

**Rain forest dynamics and response to drought in a Bornean
primary lowland dipterocarp forest**

Inauguraldissertation
der Philosophisch-naturwissenschaftlichen Fakultät
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Marcus Lingenfelder
von Deutschland

Leiter der Arbeit:
Prof. Dr. D. M. Newbery
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Der Dekan:
Prof. Dr. P. Messerli

To Anna-Luise and Karl Lingenfelder

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I. Summary / Zusammenfassung

Tropical rain forests are highly dynamic and changing. This thesis attempts to describe the dynamics and the responses of the tree vegetation in relation to disturbances by droughts in an aseasonal rain forest at Danum in Sabah, Bornean Malaysia. Over a 15-year period, dynamics were followed. Two 4-ha research plots in a primary lowland dipterocarp forest had been set up and enumerated in 1986 and re-measured in 1996. During the course of the present work, the plots were enumerated for the third time in 2001. Almost 19000 trees ≥ 10 cm girth at breast height (gbh) were examined. These were scored for alive/dead status and living trees were measured for gbh. Trees recruiting above 10 cm gbh were included into the population. Existing taxonomic information was re-checked, improved and new trees were named. 99.8% of the trees were identified to distinct species. With the variables measured in the field, dynamics could be assessed in terms of growth, mortality, recruitment and species composition.

A new model to estimate drought intensity was developed: antecedent rainfall history includes yearly running anomalies of precipitation and is considered to reflect soil water relations ecologically more meaningful than the widely used threshold of 100 mm during one month.

The 1997/98 ENSO-related drought was found to have been the most severe at Danum since 1985. During the study period two moderate (in 1987 and 1992) and several mild droughts occurred additionally. Thus, none of the periods studied were free of droughts and forest dynamics were influenced by these disturbances, particularly in the second period (1996 – 2001).

The structure of the forest changed in respect to density and basal area: the former declining across both periods, the latter increasing in the first, but declining in the second period. Although rare species dropped out, new species entered the population and overall diversity hardly changed.

Recruitment rate increased between the periods from 1.24% y^{-1} to 1.39% y^{-1} . Mortality increased from 1.87% y^{-1} to 2.34% y^{-1} – even though the average mortality rate of the first period was adjusted to an interval length of five years to make it comparable to the second period (and rates thereby becoming more similar). Mean relative growth rate increased from 11.14 mm $m^{-1} y^{-1}$ to 12.48 mm $m^{-1} y^{-1}$.

Additional information was incorporated by including a partial enumeration in 1999,

when small trees (10 – < 50 cm gbh) in 32% of the plots were measured. It showed that mortality increased across the three periods. Growth, however, decreased from 11.12 mm m⁻¹ y⁻¹ in the first period to 6.90 mm m⁻¹ y⁻¹ in the second period, but increased again in the third period to 13.68 mm m⁻¹ y⁻¹.

These results imply a strong impact of the 1997/98 drought on the forest at Danum. The trees were affected immediately (in terms of reduced growth) or with a lag (in terms of increased mortality), but they started to recover soon after the drought (in terms of growth rates two years after the strong drought that exceeded the pre-drought growth rates).

Trees responded differently depending on species, size class and topographic location, and a clear general pattern could not be found. Generally, it appears that small trees in the forest understorey were less affected by the drought. However, among the canopy-forming Dipterocarpaceae, mortality decreased with size. Species-specific responses were very variable although some species showed trends towards specialisation on either ridges or lower slopes. Species appear to have adapted to the environment at Danum using different strategies: they may be resistant in terms of being only slightly affected or resilient in terms of recovering fast after a disturbance.

The forest at Danum is known to have been subject to frequent weak to moderate and occasional strong droughts and these disturbances are seen as an integral part of the ecosystem. The present results confirm that the forest is well-adapted to the current intensity and frequency of droughts and exists in a dynamic equilibrium. Nevertheless, the disturbance events lead to repeated set-backs to the growth of the forest. From the results of the present work, predicted increase in the severity of droughts may pose a threat to the structural stability of lowland dipterocarp forests across South-East Asia.

Zusammenfassung

Tropische Regenwälder sind sehr dynamisch und laufenden Veränderungen unterworfen. Diese Arbeit versucht, die Dynamiken des Waldes und die Reaktionen der Bäume auf Trockenheiten in einem immergrünen Wald ohne jährliche Trockenzeiten bei Danum in Sabah, einem malaysischen Bundesstaat auf Borneo, zu beschreiben. Die Dynamik wurde über einen Zeitraum von 15 Jahren beobachtet. Zwei vier Hektar grosse Versuchsflächen in einem Tiefland-Primärwald (mit den bestandesbestimmenden Dipterocarpaceen) wurden 1986 angelegt und gemessen; 1996 fand eine zweite

Aufnahme statt. Im Rahmen der Arbeit an dem vorliegenden Projekt wurden die Flächen 2001 zum dritten Mal aufgenommen. Annähernd 19000 Bäume mit einem Umfang in 1.3 m Höhe von ≥ 10 cm wurden untersucht. Es wurde aufgezeichnet, ob die Bäume lebten oder abgestorben waren. Bei den lebenden wurde der Umfang gemessen. Über den Mindestumfang einwachsende Bäume wurden neu aufgenommen. Die Taxonomie der Baumarten aus früheren Aufnahmen wurde überprüft und verbessert und die neuen Bäume wurden identifiziert. Damit waren 99.8% der Individuen bis auf Artebene bestimmt. Mit den gemessenen Variablen konnten die Dynamiken des Waldes in Bezug auf Wachstum, Mortalität und Einwuchsraten eingeschätzt werden.

Ein neuer Ansatz zur Abschätzung der Stärke von Trockenheiten wurde entwickelt: der Verlauf von Niederschlägen wurde über die jährlich gleitende Abweichung vom Mittelwert berechnet. Dies wird als geeigneter angesehen als der oft genutzte, einfache Schwellenwert von 100 mm Regen während 30 Tagen, da hierbei die Bodenwasserverhältnisse ökologisch sinnvoller gewichtet werden.

Die Trockenheit, die 1997/98 in Verbindung mit einer ENSO auftrat, war die strengste in Danum seit 1985. Während des untersuchten Zeitraumes ereigneten sich zwei weitere mittelstarke (1987 und 1992) und mehrere schwache Trockenheiten. Daher war keine der untersuchten Perioden ohne Trockenheiten, was die Walddynamik beeinflusste, am intensivsten in der zweiten Periode (1996 bis 2001).

Die Struktur des Waldes hat sich dahingehend verändert, dass die Dichte der Bäume kontinuierlich abnahm und sich die Bestandesgrundfläche nach einem Anstieg in der ersten Periode, in der zweiten ebenfalls verringerte. Die Baumartenzusammensetzung änderte sich leicht, da seltene Arten ausfielen und neue Arten hinzukamen, aber die Artenvielfalt veränderte sich kaum.

Jährliche Einwuchsraten erhöhten sich von $1.24\% \text{ y}^{-1}$ auf $1.39\% \text{ y}^{-1}$ zwischen den Perioden. Die jährliche Mortalitätsrate stieg von $1.87\% \text{ y}^{-1}$ auf $2.34\% \text{ y}^{-1}$ an – trotz der Anpassung der Mortalitätsraten der ersten Periode auf ein Zeitintervall von fünf Jahren, um sie mit denen der zweiten Periode vergleichen zu können (wodurch die Raten ähnlicher wurden). Der jährliche relative Zuwachs erhöhte sich von $11.14 \text{ mm m}^{-1} \text{ y}^{-1}$ auf $12.48 \text{ mm m}^{-1} \text{ y}^{-1}$.

Zusätzliche Informationen konnten eingearbeitet werden, indem eine Teilaufnahme der Versuchsflächen von 1999 berücksichtigt wurde. Bei dieser wurden auf 32% der Fläche die kleinen Bäume (10 – < 50 cm Umfang) gemessen. Dabei zeigte sich, dass die Mortalität über die drei Perioden anstieg. Das Wachstum jedoch verringerte sich

von $11.12 \text{ mm m}^{-1} \text{ y}^{-1}$ in der ersten Periode auf $6.90 \text{ mm m}^{-1} \text{ y}^{-1}$ in der zweiten, erhöhte sich dann aber wieder auf $13.68 \text{ mm m}^{-1} \text{ y}^{-1}$ in der dritten Periode.

Diese Ergebnisse lassen auf eine starke Wirkung der 1997/98er Trockenheit auf den Wald bei Danum schliessen: die Bäume wurden einerseits unverzüglich (Abfall der Wachstumsraten) und verzögert (laufend ansteigende Mortalität) beeinträchtigt, andererseits erholten sie sich schon bald nach der Trockenheit (Wachstumsraten zwei Jahre nach der Trockenheit waren höher als jene davor).

Abhängig von Baumart, Grösse und Standort (Ober-/Unterhang), reagierten die Bäume unterschiedlich, wobei kein klares Muster erkennbar war. Allgemein scheinen die kleinen Bäume im Unterstand des Waldes weniger stark durch die Trockenheit beeinträchtigt zu sein. Allerdings nahm die Mortalität der Dipterocarpaceen, die die Oberschicht des Waldes bilden, mit steigender Grösse ab. Baumarten-spezifische Reaktionen waren sehr variabel, obwohl einige Arten tendenziell besser am Unter- oder Oberhang wuchsen. Die Baumarten haben sich scheinbar mit verschiedenen Strategien an die Umweltbedingungen in Danum angepasst: sie sind teilweise widerstandsfähig (wenn sie nur leicht zu beeinträchtigen sind) oder federn die Beeinträchtigungen ab, indem sie fähig sind, sich bald nach der Störung wieder zu erholen.

Es ist bekannt, dass der Wald bei Danum oft von schwachen bis mässig starken und gelegentlich von starken Trockenheiten heimgesucht wird. Diese Störungen werden als ein fester Bestandteil des Ökosystems gesehen. Die vorliegenden Ergebnisse bestätigen, dass der Wald gut an die gegenwärtige Häufigkeit und Stärke von Trockenheiten in einem dynamischen Gleichgewicht angepasst ist. Dennoch wird das Wachstum des Waldes durch diese Störungen immer wiederkehrend zurück geworfen. Die vorausgesagte Zunahme der Strenge von Trockenheiten könnte nach den Ergebnissen der vorliegenden Arbeit eine Bedrohung für die strukturelle Stabilität von Tiefland-Regenwäldern in Südost-Asien darstellen.

II. Introduction

The universe is change.

Marcus Aurelius (121 - 180), Meditations

The dynamic nature of ecosystems has been recognized by ecologists, change being the normal course of events. Consequently, even without direct human interference, which may feed back on regional climate, tropical rain forests are neither stable nor unchanging. There is no competitive equilibrium (which would lead to increasing extinctions of species and eventually low diversity) among organisms and no equilibrium of the community with the environment (Huston 1994), "uniform stable environments never exist in nature" (Huston 1979). The environment of tropical rain forests is variable over longer time scales (Newbery *et al.* 1999a) and their highly diverse tree communities "are unlikely to be constant in their species composition, or to show stable equilibria in their dynamics" (Newbery *et al.* 1999b). Instead, a dynamic equilibrium between low rates of competitive displacement and a moderate to low frequency of disturbance has been postulated (Huston 1979, 1994, Newbery *et al.* 1999b). Adding to the dynamics at the species level in a state of non-equilibrium is that the composition of a forest in any one location is highly special and dependent on its local history including climate, site and biogeography.

Therefore, if the term equilibrium implies the tendency of an ecosystem to show similar characteristics in terms of biomass, structure and species composition on average over long time scales (decades to centuries) and/or larger spatial scales, dynamic equilibrium may be exhibited by ecosystems (Connell and Sousa 1983, Newbery *et al.* 1999b). The dynamism is then triggered by forces (internal or external) which may affect growth by deceleration, damage or removal and the following responses of the vegetation. These may be either resistance (unaffected), persistence (the ability to tolerate stress – conditions when resources are below the optimum or they cannot be utilized optimally – across extended periods) or resilience (the ability to recover within time before the next negative force operates) or a substantial change (gradual or rapid) to the vegetation. These disturbances drive the dynamic nature of ecosystems and their interactions with the vegetation are essential to the understanding of ecological

processes.

Frequent disturbance events through drought, fire, floods, or hurricanes appear to occur largely at random and are difficult to predict (Newbery *et al.* 1999b), even more so for infrequent very strong disturbances. These stochastic events define the boundaries within which species' persistence is possible (Connell and Sousa 1983) or outside of which population reductions lead to change of species composition and structure, loss of species and biomass. The need to reliably measure disturbances (including extent, frequency and mode) and quantify changes in the forest ecosystem has been identified (Newbery *et al.* 1999a).

Droughts are the major cause of disturbance across much of South-East Asia. In aseasonal tropical rain forests droughts potentially determine forest structure and tree species composition. These droughts are generally associated with the El Niño – Southern Oscillation (ENSO) cycle and increasing knowledge about this connection as a global phenomenon, together with the recognition that rain forest ecosystem responses to these climatic anomalies are poorly understood, drew attention to ecologists who were able to study some effects in permanent research plots that had been established to study rain forest dynamics. With this aim, one research site was set up in the Danum Valley Conservation Area (Sabah, Borneo, Malaysia) in 1985/86.

The episodic cycle of the ENSO originates in sea surface temperature anomalies in the Pacific Ocean combined with sea level pressure changes at Darwin, Australia (the atmospheric component) (Trenberth 1997, Trenberth and Hoar 1997). The warm phase of the cycle is referred to as El Niño and can lead to a variety of climatic anomalies of which reduced precipitation on the west coast of southern America and across South-East Asia might be the most important.

The ENSO goes back 130000 years (Cane 2005) and ENSO-events are known to have affected Borneo for at least 18000 years (Walsh and Newbery 1999). These result in occasional weak to moderate droughts which are seen as an integral part of the ecosystem (Walsh and Newbery 1999), building a moderate disturbance regime, to which the lowland dipterocarp forest at Danum seems to be adapted (Newbery *et al.* 1999b, Walsh and Newbery 1999, Gibbons and Newbery 2003, Newbery and Lingenfelder 2004). However, during the last *c.* 30 years, the frequency and intensity of ENSO-events has increased compared to the previous 100 years and in recent decades droughts (in some regions) have also become more frequent and intense (IPCC 2001). In a future scenario,

including increased greenhouse-gas concentrations in the atmosphere, the annual cycle in the tropical Pacific and the frequency of El Niño-like conditions are expected to intensify (Timmermann *et al.* 1999, 2004). Even though not all models predict more ENSO-activity – some indicate less or little change (IPCC 2001, Cane 2005, Collins 2005) – the risk of droughts is expected to increase during future El Niño-events (IPCC 2001).

The last strong ENSO-related drought in 1997/98 raised attention to the question of how forests respond to droughts. In South-East Asia (apart from other locations in the tropics), several studies were carried out and allowed the study of ecological effects (Hämmerli 1999, Nakagawa *et al.* 2000, Harrison 2001, Delissio and Primack 2003, Potts 2003, Ichie *et al.* 2004, Newbery and Lingenfelder 2004, Slik 2004). These studies variously concluded that the forests were either well adapted to a moderate drought-regime or not adapted to the magnitude of the 1997/98-event. The focus was mainly on mortality: growth and recruitment were hardly studied and plot sizes were mostly small. In addition, drought was mainly defined by some simple measures to take effect when the 30-day running total of rainfall fell below 100 mm.

However, since drought as a factor is complex and stochastic, frequency and intensity have to be considered. Status of the soil water before and during the event, as well as replacement of depleted soil water after it, has to be taken into account in a dynamic hydrological model.

Tropical rain forest trees typically live for 100 – 400 years (Richards 1996, Newbery *et al.* 1999a) and stochastic climatic variations occur at the scales of decades to centuries. Therefore, only long-term monitoring can come close to capturing dynamics.

From previous work, it has been concluded that the forest at Danum is currently recovering from a major very strong drought *c.* 120 years ago, that it is well-adapted to repeated droughts and, although set back at stages in terms of drought-related loss of biomass, it is structurally stable and in a state of dynamic equilibrium at the scale of centuries (Newbery *et al.* 1992, 1996, 1999b, Newbery and Lingenfelder 2004). But it remains unknown how far the forest is from an equilibrium state, whether its resilience still allows recovery after the next strong disturbance or the forest is affected in a way that does not permit restitution before another drought.

From the above and from previous work at Danum, the main questions that arose were: how can drought intensity be assessed dynamically when taking into account the rainfall history at the site? How adapted is the forest to the existing moderate drought disturbance regime? To what extent are species resistant or resilient to drought? If there is resilience, what are the rates of recovery? Does the forest show immediate or rather lagged responses to droughts? Above what intensity is the ecosystem unable to tolerate droughts?

In the present study therefore, an attempt has been made to answer these questions by assessing the impact of the existing moderate drought disturbance regime and especially the 1997/98 severe drought. As the impact of droughts on tree species, different sizes, topographic gradients and position within canopy layers is thought to take effect at different times and to a differing extent, the impacts were sought in the dynamics variables, growth, mortality and recruitment on different organizational levels (species, sizes, location), and by comparing dynamics between the periods to advance a model of forest response dynamics with respect to disturbance by drought at Danum.

III. Study site

Research was conducted in the eastern Malaysian state of Sabah, *c.* 66 km inland of Lahad Datu at Darvel Bay on the north-east coast of Borneo. The study sites lie within the 438-km² Danum Valley Conservation Area (DVCA) (Figure 1), which is part of the 972.8-km² Yayasan Sabah Concession Area (Marsh and Greer 1992). The area has not been commercially logged to date and there are no settlements within. The Danum Valley Field Centre (DVFC), a touristic development (Borneo Rainforest Lodge) and temporary logging camps have been the only dwellings nearby in recent times. Old coffins and other human artefacts have been discovered within DVCA, so there might have been some settlements or regular visits in earlier times (Marsh and Greer 1992). Geographic coordinates of the 'Meteorological Hill' at Danum Valley Field Centre (DVFC) on the River Segama just east of the Conservation Area's boundary are 4°57'48" N and 117°48'10" E at an elevation of 152 m above sea level (a.s.l.) (Anon. 2000).

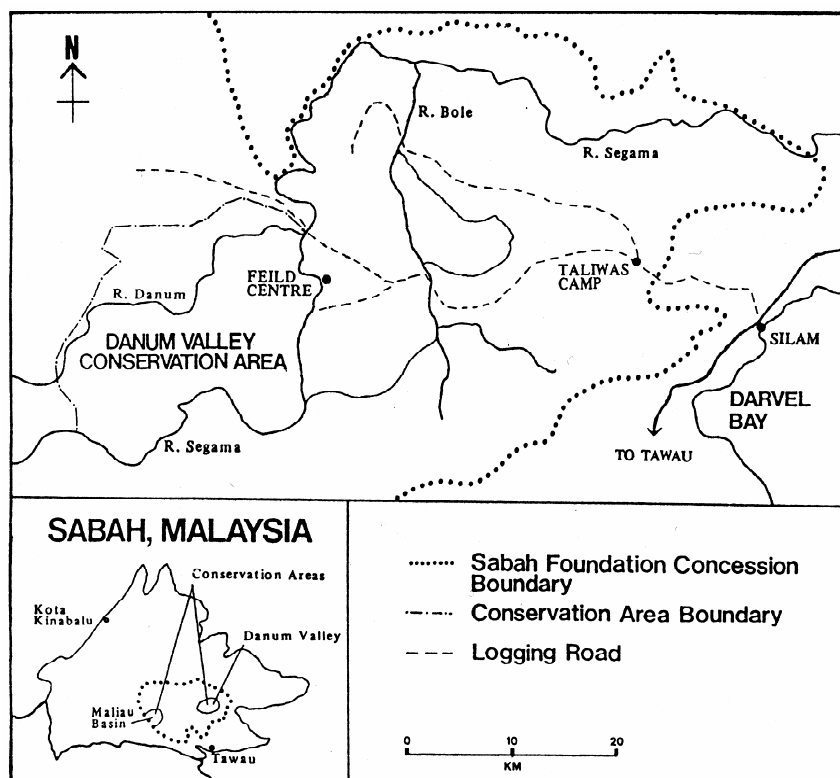


Figure 1: Map indicating the study area within Sabah (small frame) and the area west of Silam / Lahad Datu with the Danum Valley Conservation Area and the location of the Danum Valley Field Centre (large frame). Map modified from Marsh and Greer (1992)

Topography, vegetation and soils

Topography within DVCA is gently undulating at low elevations, mainly below 760 m (a.s.l.) with Mt. Danum in the centre reaching 1093 m (Marsh and Greer 1992). The area where the research plots were established lies *c.* 200-300 m a.s.l.

The vegetation of DVCA is mainly composed of primary lowland dipterocarp forest (91%, the rest being lower montane forest (Marsh and Greer 1992)). The forest at Danum is of the *Parashorea malaanonan* category (Fox 1972) and soils at Danum belong to the Bang Association (Wright 1975), although from both original publications the affiliation of DVCA is not explicit. Soils are mainly orthic acrisols developed on sandstone and mudstone of the geological Kuamut-Formation (Wright 1975). Acrisols are strongly weathered acid soils with low base saturation and a general paucity of plant nutrients (Driessen *et al.* 2001). Subjacent rocks are visible in some places.

Climate

Meteorological data for Danum were recorded at a station at DVFC since July 1985. Data presented here include the year 2003 resulting in records for 18.5 years. Data were collected for Malaysian Meteorological Service by DVFC staff under the supervision of the Royal Society (R. Walsh, University of Swansea, UK) and are used with permission.

Monthly mean temperatures ranged 1.8° C around the annual mean temperature of 26.8° C while the mean daily range was 8.6° C. The highest temperature was recorded in April 1992 with 36.5° C, the lowest in January 1993 with 16.5° C. Mean relative humidity was 95.3% at 08:00 and 78.3% at 14:00. These values are typical of equatorial rainforest locations (Walsh and Newbery 1999).

Mean annual rainfall across all full years available (1986 to 2003) was (\pm SE) 2825.3 \pm 109.9 mm with a range from 1918.4 mm (in 1997) to 3538.6 mm (in 2003) (Figure 2). Considering only those years that fully covered the study period (1986 to 2001), mean annual rainfall was 2786.7 \pm 114.6 mm.

Annual monthly rainfall (mean of each month across the years) from July 1985 to December 2003 was (\pm SE) 235.4 \pm 13.2 mm ranging from 158.3 mm (April) to 311.9 mm (January) (Figure 3). For the study period only (July 1985 to February 2002), annual monthly rainfall was 232.1 \pm 13.2 mm. Mean rainfall in the month of April was

significantly different from the annual monthly mean 1985 – 2003 (Mann-Whitney U-test: exact probability = 0.006, $U = 77.0$), but it varied considerably from 11.3 mm in 1998 – the lowest monthly value on record – to 433.3 mm in 1999, the wettest month of that year. With 701.2 mm of rain, December 2003 was the wettest month on record at Danum.

Although rainfall in the months of April and July/August on average was well below the annual monthly mean, rainfall varied considerably between years as well as between months and there is no clear dry season, indicating that Danum has an aseasonal tropical climate.

Since the start of meteorological data collection, Danum experienced 38 droughts – defined as periods with running 30-d rainfall total <100 mm (Brünig 1969, Walsh 1996b, Malhi and Wright 2004). These include two ENSO-related drought events in 1991/92 and in 1997/98. Before that, in 1982/83 a strong ENSO-event affected Sabah and may have had effects at Danum and very strong droughts have been recorded in the late 19th and early 20th centuries at regional scales throughout Sabah (Walsh 1996b).

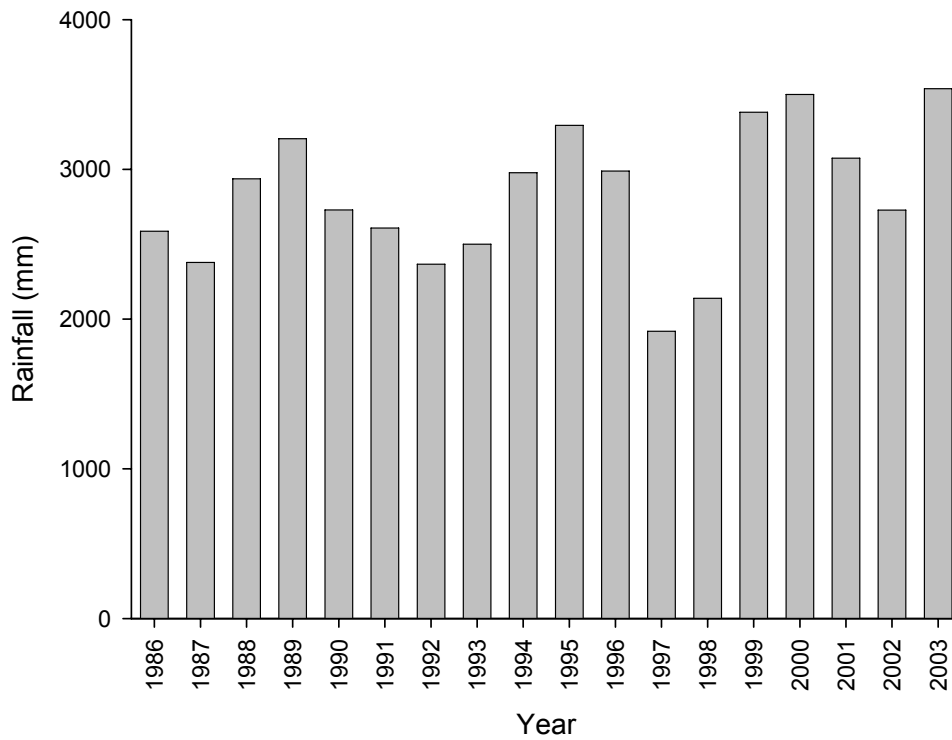


Figure 2: Annual rainfall at DVFC in the period 1986 to 2003.

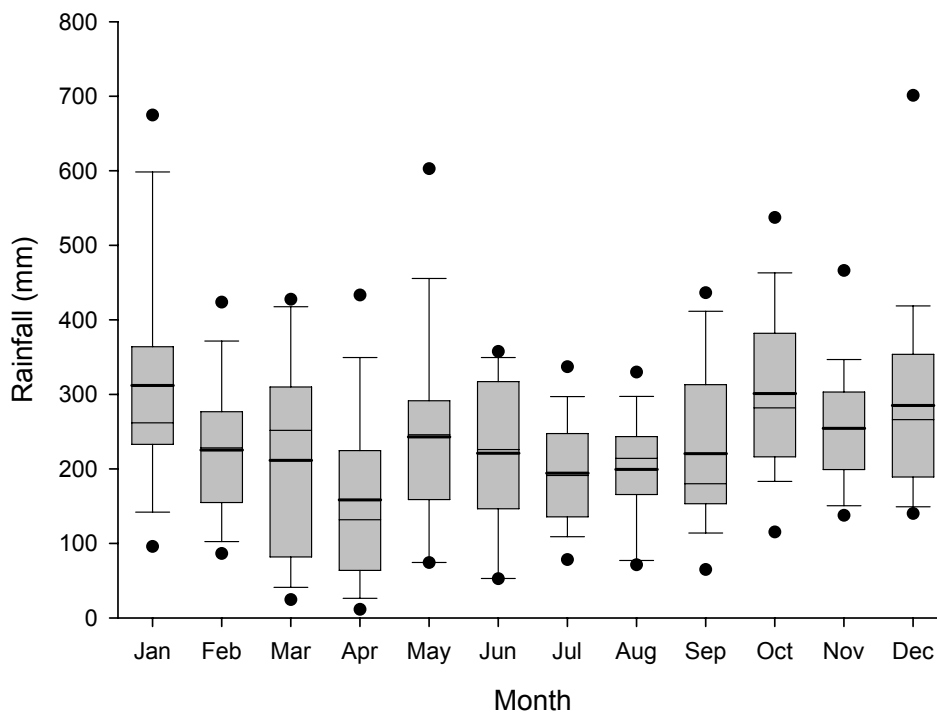


Figure 3: Box plots of monthly rainfall at DVFC in the period July 1985 to December 2003. Horizontal lines indicate the mean (thick) and the median (thin), boxes the lower and upper quartiles, whiskers the 10th and 90th percentiles and points show the extreme outliers.

IV. Methods

1. Field measurements

During all works executed in the research plots, disturbance was kept to a minimum.

(a) Measurements made prior to the present study

Plot set-up and first enumeration (1986):

In 1985 – 1986, two permanent plots were set up by D. M. Newbery at Danum (Newbery *et al.* 1992). They lie *c.* 0.8 km north-west of DVFC, just north of Danum's 'Main Trail West' (Figure 4) on gently undulating terrain with elevations (measured at each 20-m x 20-m grid point) of *c.* 208 – 254 m a.s.l.. These main plots (MP1 and MP2) are rectangular in shape (each 100 m x 400 m, 4 ha) with the long sides oriented south-north. The gradient in elevation within each plot (*c.* 35 m) and the slopes (mean across 0.25 ha areas: 23°, range: 10-35°) are similar for the main plots. MP2 lies *c.* 280 m parallel to, and west of, MP1. Each plot was divided into 100 20-m x 20-m subplots and their corners marked with belian (ironwood) posts. Subplots were labelled by 20 rows (with letters) and five columns (with numbers; e.g. M4 has the coordinates $x_1=60$; $y_1=220$; $x_2=80$, $y_2=240$) (Figure 5).

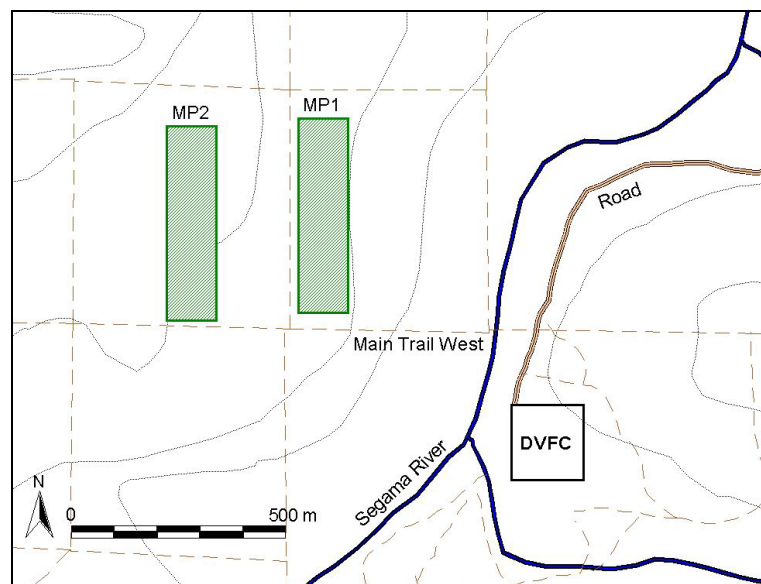


Figure 4: Location of the permanent research plots at Danum Valley: main plots 1 and 2 (shaded green) in the Danum Valley Conservation Area, trail system (dashed lines), River Segama (blue line), road to Lahad Datu (brown line) and the Danum Valley Field Centre (DVFC). Note that this map is approximate and not exactly to scale.

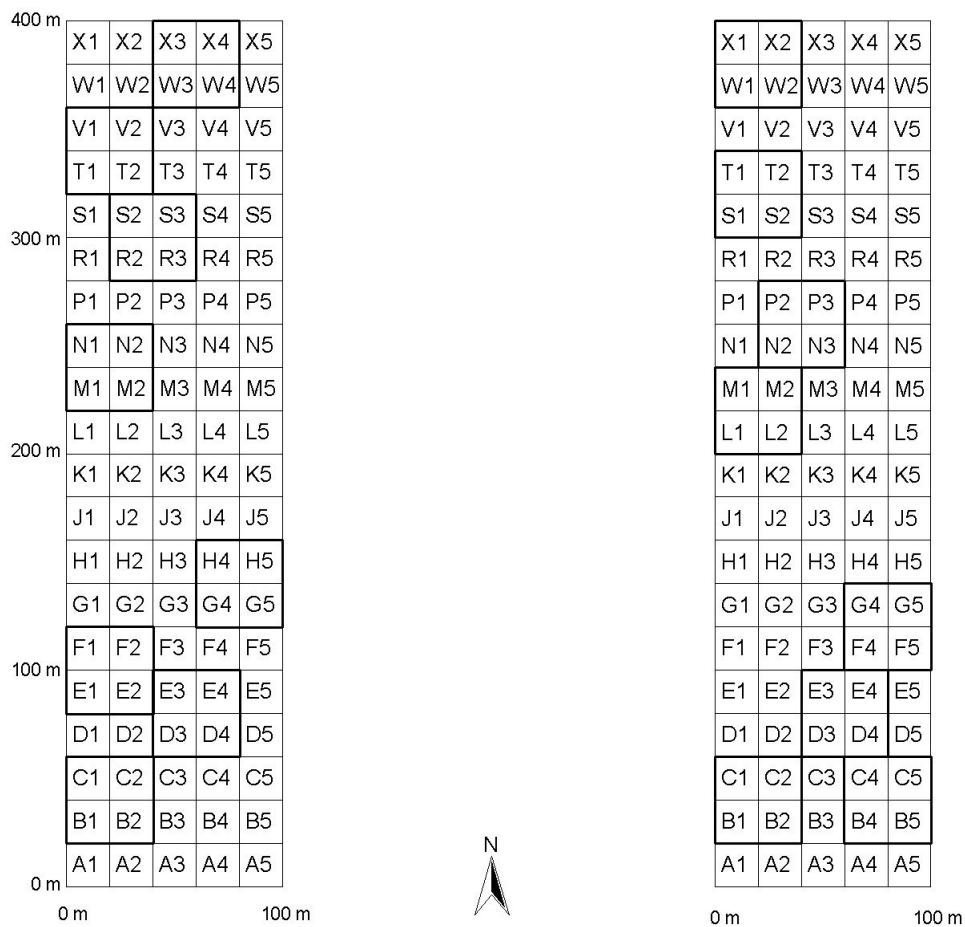


Figure 5: Setup of the two main plots at Danum Valley. 20-m x 20-m subplots are shown with their labels and the 40-m x 40-m subplots of the partial enumeration in 1999 are indicated by thicker surrounding lines.

After plot set-up in July 1985, the enumeration was conducted by E. J. F. Campbell, M. J. Still and assistants, from September 1985 to March 1986 in MP1 and from November to December 1986 in MP2 (exact dates are given in Table 2).

Within each subplot, every living tree with a minimum girth at breast height (gbh) of 10 cm was mapped to the nearest 0.1 m and its coordinates were recorded. The trees were permanently marked with a unique (for each MP) numbered aluminium tag. Tags were attached to trees with nylon fishing line using a slip-knot system to allow the sling to increase its size with tree growth. Only in the case of very large trees, was the tag nailed to the tree. The point of measurement was marked by a short horizontal stripe of yellow paint at 1.3 m above the ground (or above any buttresses; the size of a tree at the point of measurement will then still be referred to as the gbh, i.e. this term is equivalent to a reference height) and trees were measured for gbh to the nearest mm over the paint mark.

Botanical specimens were taken – except for very common and in-the-field reliably identifiable species (e.g. *Mallotus wrayi*) – between 1985 and 1987 for every tree whose leaves could be reached, named at the Sabah Forestry Department (SFD) Herbarium (Sandakan, Malaysia), and further confirmed at the Rijksherbarium (Leiden, Netherlands). Some trees of which a specimen could not be obtained were identified on fallen leaves and bark characters in the field. In a second phase of tree identification 1988 to 1990, all surviving enumerated species were re-checked and further material of unknown or uncertain taxa collected. All collections were cross-referenced at the Rijksherbarium (Newbery *et al.* 1992, 1996).

Second enumeration (1996):

Between November 1995 and February 1997, D. N. Kennedy, G. H. Petol and assistants performed the second enumeration of the main plots. Field work was done hectare-wise from south to north, alternating between the main plots, starting in MP1. All trees (i.e. those ≥ 10 cm gbh) of the first enumeration were revisited with the help of maps (one per subplot) drawn from the tree coordinates that were recorded in 1986. Every tree was inspected and if it was alive, gbh was measured. Trees that were not recorded previously but reached a gbh of ≥ 10 cm were recorded as new recruits (tag numbers in the series 12001-13000 and 14001-15000 in MP1; and in series 11001-12000 and 13001-14000 in MP2), their gbh was recorded and coordinates were taken. The status of each tree (separately for survivors and non-survivors), the condition of the stem at the point of measurement, the method of measurement and the point of measurement itself were recorded using a system of tree codes (Table 1).

The measurement procedure used in 1996 was adopted in 2001 and is described in detail in the section on the third enumeration further below.

Specimens of each recruit were collected and identified at SFD Herbarium and Rijksherbarium. Correct matching of the material with the collated collections of the first enumeration at Rijksherbarium was important (Newbery *et al.* 1999b).

Partial enumeration (1999):

A total of 2.56 ha (32% of the MP area) was measured between December 1998 and March 1999 as a partial enumeration by A. Hämmerli and assistant. Resources did not allow for a full enumeration at that time. After calculating a weighted average from the elevations at the 20-m x 20-m grid points, 40-m x 40-m squares with mean (relative) elevations of ≥ 25 m were defined as ridge subplots and those of 3 – 12 m elevation as lower slope subplots. Neighbouring subplots were allowed to border by 20 m but not to overlap. In this manner, eight 40-m x 40-m subplots in each MP, half of them on lower slopes and the other half on ridges, were randomly selected (Figure 5). Measurements were made by subplots in a random order.

All previously recorded trees ≥ 10 cm gbh were scored for alive/dead status and all living trees within a gbh-range of ≥ 10 cm to < 50 cm were re-measured, applying the 1996-procedure (see third enumeration below). Tree status and condition codes were noted similarly as in 1996 (Table 1) but were slightly simplified; observations on the point of measurement, method of measurement and number of stems were not made. Recruits were not recorded and no taxonomic work was carried out (Hämmerli 1999, Newbery and Lingenfelder 2004).

(b) Measurements made in the present study

Third enumeration (2001):

The third full enumeration of the main plots was conducted between February 2001 and October 2001. A few trees with unexpected values – mainly on the basis of comparison with data from the previous enumerations – were double-checked in February 2002 and girths and/or status codes were changed for 28 of them.

Data collection in the forest was performed by a small team consisting of the author – carrying and updating the maps and recording tree variables – and one to two assistants doing the measurements.

Measurements were made by taking rows at random from both plots so that there would be no time bias in the MP's mean values. At two instances, this procedure had to be modified and rows closest to the trail in MP1 had to be visited because of (i) elephants present in MP2 and (ii) injury to the author.

Maps were again made for all 20-m x 20-m subplots, based on the updated tree-coordinates recorded in 1996, with 2-m x 2-m grid lines, different symbols for size classes and dead trees, labelled with tree numbers and with tree species' codes in the legend - and printed on water-proof paper (Figure 6). These maps facilitated orientation within the subplots and allowed documentation of work progress through the possibility of marking the trees that were visited and inserting new recruits. They helped to relocate trees from previous enumerations, even if a tree had lost its number tag. Data recording sheets were prepared for every subplot including tree numbers, coordinates, tree status codes and heights at which stems were measured (if not at 1.3 m) from the previous enumerations.

During the measurements it was found to be useful to have the 1996-gbh values present on the recording sheets. These values were not looked at beforehand but compared with each individual tree measurement afterwards and trees that had a smaller girth than in 1996 were measured again as a double-check. In addition, the 1996 girths helped to find trees that had lost their number tags by comparing the searched-for gbh with the trees in the field. Recording sheets included empty fields for date, gbh and remarks in 2001.

In each subplot, work was started in the SW corner and progressed in a clockwise manner. Every tree that was potentially ≥ 10 cm gbh was inspected for a number tag and if it was present, the number was compared with those of the trees at that position on the map to confirm the identity of the tree. In rare cases (45 trees), the coordinates of a tree proved to be wrong and had to be corrected. If the tree did not have a tag, it was inspected for a paint mark and if that was found, position, size and species were compared with the data on the map and on the recording sheet. Combining these observations identified trees with great certainty. Once the identity of a tree was confirmed (i.e. it was the same tree as in previous enumerations), the tree was scored for alive/dead status and work proceeded as described below.

IV. Methods

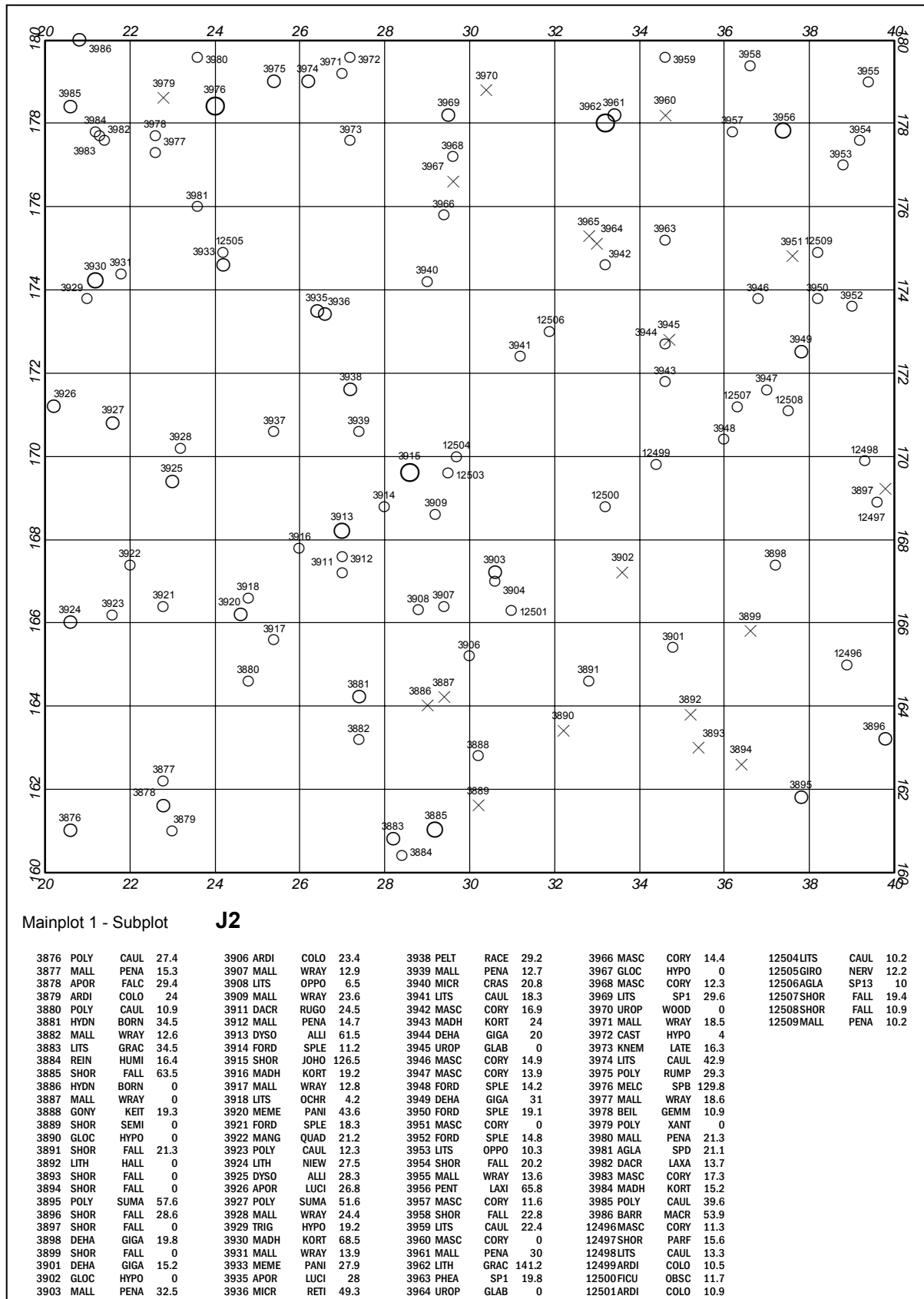


Figure 6: Example of subplot-maps with location, status (dead/alive), size, tree numbers and species codes of the trees of the enumeration in 1996 that were used for the field work in 2001.

Non-survivors

Trees that died since 1996 were recorded in five different classes, describing their status (e.g. dead standing, dead broken, etc.; Table 1). In rare cases, where no number tag or paint mark could be found, but remains of the tree could undoubtedly be identified (through position and size), these codes were still assigned, but a remark about the missing tag/paint was made. Only if there were no signs of the tree at or around the expected position was it recorded as 'missing, assumed dead'.

Survivors

The status of trees surviving from the 1996 enumerations was recorded in seven nominal classes (e.g. undamaged, broken, etc.; Table 1).

Stems of surviving trees were inspected at the paint-mark of the previous point of measurement (PoM), which was in most cases (*c.* 90% of survivors) at 1.3 m. If the paint-mark was lost, a new PoM 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, obstructing lianas, etc. The same procedure was followed if a stem was broken below the old PoM and a new shoot had to be measured. For a few trees, the PoM had to be moved because of stem deformations or emerging branches at the original PoM. Unless the deformation was too heavy to allow a measurement, girth at the old PoM was still measured and additionally an alternative PoM was established at the nearest suitable point and measured. An alternative PoM was also established if buttress growth was already influencing stem growth, or was seen likely to do so at future enumerations. In the latter case, the PoM was moved 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 is measured at the same PoM (and therefore resulting in valid growth rates). Alternative PoMs established in 1996 were utilized in 92 instances in 2001.

The condition of the stem at the point of measurement (CoS; e.g. stem normal, deformed, etc.) and the point of measurement itself (e.g. measurement taken at the original PoM, new PoM established, etc.) were recorded in 16 and six nominal classes respectively (Table 1). The height of the PoM (if not at 1.3 m) was noted.

Girth was measured using a thin 2-m long steel tape; for larger trees a wider 5-m long one was used. After lightly wiping across the PoM to remove any moss, debris or very loose bark (cautiously avoiding that anything substantial from the stem was removed that would introduce an error to the measurement), the tape was aligned with the top of the paint mark and pulled tight – without constriction – around the stem, under any lianas. Gbh was read to the nearest mm. If a tree had multiple stems and of which at least one was ≥ 10 cm gbh, this tree was measured, including additional stems if they were ≥ 5 cm gbh. The overall girth of these trees was calculated as the circumference of a hypothetical tree with basal area equivalent to the sum of the basal areas of all included stems of the multiple-stemmed tree. The number of stems (if >1) was recorded.

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 above *c.* 2 m, a ladder was used to reach the paint mark and measure girth. Depending on the composition of the ground close to the base of the tree and on the form of the trunk (buttresses), this was usually possible until *c.* 4 m. In 48 cases, the PoM had to be moved above that height and the diameters of these trees had to be measured optically with a ranging instrument (Criterion 400 Survey Laser Instrument; Laser Technology Inc., Centennial, USA). It was used on a tripod and two readings were made at 90° to one another. Azimuth and distance to the tree were also noted for future re-measurements. The method of measurement (e.g. with tape, callipers, etc.; Table 1) was recorded in five nominal classes.

New marks at the PoM were temporarily made with a pen or ribbon. Later these and any fading older ones were painted fresh. An estimated number of 750 tags (*c.* 5% of survivors) were lost since 1996 and have been replaced.

Recruits

All unmarked and unlabelled trees that were potentially larger than the minimum size limit were roughly measured around breast height. If gbh was close to 10 cm, they were measured at 1.3 m from the up-slope side of the tree (avoiding any stem deformations/lianas) and if their girth proved to be ≥ 10 cm, they were recorded as recruits. The PoM was then marked with yellow ribbon (and later painted) and the tree was tagged with a new number (in the series 20001-21000 in MP1 and 21001-22000 in

MP2). Taking the compass bearing and the distance from a nearby known tree or a corner post allowed the coordinates of the recruit to be found.

Any additional remarks about the trees (e.g. leaning, heavy damage, coordinates wrong) were noted. This especially later helped to decide whether a measurement was valid for growth calculation.

Table 1: Tree codes used in 1996, 1999 and 2001. Note that not all codes were used at all enumerations; the more detailed definitions given here apply to the 2001 enumeration.

<u>Code</u>	<u>Status of tree, non-survivors:</u>
DB	dead, broken at the base
DA	dead, broken above the base
DU	dead, uprooted
DS	dead, standing
DM	dead, missing
DN	dead, no details recorded
	<u>Status of tree, survivors:</u>
AA	alive, apparently undamaged
AB	alive, broken (at any point) above the point of measurement, old stem measured below break
AC	alive, broken below the point of measurement and coppicing, old stem dead and new stem measured (if it was ≥ 5 cm gbh)
AD	alive, old stem dead standing, coppicing, new stem measured (if it was ≥ 5 cm gbh)
AH	alive, half broken below the point of measurement, but old stem alive at point of measurement; or one or more of multiple old stems broken
AL	alive, leafless
AU	alive, (partially) uprooted, tree \pm prone
AX	original status of 1996 and 1999 corrected in 2001
	<u>Condition of stem at point of measurement (CoS):</u>
OK	stem normal
DI	deformed: irregular stem (any major deviation from the circle-form; if there was a wound, it is closed)
DC	deformed: cracked/split stem or bark (wound still open)
DL	deformed: by liana (which is usually now dead)
DF	deformed: fluted stem (tree has regularly deformations (>1 cm) all around the stem)
DH	deformed: hollow stem
DE	deformed: excrescence
LF	liana fused: callipers used for measurement
LE	girth over liana embedded in or \pm enclosed by tree stem
LO	girth over fused liana
PB	part stem: bark stripped
PD	part stem: stem partially dead/rotten (but intact)
PS	part stem: stem split/broken/delaminated
TE	stem termite-encrusted
BJ	girth measured at top or just above buttresses
BO	girth measured over buttresses

Table 1 continued:

	<u>Point of measurement (PoM):</u>
O	original: tree measured at old (1996) PoM
N	new: old paint mark not found, new mark established
M	moved: old PoM unusable because of branch, new shoot, liana, etc.
L	old stem broken or dead, new stem <5 cm gbh (i.e. too little to be measured).
A	alternative: tree measured in 2001 at alternative PoM established in 1996
AN	alternative new: tree measured in 2001 at alternative PoM established in 1996, but no paint was found (applies to optical measurements with relascope or laser)
	<u>Method of measurement (MeM):</u>
GT	girth, using tape
DC	diameter, using callipers because of fused liana
DR	diameter, PoM too high to be reached, above buttresses or deformations, using wide-scale relascope
DX	diameter, PoM too high to be reached, above buttresses or deformations, using Criterion-laser

2. Taxonomic identifications

The first identifications of recruits were made in the field by L. Madani (SFD Herbarium) during 2001. If the trees could not be identified easily on-site, specimens were taken to SFD for further investigation and comparison with herbarium material.

In January to May 2002, L. Madani and C. E. Ridsdale (Rijksherbarium) performed an intensive inspection of uncertain taxa in the primary forest plots to further improve the quality of the state of taxonomic identification. Specimens of that inspection were collected, dried and taken to Rijksherbarium by C. E. Ridsdale to collate the material with that of the previous enumerations for identification and to keep the vouchers stored.

Subspecies (*ssp.*), varieties (*v./var.*), 'forma' (*f.*) and 'affinis' (*aff.*) were considered as distinct ecological taxa in this study. 'Confer' (*cf.*) is used in the sense that the species putatively is the one referred to and not distinct from it. This resulted in seven such taxa in addition to the species *sensu stricto*.

Authorities for the most abundant species are given in the Appendix. For authorities of the other species it is referred to the International Plant Names Index (2004) of the Royal Botanic Gardens Kew, the Harvard University Herbaria and the Australian National Herbarium, published on the Internet <http://www.ipni.org> (accessed 1 May 2005).

3. Definition of periods

3.1. Lengths of enumerations

Based on the days spent in the field, the first and the second enumerations were each spread over *c.* 1.3 y (Newbery *et al.* 1992, Newbery *et al.* 1999b), the present third one in 2001 covered nearly 1 y. The partial enumeration in 1999 took 3 mo (Hämmerli 1999, Hämmerli, pers. comm.) (Table 2).

Table 2: Dates, durations and days in the field of three full and one partial (1999) enumerations of the main plots at Danum. Abbreviations used hereafter: d = day(s), mo = month(s), y = year(s).

	Enumeration year			
	1986	1996	1999	2001
Start	24.08.85	08.11.95	20.12.98	26.02.01
End ¹	15.12.86	23.02.97	29.03.99	04.02.02
Mean date	13.06.86	15.06.96	29.01.99	14.06.01
Median date	15.03.86	18.06.96	25.01.99	29.06.01
Enumeration length:				
d	478	473	99	343
y	1.31	1.30	0.27	0.94
Days with measurements (n)	n.a.	247	37	109

¹ the last date in the database of the first enumeration for MP2 is 30.11.1986; this is the middle date of the enumeration in MP2, actual measurements went from mid-November to mid-December 1986; to indicate a correct duration of the enumeration, the date of 15.12. is given here. Mean and median dates for 1986 are based on 30.11.1986.

