On the detection of dynamic responses in a drought-perturbed tropical rainforest in Borneo

M. Lingenfelder · D. M. Newbery

Abstract The dynamics of aseasonal lowland dipterocarp forest in Borneo is influenced by perturbation from droughts. These events might be increasing in frequency and intensity in the future. This paper describes drought-affected dynamics between 1986 and 2001 in Sabah, Malaysia, and considers how it is possible, reliably and accurately, to measure both coarse- and fine-scale responses of the forest. Some fundamental concerns about methodology and data analysis emerge. In two plots forming 8 ha, mortality, recruitment, and stem growth rates of trees ≥10 cm *gbh* (girth at breast height) were measured in a 'pre-drought' period (1986–1996), and in a period (1996–2001) including the 1997–1998 ENSO-drought. For 2.56 ha of subplots, mortality and growth rates of small trees (10–<50 cm *gbh*) were found also for two sub-periods (1996–1999, 1999–2001). A total of *c*. 19 K trees were recorded. Mortality rate increased by 25% while both recruitment and relative growth rates increased by 12% for all trees at the coarse scale. For small trees, at the fine scale, mortality increased by 6% and 9% from pre-drought to drought and on to 'post-drought' sub-periods. Relative growth rates correspondingly decreased by 38% and increased by 98%. Tree size and topography interacted in a complex manner with between-plot differences. The forest appears to have been sustained by off-setting elevated tree mortality by highly resilient stem growth. This last is seen as the key integrating tree variable which links the external driver (drought causing water stress) and population dynamics recorded as mortality and recruitment. Suitably sound measurements of stem girth, leading to valid growth rates, are needed to understand and model tree dynamic responses to perturbations. The proportion of sound data, however, is in part determined by the drought itself.

Keywords Dynamics · Perturbation · Drought · Stem growth · Tree mortality · Validity

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Introduction

Stochastic fluctuations in the environment are thought to play an important role in driving the long-term dynamics of tropical rain forests and in determining their structure and species composition (Newbery and Lingenfelder 2004, 2009). Droughts, fires, floods and hurricanes are notably examples of such external climatic influences. In South-East Asia, under normally aseasonal climatic conditions, it is droughts that probably have the most sustained and repeated

effects on the forests. These periods of reduced precipitation are often associated with the El Niño-Southern Oscillation (ENSO) cycle (Walsh 1996; Walsh and Newbery 1999), a global process with its origins in changes in sea-surface temperature and air pressure in the Pacific Ocean (Trenberth 1997; Trenberth and Hoar 1997).

The ENSO reaches back 130,000 years and events are known to have affected Borneo for at least 18,000 years (Walsh and Newbery 1999; Cane 2005). They result in occasional moderate droughts which are an integral component of the environment (Walsh and Newbery 1999). Away from the eastern coast of Borneo, at the inland site of Danum (in Sabah, Malaysia) for instance, the tree species of the lowland dipterocarp forests appear well adapted to the correspondingly moderate perturbations to the ecosystem that the droughts cause (Newbery et al. 1999; Gibbons and Newbery 2003; Newbery and Lingenfelder 2004, 2009).

Compared to the preceding century, the last 30 years have shown an increase in the frequency and intensity of ENSO events (Trenberth et al. 2007). The trend had been expected by the earlier analyses of Hulme and Viner (1998), Timmermann et al. (1999, 2004) and IPCC (2001). Other recent models, however, lend less support to an increase continuing in the near future (Cane 2005; McPhaden et al. 2006; Meehl et al. 2007), even though when ENSO events do occur they may lead to a higher risk of strong drought (Christensen et al. 2007). Given that the prognoses are weak it remains important to be prepared for either an increase in droughts or a stabilization of the earlier pattern because it certainly will have profound implications on how the forests should be best conserved and managed.

All tropical rain forests can be viewed as being continuously in various complex and overlapping states of recovery from past perturbations, whether these are singular or closely timed multiple events, happening recently or in the more distant past (Newbery et al. 1999; Newbery and Lingenfelder 2004). Measuring precisely how the forests respond to currently occurring perturbations may lead nearer to reliable models which can estimate how increases and decreases in frequency and/or intensity of perturbation might affect their persistence.

After the last strong ENSO-related drought in 1997/1998 several studies have been conducted on the ecological effects of such short, but significant periods of drought stress on trees in South-East Asia (Nakagawa et al. 2000; Harrison 2001; Potts 2003; Ichie et al. 2004; Newbery and Lingenfelder 2004; Slik 2004). They variously concluded that some forest's species were well adapted to a moderate drought regime whereas for those of other forests this was not so evident. The focus was also mainly on recording mortality—growth and recruitment receiving less attention—and drought was simply defined to take effect when the 30-day running total (30-d-rt) of rainfall fell <100 mm. Plots and tree sample sizes were sometimes quite small, and the area measured may not have been fully representative of local topographic variation.

Drought is a stochastic factor and frequency and intensity of its complex effects requires careful consideration. Soil water status before and during an event, as well as the replacement of depleted soil water after it, need to be taken in to account using a dynamic approach based, for example, on the idea of 'antecedent rainfall history' proposed by Newbery and Lingenfelder (2009). In addition, since climatic variation is occurring at the scale of decades, and not annually or per century, only long-term measurements over 20–30 years that capture forest dynamics before and after a drought for several years (at minimum close to the return time of the event) are likely to provide enough ecologically meaningful information. To have such records for repeated droughts at the same and other replicated locations would of course be ideal.

From previous work in Borneo, it was concluded that the forest at Danum is most likely still recovering from a very strong drought c. 130 years ago and that it is well adjusted to coping with repeated lesser droughts that have happened since then. Seen at the scale of many centuries, the forest is perhaps in a state of dynamics equilibrium, with variously large and small 'set backs' occurring at different points in time (Newbery et al. 1992, 1996, 1999). Behind this process lies the dynamics of the individual species and how they are adapted to the actual physiological effects of the drought perturbations (Newbery and Lingenfelder 2004, 2009). Their responses will collectively determine the resilience of the ecosystem, i.e., how fast and to what extent it can recover after perturbation. In this context the pressing question, for both natural and secondary managed forests,

is whether species selected under the past environmental history are able to survive as well as before when droughts come more intensely and closer together in the future.

Species-specific tree responses to the moderate perturbation regime at Danum have been presented recently by Newbery and Lingenfelder (2009). The present paper describes the structure of the permanent research plots at Danum and analyses tree dynamics between 1986 and 2001 in detail at the plot and subplot levels. The focus here is on the response of the whole forest to drought, particularly to the 1997/1998 ENSO-related event, in terms of mortality, recruitment and growth rates. Several field methodological and data analytical problems are tackled. These have wider relevance to tropical forest dynamics in general, and highlight some important limitations to conclusions that can be drawn from recensussing studies. The aims of the present study were thus: (1) to quantify the effect of the 1997/1998 main drought on forest dynamics at Danum, (2) to investigate the interactions between tree size and topography on dynamics, (3) to refine the treatment of stem growth estimates for aims 1 and 2, and (4) to place the dynamics responses into the frame of the forest ecosystem.

Methods

Study site

Location

The study site lies within the 438-km^2 Danum Valley Conservation Area (DVCA), Sabah, Malaysia, 66 km inland of Lahad Datu on the N.-E. coast of Borneo. The DVCA is an uninhabited and unlogged part of the 9730-km^2 Yayasan Sabah Concession Area; human artefacts suggest that there might have been some earlier settlement or visitation (Marsh and Greer 1992). The vegetation around the site is primary lowland dipterocarp forest of the *Parashorea malaanonan* category (Fox 1972). The topography is gently undulating, and the soils are mainly orthic acrisols of the Bang association which developed on sandstone and mudstone of the geological Kuamut-Formation (Wright 1975). Further details of the site are given in Newbery et al. (1992, 1996, 1999).

Climate

The climate at Danum Valley Field Centre (DVFC, 4°57′48″ N, 117°48′10″ E, 152 m a.s.l.) is typical of equatorial rainforest locations (Walsh and Newbery 1999) with the mean daily range of temperature (8.6°C) being larger than the monthly mean range (1.8°C) about an annual mean temperature of 26.8°C, high relative humidity and high annual rainfall (mean *c.* 2800 mm). There is no clear dry season indicating that Danum has a generally aseasonal tropical climate. Further details can be found in Newbery and Lingenfelder (2009).

Between 1985 and 2003, Danum experienced 19 low precipitation events of which one was ecologically severe (event centred in 1998), two moderately strong (1987 and 1992) and five of weaker intensity, as shown by antecedent rainfall history analysis (Newbery and Lingenfelder 2009). Severe droughts across large parts of Borneo that were probably stronger than the one in 1997/1998 were recorded in 1877/1878, 1914/1915 and just before the setting up of the main plots at Danum in 1982/1983 (Beaman et al. 1985; Walsh 1996; Walsh and Newbery 1999) and most likely affected them. The events of 1877/1878, 1982/1983, and 1997/1998 were the three strongest El Niño-events in terms of sea-surface temperature anomalies in the 'ENSO 3'-region since 1876, where reliable reconstructions can be made (IPCC 2001). Since that time droughts of weak to moderate intensity have occurred frequently across Sabah (3.25 times per 20 years) and the frequency of strong droughts at Danum was 1.54 per 20 years on average (Walsh 1996; Walsh and Newbery 1999).

Design

In 1985–1986, two permanent plots were first set up and enumerated (Newbery et al. 1992, 1996). They are located *c.* 0.8 km NW of DVFC, just north of Main Trail West on gently undulating terrain with elevations of 208–254 m a.s.l. Plot 2 lies *c.* 280 m parallel to, and west of, plot 1. The plots are rectangular in shape (each 100 m × 400 m, area = 4 ha) with the longer sides oriented north-south. Each was divided into 100 units of 20 m × 20 m (small subplots) and their corners marked with belian (ironwood) posts.

