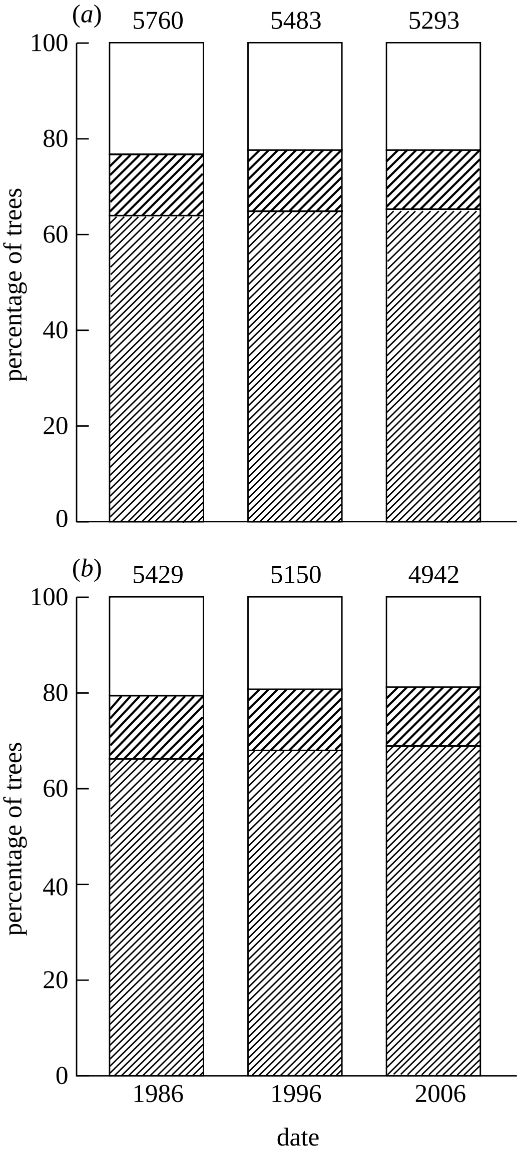

Figure 8. For the small trees (10–< 50 cm gbh) of the 49 species in common to the two plots at Danum, the proportion of trees in three structural classes u, understorey (double hatched); i, intermediate-storeyed (single hatched); and o, overstorey (open), as recorded in 1986 and 1996, and predicted by 2006 from the percentage change (ch_p) estimates in (*a*) plot 1 and (b) plot 2 at Danum. Values above the columns are total numbers of trees in the size class (cf. end table 5).

with $m_p = 5.4$ to 17.3%, and four very low m_p species (1.9–2.7%): *Dehaasia gigantifolia*, *Madhuca korthalsii*, *Knema latericia* and *Barringtonia lanceolata*.

Mean plot r_p values were much less easy to partition (figure 5*d*): 39 species lay between 0.8 and 15.6% but ten had higher recruitment (18.3–31.9%): *Shorea fallax*, *Litsea caulocarpa*, *Mallotus penangensis*, *Lophopetalum beccarianum*, *Shorea parvifolia*, *Knema latericia*, *Ardisia colorata*, *Polyalthia xanthopetala*, *Fordia spendidissima* and *Shorea johorensis*.

Mean plot rgr (figure 5*f*) showed one main group of 47 species with rgrs ranging from 3.0 to 23.0 mm mm^{-1}yr^{-1} × 10^3 but *Shorea johorensis* and *S. parvifolia* with very much higher values (49–61 mm mm^{-1}yr^{-1} × 10^3). The 13 lowest ranked species—the slow-growers (3.0–5.9 mm mm^{-1}yr^{-1} × 10^3)—are noteworthy: *Antidesma neurocarpa*, *Popowia pisocarpa*, *Xanthophyllum vitellianum*, *Hydnocarpus borneensis*, *Aglaia odoratissima*, *Magnolia candollei* var. *singapurensis*, *Polyalthia caulocarpa*, *Magnolia gigantifolia*, *Diospyros elliptifolia*, *Popowia odoardoi*, *Dehaasia gigantocarpa*, *Syzygium elopurae* and *Dimorphocalyx muricatus*.