3.2. Overall period lengths

Table 3 shows the lengths of time intervals between enumerations based on all trees (including regressors and dead trees) that had a date both at the start and at the end of an interval, calculated as the mean of trees in MP1, MP2 and in both plots combined respectively. Calculations of mortality and recruitment rates on the plot- or subplot-level, for species or size classes were done with the mean intervals of each individual group. Growth rate calculations were based on intervals of each individual tree.

Table 3: Lengths of time intervals between enumerations, showing numbers of trees (n) and means and ranges in interval length (t) for main plot 1 (MP1), main plot 2 (MP2) and both plots combined (MP) respectively.

		1986-1996			1996-2001			1996-1999			1999-2001		
		MP1	MP2	MP	MP1	MP2	MP	MP1	MP2	MP	MP1	MP2	MP
n		8971	8971	17942	8746	8897	17643	3244	3183	6427	2768	2844	5612
	mean	10.39	9.60	10.00	5.06	4.94	5.00	2.71	2.52	2.62	2.42	2.41	2.41
t (y)	range	10.14	9.05	9.05	4.03	4.04	4.03	1.90	1.83	1.83	2.02	2.01	2.01
		-11.49	-10.24	-11.49	-6.25	-5.92	-6.25	-3.32	-3.06	-3.32	-3.10	-3.12	-3.12

3.3. Naming of periods and populations included

Most of the analysis of the present work was focused on the three full enumerations that provided the most extensive data available. The resulting two time intervals will be referred to as 'period 1' (1986 – 1996) and 'period 2' (1996 – 2001) hereafter. The investigated tree community was that of the whole main plots (MP, i.e. both plots combined, with MP1 and MP2).

In Chapter V.5., possible immediate and/or lagged effects of the 1997/98-drought were investigated. This was possible through the inclusion of the 1999-measurements. Adding the data of the partial enumeration in 1999 – which lay in the middle of period 2 – allowed the comparison of variables from three intervals that will be referred to as 'period 1' (1986 – 1996), 'period 2a' (1996 – 1999) and 'period 2b' (1999 – 2001). As only a proportion of the plots and trees could be measured in 1999, analysis had to be restricted to (a) the area of the 16 subplots included in 1999 (2.56 ha, Figure 5) and (b) the subset of small trees (10 – < 50 cm gbh) at the start of each respective enumeration for growth rates. Furthermore (c), recruits had not been recorded in 1999 and mortality rates of period 2b would be overestimated in comparison with periods 1 and 2a as the reference – the number of trees at the start of period 2b in 1999 without recruits – was lower than it would have been if recruits had been recorded. To overcome this problem, all recruits were excluded from analysis for this subset. In addition (d), regressors could not be clearly separated from trees \geq 50 cm gbh in all cases (they had the same coding in the data-base of Hämmerli) and therefore a calculation of rates of losses and gains was not possible. Restrictions (c) and (d) meant that for mortality rates, too, only small (at start of each interval) trees could be analysed.

It was refrained from applying models which would interpolate growth and recruitment rates and proportions of regressing trees to find numbers of recruits and regressors in 1999 to overcome the limitations of the data-set because it is not known how those rates would have changed under the influence of the 1997/98 drought.

In summary, Chapter V.5. analyses the effects of drought on trees in the forest understorey within 2.56 ha of the main plots. The subplots used will be referred to as 'PEP' (partial enumeration plots) with single subplots numbered PEP1 to PEP16.

4. Topography

Elevations with reference to the local starting point in each main plot (SW-corner: $x = 0, y = 0, z = 0$) were recorded by D. M. Newbery before the first enumeration in 1986 at each 20-m x 20-m grid point (including the plot boundary lines). For the present study, these elevations were interpolated across each MP, using GIS software (ESRI 2000) to draw topographic maps. A software extension (Jenness 2004) was used to find elevations and slopes for positions of individual trees. This enabled a classification of every individual tree into ridge or slope, steep or flat categories. Ridges were defined as being ≥ 25 m and lower slopes as lying < 12 m, leaving the elevations of 12 – 25 m as intermediate (Hämmerli 1999, Newbery and Lingenfelder 2004).

To assess the effect of the inclination of the terrain, those trees positioned at locations where the inclination was $\geq 20^\circ$ were classified as growing on steep slopes and those on positions with $< 10^\circ$ inclination as being situated in flat areas.

5. Population changes

5.1. Mortality and recruitment vs. losses and gains

As soon as more than two enumerations are to be considered, a problem with regressing trees arises. Trees that were above the minimum gbh-limit at the first measurement might – due to natural shrinking, bark loss or slight measurement errors or because multiple-stemmed trees lost one or more of their stems – be too small at the second enumeration, where they are omitted from the population (and noted as regressors). As they are still alive at the time of measurement, three things could happen until the third measurement: (i) the regressor dies, (ii) it remains in gbh below the

minimum value, or (iii) it re-grows above the minimum gbh again. As it is not a new recruit in the sense that it was already part of the population ≥ 10 cm gbh at an earlier enumeration, it will be recorded under the original tag number. In addition to 'dead trees' and 'recruits' it is appropriate to use the terms 'losses' and 'gains' to the population of trees ≥ 10 cm gbh.

'Losses' are those trees that were lost during one interval from the population of trees ≥ 10 cm gbh; they consist of the number of trees dying in an interval (n_d) minus the dying trees that were < 10 cm gbh at the end of the previous period (dead regressors; $n_{d_reg_p1}$) plus the new regressors of the current period (n_{reg_new}):

$$n_{losses} = (n_d - n_{d_reg_p1}) + n_{reg_new}$$

'Gains' are those trees that were new to the population ≥ 10 cm gbh in a period; they consist of recruits that were not part of the population before (because they were too small) but have now grown into the relevant size (n_{rec}) plus these trees of the former regressors that re-grew into the population ($n_{reg_p1_ \geq 10}$):

$$n_{gains} = n_{rec} + n_{reg_p1_ \geq 10}$$

Mortality – in the general sense that it is widely used – includes all trees of a given population with no regard to size class. If a tree dies it is counted as dead, even if it was regressing below the minimum gbh in the previous period. A tree that, for example, broke below the point of measurement but was coppicing, was still alive and was classified as such when calculating mortality rates.

The same line of reasoning applies to recruitment: trees that reached the minimum value in size during a period were labelled as recruits and remained part of the population even if their gbh fell below this minimum.

The above mentioned difficulties with more than two enumerations (i.e. more than one period), inevitably lead to an alternative approach in quantifying the structural dynamics of a population: regressors are not part of the population anymore, they are classified as lost but not dead, and they might become part of it again if they re-grow into the minimum size class as gains (not recruits).

Therefore, rates of mortality and recruitment and of losses and gains were calculated. Mortality and recruitment rates included regressors, so that the number of

dead trees (n_d) or recruits (n_{rec}) respectively in a period was related to the number of all trees at the start (n_{start}). Rates of losses and gains used only trees above the minimum gbh in which case the number of losses (n_{losses}) or number of gains (n_{gains}) respectively was related to the number of trees ≥ 10 cm gbh at the start of the interval ($n_{start \geq 10}$).

5.1.1. Rate calculations

Periodic rates (%) were found from the following equations:

$$\text{mortality: } m_p = \frac{n_d}{n_{start}} \cdot 100$$

$$\text{recruitment: } r_p = \frac{n_{rec}}{n_{start}} \cdot 100$$

$$\text{losses: } l_p = \frac{n_{losses}}{n_{start \geq 10}} \cdot 100$$

$$\text{gains: } g_p = \frac{n_{gains}}{n_{start \geq 10}} \cdot 100$$

and annualized rates (% y^{-1}) from:

$$\text{mortality: } m_a = \left(1 - \left(1 - \frac{n_d}{n_{start}} \right)^{\frac{1}{i}} \right) \cdot 100 \quad (\text{Alder 1995, Sheil } et al. \text{ 1995})$$

$$\text{recruitment: } r_a = \left(\left(1 + \frac{n_{rec}}{n_{start}} \right)^{\frac{1}{i}} - 1 \right) \cdot 100 \quad (\text{Alder 1995, Sheil } et al. \text{ 1995})$$

$$\text{losses: } l_a = \left(1 - \left(1 - \frac{n_{losses}}{n_{start \geq 10}} \right)^{\frac{1}{i}} \right) \cdot 100$$

$$\text{gains: } g_a = \left(\left(1 + \frac{n_{gains}}{n_{start \geq 10}} \right)^{\frac{1}{i}} - 1 \right) \cdot 100$$

For comparison, the widely used (Phillips *et al.* 1994, Potts 2003, Condit *et al.* 2004) exponential mortality coefficient (% y^{-1}) *sensu* Sheil *et al.* (1995) was calculated from:

$$\lambda = \left(\frac{\ln(N_0) - \ln(N_t)}{t} \right) \cdot 100$$

where N_0 and N_t are the numbers of trees at start and end of interval, respectively and t is the time interval in years.

5.1.2. Correction of annualised mortality rates for time interval difference

Annualised mortality is dependant on the length of the time interval between enumerations if the sample population is heterogeneous in respect to differing mortality rates between groups (e.g. species) (Sheil and May 1996): mortality decreases with time. Comparing mortality rates of two periods with unequal time interval as in the present study (period 1: 10 y; period 2: 5 y) and a highly diverse tree community would be erroneous because the differences between the periods would be partly due to an artefact. Hämmerli (1999) and Newbery and Lingenfelder (2004) used the equation suggested by Sheil and May (1996) to calculate an overall average mortality (m_{all}) that takes into account different mortality rates of species and further introduced a new variable, the minimum number of individuals per species (n_{min}): in species-rich forests, a large proportion of species is rare with < 5 individuals present and for those species, sample size for the calculation of mortality rate is of low reliability, resulting in many species with mortality rates of 0% or 100%. The optimisation between reliable estimates of mortalities for each species and minimized standard error of m_{all} (which increases with n_{min}) was found at $n_{min} = 2$ (Hämmerli 1999, Newbery and Lingenfelder 2004).

This correction procedure was adopted and applied to both the whole main plots (period 1 only, see below) and the selection of subplots that were measured additionally in 1999 (period 1, period 2a and period 2b), correcting mortality rates to a common time interval of $t = 5$ y.

The correction proved to be problematic when the actual time interval and the interval to which it was corrected were very similar and it was therefore not applied to period 2 (mean interval of MP1 = 5.06 y; MP2 = 4.94 y; overall mean = 5.00 y).

Overall average mortality (% y^{-1}) was calculated as:

$$m_{all}(t^*) = \left(1 - \left(\frac{\sum_{i=1}^S (n_{i0} (1 - m_i)^{t^*})}{\sum_{i=1}^S n_{i0}} \right)^{\frac{1}{t^*}} \right) \cdot 100$$

where S is the number of groups (here: species), n_{i0} the number of individuals of group i at time 0, m_i the true annual mortality (m_a ; as a proportion, i.e. not in percentages) of group i and t^* the time interval in y (Sheil and May 1996).

The rate of decline in $m_{all}(t)$, when calculated across several years, could serve as an "estimate of the community-wide variance in mortality rates" (Sheil and May 1996) and therefore characterize the underlying distribution of species' mortalities, i.e. the variation in life expectancies, which Sheil and May (1996) termed 'dynamic diversity'. This estimate was calculated for the different (sub-) populations examined and used to explain the outcome of the interval correction procedures.

Dynamic diversity was derived from the variance of m_{all} across time:

$$\sigma^2 \approx \frac{2 \cdot (m_{all}(1) - m_{all}(t^*)) \cdot (1 - m_{all}(1))}{t - 1} \quad (\text{Sheil and May 1996}),$$

with t^* set to 15 y and given as the mortality rate standard deviation (SD) in % y^{-1} .

5.2. Growth rates

Stem growth rates were found as follows (Hunt 1990, Alder 1995):

absolute growth rate (agr) in $mm y^{-1}$:

$$agr = \frac{(gbh_{end} - gbh_{start})}{t} \cdot 10$$

and relative growth rate (rgr) in $mm m^{-1} y^{-1}$:

$$rgr = \frac{(\ln(gbh_{end}) - \ln(gbh_{start}))}{t} \cdot 10^3$$

with gbh_{start} and gbh_{end} being the gbh (in cm) at the start and at the end of a time interval (t , in y) respectively.

Definition of 'valid' trees for growth calculations:

Growth rates were calculated only if the following conditions applied: for each enumeration (except the one of 1986, when this information was not gathered) every tree was reviewed for reliability of its measurements and assigned a code: 1 = valid, 0 = invalid. Assessed as being not reliable and therefore invalid for growth calculations were those measurements where 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. If the CoS indicated major deformations through buttresses, cracked or split bark or stems, excrescence, fluted or hollow stems, termites or lianas, those trees were also excluded (an irregular stem (CoS = DI) was not considered a major deformation unless additional notes in the remarks revealed this (e.g.: 'heavy', 'extremely oval', 'spiral growth', etc.)). Moved or newly established (except on recruits) PoMs made the measurement invalid, too, as did the use of the optical measurement instrument. The use of callipers on liana fused trees was only considered a reason for exclusion if it was not possible to take two measurements or if the callipers proved to be too small for the tree.

Growth was then calculated with those trees that were valid both at the start and the end of an interval. From the resulting rates, some trees had to be additionally excluded because they had negative growth rates below an operational threshold (see V.3.4.1.).

5.3. Diversity measures

Species diversity was expressed in the form of the Shannon index and Pielou's measure of evenness, the former calculated as $H' = -\sum (p_i \cdot \ln(p_i))$, the latter as

$E = \frac{H'}{H'_{\max}}$, where p_i is the proportion of individuals in the i -th species (estimated as n_i/N)

and H'_{\max} is the maximum possible diversity (i.e. where all species were equally abundant), calculated as $\ln(S)$ (the total number of species) (Magurran 1988).

6. Size classes

Analysis within different sizes was performed on the following gbh limits:

≥ 10 cm gbh (≥ 3.2 cm dbh)	- 'all' trees
10 – < 50 cm gbh (3.2 – < 15.9 cm dbh)	- 'small'

50 – < 100 cm gbh (15.9 – < 31.8 cm dbh)	- 'medium'
≥ 100 cm gbh (≥ 31.8 cm dbh)	- 'large'

To allow reference to other studies, measures were also given for the population of trees with a diameter at breast height (dbh) of ≥ 10.0 cm (≥ 31.4 cm gbh). In addition, where it was appropriate, 10-cm gbh size classes were formed.

7. Light environment

During the period of the third full enumeration, hemispherical photographs were taken at each 20-m x 20-m grid-point in the main plots. Excluding points along the edges of the plots, this resulted in 76 photographs per MP. Five sets of photographs were taken: in April, June, August and October 2001 and in January 2002. On each occasion they were taken early in the morning before the sun was above the horizon to avoid reflections of direct sunlight (Whitmore *et al.* 1993). Pictures were taken with a FC-E8 fisheye lens and Nikon Coolpix 950 camera. The system was mounted on a levelled bracket (Delta-T Devices Ltd., Cambridge, UK), at a height of 1 m above the ground and oriented towards magnetic north.

The light environment at each point was calculated with Gap Light Analyzer Software (Frazer *et al.* 1999). The solar model settings were: solar constant 1370 W m^{-2} , (direct) beam fraction 0.39 (Whitmore *et al.* 1993), spectral fraction 0.51 (Stigter and Musabilha 1982), cloudiness index 0.45 (calculated from the sunshine data at Danum between 1996 and 2001 (Bischoff 2001)). Transmission coefficient under standard overcast sky was set at 0.4 (Whitmore *et al.* 1993). The magnetic declination at Danum during the photo sampling period was $0^\circ 32' \text{ E}$.

8. Data analysis

A data base (using MS-Access, Microsoft Corporation, Redmond, USA) was created with data from previous enumerations and the new data from the 2001-enumeration. Analysis was mainly carried out with SQL-scripts within MS-Access. Statistical analysis was performed with GenStat (7th edition, Lawes Agricultural Trust, Rothamsted, UK). ArcView 3.2a (ESRI 2000) was used to prepare maps for the 2001 field work and to analyse topography within the plots.

V. Results

1. Drought intensity derived from 'antecedent rainfall history'

For 'typical' rain forest vegetation (i.e. not heath forest etc.) on 'normal' soils (i.e. not sandy etc.), water stress is assumed to set in when the monthly mean rainfall drops below 100 mm, the estimated value for evapotranspiration in the tropics (Brüning 1969, 1971, Walsh 1996b, 1996a, Walsh and Newbery 1999, Malhi *et al.* 2002, Malhi and Wright 2004). With daily rainfall data available, this threshold can be applied to 30-day running totals (30-d-rt). Droughts can be assessed by calculating an intensity index that takes into account the deficit (30-d-rt - 100) and the drought duration (Newbery and Lingenfelder 2004).

However, this approach neglects the rainfall preceding the 30-day periods. A period of rainfall below 100 mm that had low rain in the days, weeks or months before would – assuming that the soil water reservoir is already depleted – likely be more severe to the trees than such a period with high preceding rain, in which case water would probably be still available from storage in the soil (Malhi and Wright 2004, R. Walsh pers. comm.). Malhi *et al.* (2002) remarked that water stress through a deficit in soil water affects the forest immediately (< 15 d) but that it takes some time (*c.* 60 d in their study in central Amazonian rain forest) for the soil to be recharged with water after a dry season.

Antecedent rainfall history is proposed to be taken into account in an assessment of drought intensity by a simple model: daily rainfall across the available 18.5 y was averaged to give a mean value of what the vegetation can 'expect', the amount of rain that it is adapted to (termed MDR hereafter; see Table 4 for a summary of terms used in this chapter). The difference between the actual daily rainfall (ADR) and MDR (ADR – MDR = DRA, the 'daily rainfall anomaly') was accumulated across 30 (not shown), 90, 180 and 365 d prior to each day (the 'accumulated rainfall anomaly', ARA). Figure 7 illustrates the origination of ARA by plotting 30-d-rt of both the MDR (which, as an annual pattern, is repeating itself over each of the 18.5 y) and the ADR in 1998, the last ENSO-year.

Table 4: Glossary of terms used to describe drought intensity (the symbol '|' stands for 'or').

30-d-rt	30-day-running-total of rainfall
MDR	mean (across 18.5 y) daily rainfall
ADR	actual daily rainfall
DRA	daily rainfall anomaly: $ADR - MDR$
ARA90 180 365	accumulated rainfall anomaly: running totals of DRA across 90 180 365 d
CARA100 232	conditional ARA365: 365-d running totals of DRA only when 30-d-rt < 100 mm < 232 mm
DEFARH0 100 232	deficit of rainfall derived from antecedent rainfall history: sum of DRA when ARA365 < 0 mm sum of DRA when ARA365 < 0 mm and CARA100 232 = true

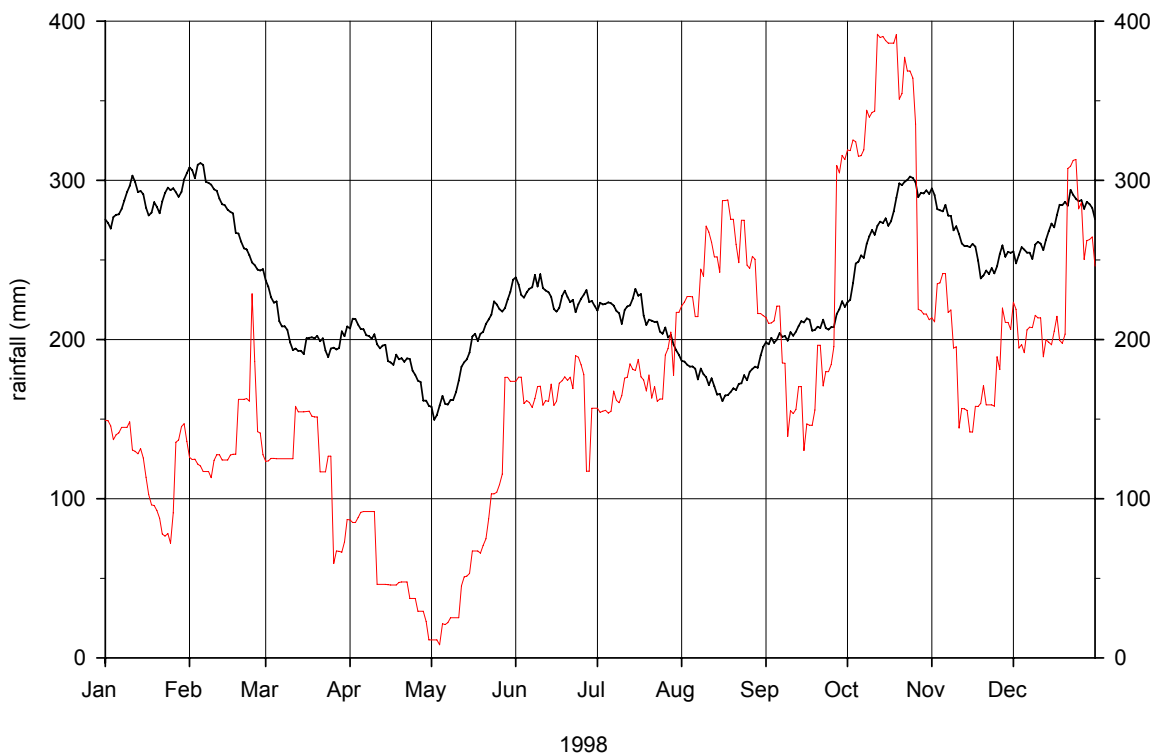


Figure 7: Rainfall at DVFC in 1998: 30-d-rt of MDR (18.5-y-mean daily rainfall; black line) and of ADR (actual daily rainfall; red line) in 1998. The year shown includes the ENSO-related drought event with 30-d-rt rainfall < 100 mm from 26 March – 22 May.

ARA gave, on any one day, the sum of rainfall across the selected period that was missing (or a surplus) to the expected average of that period.

Figure 8 shows – in relation to the 30-d-rt of MDR and of ADR – the ARAs across 90, 180 and 365 d. The three latter curves are mostly running more or less in parallel, with the 1-y-curve having the strongest amplitudes both in rainfall deficit and surplus. At

some points in time, e.g. the second half of 1989, ARA90 (3 mo) indicates a strong deficit, while ARA365 (1 y) is well in the positive range, benefiting from more-than-average rainfall earlier in 1989. Only the accumulation of anomalies across 1 y is assumed to adequately reflect water conditions and to reveal the severity of drought events: it shows the precipitation history for the preceding 365-d period and reflects depletion or saturation of soil water contents while giving the amount for the deficit/surplus and therefore quantifying water anomalies, not only stating that it is below or above a certain threshold value.

As vegetation on soil that is already water saturated would not be able to make use of more rainfall, it seems sensible not to accumulate rainfall above a certain limit. Setting this limit to $30\text{-d-rt} = 100$ mm, i.e. only including those DRAs when the 30-d-rt is below evapotranspiration, is one possibility. The other is to incorporate the DRAs every time rainfall is below the mean value (the mean 30-d-rt of MDR = 232.2 mm), when the forest receives less water than 'expected'.

Figure 9 explores these possibilities by showing, across the complete period, the 30-d-rt of MDR and ADR, ARA365 and in addition the accumulation only in those cases where 30-d-rt was < 100 mm and < 232 mm, respectively. Both 'conditional accumulations' (CARA100, CARA232) are capable of showing the main droughts at Danum during the record. However, they do not indicate any occurring water surplus and are therefore showing water deficits when ARA365 is positive (e.g. 1995-96).

If a low precipitation event is taken to occur when $\text{ARA365} < 0$ (events were allowed to be interrupted by up to 8 d without breaking continuity), i.e. below average, 19 such events have occurred at Danum from July 1985 to December 2003 (Table 5). Six events have been shorter than 10 d. The longest lasting event was that in 1990-93, followed by the events in 1997-98, 1986-88 and 1993-94. Drought intensity can finally be expressed as the sum of all daily rainfall anomalies (total DRA) within an event, which is the deficit of rainfall derived from the antecedent rainfall history: 'DEFARH'.

When neglecting 30-d-rt rainfall > 100 mm (CARA100), the event in 1990-93 with 883 d was also the severest with $\text{DEFARH} = -750$ mm across that period, followed by the event in 1997-99 with 818 d duration and $\text{DEFARH} = -602$ mm (Table 5: DEFARH100). Through the inclusion of those periods where the 30-d-rt was up to its mean (CARA232), this ranking is reversed: the event in 1997-99 was more severe ($\text{DEFARH} = -1846$ mm)

than that in 1990-93 (DEFARH = -1567 mm) (Table 5: DEFARH232). This is further emphasized when summing up all DRAs during the times that ARA365 was < 0 (Table 5: DEFARH0). Three events are consistently shown as strong by the considered possibilities of deficit-calculation and when ranked by either possibility that takes water surpluses into account, the most severe drought at Danum between July 1985 and December 2003 was the one centered in 1998, followed by the one centered in 1992 and that of 1987 (Table 5).

The by far longest drought-free period was between April 1999 and March 2002, which is consistent with the persistence of a long La Niña (the cold phase of the climatic cycle) reported by the IPCC (2001).

Table 5: Low precipitation events at Danum 1985 – 2003 (see text for explanations).

Event number ^a	Start	End	Duration (d)	DEFARH100 (mm) ^b	DEFARH232 (mm) ^c	DEFARH0 (mm) ^d
1	30.08.1986	01.05.1988	610	-326.1	-905.1	-438.0
2	07.11.1988	07.12.1988	31		-38.1	114.4
3	13.02.1989	20.02.1989	8		-7.5	-7.5
4	29.03.1989	13.05.1989	44		48.9	41.1
5	01.06.1989	06.06.1989	6			39.7
6	23.10.1990	23.03.1993	883	-749.7	-1566.9	-846.0
7	18.06.1993	03.06.1994	351	5.2	-357.3	-1.3
8	15.06.1994	23.06.1994	9		-65.8	-65.8
9	15.09.1994	23.09.1994	5		-17.8	-17.8
10	25.10.1994	01.11.1994	6		-28.5	-28.5
11	02.04.1995	27.05.1995	56	-35.1	-8.6	78.2
12	29.06.1995	13.08.1995	44		-91.8	-91.8
13	18.01.1997	15.04.1999	818	-602.2	-1846.0	-1355.8
14	18.03.2002	26.06.2002	101	-105.0	-25.4	-36.0
15	10.07.2002	02.09.2002	54	1.6	21.7	8.6
16	01.11.2002	25.11.2002	23		-73.9	-73.9
17	04.12.2002	26.03.2003	112		-126.4	-167.7
18	27.06.2003	29.06.2003	3		9.8	9.8
19	03.09.2003	26.09.2003	24	-33.6	17.0	142.7

^a: when ARA365 < 0

^b: (total DRA) when ARA365 < 0 and 30-d rt < 100

^c: (total DRA) when ARA365 < 0 and 30-d rt < 232

^d: (total DRA) when ARA365 < 0

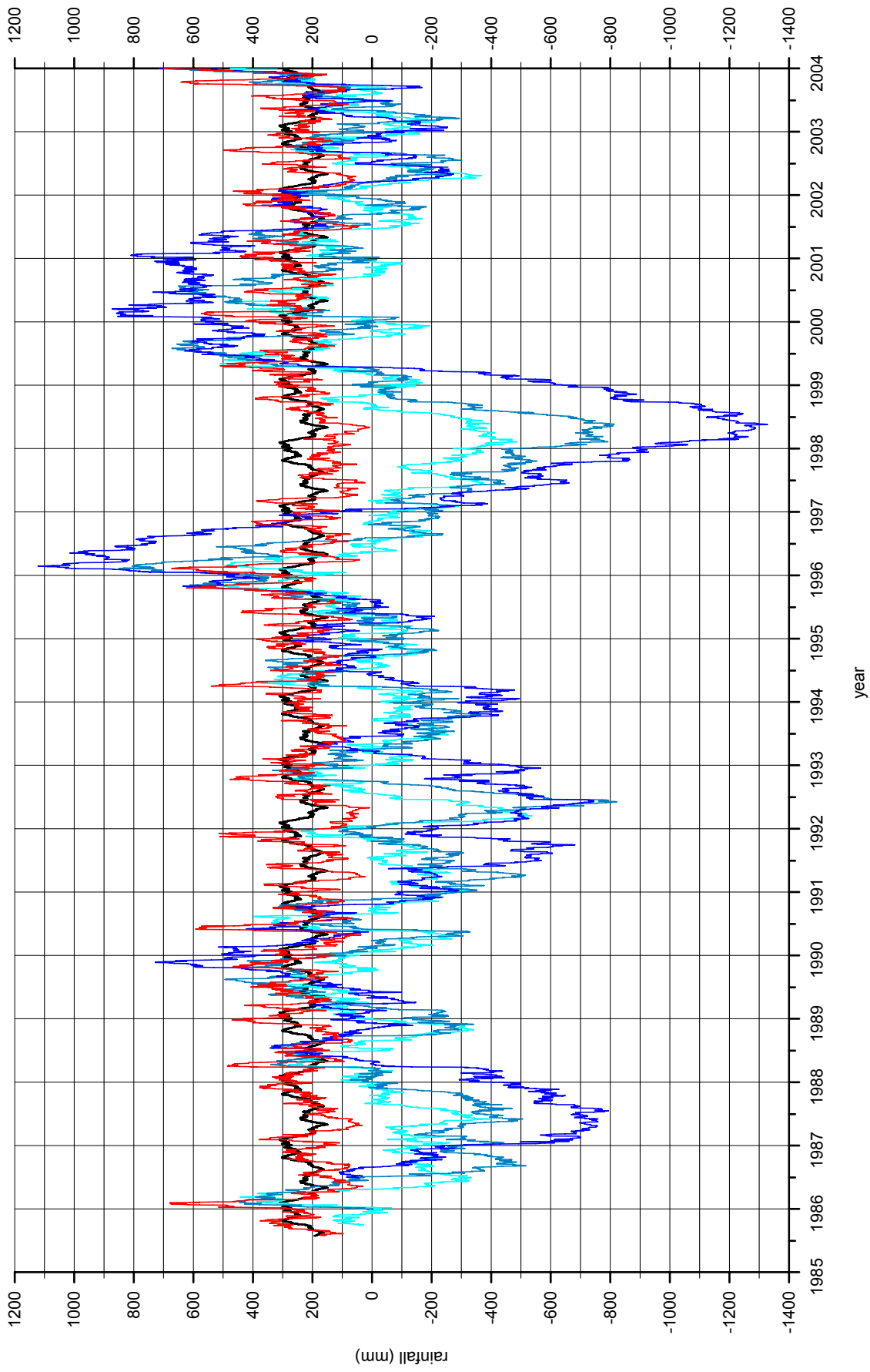


Figure 8: Accumulated rainfall anomalies (ARA) at Danum, 1985 – 2003: 30-d-rt of mean daily (MDR; black line) and actual (ADR; red) rainfall and ARAs across 90- (ARA90; cyan), 180- (ARA180; turquoise) and 365- (ARA365; blue) d.

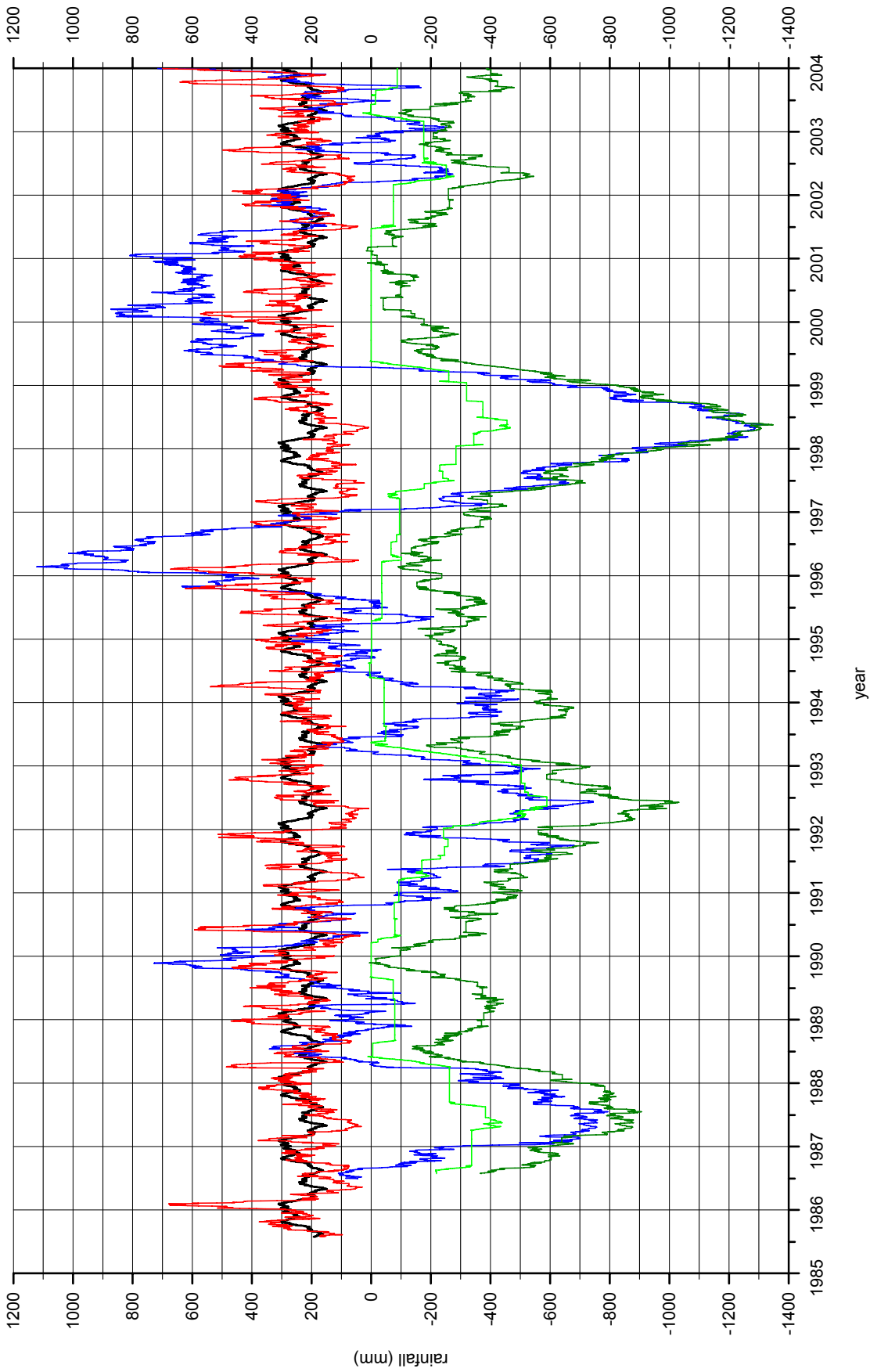


Figure 9: Accumulated rainfall anomalies (ARA) with conditions applied at Danum, 1985 – 2003: 30-d-rt of mean daily (MDR; black line) and actual (ADR; red) rainfall, ARA365 (blue) and accumulation only when 30-d-rt <100 mm (CARA100; light green) and <232 mm (CARA232; dark green), respectively.

2. Topography

The main plots at Danum gradually increase in elevation from south to north by *c.* 39 m (MP1) and 43 m (MP2). The local origins ($x = 0$; $y = 0$) of MP1 and MP2 are *c.* 206 m and 221 m a.s.l., respectively (Samat *et al.* 1997-2000). MP1 includes steep slopes facing east in its northern half. In MP2 an episodic small stream cuts two ridges with steep slopes.

Interpolating the elevations resulted in ridge areas (≥ 25 m) covering *c.* 18.4% and 33.3% and lower slope areas (< 12 m) on *c.* 32.2% and 36.3% of the planimetric surfaces of MP1 and MP2, respectively (Figure 10). Slope estimates showed that in MP1 *c.* 31% of the area is flat ($< 10^\circ$ inclination) and *c.* 14% is steep ($\geq 20^\circ$; maximum *c.* 33°). In MP2 the respective values are *c.* 26% and *c.* 18% (maximum *c.* 31°). More than half of the area of each MP lies on intermediate slopes (10 - 20°).

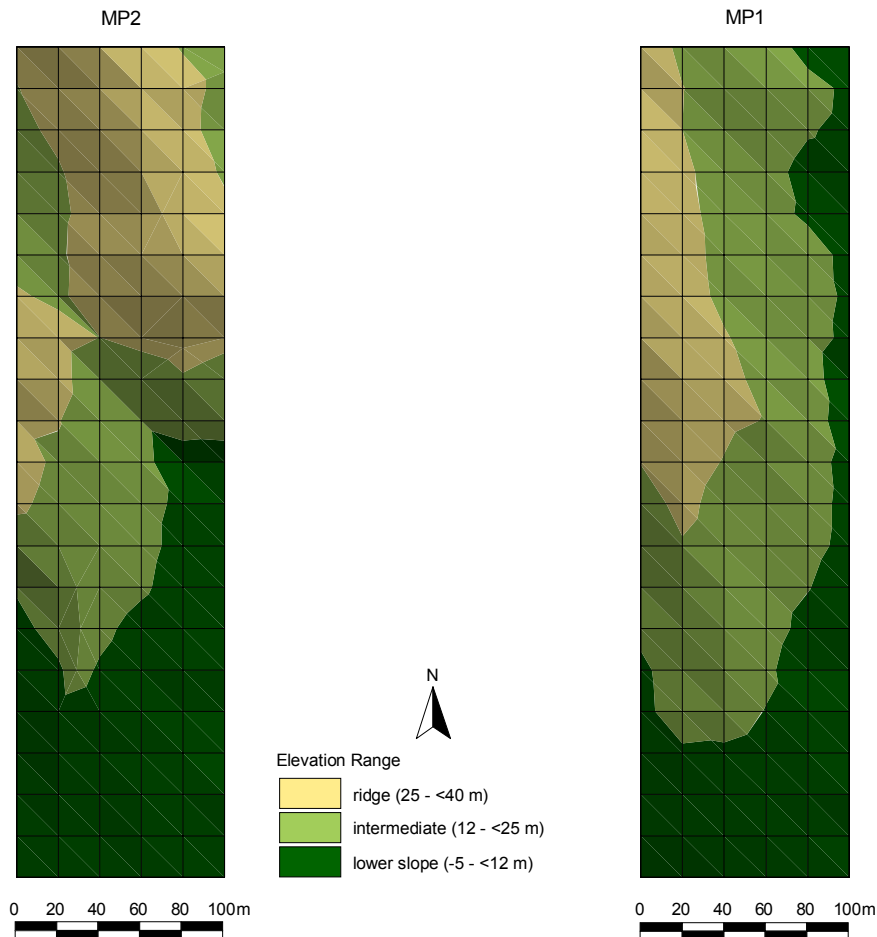


Figure 10: Topographic map of main plots at Danum. Elevations relative to each plots' origins were derived from 20-m x 20-m grid points and surfaces were interpolated. Elevation classes (ridge, intermediate, lower slope) reflect the divisions used in analysis.

3. The Danum main plots in 2001

For an overview of structural and dynamics' data, see tables in Chapter V.4.

3.1. Structure

3.1.1. Tree numbers (including losses and gains)

The main plots in Danum in 2001 consisted of 16623 trees with a gbh of ≥ 10 cm. Main plots 1 and 2 had 8268 and 8355 trees respectively. In 2001, 1938 trees were recorded as dead (MP1: 979; MP2: 959), but of these 182 had been regressors in 1996 (i.e. they were < 10 cm gbh and therefore not part of the 1996 population). The number of dead trees in 2001 corrected for regressors was 1756 (MP1: 891; MP2: 865). Of the survivors in 2001, 341 trees were found to be below the minimum gbh limit and of these 166 had been < 10 cm gbh in 1996 already, so 175 new regressors were counted. A total of 1259 new trees recruiting into the population (i.e. reaching ≥ 10 cm gbh) was recorded; MP1 had more recruits (685) than MP2 (574). Additional gains to the population were trees that had regressed below 10 cm gbh between 1986 and 1996, but re-grew to ≥ 10 cm gbh between 1996 and 2001: 22 trees in MP1 and 8 trees in MP2, adding up to a total number of gains (recruits plus re-growths) of 1289 trees (Table 11).

3.1.2. Density and basal area

The density of all trees across the main plots in 2001 was 2078 ha^{-1} (MP1: 2067 ha^{-1} , MP2: 2089 ha^{-1}) (Table 12). Almost 90% of these were between 10 and 50 cm gbh (1862 ha^{-1}), 3% (66 ha^{-1}) were ≥ 100 cm gbh (Figure 13). There were 158 recruits ha^{-1} and 220 dead trees ha^{-1} (Table 12). Density of trees ≥ 10 cm dbh (≥ 31.4 cm gbh) was 435 ha^{-1} (Table 12).

Average basal area of MP1 and MP2 for all trees was 32.5 $\text{m}^2 \text{ha}^{-1}$ (Table 13). Small trees contributed 21% (6.75 $\text{m}^2 \text{ha}^{-1}$), medium-sized trees 18% (5.85 $\text{m}^2 \text{ha}^{-1}$) and large trees 61% (19.9 $\text{m}^2 \text{ha}^{-1}$) to the total basal area (Figure 14). Using 10 cm dbh as the lower size limit, basal area was 28.4 $\text{m}^2 \text{ha}^{-1}$ (Table 13). Since 1996, 0.15 $\text{m}^2 \text{ha}^{-1}$ were gained through recruits and 4.05 $\text{m}^2 \text{ha}^{-1}$ were lost through trees that had died since the last enumeration (Table 13).

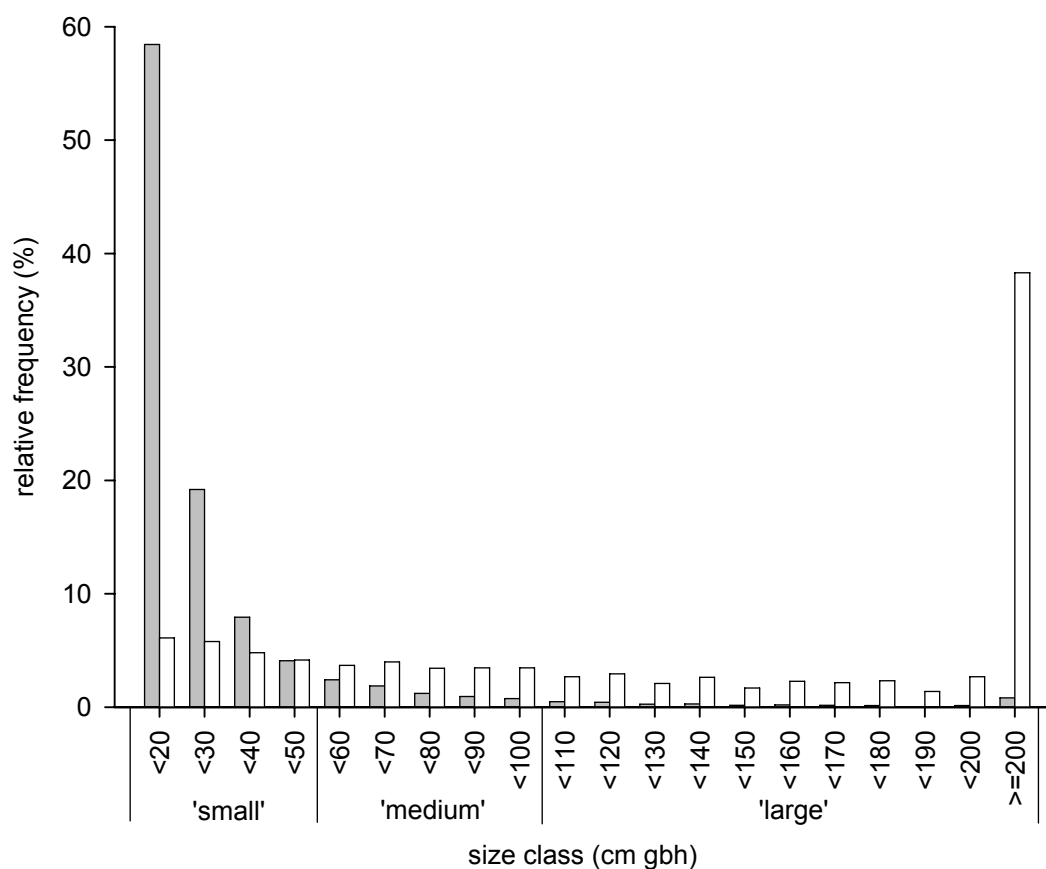


Figure 11: Frequency distribution of tree numbers (grey bars) and basal area (open bars) in the Danum main plots in 2001 for 10-cm gbh classes; the vertical lines below the x-axis separate the three main size classes (small: 10 – <50 cm; medium: 50 – <100 cm; large: \geq 100 cm).

3.2. Floristic composition of Danum main plots in 2001

3.2.1 Taxonomic revisions in 2001

In the main plots, 2686 trees were revised for tree species codes which included some minor changes in the species' codes themselves or spelling corrections. The revised trees belonged to 317 species in 1996 and were condensed to 211 species in 2001. For 390 trees which were not identifiable to species level or denoted as distinct (but unnamed) taxa in 1996, a taxonomic name could be given in 2001.

General nomenclatural changes were made on 51 taxa, of which the most important (numerous) were: *Ardisia colorata* to *A. sanguinolenta* (677 trees), *Cleisthantus glaber* to *C. contractus* (307 trees), *Baccaurea stipulata* to *B. tetrandra* (260 trees), *Litsea*

angulata to *L. machilifolia* (64 trees) and all remaining *Eugenia* spp. to *Syzygium* spp. (41 trees). A complete species list is given in Appendix Table 1.

3.2.2. Quality of taxonomic identifications

Of 16623 trees alive with gbh \geq 10 cm in 2001, 98% (16297) were identified to the species (ssp./var./f./aff.) level. For 1.76% (293 trees) the species could not be named, but they were identified as distinct species; 0.16% (27 trees) were identifiable to genus (MP1: 17 trees; MP2: 10 trees) and 0.01% (two trees, one in each MP) to family only (of which one was assigned a distinct taxon within the family). Four trees (three in MP1, one in MP2) were completely unknown because they were dead, missing or broken at the time of identification and were assigned to the family 'various'. Thus, 16591 or 99.8% of the 16623 trees alive in 2001 in the main plots were identified to a distinct species.

3.2.3. Floristic composition

Excluding the 32 taxonomically uncertain trees, the main plots at Danum in 2001 consisted of 16591 trees with a gbh \geq 10 cm, these being of 489 species in 175 genera and 59 families.

Almost half of the species (49.7%) had $<$ 5 and over one quarter (26.6%) only one individual. Considering only common species (those species with \geq 5 individuals; see Newbery *et al.* (1996)), the counts were 16164 trees in 246 species, 107 genera and 44 families (Table 6).

The two main plots differed only slightly in their numbers of species: MP1 had 374 species in 153 genera and 56 families; MP2 had 379 species in 147 genera and 52 families. MP1 and MP2 had 264 species in common, 110 species were found only in MP1, 115 only in MP2.

With increasing size classes, the contribution of species with less than five or only one individual (frequency, *f*) became larger: while in the small tree size class still almost half of the species (both main plots combined) had \geq 5 individuals and only 27% just one tree, in medium-sized trees 32% of the species had $f \geq$ 5 and 37% had $f = 1$ and in the

large size class only one quarter of the species had ≥ 5 trees and half of them had only one tree (Table 6).

Only 68 of the 489 species in the main plots were found across all sizes. In the enumeration of 2001, 265 species did not reach gbhs ≥ 50 cm and were limited to the small-tree size class and 14 rare species each were found solely within the medium- (15 trees) and the large- (19 trees) tree size classes, respectively.

Applying the widely used minimum size limit of 10 cm dbh (31.4 cm gbh), the main plots at Danum consisted of 295 species in 131 genera and 50 families in 2001.

Table 6: Floristic composition of the Danum main plots in 2001 in different size classes, including all species ($f \geq 1$) and only those species with $f \geq 5$ and showing the relative contributions of species with < 5 and those with only one individual, for MP1, MP2 and both combined (MP).

	MP1		MP2		MP	
	$f \geq 1$	$f \geq 5$	$f \geq 1$	$f \geq 5$	$f \geq 1$	$f \geq 5$
I. all trees (gbh ≥ 10 cm)						
families (n)	56	39	52	41	59	44
genera (n)	153	92	147	95	175	107
species (n)	374	188	379	192	489	246
trees (n)	8247	7936	8344	8003	16591	16164
trees (n ha ⁻¹)	2062	1984	2086	2001	2074	2021
	n	%	n	%	n	%
species ($f < 5$)	186	49.7	187	49.3	243	49.7
species ($f = 1$)	109	29.1	100	26.4	130	26.6
II. small trees (gbh 10 – < 50 cm)						
	$f \geq 1$	$f \geq 5$	$f \geq 1$	$f \geq 5$	$f \geq 1$	$f \geq 5$
families (n)	54	38	52	41	57	44
genera (n)	142	90	139	93	165	105
species (n)	349	178	356	184	458	237
trees (n)	7380	7090	7495	7185	14875	14503
trees (n ha ⁻¹)	1845	1773	1874	1796	1859	1813
	n	%	n	%	n	%
species ($f < 5$)	171	49.0	172	48.3	221	48.3
species ($f = 1$)	101	28.9	91	25.6	124	27.1
III. medium trees (gbh 50 – < 100 cm)						
	$f \geq 1$	$f \geq 5$	$f \geq 1$	$f \geq 5$	$f \geq 1$	$f \geq 5$
families (n)	36	14	36	15	41	22
genera (n)	77	23	72	25	94	38
species (n)	134	34	133	34	185	59
trees (n)	622	443	571	390	1193	958
trees (n ha ⁻¹)	156	111	143	98	149	120
	n	%	n	%	n	%
species ($f < 5$)	100	74.6	99	74.4	126	68.1
species ($f = 1$)	56	41.8	51	38.3	68	36.8
IV. large trees (gbh ≥ 100 cm)						
	$f \geq 1$	$f \geq 5$	$f \geq 1$	$f \geq 5$	$f \geq 1$	$f \geq 5$
families (n)	24	6	27	8	33	12
genera (n)	44	9	48	12	63	19
species (n)	74	15	70	16	110	28
trees (n)	245	158	278	195	523	403
trees (n ha ⁻¹)	61	40	70	49	65	50
	n	%	n	%	n	%
species ($f < 5$)	59	79.7	54	77.1	82	74.5
species ($f = 1$)	39	52.7	35	50.0	56	50.9
V. trees ≥ 10 cm dbh (gbh ≥ 31.4 cm)						
	$f \geq 1$	$f \geq 5$	$f \geq 1$	$f \geq 5$	$f \geq 1$	$f \geq 5$
families (n)	43	28	43	32	50	34
genera (n)	105	52	107	59	131	71
species (n)	219	82	224	92	295	131
trees (n)	1732	1486	1736	1509	3468	3178
trees (n ha ⁻¹)	433	372	434	377	434	397
	n	%	n	%	n	%
species ($f < 5$)	137	62.6	132	58.9	164	55.6
species ($f = 1$)	72	32.9	72	32.1	92	31.2

3.2.4. Tree diversity

The 489 species (all trees) in both plots combined gave a Shannon diversity index (H') of 4.65 with an evenness (E_H) of 0.75. MP1 ($H' = 4.51$, $E_H = 0.76$) was slightly less diverse than MP2 ($H' = 4.61$, $E_H = 0.78$) in 2001 (Table 22).

The Euphorbiaceae was by far the most abundant family in terms of tree numbers (in each main plot and in both main plots combined alike), having had more than three times as many trees as the second-ranked family Dipterocarpaceae. Table 7 shows the 10 most abundant families.

Table 7: The ten most abundant families in 2001 in the Danum main plots (MP1, MP2 and MP) with their numbers of trees (n) and percentage contributions to the total (%), ranked according to the combined values (gbh \geq 10 cm).

Family	MP1		MP2		MP	
	n	%	n	%	n	%
Euphorbiaceae	2235	27.0	2435	29.1	4670	28.1
Dipterocarpaceae	622	8.9	886	10.6	1508	9.1
Annonaceae	734	7.5	516	6.2	1250	7.5
Meliaceae	541	7.0	507	6.1	1048	6.3
Lauraceae	582	6.5	463	5.5	1045	6.3
Leguminosae	391	4.7	287	4.4	678	4.1
Myrtaceae	379	4.6	266	3.4	645	3.9
Myrsinaceae	256	4.5	368	3.2	624	3.8
Sapotaceae	368	3.1	213	2.5	581	3.5
Rubiaceae	254	3.1	196	2.3	450	2.7
other	1903	23.0	2217	26.5	4120	24.8

Of the 59 families across both plots, Euphorbiaceae was the most species-rich, followed by Lauraceae and Dipterocarpaceae and 13 additional families with 10 or more species each (Table 8).

Of 175 genera, 19 were in Euphorbiaceae, 14 in Rubiaceae, 13 in Annonaceae, 10 in Lauraceae and 10 in Leguminosae (Table 8).