Relative differences in elevation and slopes within the plots are very similar (39–43 m; Fig. 1). Plot 1

includes steep east-facing slopes in its northern half: in plot 2 an episodic small stream cuts two small ridges with steep slopes. Interpolating from 20-m × 20-m-grid elevational data, ridge areas (≥25 m, relative to SW-plot corners of 0 m) covered 18% and 33%, and lower slope areas (<12 m) 32% and 36% of the planimetric surfaces of plots 1 and 2, respectively. Of plot 1, 31% is flat (<10° inclination) and 14% is steep (≥20°; max. 33°). In plot 2, the corresponding values are 26% and 18% (max. 31°). More than half of the area of each plot lies on intermediate slopes (10–20°).
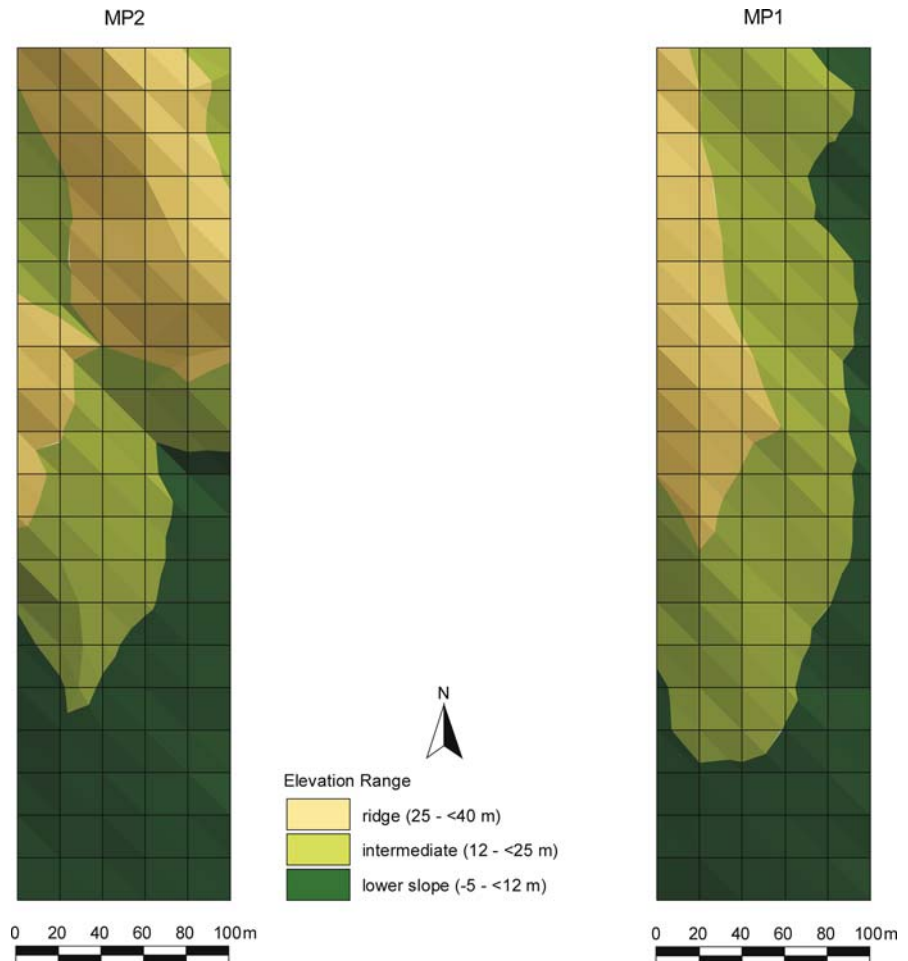
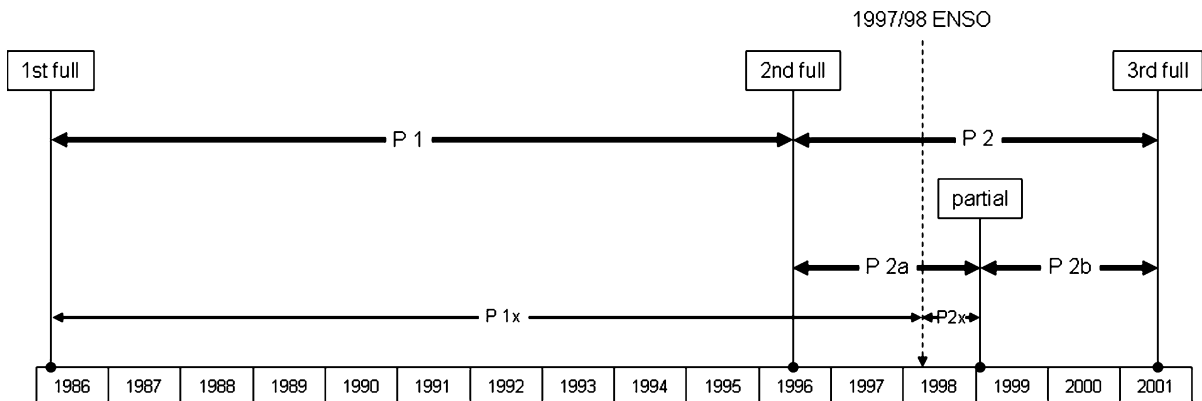Enumerations

Previous to 2001: background

The first enumeration of the plots was between 24 August 1985 and 15 December 1986 (median 15 March 1986; Fig. 2). Within each subplot, every living tree with a minimum stem girth at breast height (*gbh*) of 10 cm (≥3.2 cm *dbh*) was mapped, tagged, (and identified) and its *gbh* measured at a painted mark, usually 1.3 m above ground (see Newbery et al. 1992, for details). The second enumeration was between 8 November 1995 and 23 February 1997 (median 18 June 1996; Fig. 2), in which all trees were recorded for alive/dead status and the *gbh* of survivors remeasured. Surviving trees that had grown to ≥10 cm *gbh* (recruits) were mapped, tagged, identified, and measured (see Newbery et al. 1999). The first and second enumerations each lasted 1.3 years. The mean time interval for the two plots was 10.0 years.

Eight 40-m × 40-m (large) subplots in each main plot, half of them on lower slopes and the other half on ridges, had been measured between 20 December 1998 and 29 March 1999 (median 25 January 1999;

Fig. 1 Topographic variation within the two 4-ha permanent plots in the Danum Valley Conservation Area, Sabah, Borneo

MP2

MP1

N

Elevation Range

ridge (25 - <40 m)

intermediate (12 - <25 m)

lower slope (-5 - <12 m)

0   20   40   60   80   100m

0   20   40   60   80   100m

Fig. 2 The sampling scheme at Danum showing the dates of the three full and one partial enumeration, the timing of the 1998 ENSO drought and the corresponding periods (P1, P2) and subperiods (P2a, P2b), and the extension of P1 (P1x) and the estimated immediate post-drought sub-period (P2x)

Fig. 2). Each consisted of four small subplots in a square, as defined in Newbery and Lingenfelder (2004). Subplots were selected in a stratified random manner and represented 2.56 ha (32%) of the main plot area. In 1999, all 1996-recorded trees ≥10 cm *gbh* were scored for alive/dead status and surviving small trees (10 – <50 cm *gbh*) remeasured: recruits and regressors were not registered in 1999.

In 2001: advancements

The third full enumeration of the plots was conducted between 26 February 2001 and 4 February 2002 (median 29 June 2001, Fig. 2), taking nearly 1 year (109 field days). The mean time interval from the second enumeration was 5.0 years (Lingenfelder 2005). Dead trees were recorded in five status classes (e.g., dead standing or dead-broken: missing stems were assumed to be dead. Status of survivors was recorded in seven classes, e.g., undamaged or broken (see Supplementary materials—Appendix 1).

Stems of surviving trees were inspected at the paint-mark of the previous point of measurement (PoM). If the paint-mark was lost, a new one was established at 1.3 m on the uphill side of the tree or at the nearest suitable point on the stem avoiding stem deformations and obstructions. The same procedure was followed if a stem was broken below the old PoM and a new shoot had to be measured. Unless deformation was too great to allow remeasurement, *gbh* at the old PoM was measured and an alternative PoM was established at the nearest suitable point, and measured. An alternative PoM was also established if

buttresses were already influencing stem growth, or was seen likely to do so in the next 5 years. In the latter case, the PoM was moved to at least 1 m above the buttress. This strategy of adding alternative PoMs was started in 1996 to ensure that at least in two consecutive enumerations the tree was measured at the same PoM. Alternative PoMs established in 1996 were utilized in 92 instances in 2001 (Lingenfelder 2005). PoM (original, new, etc.) and condition of the stem (CoS; e.g., stem normal or deformed) at that point were recorded in six and 16 classes, respectively (Supplementary materials—Appendix 1). Height of the PoM (if not at 1.3 m) was also noted.

Girth (*gbh*, to nearest mm) was measured with a thin 2-m steel tape, and for larger trees a wider 5-m one, after lightly cleaning the bark at the PoM. Trees with multiple stems ≥5 cm *gbh*, and of which one was ≥10 cm *gbh*, were included and a single hypothetical *gbh*-value found from their combined basal areas. When it was impossible to insert the tape under a constricting liana, callipers were used to measure tree diameter, taking two readings at 90° to one another. For trees where the PoM had to be moved upwards to > *c*. 2 m, a ladder was used. For trees with PoMs at *c*. >4 m (*n* = 48 trees), stem diameter was measured optically with a laser ranging instrument (Criterion 400, Laser Technology Inc., Centennial, USA), again with two readings taken at 90° apart. Method of measurement was recorded in five classes (Supplementary materials—Appendix 1). Recruits surviving the interval since the second enumeration, were mapped, tagged, painted, (identified) and measured.

To make use of the additional 1999 partial enumeration of the large subplots, trees of the same size class and subplots in the 1986, 1996 and now 2001—enumerations were selected. Because no recruits were recorded in 1999, n_{99} was lowered, and to have used this value mortality rates in sub-period 2b would have been overestimated. Accordingly, recruits in 1996 and 2001 were also excluded from the subplot data set. Individual trees were allocated to the three topographic classes as defined for the main plots; numbers of trees in the intermediate locations were c. half those on the ridges and lower slopes.

Calculations

The three sets of measurements are referred to as the '1986-', '1996-', '1999-' and '2001-enumerations'; the resulting time intervals as 'period 1' (1986–1996) and 'period 2' (1996–2001). Period 2 divided into two sub-periods: 2a (1996–1999, 2.6 years) and 2b (1999–2001, 2.4 years) when including the 1999-enumeration on the subplot level (Fig. 2). These periods and subperiods might be thought of as 'pre-drought', 'drought' and post-drought', except that period 1 was not free of any droughts (Newbery and Lingenfelder 2004), the length of the sub-period encompassing the 1997–1998 major event is arbitary, and post-drought effects did begin well before 1999. Analysis within different sizes was performed for trees with the following gbh limits: all, ≥10 cm gbh (≥3.2 cm dbh); small, 10–<50 cm gbh (3.2–<15.9 cm dbh); medium, 50–<100 cm gbh (15.9–<31.8 cm dbh); and large, ≥100 cm gbh (≥31.8 cm dbh). To allow comparison with some other studies, measures were also found for the population of trees with a dbh of ≥10.0 cm (≥31.4 cm gbh).

Some trees above the minimum gbh-limit at first measurement were (due to natural shrinking, bark loss, slight measurement errors, or because multiple-stemmed trees lost one or more of their stems) too small at the second enumeration, and not being part of the population they were labelled 'regressors'. Between the second and third enumerations regressors either died, remained with gbh less that the minimum value, or regrew above that value. In the last case, a regressor was not viewed as a new recruit because it was a member of the population of trees ≥10 cm gbh at an earlier enumeration (original tag number used). This problem of trees regressing below the minimum size and potentially re-growing above that limit in a subsequent enumeration is addressed in Supplementary materials—Appendix 2 ('Losses and gains').

Basic dynamic rates

Periodic (m_p, r_p; %) and annualized (m_a, r_a; % year^{-1}) rates were found for mortality and recruitment, respectively, after Alder (1995) and Sheil et al. (1995), on the plot or subplot level for different size classes, using the mean time intervals of each individual group (see Supplementary materials—Appendix 3 for formulae). Confidence limits (95%) of m_a and r_a were estimated with an approximation based on the F-distribution. Correction of m_a for the differences in length of time interval (5-year basis) followed the method of Sheil and May (1996), as applied to the Danum data set in Newbery and Lingenfelder (2004). Absolute (agr; mm year^{-1}) and relative (rgr; mm m^{-1} year^{-1}) stem growth rates were similarly found (Supplementary materials—Appendix 3).

Growth rate calculations were based here on intervals of each individual tree. As frequency distributions of rgr values were always very strongly positively skewed, and no transformation could normalize, or a suitable probability density function be found as yet to model them, a bootstrapping procedure ($N = 2000$ runs) was used to find means and 95% confidence limits of these variables. Comparisons on this basis are to be made within each period separately. The database was handled in Microsoft Access and statistical analyses performed with GenStat versions 7 and 8 (Payne et al. 2007). Individual growth values were used for two reasons: (1) interest lay in topographic effects and differences between tree size classes, which were nested within plots; and (2) the limits would correspond to those derived for mortality rates which are de facto within-plot estimates also. Where confidence limits did not overlap means were judged to be significantly different ($\alpha = 0.05$). Growth rates were also found separately for trees that lived, and those that died, in a successive period.