Of the three species highlighted as associated with ridges (Newbery *et al*. 1996), *Dimorphocalyx muricatus*, *Cleistanthus glaber* and *Lophopetalum beccarianum* (lines 2, 10 and 14: table 5), the first two had unremarkable dynamics characteristics while the third had above average recruitment in both plots. *Mallotus wrayi*, the most abundant (understorey) species in both plots was the only one out of 49 in table 5 with the trait combination M—, viz high mortality but average in all other respects.

4. DISCUSSION

(a) *Sampling considerations*

Several important sources of inaccuracy and uncertainty entered into the calculations of the interval-based dynamics. (i) The plots at Danum were each only 4 ha in area and therefore the numbers of large trees (⩾50 cm gbh) were low at close to 10% of all trees ⩾10 cm gbh (table 1). Most of the canopy species had few representatives per hectare. (ii) The time interval was long (ten years) meaning that while the absolute changes are accurate, the annual rate of recruitment was underestimated and any annualized rates assume constancy. For this reason the use of annual rates was mostly avoided. (iii) Even for small trees (10–< 50 cm gbh), sample sizes per plot were small when the confidence limits to binomial variables were considered. For a species with $m_p = 0.1$, $n = 50$ leads to 98% confidence limits of 0.031 and 0.224, but $n = 500$ to 0.074 and 0.131 (cf. figure 1). Only one species (*Mallotus wrayi*) had > 500 trees in each plot and one other (*Dimorphocalyx muricatus*) > 500 trees in one plot (table 5). The implications of the binomial distribution for tropical rainforest mortality estimates have been recently discussed by Alder (1995), Condit *et al*. (1995), Sheil & May (1996) and Hall *et al*. (1998).

Simple population models of trees dying and recruiting may give a direct count of tree numbers but these individuals vary greatly in size. Trees recruiting above the minimum gbh are necessarily small and of low basal area abundance, but mortality involves all size classes including very large trees. Percentage change and turnover estimates for all trees therefore bear little relationship to biomass and the competition for space and resources. Using the smaller trees (10–< 50 cm gbh) brings m_p and r_p more into a direct relationship, especially when allowance is also made for the trees growing out of the 50-cm gbh class. Nevertheless, estimates of r_p at the species level are not very reliable given the taxonomic problems with infertile material.

A large majority of the species had mortality and recruitment rates that fell within confidence limits based on the pooled population estimates. Thus for most species the dynamics parameters had very large errors. The scientific value of plot replication (unusual in tropical studies) was that for at least the more abundant species (*ca*. first 50 in common) there was good rank agreement in the relative rates of mortality, recruitment and growth, suggesting that despite these within-plot errors for species, the forest at the community level had a highly species-specific dynamics. Plots did differ slightly overall so points fell more to one side of the 1:1 line than the other. If species were simply random subsets of the whole forest's trees then figures 5 and 6 would show no trends. The plots were not far apart spatially, and both encompassed similar topographic gradients, so these factors may have had a forcing effect on the plot similarity. Each common species, however, appears to show its own reaction to the local conditions at Danum.

(b) *Comparisons*

Comparison with other sites in the tropics has many difficulties and is of limited value given the huge range in conditions, methods of measurement and dates of study. Many major studies are from seasonal Central American sites (e.g. Condit *et al.* 1995) and present a very different environment to north-west Borneo. Even though droughts in the New World can intensify the dry season (Condit *et al*. 1996; Condit 1998) this is likely to lead to a different type of response from the one at Danum, with its intermittent events disturbing a 'normally' aseasonal regime. Nevertheless, taking the six values from Phillips *et al.* (1994) table 1, with census intervals of 9–12 years only (annual mortality estimates are time-period dependent; see Sheil & May 1996), and for $\geqslant 10$ cm dbh trees, the mean annual mortality rate was 1.90 ± 0.24 (s.e.). Typical values across all sites in this and other summaries (e.g. Swaine *et al.* 1987) suggest that rainforests typically have mortalities of 1–2% per annum. However, these values do not include estimates following large disturbances (e.g. fire); and if these did occur in a long census interval the temporarily increased mortality would have been largely averaged out. Many estimates of forest dynamics have been based on very small plots. The values for Danum are therefore not at all unusual and do not suggest the effects of large recent events killing high proportions of trees, as found by Leighton & Wirawan (1984), Beaman *et al.* (1985) and Woods (1989) in eastern costal parts of Borneo after the 1982–1983 severe drought and then fires in these parts. This is one argument for concluding a structural stability at Danum.