The most species rich genera were *Syzygium* (the only genus in Myrtaceae, 22 species), *Shorea* (Dipterocarpaceae, 21), *Litsea* (Lauraceae, 19), *Aglaia* (Meliaceae, 15), *Polyalthia* (Annonaceae, 15), *Diospyros* (the only genus in Ebenaceae, 11) and *Drypetes* (Euphorbiaceae, 10). Other genera had < 10 species.

Table 8: Species and genera richness of families in 2001 (gbh \geq 10 cm; \geq 10 species per family) in the Danum main plots (MP1, MP2, MP), ranked according to the number of species per family in both plots combined.

Family	MP1		MP2		MP	
	species	genera	species	genera	species	genera
Euphorbiaceae	42	16	42	16	54	19
Lauraceae	44	10	39	8	52	10
Dipterocarpaceae	24	5	30	6	37	6
Meliaceae	31	6	25	7	36	7
Annonaceae	22	11	23	11	30	13
Myrtaceae	18	1	19	1	22	1
Rubiaceae	13	11	17	13	19	14
Leguminosae	13	9	13	8	17	10
Burseraceae	14	3	10	3	16	3
Anacardiaceae	11	5	13	5	16	5
Fagaceae	10	3	12	3	13	3
Sapotaceae	9	5	8	4	12	5
Myristicaceae	8	3	11	4	12	4
Ebenaceae	7	1	11	1	11	1
Melastomataceae	7	3	9	2	10	3
Moraceae	7	2	7	3	10	3

Five species in both Danum main plots combined occurred with more than 500 individuals: *Mallotus wrayi* (Euphorbiaceae, 2164 trees), *Dimorphocalyx muricatus* (Euphorbiaceae, 792), *Ardisia sanguinolenta* (Myrsinaceae, 608), *Fordia splendidissima* (Leguminosae, 544) and *Madhuca korthalsii* (Sapotaceae, 523).

3.2.5. Most abundant species

As many species had each few individuals, analysis at the species level could not include all of them. Generally, growth rates across species were calculated only when a species had at least 10 trees with valid growth measurements for a given period.

Forming a subset of species with \geq 10 trees in either main plot and in either full enumeration, resulted in 181 species. Of these, 11 did not occur in MP1 and three not in MP2 at any census. In addition, when calculating mortality and recruitment rates with this subset, some species had rates of 100%, being rather a characteristic of rare species: the lower the number of individuals, the higher the probability that none or all of the trees die within an interval or a species is completely new at an enumeration through recruitment – biasing any mean species-values and overestimating mortality or recruitment. Restricting

the selection to $f \geq 10$ or ≥ 30 in each of the main plots (resulting in 108 and 51 species respectively) eliminated these extreme mortality and recruitment rates, but meant that tree numbers still could fall well below 30 in some cases for growth calculations where only valid measurements could be used. A subset of 34 species having ≥ 50 trees in each of the main plots in either 1986 or 1996 or 2001 still allowed at least 30 valid trees for growth calculations (with one exception where $n = 29$) which was considered to be an adequate sample size.

Examining the relative frequencies of species' growth, mortality and recruitment rates of the three different minimum threshold numbers of trees per species did not show any differences between the distributions that would justify the use of a different subset of species.

Therefore, the list of 34 species was formed and used further for the analysis of the most abundant species. This subset represented 59.4%, 59.8% and 59.8% of the total numbers of trees, and 46.4%, 46.4% and 45.8% of the total basal area in 1986, 1996 and 2001 respectively. No species increased in numbers from < 50 in 1986 to ≥ 50 in 1996 or 2001 in either plot. Three species decreased in numbers < 50 in 1996 or 2001 in one of the main plots, one species dropped < 50 trees in both main plots (*Alangium javanicum*). For a list of species and tree numbers, see Table 24.

Within these most abundant species, Euphorbiaceae were represented by seven species, followed by Annonaceae (all *Polyalthia* spp.) and Dipterocarpaceae (four species each).

3.3. Mortality and Recruitment

For both main plots combined, periodic mortality rate for the 5 y between 1996 and 2001 was 10.98% and periodic recruitment rate was 7.14% (Table 16).

The annualised rates were 2.30% y^{-1} for mortality and 1.39% y^{-1} for recruitment. Both periodic and annualised rates were higher for MP1 than for MP2, but the differences between the two plots were small (Table 16).

The overall rate of periodic losses was 11.18% and that of periodic gains 7.47%. The rates of annualised losses and gains were 2.34% y^{-1} and 1.45% y^{-1} , respectively. MP1's rates were again slightly higher than those of MP2 (Table 16).

These rates of losses and gains – where regressors were taken into account for the calculations – were higher than mortality and recruitment rates mainly because they were related to the numbers of trees ≥ 10 cm gbh at the start of the interval, which was lower than the reference of mortality and recruitment (i.e. all alive trees). Furthermore, the number of gains was higher than the number of recruits (and would always be at least as high), adding to higher rates of gains compared to recruitment. This was not generally true for losses, however, as the number of losses could be lower than the number of dead trees if there were more trees dying that had been regressors at the start of the interval than new regressors at the end of the interval. This was the case in MP2: out of 959 dead trees, 94 had been < 10 cm gbh in 1996 and 77 new regressors were counted in 2001 (Table 16).

Annualised rates for trees with dbh ≥ 10 cm (≥ 31.4 cm gbh) at the start of the interval were 2.61% y^{-1} for mortality and 1.86% y^{-1} for recruitment across both main plots combined.

In comparison to the here calculated annualised mortality rate, the widely used exponential mortality coefficient (see Methods, IV.5.1.) was slightly higher with 2.33% y^{-1} (MP1: 2.35% y^{-1} ; MP2: 2.31% y^{-1}).

Annualised mortality increased with size class across both plots combined: small trees (gbh at the start of the interval in 1996 10 – < 50 cm) had 9.7% lower, medium trees 6.7% and large trees 17.7% higher mortality than the average of all sizes. Within each main plot the increase of m_a between size classes was most pronounced for the largest trees in MP1 that had *c.* 42% higher mortality than medium trees but was reversed in MP2 where m_a of large trees was *c.* 18% lower than that of medium trees (Table 9).

Table 9: Mortality rates (m_a) in the Danum main plots 1996-2001 for different size classes.

	m_a (% y^{-1})		
	MP1	MP2	MP
all alive	2.32	2.28	2.30
small	2.09	2.06	2.08
medium	2.37	2.54	2.45
large	3.37	2.09	2.71

The 10 most abundant families in the MPs had higher mortality rates (weighted mean $m_a = 2.31\% y^{-1}$) than the other families (Table 10). Mortality showed a range of $2.75\% y^{-1}$ between the minimum (in Sapotaceae) and the maximum (in Rubiaceae) rates that occurred. Rubiaceae also had the largest difference between MP1 and MP2 (Table 10).

Table 10: Mortality of the 10 most abundant families in the Danum main plots for 1996 - 2001. Shown are the rates (m_a ; % y^{-1}) and tree numbers (n_{96} : alive at the start, n_{d01} : dead at the end of the period), ranked by n_{96} of both plots combined (MP).

Family	MP1			MP2			MP		
	n_{96}	n_{d01}	m_a	n_{96}	n_{d01}	m_a	n_{96}	n_{d01}	m_a
Euphorbiaceae	2298	217	1.94	2504	213	1.79	4802	430	1.87
Dipterocarpaceae	664	107	3.44	969	149	3.37	1633	256	3.40
Annonaceae	773	84	2.24	534	47	1.83	1307	131	2.07
Lauraceae	655	108	3.54	560	113	4.45	1215	221	3.95
Meliaceae	595	78	2.70	543	56	2.15	1138	134	2.44
Myrtaceae	412	39	1.96	299	35	2.50	711	74	2.18
Leguminosae	409	36	1.79	287	29	2.10	696	65	1.92
Myrsinaceae	253	28	2.30	381	40	2.22	634	68	2.26
Sapotaceae	370	20	1.10	224	16	1.45	594	36	1.23
Rubiaceae	269	43	3.38	226	48	4.73	495	91	3.98
Other	2008	207	2.17	2341	208	1.90	4349	415	2.02
Totals:	8706	967		8868	954		17574	1921	
Weighted means:			2.32			2.31			2.31

3.4. Growth

3.4.1. Negative growth rates

After the exclusion of unreliable gbh-measurements at both enumerations of the second period (i.e. the trees that were invalid in 1996 or 2001), the calculation of agr produced 6398 and 6536 values in MP1 and MP2, respectively. Of these, *c.* 6% had

negative growth rates: 386 in MP1 and 356 in MP2. Negative values were spread across 175 species (in 41 families), of which 52 had ≥ 5 individuals with negative agr and the distribution does not appear to be different from the frequencies of all trees. The most abundant species also had the most trees with negative growth rates. For most of the 24 trees with strongly negative rates (≤ -6.0 , > -30.0 mm y^{-1}), detailed inspection of gbhs at consecutive enumerations showed that these values most likely were recording or typing errors in 1996 (often by 10 cm difference, e.g.: gbh 1986 = 20.5 cm; 1996 = 35.0 cm; 1999 = 25.8 cm; 2001 = 26.0 cm). But as it was not always certain how and where the error originated and as it was not visible where the error was (if at all) for only slightly negative growth rates (< 0 , > -6.0 mm y^{-1}), it was refrained from manually correcting any gbh-values. Seriously faulty measurements were anyway detected and excluded by the following procedure.

To separate the values that resulted from faulty measurements or recording errors from those that would be part of the population (e.g. slight shrinkage because of low stem water content, unapparent loss of bark), an approach developed by Newbery *et al.* (1999) was followed and applied to the 1996 – 2001 data-set: proportions of frequency of all growth rates with $agr \leq 0$ mm y^{-1} were logit-transformed and plotted in increasingly negative agr-classes. Both plots separately and combined showed an almost linear decline to > -4.0 mm y^{-1} . Below that, the distribution increased slightly, decreased again and then flattened (Figure 12), indicating that these values were probably not part of the 'natural' population. Trees with $agr \leq -4.0$ mm y^{-1} (18 in MP1 and 15 in MP2) were thus considered as errors and excluded from analysis.

The maximum growth rate was identified for a *Parashorea malaanonan* (Dipterocarpaceae) with 75.52 mm y^{-1} in period 2. This tree also grew fast in period 1 (60.09 mm y^{-1}) and the maximum value is equivalent to an annual radial increment of 12 mm y^{-1} – which was not considered being an unrealistic growth rate. However, some strong increases in agr between period 1 and period 2 could be doubted, but no possibility was seen to correct for these and they were very few (< 20). Thus, no trees were excluded because of high growth rates

Counts for reliable, valid growth rate values were therefore 6380 and 6521 in MP1 and MP2 respectively, representing 82.1% of the survivors in each plot.

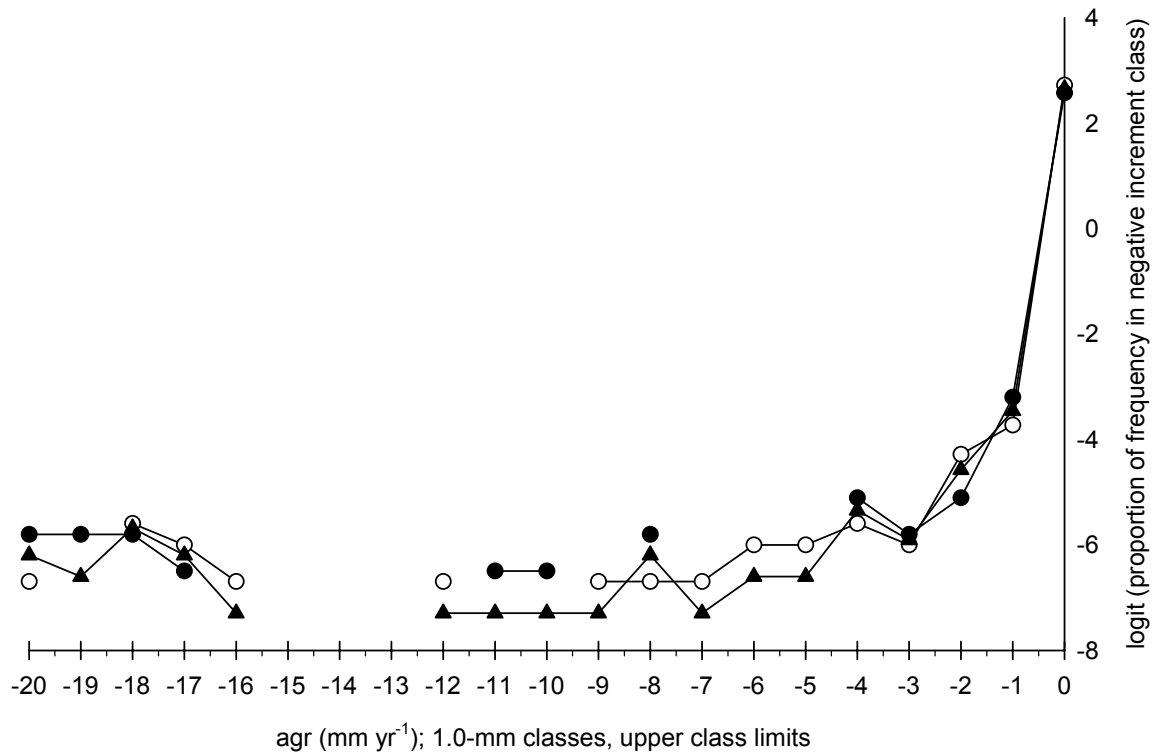


Figure 12: Logit-transformed distribution of negative growth rates in period 2 for MP1 (open circles), MP2 (closed circles) and both MPs combined (triangles).

3.4.2. Growth across main plots

With the 12901 valid growth calculations between 1996 and 2001, mean absolute growth rate across both main plots was calculated at 3.12 mm yr^{-1} (MP1: 3.33 mm yr^{-1} ; MP2: 2.90 mm yr^{-1}). Mean relative growth rate for this period was $12.48 \text{ mm m}^{-1} \text{ yr}^{-1}$ (MP1: $13.49 \text{ mm m}^{-1} \text{ yr}^{-1}$; $11.49 \text{ mm m}^{-1} \text{ yr}^{-1}$) (Table 19).

4. Lowland rainforest dynamics 1986 to 2001

4.1. Across main plots

4.1.1. Changes in structure

4.1.1.1. Revisions for 1986 and 1996

Tree numbers for the enumeration of 1986 were revised in MP1 from 8973 to 8971: one tree was reclassified as a liana and one tree was found to be outside of a plot boundary. There was no change to MP2 (n stayed at 8971).

For the 1996-enumeration, tree numbers were changed in MP1 from 8553 to 8550: one tree was found to be a liana and two trees were outside of the plot; MP2 numbers changed from 8719 to 8715 where one tree was outside and four trees were counted as one (they were coppicing from a common base).

4.1.1.2. Tree numbers

Total numbers of trees in the main plots declined by 299 in period 1 and by 679 in period 2. Considering only the population of trees with $gbh \geq 10$ cm, the decline was 677 and 642 trees in periods 1 and 2 respectively (the difference due to regressors excluded and gains included) (Table 11). On an annual basis, tree numbers ($gbh \geq 10$ cm) in period 2 declined almost twice as fast ($128 \text{ stems } y^{-1}$) as in period 1 ($68 \text{ stems } y^{-1}$).

Table 11: Tree numbers in the main plots at Danum for periods 1 and 2. Numbers at start and at end of periods with gbh ≥ 10 cm are given in bold type.

	Period 1: 1986-1996			Period 2: 1996-2001		
	MP1	MP2	MP	MP1	MP2	MP
n_{start}	8971	8971	17942	8746	8897	17643
$n_{\text{start}_{\geq 10}}$	8971	8971	17942	8550	8715	17265
n_{d}	1505	1150	2655	979	959	1938
$n_{\text{d}_{\text{reg}_{\text{p1}}}}$				88	94	182
$n_{\text{d}_{\geq 10}}$				891	865	1756
n_{s}	7466	7821	15287	7767	7938	15705
n_{reg}	196	182	378	184	157	341
(rem. old+new)				(86+98)	(80+77)	(166+175)
n_{losses}	1701	1332	3033	989	942	1931
$n_{\text{s}_{\geq 10}}$	7270	7639	14909	7583	7781	15364
n_{rec}	1280	1076	2356	685	574	1259
$n_{\text{reg}_{\text{p1}_{\geq 10}}}$				22	8	30
n_{gains}	1280	1076	2356	707	582	1289
n_{end}	8746	8897	17643	8452	8512	16964
$n_{\text{end}_{\geq 10}}$	8550	8715	17265	8268	8355	16623
$n_{\text{diff}_{\geq 10}}$	-421	-256	-677	-282	-360	-642

$n_{\text{d}_{\text{reg}_{\text{p1}}}}$: number of regressors of period 1 that were found dead in period 2

n_{reg} : number of regressors in period

(rem. old+new): remaining old regressors (from previous period) plus new regressors

$n_{\text{reg}_{\text{p1}_{\geq 10}}}$: number of regressors of previous period, gbh in 2001 ≥ 10 cm

4.1.1.3. Densities

Tree numbers declined in MP1 and MP2 for all and for small trees in the two periods (between -2.9% and -5.4%). Medium-sized and large trees increased in density in the first period (by 1.3% to 8.7%), but decreased in the second (-0.2% to -4.8%) in both main plots except for the large trees in MP2 (+2.8%). Trees ≥ 50 cm gbh were still more numerous in 2001 than in 1986 (Table 12, Figure 13). Both recruits and – less pronounced – dead trees had lower densities in period 2, but this was due to the different interval lengths: on an annual basis, recruits' density increased by *c.* 7% while the density of dead trees increased by *c.* 32%. The contribution of dead trees that had been regressors in 1996 was 1.1% of all trees (or 9.4% of all dead trees) in 2001 (Table 12).

Table 12: Densities (n trees ha⁻¹) in the main plots at Danum 1986-2001 for different size classes.

Size class (cm gbh)	MP1			MP2			MP		
	1986	1996	2001	1986	1996	2001	1986	1996	2001
all (≥ 10)	2242.8	2137.5	2067.0	2242.8	2178.8	2088.8	2242.8	2158.1	2077.9
small (10-50)	2027.3	1918.0	1849.5	2039.0	1960.5	1876.0	2033.1	1939.3	1862.8
medium (50-100)	154.5	156.5	156.3	138.3	150.3	143.0	146.4	153.4	149.6
large (≥ 100)	61.0	63.0	61.3	65.5	68.0	69.8	63.3	65.5	65.5
≥ 31.4 (≥ 10 cm dbh)	445.0	454.8	434.0	418.5	448.5	435.0	431.8	451.6	434.5
recruits		320.0	171.3		269.0	143.5		294.5	157.4
dead (≥ 10)		376.3	222.8		287.5	216.3		331.9	219.5
dead (regressors 1996)			22.0			23.5			22.8

The ratio of densities in three size classes within each main plot was *c.* 90:7:3 for small, medium and large trees respectively. The ratio stayed more or less constant across the three enumerations with only small changes. The proportion of small trees slightly declined from 1986 to 2001 in MP1 and MP2. Medium-sized trees increased their proportion in MP1 from 6.9% in 1986 steadily to 7.6% in 2001 whereas in MP2 they increased only until 1996 (from 6.2 to 6.9%) and then dropped back to 6.8% in 2001. For large trees in MP1 the proportion was 2.7% in 1986 and this increased to 2.9% in 1996 and 3.0% in 2001; the increase in proportion of large trees was more pronounced in MP2, where it increased from 2.9% to 3.1% and 3.3% in 1986, 1996 and 2001 respectively (Figure 13). Trees ≥ 10 cm dbh (≥ 31.4 cm gbh) made up *c.* 20% of all of the trees measured at each of the enumerations.

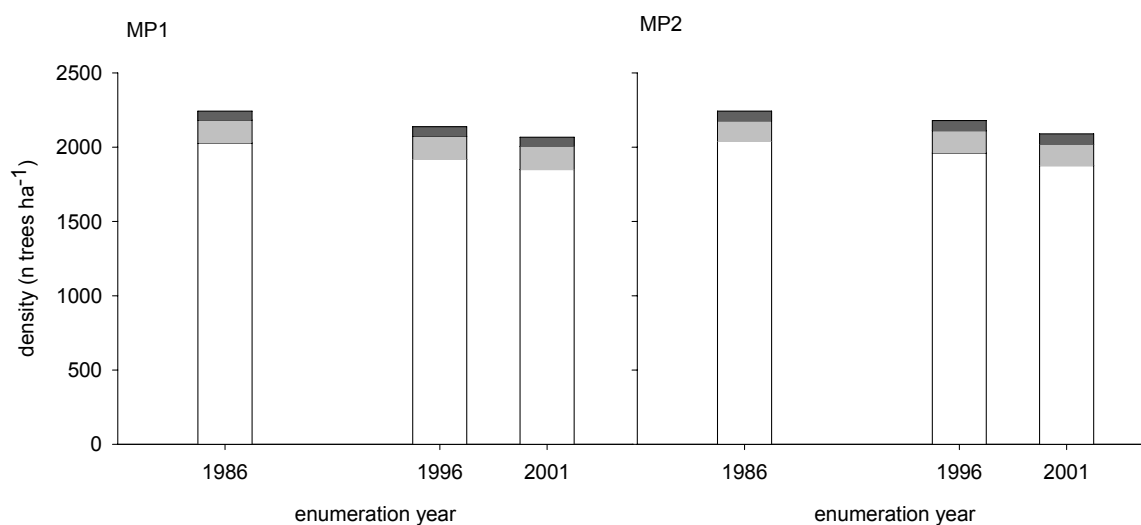


Figure 13: Change in density for MP1 and MP2 at Danum at the three full enumerations. Proportions of small (white bars), medium-sized (light grey bars) and large trees (dark grey bars) are shown.

4.1.1.4. Basal area

Basal area of all trees, which had been increasing from 1986 – 1996 (by 5.4% in MP1 and by 11.7% in MP2), decreased in the second period (MP1: -3.0%; MP2: -2.4%). In MP1 this decrease was most pronounced for small trees (-4.8%); medium-sized trees decreased by -0.8% and large trees by -3.0%. Small trees in MP2 decreased by 4.0%, but the loss in basal area in this plot was largest for medium trees (-6.5%) whereas large trees lost only 0.7% (Table 13, Figure 14).

Comparing basal area of 2001 directly with that of 1986, the change was still positive for all (2.3% and 9.1%), medium (1.9% and 4.7%) and large trees (6.2% and 14.9%), but small trees decreased in basal area by -6.8% (MP1) and -2.9% (MP2) (Table 13, Figure 14).

Table 13: Basal area ($\text{m}^2 \text{ha}^{-1}$) in the main plots at Danum 1986-2001 for different size classes.

size class (cm gbh)	MP1			MP2			MP		
	1986	1996	2001	1986	1996	2001	1986	1996	2001
all (≥ 10)	30.5	32.1	31.1	31.0	34.6	33.8	30.7	33.4	32.5
small (10-50)	7.2	7.0	6.7	7.0	7.1	6.8	7.1	7.1	6.8
medium (50-100)	6.0	6.1	6.1	5.4	6.0	5.6	5.7	6.1	5.9
large (≥ 100)	17.3	18.9	18.4	18.6	21.5	21.3	17.9	20.2	19.8
≥ 31.4 (≥ 10 cm dbh)	26.1	28.0	27.1	26.5	30.3	29.7	26.3	29.1	28.4
recruits		0.5	0.2		0.3	0.1		0.4	0.2
dead (≥ 10 cm)		4.7	4.3		3.3	3.8		4.0	4.1
dead (regressors 1996) ¹			0.002			0.003			0.002

¹: Values for dead trees that had been regressors in 1996 were estimated: out of 182 trees < 10 cm gbh in both main plots, only 29 had a gbh, 153 were not measured because they were < 5 cm gbh and for these, basal area was calculated with an estimated mean gbh of 2.5 cm

In contrast to the relative distribution of tree numbers, the proportions of the basal areas in size classes were roughly 20:20:60. Three percent of the trees (the subset of large trees) therefore accounted for 60% of the basal area. The contribution of small trees to total BA decreased in both main plots and both periods (MP1: 1986: 23.6%, 1996: 22.0%, 2001: 21.5%; MP2: 1986: 22.7%, 1996: 20.5%, 2001: 20.2%). Large trees in MP1 increased in the first period (56.8% to 58.9%) and stayed on that level until 2001. In MP2 the proportional increase from period one (60.0% to 62.1%) continued until 2001 (63.2%) (Figure 14). Trees ≥ 10 cm dbh included *c.* 87% of the total BA throughout the enumerations.

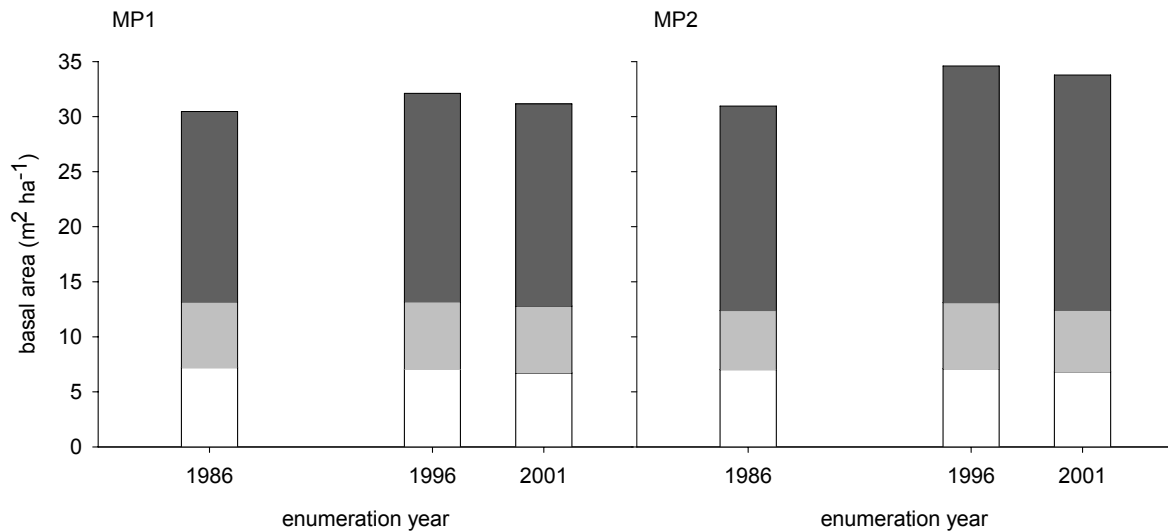


Figure 14: Change in basal area for MP1 and MP2 at Danum at the three full enumerations. Proportions of small (white bars), medium-sized (light grey bars) and large trees (dark grey bars) are shown.

Basal area growth

The difference in basal area from two consecutive enumerations was negative in the second period, as there was a relatively higher loss in basal area through trees dying than in the first period: on average, the plots lost *c.* 12% (*c.* 4 m² ha⁻¹) of their basal area in both periods, so in period 2 the same loss appeared in only half of the time as the first one.

Adjusting the differences in basal area for dead and recruiting trees as:

$$BA_{\text{grown}} = BA_{\text{diff}} + BA_{\text{dead}} - BA_{\text{recruits}}$$

where BA_{grown} is the net basal area growth, BA_{diff} the difference in basal area between two enumerations, BA_{dead} the basal area of the trees that died in the interval and BA_{recruits} the basal area of trees that were new to the population, the mean net growth of both main plots was 6.2 m² ha⁻¹ in period 1 (*c.* one fifth of the total basal area in 1986) and 3.0 m² ha⁻¹ in period 2 (*c.* one tenth of the basal area in 1996). Basal area growth in MP1 was less than in MP2 in period 1 but greater in period 2 (Table 14).

Expressing this growth on a yearly basis, the main plots on average grew 0.6 m² ha⁻¹ y⁻¹ in both periods. MP1 grew better in the second period but in MP2 this was reversed (Table 14).

Table 14: Growth of basal area (BA) in the main plots (MP1, MP2 and both plots combined, MP) at Danum 1986-2001.

		BA (m ² ha ⁻¹)		BA growth as proportion of basal area at start of period (%)		Annual BA growth (m ² ha ⁻¹ y ⁻¹)	
		period 1	period 2	period 1	period 2	period 1	period 2
MP1	BA _{diff}	1.65	-0.96				
	BA _{grown}	5.83	3.15	19.2	9.8	0.56	0.62
MP2	BA _{diff}	3.64	-0.82				
	BA _{grown}	6.57	2.86	21.2	8.3	0.68	0.58
MP	BA _{grown}	6.20	3.01	20.2	9.0	0.62	0.60

The here presented growth of basal area has to be used with caution because basal area is primarily meant as a measure of the actual state of the forest structure at a given point in time. Therefore the trees that were classified as not valid for growth analysis (see Methods, IV.5.2.) are still included in the values mentioned above.

4.1.1.5. Density and basal area in topographic classes

Both density and basal area of all, small and large trees was higher on ridges than on lower slopes (by *c.* 5% – 27%), most pronounced in large trees. There was more variability in medium-sized trees, but differences between locations and enumerations were mainly slight (Table 15). Medium and large trees continued to increase in density across both periods on intermediate locations, whereas all other size and topographical classes showed declining density in period 2. Basal area of all trees did increase in period 1 and decrease in period 2 on all locations, but small trees had decreasing basal area from 1986 onwards on all locations and large trees on lower slopes and intermediate locations increased in basal area in both periods (Table 15).

It would have been expected to find the density of recruits in 2001 to be about half of that of 1996 (*c.* 5 y *vs.* *c.* 10 y interval length). This was the case for intermediate locations and ridges, but on lower slopes, the 2001-recruits-density reached almost two thirds of that of 1996, i.e. recruitment on lower slopes was proportionally higher than expected (Table 15).

Table 15: Density and basal area for all trees, the main size classes and recruits in topographical classes (lower slope (LS), intermediate (I) and ridge (R) locations) combined for both main plots at Danum, 1986 – 2001.

		Density (n ha ⁻¹)			BA (m ² ha ⁻¹)		
		LS	I	R	LS	I	R
all	1986	2178.6	2263.2	2296.2	29.14	30.38	33.30
	1996	2068.5	2172.3	2255.1	31.97	32.39	36.62
	2001	2007.6	2066.3	2188.8	31.52	32.00	34.43
small	1986	1974.0	2053.5	2080.1	6.86	7.18	7.33
	1996	1856.3	1954.4	2026.4	6.77	7.18	7.32
	2001	1801.2	1845.0	1971.8	6.47	6.73	7.21
medium	1986	148.8	147.0	142.2	5.78	5.76	5.37
	1996	156.8	150.8	152.8	6.24	5.95	6.04
	2001	151.0	152.1	144.1	5.92	5.82	5.80
large	1986	55.8	62.7	74.0	16.49	17.44	20.60
	1996	55.4	67.1	75.9	18.96	19.26	23.26
	2001	55.4	69.3	73.0	19.13	19.45	21.41
recruits	1996	285.9	305.0	289.6	0.39	0.43	0.36
	2001	188.2	140.1	143.1	0.23	0.15	0.15

4.1.2. Dynamics

4.1.2.1. Mortality and recruitment

Periodic rates in period 2 were lower than in period 1 – apart from any dynamic effects – because the interval was only half as long. Annualized mortality was *c.* 45% higher in period 2 for both plots combined. MP1's mortality increased by *c.* 33% and MP2's by *c.* 61%. The two plots lay closer together in their mortality rates in the second than in the first period (Table 16).

For rates of losses, in addition to dead trees, regressors are considered as lost to the population and related to those trees that were ≥ 10 cm gbh at the start of a period (which generally was less than all living trees). Therefore, periodic and annual losses were higher than the corresponding rates of mortality. This was clearer and more pronounced in period 1, because it was the first period of measurements and the number of trees at the start of the period was the same for all living and trees ≥ 10 cm gbh and regressors

were recorded for the first time in 1996. The number of lost trees exceeded the number of dead trees by *c.* 14% (both main plots combined) (Table 16).

The situation in period 2 was more complex: at the start of the period, the population of all living trees was larger than that of trees ≥ 10 cm gbh, regressors from period 1 being still present or having died, and new regressors appearing. Of the trees that died between 1996 and 2001, *c.* 9% had been regressors in 1996 and were therefore not part of the losses of period 2. Where the number of new regressors exceeded the number of dead old regressors, the number of losses was still higher than the number of dead trees (as in MP1, Table 11). But if there were less new than dead old regressors, the number of losses was below that of dead trees (as in MP2, Table 11). For both main plots combined, the number of lost trees was *c.* 0.4% lower than the number of dead trees. Thus, the difference between mortality and losses is less in period 2 than in period 1 and especially small in MP2 (Table 16).

The differences of losses between the periods were not as large as in annual mortality: MP1's annual losses increased by *c.* 20% and MP2's by *c.* 28% (Table 16).

The annual recruitment rate in period 2 was *c.* 12% higher than in period 1 for both plots combined. The changes between the periods were smaller than in mortality and the two main plots rather di- than converged: MP1 had a *c.* 16% higher recruitment rate in period 2 whereas in MP2 it increased by only *c.* 7%. Thus MP1 increased its prominence in recruitment rate (Table 16).

In period 1, periodic and annual rates of gains were the same as periodic and annual recruitment rates, because recruiting trees were the only source of gains to the population and the size of the starting populations was the same for both types of rates (Table 16).

Trees that were regressors < 10 cm gbh in 1996, but re-grew ≥ 10 cm gbh between 1996 and 2001, formed an additional source of gains in period 2. These trees made up only *c.* 2.3% of the number of gains (both main plots combined), but together with the smaller starting population that the gains were related to (trees ≥ 10 cm gbh vs. all living trees), the resulting rates of gains were higher than recruitment rates (by *c.* 5% for periodic and by *c.* 4% for annual rates, both main plots combined). As a result of this constellation, the increase between period 1 and period 2 of the rate of annual gains was higher than the rate of annual recruitment (by *c.* 17%, both plots combined) (Table 16).

Table 16: Rates of mortality, recruitment, losses and gains in the main plots at Danum for periods 1 and 2.

	Period 1			Period 2		
	MP1	MP2	MP	MP1	MP2	MP
m_p (%)	16.78	12.82	14.80	11.19	10.78	10.98
l_p (%)	18.96	14.85	16.90	11.57	10.81	11.18
m_a (% y^{-1})	1.75	1.42	1.59	2.32	2.28	2.30
l_a (% y^{-1})	2.00	1.66	1.83	2.40	2.29	2.34
r_p (%)	14.27	11.99	13.13	7.83	6.45	7.14
g_p (%)	as r_p	as r_p	as r_p	8.27	6.68	7.47
r_a (% y^{-1})	1.29	1.19	1.24	1.50	1.27	1.39
g_a (% y^{-1})	as r_a	as r_a	as r_a	1.58	1.32	1.45

m_p , m_a : periodic and annual mortality (all trees, including regressors: n_d/n_{start})

l_p , l_a : periodic and annual losses (all (dead and alive) regressors excluded: $n_{losses}/n_{start_{>=10}}$)

r_p , r_a : periodic and annual recruitment

g_p , g_a : periodic and annual gains (including regressors from previous period re-growing to ≥ 10 cm gbh)

Annual mortality rates for trees with ≥ 10 cm dbh (≥ 31.4 cm gbh) at start of the interval were: period 1, MP1: 2.07% y^{-1} , MP2: 1.38% y^{-1} , both plots combined: 1.74% y^{-1} ; period 2, MP1: 2.80% y^{-1} , MP2: 2.42% y^{-1} , both plots combined: 2.61% y^{-1} . These rates were higher than those calculated for trees ≥ 10 cm gbh except for MP2 in period 1. Mortality in the ≥ 10 cm dbh size class increased on average by 50% in period 2 compared to period 1. The increase was much larger in MP2 (*c.* 75% vs. *c.* 35% in MP1) and thus – as for trees ≥ 10 cm gbh – the rates of the two main plots were closer together in period 2 than in period 1.

4.1.2.2. Mortality in size classes

Annualized mortality was calculated for the three main size classes (small, medium and large trees at the start of an interval) and additionally the class of small trees was subdivided into 10-cm-classes; this was not applied to medium and large trees, because tree numbers were low in these classes (Table 17).

Table 17: Numbers of trees (alive at start (n) and dead at end (n_d) of an interval) in size classes (10-cm-classes within the small tree size class and the main classes of small, medium and large trees) for the calculation of mortality rates of periods 1 and 2 in MP1, MP2 and both plots combined (MP) at Danum.

Size class	MP1				MP2				MP			
	n_{86}	n_{d96}	n_{96}	n_{d01}	n_{86}	n_{d96}	n_{96}	n_{d01}	n_{86}	n_{d96}	n_{96}	n_{d01}
10 – 20	5355	832	4987	475	5478	705	5129	477	10833	1537	10116	952
20 – 30	1680	295	1617	152	1673	220	1630	170	3353	515	3247	322
30 – 40	732	152	680	100	700	99	724	79	1432	251	1404	179
40 – 50	342	59	389	53	305	38	359	41	647	97	748	94
small	8109	1338	7673	780	8156	1062	7842	767	16265	2400	15515	1547
medium	618	130	626	72	553	57	601	72	1171	187	1227	144
large	244	37	251	39	262	31	272	26	506	68	523	65

For both main plots combined, m_a in period 1 was highest for medium-sized trees ($1.72\% \text{ y}^{-1}$) and lowest for large trees ($1.40\% \text{ y}^{-1}$) (Figure 15c). Within MP1 the response was similar (the relations between the classes more pronounced; Figure 15a), but in MP2 it was contrary: small trees had the highest ($1.44\% \text{ y}^{-1}$) and medium trees the lowest ($1.13\% \text{ y}^{-1}$) mortality rate (Figure 15b).

Within the small trees, mortality in period 1 was analogue in MP1, MP2 and both combined: m_a increased with size until the 30 – 40-cm-class (from $1.52\% \text{ y}^{-1}$ to $1.91\% \text{ y}^{-1}$ for both plots combined), but was lower in the 40 – 50-cm-class (MP: $1.61\% \text{ y}^{-1}$), in MP2 dropping below the rate of the smallest size class (Figure 15).

In period 2, mortality of all size classes was higher than in period 1 (by 31.0% to 93.2% for MP) (Figure 15). Across MPs combined, m_a rose from small ($1.98\% \text{ y}^{-1}$) to medium ($2.45\% \text{ y}^{-1}$) to large ($2.71\% \text{ y}^{-1}$) trees (Figure 15c). In MP1 the increase was most pronounced between medium and large trees and m_a in the latter class more than doubled to $3.37\% \text{ y}^{-1}$ (+ 119.3%) compared to period 1 (Figure 15a). In MP2, however, m_a of large trees in period 2 was similar to that of small trees and the highest mortality was calculated for medium-sized trees ($2.54\% \text{ y}^{-1}$), which, in comparison to period 1, was an increase by 125.2% (Figure 15b).

Whereas the increase in mortality within the small trees in period 2 in MP2 was linear, in MP1 and in both plots combined, the smallest two classes and the two larger classes, respectively, were similar, with a sharp step between 20 – 30 cm and 30 – 40 cm (Figure 15). Mortality rate in the 40 – 50-cm-class was lower than in the 30 – 40-cm-class, slightly so for both plots combined ($2.64\% \text{ y}^{-1}$ vs. $2.69\% \text{ y}^{-1}$), but more pronounced

in MP1 (2.84% y^{-1} vs. 3.09% y^{-1}) (Figure 15).

Although trees from all sizes responded to the 1997/98-drought-event by increased mortality, the small trees seem to have been less affected than the large trees (that had the strongest increase in m_a between the periods).

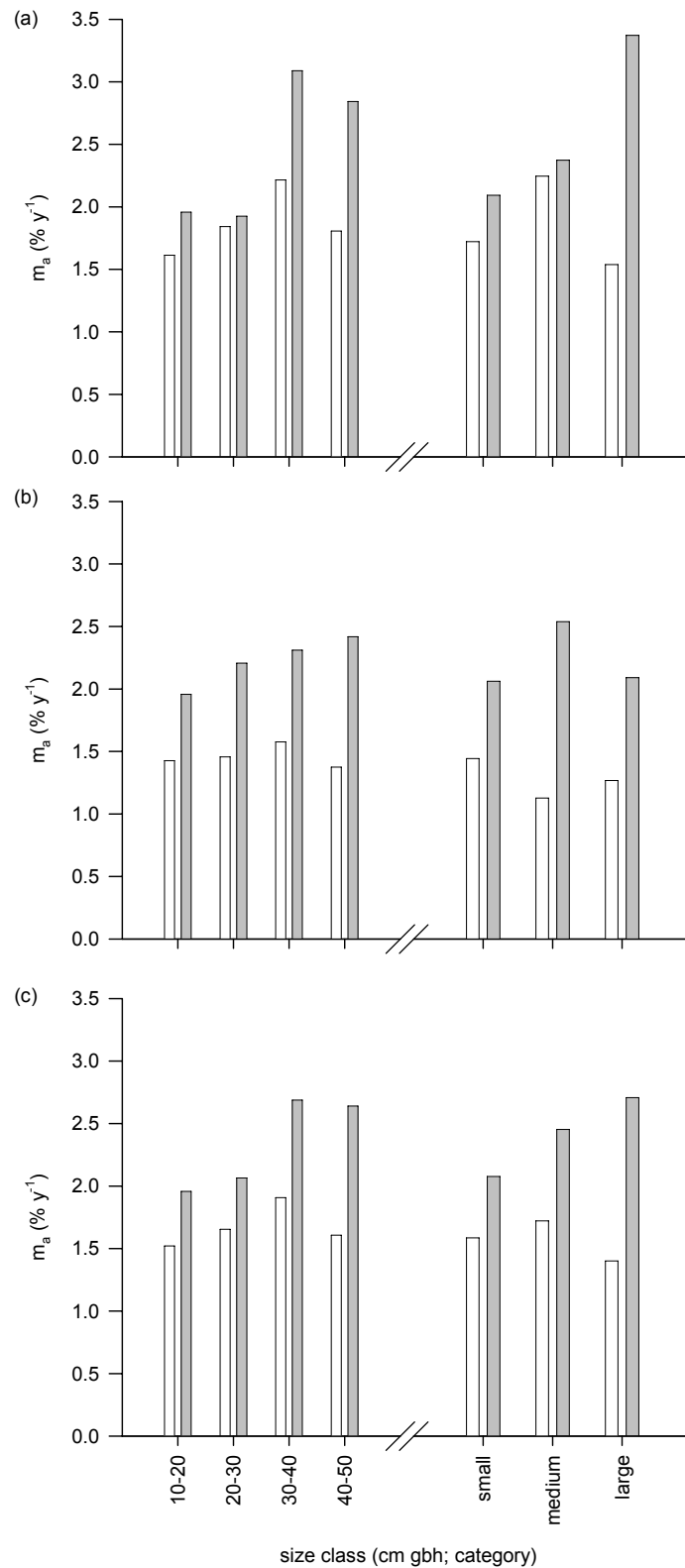


Figure 15: Mortality rates within size classes at Danum: m_a ($\% y^{-1}$) for period 1 (open bars) and period 2 (grey bars) in 10-cm-classes within the small tree size class and the main classes of small, medium and large trees in (a) MP1, (b) MP2 and (c) both plots combined.

4.1.2.3. Mortality in topographic classes

Grouped by their topographic location, trees were used to calculate mortality rates ($\% y^{-1}$) for lower slopes, intermediate locations and ridges, both for all trees and for size-classes within topographic classes. Tree numbers for both main plots combined are given in Table 18.

Table 18: Numbers of trees (alive at start (n) and dead at end (n_d) of an interval) in topographic classes for all trees and for size classes (10-cm-classes within the small tree size class and the main classes of small, medium and large trees) for the calculation of mortality rates in periods 1 and 2 for both main plots combined at Danum.

Size class	Lower slope				Intermediate				Ridge			
	n_{86}	n_{d96}	n_{96}	n_{d01}	n_{86}	n_{d96}	n_{96}	n_{d01}	n_{86}	n_{d96}	n_{96}	n_{d01}
10 – 20	3634	571	3333	343	4383	630	4085	399	2816	336	2698	210
20 – 30	1095	179	1043	93	1323	208	1267	145	935	128	937	84
30 – 40	468	73	466	65	579	117	569	68	385	61	369	46
40 – 50	216	31	248	36	265	38	313	39	166	28	187	19
small	5413	854	5090	537	6550	993	6234	651	4302	553	4191	359
medium	408	72	430	66	469	86	481	45	294	29	316	33
large	153	24	152	20	200	26	214	26	153	18	157	19
all	5974	950	5672	623	7219	1105	6929	722	4749	600	4664	411

Differences between MP1 and MP2 were mostly small and will only be referred to, when it is notable. Across all trees, mortality increased between periods 1 and 2 and in both periods m_a was highest on lower slopes and lowest on ridges, although trees on ridges experienced the strongest increase in m_a from period 1 to period 2 (by 55.7%) (Figure 16). Trees on ridges also had the lowest mortality rates within the main size classes in period 1. This was still true in period 2 for small trees, which increased in mortality by *c.* 20% – 40% in all topographic classes. But m_a of medium-sized and of large trees on ridges more than doubled (each *c.* +123%) and then lay between values of lower slopes and intermediate locations (Figure 16). Exceptionally high was the increase of m_a on ridges for large trees in MP1: in period 2 the rate was more than 5-fold that of period 1 (but tree numbers here were low: in period 1, four and in period 2, 11 out of 55 trees, respectively, died).

During period 1, large trees had the lowest mortalities of the main size classes on lower slopes and intermediate locations; on ridges, medium trees had the lowest rates. In period 2, mortality on ridges increased with main size classes. A similar pattern was

broken by medium-sized trees on intermediate locations by having had the lowest and on lower slopes by having had the highest m_a of the main size classes. Medium-sized trees on intermediate locations even had a slightly lower m_a in period 2 than in period 1 (Figure 16).

Mortality also decreased slightly for trees of the 20 – 30 cm-class on lower slopes between the periods. All other size classes within the small trees on all locations increased in m_a between periods 1 and 2, trees 30 – 50 cm gbh having had the highest mortality in period 2 (Figure 16).

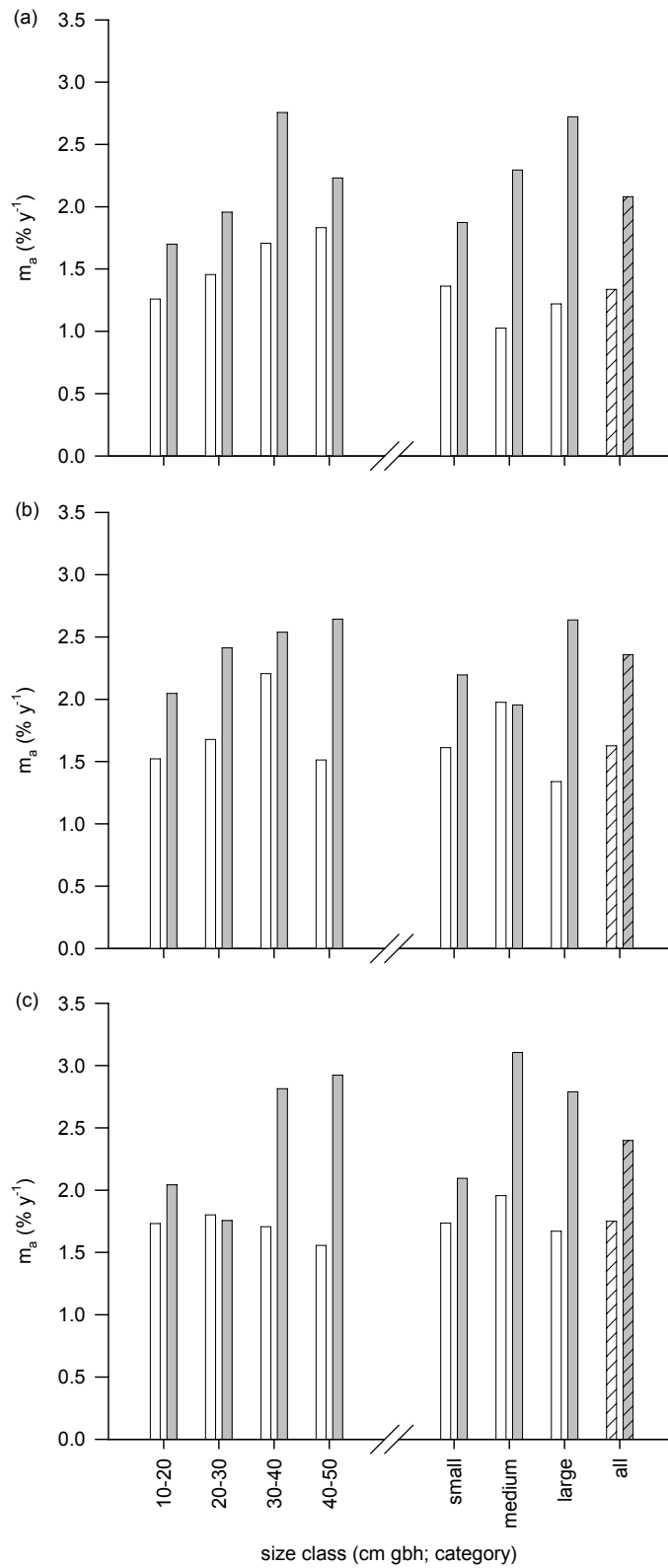


Figure 16: Mortality within topographic classes at Danum: m_a ($\% y^{-1}$) of both MPs combined for period 1 (open bars) and period 2 (grey bars) in size classes (10-cm-classes within the small tree size class and the main classes of small, medium and large trees) and for all trees (hatched pattern) on (a) ridges, (b) intermediate locations and (c) lower slopes.

4.1.2.4. Growth

Mean absolute and relative growth rates for the MPs in periods 1 and 2 are shown in Table 19. For both MPs combined, agr increased by 2.0% and rgr by 12.0% between the periods.

Table 19: Comparison of growth rates at Danum: numbers of valid trees and absolute (agr; mm y⁻¹) and relative (rgr; mm m⁻¹ y⁻¹) growth rates (\pm SE) in periods 1 and 2 for MP1, MP2 and both plots combined (MP).

	Period 1			Period 2		
	n	agr	rgr	n	agr	rgr
MP1	6467	3.19 ± 0.07	11.67 ± 0.18	6380	3.33 ± 0.07	13.49 ± 0.22
MP2	6812	2.92 ± 0.07	10.64 ± 0.17	6521	2.90 ± 0.07	11.49 ± 0.19
MP	13279	3.05 ± 0.05	11.14 ± 0.13	12901	3.12 ± 0.05	12.48 ± 0.15

4.1.2.5. Growth in size classes

Both within the small trees (10-cm-classes) and between main size classes (small, medium, large), agr increased with size in both periods and all plots (Table 20). For rgr, the opposite was the case: largest trees had the lowest rates. Within the small-tree size class, rgr was similar for all classes, although some variability occurred (Table 20).

For both MPs combined, growth declined in period 2 compared to period 1 for trees 20 – 40 cm gbh: agr by *c.* 11% and rgr by *c.* 3%. All other MP-combined rates increased in period 2, most pronounced for medium-sized trees (Table 20).

Table 20: Growth in sizes-classes: absolute (agr; mm y⁻¹) and relative (rgr; mm m⁻¹ y⁻¹) growth rates for MP1, MP2 and both main plots combined (MP) in periods 1 and 2 at Danum.

Size class	MP1		MP2		MP	
	Period 1	Period 2	Period 1	Period 2	Period 1	Period 2
<u>agr</u>						
10-20	2.00	2.20	1.75	1.79	1.87	1.99
20-30	3.30	3.13	3.14	2.59	3.22	2.86
30-40	4.99	4.23	4.43	4.21	4.70	4.22
40-50	6.33	6.48	5.60	6.25	5.97	6.37
small	2.69	2.75	2.40	2.35	2.54	2.55
medium	7.68	9.68	7.76	8.67	7.72	9.19
large	13.82	14.81	11.65	13.48	12.60	14.03
<u>rgr</u>						
10-20	11.86	14.40	10.60	11.95	11.21	13.16
20-30	11.46	11.81	10.98	9.98	11.22	10.90
30-40	12.33	11.34	11.14	11.28	11.71	11.31
40-50	12.17	13.31	11.03	12.76	11.61	13.04
small	11.83	13.57	10.74	11.53	11.27	12.53
medium	10.20	13.17	10.38	11.71	10.29	12.46
large	8.70	9.45	7.17	9.14	7.84	9.27

4.1.2.6. Growth in topographic classes

Growth across all trees in period 1 on lower slopes and on intermediate locations was similar, but less on ridges; during period 2, trees on ridges caught up, i.e. the relative increase in growth on ridges was higher (by *c.* 9% for agr and by *c.* 21% for rgr) than on the other locations (Table 21).

Further partitioning topographic locations into size classes showed that the oppositional size-dependence of agr and rgr held for all topographic classes. Between the periods, relative growth rate increased on all locations in all main size classes by *c.* 4% – *c.* 33%, only large trees on lower slopes hardly changed (Table 21).