Validity of growth rates

For each enumeration (except the one of 1986, when this information was not gathered) every tree was

reviewed for suitability of its girth measurements with regard to calculating growth rates, and assigned a code accordingly: 1 = suitable, 0 = unsuitable. Growth rates were considered valid (i.e., sound) only if both start and end measurements were suitable. Measurements were unsuitable where (1) the status code showed that the tree was broken below, half-broken or dead at the PoM, or had lost one or more of multiple stems; (2) the CoS indicated major deformations due to buttress growth, cracked or split bark or stems, excrescence, fluted or hollow stems, termites or lianas (an irregular stem (CoS = DI) was not considered a major deformation unless additional notes in the remarks revealed this, e.g., 'heavy', 'extremely oval', or 'spiral growth'); (3) POMs were moved or newly established (except on recruits), or the laser ranging instrument was used. The use of callipers on liana-fused trees was only considered a reason for exclusion where it was not possible to take two measurements or the callipers were too small.

From the resulting valid rates, some trees had additionally to be excluded because they had negative growth rates below an operational threshold. To separate those values that resulted from faulty measurements or recording errors from those that would very likely be part of the population (e.g., due to slight shrinkage because of low stem water content, unapparent loss of bark), the approach developed by Newbery et al. (1999) was followed and applied to the 1996–2001 data set: relative frequencies, expressed as proportions, of all growth rates with $agr \leq 0$ mm year^{-1} were logit-transformed and plotted in increasingly negative agr-classes. Both plots separately and combined showed an almost linear decline to -3.5 mm year^{-1}. Below that value (i.e., ≤ 4.0 mm) the distribution increased slightly, decreased again and then flattened, indicating that these values were probably not part of the 'natural' population (Lingenfelder 2005).

Spatial autocorrelation

As the growth of trees across an area might not be statistically independent from each other, the data set was explored for spatial autocorrelation (SAC). The analysis is based on mean valid relative growth rates of 10-m × 10-m subplots to account for the at-places rapidly changing topography within the main plots; a

20-m × 20-m subplot could be partly located on a flat ridge area but steeply sloping down into an intermediate elevation. Moran's test for SAC was calculated (Moran's I; using `moran.test` of the `spdep` package (Bivand 2007 in R 2.6.1, R Development Core Team 2007) and plotted at 5-m intervals across distances of 0–100 m across the whole plots as well as per hectare to investigate stationarity. Anisotropy was checked with a routine in S-Plus, Version 7.0 (Kalunsky et al. 1998). The effects of topography (elevation and slope) on rgr were investigated with a spatial conditional autoregression (CAR) model estimation by maximum likelihood (`spautolm` in `spdep`; Bivand 2007) and ordinary regression (R Development Core Team 2007). The models included linear, quadratic and cubic terms. Based on a likelihood ratio test (of the spatial coefficient; within `spautolm`) it was decided whether CAR spatial specification improved the model.

Results

Forest structure

Total numbers of trees in the main plots decreased by 299 and 679 in periods 1 and 2, respectively. Considering only trees with $gbh \geq 10$ cm, the corresponding decreases were 677 and 642. The large difference for period 1 was due to regressors being excluded and gains included (Table 1). On an annual basis, tree numbers ($gbh \geq 10$ cm) in period 2 declined almost twice as fast (128 stems year^{-1}) as in period 1 (68 stems year^{-1}). Results for the individual plots are given in Supplementary materials—Appendix 3.

With some slight variability between the plots, tree density decreased for all and for small trees in the two periods by 4% (Table 2 and Supplementary materials—Appendix 3). It increased for medium-sized and large trees in period 1 (by 5%), yet the density of medium-sized trees decreased in period 2 (by 2%) and did not change for large trees, the latter due to a 3% decrease in plot 1 but a 3% increase in plot 2. Recruits and dead trees had lower densities in period 2 than 1, largely due to the differing interval lengths. On an annual basis, the density of recruits increased by 7%, while the density of dead trees increased by 32%. The contribution of dead trees that had been regressors in 1996 was 1% of all trees (or 9% of all dead trees) in

Table 1 Numbers of trees at Danum for periods 1 (1986–1996) and 2 (1996–2001), two main plots combined, from those at the starts (n_{start}) to the ends (n_{end}), and showing the numbers that survived (n_s), died (n_d), recruited (n_r), were gained (n_{gains}) and lost (n_{losses})

	Period	
	1	2
n_{start}	17942	17643
$n_{start\_\geq 10}$	17942	17265
n_d	2655	1938
$n_{d\_reg\_p1}$		182
$n_{d\_\geq 10}$		1756
n_s	15287	15705
n_{reg}	378	341
n_{losses}	3033	1931
$n_{s\_\geq 10}$	14909	15364
n_r	2356	1259
$n_{reg\_p1\_\geq 10}$		30
n_{gains}	2356	1289
n_{end}	17643	16964
$n_{end\_\geq 10}$	17265	16623
$n_{diff\_\geq 10}$	−677	−642

The subscript ≥ 10 refers to numbers of trees with $gbh \geq 10$ cm gbh (For details at the plot level, see Supplementary materials—Appendix 3)

$n_{d\_reg\_p1}$: number of regressors of period 1 that were found dead in period 2; n_{reg}: number of regressors in period 2: old(remaining) = 166, new = 175; $n_{reg\_p1}\_{\geq 10}$: number of regressors of previous period, gbh in 2001 ≥ 10 cm

2001 (Table 2). From 1986 to 2001, density decreased for all and small trees but increased for medium-sized and large trees. The ratio of densities in three size classes within each main plot was close to 90:7:3 for small, medium and large trees, respectively, over the three enumerations (Supplementary materials—Appendix 3).

The 16 subplots, with the restrictions applied, had 5190, 4239, 3885 and 3706 in 1986, 1996, 1999 and 2001, respectively. Small trees represented 91% of all trees in 1986 and 86% at the other three enumerations. During period 1 and sub-periods 2a and 2b, 741, 237 and 213 small trees, respectively, died, so that the original population in 1986 lost 23% of its trees by 2001 through mortality, 6% (293 trees) either regressing to <10 cm gbh or advancing to ≥ 50 cm gbh. Mean density (2027 ha^{-1}) in 1986 was similar to that of the main plots (cf. Table 2), but mainly as a consequence of the missing recruits, these values

Table 2 Densities of trees (n trees ha^{-1}) in the main plots at Danum in 1986, 1996 and 2001 for three size classes of tree

	1986	1996	2001
Size class			
All (≥ 10 cm gbh)	2243	2158	2078
Small (10 to <50 cm gbh)	2033	1939	1863
Medium (50 to <100 cm gbh)	146	153	150
Large (≥ 100 cm gbh)	63	66	66
≥ 31.4 (≥ 10 cm dbh)	432	452	435
Recruits		295	157
Dead (≥ 10 cm gbh)		332	220
Dead (regressors 1996)			23

For details at the plot level, see Supplementary materials—Appendix 3

steadily declined to 1448 ha^{-1} by 2001. The mean number of small trees per subplot was 266 ($n = 16$, range, 169–386).

Coarse-scale dynamics

Basic rates

In period 1 (1986–1996) almost 15% of trees died across both plots and in period 2 (1996–2001) 11% died (Table 3). Differences between the two replicate plots were apparent in period 1: in plot 1 the periodic mortality rate was 4% above that in plot 2 (Supplementary materials—Appendix 3). In period 2 the difference between plots in m_p was much less (<1%). Annualized mortality was 45% higher in period 2 for both plots combined (Table 3a). The relative increase of m_a in plot 1 was almost twice that in plot 2 (33 vs. 61%) and m_a values in period 2 were correspondingly more similar than in period 1 (Supplementary materials—Appendix 3).

Based on a 5-year interval, the correction of m_{all} (the overall average mortality resulting from the taxa- and subplot-wise grouped mortalities) produced the expected result for period 1: shifting the annual mortality from 10 to 5 years using the correction factors (1.115 for plot 1 and 1.220 for plot 2) calculated from the data set where the rarest species were excluded ($n_{min} = 2$), increased mortality rates by 13% and 24% in plots 1 and 2, respectively. As the intervals of period 2 were similar for plot 1 (5.06 years) and plot 2 (4.94 years) and both of these were very close to an average of 5.0 years, m_{all} did

Table 3 Forest dynamics of the main plots at Danum for periods 1 (1986–1996) and 2 (1996–2001), trees ≥ 10 *gbh*: rates of mortality, recruitment and growth, and the estimated overall mortality based on species' rates

	Period	
	1	2
m_p (%)	14.80	10.98
m_a (% year^{-1})	1.59	2.30
r_p (%)	13.13	7.14
r_a (% year^{-1})	1.24	1.39
agr (mm year^{-1})	3.05	3.12
rgr (mm m^{-1} year^{-1})	11.15	12.48
m_{all} (% year^{-1})	–	2.34[a]
m_{corr}	1.87[a]	–

For details at the plot level, see Supplementary materials—Appendix 3

m_p, m_a: periodic and annual mortality (all trees, including regressors: n_d/n_{start}); r_p, r_a: periodic and annual recruitment; *agr*, *rgr*: absolute, and relative, growth rate in stem girth; m_{all}: overall average mortality with species within subplots as groups; m_{corr}: m_{all} corrected to 5-year basis (no correction for period 2)

[a] Means of plot 1 and 2 values

not need an interval correction. On this basis of the foregoing considerations, mortality increased by 20% in plot 1 and by 31% in plot 2 between periods 1 and 2. The mortality rates for both plots combined were thus 1.87 and 2.34% year^{-1} in periods 1 and 2, respectively, implying an increase by 25% between the periods. Rates for trees ≥ 10 cm *dbh* are given in Supplementary materials—Appendix 3 also.

Periodic recruitment rate in period 2 was just over half of that in period 1, as expected from the differing time intervals (Table 3). Recruitment was lower than mortality in both periods and both plots. The annualized recruitment rate in period 2 was 12%

chigher than that in period 1, for both plots combined. The changes in r_a between the periods were, however, smaller than for m_a and the two plots rather diverged than converged with time: plot 1 had a 16% higher recruitment rate in period 2 than 1 whereas in plot 2 it increased by just 7%. Thus plot 1 increased its prominence in regard to recruitment rate. Absolute (*agr*) and relative (*rgr*) growth rates were 9–17% higher in plot 1 than plot 2 (Supplementary materials—Appendix 3). Between periods 1 and 2 *agr* increased by 2.3% (from 3.05 to 3.12 mm year^{-1}) and *rgr* by 11.9% (from 11.2 to 12.5 mm m^{-1} year^{-1}; plots combined). The frequency distributions of *agr* and *rgr* were nevertheless strongly positively skewed.