It is more instructive to compare mortality rates within Sabah and for which climatic records exist in detail (Walsh 1996*a*; Walsh & Newbery, this issue). There is one site (but not for the same time period) with which to do this: the primary dipterocarp forest at Sepilok, near Sandakan, Research Plot 17 (RP 17) (Nicholson 1965*b*; Fox 1973). This 1.82-ha plot sited 15–45 m above sea level, on undulating sandstone with small sharp ridges, was measured in 1956, 1958, 1960, 1962 and then 1968 for trees

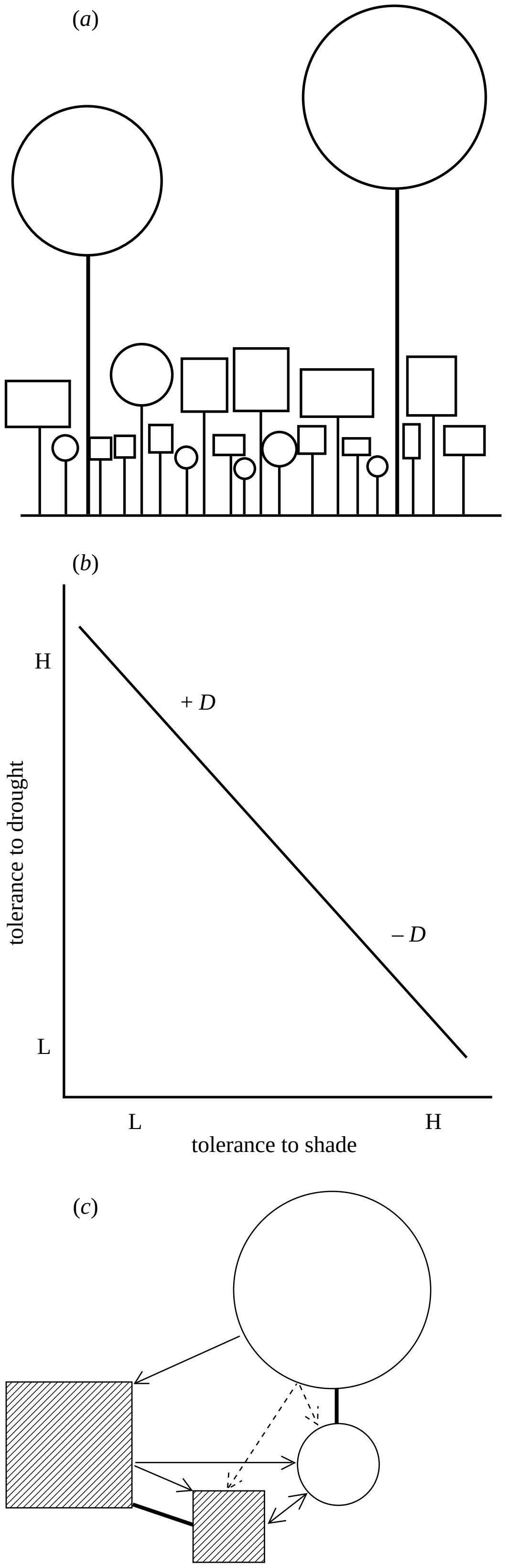

Figure 9. Structural groups' trade-offs and feedback as a proposed basis for the role of the understorey in drought-disturbed dipterocarp forest at Danum, Sabah. (*a*) Idealized forest structure (based on a profile on line L of plot 1, and general observations): circular crowns, overstorey species; box-shaped crowns, understorey species (intermediate-storeyed now shown). (*b*) Envisaged trade-off in shade and drought tolerances among understorey species, shifting with intensity–frequency of drought (± D); L, low,

Figure 9. (*Cont.*) H, high. (*c*) A simple feedback diagram for overstorey species (open circles) and understorey species (hatched squares), drawn large and small to represent the relative tree sizes in the over- and understoreys. Lines (links) with no arrows show direction of growth. Arrows in one direction indicate the positive effects of one group-size class on another, solid arrows indicating stronger effects than dashed ones. The line arrowing two directions indicates where potentially strong competition might occur.