Table 21: Growth in size classes within topographic classes: absolute (agr; mm y⁻¹) and relative (rgr; mm m⁻¹ y⁻¹) growth rates for both main plots combined in periods 1 and 2 at Danum.

Size class	Lower slope		Intermediate		Ridge	
	Period 1	Period 2	Period 1	Period 2	Period 1	Period 2
<u>agr</u>						
10-20	1.89	2.06	1.92	1.90	1.77	2.03
20-30	3.37	2.84	3.39	2.76	2.81	3.01
30-40	4.79	5.22	5.10	3.69	4.04	3.82
40-50	5.99	6.64	6.34	6.78	5.37	5.40
small	2.60	2.69	2.65	2.44	2.32	2.54
medium	7.37	8.69	8.26	9.43	7.37	9.48
large	15.17	14.85	11.36	14.32	11.70	12.96
all	3.12	3.23	3.14	3.04	2.85	3.10
<u>rgr</u>						
10-20	11.27	13.58	11.36	12.54	10.92	13.59
20-30	11.87	10.84	11.60	10.48	9.96	11.51
30-40	11.89	13.53	12.60	10.12	10.28	10.45
40-50	11.59	13.28	12.28	13.97	10.61	11.32
small	11.46	12.99	11.54	11.99	10.64	12.78
medium	9.89	11.84	10.81	12.66	10.05	12.98
large	9.37	9.38	7.15	9.52	7.25	8.87
all	11.32	12.87	11.42	12.00	10.53	12.72

4.1.3. Changes in floristic composition

4.1.3.1. Taxonomic revisions

Revising the 1986 data set after applying the changes of the taxonomic identifications in 2001 resulted in a total of 450 species (in 171 genera and 60 families), which were originally 492 species (Newbery *et al.* 1992, revised in Newbery *et al.* 1999). There were 246 species with $f \geq 5$ in 108 genera and 44 families. That is close to the number of 250 species with $f \geq 5$ reported by Newbery *et al.* (1999), indicating that revisions mostly affected rare species.

For the 1996 data-set, revision gave 466 species (in 173 genera and 60 families) for trees ≥ 10 cm gbh (originally 587 species; Newbery *et al.* 1999). Including those trees that regressed < 10 cm gbh, the counts were 474 species, 175 genera, 60 families (originally 591 species; Newbery *et al.* 1999). Counting only species with ≥ 5 trees in both main plots together gave 243 species in 108 genera and 44 families, again close to the original count of 1996 of 253 species with $f \geq 5$ individuals (Newbery *et al.* 1999).

The species richness increased between 1986, 1996 and 2001 (489 species in 175 genera and 59 families), but comparing the $f \geq 5$ estimate of 1986 and 1996 with that of 2001 (246 species, 107 genera, 44 families) showed little change in the number of taxonomic classes within the main plots. The number of common species in the main plots at Danum appears to have been stable.

4.1.3.2. Changes

Out of the 450 species present in 1986, 26 were lost through trees that died until 1996. Twenty-two had one stem only; none of these species had ≥ 5 stems. Fifty new species were gained through trees that recruited above the minimum gbh, where 28 species had one individual and two species had ≥ 5 trees (*Dysoxylum grande*, Meliaceae, $n = 6$ and *Vatica micrantha*, Dipterocarpaceae, $n = 5$). Eight species in 1996 were represented by regressors only. Thus, in summary, the number of species ≥ 10 cm gbh in 1996 was 466.

Between 1996 and 2001, out of 474 species present in 1996 (including regressors), 30 species were lost. Of these, 27 species had one individual and only one species had ≥ 5 stems (*Syzygium* species b, Myrtaceae, $n = 8$). Recruiting trees introduced 50 new species to the main plots of which 26 had one and four species had ≥ 5 stems (*Shorea macroptera*, $n = 10$; *Shorea parvistipula*, $n = 7$; *Parashorea tomentella*, $n = 6$, all Dipterocarpaceae, and *Memecylon laevigatum*, Melastomataceae, $n = 7$). Of the resulting 494 species, five occurred as regressors only and hence, in total there were 489 species with ≥ 10 cm gbh in 2001.

4.1.3.3. Diversity

Although species richness increased steadily between the enumerations, neither Shannon's H' nor evenness changed notably for all trees, both plots combined (Table 22). The slight difference in the two main plots remained since 1986 and also hardly changed. With increasing size classes, Shannon's index decreased and was lowest for large trees ≥ 100 cm gbh. The highest diversity was calculated for the group of trees ≥ 10 cm dbh where a relatively – compared to all trees – low number of trees was combined with high species richness (species-individual ratio of 0.08 to 0.09) while the species were more

equally distributed (evenness 0.83).

The above mentioned (V.3.2.4.) higher diversity in MP2 compared to MP1 for all trees was also true for small trees and trees ≥ 10 cm dbh at all enumerations and for medium-sized trees in 2001. But for large trees, this difference was reversed: diversity was higher in MP1 than in MP2 (Table 22).

Evenness was greatest for medium-sized trees and (slightly less) for large and ≥ 10 cm dbh trees. In these size classes, the dominance of *Mallotus wrayi* was much less pronounced: whereas this species made up *c.* 13% of all trees in all and small tree size classes, its share dropped to *c.* 5% for trees ≥ 10 cm dbh and $< 1\%$ for medium-sized trees. Even though the large tree size class was dominated by *Shorea* spp., no single species of that genus reached an equally high dominance as *Mallotus wrayi* (which did not occur in large trees) (Table 22).

Table 22: Diversity measures for the main plots at Danum at three enumerations in different size classes, showing numbers of trees (n), species richness (S), diversity (Shannon index, H') and evenness (E_H).

Size class	year	MP1				MP2				MP			
		n	S	H'	E_H	n	S	H'	E_H	n	S	H'	E_H
all	1986	8942	346	4.52	0.77	8954	358	4.61	0.78	17896	450	4.65	0.76
	1996	8540	350	4.50	0.77	8708	368	4.62	0.78	17248	466	4.64	0.76
	2001	8247	374	4.51	0.76	8344	379	4.61	0.78	16591	489	4.65	0.75
small	1986	8091	318	4.42	0.77	8144	338	4.53	0.78	16235	414	4.56	0.76
	1996	7666	320	4.39	0.76	7837	349	4.52	0.77	15503	433	4.54	0.75
	2001	7380	349	4.40	0.75	7495	356	4.51	0.77	14875	458	4.54	0.74
medium	1986	610	134	4.26	0.87	552	125	4.26	0.88	1162	179	4.43	0.85
	1996	624	135	4.25	0.87	600	131	4.26	0.87	1224	186	4.42	0.85
	2001	622	134	4.23	0.86	571	133	4.35	0.89	1193	185	4.44	0.85
large	1986	241	80	3.84	0.88	258	69	3.58	0.85	499	114	3.97	0.84
	1996	250	78	3.81	0.87	271	69	3.57	0.84	521	112	3.93	0.83
	2001	245	74	3.71	0.86	278	70	3.57	0.84	523	110	3.88	0.83
10 dbh	1986	1763	230	4.58	0.84	1666	226	4.65	0.86	3429	305	4.75	0.83
	1996	1813	231	4.60	0.85	1790	230	4.65	0.86	3603	306	4.75	0.83
	2001	1732	219	4.58	0.85	1736	224	4.66	0.86	3468	295	4.74	0.83

4.2. Dynamics at the species level

4.2.1. Percentage change

The frequency distribution of the change of abundances for those species that had ≥ 10 trees at the start of each interval was investigated within 5%-classes (Figure 17). The mean percentage change (\pm SE) decreased from $-4.9 \pm 1.5\%$ to $-6.5 \pm 0.9\%$ in MP1 and from $-3.3 \pm 1.1\%$ to $-6.9 \pm 1.0\%$ in MP2 between periods 1 and 2. While in both MPs during period 2 less species decreased and – even more pronounced – less species increased in tree numbers, a greater proportion of species changed only slightly in their abundances ($-5\% - +5\%$; 'static') than in period 1 (Figure 17), possibly due to different interval lengths.

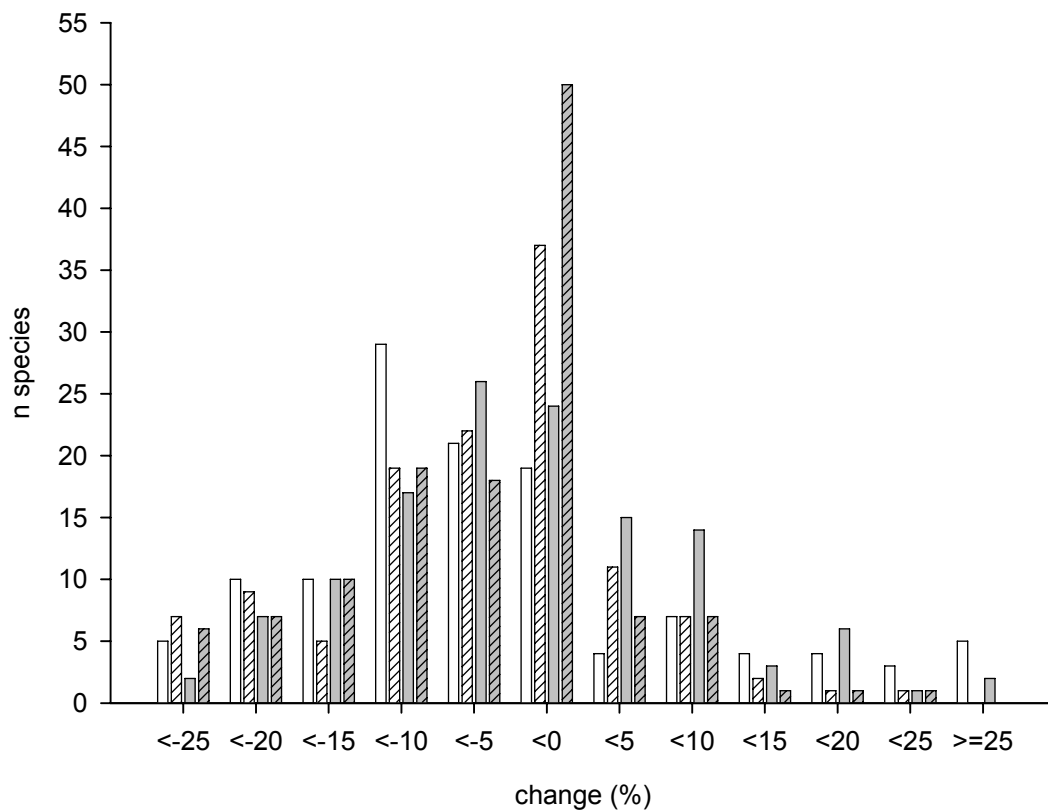


Figure 17: Percentage change of species with ≥ 10 individuals in 1986 and 1996 for MP1 (white bars) and MP2 (grey bars) in period 1 (no pattern) and in period 2 (hatched pattern). Upper class limits are given.

4.2.2. Overall average mortality and interval corrected mortality

The procedure of calculating interval corrected mortality was developed with the PEP-data set and is given in detail in Chapter V.5.4., where the additional enumeration of 1999 is included in the analysis.

Calculating annualised mortality as the mean of subplots increased the main plot estimates slightly in comparison to all data pooled across the main plots. Without correction to an equal time interval, m_{all} – the overall average mortality resulting from the taxa- and subplot-wise grouped mortalities – was slightly higher in MP1 and slightly lower in MP2 in both periods than mean m_a of subplots (Table 23).

The correction to an equal time interval was done in the same way as described in Chapter V.5.4., but the subplot size used here was 20 x 20-m and therefore only one quarter of that of the partial enumeration plots.

Based on a 5-y interval, the correction of m_{all} produces the expected result for period 1: shifting the annual mortality from *c.* 10 y to 5 y using the correction factors (MP1: 1.115, MP2: 1.220) calculated from the data set where the rarest species were excluded ($n_{\text{min}} = 2$), increased mortality rates from $m_a = 1.75\% \text{ y}^{-1}$ to $m_{\text{corr}} = 1.98\% \text{ y}^{-1}$ in MP1 (*c.* 13% increase) and from $m_a = 1.42\% \text{ y}^{-1}$ to $m_{\text{corr}} = 1.76\% \text{ y}^{-1}$ in MP2 (*c.* 24% increase) (Table 23). This procedure did not work properly for the second period: applying the correction from 5.06 (MP1) and 4.94 (MP2) to 5 y was – instead of slightly increasing the mortality in MP1 (it was a correction from 'long to short') and decreasing it slightly in MP2 ('short to long') – actually lowering mortality in both main plots, in MP1 by *c.* 4% and in MP2 by *c.* 7%. As the intervals of period 2 were very close to and on average 5.0 y, m_{all} without interval correction was considered to be the best estimate for mortality in period 2, while m_{corr} was taken as such in period 1.

On this basis, mortality increased by 19.7% in MP1 and by 30.7% in MP2 between period 1 and 2 (Table 23). The applicable mortality rates for both main plots combined were thus $1.87\% \text{ y}^{-1}$ and $2.34\% \text{ y}^{-1}$ in period 1 and 2, respectively – implying an increase of 25.1% between the periods.

Table 23: Mortality at the subplot level within the MPs at Danum for periods 1 and 2: subplots' mean annualized mortality ($m_{a_subplot}$), overall average mortality with species within subplots as groups (m_{all}) and the later with applied correction to 5-y interval length (period 1 only). All mortality rates are in % y^{-1} .

	Period 1		Period 2	
	MP1	MP2	MP1	MP2
$m_{a_subplot}$	1.78	1.44	2.35	2.31
m_{all}	1.81	1.41	2.37	2.30
m_{corr} (5 y)	1.98	1.76	-	-

4.2.3. Mortality of the most abundant species

Weighted mean m_a of the 34 most abundant species across MPs was lower than group-mortality-adjusted rates: by *c.* 17% in period 1 (m_{corr}) and by *c.* 10% in period 2 (m_{all}) (Table 23, Table 24). Mortality of most abundant species in period 2 was 36% higher than in period 1.

During both periods, 21 species had lower and 13 species had higher than average m_a . The range of species' rates was wider in period 2, but in both periods, *Knema latericia* was at the lowest end (period 1: 0.22% y^{-1} ; period 2: 0.49% y^{-1}) and *Shorea johorensis* had the highest rates (period 1: 4.01% y^{-1} ; period 2: 5.12% y^{-1}) (Table 24). *Dysoxylum cyrtobotryum* and *Maschalocorymbus corymbosus* decreased in mortality between the periods (by 13% and 4%, respectively) and five species increased by < 10% (*Dimorphocalyx muricatus* and *Cleistanthus contractus* of Euphorbiaceae and three species of Annonaceae). The remaining 27 species had > 10% higher mortalities in period 2 compared to period 1. Of these, six increased by > 100%: *Alangium javanicum*, *Pentace laxiflora*, *Litsea ochracea*, *Barringtonia lanceolata*, *Knema latericia* and *Madhuca korthalsii*, whereby the latter three species had increased mortality rates on a rather low level and still were below the average of period 2 (Table 24).

Investigating species' mortalities within size classes was difficult because in most classes, tree numbers were low and many classes were not occupied, especially in the larger sizes; furthermore, there was no clear pattern recognizable: variability of m_a between size classes was high. Generally, it appears that species of the understorey (e.g. euphorbs) increased in mortality with increasing size class, whereas species of the overstorey (e.g. dipterocarps) decreased in m_a with increasing size.

Table 24: Mortality rates (m_a ; % y^{-1}) and numbers of trees (alive at start (n) and dead at end (n_d) of an interval) in periods 1 and 2 across both main plots combined for the 34 most abundant species at Danum.

Species	n_{86}	n_{96}	n_{d96}	n_{d01}	m_aP1	m_aP2
<i>Alangium javanicum</i>	101	91	12	15	1.27	3.45
<i>Antidesma neurocarpum</i>	119	100	33	17	3.20	3.64
<i>Aporosa falcifera</i>	261	238	42	23	1.74	2.00
<i>Ardisia sanguinolenta</i>	568	591	61	53	1.14	1.87
<i>Baccaurea tetrandra</i>	250	233	25	17	1.06	1.46
<i>Barringtonia lanceolata</i>	141	147	4	10	0.29	1.41
<i>Chisocheton sarawakanus</i>	155	150	17	11	1.16	1.48
<i>Cleistanthus contractus</i>	289	273	32	16	1.17	1.26
<i>Dacryodes rostrata</i>	153	145	11	9	0.75	1.26
<i>Dimorphocalyx muricatus</i>	840	801	84	40	1.05	1.07
<i>Dysoxylum cyrtobotryum</i>	170	155	26	11	1.65	1.43
<i>Fordia splendidissima</i>	520	543	56	50	1.13	1.88
<i>Gonystylus keithii</i>	121	126	9	7	0.77	1.11
<i>Knema latericia</i>	141	166	3	4	0.22	0.49
<i>Lithocarpus nieuwenhuisii</i>	125	115	12	7	1.01	1.24
<i>Litsea caulocarpa</i>	322	319	71	57	2.45	3.88
<i>Litsea ochracea</i>	163	147	26	29	1.73	4.33
<i>Lophopetalum beccarianum</i>	234	267	18	11	0.79	0.88
<i>Madhuca korthalsii</i>	508	532	29	32	0.58	1.22
<i>Mallotus penangensis</i>	204	233	24	18	1.23	1.57
<i>Mallotus wrayi</i>	2268	2207	329	214	1.55	1.99
<i>Maschalocorymbus corymbosus</i>	403	335	126	55	3.67	3.53
<i>Parashorea malaanonan</i>	149	133	26	18	1.91	2.82
<i>Pentace laxiflora</i>	240	214	29	35	1.28	3.45
<i>Polyalthia cauliflora</i>	324	302	40	21	1.29	1.42
<i>Polyalthia rumphii</i>	141	138	13	7	0.96	1.02
<i>Polyalthia sumatrana</i>	222	221	24	13	1.14	1.19
<i>Polyalthia xanthopetala</i>	241	223	61	48	2.82	4.79
<i>Reinwardtiodendron humile</i>	262	221	60	43	2.59	4.13
<i>Shorea fallax</i>	371	395	79	59	2.35	3.25
<i>Shorea johorensis</i>	197	157	67	36	4.01	5.12
<i>Shorea parvifolia</i>	206	170	65	36	3.71	4.67
<i>Syzygium elopuræ</i>	134	120	18	10	1.42	1.77
<i>Syzygium tawaense</i>	124	120	16	14	1.37	2.44
totals	10667	10328	1548	1046		
means					1.60	2.31
SE					0.17	0.23
weighted means					1.55	2.11

The variability of m_a was also true for topography. However, by looking at the change in mortality within topographic locations between the two periods, some species seemed to show a trend towards less vulnerability on either location. In Table 25 the changes between periods are shown and a classification is given as a 'best performance' in terms of labelling that topographic location on which the respective species had a

decrease in mortality (including slight increases < 10%). Eleven species increased in m_a on all locations and were not labelled (Table 25).

From this classification, three species were responding positively (i.e. lower mortality) to the 1997/98-drought on lower slopes, seven species on intermediate locations and four species on ridges. Four species 'performed well' on lower slopes and intermediate locations, three on lower slopes and ridges (they had elevated mortality only on intermediate locations) and one species on intermediate locations and ridges. *Dysoxylum cyrtobotryum* had lower m_a in period 2 than in period 1 in all three topographic classes (Table 25).

Table 25: Change of mortality between periods 1 and 2 of the most abundant species within topographic classes (both MPs combined) at Danum. The change (m_a period 2 – m_a period 1) is indicated by: +++: $\geq 100\%$; ++: $50\% - < 100\%$; +: $10\% - < 50\%$; ~: $-10\% - < 10\%$; -: $-50\% - < -10\%$; --: $-100\% - < -50\%$; ---: $< -100\%$. Classification is done with letters for the topographic classes (lower slope: LS, intermediate locations: I, ridges: R) to indicate 'best performance' on a 'preferred' location (see text).

Species	Lower slope	Intermediate	Ridge	Class
<i>Baccaurea tetrandra</i>	+++	--	+++	I
<i>Cleistanthus contractus</i>	n.a.	--	+	I
<i>Dacryodes rostrata</i>	+++	--	++	I
<i>Gonystylus keithii</i>	++	~	+++	I
<i>Maschalocorymbus corymbosus</i>	+	-	+	I
<i>Parashorea malaanonan</i>	+	~	+++	I
<i>Syzygium tawaense</i>	+++	~	+++	I
<i>Knema latericia</i>	+++	--	---	I/R
<i>Chisocheton sarawakanus</i>	-	+++	+++	LS
<i>Mallotus wrayi</i>	~	+	+++	LS
<i>Syzygium elopuræ</i>	---	++	++	LS
<i>Aporosa falcifera</i>	~	-	++	LS/I
<i>Mallotus penangensis</i>	~	~	+++	LS/I
<i>Polyalthia cauliflora</i>	~	-	+++	LS/I
<i>Polyalthia sumatrana</i>	~	--	+++	LS/I
<i>Dysoxylum cyrtobotryum</i>	-	~	~	LS/I/R
<i>Lithocarpus nieuwenhuisii</i>	~	++	~	LS/R
<i>Lophopetalum beccarianum</i>	~	+	~	LS/R
<i>Shorea parvifolia</i>	-	++	-	LS/R
<i>Antidesma neurocarpum</i>	+	+	~	R
<i>Dimorphocalyx muricatus</i>	+++	++	-	R
<i>Polyalthia rumphii</i>	++	+	---	R
<i>Shorea johorensis</i>	+	+	~	R
<i>Alangium javanicum</i>	+++	++	++	
<i>Ardisia sanguinolenta</i>	++	++	+	
<i>Barringtonia lanceolata</i>	+++	+++	+++	
<i>Fordia splendidissima</i>	+++	+	++	
<i>Litsea caulocarpa</i>	+	+++	+	
<i>Litsea ochracea</i>	+++	++	+++	
<i>Madhuca korthalsii</i>	+	+++	+++	
<i>Pentace laxiflora</i>	+++	+++	+	
<i>Polyalthia xanthopetala</i>	+++	+	+	
<i>Reinwardtiodendron humile</i>	++	+	+++	
<i>Shorea fallax</i>	+	+	++	

4.2.4. Mortality within families

Except for the Rubiaceae (with one species only: *Maschalocorymbus corymbosus*), all families of the most abundant species increased in m_a between the periods, most pronounced ($> 100\%$) in five families (each consisting of one species only) (Table 26).

Mortality rates of the most numerous families of Euphorbiaceae, Annonaceae and Dipterocarpaceae increased by 22% to 32% between periods 1 and 2 (Table 26).

Table 26: Mortality rates (m_a ; % y^{-1}) for families of the most abundant species at Danum.

Family 2001	n_{86}	n_{96}	n_{d96}	n_{d01}	m_aP1	m_aP2
Rubiaceae	403	335	126	55	3.67	3.53
Celastraceae	234	267	18	11	0.79	0.88
Euphorbiaceae	4231	4085	569	345	1.43	1.75
Fagaceae	125	115	12	7	1.01	1.24
Dipterocarpaceae	923	855	237	149	2.90	3.79
Annonaceae	928	884	138	89	1.58	2.09
Meliaceae	587	526	103	65	1.92	2.55
Thymelaeaceae	121	126	9	7	0.77	1.11
Myrtaceae	258	240	34	24	1.39	2.11
Myrsinaceae	568	591	61	53	1.14	1.87
Leguminosae	520	543	56	50	1.13	1.88
Burseraceae	153	145	11	9	0.75	1.26
Lauraceae	485	466	97	86	2.21	4.02
Sapotaceae	508	532	29	32	0.58	1.22
Myristicaceae	141	166	3	4	0.22	0.49
Tiliaceae	240	214	29	35	1.28	3.45
Alangiaceae	101	91	12	15	1.27	3.45
Lecythidaceae	141	147	4	10	0.29	1.41

4.2.5. Turnover

Turnover – the mean of recruitment and mortality rates – as a measure of dynamics showed an increase between the periods: the mean (\pm SE) of species with ≥ 10 individuals was $1.67 \pm 0.10\% y^{-1}$ and $1.38 \pm 0.09\% y^{-1}$ in period 1 and $2.14 \pm 0.16\% y^{-1}$ and $1.95 \pm 0.13\% y^{-1}$ in period 2 for MP1 and MP2, respectively.

From the frequency distribution of turnover (Figure 18), the proportions of low ($< 1.5\% y^{-1}$) to high ($\geq 1.5\% y^{-1}$) dynamic turnover reversed between period 1 and 2: during the first interval, more than half of the species showed low, in the second one, more than half of the species showed high dynamic turnover.

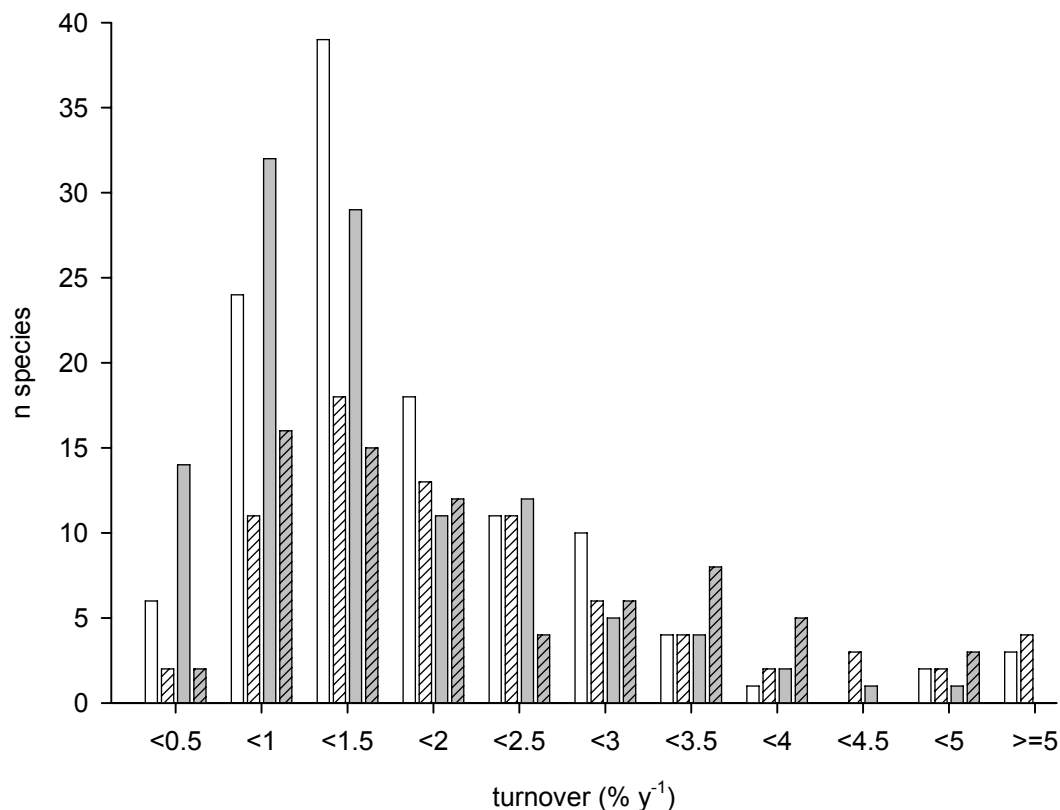


Figure 18: Turnover of species with ≥ 10 individuals in 1986 or 1996 for MP1 (white bars) and MP2 (grey bars) in period 1 (no pattern) and in period 2 (hatched pattern). Upper class limits are given.

4.2.6. Growth across species

Mean absolute growth rates of species with ≥ 10 valid individuals in both periods (105 in MP1, 113 in MP2) decreased by 3.3% in MP1 and increased by 3.5% in MP2 between period 1 and 2; relative growth rate increased by 4.3% and 6.7% in MP1 and MP2, respectively (Table 27). Mean growth rates were significantly correlated with mean gbh (variables \ln -transformed; Spearman's rank correlation coefficient for agr: 0.705 – 0.727, for rgr: 0.425 – 0.491; $P = 0$ in all cases). Species with on-average larger trees tended to have larger growth rates, more clearly so for absolute than for relative rates (Figure 19). At the upper end of this relationship, species from the Dipterocarpaceae (*Shorea* spp.) and Fagaceae (*Lithocarpus* spp. and *Quercus* spp.) and on the lower end, species mainly from the Polygalaceae and Annonaceae were found.

Table 27: Mean absolute (agr , mm y^{-1}) and relative (rgr , $\text{mm m}^{-1} \text{y}^{-1}$) growth rates \pm SE across species with ≥ 10 individuals for period 1 and 2 in MP1 and MP2 at Danum.

	MP1		MP2	
	mean	\pm SE	mean	\pm SE
agr period 1	3.96	± 0.49	3.33	± 0.35
agr period 2	3.83	± 0.41	3.45	± 0.36
rgr period 1	12.94	± 1.00	11.22	± 0.77
rgr period 2	13.50	± 0.83	11.98	± 0.74

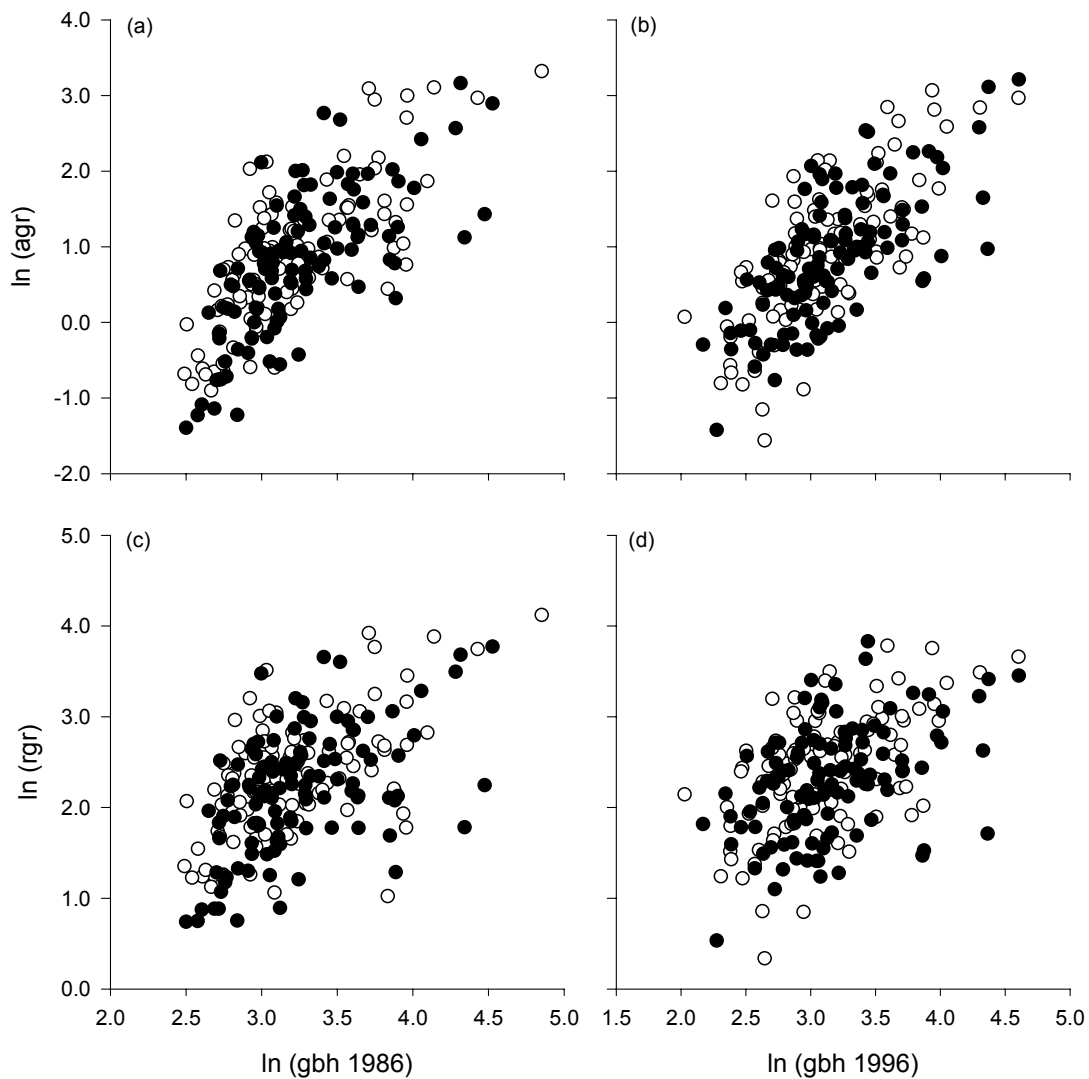


Figure 19: Growth related to gbh: mean absolute (a and b) and relative (c and d) growth rates of species with ≥ 10 valid measurements in period 1 (a and c) and period 2 (b and d) in relation to gbh at the start of each respective interval for MP1 (open circles) and MP2 (filled circles) at Danum. Untransformed units were mm y^{-1} (agr), $\text{mm m}^{-1} \text{y}^{-1}$ (rgr) and mm (gbh).

4.2.6.1. Growth of most abundant species

Weighted mean rgr of the 34 species increased by *c.* 11% (agr by *c.* 3%) between the periods. *Antidesma neurocarpum* and *Shorea parvifolia* had the lowest and highest growth rates (both MPs combined) of the most abundant species in both periods, both in agr and rgr, respectively (Table 28). Twenty-three species had higher rgr in the second than in the first period, most of these by 10% – 50%. The strongest increase in rgr was exhibited by *A. neurocarpum* (by *c.* 85%). Of the dipterocarps, only *Parashorea malaanonan* increased in rgr (by *c.* 6%), the three *Shorea spp.* decreased by 12% – 23%. Five of the seven euphorbs and all four species of the Annonaceae increased in rgr (by 7% – 85%, including the euphorb *A. neurocarpum*). The remaining two euphorbs that had a negative rgr-balance between the periods were *Aporosa falcifera* (*c.* -13%) and *Baccaurea tetrandra* (*c.* -6%) (Table 28).

Within the small trees size class, all four dipterocarps were growing less in the second period than in the first one. *Shorea johorensis* additionally had lower rgr in period 2 in large trees. If there were trees of euphorbs present in the medium and large size classes, they showed less growth in period 2, except for *Mallotus wrayi*, which increased in growth (but $n < 10$).

Table 28: Growth of the 34 most abundant species. Absolute (agr; mm y⁻¹) and relative (rgr; mm m⁻¹ y⁻¹) growth rates in periods 1 and 2 for both main plots combined at Danum.

Species	agr		rgr	
	Period 1	Period 2	Period 1	Period 2
<i>Alangium javanicum</i>	2.10	1.56	7.99	6.99
<i>Antidesma neurocarpum</i>	0.43	0.77	3.01	5.56
<i>Aporosa falcifera</i>	3.55	2.85	12.12	10.61
<i>Ardisia sanguinolenta</i>	1.93	1.82	11.24	11.33
<i>Baccaurea tetrandra</i>	1.98	1.81	8.10	7.59
<i>Barringtonia lanceolata</i>	1.58	2.03	5.47	7.11
<i>Chisocheton sarawakanus</i>	3.31	3.21	12.06	11.88
<i>Cleistanthus contractus</i>	1.17	1.54	6.89	9.60
<i>Dacryodes rostrata</i>	1.89	1.60	7.97	6.64
<i>Dimorphocalyx muricatus</i>	1.02	1.42	5.43	8.00
<i>Dysoxylum cyrtobotryum</i>	5.40	5.37	17.63	15.91
<i>Fordia splendidissima</i>	1.79	1.99	10.21	12.22
<i>Gonystylus keithii</i>	2.88	3.28	11.34	14.22
<i>Knema latericia</i>	1.99	2.31	12.24	13.02
<i>Lithocarpus nieuwenhuisii</i>	5.24	5.30	15.30	17.87
<i>Litsea caulocarpa</i>	3.32	3.97	16.26	20.36
<i>Litsea ochracea</i>	3.31	2.22	13.54	11.05
<i>Lophopetalum beccarianum</i>	3.18	3.77	15.24	18.95
<i>Madhuca korthalsii</i>	2.49	2.68	10.65	12.21
<i>Mallotus penangensis</i>	2.47	2.71	11.74	14.94
<i>Mallotus wrayi</i>	1.69	2.00	9.10	11.58
<i>Maschalocorymbus corymbosus</i>	1.24	1.47	8.24	9.90
<i>Parashorea malaanonan</i>	7.48	9.64	14.03	14.84
<i>Pentace laxiflora</i>	8.13	8.87	21.03	20.54
<i>Polyalthia cauliflora</i>	0.87	1.14	5.01	6.58
<i>Polyalthia rumphii</i>	2.52	2.89	11.95	14.03
<i>Polyalthia sumatrana</i>	4.13	4.66	15.50	17.15
<i>Polyalthia xanthopetala</i>	1.98	1.65	9.50	10.20
<i>Reinwardtiodendron humile</i>	1.29	1.28	6.19	6.43
<i>Shorea fallax</i>	5.40	4.62	17.97	15.75
<i>Shorea johorensis</i>	16.72	15.55	38.35	29.71
<i>Shorea parvifolia</i>	23.07	21.94	43.78	37.41
<i>Syzygium elopuræ</i>	1.19	1.22	5.66	6.17
<i>Syzygium tawaense</i>	3.87	3.63	13.41	15.39
Means:	3.84	3.91	12.77	13.28
SE:	0.77	0.74	1.43	1.15
Weighted means:	2.84	2.93	11.08	12.34

Analogue to mortality within topographic classes, Table 29 shows the change of rgr between periods 1 and 2. Eleven species (including the three *Shorea spp.*) decreased on all locations (or an increase was < 10%) and 10 species showed a combined positive growth-balance on two locations. Five species (including three euphorbs) increased in rgr

in all topographic classes. Three species showed better growth on lower slopes, two species on intermediate locations and three species on ridges (Table 29).

Table 29: Change of relative growth rate between periods 1 and 2 of the most abundant species within topographic classes (both MPs combined) at Danum. The change (rgp period 2 – rgr period 1) is indicated by: +++: $\geq 100\%$; ++: $50\% - < 100\%$; +: $10\% - < 50\%$; ~: $-10\% - < 10\%$; -: $-50\% - < -10\%$; --: $-100\% - < -50\%$; ---: $< -100\%$. Classification is done with letters for the topographic classes to indicate ‘best performance’ on a ‘preferred’ location (see text).

Species	Lower slope	Intermediate	Ridge	Class
<i>Alangium javanicum</i>	-	+	-	I
<i>Lithocarpus nieuwenhuisii</i>	-	++	~	I
<i>Barringtonia lanceolata</i>	~	++	+	I/R
<i>Cleistanthus contractus</i>	n.a.	+	+	I/R
<i>Knema latericia</i>	-	+	+	I/R
<i>Mallotus penangensis</i>	~	+	+	I/R
<i>Gonystylus keithii</i>	++	~	~	LS
<i>Polyalthia sumatrana</i>	+	~	~	LS
<i>Polyalthia xanthopetala</i>	+	~	~	LS
<i>Litsea caulocarpa</i>	++	+	~	LS/I
<i>Madhuca korthalsii</i>	+	+	~	LS/I
<i>Maschalocorymbus corymbosus</i>	+	+	~	LS/I
<i>Syzygium tawaense</i>	++	+	-	LS/I
<i>Antidesma neurocarpum</i>	+	+++	+	LS/I/R
<i>Dimorphocalyx muricatus</i>	++	++	+	LS/I/R
<i>Fordia splendidissima</i>	+	+	+	LS/I/R
<i>Mallotus wrayi</i>	+	+	+	LS/I/R
<i>Polyalthia cauliflora</i>	+	+	++	LS/I/R
<i>Chisocheton sarawakanus</i>	+	-	+	LS/R
<i>Polyalthia rumphii</i>	+	~	++	LS/R
<i>Lophopetalum beccarianum</i>	~	~	+	R
<i>Parashorea malaanonan</i>	-	~	+++	R
<i>Syzygium elopuræ</i>	-	~	++	R
<i>Aporosa falcifera</i>	~	-	-	
<i>Ardisia sanguinolenta</i>	~	~	~	
<i>Baccaurea tetrandra</i>	~	-	-	
<i>Dacryodes rostrata</i>	-	-	~	
<i>Dysoxylum cyrtobotryum</i>	-	~	~	
<i>Litsea ochracea</i>	-	~	-	
<i>Pentace laxiflora</i>	~	~	-	
<i>Reinwardtiodendron humile</i>	~	~	~	
<i>Shorea fallax</i>	~	-	-	
<i>Shorea johorensis</i>	-	-	~	
<i>Shorea parvifolia</i>	-	~	-	

4.2.7. Comparison of growth rates for the most abundant species

Selecting all valid growth rates of the 34 most abundant species resulted in 3740 to 4088 values (Table 30a). Mean agr in MP1 increased by 9.3% and mean rgr by 17.5% between period 1 and period 2. In MP2, agr decreased by 3.8% and rgr increased by 4.2% between the periods (Table 30a).

To perform statistical tests on the changes of growth rates between the periods, two different approaches were followed: firstly, only trees with valid rates in both periods ('pairs of growth rates') were considered and secondly, growth of period 1 was projected to period 2 using linear regression and these predicted growth rates were compared with the rates calculated from actual measurements.

4.2.7.1. 'Pairs of growth rates'

The selection of valid rate pairs (i) lowered the number of values (by *c.* 13% – 17%) and (ii) altered the difference in growth rates: on average rate differences were reduced (Table 30b).

Table 30: Comparison of growth rates for the 34 most abundant species: numbers of values available for calculation of differences in growth (n) and weighted means of absolute (agr; mm y⁻¹) and relative (rgr; mm m⁻¹ y⁻¹) growth rates for main plots 1 and 2 at Danum, for (a) all valid and (b) paired growth rates separately.

	MP1			MP2		
	n	agr	rgr	n	agr	rgr
<u>(a) all valid trees</u>						
period 1	4088	2.89	11.43	3940	2.79	10.71
period 2	4056	3.16	13.43	3740	2.68	11.16
period 2 - period 1		0.27	2.00		-0.11	0.45
<u>(b) pairs of growth rates</u>						
period 1	3379	2.90	11.83	3251	2.75	11.04
period 2	3379	3.03	11.17	3251	2.67	9.74
period 2 - period 1		0.13	-0.66		-0.08	-1.30

Within species, growth rates might be changed in either direction and the change can be considerable. Table 31 shows the example of *Mallotus wrayi* in MP2. With all valid trees, agr increased by 8% and rgr by 17% between the periods. Using pairs of valid trees only, this is reversed to a decrease in agr by 4% and in rgr by 7%. Standard errors

were similar (3.3 – 5.0% of mean) but minima were more negative for the 'all valid trees' subset than for the 'pairs' (Table 31). This could be a hint towards the reliability of rates: when there are three qualitatively good measurements for an individual tree, the resulting growth rates (two periods) might be more credible than a rate derived from only two measurements (one period) where that tree had e.g. stem deformations in the previous or the following period. More importantly, however, pairs of valid trees are excluding trees that recruited into the population between 1986 and 1996 (123 trees in the *M. wrayi* example) and those trees that died between 1996 and 2001 (79 trees). As growth of dying trees is slowed down prior to death (see Chapter V. 5.6.2.), exclusion of growth rates in period 1 from trees that died in period 2 therefore increased mean agr in period 1 (mean agr of these unpaired 140 trees in period 1 was 1.37 mm y⁻¹). The opposite effect took place in period 2: the recruits of 1996 that did not have corresponding growth rates in period 1, grew better than average (2.68 mm y⁻¹) and thus their exclusion in period 2 led to a lower mean agr for the paired rates compared to 'all valid trees'. Consequently, differences in growth rates for *M. wrayi* were reversed from positive ('all valid trees') to negative ('pairs of valid trees') (Table 31).

Comparison of paired growth rates for that reason has to be considered as an estimate for cohorts of trees that were part of the population from the beginning until the end of the measurements.

Table 31: Example of changed growth rate-values of *Mallotus wrayi* in MP2 resulting from the reduction of usable values for all valid (a) and paired (b) growth rates separately, showing number of trees (n), mean (\pm SE) and range of agr and rgr in the two periods and the difference of both (P2-P1).

	agr (mm y ⁻¹)			rgr (mm m ⁻¹ y ⁻¹)		
	Period 1	Period 2	P2-P1	Period 1	Period 2	P2-P1
<u>(a) all valid trees</u>						
n	796	780		796	780	
mean	1.73	1.87	+0.14	9.46	11.09	+1.63
\pm SE	\pm 0.060	\pm 0.084		\pm 0.315	\pm 0.491	
min	-2.42	-2.03		-9.94	-16.72	
max	12.30	25.47		63.66	115.63	
<u>(b) pairs of growth rates</u>						
n	655	655		655	655	
mean	1.80	1.73	-0.07	10.01	9.27	-0.74
\pm SE	\pm 0.065	\pm 0.087		\pm 0.345	\pm 0.448	
min	-0.52	-1.66		-4.62	-8.46	
max	12.30	25.47		63.66	115.63	

For the following procedures, only relative growth rates were considered because they were less dependent on tree size and more sensitive to changes.

Statistical tests for differences in growth rates between periods:

Only very few species had growth rates that were normally distributed; and rates of individual trees in period 2 were not independent of their rates in period 1. Non-parametric tests were therefore needed, Wilcoxon-Matched-Pairs (or Signed-Ranks) test being the most appropriate. The other possibility was to use the Mann-Whitney U-test, but to overcome the dependency-problem, subsets of one half of the trees in period 1 were drawn 100 times at random and compared with the other halves of the trees in period 2. The number of instances in which a significant result ($\alpha = 0.05$) was achieved was counted.

A major concern in multiple hypothesis testing problems is the rejection of even one true null hypothesis (type I errors; 'false positives'), termed 'family-wise error-rate', FWER (Benjamini and Hochberg 1995, Benjamini and Yekutieli 2001). To control FWER, Bonferroni one-step procedure (Garcia 2004) was applied to U-tests: H_i is rejected while $P_i \leq \alpha/n$, otherwise H_i is accepted, i.e. to reach an overall $P \leq 0.05$ individual tests had to have $P \leq 0.0005$. The numbers of individual tests with $P \leq 0.0005$ were counted. The probability of exactly n tests being statistically significant due to chance alone can be calculated with the Bernoulli-equation (Moran 2003):

$$P = (N!/(N-K)!K!) * \alpha^K (1-\alpha)^{N-K}$$

where N is the number of tests and K the number of tests with $P \leq \alpha$. With $N = 100$ and $\alpha = 0.05$, setting $K = 3$ leads to a probability of these three significant outcomes resulting from chance alone of ≤ 0.0005 (exactly 0.000019255). Therefore, an overall significance was considered achieved when ≥ 3 individual test runs yielded $P \leq 0.0005$ (Table 33).

A less restrictive approach than the Bonferroni procedure is the control of the 'false discovery rate', FDR (Benjamini and Hochberg 1995, Benjamini and Yekutieli 2001, Garcia 2004): P-values of tests are ranked in ascending order and, starting with the highest P-value, each P is checked if it is $\leq k$ (the rank) times α divided by n ; at the first P that meets this requirement its corresponding null hypothesis and all those having smaller P 's are rejected (Garcia 2004). This results again in a count of individual test runs that

reached significance (at a given α). To achieve an overall significance, those P's that first met the requirements were inserted in the above given Bernoulli-procedure and the number of tests needed to reach $P \leq 0.0005$ was found (Table 32).

Table 32: Tests for differences in growth: species with ≥ 1 significant tests (out of 100) when applying FDR procedure; first P-values of U-tests that met the requirements and minimum number of test runs required to achieve probability of n type I errors ≤ 0.0005 (n_{\min}) (see text for explanations).

Plot	Species	'first P'	runs _{min}
MP1	<i>Aporosa falcifera</i>	0.0005	3
MP1	<i>Dimorphocalyx muricatus</i>	0.0130	7
MP1	<i>Fordia splendidissima</i>	0.0010	3
MP1	<i>Lophopetalum beccarianum</i>	0.0005	3
MP1	<i>Mallotus wrayi</i>	0.0002	2
MP1	<i>Parashorea malaanonan</i>	0.0003	2
MP1	<i>Polyalthia xanthopetala</i>	0.0002	2
MP1	<i>Reinwardtiodendron humile</i>	0.0022	4
MP1	<i>Shorea fallax</i>	0.0024	4
MP1	<i>Shorea johorensis</i>	0.0151	8
MP1	<i>Shorea parvifolia</i>	0.0390	12
MP2	<i>Aporosa falcifera</i>	0.0147	8
MP2	<i>Ardisia sanguinolenta</i>	0.0454	13
MP2	<i>Cleistanthus contractus</i>	0.0043	5
MP2	<i>Dimorphocalyx muricatus</i>	0.0275	10
MP2	<i>Dysoxylum cyrtobotryum</i>	0.0003	2
MP2	<i>Litsea caulocarpa</i>	0.0327	11
MP2	<i>Litsea ochracea</i>	0.0226	9
MP2	<i>Mallotus wrayi</i>	0.0373	12
MP2	<i>Pentace laxiflora</i>	0.0075	6
MP2	<i>Shorea fallax</i>	0.0439	13
MP2	<i>Shorea parvifolia</i>	0.0042	5
MP2	<i>Syzygium elopuræ</i>	0.0001	2

V. Results

Table 33: Differences in relative growth rates between period 1 and period 2 for the 34 most abundant species in MP1 and MP2 at Danum. Numbers of trees used for growth calculations, rgr (mm m⁻¹ y⁻¹) and percentage change (%ch) of rgr between the periods are shown for 'all valid trees' and for 'pairs of growth rates'. Results of statistical tests for the 'pairs' are given as: randomized U-tests (MWU), showing numbers of tests with (A) P ≤ 0.05, (B) P ≤ 0.0005 (one-step Bonferroni) and (C) P ≤ P_{FDR} (FDR procedure); results of conventional Wilcoxon-matched-pairs tests are shown in the last column (WIL) with *: P ≤ 0.05; **: P ≤ 0.02; ***: P ≤ 0.01. Overall significant different growth for a species (see text) is indicated by bold values (columns MWU B and C).