Effects of tree size and topography

In periods 1 and 2 m_a was higher on intermediate positions and lower slopes than on ridges (Table 4), and did not differ greatly between size classes within topographic classes (Fig. 3). Considering the individual plots, however, the m_a of medium-sized trees in plot 1 was approximately double that in plot 2, a much larger difference than in the other size classes (Supplementary materials—Appendix 4). In period 2, m_a increased with size for all topographic classes combined (Fig. 3d), a reflection especially of the large (1.6-fold) difference between small and large trees in plot 1 (Supplementary materials—Appendix 4). This increasing trend with size was most clearly shown on the ridges (Fig. 3a), while on the lower slopes m_a was highest among the medium-sized trees (Fig. 3c), and intermediate positions had a complex pattern in between (Fig. 3b). In the small, medium and large size classes, m_a was overall 31, 42 and 94%, respectively, higher in period 2 than 1. The increase in m_a across periods was strongest for

Table 4 Comparison of annualized mortality (m_a, % year^{-1}), recruitment (r_a, % year^{-1}) and relative stem growth rates (*rgr*, mm m^{-1} year^{-1}) in plots 1 and 2 combined at Danum in three topographic classes for periods 1 (1986–1996) and 2 (1996–2001)
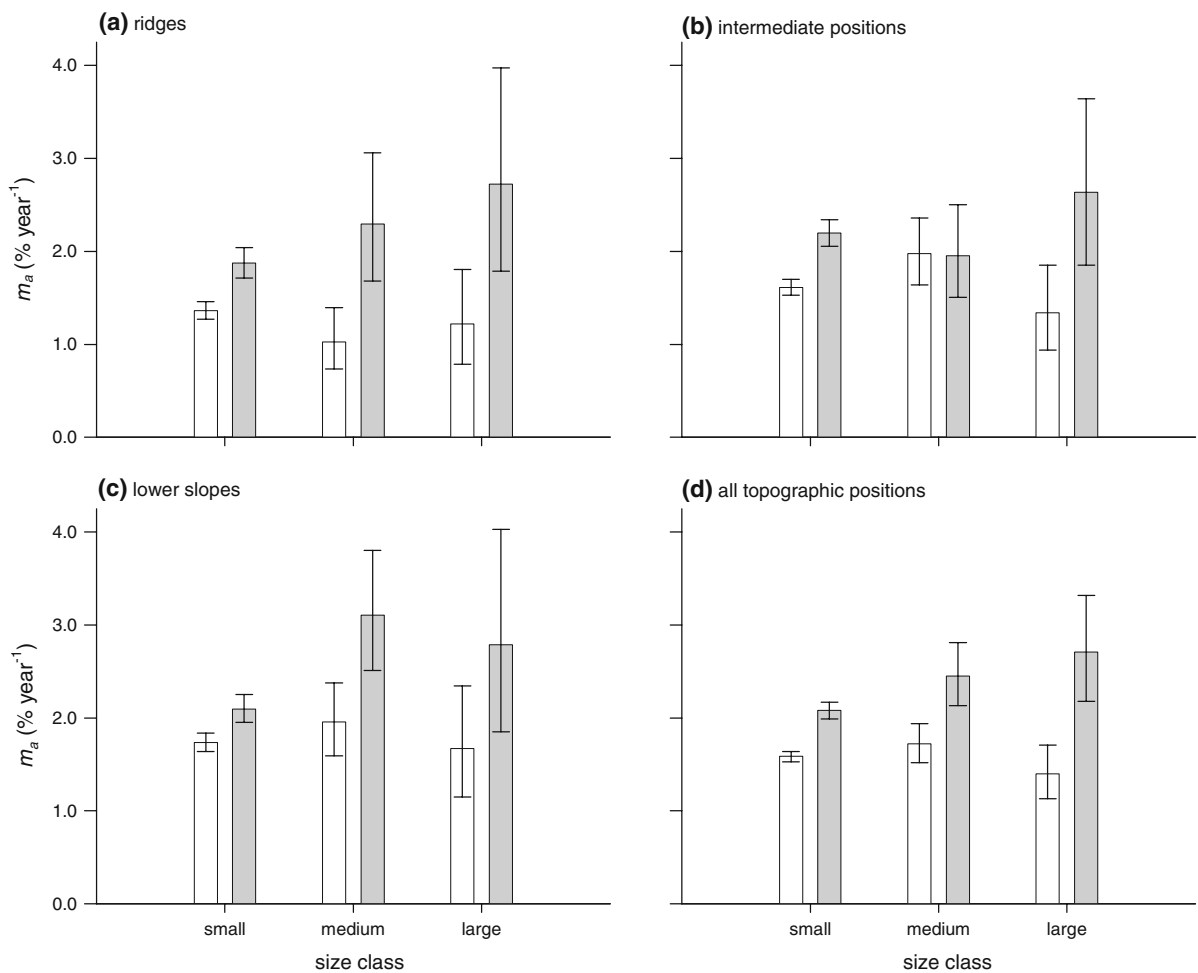
Topographic class	m_a		r_a		*rgr*	
Period:	1	2	1	2	1	2
Ridge	1.34 [1.25–1.43]	1.93 [1.78–2.09]	1.19 [1.12–1.26]	1.31 [1.19–1.43]	10.52 [10.10–11.00]	12.71 [12.22–13.30]
Intermediate	1.63 [1.55–1.71]	2.19 [2.06–2.33]	1.26 [1.20–1.32]	1.27 [1.17–1.36]	11.43 [11.04–11.83]	11.99 [11.59–12.49]
Lower slope	1.75 [1.66–1.85]	2.19 [2.05–2.34]	1.27 [1.20–1.33]	1.67 [1.56–1.78]	11.32 [10.90–11.78]	12.88 [12.36–13.42]

Numbers in square brackets are the 95% confidence limits (bootstrapped in case of *rgr*). Numbers of trees at the starts of the intervals (m_a) or numbers of valid trees (*rgr*) are found in Supplementary materials—Appendix 4

medium-sized trees in plot 2 with a 2.25-fold increase (Supplementary materials—Appendix 4). Again, it was the intermediate position (averages over size classes) that showed the largest differences between plots (plot 2 almost 40% higher than plot 1). Considering interactions between size class, topography and plot, the most marked changes were the increase in m_a of large trees on ridges plot 1 (period 2 > 5-fold period 1), and the amelioration for medium-sized trees in the intermediate position in plot 2. Small trees were in general much less affected. Between plot differences were important.

Recruitment was also lowest on ridges although differences between locations were smaller than for mortality (Table 4). Furthermore, r_a hardly changed

on intermediate locations between periods, increased moderately (10%) on ridges but rather strongly (32%) on lower slopes (Table 4). Relative growth rates were higher in period 2 than 1 by 11, 21 and 18% in small, medium and large size classes, respectively (Table 4, Fig. 4d). Except for medium-sized trees in period 1, growth rates were higher in plot 1 than 2 in both periods, especially strongly for the small trees (Supplementary materials—Appendix 4). Relative growth rates generally decreased with increasing size class in both plots and both periods, more pronounced on ridges and intermediate positions (Fig. 4a, b) than on lower slopes in period 1 (Fig. 4c), while in period 2 the trend was broken by medium-sized trees on the intermediate positions performing marginally better

Fig. 3 Mortality rates within size and topographic classes in the main plots at Danum: m_a (% year^{-1}) for period 1 (*open bars*) and period 2 (*grey bars*) in the main classes of small,

medium and large trees **a** on ridges, **b** at intermediate positions, **c** on lower slopes, and **d** for all topographic classes combined. Bars indicate 95% confidence limits
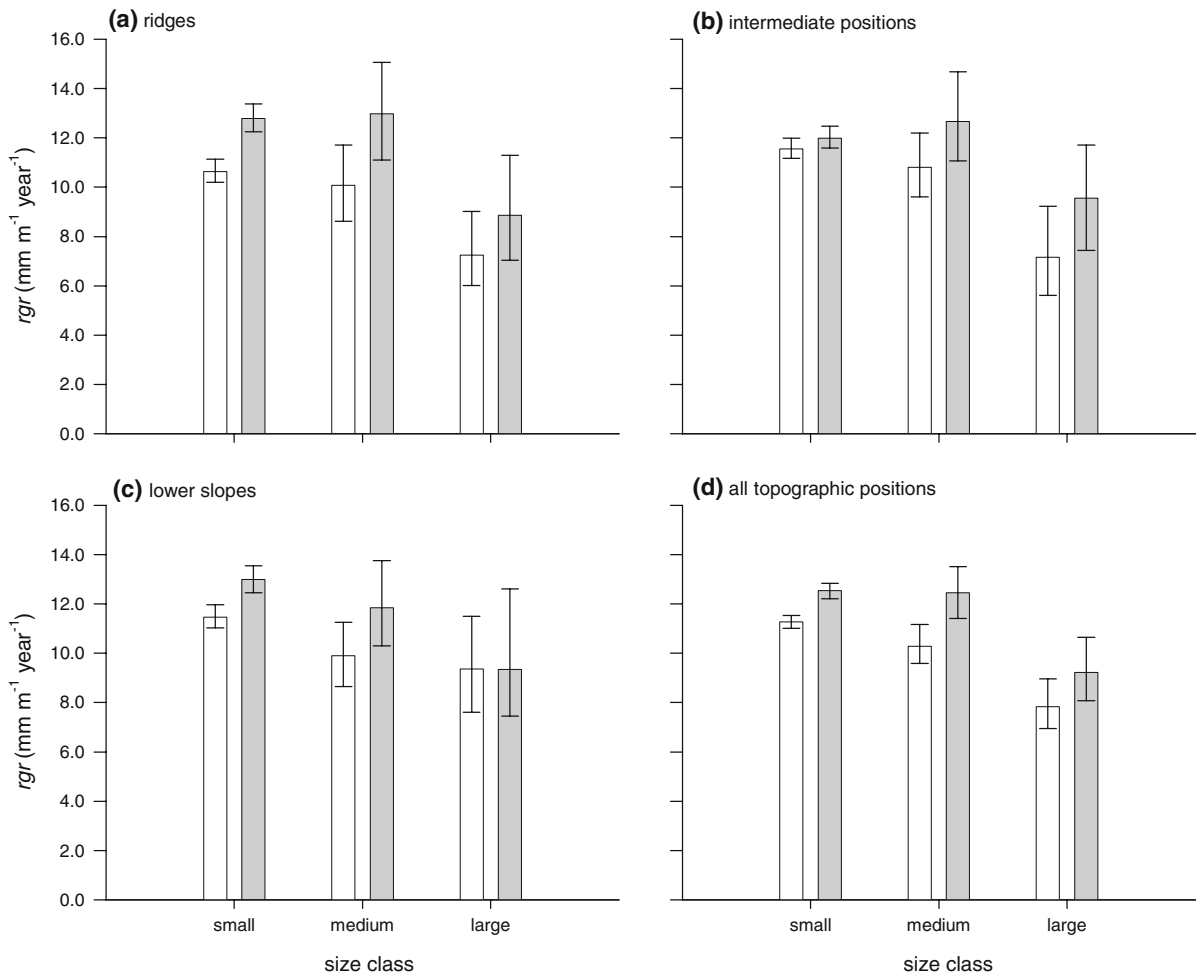
Fig. 4 Relative growth rates within size and topographic classes in the main plots at Danum: *rgr* (mm m^{-1} year^{-1}) for period 1 (*open bars*) and period 2 (*grey bars*) in the main classes of small, medium and large trees **a** on ridges, **b** at intermediate positions, **c** on lower slopes, and **d** for all topographic classes combined. Bars indicate 95% confidence limits

relative to the other size classes. Trees on intermediate positions had 22% and 39% higher mean *rgr* in plot 1 than 2 in periods 1 and 2, respectively (Supplementary materials—Appendix 4). Among the plot–plot differences (far fewer than for m_a) only one more is noteworthy: a >50% lower *rgr* in plot 2 than plot 1 for large trees in intermediate positions in period 1.