$\geqslant$30.5 cm gbh or 9.7 cm dbh. Calculating annualized mortality rates (m_a, using the formula in § 2) from the data in Fox (1973) gave 1.18, 0.56, 1.51 and 1.72%, respectively. Fox commented that two-thirds of the mortality was within the smallest girth class (9.7–19.4 cm dbh or 31–61 cm gbh, i.e. understorey; cf. Danum study). If the three estimates for the first six years are averaged, the rate of 1.08% is much lower than the rate for the second six years. Within this 12-year period, according to Walsh (1996*a*) only 1957 and 1968 had weak droughts of three months' duration, coming near the start and at the very end of the Sepilok records. Thus the latter six-year RP 17 mortalities were also from a relatively benign period, and compare well with the Danum values of 1.3–2.1% across plots. A nearby RP 18 (Fox 1973) of 1 ha on a wet alluvial site showed a similar pattern of mortalities over the three intervals of 1957, 1961, 1966 and 1969 (also trees $\geqslant$9.7 cm dbh) with m_a 1.34, 2.39 and 2.08%, respectively.

(c) *The understorey*

Small trees (10–< 50 cm gbh), i.e. understorey individuals, made up 90% of the populations $\geqslant$10 cm gbh in each plot at Danum. These included understorey species *per se*, those that stay in the shade of the main canopy and rarely exceed 50 cm gbh, and individuals of the overstorey (canopy and emergent species) which have the potential to grow into much larger trees. While the 50-cm limit was selected on the grounds of sample sizes afforded, structural proportions and the floristic analyses of Newbery *et al.* (1996), the main results of this paper would be unlikely to change much had 45 or 55 cm been chosen. The Danum forest has few pioneer species (short-lived, highly light-responsive trees) as there have been few small gaps recently (Newbery *et al.* 1992), so the forest can be thought of as being composed of these two main groups, the one of short, small trees tolerant of the shade and the other of potentially taller, larger trees responsive to increases in light once established as large saplings or small trees. The classification into storeys is a simple device whereas in reality all species lie along a continuum.

Numerous studies have shown a close relationship between gbh and height (e.g. Hallé *et al.* 1978) so height can be reasonably inferred from gbh in the general case. The strongest interactions between trees should occur between individuals in this small-tree class, this being composed principally of nearest-neighbour competitive interferences between overstorey and understorey species' trees, both inter- and intra-group. The analyses showed that in this size class local density was high and variable and appeared to affect r_p and rgr. The larger trees may have had relatively little influence on this stratum being much too high and widely spaced to create direct shading (except near midday) and probably with deeper root systems than smaller trees. The degree of influence of the larger trees probably declines rapidly and nonlinearly above 50 cm gbh. These big trees nevertheless form a substantial part of the forest biomass and 'holding structure' for the smaller ones.

If spatially explicit neighbour interactions do contribute to the outcome of interactions at the species level, and site and climate have selecting effects on species performance and fitness, then it may be postulated that the strongest deterministic component of community interactions is among these small pole and subcanopy trees. For seed input, establishment of seedlings, saplings and then very small trees, chance plays a major role in species survival (Still 1993, 1996; for Danum), and for the very big trees mortality is also largely stochastic (Whitmore 1984; in general). This 'funnelling' effect towards the small trees means that wherever growing conditions, especially those regarding light levels and water availability, temporarily improve, then trees can grow faster and as overstorey species move out of this competitive layer they rapidly accelerate into generally freer space above. Indeed the silvicultural practice of thinning out understorey species to 'release' dipterocarp saplings testifies to this effect (Nicholson 1965*a*).