Species	MP1													
	All valid trees					Pairs of growth rates								
	growth P1		growth P2		%ch	growth P1		growth P2		%ch	MWU			WIL
	n	rgr	n	rgr	rgr	n	rgr	n	rgr	rgr	A	B	C	
<i>Alangium javanicum</i>	35	7.62	30	7.76	2	26	7.81	26	6.20	-21	2	0	0	
<i>Antidesma neurocarpum</i>	43	3.08	40	6.04	96	34	3.20	34	5.42	70	12	0	0	
<i>Aporosa falcifera</i>	81	11.67	73	10.49	-10	66	12.57	66	9.33	-26	29	2	2	***
<i>Ardisia sanguinolenta</i>	158	10.19	174	14.06	38	134	10.64	134	10.73	1	1	0	0	
<i>Baccaurea tetrandra</i>	105	7.71	93	6.72	-13	86	8.09	86	6.11	-24	10	0	0	
<i>Barringtonia lanceolata</i>	67	7.18	63	9.60	34	56	8.17	56	8.66	6	4	0	0	
<i>Chisocheton sarawakanus</i>	63	13.73	63	13.41	-2	55	15.17	55	12.50	-18	4	0	0	
<i>Cleistanthus contractus</i>	54	7.62	50	7.53	-1	48	7.03	48	6.82	-3	4	0	0	
<i>Dacryodes rostrata</i>	51	10.08	46	8.27	-18	43	9.80	43	7.62	-22	1	0	0	
<i>Dimorphocalyx muricatus</i>	238	7.24	238	10.72	48	212	7.46	212	10.68	43	50	6	31	***
<i>Dysoxylum cyrtobotryum</i>	60	14.96	56	13.90	-7	51	15.12	51	12.68	-16	7	0	0	
<i>Fordia splendidissima</i>	242	10.76	254	11.40	6	204	11.23	204	9.52	-15	30	1	3	**
<i>Gonystylus keithii</i>	60	13.49	61	16.95	26	51	12.83	51	14.49	13	2	0	0	
<i>Knema latericia</i>	54	12.04	59	10.70	-11	47	11.57	47	10.69	-8	2	0	0	
<i>Lithocarpus nieuwenhuisii</i>	42	12.77	32	19.38	52	31	13.35	31	19.18	44	5	0	0	
<i>Litsea caulocarpa</i>	101	17.24	120	24.48	42	78	18.79	78	19.33	3	7	0	0	
<i>Litsea ochracea</i>	49	15.51	46	13.76	-11	36	13.63	36	10.41	-24	8	0	0	*
<i>Lophopetalum beccarianum</i>	99	19.36	112	24.86	28	80	20.08	80	23.44	17	12	1	1	
<i>Madhuca korthalsii</i>	282	10.76	284	12.80	19	247	10.81	247	11.48	6	3	0	0	
<i>Mallotus penangensis</i>	93	12.82	115	15.40	20	83	12.92	83	13.06	1	3	0	0	
<i>Mallotus wrayi</i>	985	8.81	943	11.97	36	798	9.36	798	9.81	5	17	1	1	
<i>Maschalocorymbus corymbosus</i>	139	8.42	143	11.13	32	112	9.34	112	8.55	-8	4	0	0	
<i>Parashorea malaanonan</i>	48	15.28	44	13.22	-13	37	16.34	37	12.85	-21	20	1	1	*
<i>Pentace laxiflora</i>	79	22.07	73	22.88	4	63	24.65	63	20.04	-19	20	0	0	***
<i>Polyalthia cauliflora</i>	184	5.29	177	7.28	38	166	5.37	166	6.67	24	4	0	0	***
<i>Polyalthia rumphii</i>	62	12.29	63	12.91	5	56	12.04	56	9.87	-18	6	0	0	
<i>Polyalthia sumatrana</i>	90	15.19	84	17.36	14	77	15.07	77	17.16	14	2	0	0	
<i>Polyalthia xanthopetala</i>	122	8.78	111	9.82	12	81	10.08	81	7.92	-21	16	1	1	*
<i>Reinwardtiodendron humile</i>	76	6.16	61	5.14	-17	57	6.70	57	4.64	-31	34	1	2	
<i>Shorea fallax</i>	135	16.86	163	16.14	-4	112	17.48	112	12.46	-29	39	2	6	***
<i>Shorea johorensis</i>	47	42.37	43	32.75	-23	33	42.44	33	25.22	-41	45	2	31	***
<i>Shorea parvifolia</i>	56	48.63	59	42.76	-12	45	55.02	45	26.77	-51	85	20	81	***
<i>Syzygium elopuræ</i>	51	6.35	49	7.34	16	45	6.30	45	6.70	6	1	0	0	
<i>Syzygium tawaense</i>	37	14.60	34	18.92	30	29	12.82	29	16.36	28	3	0	0	
Totals:	4088		4056			3379		3379						
Weighted means:		11.43		13.43			11.83		11.17					

Table 33 continued:

Species	MP2													WIL
	all valid trees					pairs of growth rates								
	growth P1		growth P2		%ch	growth P1		growth P2		%ch	MWU			
	n	rgr	n	rgr	rgr	n	rgr	n	rgr	rgr	A	B	C	
<i>Alangium javanicum</i>	34	8.37	30	6.213	-26	25	8.29	25	6.52	-21	3	0	0	
<i>Antidesma neurocarpum</i>	34	2.919	30	4.927	69	27	2.56	27	3.47	36	8	0	0	
<i>Aporosa falcifera</i>	76	12.59	70	10.72	-15	62	14.19	62	9.28	-35	57	3	30	***
<i>Ardisia sanguinolenta</i>	272	11.86	270	9.568	-19	226	11.87	226	8.41	-29	92	28	92	***
<i>Baccaurea tetrandra</i>	84	8.598	75	8.656	1	72	9.20	72	8.02	-13	3	0	0	
<i>Barringtonia lanceolata</i>	62	3.624	57	4.35	20	56	3.67	56	4.07	11	2	0	0	
<i>Chisocheton sarawakanus</i>	53	10.08	42	9.574	-5	38	11.00	38	8.33	-24	7	0	0	
<i>Cleistanthus contractus</i>	169	6.651	162	10.24	54	149	6.23	149	8.73	40	33	1	4	***
<i>Dacryodes rostrata</i>	79	6.614	72	5.604	-15	71	6.01	71	5.61	-7	1	0	0	
<i>Dimorphocalyx muricatus</i>	429	4.432	407	6.407	45	384	4.54	384	6.04	33	64	6	56	***
<i>Dysoxylum cyrtobotryum</i>	69	19.96	66	17.62	-12	61	19.52	61	16.99	-13	8	1	1	
<i>Fordia splendidissima</i>	152	9.338	160	13.51	45	126	9.45	126	10.97	16	9	0	0	
<i>Gonystylus keithii</i>	44	8.419	40	10.05	19	38	9.30	38	9.30	0	2	0	0	
<i>Knema latericia</i>	74	12.38	81	14.6	18	70	12.82	70	15.80	23	6	0	0	
<i>Lithocarpus nieuwenhuisii</i>	52	17.34	38	16.6	-4	42	18.56	42	17.08	-8	4	0	0	
<i>Litsea caulocarpa</i>	96	15.22	95	15.14	-1	64	16.70	64	8.43	-50	91	28	90	***
<i>Litsea ochracea</i>	66	12.07	49	8.502	-30	46	12.51	46	7.55	-40	63	5	49	***
<i>Lophopetalum beccarianum</i>	101	11.21	109	12.87	15	94	11.43	94	10.47	-8	3	0	0	
<i>Madhuca korthalsii</i>	151	10.45	145	11.05	6	130	10.89	130	10.38	-5	0	0	0	
<i>Mallotus penangensis</i>	79	10.48	81	14.28	36	66	10.71	66	12.21	14	5	0	0	
<i>Mallotus wrayi</i>	796	9.462	780	11.09	17	655	10.01	655	9.27	-7	87	22	85	***
<i>Maschalocorymbus corymbosus</i>	106	7.994	100	8.134	2	80	8.21	80	6.61	-20	12	0	0	
<i>Parashorea malaanonan</i>	63	13.07	49	16.29	25	46	15.06	46	15.80	5	5	0	0	
<i>Pentace laxiflora</i>	84	20.06	72	18.17	-9	63	23.48	63	17.63	-25	36	2	14	***
<i>Polyalthia cauliflora</i>	87	4.409	81	5.031	14	76	4.82	76	4.20	-13	2	0	0	
<i>Polyalthia rumphii</i>	57	11.58	56	15.28	32	52	12.01	52	14.57	21	3	0	0	
<i>Polyalthia sumatrana</i>	102	15.77	102	16.97	8	89	15.87	89	15.78	-1	2	0	0	
<i>Polyalthia xanthopetala</i>	50	11.27	45	11.13	-1	33	12.66	33	8.35	-34	9	0	0	
<i>Reinwardtiodendron humile</i>	90	6.218	79	7.422	19	67	6.76	67	6.69	-1	3	0	0	
<i>Shorea fallax</i>	129	19.15	135	15.27	-20	99	22.46	99	12.59	-44	91	34	90	***
<i>Shorea johorensis</i>	35	32.97	29	25.19	-24	26	40.12	26	25.63	-36	15	0	0	***
<i>Shorea parvifolia</i>	68	39.79	45	30.39	-24	38	46.22	38	26.55	-43	39	2	8	***
<i>Syzygium elopuræ</i>	49	4.935	48	4.972	1	45	5.26	45	4.50	-15	10	1	1	
<i>Syzygium tawaense</i>	48	12.49	40	12.39	-1	35	13.94	35	11.30	-19	7	0	0	*
Totals:	3940		3740			3251		3251						
Weighted means:		10.71		11.16			11.04		9.74					

When defining significance with the Bonferroni procedure, rgr increased significantly in one species in each MP and decreased significantly in one (MP1) and six (MP2) species between period 1 and period 2. With the less conservative FDR procedure, three (MP1) and two (MP2) additional species showed a significant decline in growth rates. The Wilcoxon tests included six (one with positive, five with negative rgr-balance) additional species in MP1 and three (one positive, two negative) in MP2 at $P \leq 0.05$ (Table 33).

The only species that showed a consistent pattern across both MPs and U- and Wilcoxon-tests was *Dimorphocalyx muricatus*, growing significantly better in period 2 than in period 1. When only considering the FDR procedure, *Shorea fallax* and *S. parvifolia* decreased significantly in growth rates between periods in both MP1 and MP2 (Table 33).

4.2.7.2. 'Projected growth rates'

Including all valid rates, for each of the 34 most abundant species, linear regression was performed with relative growth rate of a period as the response variate and gbh at the start of a period as the explanatory variate (excluding again those trees with $\text{agr} < -4.0$ mm; due to the remaining slight negative rates, ln-transformation was not applied). The resulting regression lines showed that species' growth rates were (more or less) dependant on tree size (Figure 20 shows the relationships in period 1). Applying the tree-wise, within-species regressions on between-species regressions (i.e. predicting growth of a species in a period by applying the regression-equation of the species to gbh at the start of the same period) showed a highly significant fit (adjusted $R^2 > 0.985$; F probability < 0.001).

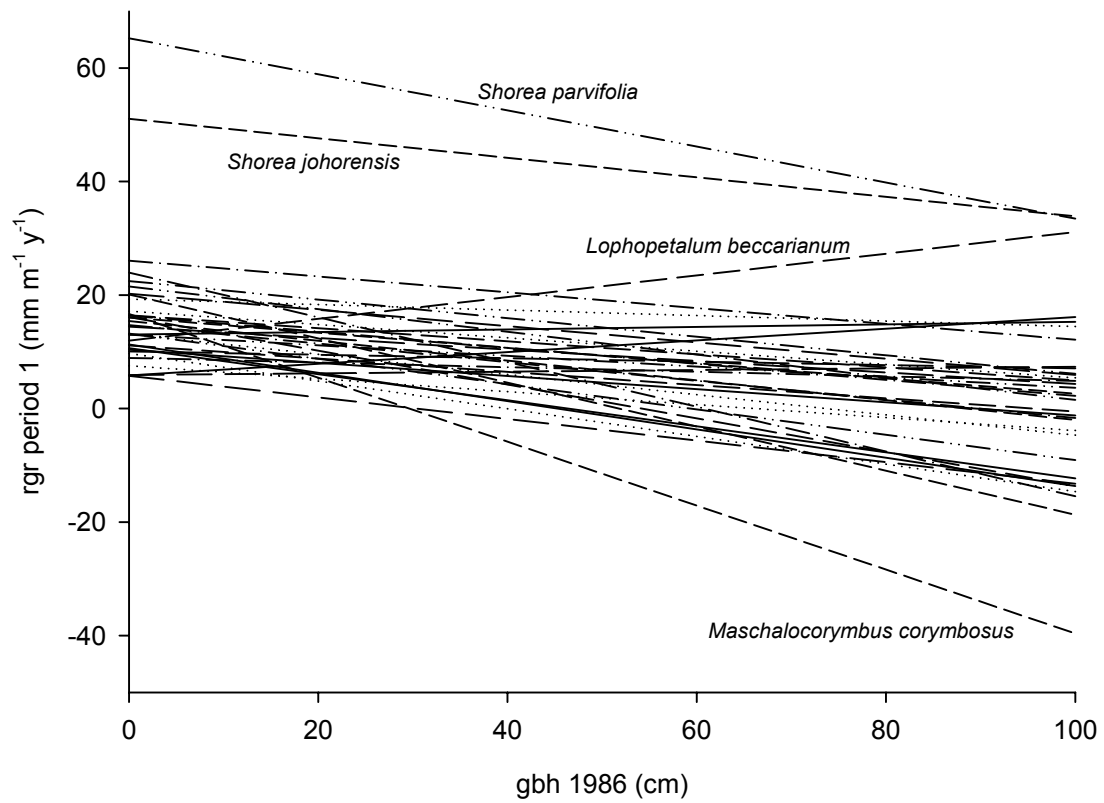


Figure 20: Regression lines of the relationships between growth and tree size within each of the 34 most abundant species in period 1, both MPs combined.

The derived species' regression equations of period 1 were used on the gbhs of every single tree measured in 1996 to predict rgr for period 2. The species-wise relationship of predicted *vs.* actual rgr in period 2 is shown in Figure 21.

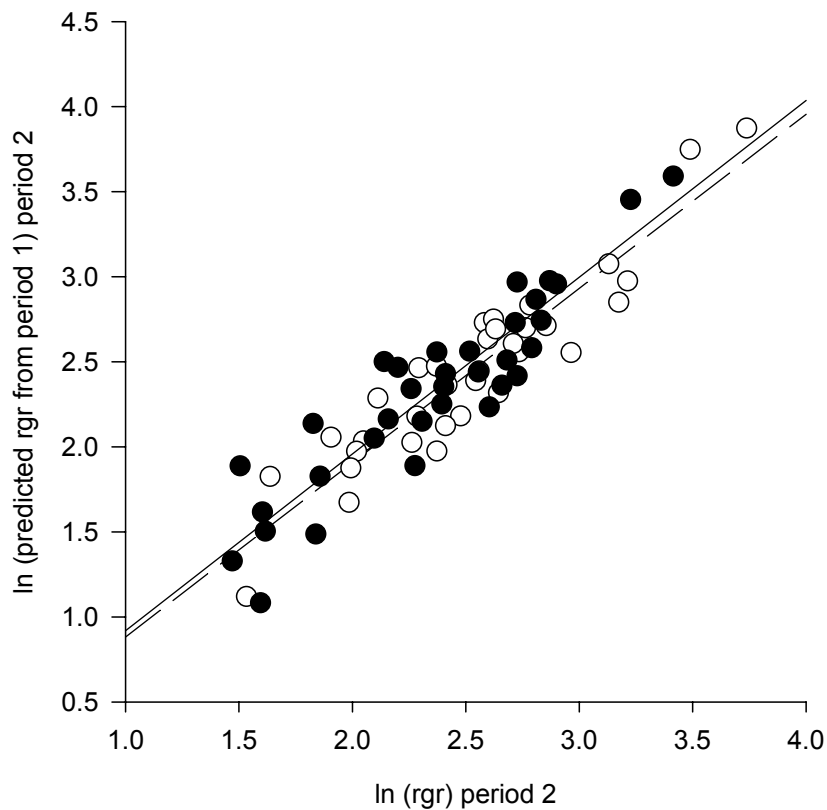


Figure 21: Relationship of predicted and actual relative growth rates of the 34 most abundant species (trees with reliable measurements) in period 2 for MP1 (open circles) and MP2 (closed circles); regression fit for MP1 (dashed line): adjusted $R^2 = 0.865$; F probability < 0.001 ; and for MP2 (solid line): adjusted $R^2 = 0.835$; F probability < 0.001 . Untransformed units were $\text{mm m}^{-1} \text{y}^{-1}$.

Across all 34 species investigated, actual rgr of period 2 was 15.9% and 6.2% above the predicted rates (percentage difference of weighted means) in MP1 and MP2, respectively (Table 34). The weighted means of relative growth rates predicted for period 2 were slightly different from rgr in period 1: +1.4% in MP1 and -1.9% in MP2.

The predicted rates of period 2 were compared with those calculated from the actual measurements in 1996 and 2001 to assess any differences in growth between the periods with Wilcoxon-Matched-Pairs tests (Table 34). With this approach, five species showed a consistent pattern across both main plots: *Aporosa falcifera*, *Baccaurea tetrandra*, *Litsea ochracea*, and *Shorea fallax* had actual relative growth rates in period 1 that were significantly below (by 0.5% - 30.3%) the expected values if growth would have continued at the same pace as in period 1. *Dimorphocalyx muricatus* exceeded the predicted rgr by 48.7% (MP1) and 42.2% (MP2), i.e. grew better than expected.

Increased rgr was also shown by *Lophopetalum beccarianum* in MP1 (26.9%) and by *Cleistanthus contractus* in MP2 (47.2%), the latter species also showed a trend towards better rgr in MP1 (4.6%). The growth in period 2 of *Shorea johorensis* and *S. parvifolia* in MP1 and *Ardisia sanguinolenta*, *Dacryodes rostrata*, *Dysoxylum cyrtobotryum* and *Litsea caulocarpa* in MP2 was poorer (by 1.2% – 31.8%) than expected, with *S. johorensis* and *D. rostrata* expressing trends in the same direction in the respective other main plot (-22.9% and -16.0%, respectively). For *A. sanguinolenta* and *L. caulocarpa*, growth in MP1 showed a trend in the opposite direction as in MP2, where these species were growing better than expected (by c. 38%). Six more species showed trends towards better or poorer growth than expected in either one or both MPs, including the most abundant overall species *Mallotus wrayi*, with a trend of better-than-expected rgr in MP1 (34.3%) and MP2 (15.3%) (Table 34).

When combining both MPs, eight species had actual rgrs that were significantly lower than those from the predictions: *Alangium javanicum*, *Dacryodes rostrata*, *Shorea johorensis*, *S. fallax*, *S. parvifolia*, *Aporosa falcifera*, *Baccaurea tetrandra* and *Litsea ochracea*. Three species exceeded the predicted values: *Antidesma neurocarpum*, *Dimorphocalyx muricatus* and *Ardisia sanguinolenta*. *Chisocheton sarawakanus* and *Dysoxylum cyrtobotryum* showed a trend of poorer and *Lophopetalum beccarianum*, *Mallotus penangensis* and *Pentace laxiflora* of better growth than predicted. Three of the four dipterocarps (all of the genus *Shorea*) present in the most abundant subset therefore decreased in growth in the second period (*Parashorea malaanonan*, the fourth dipterocarp, did have increased rgr, but not significantly so). Five of the seven euphorbs in the subset showed at least a trend towards different growth between the periods: two species with poorer, three with better growth in period 2 (the remaining two species, *Cleistanthus contractus* and *Mallotus wrayi*, both showed (insignificantly) increased rgr, too).

Table 34: Comparisons of predicted (pred) with actual (act) relative growth rates (rgr; $\text{mm m}^{-1} \text{y}^{-1}$) in period 2 for the 34 most abundant species in MP1 and 2 at Danum. Numbers of trees used for calculations and the resulting growth rates are shown and differences between rates are given as percentage of actual rgr in relation to predicted rgr (diff (%)); P-values of Wilcoxon-Matched-Pairs tests are shown and significance is indicated by stars as: $P \leq 0.05$: *, $P \leq 0.02$: **, $P \leq 0.001$: ***. Species with a significant ($P \leq 0.05$) difference between actual and predicted rgr across both MPs pooled are given in bold type.

Species	MP1					MP2				
	rgr period 2		n trees	diff(%)	P	rgr period 2		n trees	diff(%)	P
	act	pred				act	pred			
Alangium javanicum	7.76	7.65	30	1.4	0.2710	6.21	8.48	-26.7	0.0667	
Antidesma neurocarpum	6.04	3.07	40	96.9	0.0514	4.93	2.95	66.8	0.1094	
Aporosa falcifera	10.49	11.76	73	-10.8	0.0250	10.72	12.90	-16.9	0.0163	
Ardisia sanguinolenta	14.06	10.16	174	38.5	0.0993	9.57	11.79	-18.8	0	
Baccaurea tetrandra	6.72	7.82	93	-14.0	0.0158	8.66	8.70	-0.5	0.0151	
Barringtonia lanceolata	9.60	7.58	63	26.6	0.6708	4.35	3.78	15.2	0.2385	
Chisocheton sarawakanus	13.41	13.93	63	-3.7	0.2394	9.57	10.40	-7.9	0.0504	
Cleistanthus contractus	7.53	7.19	50	4.6	0.0594	10.24	6.60	54.8	0.0252	
Dacryodes rostrata	8.27	9.84	46	-16.0	0.0678	5.60	6.60	-15.2	0.0082	
Dimorphocalyx muricatus	10.72	7.21	238	48.7	0.0050	6.41	4.42	44.8	0.0218	
Dysoxylum cyrtobotryum	13.90	14.78	56	-6.0	0.3702	17.62	19.61	-10.2	0.0410	
Fordia splendidiissima	11.40	10.63	254	7.2	0.0889	13.51	9.34	44.6	0.1051	
Gonystylus keithii	16.95	13.57	61	24.9	0.6276	10.05	8.58	17.0	0.8264	
Knema latericia	10.70	11.87	59	-9.9	0.0636	14.60	12.30	18.6	0.6871	
Lithocarpus nieuwenhuisii	19.38	12.86	32	50.7	0.1776	16.60	17.58	-5.5	0.3728	
Litsea caulocarpa	24.48	17.29	120	41.6	0.0503	15.14	15.33	-1.2	0.0060	
Litsea ochracea	13.76	15.66	46	-12.1	0.0351	8.50	12.19	-30.3	0.0029	
Lophopetalum beccarianum	24.86	19.59	112	26.9	0.0082	12.87	11.48	12.2	0.7748	
Madhuca korthalsii	12.80	10.90	284	17.4	0.9318	11.05	10.54	4.9	0.1627	
Mallotus penangensis	15.40	12.92	115	19.2	0.1871	14.28	10.62	34.5	0.1869	
Mallotus wrayi	11.97	8.86	943	35.1	0.0646	11.09	9.50	16.7	0.0520	
Maschalocorymbus corymbosus	11.13	8.37	143	33.1	0.1064	8.13	7.77	4.7	0.1312	
Parashorea malaanonan	13.22	15.34	44	-13.9	0.1228	16.29	13.22	23.2	0.3633	
Pentace laxiflora	22.88	21.67	73	5.6	0.3521	18.17	19.24	-5.6	0.0963	
Polyalthia cauliflora	7.28	5.33	177	36.5	0.0657	5.03	4.50	11.8	0.4040	
Polyalthia rumphii	12.91	11.54	63	11.9	0.4644	15.28	11.22	36.1	0.2785	
Polyalthia sumatrana	17.36	15.06	84	15.3	0.5328	16.97	15.55	9.1	0.6133	
Polyalthia xanthopetala	9.82	8.85	111	10.9	0.2901	11.13	11.36	-2.0	0.3075	
Reinwardtiodendron humile	5.14	6.21	61	-17.2	0.1805	7.42	6.22	19.3	0.9206	
Shorea fallax	16.14	16.99	163	-5.0	0.0021	15.27	19.46	-21.5	0	
Shorea johorensis	32.75	42.48	43	-22.9	0.0225	29	31.61	-20.3	0.0837	
Shorea parvifolia	42.76	48.15	59	-11.2	0.0349	30.39	36.28	-16.2	0.2340	
Syzygium elopurae	7.34	6.52	49	12.5	0.6430	4.97	5.04	-1.4	0.7488	
Syzygium tawaense	18.92	14.88	34	27.1	0.8793	12.39	12.96	-4.4	0.2826	
Totals:			4056			3740				
Weighted means:	13.43	11.59		15.9		11.16	10.51	6.2		

4.3. Growth and mortality of commercial timber species

Thirty-eight dipterocarp-species that occurred in the Danum main plots (excluding two *Shorea spp.* of distinct, but unknown species) were placed into (wood-density-based) timber-groups according to Newman *et al.* (1996, 1998): light hardwoods (LH) included mainly *Shorea spp.* from the 'meranti'-series and *Parashorea spp.* ('white seraya'); medium and heavy hardwoods were combined (MHH) and included *Shorea spp.* from the 'selangan batu'-series and *Dipterocarpus spp.* from the 'keruing'-series (Table 35). All remaining species were placed into 'other timber' (OTH) which is – because of usually small size and poor form – not commercially logged (Newman *et al.* 1998).

Table 35: Classification of 38 dipterocarp-species from the Danum main plots into timber-groups (LH: light hardwoods; MH: medium hardwoods; HH: heavy hardwoods; MHH: combined MH and HH; OTH: other timber) with tree numbers in 2001 (n 2001).

Species	n 2001	Timber group
<i>Anisoptera costata</i>	8	LH
<i>Parashorea malaanonan</i>	119	LH
<i>Parashorea tomentella</i>	6	LH
<i>Shorea agamii</i>	5	LH
<i>Shorea angustifolia</i>	40	LH
<i>Shorea argentifolia</i>	48	LH
<i>Shorea fallax</i>	376	LH
<i>Shorea gibbosa</i>	2	LH
<i>Shorea johorensis</i>	138	LH
<i>Shorea laxa</i>	3	LH
<i>Shorea leprosula</i>	38	LH
<i>Shorea macrophylla</i>	2	LH
<i>Shorea macroptera</i>	10	LH
<i>Shorea parvifolia</i>	162	LH
<i>Shorea parvistipula</i>	7	LH
<i>Shorea pauciflora</i>	72	LH
<i>Shorea pilosa</i>	103	LH
<i>Shorea smithiana</i>	2	LH
<i>Shorea symingtonii</i>	13	LH
<i>Dipterocarpus acutangulus</i>	3	MHH (MH)
<i>Dipterocarpus caudiferus</i>	3	MHH (MH)
<i>Dipterocarpus kerrii</i>	65	MHH (MH)
<i>Shorea atrinervosa</i>	23	MHH (HH)
<i>Shorea falciferoides</i>	4	MHH (HH)
<i>Shorea seminis</i>	2	MHH (HH)
<i>Shorea superba</i>	3	MHH (HH)
<i>Hopea nervosa</i>	129	OTH
<i>Vatica albiramis</i>	3	OTH
<i>Vatica dulitensis</i>	89	OTH
<i>Vatica micrantha</i>	5	OTH
<i>Vatica oblongifolia</i>	6	OTH
<i>Vatica oblongifolia ssp. multinervosa</i>	1	OTH
<i>Vatica sarawakensis</i>	24	OTH
<i>Vatica sp.</i>	1	OTH
<i>Vatica species a</i>	0	OTH
<i>Vatica species b</i>	1	OTH
<i>Vatica umbonata</i>	11	OTH
<i>Vatica vinosa</i>	2	OTH
Total (2001):	1529	

Within the dipterocarps, LH were the dominating group (c. 80% in 1986), but as their tree numbers decreased in both periods (by c. -6% and -8%, respectively) their contribution declined over the years (to c. 75% in 2001), mainly to the benefit of OTH (c. 14% in 1986 to c. 18% in 2001). MHH proportion was with c. 6% – 7% similarly low at all three enumerations (Table 36). Both MHH and OTH were still increasing in absolute numbers in period 1 (by c. 4% and c. 15%, respectively), but decreased slightly (< 3%) in period 2 (Table 36).

The contribution of LH to all dipterocarps increased with increasing size class, reaching 86% – 87% for the large (≥ 100 cm gbh) trees (Table 36). The proportions of MHH were not very different between size classes (5% – 7%). The observed loss of contributions in all trees of LH in favour of OTH is mainly attributable to a shift in proportions of small trees: whereas tree numbers of LH decreased across the enumerations, those of OTH increased in the first period and remained constant in the second. This led to an increase of the relative contribution of OTH to the small tree size class from 15% in 1986 to 20% in 1996 and to 22% in 2001 (Table 36).

Table 36: Tree numbers (at the start of a period and trees valid for growth calculations in a period) of dipterocarp-species within timber-groups.

		Timber-group		
		LH	MHH	OTH
n ₈₆	all	1334	102	241
	small	994	82	192
	medium	147	9	29
	large	193	11	20
n ₉₆	all	1250	106	276
	small	834	82	225
	medium	200	13	25
	large	208	11	22
n ₀₁	all	1154	103	272
	small	744	78	226
	medium	173	12	18
	large	222	13	21
n valid period 1	all	823	83	172
	small	623	72	135
	medium	109	5	24
	large	91	6	13
n valid period 2	all	806	82	201
	small	591	68	174
	medium	139	9	13
	large	76	5	14

Light hardwoods had the highest mortality rates of all timber groups: 2.94% y^{-1} and 3.79% y^{-1} in periods 1 and 2, respectively (Figure 22a). Mortality of MHH, which was low in period 1 (0.62% y^{-1}) increased relatively even more in period 2 (1.66% y^{-1}). Remarkably, mortality of OTH did not increase in period 2, instead, there was hardly any change (period 1: 2.37% y^{-1} ; period 2: 2.36% y^{-1}). Recruitment was highest for OTH in period 1 (3.17% y^{-1}), but in period 2 (1.88% y^{-1}), this rate dropped close to that of LH, which was similar in both periods (1.80% y^{-1} and 1.89% y^{-1} for periods 1 and 2, respectively). Also, recruitment rate of MHH hardly changed between period 1 (0.96% y^{-1}) and period 2 (0.99% y^{-1}) (Figure 22a). Consequently, turnover of MHH showed low ($< 1.5\%$), that of LH and OTH high ($\geq 1.5\%$) dynamics.

Absolute growth rates of LH (period 1: 11.14 mm y^{-1} ; period 2: 9.93 mm y^{-1}) were *c.* 2.2 – 2.5-fold that of MHH and OTH in both periods (Figure 22b). The difference was less pronounced for relative growth rates and here, rates of OTH were slightly higher than those of MMH (Figure 22b).

Mortality rates of LH increased in all size classes and the raise was becoming more pronounced with increasing size class (Figure 23a). Those rates of MHH did increase nearly 3-fold in small trees, but no trees ≥ 50 cm gbh died in either period. The group of OTH had lower m_a in period 2 than in period 1 in small (*c.* -27%) and large (*c.* -12%) size classes, but mortality of medium sized trees increased more than 7-fold to 5.19% y^{-1} in period 2 (Figure 23a).

Relative growth rate within size classes showed that the lead of LH was only true for trees < 100 cm gbh (most pronounced for medium trees in period 2): in the large size class, LH growth rates were similar to those of MHH (Figure 23b). Growth was increasing between the periods in all size classes (but not evenly strong, range: *c.* 1% – 59%) except for small trees in LH and medium trees in MHH, where rgr decreased by 22% and 52%, respectively (Figure 23b).

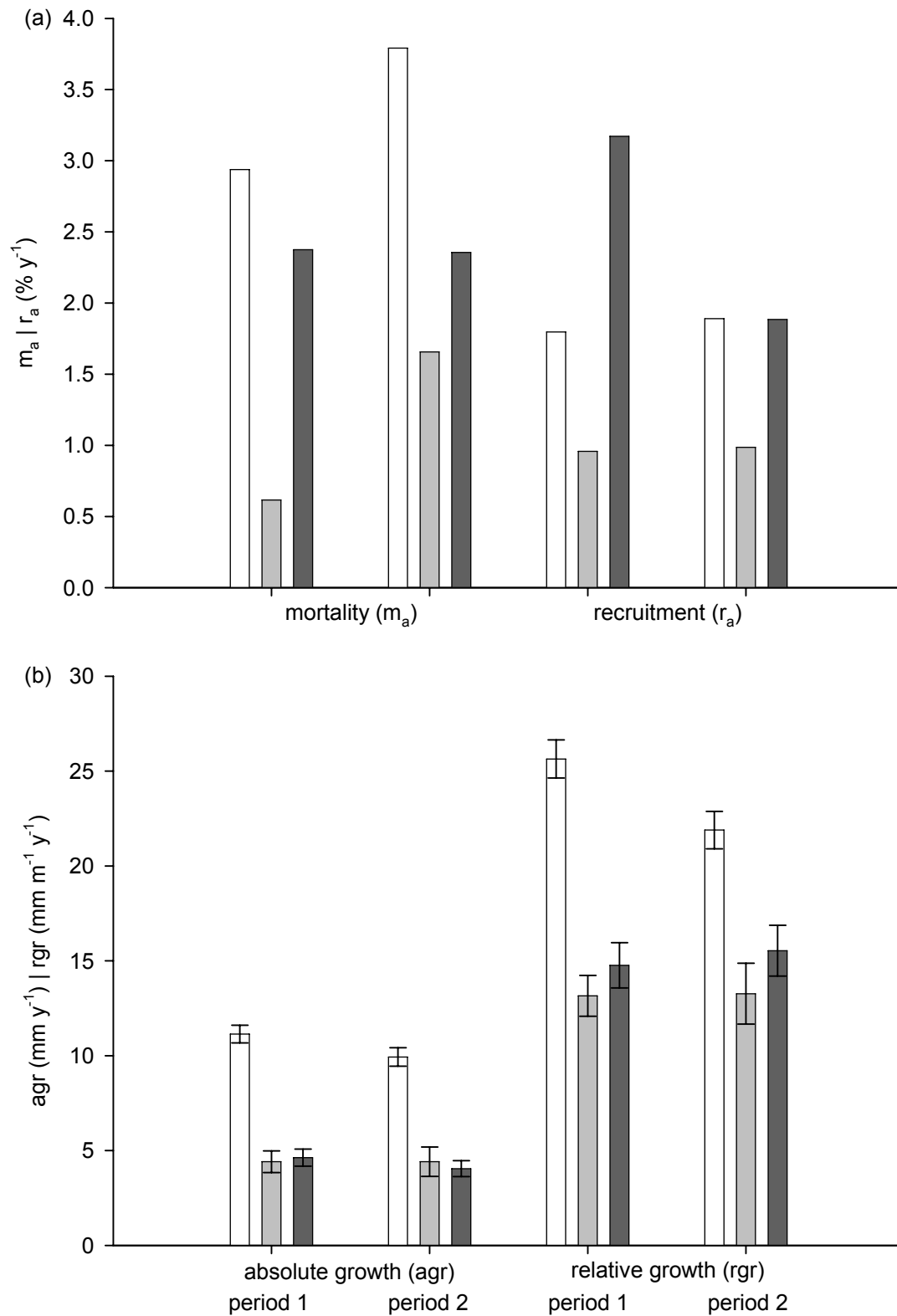


Figure 22: Growth and mortality of dipterocarp-species within timber-groups: mortality and recruitment rates (a), absolute and relative growth rates (\pm SE) (b) for periods 1 and 2 are shown for LH (open bars), MHH (light grey bars) and OTH (dark grey bars).

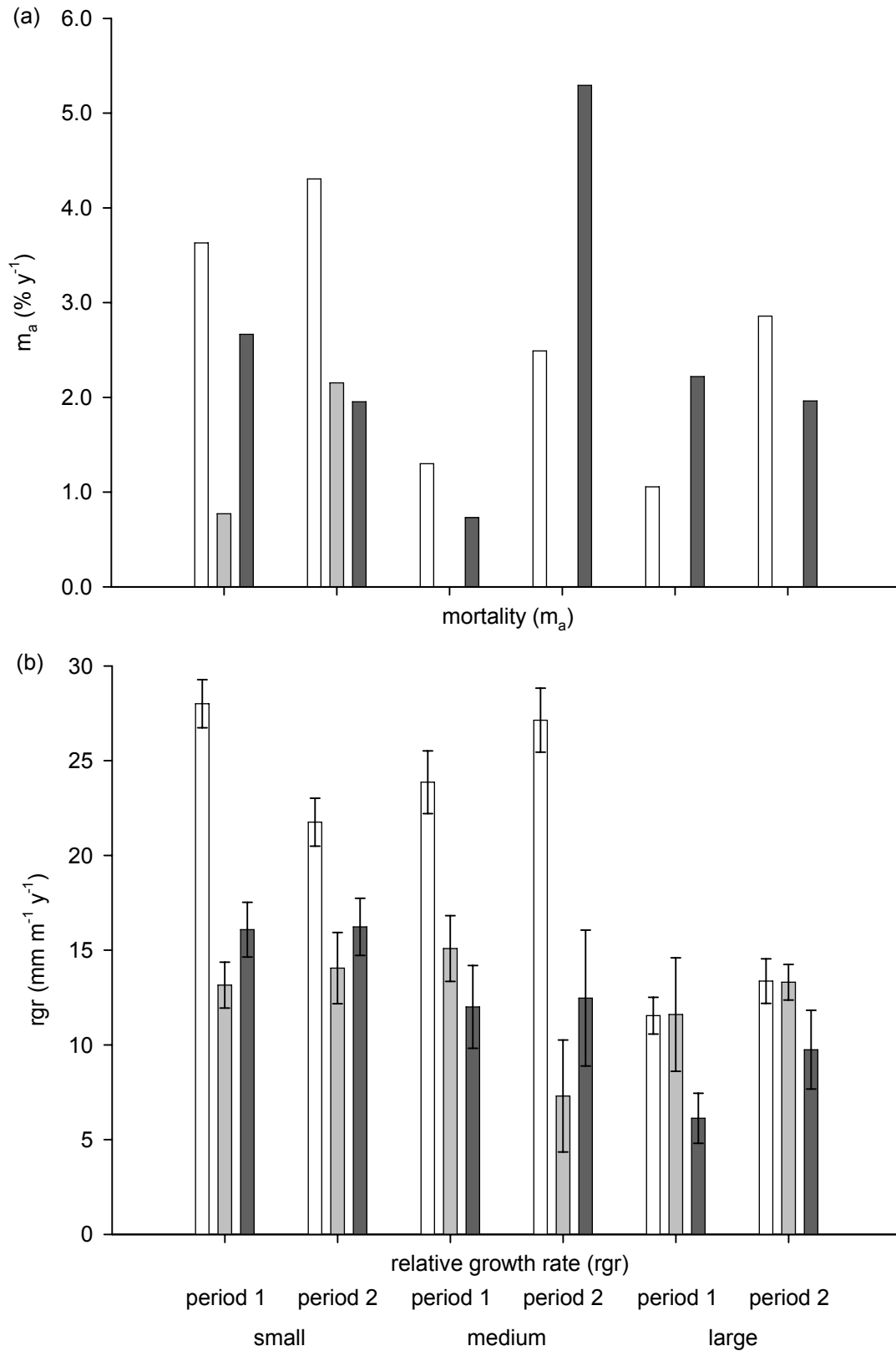


Figure 23: Growth and mortality of dipterocarp-species within timber-groups for size classes: mortality rates (a), relative growth rates (\pm SE) (b) for small (10 – < 50 cm gbh at start of interval), medium (50 – < 100 cm gbh) and large (\geq 100 cm gbh) in periods 1 and 2 are shown for LH (open bars), MHH (light grey bars) and OTH (dark grey bars).

5. Possible lagged effect of drought in the understory

5.1. Structure

After applying the necessary restrictions regarding sample area, tree sizes, regressors and recruits to the data set (see Methods, V.3.3.), the subset of small trees (10 – < 50 cm gbh) within the PEPs was composed of 5190 trees in 1986, 4239 in 1996, 3885 in 1999 and 3706 in 2001. Small trees represented *c.* 91% of all trees in 1986 and *c.* 86% at the other three enumerations. During period 1, 741 small trees died, 237 during period 2a and 213 during period 2b, so that the original population in 1986 lost *c.* 23% of its trees by 2001 through mortality. A further *c.* 6% (293 trees) was lost to the small trees' subset either through trees regressing < 10 cm gbh or through trees advancing \geq 50 cm gbh.

Mean density and mean basal area in 1986 was similar to that of the main plots, but due to the missing recruits, tree numbers and basal area steadily declined (Table 37). The 16 PEPs had on average 266 small trees (range: 169 - 386) each.

Table 37. Densities of alive (n) and of dead trees (n_d) and basal area (BA) in the PEPs at Danum 1986 - 2001 for small trees (10 cm – < 50 cm gbh).

	1986	1996	1999	2001
n_d (ha^{-1})	n.a.	290	93	83
n (ha^{-1})	2027	1656	1518	1448
BA ($m^2 ha^{-1}$)	6.98	6.61	6.13	6.05

5.2. Floristic composition

Twelve trees had to be excluded because they were of unknown species in 1986, whereas in all following enumerations only one tree each had to be excluded. The subset represented 299 species in 1986. Nineteen, five and again five species were lost in 1996, 1999 and 2001 respectively, leading to 270 species in 2001. Hereby – contrary to the 'all trees' population – the loss of species to this size class of small trees could be due to all individuals of a species (i) dying, (ii) regressing < 10 cm gbh, (iii) advancing \geq 50 cm gbh or (iv) a combination of these outcomes. The maximum number of individuals present before a species disappeared (i.e. was lost completely within a period) was three.

Eighty-three of the 270 species of 2001 did not lose stems between the first and

the last enumeration, 60 species lost < 25%, 63 species 25% – 50% and 93 species \geq 50% of their stems (21 species of the latter had one individual only).

The counts for species with \geq 5 individuals were 161, 140, 133 and 124 at the four successive enumerations.

Euphorbiaceae was the most abundant family, followed by Annonaceae. Dipterocarpaceae, the second-ranked family of all trees in the main plots in 1986, was at fifth rank within small trees (at all enumerations). *Mallotus wrayi* was the most numerous species (14% – 15% of small trees), followed by *Dimorphocalyx muricatus* (5% – 6%) (at all enumerations).

Forming a list of most abundant species within the small trees subset with $n \geq$ 50 trees in 1986 resulted in 22 species (see most abundant small species, Table 42).

5.3. Fate of trees

Data, collected at the 1996, 1999 and 2001 enumerations, of the status of alive trees, of those trees that were found dead and of the condition of the stem (at PoM) were investigated for indications of possible increased damage after the 97/98 drought. As these categories had not been defined strictly, were sometimes difficult to assess (e.g. 'AB' – crown damage of larger trees was not easily visible where the understorey was dense) and were gathered by three different persons, the results might be influenced by the observers' subjectivity and not be directly comparable and thus have to be treated with caution. However, they may still supply valuable additional information.

The proportions of undamaged and damaged living trees were consistent between 1996 and 2001. In 1999, fewer trees were classified as being damaged. The status of dead trees (which was more clearly recognizable) changed very much: the proportion of trees found dead standing in 1999 was 7-fold that of 1996. In 2001, more than half of the dead trees were damaged, possibly including many of those trees that were still standing in 1999 (given that 'dead standing' was not interpreted differently in 1999). If irregular stems (the most difficult to assess) were taken as undamaged, there would not be much change in the proportion of 'OK'-trees. The decline and rise of damaged stems is rather unexpected and is thought to be due to the different interpretation of the criteria. But the

proportion of trees that were obstructed or damaged by lianas should not have been subject to individual interpretations by the observers and reveals an interesting steady increase of liana-affected trees from 1996 to 2001, possibly indicating an overall increase in abundance of lianas (Table 38).

Table 38: Proportions of healthy and of damaged trees in the Danum MPs 1996-2001, based on tree status and condition of stem categories (for explanations of tree codes see Table 1).

Category	1996	1999	2001
<u>Status alive</u>			
n	17643	5276	16964
apparently undamaged (AA) (%)	92.2	96.1	92.4
alive damaged (AB, AC, AD, AH, AL, AU) (%)	7.8	2.7	7.6
<u>Status dead</u>			
n	2655	338	1938
dead damaged (DB, DA, DU) (%)	46.1	26.0	54.6
dead missing (DM, DN) (%)	48.1	33.4	32.2
dead standing (DS) (%)	5.8	40.5	13.1
<u>Condition of stem</u>			
n	17389	5276	16744
undamaged (OK) (%)	97.0	93.3	86.9
irregular (DI, DF) (%)	0.5	4.2	5.6
damaged (DC, DE, DH, DS, PB, PD, PS, TE) (%)	1.5	0.7	2.7
liana (DL, LE, LF, LO) (%)	0.8	1.8	3.8
buttress (BJ, BO) (%)	0.2	n.a.	1.1

5.4. Mortality

Mean mortality rates, i.e. for all trees across the PEPs – regardless of any groups – pooled together, were calculated in the form of four different rate types (respectively variations) and are given in Table 39.

5.4.1. Simple mortality rates across all trees

Both true annual mortality (m_a) and the exponential mortality coefficient (λ) increased substantially by *c.* 41% and *c.* 35% respectively in period 2a compared to period 1 and less pronounced by *c.* 7% and *c.* 3% in period 2b compared to period 2a (Table 39).

5.4.2. Overall average mortality with species as groups

Considering the dependency of mortality rates on time interval length when mortalities of the population are not homogeneous, the equation for the overall average mortality rate (m_{all}) was applied to all periods respectively.

The calculation of m_{all} – across all trees and subplots, but with species as groups – resulted in slightly lower mortality rates compared to m_a (Table 39). The decline of m_{all} for each of the three periods, when calculated with $t = 1$ y to $t = 15$ y, was rather small, especially for period 1 (Figure 26).

The underlying distribution of m_a was strongly right skewed, where 48% to 68% of the species had zero mortality and 1.1% to 2.3% of the species died out completely (i.e. lost all of their individuals) (Figure 24). The distributions of m_a in periods 2a and 2b were significantly different from that of period 1 (chi-squared goodness-of-fit test; $\chi^2 = 31.06$, $df = 6$, $P < 0.001$ and $\chi^2 = 46.51$, $df = 6$, $P < 0.001$, respectively) while distributions of periods 2a and 2b were not significantly different from each other ($\chi^2 = 4.20$, $df = 6$, $P = 0.650$).

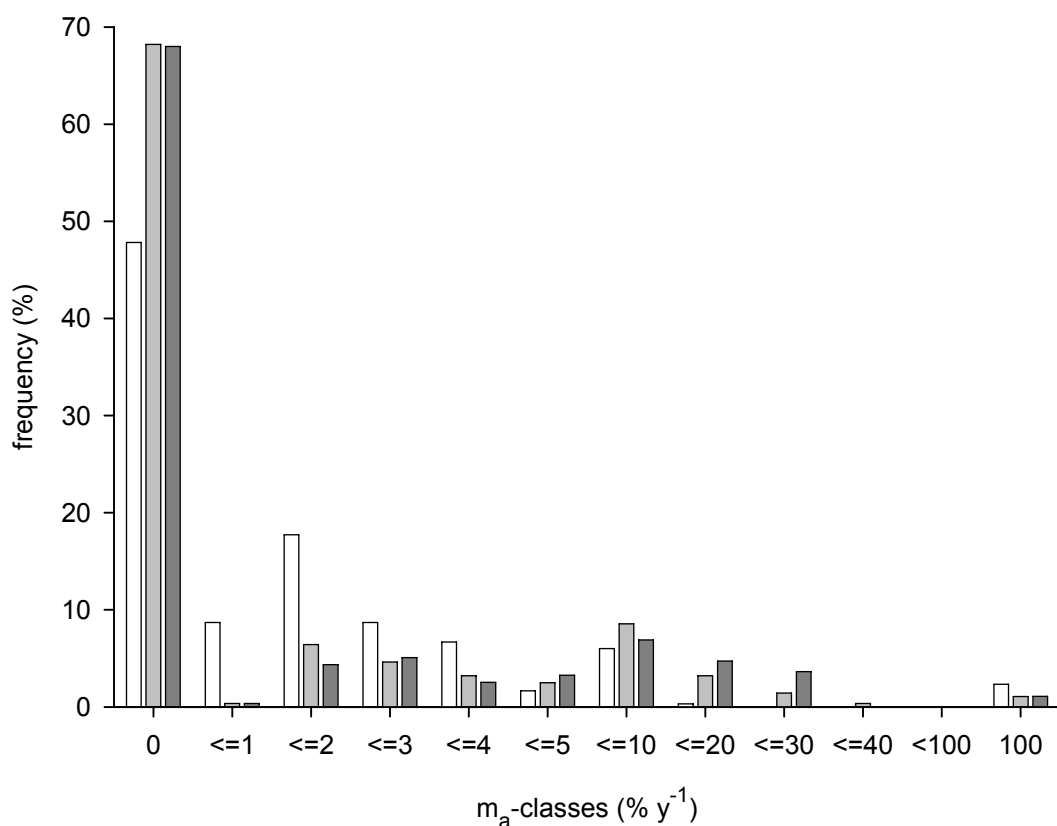


Figure 24. Relative frequency distributions of m_a within species for periods 1 (open bars), 2a (light grey bars) and 2b (dark grey bars) in the PEPs at Danum.

With period 1 being four times as long as periods 2a and 2b, individual species were more likely to lose individuals and therefore show mortality rates > 0 . In period 1, hence, the proportion of species with zero mortality was lower, while more species had $m_a > 0 \leq 4\% \text{ y}^{-1}$ compared to periods 2a and 2b.

The 'dynamic diversity' (or community-wide variance in mortality rates; *sensu* Sheil & May (1996)) gave mortality rate SDs of 1.94%, 2.53% and 2.85% for periods 1, 2a and 2b respectively.

Setting the time interval to $t = 5 \text{ y}$, i.e. handling the three periods as if their intervals had been 5 y, yielded a higher m_{all} for period 1 and lower m_{all} for periods 2a and 2b compared to m_a (Table 39, Figure 26).

Table 39. Simple mean (across all species and subplots) mortality rates and overall average (with species as groups) mortality rate calculations for periods 1, 2a and 2b in the PEPs at Danum.

Mortality rate type	Mortality rate ($\% \text{ y}^{-1}$)		
	Period 1	Period 2a	Period 2b
true annual mortality (m_a)	1.53	2.17	2.32
exponential mortality coefficient (λ) ^a	1.54	2.08	2.16
overall average mortality (m_{all})	1.51	2.16	2.31
overall average mortality at $t = 5 \text{ y}$ (m_{all_t5})	1.57	2.06	2.18

^a to calculate λ , n_t was obtained by subtracting n_d from n_0

Using the proposed variable for an interval correction (n_{min} ; see V.5.4.4. below) was not feasible here as the lines for $n_{\text{min}} = 1, 2$ and 3 lay very close together (Figure 26): exclusion of species with only one or two individuals did not change the distribution of m_a much (Figure 25) (chi-squared goodness-of-fit tests showed no significant differences between the distributions of m_a with $n_{\text{min}} = 1, 2$ and 3 within each period except for P1 with $n_{\text{min}} = 1$ compared to $n_{\text{min}} = 3$ ($\chi^2 = 15.81$, $df = 5$, $P = 0.015$; but with low n in the higher classes)).

Figure 26 also shows the discrepancy between m_a and m_{all} : the longer the time interval, the more is m_a affected by the heterogeneity of the population with different mortality rates between groups (here: species), i.e. the more it is deviating from the declining curve of m_{all} (0.02% in period 1, 0.01% in periods 2a and 2b).

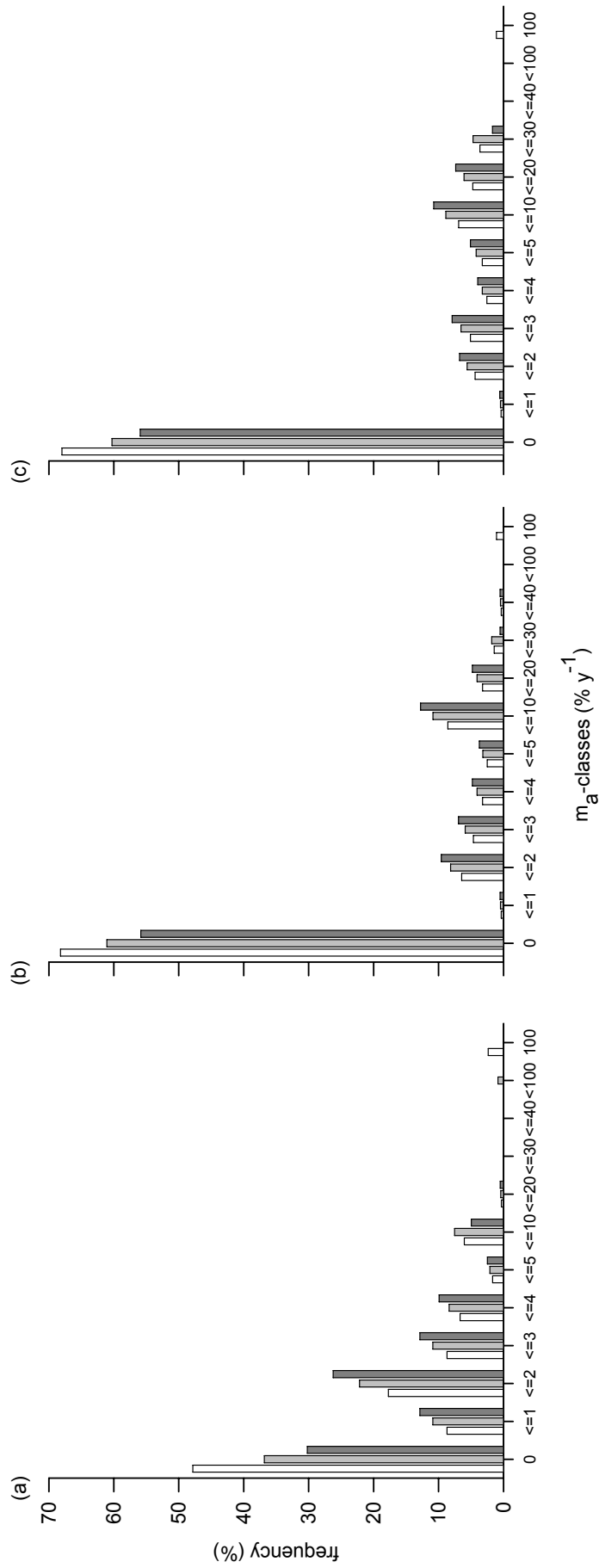


Figure 25. Relative frequency distributions of mortality (m_a) among species for periods 1 (a), 2a (b) and 2b (c) showing the effect of exclusion of rare species: all species included (white bars), species with one individual only excluded ($n_{\min} = 2$; light grey bars) and species with one and two individuals only excluded ($n_{\min} = 3$; dark grey bars).