Growth, topography and spatial autocorrelation

Spatial autocorrelation (Moran's I) was detected for distances up to 25 m (period 1) in main plot 1 and up to 60 m (period 2, when neglecting the significant cases after some insignificant distances) in main plot 2 (Supplementary materials—Appendix 5). There was no sign of anisotropy but SAC showed non-stationarity, i.e., varying effect across both plots. Regular regression models showed very mixed results. There was a significant fit for main plot 1 of *rgr* on just elevation in period 1 ($P < 0.01$) and on slope in period 2 ($P < 0.01$), however, the variance accounted for in those cases was very small (2.5% and 1.7%, respectively). Likewise, for plot 2, the fit of *rgr* on elevation was significant in periods 1 and 2 ($P < 0.001$) but only for slope in period 2 ($P < 0.01$): r^2 lay between 3.2% and 9.2% in those cases. Spatial specification led to an improvement of the model in main plot 2: CAR of *rgr* on elevation and on slope

had a significantly improved fit in periods 1 and 2 (LR probability <0.001 in three cases, <0.05 in one case). In plot 1, CAR led to no significantly improved fits. Interaction between the periods and elevation and slope was low.

Fine-scale dynamics

Basic rates

Annualized mortality rate (m_a) increased by 42% between period 1 and sub-period 2a, but by only 7% between sub-periods 2a and 2b (Table 5a). Correcting to the basis of $t = 5$ years and $n_{min} = 2$ (correction factors = 1.109, 0.834 and 0.849 for (sub-) periods 1, 2a and 2b, respectively; see Lingenfelder 2005), m_{corr} increased by just 6% between period 1 and sub-period 2a, and by 9% between sub-period 2a to 2b. Mean relative growth rates across subplots declined by 38% between period 1 to sub-period 2a but recovered substantially by 98% in sub-period 2b, 23% higher than in period 1 (Table 5b). All 16 subplots had lower *rgr* (−4 to −82%) in period 2a than in period 1, but only two decreased further in *rgr* (−8 to −16%) during period 2b. Of the 14 subplots with higher *rgr*, seven increased by >100% (up to 275%) compared to period 2a. Against period 1, seven subplots had lower *rgr* in period 2b, but in nine subplots growth was still elevated above the level of the pre-drought period (three subplots with >100%). Variability of growth rates was higher in sub-period 2b than before, pointing—after the more uniform reaction (reduced growth) immediately after the drought—to a strong

positive, but spatially diverse response of trees starting *c*. 1 year after the drought.

Effects of tree size and topography

Small trees were divided into four 10-cm size classes, and in all of these mortality rates of sub-periods 2a and 2b were higher than in period 1 (Fig. 5a). The strongest increase in mortality of sub-period 2a over period 1 was in the 30–40 cm class (80%) with a smaller increase in sub-period 2b (10%), so that m_a in this size class almost doubled between period 1 and sub-period 2b. The 20–30 cm size class exhibited the strongest increase in m_a between sub-periods 2a and 2b (22%). All trees were affected immediately in sub-period 2a, most severely those 30 − <50 cm *gbh*. In sub-period 2b, trees 20–<40 cm still had increasing m_a but those 10–<20 and 40–<50 cm *gbh* appeared to be relatively less affected (Fig. 5a).

Small trees on lower slopes experienced higher m_a in period 1 than those on ridges and intermediate locations. In sub-period 2a, mortality in all topographic classes increased strongly by 25–65%, but the differences between classes were smaller than in period 1, trees on ridges showing a slightly higher mortality than those on lower slopes. Period 2b showed a further increase of mortality on the ridges (9%) and intermediate elevations (48%), but a decrease (16%) on lower slopes. Trees on intermediate elevations reached the highest mortality rates across the three topographic classes and periods (3.05% year^{-1}). Comparing m_a of sub-period 2b with that of period 1, the intermediate class more than

Table 5 Estimates of annualized mortality rate for small trees in subplots, and the rate corrected for differences in interval length for period 1 and sub-periods 2a and 2b at Danum, and the corresponding mean subplot (±SE) absolute (*agr*) and relative (*rgr*) stem growth rates

	Period / Subperiod		
	1	2a	2b
(a) Annualized mortality (% year^{-1}):			
Mean (m_a)[a]	1.53	2.17	2.32
Overall mean at $t = 5$ years (m_{all})	1.57	2.06	2.18
Corrected overall mean (m_{corr})	1.70 ± 0.11	1.81 ± 0.10	1.97 ± 0.23
(b) Growth rates:			
agr (mm year^{-1})	2.44 ± 0.18	1.60 ± 0.13	2.91 ± 0.33
rgr (mm m^{-1} year^{-1})	11.12 ± 0.79	6.90 ± 0.54	13.68 ± 1.56

[a] Weighted mean m_a values across subplots were almost identical
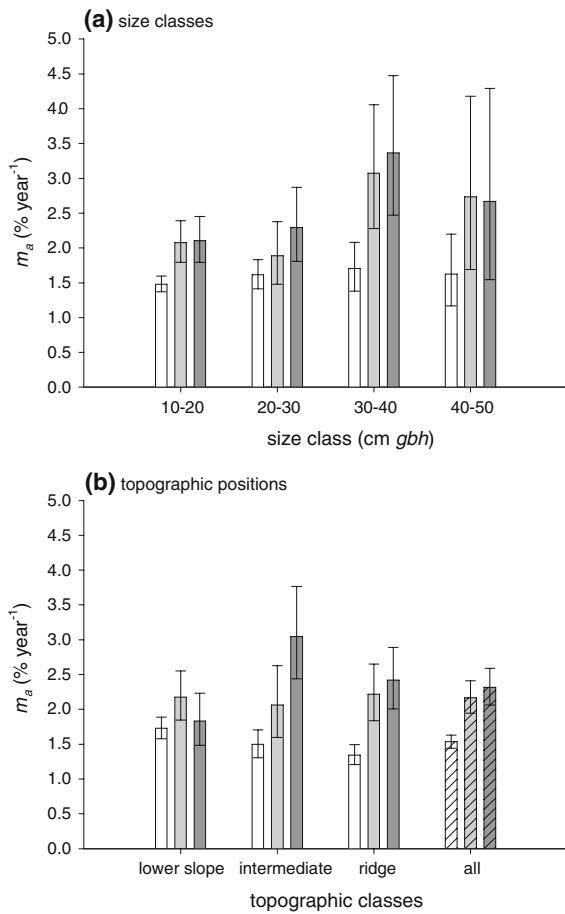
Fig. 5 Mortality rates of small trees in the subplots at Danum (m_a, % year^{-1}) for period 1 (*open bars*), and subperiods 2a (*light grey bars*) and 2b (*dark grey bars*): **a** in four 10-cm *gbh* classes, and **b** for three topographic classes. Bars indicate 95% confidence limits

doubled (increased by 104%) in mortality and ridges had 80% higher mortality but m_a for trees on lower slopes was elevated by only 6% (Fig. 5b).

The decline of *rgr* between period 1 and sub-period 2a, and subsequent recovery between sub-periods 2a and 2b was apparent across all size classes, this becoming less pronounced with increasing size (Fig. 6a). Mean growth rate of the smallest trees (10–<20 cm *gbh*) in sub-period 2a was 45% lower than in period 1 but increased by 129% between period 1 and sub-period 2b. All size classes had higher *rgr* in sub-period 2b compared to period 1 (by 16–25%). Differences in growth between size classes were small in period 1 and more variable in sub-periods 2a and 2b. During sub-period 2a, growth rates

increased with size class: the smallest trees were most affected by the drought (Fig. 6a). Trees on intermediate topographic locations had the highest *rgr* in period 1, and also showed the greatest decline between period 1 and sub-period 2a (−45%) compared to trees on ridges and lower slopes (Fig. 6b). Trees on lower slopes grew slightly better than those on ridges in period 1 and sub-period 2a. Trees on ridges were more affected in sub-period 2a (40% less *rgr* than in period 1) but recovered better than those on lower slopes in sub-period 2b (135 vs. 65%, respectively, compared to period 2a) and then displayed the strongest gain in growth compared to period 1 (42%) and the highest rates of all topographic classes in all periods (Fig. 6b). Analysis for
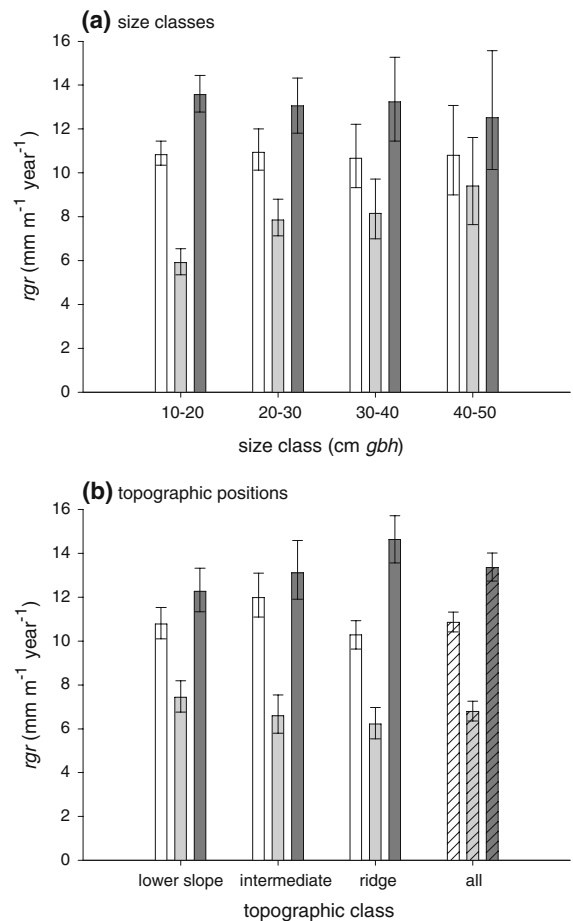
Fig. 6 Relative growth rates of small trees in the subplots at Danum (*rgr*, mm m^{-1} year^{-1}) for period 1 (*open bars*), and subperiods 2a (*light grey bars*) and 2b (*dark grey bars*): **a** in four 10-cm *gbh* classes, and **b** at three topographic classes. Bars indicate 95% confidence limits

SAC in subplots showed even fewer significant fits than on the whole plot level, again with little variance accounted for. Including the CAR model only proved to be useful in one case (main plot 1, sub-period 2b).
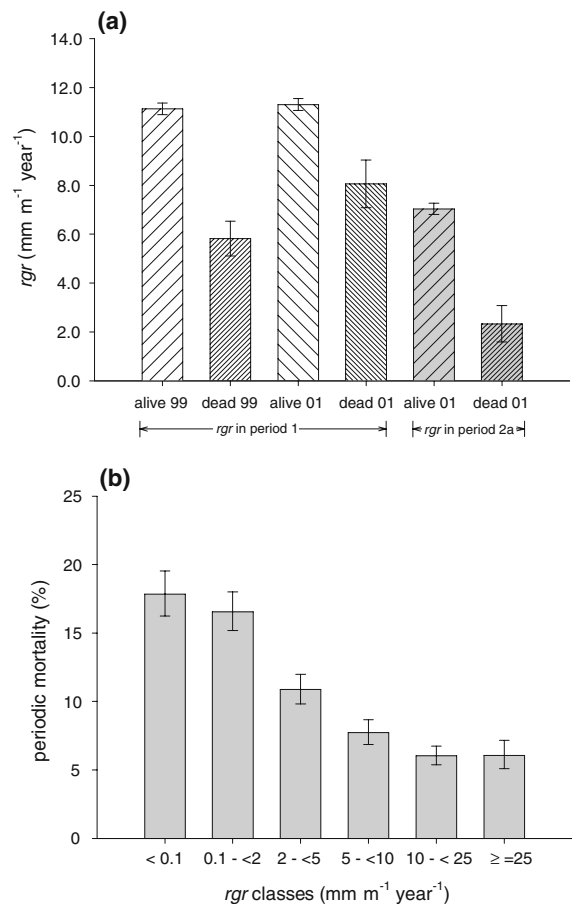
Growth and subsequent mortality

In period 1, the growth of trees that died between 1996 and 1999 was a little more than half of that of trees that were still alive in 1999 (Fig. 7a). This effect was again visible for trees that died between 1999 and 2001: their growth rates of period 1 lay still well below those of the alive-trees in 2001 (29% for *rgr*, less pronounced with 21% for *agr*). Growth in sub-period 2a of trees that died during sub-period 2b was even two-thirds lower than that of the trees that still lived in 2001 (Fig. 7b). Both Mann–Whitney *U*-test and Kolmogorov–Smirnov test showed highly significant ($P < 0.001$) differences between all combinations. Periodic mortality in period 2 fell nearly 3-fold between trees with <2 and those with ≥ 10 mm m^{-1} year^{-1} *rgr* in period 1 (from 17 to 6%; Fig. 7b).