(d) *Forest structure*

The structure of the forest at Danum accords with this model (figure 9*a*). The understorey is well defined, the canopy between the large emergent stems is relatively low (*ca.* 20 m) and the canopy both from within and from above has a rough and uneven appearance (D. M. Newbery, personal observation). Gaps at mid-height are very obvious and the emergent trees rarely adjoin. This, combined with the low basal area and the irregular frequency distribution among medium to large trees and the high abundance of lianas, suggests a forest that has been and is disturbed, a forest in recovery (Newbery *et al.* 1992; Campbell & Newbery 1993).

The increasing basal area, mainly among larger trees, suggests that at Danum this forest is continuing to aggrade. The basal areas agree closely with those from the relascope survey, and from ten 0.16-ha satellite plots (five ridge, five lower-slope) showing a mean and s.e. of 35.1 ±3.19 $\mathrm{m^2\,ha^{-1}}$ (98% confidence limits, 26.1 and 44.1 $\mathrm{m^2\,ha^{-1}}$) for trees $\geqslant$10 cm gbh (D. M. Newbery and G. H. Petol, unpublished data). Thus, the low basal area reported in Newbery *et al.* (1992) for the two 4-ha plots, in comparison with other north-east and east Borneo sites, seems not to be a sampling artefact but representative of the surrounding 100 ha.

Fox (1972) also commented on the openness of the canopy in primary forest at Segaliud-Lokan, in eastern Sabah, and a forest close in basal area to that of Danum (Newbery *et al.* 1992). His profile diagrams are remarkably similar to the one (D. M. Newbery and M. J. Still, unpublished data) for Danum and agrees with our personal observations. Fox commenting on this forest wrote (p. 98) 'There is no evidence of past disturbance but patchiness may be due to higher mortality following faster growth rates than in some other types [of forest].' Dominated by *Parashorea tomentella* and *Eusideroxylon zwageri*, the Segaliud-Lokan forest also had a great abundance of lianas. This forest lies *ca.* 50 km south-west of Sandakan, with a climate probably very like that of Danum, or slightly more drought prone, judging from the maps of Walsh (1996*a*) and Walsh & Newbery (this issue). Furthermore, Ashton & Hall (1992) have observed a range of canopy openness across several dipterocarp stands in Sarawak and suggested that this might be related to the incidence of drought.

Plot 1 increased in basal area (trees $\geqslant$10 cm gbh) at 0.18 $\mathrm{m^2\,yr^{-1}}$ and plot 2 by 0.40 $\mathrm{m^2\,yr^{-1}}$. On a simple linear projection, 35 $\mathrm{m^2\,ha^{-1}}$ would be reached on average in 25 years, by *ca.* 2020. However, it is possible that a major drought or two to three smaller ones will have set back the growth by then. Estimating the probability of that happening is presently not possible without longer-term data.

(e) *Stabilizing processes*

The small tree-pole stage could thus be expected to be very responsive to the environment. Recruitment into, and loss from, this layer (by mortality or advanced growth) could lead to a structural stability that slowly changes over time, one adjusting to disturbance intensity and frequency. While individual species may fluctuate over decades, reacting locally and particularly to site and climatic factors, the complement of understorey versus overstorey stems will be expected to be constant. This is suggested by the data for Danum. It also corresponds to the notion of the two ecophysiological groups which have a reciprocal feedback (figure 9) on each other's dynamics in the following way. The understorey species require shade from the canopy of the overstorey species to survive, and the overstorey, as even smaller stems (Still 1993, 1996), also require the understorey under which to establish, though eventually they require light and space to advance. This upward movement of trees as and when light availability permits, moderated by water stress, accords with the typification of Oldeman & van Dijk (1991) of 'strugglers' (i.e. understorey) and 'gamblers' (i.e. overstorey), explained in greater detail in Oldeman (1987). Bongers & Sterck (1998) have modelled tree growth as a series of slow and fast growth phases as the vegetation around an individual subtly changes over decades. If the understorey becomes too dense then the chances that overstorey saplings can grow will decrease and mortality follows. The proposed self-stabilizing processes will have lagged growth effects. These arguments point to the understorey–overstorey balance being an important indicator of successional stage and of site conditions, and to the essential 'nursing' role of the understorey for overstorey regeneration in the long term (i.e. centuries-scale of forest regeneration).