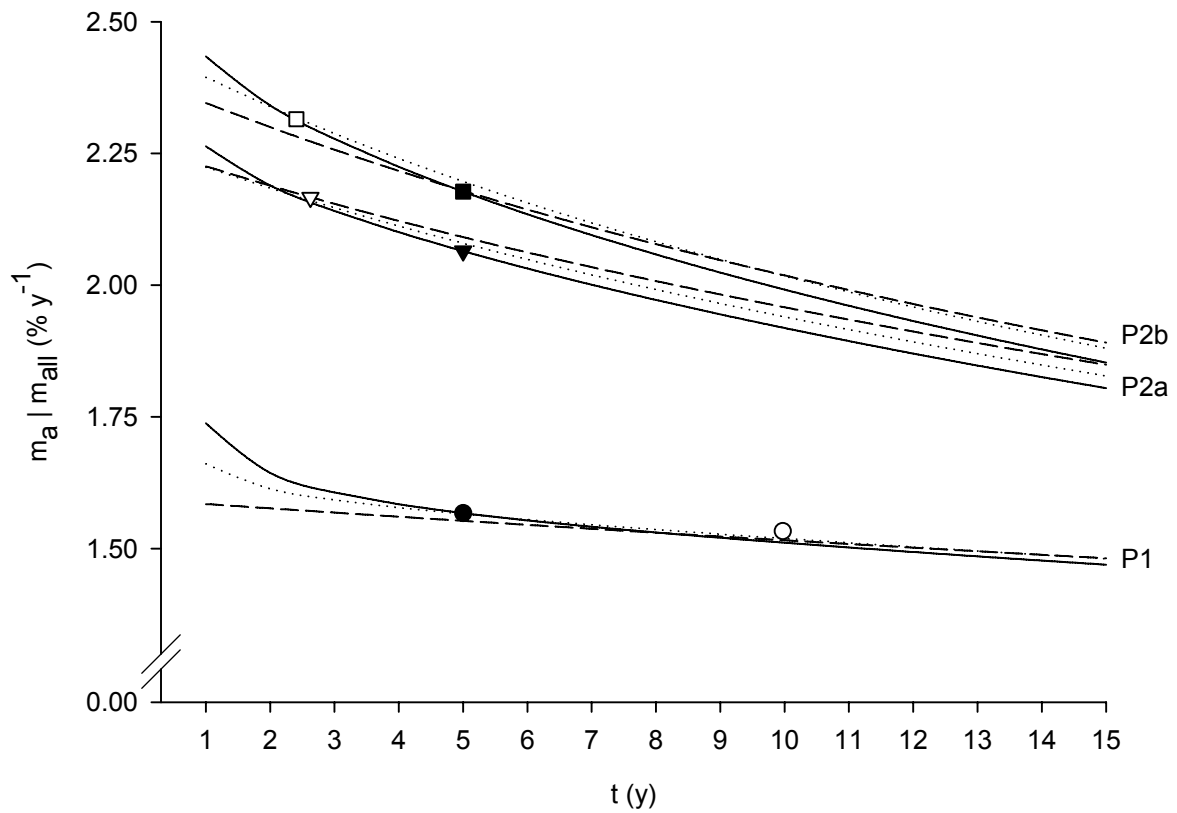


Figure 26. Mortality rates in PEPs: m_{all} with species as groups for $t = 1 - 15$ y (lines) with $n_{min} = 1$ (solid lines), $n_{min} = 2$ (short dashed lines) and $n_{min} = 3$ (long dashed lines), m_a (open symbols) and m_{all} at $t = 5$ y (filled symbols) for periods 1, 2a and 2b.

5.4.3. Overall average mortality with species within subplots as groups

The concept of mortalities at the group level was followed further by examining m_a with species within subplots as groups and calculating m_{all} .

The calculation of simple m_a within the 16 PEPs gave mean values (weighted by n_{start} ; \pm SE) of $1.54 \pm 0.10\% \text{ y}^{-1}$ for period 1, $2.17 \pm 0.12\% \text{ y}^{-1}$ for period 2a and $2.32 \pm 0.27\% \text{ y}^{-1}$ for period 2b.

Using each species' individual subplot m_a and t in the calculation, m_{all} (\pm SE) at all enumerations was slightly lower compared to m_a : period 1: $1.51 \pm 0.10\% \text{ y}^{-1}$; period 2a: $2.16 \pm 0.12\% \text{ y}^{-1}$; period 2b: $2.30 \pm 0.27\% \text{ y}^{-1}$. In addition to the inclusion of heterogeneous subpopulations, slight differences compared to m_a came through the exclusion of uncertain taxa for the calculation of m_{all} .

Dynamic diversity for this community under the prevailing conditions was (mortality rate SD) 6.12% in period 1, 5.12% in period 2a and 5.27% in period 2b, pointing to a relatively large (*c.f.* V.5.4.2. Overall average mortality with species as groups only) decline of m_{all} across time (1 – 15 y) and thus indicating that the variability in mortality rates was higher with species within subplots as groups than when the groups were formed with species alone (Figure 28, at $n_{min} = 1$).

5.4.4. Interval-corrected overall average mortality

To explore the suggested time interval correction to the data set with the proposed variable – the minimum number of individuals per species –, m_{all} and its SE was found for a range of $t = 1 \text{ y}$ to $t = 15 \text{ y}$ and $n_{min} = 1$ to $n_{min} = 10$ for each period separately (Figure 27).

In all periods, m_{all} at $n_{min} = 1$ (i.e. all species included) declined with increasing t , steeply so from $t = 1$ to *c.* $t = 4$, and then more gradually (Figure 27). This decline was less pronounced with increasing n_{min} , when more and more species were excluded, with the largest reduction being between $n_{min} = 1$ and $n_{min} = 2$. M_{all} decreased with increasing n_{min} at $t = 1$, but more (periods 2a and 2b) or less (period 1) increased at $t = 15$.

Standard errors were smallest at $t = 15$ at all enumerations, with $n_{min} = 2$ in period 1 and $n_{min} = 1$ in periods 2a and 2b. They generally increased from low n_{min} and

long intervals to high n_{\min} and shorter intervals, but this pattern was broken by slight (period 2a) or strong irregularities (periods 1 and 2b): Period 1 showed the strongest decrease in SE at $n_{\min} = 1$ across the 15 y, then flattened until $n_{\min} = 4$, but nearly reached the maximum steepness again at $n_{\min} = 7$ before being levelled out at $n_{\min} = 10$. In period 2a, SEs decreased only slightly between $n_{\min} = 1$ and $n_{\min} = 3$, most pronounced at $t = 1$ and then increased almost linearly with time across $n_{\min} = 3$ to $n_{\min} = 10$. The pattern in period 2b was wave-like across increasing n_{\min} (Figure 27).

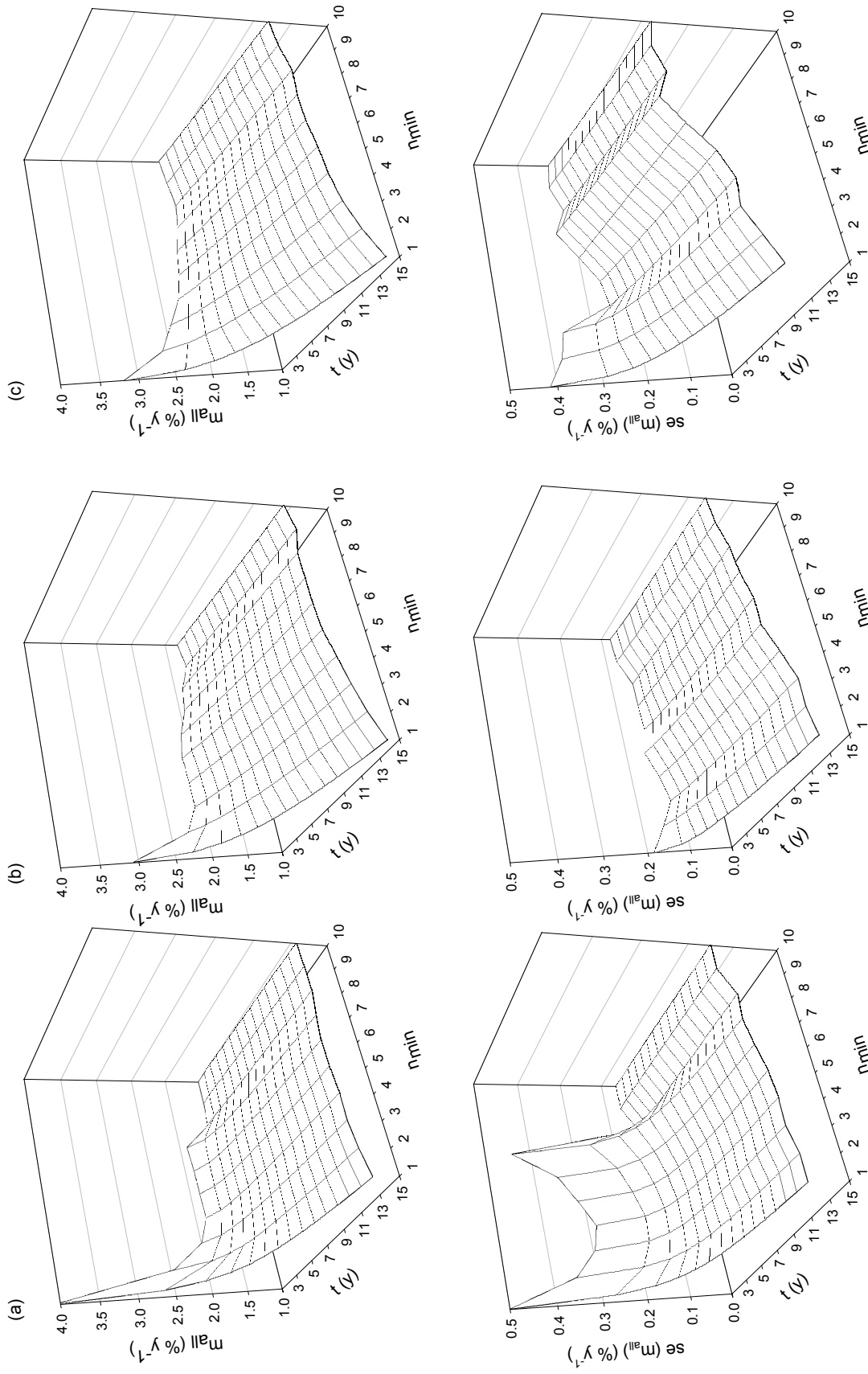


Figure 27. Overall mean mortality rates (m_{all} , upper row) and their standard errors ($se(m_{all})$, lower row) with $t = 1 - 15$ y and $n_{min} = 1 - 10$ for (a) period 1, (b) period 2a and (c) period 2b in PEPs at Danum, small trees..

Plotting the dynamic diversity of each period while subsequently excluding species (i.e. increasing n_{\min}) showed the same result: the initial variability as well as the decline in variability of m_{all} across time was greatest in period 1 at $t = 1$ and the steepest decline was visible between $n_{\min} = 1$ and $n_{\min} = 2$, indicating that a large proportion of variability was eliminated at $n_{\min} = 2$ (Figure 28). In contrast to SE of the subplots' m_{all} , dynamic diversity shows variation of m_{all} across time. Thus, Figure 28 indicates that with increasing n_{\min} , the dynamic diversity of the longest period dropped below that of the shorter ones (at $n_{\min} = 2$ for period 2b and at $n_{\min} = 3$ for period 2a), except for the hump at $n_{\min} = 7$, which was visible in the SEs of the first period's mean subplot m_{all} (Figure 27). This peak was caused by a single species in one subplot: *Shorea leprosula* in PEP4 had seven individuals in 1986 that all died until 1996. PEP4 was the only subplot where 100%-mortalities occurred at such high numbers of individuals within a species and thus had a range in m_a of 0-100%.

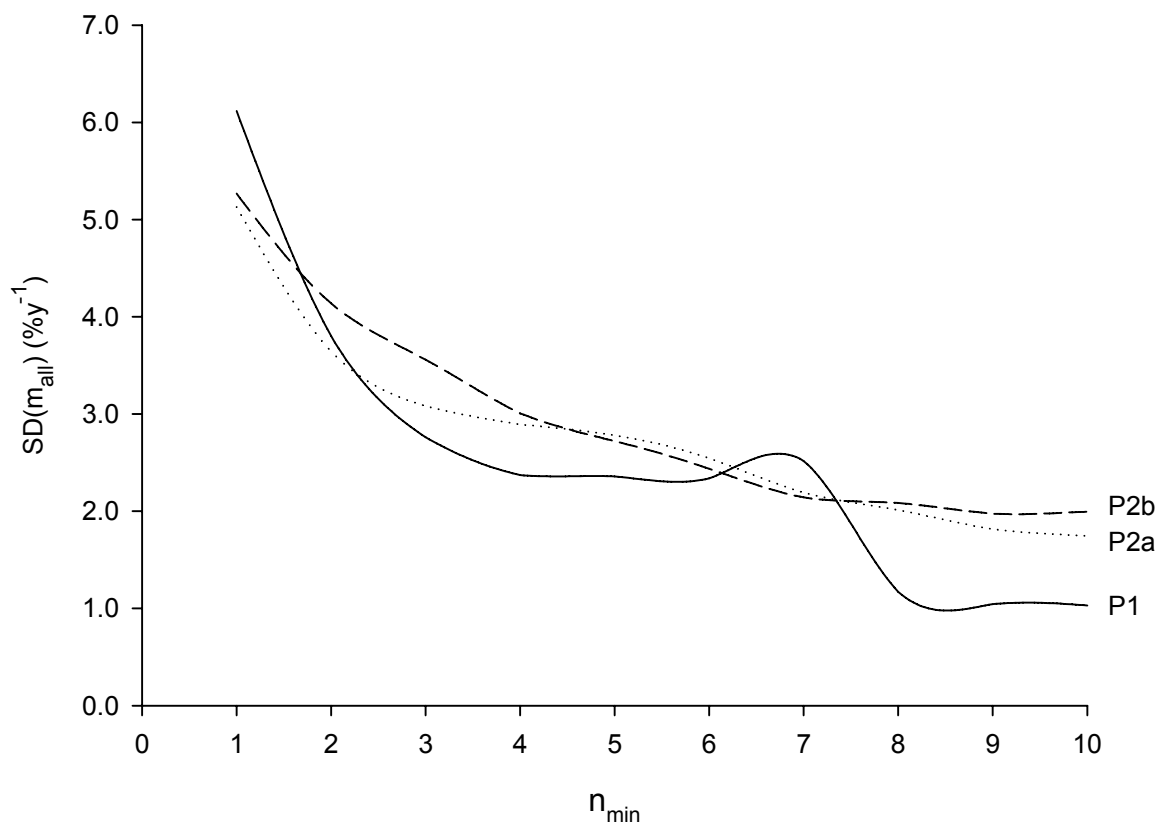


Figure 28. Dynamic diversity (SD of m_{all} across $t = 1-15$ y) of m_{all} of small trees with subplot species as groups, with increasing n_{\min} for periods 1, 2a and 2b in PEPs at Danum.

Closer examination of m_{all} in each individual subplot revealed that the steep decline of m_{all} with increasing t at low n_{min} is due to the proportion of underlying m_a with 100%: PEPs that had species that were completely lost between two enumerations did show this decline, but in those subplots that did not have any total losses of species the decline was slight and linear (Figure 29, Figure 30, Figure 31). While at $n_{\text{min}} = 1$ only few PEPs showed this response, when more and more rare species were excluded, the proportion of PEPs without $m_a = 100\%$ increased and at $n_{\text{min}} = 5$ all PEPs in periods 2a and 2b showed a linear decline in m_{all} across time. In period 1, this was achieved only at $n_{\text{min}} = 8$, after *Shorea leprosula* in PEP 4 dropped out (see above). At $n_{\text{min}} = 10$ most PEP's m_{all} were flat and distributed over a wider range of values than at lower n_{min} (down to $n_{\text{min}} = 5$ as it is visible in period 2b (Figure 31)): exclusion of rare species led to more intra-subplot homogeneity of mortality but between PEPs the species composition was less similar and thus the inter-subplot heterogeneity increased.

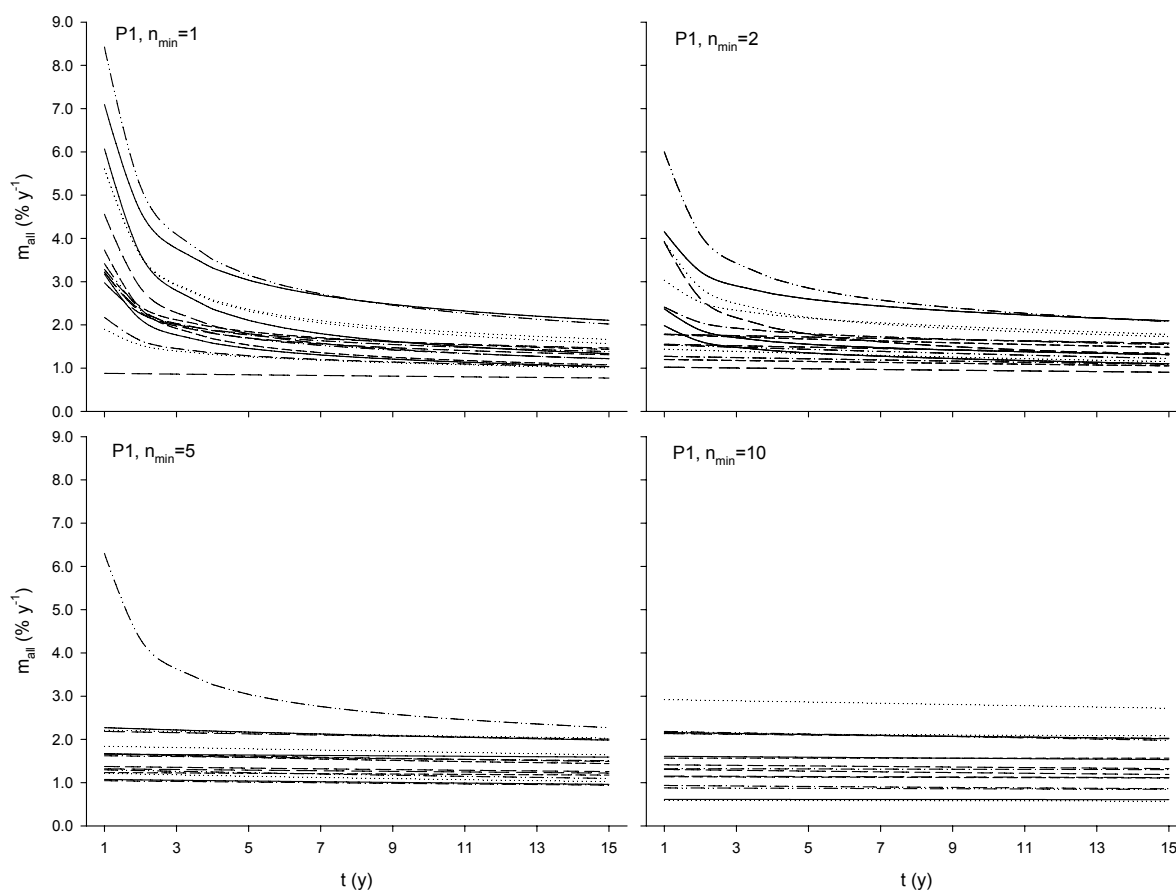


Figure 29. Overall average mortality (m_{all}) individually for 16 PEPs at Danum with $n_{\text{min}} = 1, 2, 5$ and 10 in period 1, simulated across 15 y.

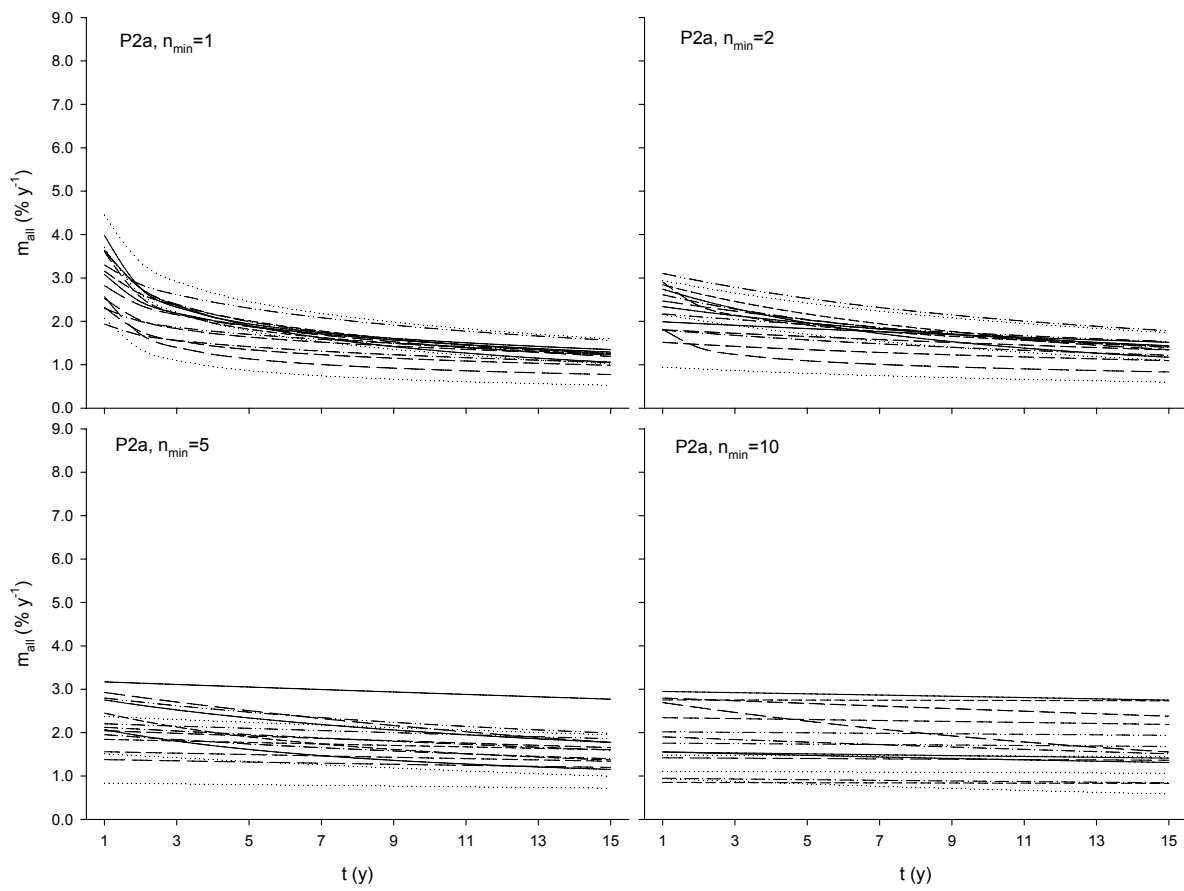


Figure 30. Overall average mortality (m_{all}) individually for 16 PEPs at Danum with $n_{min} = 1, 2, 5$ and 10 in period 2a, simulated across 15 y.

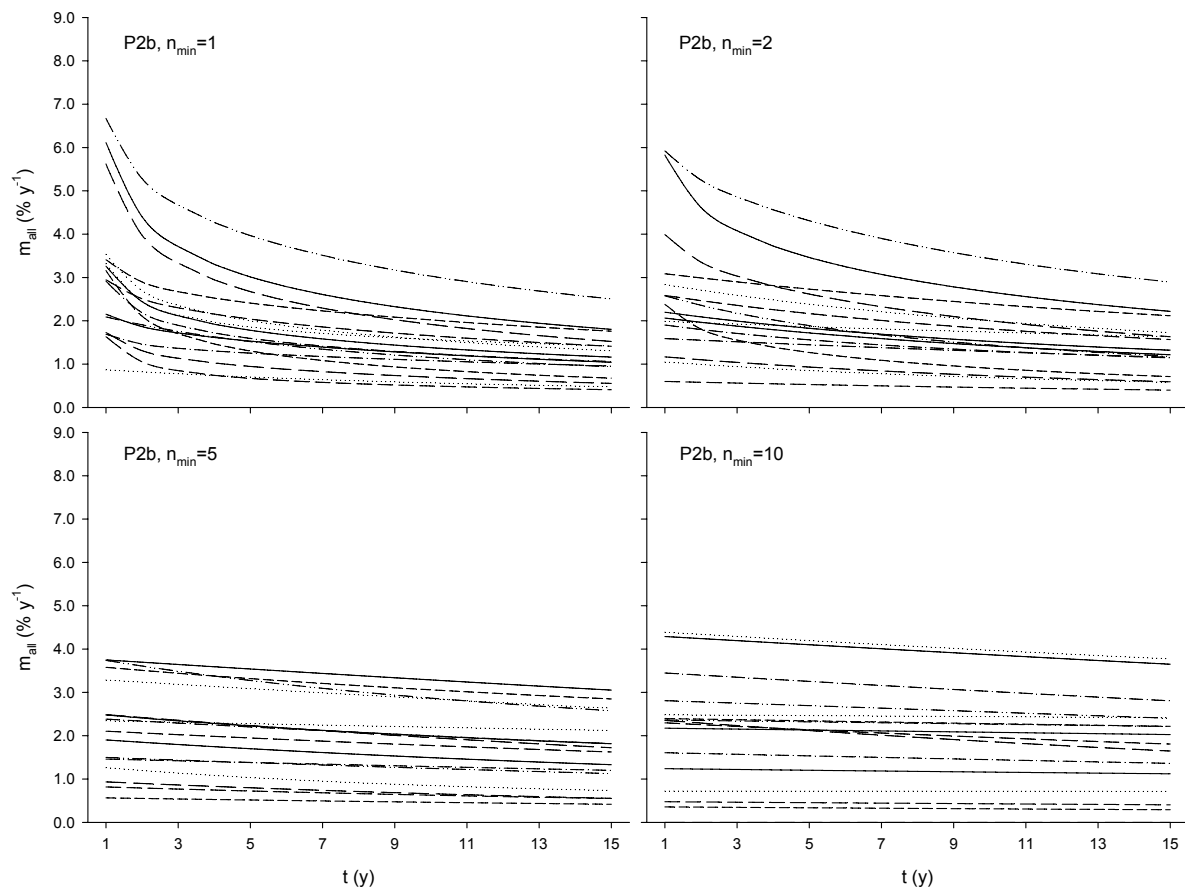


Figure 31. Overall average mortality (m_{all}) individually for 16 PEPs at Danum with $n_{min} = 1, 2, 5$ and 10 in period 2b, simulated across 15 y.

As the exclusion of those species with only one individual resulted in the largest decline in variability, m_{all} was based on $n_{min} = 2$ to calculate the interval correction factor. Calculated rates at $n_{min} = 2$ could fall below the values at $n_{min} = 1$, and this had consequences for the correction procedure: a correction factor individually calculated for each PEP, using the shift from m_{all} at $t =$ the species' subplot interval and $n_{min} = 1$ to $t = 5$ y and $n_{min} = 2$ could lead to a reduction in mortality, even when correcting from the longer to the shorter interval (where an increase would be expected). Thus, the correction procedure had to be based on the mean m_{all} across PEPs (Table 40).

Table 40. Time-interval correction factor for overall average mortality rates from m_{all} at $t = 5$ and $n_{\text{min}} = 2$ related to m_a (weighted mean across subplots) for PEPs at Danum.

	Period 1	Period 2a	Period 2b
m_a	1.54	2.17	2.32
$m_{\text{all}} (t = 5; n_{\text{min}} = 2)$	1.70	1.81	1.97
correction factor	1.109	0.834	0.849

Each correction factor was applied to each PEPs' m_{all} and the corrected mortality rate (m_{corr}) was calculated as the mean of the corrected PEP-mortalities (Table 41).

With this approach, consequently m_{corr} was raised by 10.9% in period 1 and lowered by 16.6% and 15.1% in period 2a and period 2b, respectively (Figure 32).

The resulting annualised overall average mortality rates, based on species' m_a within subplots and corrected to the common interval length of 5 y ($m_{\text{corr}} \pm \text{SE}$) were therefore in period 1: $1.70 \pm 0.11\% \text{ y}^{-1}$; in period 2a: $1.81 \pm 0.10\% \text{ y}^{-1}$; and in period 2b: $1.97 \pm 0.23\% \text{ y}^{-1}$, a continuous increase across intervals (Table 41).

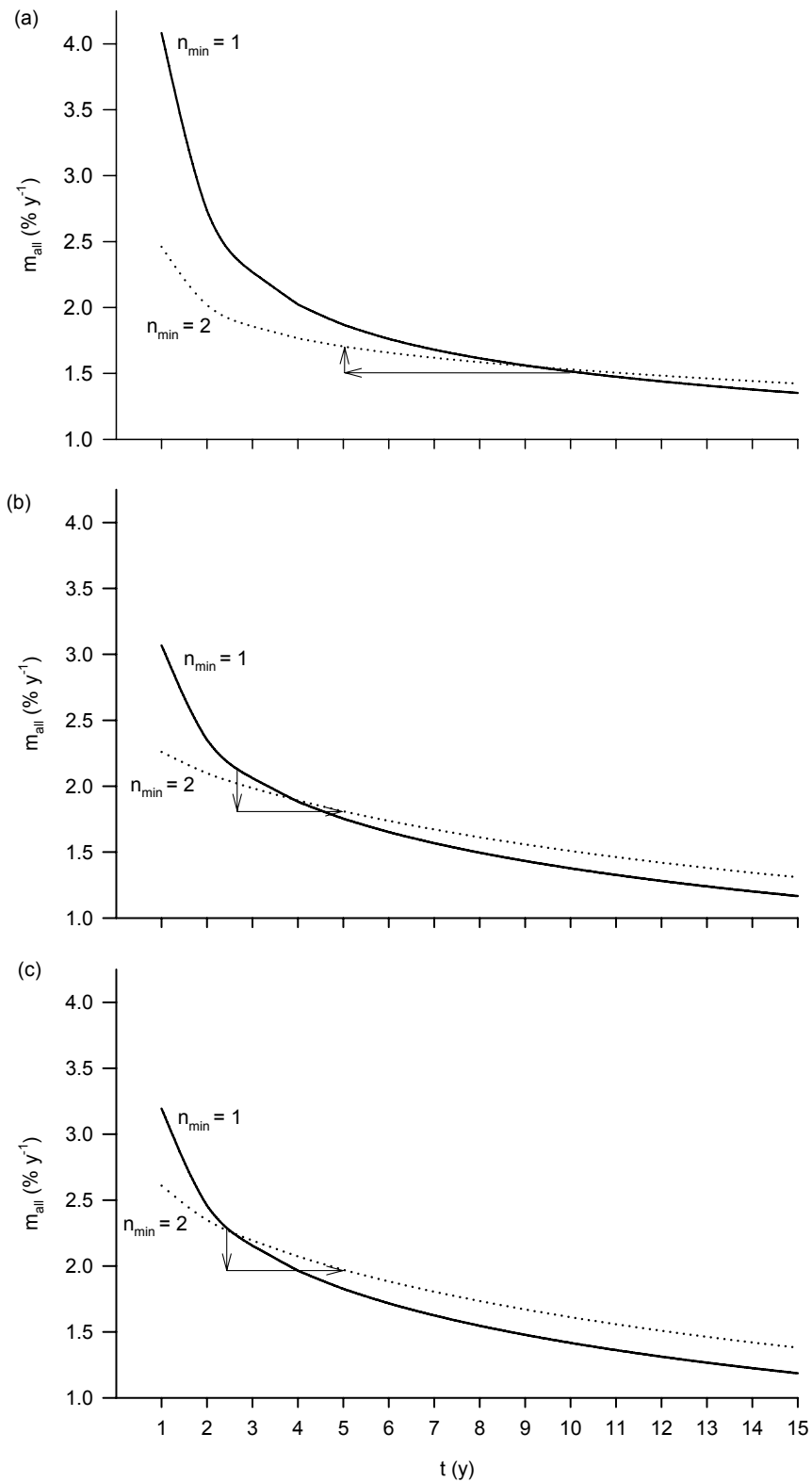


Figure 32. Time-interval correction procedure for mortality: overall average mortality (m_{all}) across $t = 1 - 15$ y for $n_{min} = 1 - 2$ in periods 1 (a), 2a (b) and 2b (c). The correction factor is indicated by the arrows, leading from m_a at $t =$ the actual interval length and $n_{min} = 1$ to $t = 5$ y (the common interval length) and $n_{min} = 2$.

Table 41. Interval-corrected overall average mortality rates for each PEP at Danum, 1986 to 2001; showing subplot-number (PEP), topographic location of PEP (topo; S = lower slope, R = ridge) tree numbers (alive at start of interval (n), dead at end of interval (n_d)), mean interval length, annualized uncorrected mortality rate (m_a) and interval-corrected overall average mortality rate (m_{corr}). Correction factors applied: period 1: 1.109; period 2a: 0.834; period 2b: 0.849. Means were weighted by n_{start} . Note that n , n_d , Int and m_a were based on all trees within PEPs while m_{corr} excluded taxonomical uncertain trees.

PEP	Topo	Numbers of trees										Interval length (y)						Mortality rates (% y^{-1})					
		n_{86}	n_{d96}	n_{96}	n_{d99}	n_{99}	n_{d01}	n_{01}	P1	P2a	P2b	m_a	m_{corr}	Period 1	Period 2a	Period 2b	m_a	m_{corr}	m_a	m_{corr}			
1	S	378	83	275	18	243	10	241	10.20	3.09	2.28	2.40	2.66	2.17	1.81	1.83	1.55						
2	S	321	56	253	22	221	4	220	10.21	3.11	2.25	1.86	2.06	2.88	2.41	0.81	0.69						
3	S	352	53	283	20	256	12	248	10.16	3.10	2.60	1.59	1.77	2.34	1.95	1.83	1.55						
4	S	272	59	199	10	174	8	169	10.44	2.69	2.56	2.31	2.57	1.89	1.58	1.82	1.55						
5	R	352	54	283	16	263	22	244	10.36	2.59	2.29	1.59	1.77	2.23	1.86	3.75	3.18						
6	R	285	32	246	10	230	11	217	10.36	2.57	2.33	1.14	1.27	1.60	1.34	2.08	1.77						
7	R	350	48	286	11	264	6	265	10.56	2.32	2.41	1.39	1.54	1.68	1.40	0.95	0.81						
8	R	264	42	206	12	192	19	173	10.57	2.27	2.60	1.63	1.80	2.60	2.17	3.93	3.34						
9	S	272	44	217	7	198	12	187	9.23	2.95	2.46	1.89	2.10	1.10	0.92	2.51	2.13						
10	S	293	32	245	15	227	16	212	9.29	2.80	2.61	1.24	1.37	2.23	1.86	2.76	2.34						
11	S	386	48	323	23	295	33	265	9.41	2.76	2.31	1.40	1.55	2.64	2.20	5.00	4.24						
12	S	323	25	290	11	273	8	265	9.52	2.55	2.40	0.84	0.93	1.50	1.25	1.23	1.05						
13	R	341	47	273	17	251	8	246	9.67	2.49	2.30	1.52	1.69	2.55	2.13	1.40	1.19						
14	R	376	50	315	14	296	17	281	9.82	2.31	2.43	1.44	1.60	1.95	1.62	2.41	2.04						
15	R	336	38	290	17	269	14	252	9.90	2.26	2.29	1.20	1.34	2.64	2.20	2.31	1.96						
16	R	289	30	255	14	233	13	221	9.92	2.24	2.53	1.10	1.22	2.49	2.08	2.24	1.90						
Totals:		5190	741	4239	237	3885	213	3706															
Weighted means:								9.97	2.63	2.41	1.54	1.70	2.17	1.81	2.32	1.97							
± SE:								0.10	0.11	0.12	0.10	0.11	0.12	0.10	0.27	0.23							

Comparison of the calculated mortality rates showed that again (*c.f.* Table 39) m_a was slightly higher than m_{all} (at $n_{min} = 1$, $t = int$) with the largest difference at the longest time interval (period 1, $0.03\% y^{-1}$), due to the decline in rate of mortality across time in heterogeneous populations.

In relation to m_a , m_{corr} brought the mortality rates closer together – which was expected from the time intervals present and the correction to a mean interval in between (5 y) – but still showed marked differences between the periods (Figure 33).

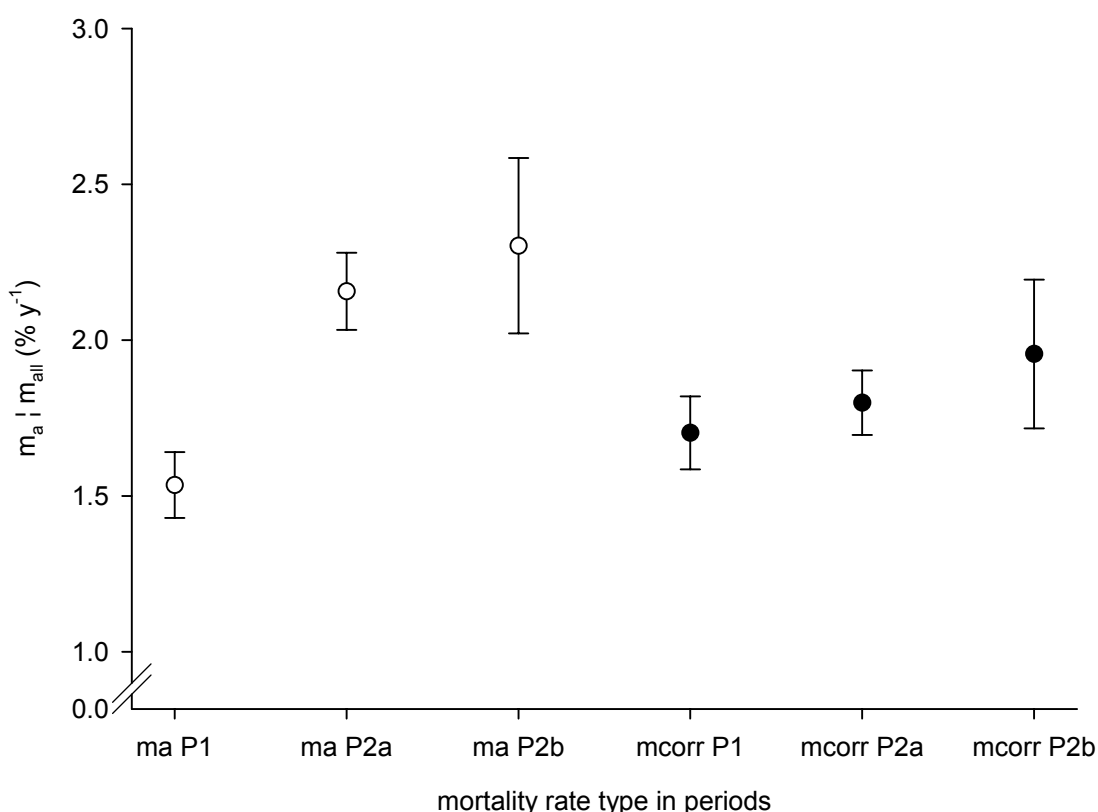


Figure 33. Comparison of subplots' annualised (m_a ; open circles) and interval corrected overall average (m_{corr} ; filled circles) mortality rates \pm SE for periods 1, 2a and 2b in PEPs at Danum:

M_{corr} , the interval corrected overall average mortality was taken as the best estimate for mortality because it accounted for the apparent rate decline in heterogeneous populations and adjusted for differences in time intervals, making the rates between different enumerations comparable. M_{corr} in the present setting is conservative in the sense that it is not overestimating differences in mortality between periods.

Consequentially, mortality in the PEP-subset increased by 6.2% from period 1 to period 2a and by 8.9% from period 2a to period 2b.

The rise in variability of m_{corr} (SE in Table 41, and Figure 33) points to a mixed spatial response of trees to drought: whereas in period 2a mortality rose rather uniformly within subplots (12 out of 16 subplots had increased mortality), in period 2b subplot rates were spread over a wider range and drifted more apart (seven subplots had higher, nine had lower mortality rates than in the previous period). Differentiating between those PEPs that lay on lower slope and those that lay on ridge locations showed that seven ridge-PEPs and five lower-slope-PEPs (out of eight each) increased in mortality between period 1 and period 2a; between periods 2a and 2b, four and three PEPs still increased in mortality on ridges and lower slopes, respectively (Table 41). This could hint towards a higher vulnerability to droughts of trees on ridges. It is investigated in more detail in Chapter V.5.4.7., further below.

5.4.5. Mortality of the most abundant species

Mean m_a (weighted by n_{start}) and m_{all} of the 22 most abundant species increased between the first two periods, but it did not change in period 2b (Table 42). The magnitude of change and the range of values were different from those of the subplot mortalities: m_{all} increased by 50.1% between periods 1 and 2a and remained constant in period 2b (Table 42).

Individual species' mortalities (m_a), which had a range of $0.55\% \text{ y}^{-1} - 3.86\% \text{ y}^{-1}$ in period 1, became more variable in periods 2a and 2b, where two species each had zero mortality and the maximum values were $9.96\% \text{ y}^{-1}$ and $8.28\% \text{ y}^{-1}$, respectively (Table 42).

Sixteen of the 22 most abundant species showed an increase in mortality in period 2a compared to period 1: most of these species (eight) by 0% – 50% and six by > 100%. Six species decreased in mortality: four by 0% – 50% and two dropped to zero. Between periods 2a and 2b, twelve species increased (six by 0% – 50%, four by > 100%) and nine species decreased in mortality (three by 0% – 50%, five by 50% – 100% and one fell to zero). One additional species stayed at zero mortality (Table 42).

When comparing the changes of individual species' mortality rates between periods 1 and 2a and periods 2a and 2b, 12 species showed contrasting behaviours, either increasing between the first two periods and then decreasing (eight species) or decreasing first and then increasing (four species). In eight species mortality rose, in one species mortality declined across all periods and one species dropped to and then stayed at zero mortality. *Maschalocorymbus corymbosus* (Rubiaceae) had the highest m_a in period 1, decreased slightly in period 2a, but had again the highest mortality rate in period 2b (Table 42).

Strongest reactions between periods 1 and 2a – with > 200% mortality increase – were expressed by *Dacryodes rostrata* (Burseraceae), *Polyalthia xanthopetala* (Annonaceae; showing the highest mortality rate of all 22 species and all three periods with 9.96% γ^{-1} in period 2a) and *Litsea caulocarpa* (Lauraceae). Between periods 2a and 2b, only *Litsea ochracea* (Lauraceae) increased by > 200%. Increases of > 100% were shown by *M. corymbosus*, *Madhuca korthalsii* (Sapotaceae) and *Polyalthia rumphii* (Annonaceae). A net increase in mortality between the start and the end of the enumerations (*i.e.* 1986 – 2001) was seen in 18 species. Four of these had a m_a in period 2b of > 200% above that in period 1: *L. ochracea*, *P. rumphii*, *Fordia splendidissima* (Leguminosae) and *M. korthalsii* (Table 42).

P. rumphii did have zero-mortality in period 2a, as did *Lophopetalum beccarianum* (Celastraceae), which also did not lose any stems during period 2b. The second species with mortality at zero in period 2b was *Mallotus penangensis* (Euphorbiaceae).

Apart from *L. beccarianum* and *M. penangensis*, only *Dimorphocalyx muricatus* (Euphorbiaceae) and *Dysoxylum cyrtobotryum* (Meliaceae) had lower m_a in period 2b than in period 1 (Table 42).

It is noteworthy that only seven of the most abundant species had substantially (> 10) additional trees with a gbh \geq 50 cm, *i.e.* being represented outside the small trees' size class. This indicates that the other 15 species belonged to the understorey or intermediate storeys of the forest at Danum.

Table 42. Numbers of trees at start of each period (n) and of trees dying within a period (n_d) and annualised mortality rates (m_a , % y^{-1}) for the 22 most abundant species within PEPs at Danum for periods 1, 2a and 2b.

Species	Numbers of trees							m_a		
	n_{86}	n_{d96}	n_{96}	n_{d99}	n_{99}	n_{d01}	n_{01}	P1	P2a	P2b
<i>Aporosa falcifera</i>	74	6	65	2	62	2	59	0.85	1.17	1.35
<i>Ardisia sanguinolenta</i>	166	20	138	5	130	8	123	1.28	1.45	2.59
<i>Baccaurea tetrandra</i>	76	9	66	2	62	3	58	1.27	1.12	2.07
<i>Cleistanthus contractus</i>	118	14	103	3	97	3	97	1.24	1.23	1.30
<i>Dacryodes rostrata</i>	58	4	54	5	48	2	47	0.72	3.54	1.74
<i>Dimorphocalyx muricatus</i>	276	25	250	11	236	2	234	0.95	1.78	0.37
<i>Dysoxylum cyrtobotryum</i>	53	10	41	3	36	1	36	2.10	2.90	1.16
<i>Fordia splendidissima</i>	157	15	134	8	122	9	116	0.99	2.31	3.09
<i>Litsea caulocarpa</i>	105	22	72	13	56	4	52	2.32	7.39	3.04
<i>Litsea ochracea</i>	60	8	49	2	45	6	39	1.43	1.58	5.83
<i>Lophopetalum beccarianum</i>	71	4	66	0	63	0	64	0.57	0.00	0.00
<i>Madhuca korthalsii</i>	112	6	103	2	98	4	95	0.55	0.72	1.70
<i>Mallotus penangensis</i>	57	8	48	2	45	0	46	1.47	1.41	0.00
<i>Mallotus wrayi</i>	713	99	612	32	573	27	548	1.49	2.00	1.99
<i>Maschalocorymbus corymbosus</i>	120	39	80	7	71	13	60	3.86	3.44	8.28
<i>Pentace laxiflora</i>	58	12	36	4	31	2	27	2.31	4.14	2.72
<i>Polyalthia cauliflora</i>	123	15	108	4	104	5	99	1.28	1.41	2.03
<i>Polyalthia rumphii</i>	53	5	48	0	47	4	44	1.00	0.00	3.59
<i>Polyalthia sumatrana</i>	50	5	43	3	36	2	36	1.06	2.70	2.31
<i>Polyalthia xanthopetala</i>	59	16	42	10	32	3	29	3.06	9.96	4.01
<i>Reinwardtiodendron humile</i>	76	21	55	6	48	5	44	3.18	4.06	4.45
<i>Shorea fallax</i>	85	16	64	7	55	6	49	2.10	4.57	4.76
Totals:	2720	379	2277	131	2097	111	2002			
Weighted means:								1.52	2.26	2.26
± SE:								0.19	0.49	0.41
Overall average mortality (m_{all})								1.49	2.24	2.24

5.4.6. Mortality in size classes

Subdividing the small trees further into 10-cm size classes, and using these four classes as groups to calculate the overall average mortality rate, resulted in exactly the same rates as the weighted mean of m_a in the four classes (which is the same as the simple annualised mortality rate of the small trees' subset): 1.53% y^{-1} , 2.17% y^{-1} and

2.32% y^{-1} in periods 1, 2a and 2b, respectively. Obviously, mortality between size classes was not differing enough to result in a reduction of m_{all} in the longest period (period 1, 9.97 y; m_a range: 1.48 – 1.70% y^{-1}) and although the variability of m_a in periods 2a (range: 1.89 – 3.07% y^{-1}) and 2b (range: 2.10 – 3.37% y^{-1}) was high, time intervals were too short (2.63 y and 2.41 y) to show an effect on m_{all} .

Tree numbers, especially the counts of dead trees, in the classes ≥ 30 cm were too low (Table 43) to perform the calculation of m_{all} with species within size classes as groups.

In all size classes, mortality rates of periods 2a and 2b were higher than in period 1 (Figure 34). The strongest increase in mortality of period 2a compared to period 1 was observed in the 30 – 40 cm class (by *c.* 80%) which showed another increase in period 2b (by *c.* 10%) so that mortality in this size class almost doubled between 1986 – 1996 and 1999 – 2001 from 1.70% y^{-1} to 3.37% y^{-1} . The 20 – 30 cm size class exhibited the strongest increase in mortality in between periods 2a and 2b (by *c.* 22%). Only in the size class of 40 - 50 cm – after an increase of *c.* 68% between periods 1 and 2a – did mortality decrease slightly (by *c.* 2%) between periods 2a and 2b. The increase of mortality in the 10 – 20 cm class between periods 2a and 2b was small (by *c.* 1%) (Figure 34). All size classes were immediately affected by the drought of 1997/98, most severely those trees $\geq 30 < 50$ cm gbh and still showed elevated mortality during the period after the drought, where the smallest trees < 40 cm still had increasing mortality but trees 40 – < 50 cm seem to have begun to recover.

Table 43. Tree numbers in size classes (upper and lower limits; cm gbh) in PEPs at Danum, 1986 – 2001. Numbers at the start of interval (n) and numbers of dead trees at the end of interval (n_d) are shown.

Size class (cm gbh)	n_{86}	n_{d96}	n_{96}	n_{d99}	n_{99}	n_{d01}
10 - 20	3446	476	2535	136	2286	114
20 - 30	1114	167	1046	51	994	54
30 - 40	431	68	446	35	416	33
40 - 50	199	30	212	15	189	12
Totals:	5190	741	4239	237	3885	213

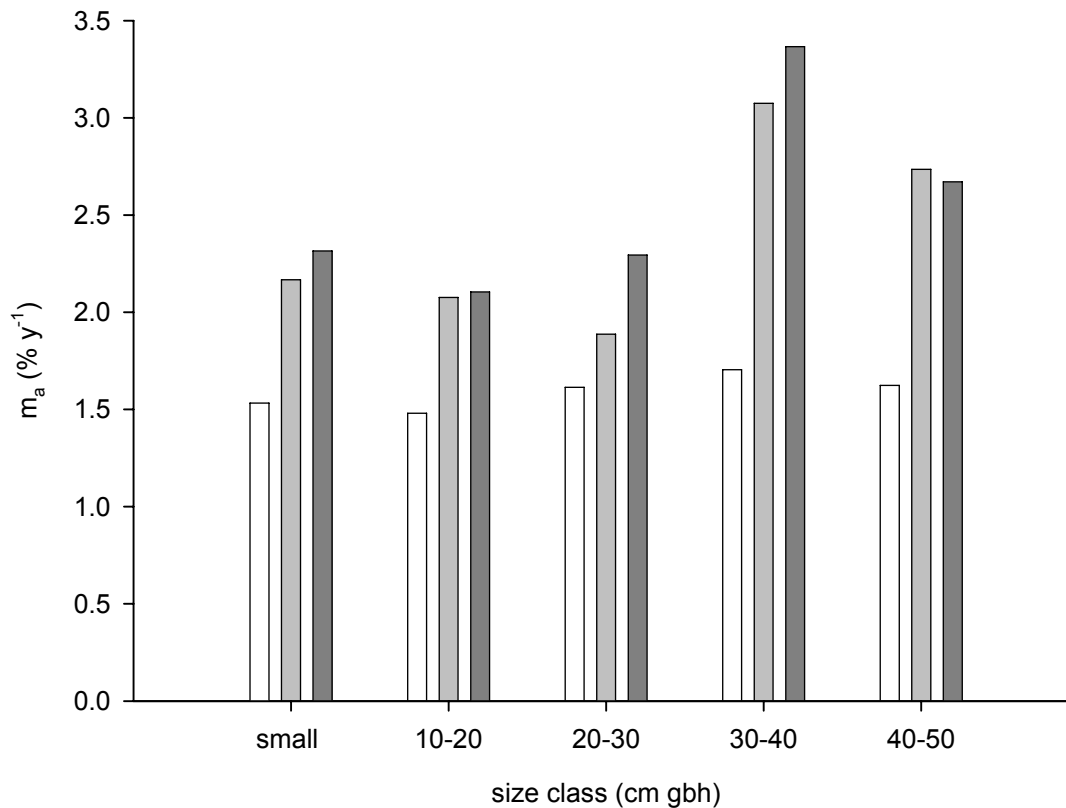


Figure 34. Mortality rates for small trees (10 – <50 cm gbh) and separately for 10-cm size classes in PEPs at Danum for periods 1 (white bars), 2a (light grey bars) and 2b (dark grey bars).

5.4.7. Mortality in topographic classes

Mortality rates (m_a) of trees growing on ridges or lower slopes showed that in period 1, trees on lower slopes experienced higher mortality ($1.73\% \text{ y}^{-1}$) than those on ridges ($1.34\% \text{ y}^{-1}$) and those on intermediate locations ($1.50\% \text{ y}^{-1}$) (Figure 35). In period 2a, mortality in all topographic classes increased strongly by *c.* 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 (by *c.* 9%), but a strong decrease (by *c.* 16%) on lower slopes. Trees on intermediate elevations (with approximately only half the tree numbers than in ridge and lower slope classes (Table 44)) increased in mortality in period 2b even more than those on the ridges (by *c.* 48%) and reached the highest mortality rates across the three topographic classes and periods ($3.05\% \text{ y}^{-1}$). Comparing m_a of period 2b with that

of period 1, the intermediate class more than doubled (by *c.* 104%) in mortality, ridges had *c.* 80% higher mortality but m_a for trees on lower slopes was elevated by only *c.* 6% (Figure 35).

The calculation of m_{all} with topographic classes as groups did not change the average rates for periods 2a and 2b and only very slightly reduced that of period 1 (to 1.53% y^{-1}).

All topographic locations were affected by the drought, ridges and intermediate elevations still increased in mortality two years after the drought, but lower slopes reached a rate close to that before the drought shortly after the disturbance.

Table 44. Tree numbers in topographic classes in PEPs at Danum, 1986 – 2001. Numbers of trees at the start of a period (n), numbers of dead trees at the end of a period (n_d) are shown.