Valid and invalid growth rates

Proportions invalid and sources of invalidity

The number of trees that were classified as having unsuitable *gbh* measurements decreased by 10% between 1996 and 2001 (Supplementary materials—Appendix 6; information was not available for the first enumeration of 1986). This was largely because of the much smaller ($<50\%$) number of trees where a new PoM had to be established (or an existing PoM moved) in 2001 compared to 1996—understandable given the higher probability of losing a paint mark in the longer (10-year) interval. Conversely though, measurements were more affected by unsuitable stem conditions in 2001 than 1996 (Supplementary materials—Appendix 6).

During the part-enumeration of 1999 (where only 'tree status' and 'condition of stem' had been recorded), the status 'standing' (DS) was attributed to almost half of the dead trees, compared to much lower proportions in 1996 and 2001. Close to a third of dead stems were recorded as 'damaged' (DB, DA, DU) in 1999, but this status was attributed to around half of the trees in 1996 and 2001. Notably, the proportion of trees with lianas or liana damage

Fig. 7 Growth and subsequent mortality at Danum: **a** Relative growth rates of small trees in subplots for period 1 (*open bars*) and subperiod 2a (*grey bars*) categorized according to whether they lived (wide hatching) or died (narrow hatching) in subsequent subperiods; bars are SEs of subplot means. **b** Change in periodic mortality in period 2 of trees with increasing (valid) relative growth rate in period 1. Sample sizes of the six successive classes were 1508, 1950, 2336, 2483, 3447 and 1550. Bars indicate 95% confidence limits

increased steadily between 1996, 1999 and 2001 (Supplementary materials—Appendix 6).

The number of invalid growth rates increased by 40% (from 1754 to 2453), however, because mainly the newly unsuitable measurements in 2001 were not all for the same trees as in 1996—in 954 cases (Table 6). (The remaining difference in unsuitable measurements versus invalid rates in both periods/ enumerations was due to (a) trees regressing <10 cm *gbh*, and (b) growth rates additionally excluded because *agr* ≤ -4 mm year^{-1}.) In periods 1 and 2, 12% and 16%, respectively, of the *rgr* values were invalid. Losing old PoMs and damage to stems were

Table 6 Relative contributions (%) of the causes of unsuitability that led to invalid growth rates

	Period	
	1	2
Damaged	26.4	25.1
Lianas	5.1	7.4
Moved PoM	7.8	1.2
New PoM	56.6	16.4
Relascope/laser/callipers	0.6	0.0
Buttresses	0.2	2.1
Irregular stem	2.5	5.8
Absolute growth rate ≤ -4 mm	1.0	1.3
Invalid at start of period		38.4
Other reasons (regressors, etc.)		2.4

See main text for numbers of invalid rates per period and Supplementary material—Appendix 6 for totals

the other main reasons why some growth values became invalid (although this ranking does depend on the importance given to the individual categories because the classifications concerned multiple aspects (CoS, PoM, MeM, etc.), a stem could have been damaged and been measured at a new PoM: the ranking chosen here is as shown in Table 6 (from top to bottom). Across size classes, the proportion of invalid growth rates increased with size, with a similar shape in both periods (Fig. 8a).

Comparison of valid with invalid growth rates

Being influenced by very negative values, the mean of the invalid rates lay well below (by 26–68%) the mean of the valid rates and in sub-period 2a the mean invalid *rgr* was negative (Fig. 8b). Both the increases in *rgr* between periods 1 and 2 and between sub-periods 2a and 2b, as well as the decrease between period 1 (subplots, small trees) and sub-period 2a, were much less pronounced for valid compared to invalid growth rates, indicating an underestimation of the changes between periods.

Setting those growth rates to zero where *agr* was >-4.0 and <0 mm year^{-1} and dropping the large negative values ≤ -4 mm year^{-1} (which yielded very similar results as when setting all *agr* values <0 mm year^{-1} to zero), resulted in elevated *rgr* compared to the preferred approach, only slightly (up to 1%) in periods 1 and 2, and in period 1 for small

trees, but much more (20–43%) in sub-periods 2a and 2b. The consequence would have been a decrease in *rgr* between period 1 (small) and sub-period 2a by only 11% and an increase between sub-periods 2a and 2b by only 65%. Including the small negative rates (>-4 and <0 mm year^{-1}) but setting all invalid ones to zero growth, i.e., adding 304 to 2567 (depending on the period) *rgr* values of 0, growth rates would have been substantially lowered (by 8–17%) with the effect that the change in *rgr* would have been only 6% between periods 1 and 2 but similar between the sub-periods (P1 to P2a: +38%, P2a to P2b: +103%) when compared again to the preferred 'problem-free' approach.

Immediate effect of 1997/1998-drought

Mortality and growth rates of period 1 (1986–1996) were assumed to hold constant until the onset of the 1998-drought on 4 April 1998, the date on which the *30-d-rt* of precipitation had fallen <100 mm for 10 days. Period 1 was extended to t_{P1x}, by 1.84 years, leaving a drought sub-period 2x of 0.78 years (see Fig. 2). The number of trees present at the start of sub-period 2x (n_{98}) was estimated from: $n_{98} = n_{96} (1 - m_{a\_P1})^{t_{P1x} - t_{P1}}$. The number of trees dying in extension was: $n_{d1x} = n_{96} - n_{98}$, and consequently those dying in sub-period 2x: $n_{d2x} = n_{d99} - n_{d1x}$. The resulting m_a for sub-period 2x was 3.64% year^{-1} ($n_{96} = 4239$, $n_{98} = 4120$, $n_{d99} = 237$). Using m_a estimates uncorrected for interval length (1.53% year^{-1}), m_a more than doubled (increase of 138%) between period 1 (and sub-period 1x) and sub-period 2x. Applying the correction procedure developed for sub-periods 2a and 2b (above, and Lingenfelder 2005), and tentatively extrapolating the curve back from 1.0 to 0.78 years, an approximate correction factor which places m_{a_2x} on a 5-year interval basis is 0.90. This led to a corrected value of 3.28% year^{-1}, a slightly less-than-doubling in m_a (increase of 93% on 1.70% year^{-1} in Table 5). The absolute growth rates of period 1 were applied at the start of sub-period 1x to the *gbh* values of 1996. From the *gbh* values in 1998 so estimated, *rgr* for sub-period 2x could be found (trees $10 - <50$ cm *gbh*). Mean growth rates in sub-period 2x were negative: $agr = -0.44$ mm year^{-1}, $rgr = -2.38$ mm m^{-1} year^{-1}. During sub-period 2x small trees on average therefore decreased by 0.34 mm *gbh* (or 0.11 mm *dbh*).
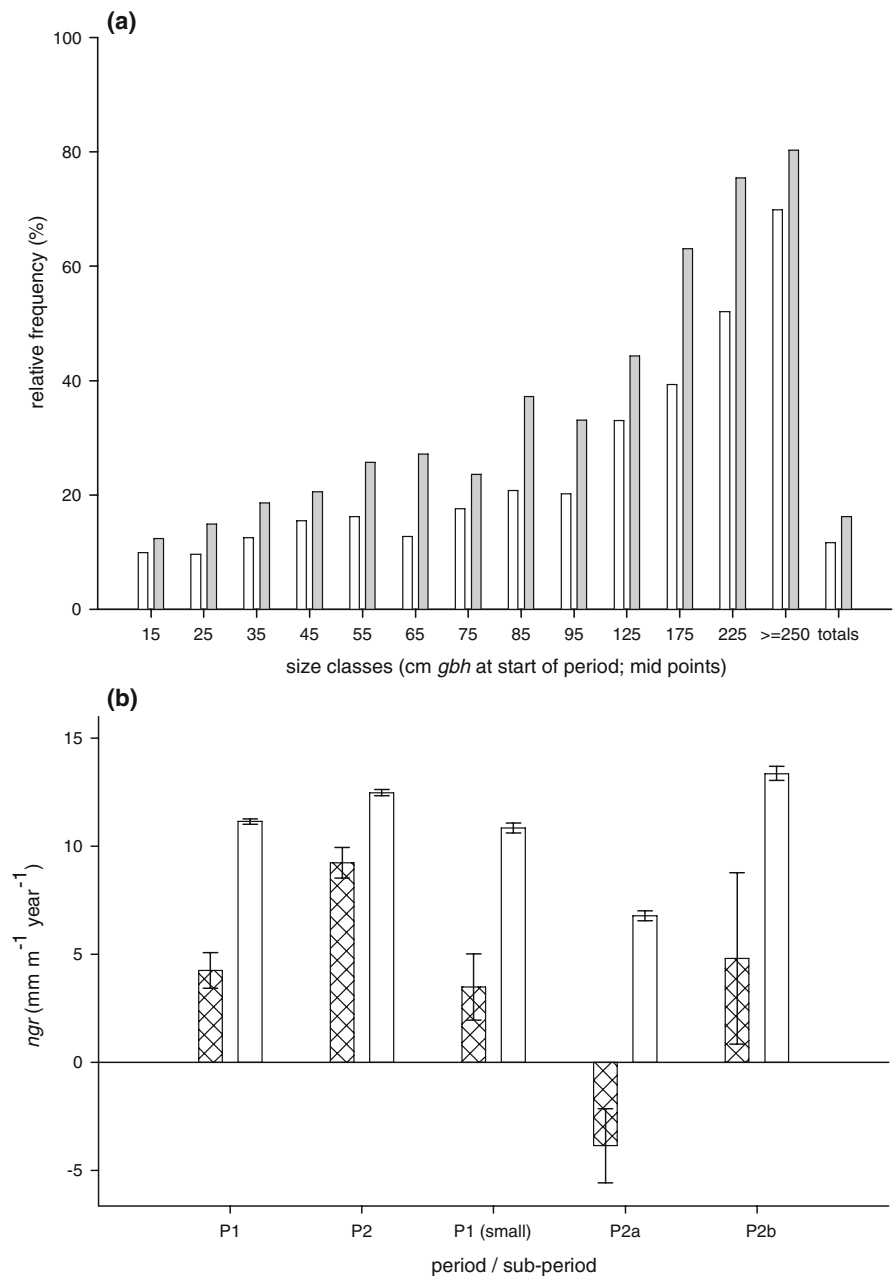
Discussion

Methodological and analytical considerations

Mortality and recruitment

The dynamics of the forest at Danum was based on
measurements of two replicate 4-ha plots containing
c. 19 K trees ≥10 cm *gbh* spanning 15 years.