Across the understorey and overstorey groups a wide range in m_p and r_p values for species was found, meaning that for both of these some species are more or less dynamic, but within a structural group they balance or compensate one another to suggest a stable convergence. What, however, separates the overstorey from the understorey species is rgr potential, typified by the fast-growing dipterocarps and slow-growing euphorbs. When a dipterocarp occurs in a favourable mid-canopy gap it will grow on very fast; and conversely a euphorb will sustain slow growth in the shade. This interactive dynamic between the groups captures the principal forest processes.

At the subplot level, mortality and recruitment were unrelated to topography, though locally high rgr and r_p occurred across the plots. This relationship was strongest when only the 10–< 50 cm trees were considered: where their density and basal area was lowest (probably due to a large tree death or localized disturbance created by drought) light levels were presumably higher and hence regeneration could increase. This is a largely stochastic process in time and space and which further leads to a high chance component for mortality and recruitment of seedlings.

(f) *Physiological traits*

Fast and slow growth both have costs and for this forest a trade-off in life-history traits can be imagined. The overstorey species (not all, but many) can have potentially high growth rates but the cost is a high mortality for those that fail to be positioned by chance near to a canopy opening. This mortality must be matched by high recruitment for the species' populations to be maintained. In contrast, for understorey species survival in the shade is of selective advantage but at the cost of low rgr. Survival implies low mortality (and under equilibrium low recruitment being necessary), yet for several understorey species the Danum data do show high mortality and recruitment rates (figure 5*c*). The answer to this paradox may lie in the fact that this forest is not in equilibrium due to drought disturbances, and some species within the understorey showed temporarily high recruitment and mortality, possibly due to increased light availability. There must be some continual readjustment among the understorey species in the form of a second important trade-off (figure 9*b*) which relates to degree of tolerance to shade versus tolerance to water-stress (see Smith & Huston 1989; Huston 1994) and exposure to higher temperatures. Departure from these expected trade-offs for some understorey species is perhaps a measure of the reaction of this forest to disturbance.

(g) *Drought hypothesis*

At Danum the extent to which the 1982–1983 drought affected the forest is unrecorded but if observations over the rest of the state are indicative then probably it did suffer some disturbance. The first enumeration was in 1985–1986 so the forest would have had three to four years of recovery before plot establishment. However, large tree falls and gap formation were scarce, suggesting that tree death was negligible, possibly only temporary defoliation being the reaction if any at all. Drought effects can be very localized in intensity (Walsh 1996*a*,*b*). In the interval of the two permanent plots' measurement there was no major drought recorded, except for a short spell in 1992 probably of very little consequence to the forest. More recently since the second enumeration in 1995–1996 there has been a major drought period in 1997–1998 (Walsh & Newbery, this issue). Thus the period of dynamics recorded was relatively benign and acts as a background control, although lag effects after 1983 might have been inherent. (For instance, the putative drought tolerant species showed no particular reaction during this 1986–1996 period.) Estimates of mortality from the intermediate 1989 recensus (Newbery *et al.* 1992) were much lower at 1.10 and 1.05% yr^{-1} than the annual rates based on the ten-year period of 1.75 and 1.42% yr^{-1} (table 2), suggesting perhaps an alleviation in tree deaths at the start of the inter-drought interval.