Topographic class	n_{86}	n_{d96}	n_{96}	n_{d99}	n_{99}	n_{d01}
Ridge	1926	246	1613	84	1495	85
Lower slope	2164	340	1720	106	1555	68
Intermediate	1100	155	906	47	835	60
All	5190	741	4239	237	3885	213

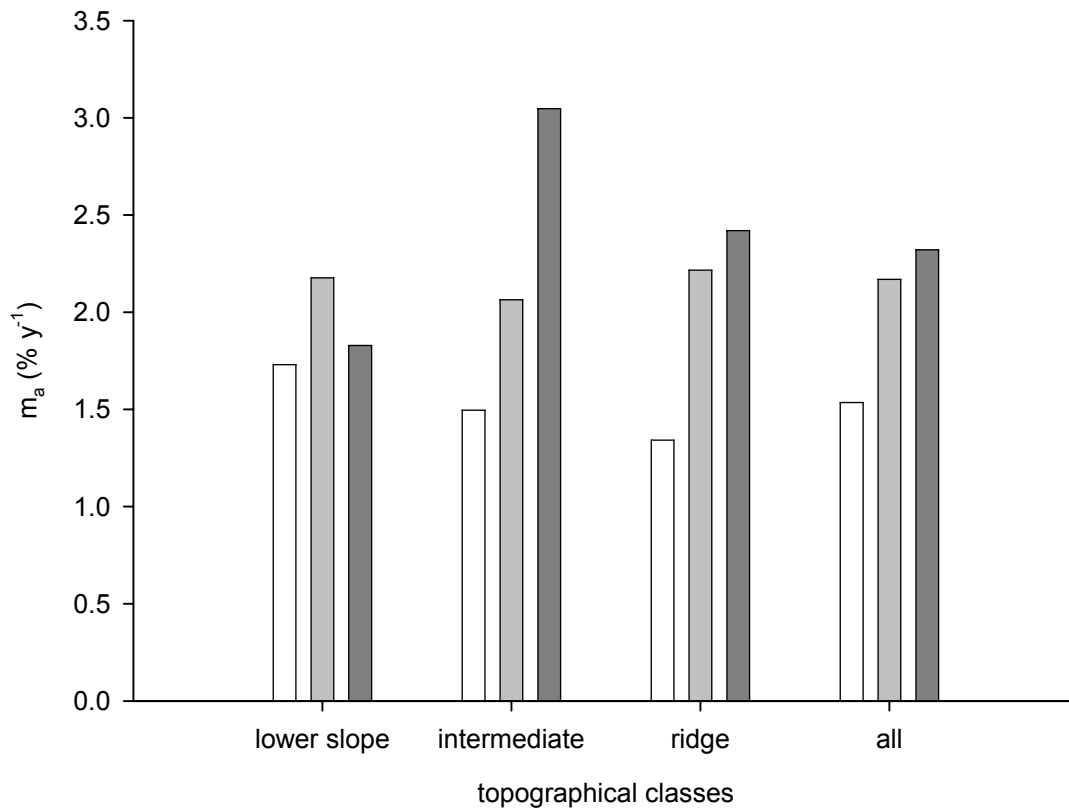


Figure 35. Mortality rates within topographic classes and across all locations in PEPs at Danum for periods 1 (white bars), 2a (light grey bars) and 2b (dark grey bars).

5.5. Growth

5.5.1. Growth across subplots

Mean growth rates across subplots declined very much in period 2a compared to period 1 (relative growth rate by 35.6%) but recovered tremendously in period 2b (rgr by 93.8%) and were still higher (rgr 24.7%) than in period 1 (Table 45, Figure 36).

All of the 16 subplots had lower rgrs (*c.* 4% – 82%) in period 2a than in period 1, but only two further decreased in rgr (*c.* 8 – 16%) during period 2b. Of the 14 PEPs with higher rgr, seven increased by > 100% (up to *c.* 275%) compared to period 2a. Against period 1, seven PEPs had lower rgrs in period 2b, but in nine subplots growth was still elevated above the level of the pre-drought period (three > 100%) (Table 45).

Variability of growth rates was higher in the third compared to the first two periods, pointing – after the more uniform reaction (reduced growth) immediately after

the drought - to a strong positive, but spatially diverse response of trees starting *c.* one year after the drought.

Table 45. Growth rates in PEPs at Danum, 1986 – 2001; gbh at start of interval: ≥ 10 <50 cm; showing numbers of trees valid for growth rate calculations, mean absolute (agr; mm y^{-1}) and mean relative growth rates (rgr; $\text{mm m}^{-1} \text{y}^{-1}$) for each period within each subplot. Mean time interval lengths were: period 1: 9.98 y, period 2a: 2.63 y and period 2b: 2.42 y.

PEP number	n trees valid			mean agr (mm y^{-1})			mean rgr ($\text{mm m}^{-1} \text{y}^{-1}$)		
	P1	P2a	P2b	P1	P2a	P2b	P1	P2a	P2b
1	267	219	214	2.88	1.94	3.02	10.54	8.41	13.36
2	247	209	204	1.98	1.58	2.95	8.66	8.13	13.10
3	266	229	225	2.89	1.53	2.37	12.54	6.97	11.22
4	174	149	143	3.42	3.10	2.58	16.10	12.51	10.47
5	256	230	226	1.22	1.04	2.15	5.97	4.98	11.66
6	213	196	190	2.39	1.88	5.93	12.71	7.56	28.35
7	271	241	234	3.16	1.72	2.21	15.00	7.51	10.13
8	198	171	155	3.05	1.49	2.90	14.87	6.98	14.85
9	194	172	164	3.06	1.99	5.26	13.24	7.96	23.29
10	221	196	191	1.88	1.04	1.25	8.74	4.14	5.80
11	294	265	239	1.72	1.39	3.43	7.60	6.18	17.38
12	272	257	251	2.08	1.60	1.52	10.90	7.75	7.15
13	234	200	217	3.41	0.78	1.67	14.40	2.56	7.49
14	298	274	257	2.09	1.58	2.44	9.11	6.35	11.45
15	285	255	230	1.40	1.43	2.33	6.58	6.31	11.05
16	236	210	196	2.36	1.52	4.60	10.98	6.02	22.13
Totals	3926	3473	3336						
Means				2.44	1.60	2.91	11.12	6.90	13.68
\pm SE				0.176	0.129	0.330	0.789	0.540	1.558

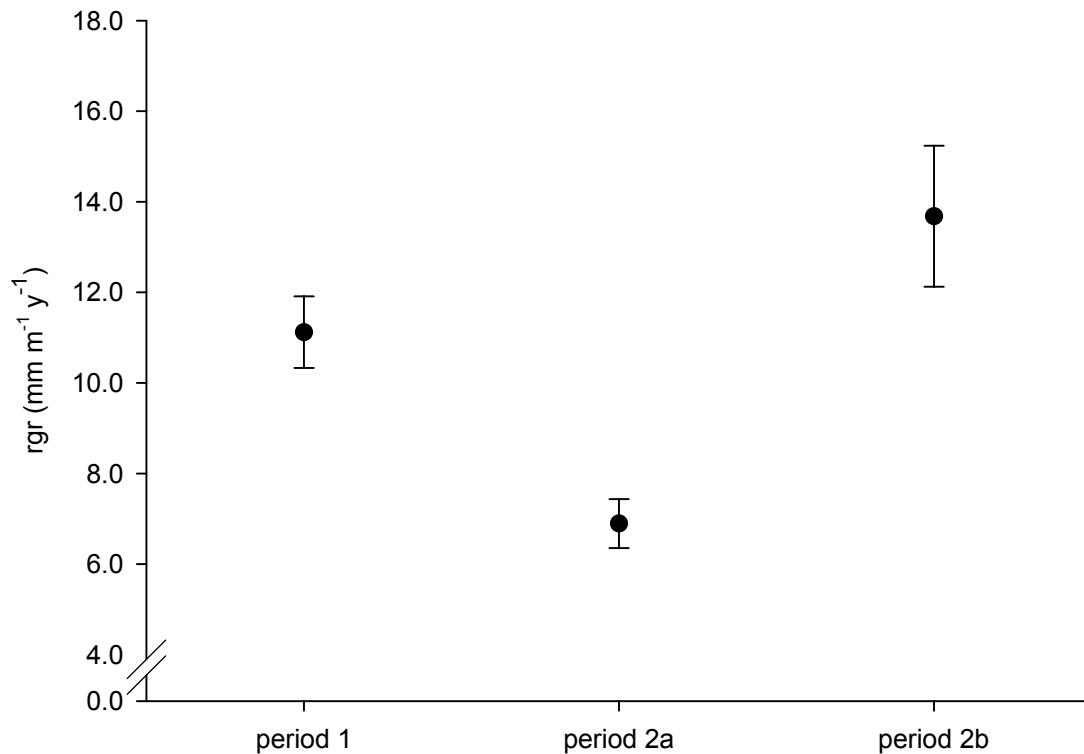


Figure 36: Mean relative growth rates (\pm SE) across PEPs at Danum for the three periods covering 1986 – 2001.

5.5.2. Growth of most abundant species

Growth rates of the 22 most abundant species (small trees) showed the same pattern as those within subplots: a sharp decline in growth between periods 1 and 2a (rgr by *c.* 39.8%), followed by a strong increase in growth between periods 2a and 2b (by *c.* 131.9%), above the level of period 1 (*c.* 39.6%) (Table 46). All of the 22 species had lower rgr in period 2a than in period 1, five of them decreased in growth by > 50%, fifteen by 10% – 50% and two by < 10%. The latter - *Lophopetalum beccarianum* and *Dacryodes rostrata* - being the only species with a positive agr balance between periods 1 and 2a. *Reinwardtiidendron humile* displayed a mean negative growth rate in period 2a: 23 out of 42 valid trees had slightly smaller gbhs in 1999 than in 1996 and therefore growth rates < 0 (Table 46).

All species increased in both absolute and relative growth rates between periods

2a and 2b, ten species with an increase in rgr of > 100%. *Dimorphocalyx muricatus* increased in rgr more than 4-fold, *Cleistanthus contractus* and *Baccaurea tetrandra* more than 3-fold. Sixteen species thereby reached rgrs that were > 10% higher than in period 1, with the rgr of *D. muricatus* three times and *Polyalthia rumphii*'s twice as high. Of four species that did not attain the rgr-levels of the first period, three lay well below the rates of period 1: *Shorea fallax* (-50.5%), *Litsea ochracea* (-40.0%) and *Aporosa falcifera* (-25.6%) (Table 46).

Table 46. Growth of most abundant species (gbh: 10 – < 50 cm at start of interval) within PEPs at Danum, for periods 1, 2a and 2b. Numbers of trees that were valid for growth calculations are shown with mean absolute (agr, mm y⁻¹) and mean relative (rgr, mm m⁻¹ y⁻¹) growth rates.

Species	n valid trees			agr			rgr		
	P1	P2a	P2b	P1	P2a	P2b	P1	P2a	P2b
<i>Aporosa falcifera</i>	57	54	57	2.89	1.39	2.42	12.80	5.42	9.52
<i>Ardisia sanguinolenta</i>	125	114	109	2.13	1.08	2.41	12.35	4.88	13.59
<i>Baccaurea tetrandra</i>	57	52	55	2.00	1.14	2.84	8.37	3.92	12.49
<i>Cleistanthus contractus</i>	85	75	86	1.39	0.67	2.76	7.81	4.03	14.93
<i>Dacryodes rostrata</i>	51	45	40	1.51	1.67	1.92	7.49	6.99	9.06
<i>Dimorphocalyx muricatus</i>	227	209	213	0.92	0.74	2.89	5.26	3.72	16.54
<i>Dysoxylum cyrtobotryum</i>	39	32	32	5.52	3.81	5.45	20.28	12.56	18.76
<i>Fordia splendidissima</i>	119	105	101	1.71	1.20	2.28	9.52	5.99	12.22
<i>Litsea caulocarpa</i>	66	52	46	3.77	2.67	4.18	18.20	11.58	18.23
<i>Litsea ochracea</i>	47	42	35	4.12	1.91	2.61	16.98	8.08	10.19
<i>Lophopetalum beccarianum</i>	64	60	56	2.92	3.24	5.31	15.11	14.32	24.39
<i>Madhuca korthalsii</i>	97	89	86	1.99	1.73	2.44	10.35	7.71	12.44
<i>Mallotus penangensis</i>	48	44	44	1.99	1.44	2.35	12.10	8.35	13.87
<i>Mallotus wrayi</i>	569	517	493	1.60	1.04	2.78	9.08	5.73	14.83
<i>Maschalocorymbus corymbosus</i>	65	58	52	1.34	0.85	1.99	8.44	4.45	11.80
<i>Pentace laxiflora</i>	34	27	26	3.98	3.08	4.85	16.03	9.03	16.41
<i>Polyalthia cauliflora</i>	104	97	94	0.85	0.57	1.28	4.77	2.63	7.37
<i>Polyalthia rumphii</i>	46	45	41	1.77	1.38	3.67	8.60	6.81	17.91
<i>Polyalthia sumatrana</i>	45	35	31	3.61	3.22	5.17	17.54	15.18	23.57
<i>Polyalthia xanthopetala</i>	41	30	26	2.49	1.95	2.50	11.17	9.01	12.50
<i>Reinwardtiodendron humile</i>	49	42	40	0.99	-0.08	1.27	4.97	-2.46	7.84
<i>Shorea fallax</i>	62	51	43	4.99	2.47	3.24	17.51	6.80	8.67
Totals:	2097	1875	1806						
Weighted means:				2.01	1.33	2.81	10.11	6.08	14.11

5.5.3. Growth in size classes

Numbers of trees that were valid for growth rate calculations were sufficient: even in the 40 – < 50 cm-class, there were > 100 trees available (Table 47).

The decline of rgr between periods 1 and 2a and subsequent recovery between periods 2a and 2b was visible across all size classes, gradually becoming less pronounced with increasing size (Figure 37). Growth of the smallest trees (10 – < 20 cm gbh) in period 2a was *c.* 45% below that of period 1 but increased by *c.* 129% during period 2b. All size classes had higher rgr in period 2b compared to period 1 (*c.* 16% – 25%).

Differences in growth between size classes were slight during period 1, but more variability was seen in periods 2a and 2b. During period 2a, growth rates increased with size class: the smallest trees seemed to be most affected by the drought (Figure 37).

Table 47. Numbers of trees valid for growth calculations in 10-cm size classes for periods 1, 2a and 2b in PEPs at Danum.

Size class (cm gbh)	n valid trees		
	P1	P2a	P2b
10 – < 20	2623	2109	2004
20 – < 30	847	851	843
30 – < 40	319	352	349
40 – < 50	137	161	140
Totals:	3926	3473	3336

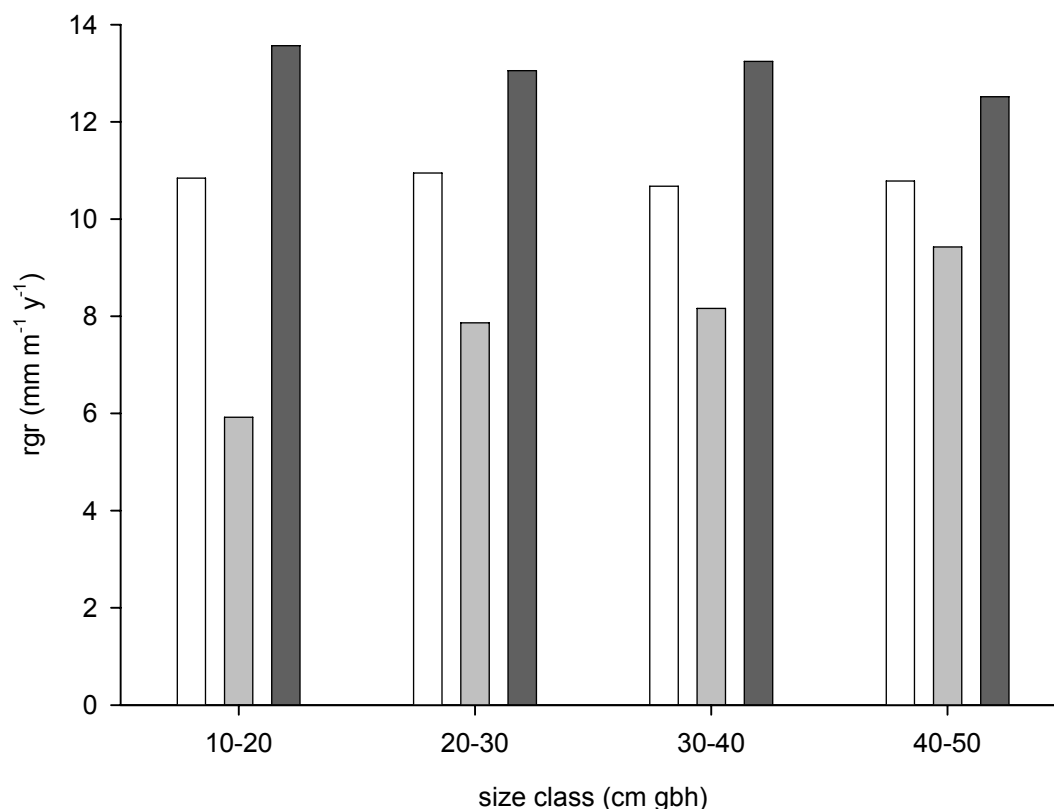


Figure 37. Mean relative growth rates within size classes (limits are \geq and $<$) in PEPs at Danum in period 1 (open bars), period 2a (light grey bars) and period 2b (dark grey bars).

5.5.4. Growth in topographic classes

Trees on intermediate topographic locations (with just more than half of the trees as in the other two classes; Table 48) had the highest relative growth rates in period 1, and also showed the greatest decline between periods 1 and 2a (*c.* -45%) compared to trees on ridges, lower slopes (Figure 38) or all locations pooled. Trees on lower slopes grew slightly better than those on ridges in periods 1 and 2a. Trees on ridges were more affected in period 2a (*c.* -40% compared to period 1) but recovered better than on lower slopes in period 2b (*c.* 135% vs. *c.* 65% respectively, compared to period 2a) and then displayed the strongest gain in growth compared to period 1 (*c.* 42%) and the highest rates of all topographic classes in all periods (Figure 38).

Table 48. Numbers of trees valid for growth rate calculations within topographic classes in PEPs at Danum, 1986 – 2001.

Topographic class	n valid trees		
	P1	P2a	P2b
ridge	1497	1339	1280
lower slope	1598	1391	1359
intermediate	831	743	697
Totals:	3926	3473	3336

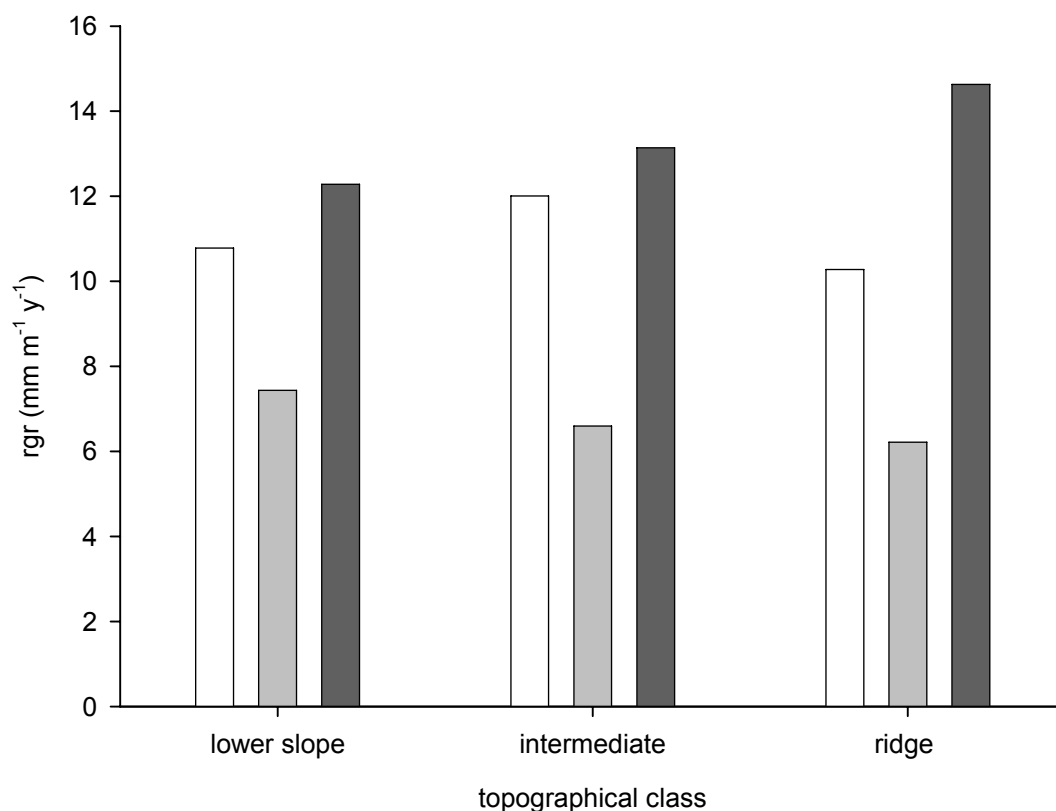


Figure 38. Mean relative growth rates for trees on lower slope, intermediate and ridge locations in PEPs at Danum in period 1 (open bars), period 2a (light grey bars) and period 2b (dark grey bars).

5.6. Growth and mortality

5.6.1. Species-specific responses to drought

The joint results of mortality and growth changes across periods for the most abundant species of the small-tree population in the PEPs (Table 49) suggest species-specific reactions to the 1997/98 drought.

All species showed an immediate negative reaction in growth shortly after the drought (period 2a), but recovered already in period 2b. In most species (19), mortality was either immediately (in period 2a) or with some lag (in period 2b) negatively affected (*i.e.* increased mortality rates). Twelve species that showed this response had mortality rates in period 2b that were elevated above the level in period 1, but also reached growth rates well above (> 10%) those of period 1. This group included *Mallotus wrayi*, the ubiquitous and overall most abundant species (Table 49).

Two species displayed a fast recovery from high mortality of period 2a in period 2b with rates dropping much (by *c.* 45 – 61%) below the first-period levels: *Dysoxylum cyrtobotryum* – with growth rates in period 2b that came close (within > 90%) to those of period 1 again – and *Dimorphocalyx muricatus* – which had a mean rgr in period 2b that was more than three times as high as in period 1. Two more species recovered in period 2b from high mortality rates in period 2a but not below the levels of period 1 and had growth rates in period 2b within \pm 10% of those in period 1 (*Litsea caulocarpa* and *Pentace laxiflora*; Table 49).

For six species, a response to the drought was more clearly identifiable: three species did not recover in mortality – the increase in mortality rates was immediate in period 2a and persistent, either remaining on that elevated level or even increasing further in period 2b, resulting in mortality rates > 50% above those of period 1 – and could not reach the growth levels of period 1 in period 2b (-10% to -50%), indicating a severe and at least medium-term negative effect of the drought on *Aporosa falcifera*, *Litsea ochracea* and *Shorea fallax* (Table 49). Relatively unaffected by the drought in terms of mortality or even displaying overall reduced mortality and at the same time exceeding the growth rates of period 1 in period 2b were: *Mallotus penangensis*, *Cleistanthus contractus* and *Lophopetalum beccarianum* (Table 49). The latter species' rgr was also least affected in period 2a compared to period 1 (-5.2%).

Dimorphocalyx muricatus, *C. contractus* and *L. beccarianum* had also been identified as being drought tolerant / avoiding in earlier work at Danum (Newbery *et al.* 1996).

No family-specific reaction was visible, except that all four species of the Annonaceae showed persistent high mortality while their growth recovered. Euphorbiaceae were represented in four out of five proposed groups of a classification for the species responses to drought (Table 49).

Table 49. Species specific responses to drought: changes in mortality rates and relative growth rates between periods 2a and 1, 2b and 2a, 2b and 1 and the resulting species grouping for the 22 most abundant species (small trees) at PEPs, Danum, 1986 – 2001. Change of mortality rates is expressed as: +++: $\geq 100\%$ increase; ++: 50-100% increase; +: 10-50% increase; \approx : 0-10% increase or decrease; ---: $\geq 100\%$ decrease; --: 50-100% decrease; -: 10-50% decrease. Full family names and their codes are given in Appendix Table 1.

Species	Family	change in mortality				change in growth				response to drought
		2a vs. 1	2b vs. 2a	2b vs. 1	2a vs. 1	2b vs. 2a	2b vs. 1	2a vs. 1		
<i>Cleistanthus contractus</i>	Euph	\approx	\approx	\approx	-	+++	++			
<i>Lophopetalum beccarianum</i>	Cela	---	\approx	---	\approx	++	++		drought resistant	
<i>Mallotus penangensis</i>	Euph	\approx	---	---	-	++	+			
<i>Aporosa falcifera</i>	Euph	+	+	++	--	++	-			
<i>Litsea ochracea</i>	Laur	+	+++	+++	--	+	-		persistently affected	
<i>Shorea fallax</i>	Dipt	+++	\approx	+++	--	+	--			
<i>Litsea caulocarpa</i>	Laur	+++	--	+	-	++	\approx		(persistently affected)	
<i>Pentace laxiflora</i>	Tili	++	-	+	-	++	\approx			
<i>Dimorphocalyx muricatus</i>	Euph	++	--	--	-	+++	+++		immediately affected, recovered: resilient	
<i>Dysoxylum cyrtobotryum</i>	Meli	+	--	-	-	+	\approx			
<i>Ardisia sanguinolenta</i>	Myrs	+	++	+++	--	+++	+			
<i>Baccaurea tetrandra</i>	Euph	-	++	++	--	+++	+			
<i>Dacryodes rostrata</i>	Burs	+++	--	+++	\approx	+	+			
<i>Fordia splendidissima</i>	Legu	+++	+	+++	-	+++	+			
<i>Madhuca korthalsii</i>	Sapo	+	+++	+++	-	++	+		immediately or lagged but persistent high mortality, growth recovered	
<i>Mallotus wrayi</i>	Euph	+	\approx	+	-	+++	++			
<i>Maschalocorymbus corymbosus</i>	Rubi	-	+++	+++	-	+++	+			
<i>Polyalthia cauliflora</i>	Anno	\approx	+	++	-	+++	++			
<i>Polyalthia rumphii</i>	Anno	---	+++	+++	-	+++	+++			
<i>Polyalthia sumatrana</i>	Anno	+++	-	+++	-	++	+			
<i>Polyalthia xanthopetala</i>	Anno	+++	--	+	-	+	+			
<i>Reinwardtiodendron humile</i>	Meli	+	\approx	+	---	+++	++			

5.6.2. Growth and subsequent mortality

Growth rates were calculated separately for trees that were still alive in the following period and for those that died until the next enumeration to detect whether trees already showed reactions before they actually died, if death is following a preceding weakening of the trees. As there were few counts of dead trees even within the most abundant species (mean 5 – 6), it was not possible to do these calculations on species level and thus were performed across all trees only.

In period 1, the growth of trees that died between 1996 and 1999 was just more than half of that of trees that were still alive in 1999 (Figure 39). 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 (*c.* 29% for rgr, less pronounced with *c.* 21% for agr). Growth in period 2a of trees that died during period 2b was even two thirds lower than that of the trees that still lived in 2001 (Figure 39). Both Mann-Whitney U and Kolmogorov-Smirnov tests showed highly significant ($P < 0.001$) differences between all combinations mentioned.

Imminent tree deaths seem to be indicated by reduced growth rates.

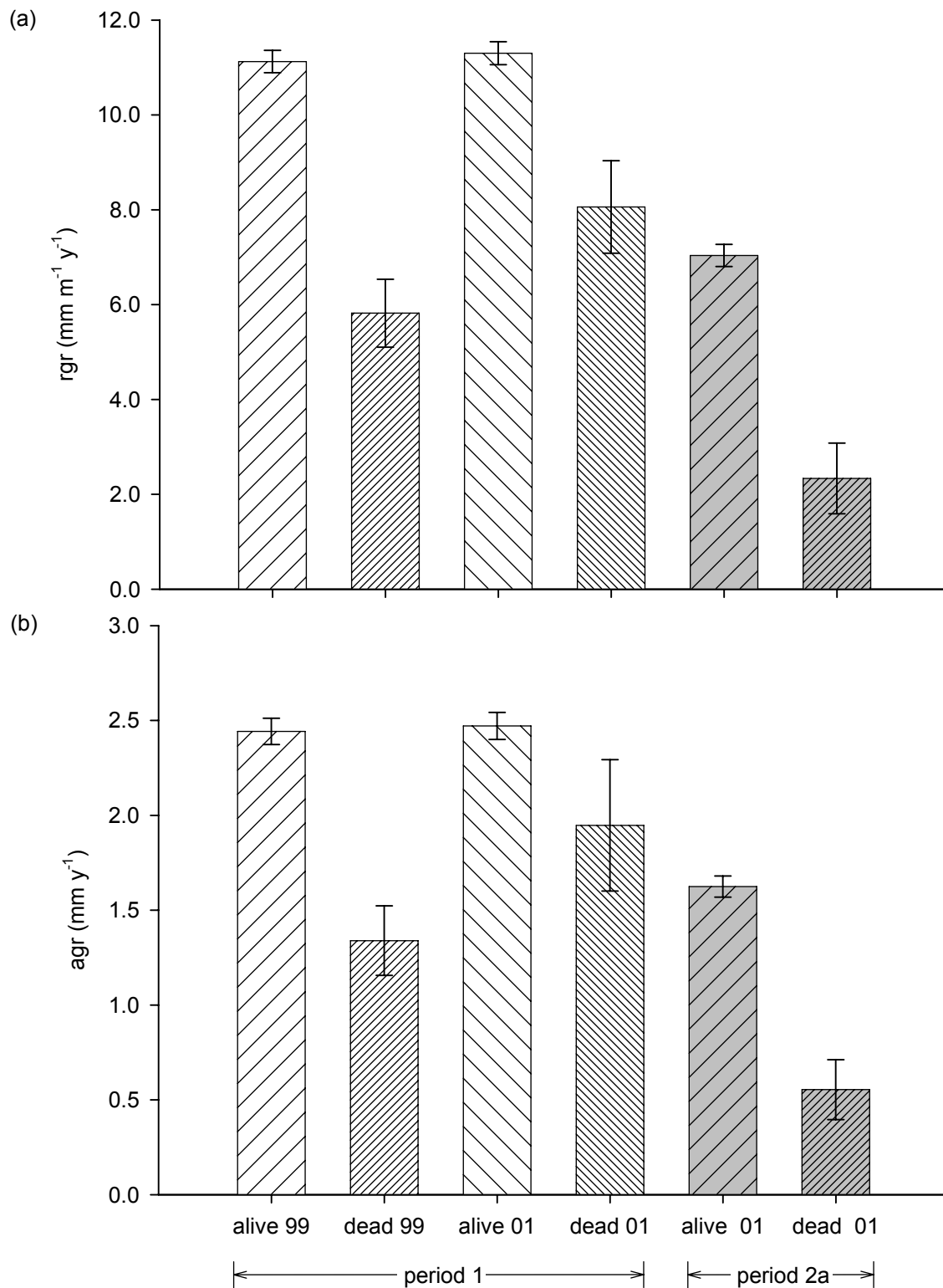


Figure 39. Growth and subsequent mortality (\pm SE) in PEPs at Danum: rgr (a) and agr (b) in periods 1 (white bars) and 2b (grey bars) for trees that were alive (coarse pattern) and those that were dead (fine pattern) in the following period(s). Tree numbers included ranged from 3289 – 3720 for alive and from 184 – 206 for dead trees.

5.6.3. Estimation of the immediate effect of the 1997/98-drought on mortality and growth

Mortality and growth rates of period 1 (1986-1996) were assumed to be valid until the onset of the 1998-drought. The starting point of that disturbance event was set to 04.04.1998, when the 30-d rt of rainfall was < 100 mm for 10 d.

As mortality between individual PEPs varied in the manner that some subplots had lower m_a in period 2a than in period 1 and therefore estimated numbers of dead trees for 1999 could be higher than the number actually found (this was the case for one PEP), the estimation of rates was performed across all trees pooled.

Mortality

If m_a of period 1 is taken as being constant until the drought of 1998 (the estimated period 1e, 1986 – 1998), then the number of trees present at the new starting point in 1998 (n_{98e}) can be calculated by (Sheil and May 1996): $n_{98e} = n_{96} (1 - m_a P1)^{IntP2x}$, with IntP2x being the interval of 1996 – 1998.

The number of dead trees in 1998 (n_{d98e}) resulted from $n_{96} - n_{98e}$. These trees had to be subtracted from the trees that were recorded in the field in 1999 as being dead, i.e. having died between 1996 and 1999, to get the number of trees that died between 1998 and 1999, the new period for which the mortality rate is sought (period 2e): $n_{d99e} = n_{d99} - n_{d98e}$.

The resulting annualised mortality rate for period 2e is therefore estimated to be 3.64% y^{-1} . As this value is not corrected for group mortalities or time interval differences, it has to be compared with the simple annualized rates from period 1 and period 2b. Thus, mortality in period 2e – in the nine months during and immediately after the 1998-drought – would have more than doubled compared to that of period 1. The rate in the post-drought period 2b would have been lowered by more than a third (Table 50).

These comparisons have to be treated with caution in respect to the differing interval lengths, though: mortality in period 1e (c. 12 y) is most likely underestimated, mortality in periods 2e (c. 1 y) and 2b (c. 2.5 y) overestimated and m_{corr} would bring these rates closer together.

Table 50. Estimation of the immediate effect of the 1998-drought on mortality in PEPs at Danum. Variables needed to derive the drought mortality (Int: interval length; n: number of trees) and pre-, drought and post-drought mortality rates (m_a) are shown. For explanations, see text.

Variable		Mortality rate		
IntP1e:	11.83 y			
IntP2x:	1.84 y			
IntP2e:	0.78 y			
n_{98} :	4239			
n_{98e} :	4120			
n_{d98e} :	119	m_aP1e :	1.53	% y^{-1}
n_{d99} :	237	m_aP2e :	3.64	% y^{-1}
n_{d99e} :	118	m_aP2b :	2.32	% y^{-1}

For the 22 most abundant species within the PEPs, mean m_a of P2e is estimated at 4.10% y^{-1} . This would be a 2.7-fold increase compared to period 1 and then a decrease by *c.* 45% into period 2b (Table 51).

Two species' rates had to be adjusted: *Polyalthia rumphii* and *Lophopetalum beccarianum* would have negative mortality rates because they did not have any dead trees in 1999, but the continued rate of period 1 would have predicted some and thus their n_{d99e} was estimated to be higher than the dead trees actually found. Mortality for these two species was therefore set to zero (Table 51).

All other species increased in mortality in period 2e compared to period 1 by up to > 10-fold (*Dacryodes rostrata*) (Table 51). Thirteen species then showed lower m_a in period 2b compared to period 2e, but seven species further increased in m_a .

Table 51. Mortality of the most abundant species in the estimated period 2e (1998 – 1999) in PEPs at Danum. Table is sorted ascending by m_a P2e. Two species' rates (^a) were manually adjusted to 0%; see text for explanation. Fractions of tree numbers are given because these are estimated rates and when omitting the decimal, the rates would partially not be plausible (e.g. *B. tetrandra*).

Species	n_{98e}	n_{d99e}	m_a P2e (% y^{-1})
<i>Polyalthia rumphii</i> ^a	47.1	0.0	0.00
<i>Lophopetalum beccarianum</i> ^a	65.4	0.0	0.00
<i>Baccaurea tetrandra</i>	64.4	0.4	0.73
<i>Madhuca korthalsii</i>	101.9	0.9	1.16
<i>Cleistanthus contractus</i>	101.0	1.0	1.20
<i>Mallotus penangensis</i>	46.5	0.5	1.27
<i>Polyalthia cauliflora</i>	105.4	1.4	1.72
<i>Ardisia sanguinolenta</i>	135.0	2.0	1.83
<i>Litsea ochracea</i>	47.7	0.7	1.94
<i>Aporosa falcifera</i>	64.0	1.0	2.00
<i>Maschalocorymbus corymbosus</i>	74.5	1.5	2.53
<i>Mallotus wrayi</i>	594.9	14.9	3.21
<i>Dimorphocalyx muricatus</i>	246.0	7.0	3.51
<i>Dysoxylum cyrtobotryum</i>	39.4	1.4	4.58
<i>Fordia splendidissima</i>	131.6	5.6	5.41
<i>Reinwardtiodendron humile</i>	51.5	2.5	6.29
<i>Polyalthia sumatrana</i>	42.1	2.1	6.43
<i>Pentace laxiflora</i>	34.4	2.4	8.81
<i>Shorea fallax</i>	61.7	4.7	9.76
<i>Dacryodes rostrata</i>	53.3	4.3	10.07
<i>Litsea caulocarpa</i>	69.0	10.0	18.06
<i>Polyalthia xanthopetala</i>	39.7	7.7	24.17
Totals:	2216.4	71.9	
Weighted means:			4.10

Growth

Mean absolute growth rate of period 1 was applied to the gbh of 1996 with the new end date (interval length: 1.84 y) to get gbhs in 1998. These were restricted to the range 10 – < 50 cm and used to calculate absolute and relative growth rates 1998-1999, the estimated period 2e (0.78 y). Rates were then compared between periods 1e (interval length: 11.80 y; same rates as for period 1), 2e and the unchanged period 2b (2.42 y).

The resulting growth rates for period 2e were negative: $agr = -0.44 \text{ mm } y^{-1}$ (range: -287.90 – 92.72); $rgr = -2.38 \text{ mm m}^{-1} y^{-1}$ (range: -871.86 – 543.18). The extreme values point to some possible difficulties with measurements for a few trees in this

approach. However, excluding those values at the ends of the range would presumably not change the mean substantially as the distribution is symmetric. Furthermore, logit-transformed agrs did not reveal a break in the distribution (positive or negative) that would justify the cut-off of certain values (Figure 40).

Hence, during the time from April 1998 to January 1999, including 48 d of drought and the *c.* eight following months, small trees in the PEPs on average decreased in girth by -0.34 mm, equivalent to a shrinkage in diameter of 0.11 mm.

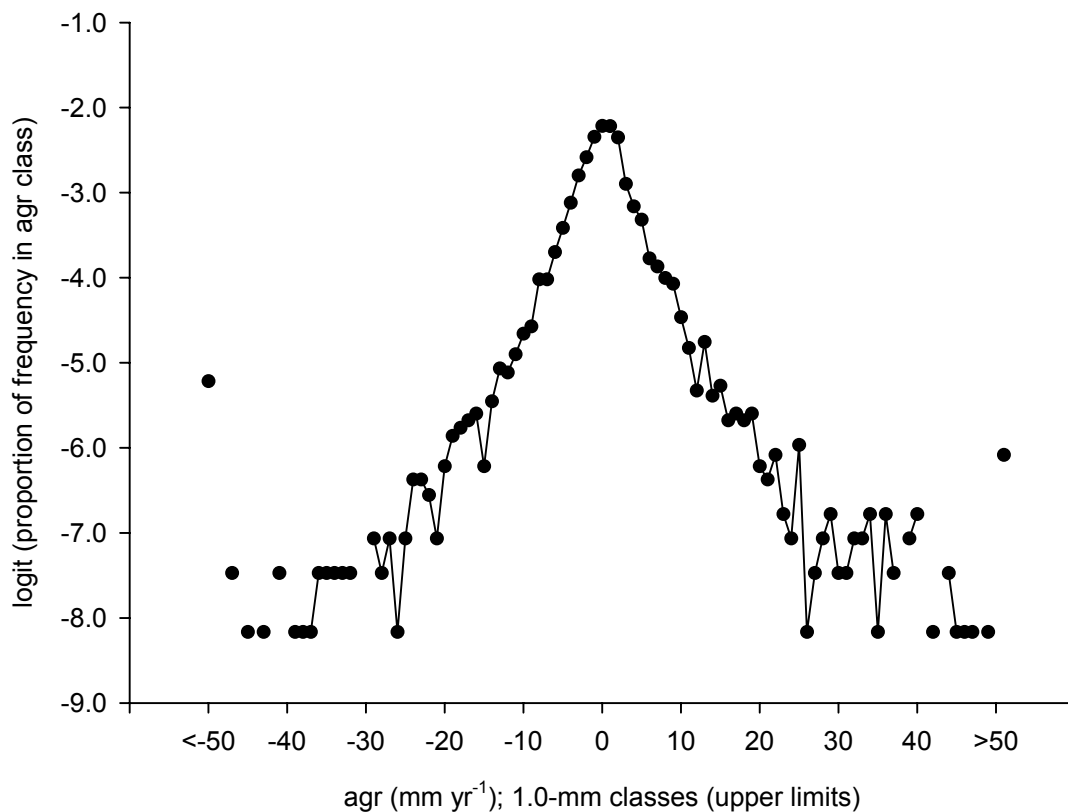


Figure 40. Logit-transformed distribution of growth rates within the estimated period 2e (1998-1999) in PEPs at Danum.

The mean agr of the most abundant species was even lower than the average across all trees: -1.06 mm y⁻¹ (Table 52). Sixteen of the most abundant species showed a negative agr-estimate in period 2e, with *Litsea ochracea* having had the most negative rate. Only six species continued to grow during the drought period, and only *Polyalthia sumatrana* is estimated to have grown better than in period 1 (Table 52).

Table 52. Growth of most abundant species in the estimated period 2e (1998-1999) in PEPs at Danum. Table is sorted ascending by agr P2e.

Species	n valid trees	agr P2e (mm y ⁻¹)	rgr P2e (mm m ⁻¹ y ⁻¹)
<i>Litsea ochracea</i>	43	-5.25	-15.85
<i>Cleistanthus contractus</i>	81	-4.81	-19.94
<i>Ardisia sanguinolenta</i>	120	-3.58	-21.53
<i>Reinwardtiodendron humile</i>	41	-3.01	-20.02
<i>Shorea fallax</i>	50	-2.22	-10.27
<i>Aporosa falcifera</i>	54	-1.45	-7.02
<i>Pentace laxiflora</i>	28	-1.34	-18.52
<i>Baccaurea tetrandra</i>	53	-1.34	-7.61
<i>Mallotus wrayi</i>	525	-1.30	-4.82
<i>Fordia splendidissima</i>	109	-1.15	-4.90
<i>Dysoxylum cyrtobotryum</i>	33	-0.87	-2.07
<i>Polyalthia cauliflora</i>	99	-0.57	-4.47
<i>Dimorphocalyx muricatus</i>	216	-0.53	-3.06
<i>Maschalocorymbus corymbosus</i>	57	-0.22	-2.88
<i>Mallotus penangensis</i>	44	-0.17	0.45
<i>Polyalthia xanthopetala</i>	30	-0.07	3.51
<i>Litsea caulocarpa</i>	52	0.11	1.15
<i>Polyalthia rumphii</i>	45	0.52	4.71
<i>Madhuca korthalsii</i>	89	0.86	2.96
<i>Dacryodes rostrata</i>	46	1.27	4.11
<i>Lophopetalum beccarianum</i>	62	2.87	10.51
<i>Polyalthia sumatrana</i>	35	3.35	16.90
Totals:	1912		
Weighted means:		-1.06	-5.14

Revised species-specific responses of growth and mortality

The classification of species-specific responses to the 1998-drought in respect to growth and mortality (see 5.5.1. above) has to be revised as there do not seem to be true 'drought resistant species'. The relations between periods 1 and 2b do not change, but different responses are revealed between periods 1 and 2e and periods 2e and 2b.

With the exception of *Polyalthia sumatrana* – which slightly increased in rgr by 6.50% (but had high persistent mortality) – all species showed reduced growth between periods 2e and 1. The three species termed drought resistant above (constant or decreasing mortality and only slightly decreasing rgr between periods 1 and 2a, but strongly increasing into period 2b) were shown to be affected immediately by the drought in reduced rgr by *c.* 31 – > 100%. However, they still recovered into period 2b in growth

and their mortality relations hardly changed. A better classification could be 'drought resistant in regard to mortality, immediately affected but resilient in regard to growth'.

Five species showed, in contrast to the above, reduced mortality in period 2b compared to period 2e, i.e. they started to recover from the drought: *Aporosa falcifera*, *Shorea fallax*, *Fordia splendidissima*, *Mallotus wrayi* and *Reinwardtiidendron humile*, but their rates remained above the level of period 1.

6. Light in the understorey

A possible influence of the light conditions in the understorey on basal area, mortality, recruitment and growth was investigated with the results from hemispherical images taken in the main plots between April 2001 and January 2002. For this analysis, it was assumed that the conditions calculated from the hemiphotos were valid throughout period 2 (1996 – 2001) and could have affected tree growth and survival. Mean canopy openness (COP, %) – calculated with GLA-software – of five images taken at each of the 76 photo-points in each MP was used to assess the light environment.

Light levels in both MPs were similarly low: the mean across MP1 was (\pm SE) 4.99 ± 0.14 % (median: 4.59%; range: 3.62 – 9.36%) and across MP2 it was 4.92 ± 0.10 % (median: 4.78%; range: 3.36 – 8.41%). The frequency distribution of canopy openness at the photo-points was right skewed and the largest proportion of points had $COP \leq 5\%$ (51 points in each MP). Only eight points in MP1 and four in MP2 had $COP > 7\%$ (Figure 41). These were taken as 'high light' points and compared with the equal number of those points with the lowest COP in each MP and for both MPs combined. A second comparison included the eight brightest and the eight darkest points in each MP, given for both plots pooled.

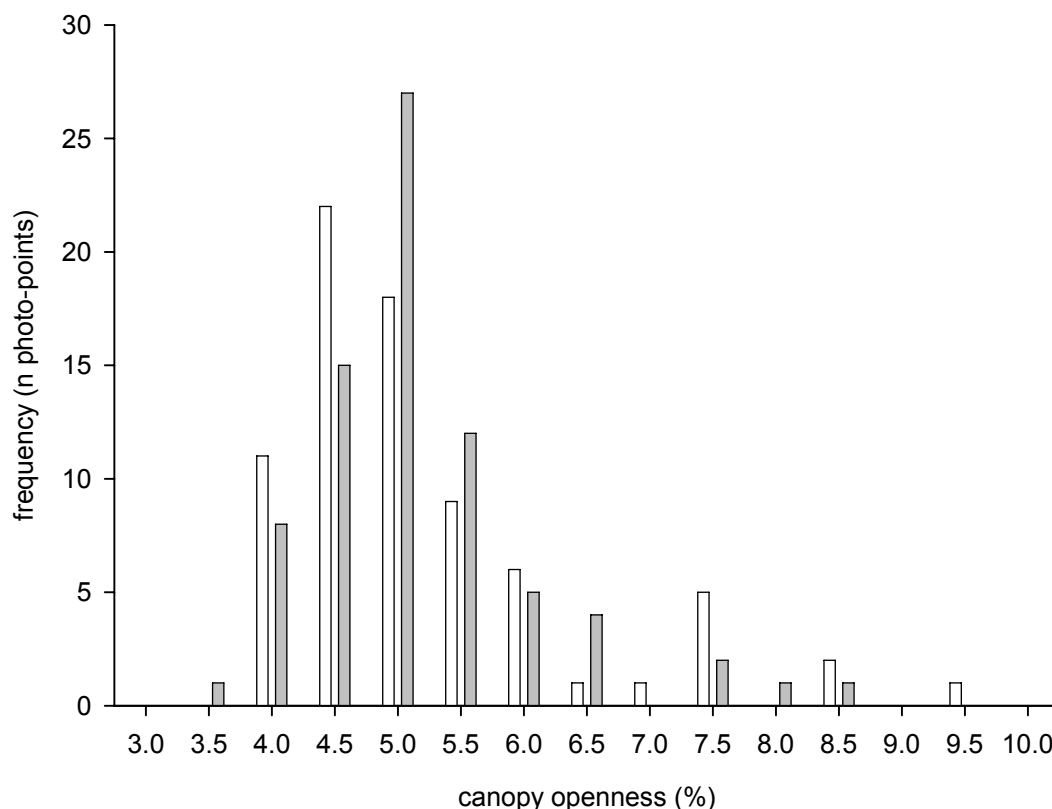


Figure 41: Frequency distribution of mean canopy openness (upper class limits) at hemiphoto-points in MP1 (open bars) and MP2 (grey bars) at Danum for the period April 2001 – January 2002.

Variables (n trees dead/alive, gbhs) were found within circles around each selected photo-point with two different runs for circle areas of 500 m² and 1000 m². Recruitment, mortality and growth rates of period were calculated for all trees (gbh 1996 ≥ 10 cm) and – since hemiphotos were taken at 1 m height and therefore represent light conditions in the lower vertical stratum – for the smallest trees (gbh 1996 10-15 cm gbh). Mean tree numbers within the selected circles ranged from 40 (smallest trees, 500 m²) to 219 (all trees, 1000 m²) and did not fall < 20. The possibility that the light conditions calculated from the hemiphotos might only be valid for even smaller circle areas (100 m²) could not be analysed as tree numbers within such small circles dropped to < 10 at most of the points.

Differences between high and low light points were analysed using one-way ANOVA (no blocking) with light as the treatment (runs with MWU-tests gave very similar results regarding significances) (Table 53).

The results of the comparison did not detect any differences in basal area and recruitment rate between high and low light points in any of the tested combinations (Table 53). None of the variables tested in MP2 were significantly different between high and low light points (only four points each; Table 53a).

Only in MP1, when all trees were included and within the 500 m² -circles, growth rates (agr and rgr) were significantly higher at high than at low light points. This effect disappeared in 1000-m² circles or when using the smallest trees only and was not visible in any other case (Table 53a).

Mortality rate did show a more consistent pattern across several plots, size classes and areas: in the comparison of points with COP \leq 5% and \geq 7%, m_a was significantly higher at high light than at low light points in MP1 for all trees in 500-m² and 1000-m² circles and for the smallest trees in 500-m² circles and also when combining both MPs for all trees in 500-m² circles (Table 53a). When comparing the brightest with the darkest points, m_a is again higher at high light points for all trees in both circle areas and for the smallest trees in 500 m² circles (Table 53b).

Table 53: Comparison of structural and dynamic variables of period 2 between high and low light points within the main plots at Danum for all and for the smallest (gbh 10-15 cm) trees in 500 m² and 1000 m² circles. (a) includes eight high (canopy openness, COP > 7%) and eight low (COP ≤ 5%) light points of MP1 and four each of MP2. (b) compares the eight brightest with the eight darkest points of each MP. Significant results from the ANOVAs are given in bold type.

			500 m ²			1000 m ²		
variable			mean		ANOVA	mean		ANOVA
			high light	low light	F prob.	high light	low light	F prob.
(a)	MP1	COP (%)	7.83	3.81	(df = 15)			
	all trees	ba (m ²)	1.68	1.33	0.360	3.21	3.74	0.295
		r _a (% y ⁻¹)	1.86	1.40	0.171	1.55	1.32	0.510
		m _a (% y ⁻¹)	4.05	1.48	<0.001	2.79	1.60	0.002
		agr (mm y ⁻¹)	4.31	3.58	0.039	3.84	3.49	0.252
		rgr (mm m ⁻¹ y ⁻¹)	18.59	14.76	0.041	16.86	14.17	0.067
	smallest	ba (m ²)	0.04	0.05	0.063	0.09	0.09	0.687
		m _a (% y ⁻¹)	3.40	1.05	0.009	2.42	1.33	0.055
		agr (mm y ⁻¹)	2.80	2.33	0.268	2.56	2.19	0.190
		rgr (mm m ⁻¹ y ⁻¹)	21.00	17.00	0.157	19.29	16.04	0.092
	MP2	COP (%)	7.54	3.55	(df = 7)			
	all trees	ba (m ²)	1.81	1.20	0.243	3.49	2.77	0.213
		r _a (% y ⁻¹)	0.91	1.41	0.441	0.84	1.34	0.288
		m _a (% y ⁻¹)	2.83	3.23	0.525	2.33	2.76	0.460
		agr (mm y ⁻¹)	2.57	3.09	0.509	2.76	3.14	0.665
		rgr (mm m ⁻¹ y ⁻¹)	10.00	15.00	0.407	10.60	13.70	0.509
	smallest	ba (m ²)	0.05	0.04	0.382	0.10	0.09	0.474
		m _a (% y ⁻¹)	2.40	3.20	0.424	1.80	3.10	0.064
		agr (mm y ⁻¹)	1.50	2.55	0.374	1.52	2.09	0.509
		rgr (mm m ⁻¹ y ⁻¹)	11.60	18.80	0.396	11.90	15.60	0.558
	MP	COP (%)	7.73	3.73	(df = 23)			
	all trees	ba (m ²)	1.72	1.29	0.134	3.30	3.42	0.767
		r _a (% y ⁻¹)	1.54	1.40	0.644	1.32	1.33	0.964
		m _a (% y ⁻¹)	3.64	2.06	0.005	2.63	1.98	0.051
		agr (mm y ⁻¹)	3.73	3.42	0.438	3.48	3.37	0.763
		rgr (mm m ⁻¹ y ⁻¹)	15.70	14.80	0.706	14.78	14.01	0.678
	smallest	ba (m ²)	0.04	0.05	0.390	0.09	0.09	0.783
		m _a (% y ⁻¹)	3.07	1.76	0.064	2.22	1.92	0.529
		agr (mm y ⁻¹)	2.37	2.40	0.938	2.22	2.16	0.858
		rgr (mm m ⁻¹ y ⁻¹)	17.90	17.60	0.936	16.80	15.90	0.687
(b)	MP	COP (%)	7.35	3.77	(df = 31)			
	all trees	ba (m ²)	1.84	1.44	0.122	3.41	3.35	0.839
		r _a (% y ⁻¹)	1.51	1.31	0.437	1.31	1.31	0.996
		m _a (% y ⁻¹)	3.43	1.97	0.002	2.58	1.88	0.008
		agr (mm y ⁻¹)	3.63	3.24	0.258	3.36	3.22	0.638
		rgr (mm m ⁻¹ y ⁻¹)	15.09	13.85	0.529	14.07	13.39	0.657
	smallest	ba (m ²)	0.04	0.05	0.252	0.09	0.09	0.707
		m _a (% y ⁻¹)	2.76	1.66	0.043	2.17	1.86	0.394
		agr (mm y ⁻¹)	2.32	2.15	0.664	2.11	2.02	0.734
		rgr (mm m ⁻¹ y ⁻¹)	17.60	16.00	0.561	16.13	17.98	0.563

VI. Discussion

1. Methodological and conceptual considerations

The data-set of the present work is unique for the following reasons:

(i) High quality.