Taxonomic identification was almost 100% and done
to a high level, with revisions at later enumerations
reducing the proportion of singletons. Mortality,
recruitment and stem growth rates of all trees from
1986 to 1996, and from 1996 to 2001 (periods 1 and
2) could be estimated at the plot level but only
mortality and growth rates of small trees, from 1996
to 1999 and 1999 to 2001 (sub-periods 2a and 2b)
were achievable at the subplot level (*c*. 1/3 of the plot

area). Care was taken to confirm that trees recorded as having died really were dead (ideally for any enumeration this should be checked 3–6 months after), and that recruits corresponded precisely to the ≥ 10 cm lower *gbh* limit. At the plot level, rates in period 2 included trees that recruited at the end of period 1. By contrast, at the subplot level rates in sub-periods 2a and 2b were based on only the survivors of the previous period or sub-period. Accordingly, the results given here are slightly different from those of Newbery and Lingenfelder (2004) where the 1996-recruits for sub-period 2a were included. The important contribution of regressors in the dynamics calculations (leading to alternative calculations of gains and losses to the population, Supplementary materials—Appendix 2) was, accordingly, only possible at the plot level and for period 2.

Periodic mortality rates were slightly higher than recruitment rates in both periods, this being in part due to the underestimation of true recruitment rates. Without assuming unrealistic population equilibrium conditions, even for period 1, there is to date no fully satisfactory way of accounting for recruits which die within a period and go unrecorded at the next enumeration. The best corrected value for m_a increased by 25% between periods 1 and 2, while r_a (uncorrected) increased only 12%, giving the impression that recruitment lagged behind mortality. However, the lower r_a (than m_a) was probably due to a combination of the evident long-term succession (Newbery et al. 1992), the influence of the most recent drought (Newbery and Lingenfelder 2004) and the methodological underestimation. It means further that such a data set on tree dynamics—based on plots remeasured at intervals of several years—cannot be complete. It is not justified even to assume that m_a and r_a are constant with time, which on the one hand raises a problem for corrections of m_a for interval length (Sheil and May 1996; Newbery and Lingenfelder 2004), and on the other hand questions whether r_a can be similarly corrected (possibly in the way Lewis et al. 2004 have suggested), given that recruits of different species will also have their own different mortality rates.

Tree death is likely in part to be a consequence of reduced growth rate. Very low to zero, or negative growth rates, are often associated with trees in their last months or years before dying (Kobe 1996; Kobe and Coates 1997). Of particular interest for Danum

is—apart from the time lag—that the difference in *rgr* of 2001 alive and dead trees was much larger for sub-period 2a than period 1, the former being directly associated with the 1998 drought perturbation. The larger difference for the 1999 than 2001 alive and dead trees' *rgr* in period 1 lends support in the same direction. A similar association of *rgr* with mortality has been shown by Chao et al. (2008).

Local-scale heterogeneity in forest dynamics was evident from the different responses of the two plots. Mortality rate (m_a) changed more in plot 2 than 1, but the converse was the case for r_a: plots differed less in m_a in period 2 than 1 (a convergence) but differed more in 2 than 1 for r_a (divergence). The plots differed in important details of topography especially the small stream running across plot 2, and the more exposed ridge in plot 1 (Fig. 1). It is interesting that often medium-sized trees in intermediate positions showed the largest plot–plot differences, suggesting that small (understorey species) and large (mostly canopy species) trees were adapted at the extremes of the gradient but between them drought caused the most reactivity.

Including regressors, and using a fixed population size threshold (to find alternatively losses and gains), had important consequences for these calculations. Of the two periods, evaluation of the dynamics was more complete for period 2 than 1 because information on regressors at the start of period 1 was lacking. A critical unknown concerns the dynamics of trees close to the minimum *gbh* used in the enumeration. This may perhaps be overcome in the future by closer study of subsamples of trees in the *c.* 7.5–25-cm *gbh* range over a series of shorter time intervals. More intensive sampling (with more persons involved), however, would mean more interference to the vegetation.

In the present analysis, data from the two replicate plots have been combined because overall plot differences were small compared with those over time (Newbery and Lingenfelder 2009). Confidence limits on means of m_a and *rgr* in tree-size and topographic classes approximately indicated the between-tree variability. Measurements of individuals will not be spatially or temporally independent from one another, though, and the true limits are likely to be slightly larger. Statistical comparisons between classes are inappropriate for another reason—the classes were arbitrarily defined on a continuous scale. Spatial auto-correlation was addressed in the analysis of

growth in relation to topography with individual tree elevations and slopes rather than classes. The end result was that it had a relatively very small effect.

Stem growth

In the analysis reported in this paper attention was given to the determination of the validity of stem *gbh*, and hence *rgr*, and an extensive system of coding for invalid trees in the field (CoS, MeM, PoM). In the calculation of mean growth rates of trees per plot or subplot almost all other tropical studies have sought ways of correcting questionable *gbh* values (those appearing anomalous due to measurement or recording errors for plausible reasons) or unsuitable pairs of *gbh* (due to shift in PoM, poor CoS at start and/or end of the period) so that all surviving trees had an actual or estimated growth increment, and any finally omitted from the data set were those remaining unexplainable extreme negative and positive values. A major concern of many researchers has been how to deal properly with the small negative growth values, and no standard mathematical probability density function for tree *rgr* has been found which caters for the numerous small negative as well as the few highly positive growth rates encountered. These negative rates became important in evaluating drought effects in period 2 at Danum.

Condit et al. (1993) omitted trees whose *dbh* decreased by >5% or had an *agr* of >75 mm year^{-1}, and left the smaller decreases in the data set. Later though after excluding those decreasing >25% and the same class of extreme positives, negative increments in *dbh* were removed by resetting the second *dbh* of a pair to the first *dbh* + 0.5 mm (Condit et al. 2006). No mention was made of how increments where PoM, CoS, and MeM (equivalent to the terminology of this paper) were dealt with. Condit et al. (2004) excluded trees where the second *dbh* was ≥4 SDs (of a reference remeasurement) below the first one, which was equivalent to excluding only trees with growth rates ≤−5 mm year^{-1} *dbh* (−15.7 mm year^{-1} *gbh*; positives >75 mm year^{-1} were also again excluded). Editing the data in this way will raise the mean growth increment unless the removal of the very few extreme positive values balances the many small negative ones. Clark and Clark (1999) moved the PoM when stem irregularities required it, but seemingly used the second *dbh* in finding the last period's growth

increment even if the PoM was no longer suitable: the new PoM was applying to the next period. The data of Phillips et al. (1998) rest on a method of standardizing *dbh* measurements at old and new (shifted) PoMs using 'the ratio of diameters at both PoMs' (Peacock et al. 2007), but it is not explained how this was actually achieved. Feeley et al. (2007) simply changed the growth rate to zero for all trees where the PoM had changed, presumably replacing in this way both some negative and some positive values, and Nakagawa et al. (2000) excluded all growth rates ≤−2 mm year^{-1} in diameter and set those >−2 and <0 mm to zero growth.

Nevertheless, how frequent stem irregularities were in leading to new PoMs is not mentioned in any study we could find and it is not possible from any of them to ascertain what percentage of values were edited, rounded up, or omitted. Most authors simply write the problem off as being of 'negligible' consequence, and any details pertaining are sometimes hidden in appendices. Baker et al. (2004), finding plot basal area increments in Amazonian forests, also needed to deal with aberrant *dbh* values. Those with *agr* ≤−2.0 mm year^{-1} or ≥40.0 mm year^{-1} were left out (following a recommendation of Sheil 1995, for one forest site in Africa), and those appearing unusual were replaced by either a value interpolated from *dbh* values before and after the datum in question or if at the end of a series by the median value of the other trees in its size class. Chave et al. (2008) applied a similar procedure but with class limits of −5.0 and 45.0 mm year^{-1}, and using means of *dbh* classes for substitution: PoMs were only painted when they deviated from the standard 1.3 m; a possible source of inaccuracy. In none of these studies is it explained objectively why the selected cut-off values were used or a justification of rounding negative values to zero or small positives was made. It gives the impression of practical convenience: Sheil (1995) referred to 'harmonizing' his data set on the grounds of 'common sense', and Phillips et al. (2002) call their procedure 'post measurement data checking' where so-called 'false' negatives are rounded up (to zero usually) but 'false' positives are not rounded down. In our analysis for Danum we have sought to avoid these arbitrary systems. We excluded only extreme negative values on the basis of an objective statistical technique (Newbery et al. 1999) and retained all other negative values as part of the sample of tree measurements. No

extreme positive *rgr* values were omitted because the maximum *agr* was 75.5 mm year^{-1} *gbh* (24.0 mm year^{-1} *dbh*), for a dipterocarp in period 2. While this value is well within the limits used by Condit et al. (2004, 2006) and Sheil (1995), it is not unexpectedly large for these species and forests. In the present data set, modifications of negative or invalid growth rates would have led to different growth levels (elevated or lowered) and—in the case of setting slight negative values to zero—possibly an underestimation of the response of the forest to the 1997/1998 drought.

By excluding invalid trees, estimates of mean growth rates of valid ones were highly accurate, especially for the small trees (10 − <50 cm *gbh*). Possible biases as a result of unusual growth (e.g., buttresses moving upwards or development of reaction-wood on steep slopes), stem irregularities or measurement uncertainties through the use of optical instruments for large trees, were minimized. Nevertheless, trees that were labelled invalid because their stems were defect or unsuitable might have had relatively slow growth rates if these features were indicating damage or a stage prior to death. Conversely, large trees with buttresses, especially those emerging out of the main canopy, might have had relatively fast (valid) growth rates. Recording stem growth rates more accurately and completely could be achieved by a set of 3–5 (multiple) PoMs spaced along the bole, so that at least one (preferably more) gave a valid *rgr* for any period (Dawkins 1956). This would be prohibitively intensive in field work and as a trade-off limit the number of trees and area enumerated considerably.

Including growth rates down to −4 mm year^{-1}, and not excluding every rate <0 mm year^{-1} can be defended on grounds of (i) physiology and growth, since it has been shown in the present and other studies (e.g., Sheil 2003) that shrinkage of trees due to loss of stem water does occur to this extent; (ii) there are measurement errors, so that a tree of zero growth rate can be recorded with an error of ±1 or 2 mm; and (iii) the logit-plot technique of Newbery et al. (1999) highlighted a very different frequency distribution below −4 mm compared with above it where values formed part of an (unknown) exponential-type family function.

In the treatment of growth data there are two choices: to substitute unmeasured or erroneous rates by estimates (medians, means, interpolated values,

ceven by zeros or small positives), or to leave them as unmeasured, and accept that where two *gbh* values do not meet acceptable accuracy then the *rgr* remains unknown. In the present paper, the second choice has been taken because the forest dynamics is clearly in a short-term non-equilibrium state and the response to a perturbation is being studied. Possibly in a steady-state equilibrium forest some replacement might be defended but even then it should not be necessary if 'errors' and unmeasured rates are at random and distributed proportionally across all size classes and species. To obtain *agr* and plot level basal area increments would simply require here a proportional multiplying up. Nevertheless, substitution must introduce bias and the more the system is away from a steady state the stronger the likely bias. This is an important issue given the increasing recognition that many forests are recovering from recent perturbations (Wright 2005; Chave et al. 2008).