Building on the interpretation put forward in Newbery *et al.* (1992) and linked to the floristic–topographic analyses which suggested the drought hypothesis, the current dynamics data, combined with increasing knowledge of the climatology (Walsh & Newbery, this issue), strengthens the assertion that the Danum forest is continually disturbed at intervals by these dry events, possibly coming with great intensity and consequences every 100–200 years but also with less, yet significant, intensity and greater frequency every 7–15 years. The forest is thus in a continual state of recovery, suggesting a dynamic equilibrium on the scale of centuries. This is its natural state to which most of the species, dipterocarps and ridge-top understorey species are presumably well adapted. Gibbons (1998) has recently provided experimental support for the drought hypothesis comparing ridge and lower-slope species responses to water shortage: *Dimorphocalyx muricatus* appears able to tolerate lower water potentials than *Mallotus wrayi*, for instance. In Walsh & Newbery (this issue) the mechanisms by which trees in over- and understorey might be adapted to short strong periods of drought are reviewed.

The low species richness of the Danum site relative to other Bornean forests (Newbery *et al*. 1992) fits within this prediction of the model by Huston (1979, 1994). A measure of competitive displacement is needed next. Dominance of the understorey (but not the overstorey) could be the hallmark of long-term disturbance as could the drought-tolerant guild of understorey species found on the ridge parts of the plots (Newbery *et al*. 1996). Several fast-growing *Shorea* species form the main canopy, but the slower-growing *Parashorea malaanonan* fails to reach very large sizes or canopy dominance. Fox (1972) suggests that absence of *P. malaanonan* indicates late secondary forest after fire. From soil samples and pits at Danum there is no evidence of recent fire (Newbery *et al*. 1996).

The fast growth and high turnover suggest that some dipterocarps may be adapted to disturbance; drought and the lighter-wooded species especially may outgrow the slower canopy dominants which would survive under no or less disturbance (Whitmore 1984; Goldammer & Seibert 1990). Dipterocarps may occupy a niche in disturbed late-successional Bornean forests, and within this family the faster and lighter-wooded species indicate the more droughted sites (cf. Ashton & Hall 1992). The lack of very dense-wooded, slow-growing dominants such as *Eusideroxylon zwageri* at Danum confirms an absence of fire history.

(h) *Long-term dynamics*

There are no *a priori* reasons to assume that Bornean dipterocarp forests will reach a stable or constant state in their species composition in the coming centuries or millennia. The prognosis of warming with regional climate changes (Hulme & Viner 1998; Walsh & Newbery, this issue) accompanied by more frequent and intense droughts may select for forests with more species adapted to this type of disturbance. The forest would be expected to become species-poorer, have a more uneven structure and perhaps lower stature. In Walsh & Newbery (this issue), the synthesis first proposed by Walsh (1996*a*), showing how forests respond to changing frequency and intensity of drought, is refined to incorporate the new ideas on the role of the understorey.

The long-term, dynamic equilibrium proposed here for the Danum forest ecosystem has several essential features of a feedback process (O'Neill *et al*. 1986; Pahl-Wostl 1995) that permit changing species composition within functional groups to maintain the forest structure in understorey–overstorey defined ratios by having positive and negative effects, with lags, on each other's growth and abundance (figure 9*c*). This implies a structurally stable system within certain disturbance limits. The ecophysiological and life-history traits of the two storeys, over a vertical gradient, suggest complementary trade-offs. However, the structure is determined by the level of disturbance and the greater the drought frequency the more the understorey is expected to have a protective role. Complete removal (e.g. by very severe drought, fire or heavy harvesting) would lead to a very slow recovery of the system. Moderate disturbance should be accommodated by the species adapted to the regime: lack of droughts would lead to the forest becoming larger in stature and basal area with a reduced contribution by the understorey species.

5. CONCLUSION

Water and light availability are the two principal driving factors that together allow a direct physical understanding of forest ecosystem functioning in relation to climate change. In this respect the potential role of the understorey in tropical forest dynamics has been seriously neglected. In this paper, a novel approach to interpreting species composition and structure under a regime of stochastic drought disturbance is proposed.

Two steps to test the drought–understorey hypothesis further are (i) a model incorporating the feedback process in three-dimensional continuous parameter space and time, operational for a wide range of site conditions and scenarios; and (ii) a study of forests along a gradient of increasing frequency of drought disturbance concentrating on understorey composition and dynamics, using Danum as a reference site. The coming decades of climate change may indeed put such a gradient into sharp relief.

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