Was the *rgr* in period 2 (12.5 mm m^{-1} year^{-1}) higher than in period 1 (11.6 mm m^{-1} year^{-1}) then because period 2 had a greater proportion of invalid trees than period 1, that is more trees (of largely low or negative *rgr*) were removed from the total sample in period 2 than 1? It cannot be known empirically what the valid rates of the invalid class would have been: they are undetermined. It is not even possible to reasonably assume, based on current knowledge, that they were proportional to the invalid rates with a common conversion equation applying to both periods, or that the invalid sample was a subsample of similar origins and frequency distribution in both periods. The same argument applies for the sub-periods of period 2. The situation is not satisfactory but indicates the limits of what can be measured and how far the dynamics of the system can be reliably interpreted. We recommend that in future authors could report how many trees in their samples were edited and omitted, and for what reasons.

Assuming a dynamic equilibrium in order to substitute for missing values or make the analysis tractable has been repeatedly shown to be mistaken in ecology. It is clearly the case for the forest at Danum, where the continual readjustment in response to past perturbations means that the system never comes to a constant state, remaining in flux and unpredictable. A fundamental concern is how much the drought influenced the extent of the recording of valid

growth, a problem further compounded by the need to use fine-scale time resolution to detect the dynamic response at all.

Dynamics and droughts at Danum and in relation to other tropical forests

Immediate and lagged mortality and growth

Mortality did increase after 1996 by 25% (interval corrected rates of all trees for both main plots combined). Taking the subset of small trees measured in 1999 into account, a rather moderate, continuous increase by 6% and 9% in sub-periods 2a and 2b, respectively, was indicated. However, in the calculation of these values, regressors, gains and recruits were excluded and thus they are probably overestimated. In a recent work at Danum (Newbery and Lingenfelder 2004), mortality was shown to have slightly decreased from 1996 to 1999 (the present sub-period 2a). If that is taken as the basis for the 'high drought intensity' period, then mortality started to take effect some time after the immediate perturbation—but still within the low precipitation-event—i.e., in the period between 9 months and 3 years after the drought. Also increases in growth rates did occur after 1999 (in period 2b), after a very strong decline in sub-period 2a. Even though during the partial enumeration from December 1998 to March 1999—9 months after the peak of the drought—rainfall was above average (mean 30-d-rt: 275 mm), measurements were done within the drought event that lasted until mid-April 1999, with the antecedent rainfall history still indicating a deficit (Lingenfelder 2005; Newbery and Lingenfelder 2009). It seems reasonable that under these circumstances, water storage in the outer tree compartments was not refilled by then and growth was not substantial enough to result in positive rates. Sheil (2003) reviewed different studies and performed an exploratory study on tropical diurnal tree stem diameter variation. He found that fluctuations in girth (shrinkage and expansion) of 0.5 mm–2.0 mm day^{-1} were not exceptional. In Ghana, Baker et al. (2002) observed dry-season (c. 4 months) shrinkages as much as 2.8 mm in diameter (8.8 mm in girth). Although a theoretical calculation, the average shrinkage in tree girth of 0.34 mm in c. 9 months (during sub-period 2x) shown in the present study is therefore not surprising.

Two effects successively took place at Danum during and after the strong drought of 1997/1998: (a) an immediate response in growth (negative impact) while mortality did not increase or only slightly increased (resistance, but possibly weakening), followed by (b) lagged responses in mortality (negative impact) and increased growth (resilience). Harrison (2001) hypothesised that even though droughts are not the direct trigger for flowering, they have an influence on phenology with a general increase of leaf production and flowering after droughts (offering an advantage of not flowering during times of heavy rain which could possibly damage the flowers and disrupt pollination and possibly having increased light levels due to increased mortality). Leaf shedding and flushing within 2 months of experiencing a short dry spell was found for trees in Sarawak and the flushing seemed to have induced cambium growth: 2–4 months after the flushing or 3–6 months after a dry spell, growth rates peaked on two occasions in 1996 and 1997 (Ichie et al. 2004). At Danum, extensive defoliation occurred in March 1998 and growth rates were very low at least until early 1999 when the partial enumeration took place. As the 1997/1998-drought was more intense than the brief dry periods described in Sarawak, and it is not known when flushing recommenced at Danum, it is well possible that this process of shedding and flushing occurred in a similar but slowed-down manner. Severe water stress led to abscission of senescent leaves with reduced stomatal control (Walsh and Newbery 1999), bud break and flushing assumingly soon after rainfall increased again (perhaps when 30-d-rt >100 mm), but hardly any (detectable) cambium growth until water storage in the trees was completely refilled in the first quarter of 1999 (possibly in April, when the antecedent rainfall history was turning positive again). Nutrient availability on the forest floor may have been increased by the defoliation and this additionally provided the basis for the boost in growth after April 1999.

The delayed increase in mortality after a severe drought is in contrast to results of other studies in Borneo. At two different sites within Lambir Hills National Park, Sarawak, Nakagawa et al. (2000) and Potts (2003) estimated mortality for pre-drought (1993–1997) and drought (1997–1998) periods. They found more than 3-fold higher mortality rates in the second interval that ended shortly (5–6 months) after

the 1997/1998-event. This drought was possibly more severe in that region than at Danum, indicated by *30-d-rt* <100 mm for 89 days (at Danum the equivalent value was 58 days), although the preceding rainfall history at the Lambir site is not known. However, 'true annualised mortality' (Nakagawa et al. 2000) and 'exponential mortality coefficient' (Potts 2003) for two time intervals of quite different length were compared: *c*. 4 years versus *c*. 1 year. As the decline of mortality rate in heterogeneous populations due to dependence on the interval length is especially strong from $t = 1$ to $t = 2$ (Sheil and May 1996), the high rates of the short drought period in these two studies might have been substantially overestimated. Nakagawa et al. (2000) also did not find a large decline in relative growth rates in their drought period.

A similar pattern of mortality was found in East Kalimantan (Slik 2004). Although only 'percentages of dead standing trees' were given, these were much higher shortly (8–13 months) than 4 years after the drought (15.4% compared to 4.2% in the 'undisturbed' plots). Plots in logged areas of that study had an even higher percentage of dead trees, this also hinting at the possibly increased risk to disturbed ecosystems. Sites classified as 'dry' had more dead trees than those which were 'wet' (Slik 2004). By contrast, at Sungai Wain, a site close to that of Slik's, lagged mortality was found by van Nieuwstadt and Sheil (2005): 8 months after the drought the proportion of dead trees was 18.5%, increasing to 26.3% at 21 months. In nearly all of these studies, there was no correction for interval length and the inferred drought effect was over-estimated.

Size-related effects

Across both main plots, mortality was highest for medium-sized and lowest for large trees in period 1. In the second period, mortality increased with increasing size, large trees being most affected by the drought, and this was most pronounced on ridges (although mortality was lower on ridges than on lower slopes in both periods). This pattern was not seen in Sarawak, where mortality decreased with increasing size; however, increase of mortality in the drought period was also greatest for large trees (Nakagawa et al. 2000; Potts 2003). On the other hand, in East Kalimantan, mortality increased with size (in the unburned plots) too, and the drought had

its largest impact on large trees (van Nieuwstadt and Sheil 2005). The authors of that study ascribed this effect to the hydraulic limitation hypothesis, where water stress increases with the height of trees (all else staying constant) and imposes a greater risk of cavitation. During moderate droughts, large trees with deeper-reaching roots might be less affected, but if water stress is becoming more severe, cavitation would in addition to faster depletion of their root zones affect large trees more than smaller ones (van Nieuwstadt and Sheil 2005). This generally fits with the Danum data. Yet, the trend found at Danum that understorey species followed the general pattern (of increasing mortality with increasing size), but overstorey-species decreased in mortality with increasing size (Lingenfelder 2005), is contrary to the findings of van Nieuwstadt and Sheil (2005). Although small trees in general seemed to be less affected by the drought, the impact on large overstorey-trees possibly was not severe enough to increase their mortality.

Conversely to mortality, relative growth rate decreased with increasing size in both periods and growth was higher on lower slopes than on ridges in period 1. In period 2, however, the recovery (i.e., the increase in growth) was larger on ridges. Growth of trees on ridge locations reached similar levels as that of trees located on lower slopes, with medium-sized trees on ridges even exceeding those on lower slopes in growth. Although there was some variation between plots, topography also showed an influence on growth rates in the regression models. This seems to imply that the forest species are largely adapted to where they are on the gradient of elevation and that the perturbation (seen on the 5-year scale 1996–2001) did not have a large effect.

Results of the present work provide strong evidence that forest dynamics at Danum from 1986 to 2001 were influenced by the responses to several mild-to-moderate and one severe drought. However, the perturbations were not major disturbances in the sense that the forest was vitally damaged. Elsewhere we have demonstrated highly species-specific dynamics, operating in ways that increased some and decreased other species and so apparently balancing or compensating one another (Newbery and Lingenfelder 2009). If the forest was still recovering from catastrophic droughts *c*. 90–130 years ago (Newbery et al. 1999; Newbery and Lingenfelder 2004), then the event of 1997/1998 could be called a 'set-back', one that it seems the

forest is capable of overcoming. Potentially threatening could be possible future increases in the intensity and frequency of droughts with shorter between-drought intervals for recovery that could lead to serious changes in the structure and the dynamics of lowland dipterocarp forests (Walsh 1996).

Conclusions

While recent moderate droughts affected the overall structure of the forest at Danum only slightly, showing that the forest can indeed accommodate such perturbations, the upper limits of drought frequency or intensity to which the forest is resilient remain uncertain. If, as a result of climatic change, drought events were to increase in the future, the forest might respond in either of two hypothetical ways: (1) an increase in faster growing, light-demanding species, because the canopy remains open for longer periods; or (2) an increase in drought-tolerant species, especially in the understorey, because the atmosphere and soil become drier also for longer periods. We prefer the second hypothesis because such a guild of drought-tolerant species has been demonstrated at the site, and increasing drought would presumably select them. Both outcomes would likely result in lower stature and biomass forest, with reduced densities of the dominant dipterocarp species that are largely drought-intolerant until they reach the sub-canopy. For the primary forest and its conservation, this would mean a substantially changed upper canopy, unless the understorey were to respond effectively enough to nurse the dipterocarps to the same degree as before, and in secondary logged forests it might lead to a tendency to replace pioneers by drought-tolerant understorey species, which could even increase (through nursing) dipterocarp restocking (Newbery et al. 1999). Clearly, it is essential to maintain long-term permanent plots like those at Danum which have the capability of following these changes, and use the data to model different drought scenarios.

The link variable between the external driving stress (e.g., drought perturbation) and forest dynamics is *rgr*. This rate is affected by numerous other factors, external and internal to the tree, but measured on stem size it is perhaps the best integrative measure of tree performance. Trees with very low, zero or even maintained negative rates tend to die, those with positive rates enable recruitment into the population and movement through the size classes. It is therefore critically important to measure *rgr* as accurately as possible and minimize the number of invalid trees because these introduce uncertainties and even biases in the final assessment. One way forward is to employ multiple PoMs, a second would be to use covariates of tree growth other than *gbh*. How the methodological and analytical problems highlighted in this paper are handled can clearly influence the conclusions drawn about how perturbations influence the dynamics of the ecosystem under study.

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