Special care was taken with the measurements themselves. A small team of conscientious instructed workers took the tree measurements, and the principal researcher was always in the field during data-collection, doing the recording and assessment of tree-status. Standard protocols (*c.f.* Alder and Synnott 1992, Sheil 1995, Phillips and Baker 2002) were followed, including sensitive issues regarding tree-tagging, stem deformations, buttresses, recording point of measurement etc. Taxonomic identifications were carried out thoroughly, with re-checking and comparison with herbarium material (in an exemplary good collaboration between local and European taxonomists) to achieve a level of identifications to distinct species of 99.8% with great certainty.

(ii) Extent.

A total of 18902 trees in a total area of 8 ha were visited in 2001. The relatively low size limit of the trees measured (≥ 10 cm gbh, i.e. ≥ 3.2 cm dbh) resulted in a large number of trees of the understorey being part of the population sampled; *c.* 79% of all trees were < 10 cm dbh and these would have not been recorded if that minimum size (standard for many forestry studies) would have been applied. To reach an adequate sample size for large trees (especially when partitioning into species or size classes), however, the plot-size has to be recognized as being at the lower limit.

(iii) Replication.

There were two 4-ha plots.

(iv) Elevational gradient.

To study the potential influence of water availability in relation to topography, each main plot had a lower slope to ridge gradient.

(v) Long-term record.

Three full enumerations (1986, 1996, 2001) over *c.* 15 y with this level of consistency, intensity and data quality in the tropics is relatively rare.

For the analysis of growth rates, trees with unreliable girth measurements were excluded. With this conservative approach, possible bias through 'abnormal' growth (e.g. buttresses moving upwards or development of reaction-wood on steep slopes) or measurement uncertainties through the use of optical instruments were minimized.

Detection of dead trees was not considered a problem in the field in 2001. While scanning the status of each tree, it was recognised whether crowns were damaged, leafless or whether the stem was intact or rotten, losing bark, etc. In ambiguous cases, the bark was lightly cut with a knife to find living tissue. However, some trees that were marked as dead in the 1999 partial enumeration were found to be alive in 2001 (and the data-base was accordingly adjusted). Most of them were small trees, often broken and coppicing. Errors of this kind could not be completely precluded, but particular care was taken to avoid them because the resulting bias in estimating dynamics variables, especially mortality rate, can be significant. Ideally, status 'dead' should be checked and confirmed 3 – 6 mo after an enumeration.

The partial enumeration of 1999 allowed a further valuable insight into the forests' response by being immediately after the 1997/98-drought. However, many restrictions of that data-set meant that only a limited part of the population could be analysed and interpretations had to be treated with caution until verification at the next full enumeration.

Comparison of species-specific responses to the drought of 1997/98 hint at some draw-backs of the 1999-data: smaller area sampled, lower numbers of trees, the non measurement of recruits and regressors. Those species that were resistant in terms of mortality and resilient with regard to growth (*Cleistanthus contractus*, *Lophopetalum beccarianum* and *Mallotus penangensis*) all had higher mortality rates in period 2 than in period 1 in the whole of the main plots (c. 6% – 28%). Nevertheless, most of the species-specific responses were consistent for MPs and PEPs and the trend towards a differentiation in the response of species to a disturbance event like the severe drought holds.

A step forward was taken with the recognition and formulation of the problem with regressors in multiple censuses, leading to the calculation of 'losses' and 'gains'. Although these results are not yet comparable with other rain forest locations, efforts should be undertaken to standardize procedures in this respect.

The dependence of mortality on length of time interval in heterogeneous tropical forests has been shown by Sheil and May (1996). The idea of m_{all} was followed and further developed by Hämmerli (1999) and Newbery and Lingenfelder (2004) by making m_{all} conditional on a certain minimum number of individuals per species. In the present work, this approach was also adopted and additional information on the behaviour of an interval-corrected group mortality rate was gained. However, it remains debatable whether the rather complex procedure involved is practicable.

The ecologically unrealistic assumption behind annualised rates of mortality and recruitment as being constant over time still remains. Furthermore the number of trees that recruited into the population between two enumerations will remain unknown, these having died before they could be recorded and thus are not appearing in the data-set. An equally necessary interval-correction for annual recruitment rates was not made in the present study.

A different approach to a census-correction of mortality, recruitment and turnover was presented by Lewis *et al.* (2004). It was applied to an extensive data-set from the Amazon (Phillips *et al.* 2004) where the correction of mortality strangely resulted in elevated rates, regardless of whether time intervals between enumerations were shorter or longer than the interval to which they were corrected. The approach was not tested on the Danum data as there were only three main enumerations and the disturbance occurred in the second interval.

Debatable might also be the threshold for the exclusion of negative growth rates (≤ -4 mm y^{-1}) although all positive rates were included no matter how high they were. None of the calculated large increments were unrealistic however. Including growth rates down to -4 mm y^{-1} and not excluding every rate < 0 is physiologically sensible as it was 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. For this reason also the approach of Nakagawa *et al.* (2000), who excluded all growth rates ≤ -2 mm y^{-1} in diameter and set those > -2 and < 0 mm to zero growth, was not considered feasible. The selected threshold in the present study was not as low as the one of Condit *et al.* (2004): they stated that their method of excluding trees (where the second dbh was 4 standard deviations (of a special remeasurement) below the first one), compared to excluding trees that showed negative growth rates ≤ -5 mm y^{-1} in diameter (15.7 mm y^{-1} in girth), had little influence on their estimates.

2. Drought intensity at Danum

In addition to irradiance, water availability in a regime of normally evenly distributed high annual rainfall is one of the main factors for growth in aseasonal tropical rain forests (Newbery *et al.* 1999b, Baker *et al.* 2003). When precipitation fails to provide the vegetation with the expected amount of water, drought stress takes effect. Hitherto, the threshold for stressful conditions was set at 100 mm across 30 d (the estimated average rate of evapotranspiration in the tropics (e.g. Malhi *et al.* 2002)), often using monthly rainfall records, and intensities of droughts were assessed by counting the days or months for which rainfall was below that threshold. Taking the amount by which each month of a drought fell below 100 mm into account, the cumulative rainfall deficit (Walsh 1996b) quantifies the intensity at least for the period where a drought persists. The mean drought intensity index (Newbery and Lingenfelder 2004) incorporates the deficit during a drought with the drought duration.

As outlined in Chapter IV.1., the proposed antecedent rainfall history integrates past precipitation and is able to quantify a missing component to the forest water supply, overcoming the draw-backs of simple threshold-based approaches. However, it remains unknown for how far back rainfall history has an effect on hydrology, at what rates soil water storage is depleted, and to what extent trees may be capable of using internal stores of water. Not considered among these ideas is that moisture might reach trees in the form of high air-humidity, as dew or cloud droplets.

Judging from the deficits calculated (DEFARH) and observations of an extensive defoliation at Danum in April and May 1998 (Walsh and Newbery 1999, G. Reynolds, pers. comm.), the drought event of 1997/98 was the most severe since the start of meteorological measurements at Danum in 1985. The absolute minimum ARA365 during that drought was -1327.7 mm, i.e. almost half the average annual rainfall was missing in May 1998. These findings on the severity of the 97/98-drought are in accordance with those of Walsh and Newbery (1999) and Newbery and Lingenfelder (2004). Drought-conditions during that time were widespread across Borneo and reports from Sarawak (Nakagawa *et al.* 2000, Harrison 2001, Potts 2003), Sabah (Aiba and Kitayama 2002) and East Kalimantan (Slik 2004) indicate widespread strong water-stress to the vegetation.

Notes on any possible defoliation during other droughts were not available, so it must be concluded that events with possibly < -1000 mm DEFARH0 are ecologically severe in intensity. One such event took place in the 18.5 y of the present study. Two moderate (> 600 d and DEFARH0 < -400 mm) and five weak (> 10 d and DEFARH0 < 0 mm) events occurred during that time. Droughts of weak to moderate intensity have occurred frequently across Sabah since *c.* 1875 (3.25 times per 20 y; Walsh and Newbery 1999). Severe droughts across large parts of Borneo that were probably stronger than the 1997/98-one were recorded in 1877/78, 1914/15 and just before the setup of the main plots at Danum in 1982/83 (Beaman *et al.* 1985, Walsh 1996b, Walsh and Newbery 1999) and most likely affected them. The events of 1877/78, 1982/83 and 1997/98 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). The frequency of strong droughts at Danum was 1.54 per 20 y on average (Walsh 1996b, Walsh and Newbery 1999).

In summary, the climate data show that the forest at Danum, even if this site was not so strongly affected as the more drought-prone east coast of Sabah (Walsh and Newbery 1999), experienced mild to moderate droughts frequently and stronger ones approximately once (based on the present data) in 20 y. Therefore disturbances from drought events are an integral part of the environment at Danum and the tree species should be adapted to a 'natural' frequency and intensity of droughts. Although it remains difficult to estimate at what increased intensity/frequency drought might occur in the future (IPCC 2001), they have a long-lasting and possibly significant effects on forest structure and species composition. The antecedent rainfall history variable nevertheless allows droughts to be ranked according to their ecological impact and with future remeasurements of permanent research plots, it has the potential to provide the direct quantitative link between droughts and effects on the vegetation.

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

The following paragraphs aim at discussing responses of the forest at Danum under the described drought-disturbance regime and putting the dynamics into the context of other tropical rain forest locations.

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 disturbances were not disastrous in the sense that the forest was vitally damaged. If the forest was still recovering from catastrophic droughts *c.* 80 – 120 y ago (Newbery *et al.* 1999b, Newbery and Lingenfelder 2004), then the event of 1997/98 could be called a 'set-back', one that it seems the forest is capable of overcoming.

3.1. Immediate and lagged mortality and growth

Mortality did increase after 1996 by *c.* 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 6.2% and 8.9% in 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 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 disturbance – but still within the CARA232-event, i.e. in the period between 9 mo to 3 y after the drought. Also increases in growth rates did occur after 1999 (in period 2b), after a very strong decline in period 2a. Even though during the partial enumeration from December 1998 to March 1999 – 9 mo after the peak of the drought – rainfall was above average (mean 30-d-rt: 275 mm), measurements were still done within the drought event that lasted until mid-April 1999, when 30-d accumulated rainfall anomalies (ARA30) were < 0 mm almost half of the time and the conditional accumulation of the anomalies across 1 y (CARA232) was still < 500 mm during the complete 1999-

enumeration. It seems reasonable that under these circumstances, water storage in the outer tree compartments was not refilled by then and growth was not large enough to result in positive growth rates. Sheil (2003) reviewed different studies and performed an exploratory study on tropical diurnal tree stem diameters. He found that fluctuations in girth (shrinkage and expansion) of *c.* 0.5 mm – 2.0 mm d⁻¹ were not unexceptional. Karling (1934), whose study was included in Sheil's review, reported a dry-season decline across *c.* 4 mo for one *Achras zapota* in Honduras of 5.16 mm in diameter (16.2 mm in girth). In Ghana, Baker *et al.* (2002) observed dry-season (*c.* 4 mo) shrinkages as much as *c.* 2.8 mm in diameter (8.8 mm in girth).

Although a theoretical calculation, the result of the estimation of growth rates during period 2e (1998 – 1999; Chapter IV.5.6.3.), an average shrinkage in tree girth of 0.34 mm in *c.* 9 mo, is thus not surprising.

Two effects successively took place at Danum during and after the strong drought of 1997/98:

- (i) an immediate response in growth (negative impact) while mortality did not increase or only slightly increased (resistance, but possibly weakening), followed by
- (ii) lagged responses in mortality (negative impact) and increased growth (resilience).

Harrison (2001) hypothesised that even though droughts are not the direct trigger for flowering (Ashton *et al.* 1988), 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 mo of experiencing a short dry spell was found for trees in Sarawak and the flushing seemed to have induced cambium growth: 2 – 4 mo after the flushing or 3 – 6 mo 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 1997/98-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 (Borchert 2000), bud break and flushing assumingly soon after rainfall increased again ($30\text{-d-rt} > 100 \text{ mm?}$), but no cambium growth until water storage in the trees was completely refilled in the first quarter of 1999 (in April, when $\text{ARA365} > 0?$). 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.

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 mo) after the 1997/98-event. This drought was possibly more severe in that region than at Danum, indicated by $30\text{-d-rt} < 100 \text{ mm}$ for 89 d (at Danum the equivalent value was 58 d), although the preceding rainfall history at the Lambir sites 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 y *vs.* *c.* 1 y. 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.

In another study on Mt. Kinabalu in Sabah, the 30-d-rt was $< 100 \text{ mm}$ for even 115 d in early 1998 (Aiba and Kitayama 2002). In their lowland plots, 'true annualised mortality' was 2.4- (intermediate fertile soils) to $> 3\text{-fold}$ (low fertility) higher in the drought- (1997 – 1998) compared to the pre-drought (1995 – 1997) period. Time intervals compared were therefore *c.* 12 *vs.* *c.* 20 months, resulting in the same concerns as those expressed above. Additionally, the location of the research plots on Mt. Kinabalu must be considered as being quite isolated, with extensive farmland and plantations surrounding the mountain. Size and fragmentation of the forests are known to play a role in the impact that droughts have: small, isolated patches with disrupted hydrological cycles might be more vulnerable (Harrison 2001, Laurance and Williamson 2001, Laurance *et al.* 2001) than continuous forest at Danum (which is more remotely situated, yet still surrounded by secondary forest). It is not known, how the forests at Lambir are

positioned in this respect.

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 y after the drought (15.4% compared to 4.2% in the 'undisturbed' plots) (Slik 2004). 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): percentage of dead trees was at 18.5% 8 mo after the drought, but increased to 26.3% at 21 mo.

3.2. 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 largest 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 cavitations. During moderate droughts, large trees with deeper-reaching roots might be less affected, but if water stress is becoming more severe, cavitations 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, 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.

Interestingly, the shade tolerant and slow growing 'other' timber species within

the Dipterocarpaceae did not increase in mortality in period 2 in all, small and large trees, whereas light and medium/heavy hardwoods had higher mortality rates in the second than in the first period. This led to an increasing relative contribution of the 'other' timber species across the years – an observation also made by Bischoff *et al.* (subm.) in a recent work at Danum that compared primary and secondary forest.

Conversely to mortality, relative growth rate decreased with increasing size in both periods and not surprisingly, growth was better 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.

Growth and mortality are connected in the sense that weakened trees with low growth rates have a larger probability of dying soon (Kobe and Coates 1997, for temperate forests).

3.3. Changes in structure with respect to possible effects on the carbon cycle

Tree density at Danum continued to decline but the aggregation of biomass that was observed in the first period (1986 – 1996) did not continue in the second one (1996 – 2001): basal area in 2001 was less than that in 1996. This trend and the relatively low basal area overall (compared to other sites in lowland dipterocarp forest (Newbery *et al.* 1992)) was also seen in measurements of 10 satellites to the Danum main plots (just north of MPs; total area 1.6 ha; trees ≥ 10 cm gbh) where density declined by *c.* 3.5% from 2348 trees ha⁻¹ to 2266 trees ha⁻¹ and basal area decreased by *c.* 6.3% from 34.5 m² ha⁻¹ to 32.2 m² ha⁻¹ in 1995 and 2001, respectively (D.M. Newbery and M. Lingenfelder, unpubl. data).

These results contrast with those from forests in the neotropics where increasing biomass was detected (Phillips and Gentry 1994, Phillips *et al.* 1998, Baker *et al.* 2004, Phillips *et al.* 2004). This issue is subject to a currently ongoing debate (Clark 2004, Fearnside 2004, Rolim *et al.* 2005). The coincidence of the drought and increasing growth rates shortly thereafter at Danum does not call for an interpretation in favour of improved

growth conditions due to an increased warming or elevated CO₂ in the atmosphere. The results of the present work do not preclude any such effects since basal area did increase in the first period, but if they were operating, they were overlaid by the response to the drought.

Increasing turnover as in the Amazon plots (Phillips *et al.* 2004) was detected at Danum, but again this cannot be ascribed to climate change *per se* because of the disturbance related dynamics that took place over the time period analysed at Danum. Furthermore, recruitment at Danum was lower than mortality and thus, mortality was not lagging behind recruitment (Phillips *et al.* 2004).

Stochastic drought events are altering the forest at Danum on a short time scale but the forest can accommodate them, presumably up to a certain (continuously running) intensity; but if, as a result of climatic change, drought events were to increase in frequency and intensity in the future, the forest is most likely going to be modified in the direction of higher mortality and less growth, decreasing diversity, a shift towards fast growing, light-demanding species and eventually leading to large losses of biomass. More and stronger disturbances by droughts, as predicted, could prove catastrophic for lowland dipterocarp forest in Sabah (and probably South-East Asia). These forests would, if they are not yet, at the latest by then become carbon sources. This was similarly suggested for old-growth forest in general (Clark 2004). In a model of the influence of high CO₂ on Amazonian forests, Cox *et al.* (2004) included the coupling between climate and biosphere, i.e. the feedback of changing vegetation on the climate (but ignored direct anthropogenic deforestation and natural fires). Under the 'business as usual' scenario of increasing CO₂-emissions, subsequent warming and suppressed rainfall, forest cover would rapidly decline around the year 2050 (when rainfall drops < 3 mm d⁻¹), resulting in even more CO₂-emissions and less rain (Cox *et al.* 2004). This forecast could prove realistic for Sabah, if droughts become too intense even for the (more-or-less) resistant species and too frequent to allow resilient species to recover. The forest at Danum does not seem to be able to serve as a carbon buffer against increasing anthropogenic CO₂-emissions.

3.4. Species responses as specific adaptation to the local environment

Species-specific responses of the most abundant species were very variable, mortality rates ranging from 0.22 – 4.01% y^{-1} and from 0.49 – 5.12% y^{-1} , rgr from 3.01 – 43.78 $mm\ m^{-1}\ y^{-1}$ and from 5.56 – 37.41 $mm\ m^{-1}\ y^{-1}$ in periods 1 and 2, respectively. Some species' performances indicate positive or negative responses in different size- and/or topographic classes, being somewhat drought resistant or resilient or a mixture of both in regard to mortality and growth, respectively. Even though *Dimorphocalyx muricatus* had the most clearly identifiable pattern across the full enumerations – hardly any increase in mortality, even decreasing on ridges, but significantly higher growth rate in period 2 compared to period 1 – this was broken by elevated mortality and reduced growth immediately after the drought.

Different morphological and/or physiological mechanisms have evolved in species in response to the (so far) moderate drought-disturbance regime at Danum and possibly to different environmental conditions (light (gaps) and water availability (topography)) existing at the relatively small scale as in the Danum-plots. The tree species are able to either avoid or resist disturbances or recover from them soon.

Diversity of trees in the Danum-plots was stable across the enumerations (in terms of the Shannon-index) as was the richness of common species. Overall species richness was increasing, i.e. more rare species entered the population than died out. Although not tested specifically, this could be evidence in support of the intermediate disturbance hypothesis (Connell 1978): disturbances in the form of the severe droughts of 1982/83 and 1997/98 and numerous small to moderate droughts opened the canopy – presumably during the strongest droughts more or less uniformly across the area through defoliation for a short time and after the droughts selectively scattered through trees that probably died standing without creating large treefall-gaps – and allowed species to successfully recruit into the population (bearing in mind that not seedlings, but trees $\geq 10\ cm\ gbh$ were recorded). These results do not imply complete randomness (Hubbell 2001).

3.5. The role of light in the understorey

The possibilities for the interpretation of light conditions through canopy openness calculated from hemispherical photographs remained limited because of the small variation in canopy openness near the ground, ranging from *c.* 3.4% to *c.* 9.4%. These results correspond with values from other studies at Danum who found canopy openness

at their control sites in closed forest to be 2% – 5.4% (Brown 1993, Whitmore *et al.* 1993) and 5.4%. Gap size within closed forest is generally small: Brown (1993) found 70% of the gaps he studied to have canopy openness < 10%. This has to be considered when discussing the results of the hemispherical photography.

Higher mortality at high light points might indicate a recent disturbance: since the hemispherical photographs used represent light conditions around the time of the enumeration in 2001, but mortality rates refer to the five years until the measurements, that period could have experienced tree falls at the photo-points which led to increased light levels at the ground and increased mortality. Another period after the images were taken would be needed to see whether mortality would still be elevated at high light points or if it would not be lower than at low light points, reflecting better growth/survival conditions after a canopy opening (until the gap is closed, light conditions becoming less favourable and competition is leading to elevated mortality levels again).

In those areas in MP1 that showed higher growth rates with more light, the remaining trees might have been in a 'waiting' position just before a tree fall and could take advantage of the higher light availability, releasing their growth potential.

Not revealing more dependencies of structural and dynamic variables on light conditions might be due to (i) the areas chosen being too large for an adequate representation of the results from the hemiphotos, and (ii) light conditions derived from hemiphotos at 1 m above ground might only be true for this height level and might not influence growth and mortality of the trees examined – even the smallest trees usually reach heights of several metres.

The exploration of the light conditions in the main plots was started in 2001. From the present results, the value of these measurements is considered to lie more in the documentation of changes in light levels across the years. Taking the photographs repeatedly, but rather than multiple times throughout a year, maybe once at each enumeration or even yearly, might serve this purpose better. And it could allow growth, recruitment and mortality rates to be related to gap-formation history at the photo-points and therefore demonstrate the effects of changing light conditions with time.

3.6. Dynamics 1986 – 2001 and the drought hypothesis

Different patterns in mortality and growth for Euphorbiaceae (and Annonaceae) and Dipterocarpaceae at different sizes support the hypothesis of Newbery *et al.* (1992, 1996, 1999b) on the respective roles of these three main families and the understorey. They proposed a 'nursing' role of the understorey for overstorey regeneration in the sense that the understorey protects seedlings of overstorey species that can persist in the shade but at the same time are less drought tolerant at that stage (Newbery *et al.* 1999b). After defoliation of the canopy, the understorey species could profit from increased light and improve their growth ahead of overstorey dipterocarps. The 'interactive dynamic' of faster rgr of dipterocarps against slow rgr of euphorbs (Newbery *et al.* 1999b) is then halted until supply with water is back to 'normal' and overstorey species in mid-canopy positions could take advantage of their growth potential again.

As anticipated by Newbery *et al.* (1999b), the aggradation of biomass was set back again by the 1997/98-disturbance, basal area was declining in period 2.

In contrast to Nakagawa *et al.* (2000) and Harrison (2001), who concluded that species were not or ill-adapted to droughts of the 1997/98-magnitude, the results of the present study rather confirm those from Newbery and Lingenfelder (2004), that the community at Danum is well adapted to the present moderate disturbance regime with occasional severe droughts.

VII. Conclusions

The results from the present study showed that the forest at Danum is well adapted to the moderate drought disturbance regime. A drought as severe as the 1997/98-one did have a strong impact on the forest and trees were immediately affected through decreased growth across all (of the most abundant) species and lagged through increased mortality. However, an intriguing resilience in terms of recovering growth after the drought was seen and although mortality increased in some species still three years after the disturbance, others were already demonstrating improved survivorship. A suspended oscillation pattern during and after disturbance by drought of increased mortality, reduced growth, lagged recovery and eventual 'normalisation' is therefore suggested for Danum.

On a local and short-term scale, responses of the forest at Danum to the disturbance by drought imply a state of non-equilibrium: species may not persist and those that do are affected in one way or another. However, stability of the forest ecosystem in the sense of a dynamic equilibrium across centuries where the system is not changed in such a way that it outlasts turnover time and returns to equilibrium points after being disturbed is concluded for primary lowland dipterocarp forest at Danum.

The question remains what will happen in the near future when the prognosis of an increasing amplitude and frequency of disturbances is fulfilled. Is the set-back of aggregation towards maximum biomass permanent, i.e. will there be a long-term damage to the forest ecosystem? Or rather: when are the limits that allow recovery and within which the structural stability of the forest would not be affected transcended? From the compensation effects of growth and mortality, it seems that Danum still can cope with disturbances even of the intensity of the 1997/98-drought. For 3 y after that strong event, there has been no drought and only mild ones occurred in 2002/03. If no new drought occurs until the next enumeration of the Danum plots in 2006, the prediction is lower mortality and growth (back to 'normal' levels) and increasing basal area/biomass. But if a new drought would affect the area in the meantime (an ENSO was recently predicted for 2004/05), the impact on the weakened ecosystem at Danum may be strong.

Only further monitoring of the plots will reveal whether the adaptation of the forest at Danum is effective enough to withstand stronger droughts more frequently or if the spectrum of droughts is becoming too intense and the forest at Danum will degenerate.

Supplementary measurements of soil and tree water relations and intensified search for functional tree guilds would allow increased understanding of the Danum drought dynamics. The degree of slope steepness might be worth considering in more detail in future analysis. Also promising is to examine the spatial patterns of the dynamics and especially the spatial distributions of the responses to the drought found in the present study.

These findings have strong implications for sustainable forest management, conservation and politics: tropical rain forests have to be treated carefully, harvesting systems must consider the important role of the understorey for regeneration of canopy-forming timber species; forest fragmentation must be limited, large untouched areas of primary forest must be preserved; emissions of greenhouse gases that reinforce intensity and frequency of ENSO-events must be halted. I hope that works like the present one are able to raise awareness to the problems the tropical rain forest is facing and the importance it has in global climate cycles and lead to action by policy makers.

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X. Appendix

Appendix Table 1: Species of two 4-ha main plots at Danum with numbers of trees at the three full enumerations and indication of the 34 most abundant species (by a star in column '34'). Species that were dead in 2001 and had not been re-checked retain old genus and/or species codes of 1996 only. Authorities are available on the internet site of the International Plant Names Index (IPNI) at www.ipni.org. Authorities from IPNI are given here for the 34 most abundant species.

Family	Species	n 1986	n 1996	n 2001	'34'
Alangiaceae	<i>Alangium javanicum</i> Koord.	101	110	110	*
Anacardiaceae	<i>Buchanania insignis</i>	120	121	111	
Anacardiaceae	<i>Buchanania sessilifolia</i>	6	17	19	
Anacardiaceae	<i>Gluta oba</i>	0	0	1	
Anacardiaceae	<i>Gluta sabahana</i>	0	0	2	
Anacardiaceae	<i>Gluta species a</i>	6	6	6	
Anacardiaceae	<i>Gluta species b</i>	1	1	1	
Anacardiaceae	<i>Gluta wallichii</i>	10	11	11	
Anacardiaceae	<i>Mangifera aff. odorata</i>	6	6	5	
Anacardiaceae	<i>Mangifera foetida</i>	5	6	6	
Anacardiaceae	<i>Mangifera parvifolia</i>	16	18	14	
Anacardiaceae	<i>Mangifera quadrifida</i>	11	11	8	
Anacardiaceae	<i>Mangifera swintonioides</i>	4	4	4	
Anacardiaceae	<i>Melanochyla auriculata</i>	0	1	1	
Anacardiaceae	<i>Melanochyla caesia</i>	2	2	2	
Anacardiaceae	<i>Melanochyla elmeri</i>	3	4	5	
Anacardiaceae	<i>Semecarpus bunburyana</i>	1	1	1	
Anacardiaceae	<i>Semecarpus cuneiformis</i>	1	1	1	
Annonaceae	<i>Alphonsea kinabaluensis</i>	17	19	16	
Annonaceae	<i>Annonaceae species a</i>	1	1	1	
Annonaceae	<i>Enicosanthum erianthoides</i>	0	1	1	
Annonaceae	<i>Enicosanthum grandifolium</i>	1	1	1	
Annonaceae	<i>Goniothalamus sp.</i>	0	0	1	
Annonaceae	<i>Meiogyne cylindrocarpa</i>	1	1	1	
Annonaceae	<i>Meiogyne virgata</i>	1	1	1	
Annonaceae	<i>Monocarpia euneura</i>	4	5	4	
Annonaceae	<i>Neo-uvaria acuminatissima</i>	24	29	29	
Annonaceae	<i>Orophea cf. myriantha</i>	1	1	18	
Annonaceae	<i>Orophea sp.</i>	0	0	1	
Annonaceae	<i>Phaeanthus ebracteolatus</i>	0	0	3	
Annonaceae	<i>Phaeanthus sp. 1</i>	38	40	37	
Annonaceae	<i>Phaeanthus species ?</i>	0	0	2	
Annonaceae	<i>Phaeanthus splendens</i>	10	11	13	
Annonaceae	<i>Polyalthia borneensis</i>	9	11	12	
Annonaceae	<i>Polyalthia cauliflora</i> Hook. f. & Thomson	324	343	322	*
Annonaceae	<i>Polyalthia cinnamomea</i>	54	57	60	
Annonaceae	<i>Polyalthia congesta</i>	85	88	78	
Annonaceae	<i>Polyalthia cylindrocarpa</i>	1	1	1	
Annonaceae	<i>Polyalthia hypoleuca</i>	1	1	1	
Annonaceae	<i>Polyalthia longipes</i>	0	1	1	
Annonaceae	<i>Polyalthia rumphii</i> Merr.	141	153	147	*
Annonaceae	<i>Polyalthia sclerophylla</i>	0	0	1	
Annonaceae	<i>Polyalthia sp. 2</i>	0	1	1	
Annonaceae	<i>Polyalthia sp. 3</i>	1	1	1	
Annonaceae	<i>Polyalthia sp. A</i>	3	3	3	
Annonaceae	<i>Polyalthia sp. B</i>	0	1	3	
Annonaceae	<i>Polyalthia sumatrana</i> King	222	246	232	*
Annonaceae	<i>Polyalthia xanthopetala</i> Merr.	241	288	227	*
Annonaceae	<i>Popowia odoardi</i>	82	91	72	
Annonaceae	<i>Popowia pisocarpa</i>	82	87	76	
Annonaceae	<i>Sageraea elliptica</i>	1	1	1	
Annonaceae	<i>Xylopiella elliptica</i>	27	27	26	
Apocynaceae	<i>Alstonia angustiloba</i>	2	2	2	
Apocynaceae	<i>Alstonia spatulata</i>	3	3	3	
Bombacaceae	<i>Coelostegia chartacea</i>	0	1	2	
Bombacaceae	<i>Durio acutifolius</i>	9	10	11	
Bombacaceae	<i>Durio graveolens</i>	24	30	30	
Bombacaceae	<i>Durio oxleyanus</i>	1	1	1	

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Bombacaceae	<i>Neesia strigosa</i>	26	28	27	
Bombacaceae	<i>Neesia synandra</i>	1	1	3	
Burseraceae	<i>Canarium asperum</i>	1	1	1	
Burseraceae	<i>Canarium caudatum</i>	2	2	2	
Burseraceae	<i>Canarium denticulatum</i>	52	54	51	
Burseraceae	<i>Canarium megalanthum</i>	3	3	3	
Burseraceae	<i>Canarium odontophyllum</i>	9	11	10	
Burseraceae	<i>Canarium sp. A</i>	1	1	0	
Burseraceae	<i>Dacryodes incurvata</i>	10	23	22	
Burseraceae	<i>Dacryodes nervosa</i>	1	1	1	
Burseraceae	<i>Dacryodes rostrata</i> (Blume) H.J. Lam	153	157	146	*
Burseraceae	<i>Dacryodes rostrata f. cuspidata</i>	2	2	2	
Burseraceae	<i>Dacryodes rugosa</i>	46	52	54	
Burseraceae	<i>Santiria apiculata</i>	1	1	1	
Burseraceae	<i>Santiria apiculata var. pilosa</i>	1	1	1	
Burseraceae	<i>Santiria CONF</i>	1	1	0	
Burseraceae	<i>Santiria kalkmaniana</i>	1	1	1	
Burseraceae	<i>Santiria laevigata</i>	3	4	8	
Burseraceae	<i>Santiria megaphylla</i>	7	7	7	
Burseraceae	<i>Santiria tomentosa</i>	41	47	42	
Celastraceae	<i>Bhesa paniculata</i> Arn.	0	1	1	
Celastraceae	<i>Lophopetalum beccarianum</i> Pierre & Ridl.	234	286	284	*
Celastraceae	<i>Lophopetalum javanicum</i>	1	1	1	
Chrysobalanaceae	<i>Kostermanthus heteropetalus</i>	12	14	15	
Chrysobalanaceae	<i>Parinari oblongifolia</i>	28	30	25	
Combretaceae	<i>Terminalia foetidissima</i>	3	3	3	
Compositae	<i>Vernonia arborea</i>	1	1	1	
Convolvulaceae	<i>Erycibe borneensis</i>	2	2	2	
Convolvulaceae	<i>Erycibe grandifolia</i>	1	1	1	
Cornaceae	<i>Mastixia rostrata ssp. caudatifolia</i>	3	3	3	
Cornaceae	<i>Mastixia trichotoma</i>	22	28	21	
Crypteroniaceae	<i>Crypteronia griffithii</i>	1	1	1	
Crypteroniaceae	<i>Crypteronia paniculata</i>	1	1	1	
Dilleniaceae	<i>Dillenia borneensis</i>	1	1	1	
Dilleniaceae	<i>Dillenia excelsa</i>	14	15	22	
Dilleniaceae	<i>Dillenia sp.</i>	1	1	1	
Dilleniaceae	<i>Dillenia sumatrana</i>	67	73	64	
Dipterocarpaceae	<i>Anisoptera costata</i>	10	10	8	
Dipterocarpaceae	<i>Dipterocarpus acutangulus</i>	0	0	3	
Dipterocarpaceae	<i>Dipterocarpus caudiferus</i>	2	2	3	
Dipterocarpaceae	<i>Dipterocarpus kerrii</i>	65	71	69	
Dipterocarpaceae	<i>Hopea nervosa</i>	99	162	150	
Dipterocarpaceae	<i>Parashorea malaanonan</i> Merr.	149	159	137	*
Dipterocarpaceae	<i>Parashorea tomentella</i>	0	0	6	
Dipterocarpaceae	<i>Shorea agamii</i>	7	7	6	
Dipterocarpaceae	<i>Shorea angustifolia</i>	42	53	45	
Dipterocarpaceae	<i>Shorea argentifolia</i>	78	96	71	
Dipterocarpaceae	<i>Shorea atrinervosa</i>	21	25	25	
Dipterocarpaceae	<i>Shorea falciferoides</i>	5	5	5	
Dipterocarpaceae	<i>Shorea fallax</i> Meijer	371	477	435	*
Dipterocarpaceae	<i>Shorea gibbosa</i>	0	0	2	
Dipterocarpaceae	<i>Shorea johorensis</i> Foxworthy	197	225	174	*
Dipterocarpaceae	<i>Shorea laxa</i>	0	0	3	
Dipterocarpaceae	<i>Shorea leprosula</i>	59	71	49	
Dipterocarpaceae	<i>Shorea macrophylla</i>	2	2	2	
Dipterocarpaceae	<i>Shorea macroptera</i>	0	0	10	
Dipterocarpaceae	<i>Shorea parvifolia</i> Dyer	206	235	198	*
Dipterocarpaceae	<i>Shorea parvistipula</i>	1	1	7	
Dipterocarpaceae	<i>Shorea pauciflora</i>	88	107	82	
Dipterocarpaceae	<i>Shorea pilosa</i>	116	140	120	
Dipterocarpaceae	<i>Shorea seminis</i>	5	5	3	
Dipterocarpaceae	<i>Shorea smithiana</i>	0	2	2	
Dipterocarpaceae	<i>Shorea sp. A</i>	1	1	1	
Dipterocarpaceae	<i>Shorea sp. B</i>	2	2	0	
Dipterocarpaceae	<i>Shorea superba</i>	4	4	3	
Dipterocarpaceae	<i>Shorea symingtonii</i>	8	11	14	
Dipterocarpaceae	<i>Vatica albiramis</i>	4	4	3	
Dipterocarpaceae	<i>Vatica dulitensis</i>	96	104	96	
Dipterocarpaceae	<i>Vatica micrantha</i>	0	5	5	
Dipterocarpaceae	<i>Vatica oblongifolia</i>	8	9	8	
Dipterocarpaceae	<i>Vatica oblongifolia ssp. multinervosa</i>	0	0	1	
Dipterocarpaceae	<i>Vatica sarawakensis</i>	23	26	24	
Dipterocarpaceae	<i>Vatica sp.</i>	1	1	1	

Dipterocarpaceae	<i>Vatica species a</i>	1	1	1	
Dipterocarpaceae	<i>Vatica species b</i>	1	1	1	
Dipterocarpaceae	<i>Vatica umbonata</i>	6	11	11	
Dipterocarpaceae	<i>Vatica vinosa</i>	2	2	2	
Ebenaceae	<i>Diospyros cauliflora</i>	23	23	22	
Ebenaceae	<i>Diospyros diepenhorstii</i>	2	2	2	
Ebenaceae	<i>Diospyros elliptifolia</i>	79	81	73	
Ebenaceae	<i>Diospyros euphlebica</i>	5	5	5	
Ebenaceae	<i>Diospyros foxworthyi</i>	15	16	16	
Ebenaceae	<i>Diospyros hallierii</i>	4	4	4	
Ebenaceae	<i>Diospyros macrophylla</i>	5	5	5	
Ebenaceae	<i>Diospyros mindanaensis</i>	0	1	1	
Ebenaceae	<i>Diospyros nitida</i>	0	1	1	
Ebenaceae	<i>Diospyros sp. B</i>	2	2	2	
Ebenaceae	<i>Diospyros sp. C</i>	1	1	1	
Ebenaceae	<i>Diospyros squamifolia</i>	44	56	47	
Elaeocarpaceae	<i>Elaeocarpus clementis</i>	1	1	1	
Elaeocarpaceae	<i>Elaeocarpus stipularis</i>	0	2	2	
Euphorbiaceae	<i>Antidesma neurocarpum</i> Miq.	119	133	106	*
Euphorbiaceae	<i>Aporosa acuminatissima</i>	9	9	9	
Euphorbiaceae	<i>Aporosa arborea</i>	5	5	5	
Euphorbiaceae	<i>Aporosa confusa</i>	0	0	1	
Euphorbiaceae	<i>Aporosa falcifera</i> Hook. f.	261	281	239	*
Euphorbiaceae	<i>Aporosa GRAN</i>	1	1	0	
Euphorbiaceae	<i>Aporosa lucida</i>	41	48	41	
Euphorbiaceae	<i>Aporosa LUNA</i>	1	1	0	
Euphorbiaceae	<i>Aporosa nigricans</i>	23	24	23	
Euphorbiaceae	<i>Aporosa nitida</i>	29	30	34	
Euphorbiaceae	<i>Aporosa species ?</i>	0	1	1	
Euphorbiaceae	<i>Baccaurea javanica</i>	0	1	1	
Euphorbiaceae	<i>Baccaurea macrocarpa</i>	9	9	6	
Euphorbiaceae	<i>Baccaurea parviflora</i>	1	4	4	
Euphorbiaceae	<i>Baccaurea pyriformis</i>	0	0	2	
Euphorbiaceae	<i>Baccaurea tetrandra</i> Müll. Arg.	250	260	248	*
Euphorbiaceae	<i>Baccaurea trigonocarpa</i>	33	35	29	
Euphorbiaceae	<i>Blumeodendron kurzii</i>	5	5	4	
Euphorbiaceae	<i>Botryophora geniculata</i>	0	2	2	
Euphorbiaceae	<i>Bridelia penangiana</i>	1	1	1	
Euphorbiaceae	CHAE CAST	1	1	0	
Euphorbiaceae	<i>Cleistanthus celebicus</i>	0	2	2	
Euphorbiaceae	<i>Cleistanthus contractus</i> Airy Shaw	289	309	299	*
Euphorbiaceae	<i>Cleistanthus paxii</i>	3	4	3	
Euphorbiaceae	<i>Cleistanthus PERS</i>	4	4	0	
Euphorbiaceae	<i>Cleistanthus sumatranus</i>	0	3	3	
Euphorbiaceae	<i>Dimorphocalyx muricatus</i> (Hook. f.) Airy Shaw	840	891	840	*
Euphorbiaceae	<i>Drypetes caesia</i>	4	5	8	
Euphorbiaceae	<i>Drypetes crassipes</i>	0	1	1	
Euphorbiaceae	<i>Drypetes eriocarpa</i>	3	4	4	
Euphorbiaceae	<i>Drypetes longifolia</i>	18	24	27	
Euphorbiaceae	<i>Drypetes macrostigma</i>	0	1	1	
Euphorbiaceae	<i>Drypetes microphylla</i>	0	0	1	
Euphorbiaceae	<i>Drypetes polyneura</i>	3	4	4	
Euphorbiaceae	<i>Drypetes sp. A</i>	1	1	0	
Euphorbiaceae	<i>Drypetes sp. B</i>	1	2	2	
Euphorbiaceae	<i>Drypetes sp. E</i>	45	45	41	
Euphorbiaceae	<i>Drypetes species d</i>	3	3	2	
Euphorbiaceae	<i>Elateriospermum tapos</i>	1	1	1	
Euphorbiaceae	<i>Galearia fulva</i>	12	12	15	
Euphorbiaceae	<i>Galearia sp. A</i>	1	1	0	
Euphorbiaceae	<i>Glochidion elmeri</i>	17	17	13	
Euphorbiaceae	<i>Glochidion hypoleucum</i>	10	11	4	
Euphorbiaceae	<i>Glochidion lancisepalum</i>	30	35	27	
Euphorbiaceae	<i>Glochidion lutescens</i>	0	1	1	
Euphorbiaceae	<i>Glochidion pubicapsa</i>	1	1	1	
Euphorbiaceae	<i>Glochidion rubrum</i>	5	6	11	
Euphorbiaceae	<i>Homalanthus populneus</i>	0	0	1	
Euphorbiaceae	<i>Koilocarpus laevigatum</i>	151	158	142	
Euphorbiaceae	<i>Koilocarpus longifolium</i>	0	2	6	
Euphorbiaceae	<i>Macaranga conifera</i>	2	3	3	
Euphorbiaceae	<i>Macaranga hypoleuca</i>	0	1	3	
Euphorbiaceae	<i>Mallotus eucaustus</i>	7	7	7	
Euphorbiaceae	<i>Mallotus penangensis</i> Müll. Arg.	204	258	263	*
Euphorbiaceae	<i>Mallotus species 9</i>	0	1	1	

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Euphorbiaceae	<i>Mallotus stipularis</i>	115	129	123	
Euphorbiaceae	<i>Mallotus wrayi</i> King ex Hook. f.	2268	2558	2413	*
Euphorbiaceae	<i>Neoscortechinia forbesii</i>	0	0	2	
Euphorbiaceae	<i>Neoscortechinia philippinensis</i>	99	102	92	
Euphorbiaceae	<i>Trigonopleura malayana</i>	1	2	2	
Euphorbiaceae	<i>Trigonostemon hirsutus</i>	22	23	23	
Fagaceae	<i>Castanopsis borneensis</i>	0	0	2	
Fagaceae	<i>Castanopsis costata</i>	2	2	1	
Fagaceae	<i>Castanopsis hypophoenicea</i>	11	17	20	
Fagaceae	<i>Castanopsis sp. 1</i>	1	1	0	
Fagaceae	<i>Lithocarpus cantleyanus</i>	1	2	7	
Fagaceae	<i>Lithocarpus confragosus</i>	0	1	1	
Fagaceae	<i>Lithocarpus ewyckii</i>	3	4	4	
Fagaceae	<i>Lithocarpus ferrugineus</i>	0	0	1	
Fagaceae	<i>Lithocarpus gracilis</i>	73	86	77	
Fagaceae	<i>Lithocarpus hallierii</i>	26	33	25	
Fagaceae	<i>Lithocarpus leptogyne</i>	72	95	80	
Fagaceae	<i>Lithocarpus meijeri</i>	6	7	8	
Fagaceae	<i>Lithocarpus nieuwenhuisii</i> (Seem.) A. Camus	125	131	123	*
Fagaceae	<i>Lithocarpus ruminatus</i>	1	1	1	
Fagaceae	<i>Lithocarpus sp.</i>	0	0	1	
Fagaceae	<i>Lithocarpus sp. B</i>	1	1	0	
Fagaceae	<i>Quercus argentata</i>	32	37	31	
Fagaceae	<i>Quercus gemelliflora</i>	1	1	1	
Fagaceae	<i>Quercus sumatrana</i>	1	1	1	
Flacourtiaceae	<i>Casearia tuberculata</i>	4	4	4	
Flacourtiaceae	<i>Hydnocarpus borneensis</i>	106	115	112	
Flacourtiaceae	<i>Hydnocarpus polypetalus</i>	81	83	85	
Flacourtiaceae	<i>Hydnocarpus species a</i>	1	1	1	
Flacourtiaceae	<i>Hydnocarpus subfalcata</i>	36	38	38	
Flacourtiaceae	<i>Ryparosa hullettii</i>	85	89	84	
Guttiferae	<i>Calophyllum gracilipes</i>	13	19	17	
Guttiferae	<i>Calophyllum soulattri</i>	3	3	2	
Guttiferae	<i>Garcinia benthami</i>	0	1	1	
Guttiferae	<i>Garcinia forbesii</i>	5	6	6	
Guttiferae	<i>Garcinia gaudichaudii</i>	6	6	6	
Guttiferae	<i>Garcinia nervosa</i>	1	1	1	
Guttiferae	<i>Garcinia parvifolia</i>	17	17	9	
Guttiferae	<i>Garcinia penangiana</i>	2	2	2	
Guttiferae	<i>Mesua borneensis</i>	23	27	22	
Guttiferae	<i>Mesua macrantha</i>	0	0	3	
Icacinaceae	<i>Stemonurus grandifolius</i>	16	17	14	
Icacinaceae	<i>Stemonurus malaccensis</i>	44	47	46	
Icacinaceae	<i>Stemonurus scorpioides</i>	0	0	2	
Juglandaceae	<i>Engelhardia serrata</i>	2	2	1	
Lauraceae	<i>Actinodaphne diversifolia</i>	2	7	7	
Lauraceae	<i>Actinodaphne macrophylla</i>	4	5	5	
Lauraceae	<i>Actinodaphne sp. 1</i>	1	1	0	
Lauraceae	<i>Alseodaphne bancana</i>	0	0	2	
Lauraceae	<i>Alseodaphne elmeri</i>	8	10	13	
Lauraceae	<i>Alseodaphne oblanceolata</i>	12	12	9	
Lauraceae	<i>Alseodaphne sp. ?</i>	1	1	1	
Lauraceae	<i>Alseodaphne sp. C</i>	1	1	1	
Lauraceae	<i>Beilschmiedia gemmiflora</i>	29	29	26	
Lauraceae	<i>Beilschmiedia glauca</i>	32	39	36	
Lauraceae	<i>Beilschmiedia lucidula</i>	0	0	2	
Lauraceae	<i>Beilschmiedia sp. A</i>	34	36	33	
Lauraceae	<i>Beilschmiedia sp. D</i>	1	1	0	
Lauraceae	<i>Beilschmiedia sp. F</i>	38	43	40	
Lauraceae	<i>Beilschmiedia sp. G</i>	1	1	0	
Lauraceae	<i>Beilschmiedia sp. S</i>	1	1	1	
Lauraceae	<i>Beilschmiedia species b</i>	0	1	1	
Lauraceae	<i>Beilschmiedia tawaensis</i>	19	20	17	
Lauraceae	<i>Beilschmiedia wallichiana</i>	3	3	3	
Lauraceae	<i>Beilschmiedia zeylanica</i>	16	17	16	
Lauraceae	<i>Cinnamomum griffithii</i>	1	1	1	
Lauraceae	<i>Cryptocarya crassinervia</i>	7	7	6	
Lauraceae	<i>Cryptocarya sp. D</i>	5	5	3	
Lauraceae	<i>Cryptocarya sp. S</i>	1	1	1	
Lauraceae	<i>Cryptocarya teysmanniana</i>	47	51	46	
Lauraceae	<i>Dehaasia caesia</i>	8	12	14	
Lauraceae	<i>Dehaasia cuneata</i>	6	6	6	
Lauraceae	<i>Dehaasia gigantocarpa</i>	115	122	117	

Lauraceae	<i>Dehaasia incrassata</i>	7	8	8	
Lauraceae	<i>Dehaasia sp. B</i>	0	0	1	
Lauraceae	<i>Endiandra macrophylla</i>	1	1	1	
Lauraceae	<i>Lindera POLY</i>	1	1	0	
Lauraceae	<i>Lindera sp.</i>	0	0	1	
Lauraceae	<i>Lindera sp. A</i>	5	14	15	
Lauraceae	<i>Lindera species b</i>	2	2	1	
Lauraceae	<i>Litsea caulocarpa</i> Merr.	322	415	375	*
Lauraceae	<i>Litsea costata</i>	0	0	1	
Lauraceae	<i>Litsea cuprea</i>	3	3	3	
Lauraceae	<i>Litsea fenestrata</i>	12	14	14	
Lauraceae	<i>Litsea ferruginea</i>	20	23	21	
Lauraceae	<i>Litsea gracilipes</i>	42	45	37	
Lauraceae	<i>Litsea grandis</i>	1	1	1	
Lauraceae	<i>Litsea insignis</i>	0	1	1	
Lauraceae	<i>Litsea lanceolata</i>	9	9	5	
Lauraceae	<i>Litsea lancifolia</i>	26	29	31	
Lauraceae	<i>Litsea machilifolia</i>	58	64	62	
Lauraceae	<i>Litsea macrophylla</i>	0	0	1	
Lauraceae	<i>Litsea mappacea</i>	0	0	3	
Lauraceae	<i>Litsea ochracea</i> Boerl.	163	179	164	*
Lauraceae	<i>Litsea resinosa</i>	19	25	19	
Lauraceae	<i>Litsea robusta</i>	13	17	18	
Lauraceae	<i>Litsea sessilis</i>	23	25	26	
Lauraceae	<i>Litsea sp. D</i>	1	1	0	
Lauraceae	<i>Litsea sp. G</i>	0	0	1	
Lauraceae	<i>Litsea sp. I</i>	0	0	1	
Lauraceae	<i>Litsea sp. X</i>	1	1	1	
Lauraceae	<i>Litsea species 1</i>	8	8	5	
Lauraceae	<i>Litsea species 2</i>	3	3	1	
Lauraceae	<i>Litsea species 3</i>	1	1	1	
Lauraceae	<i>Litsea species e</i>	1	1	1	
Lauraceae	<i>Litsea tomentosa</i>	6	6	4	
Lauraceae	<i>Nothaphoebe cuneata</i>	1	1	1	
Lauraceae	<i>Nothaphoebe heterophylla</i>	1	1	1	
Lauraceae	<i>Nothaphoebe sp. D</i>	1	1	0	
Lauraceae	<i>Nothaphoebe sp. G</i>	0	1	1	
Lauraceae	<i>Nothaphoebe species a</i>	28	28	21	
Lauraceae	<i>Nothaphoebe species b</i>	3	3	2	
Lauraceae	<i>Nothaphoebe umbelliflora</i>	0	0	1	
Lauraceae	<i>Phoebe macrophylla</i>	35	49	56	
Lecythidaceae	<i>Barringtonia gigantostachya</i>	1	1	1	
Lecythidaceae	<i>Barringtonia lanceolata</i> (Ridl.) Payens	141	151	155	*
Lecythidaceae	<i>Barringtonia macrostachya</i>	13	15	14	
Lecythidaceae	<i>Barringtonia sarcostachys</i>	14	15	15	
Lecythidaceae	<i>Barringtonia sp. A</i>	4	4	4	
Leguminosae	<i>Archidendron cockburnii</i>	2	11	11	
Leguminosae	<i>Archidendron fagifolium</i> v. <i>borneensis</i>	0	0	1	
Leguminosae	<i>Archidendron microcarpum</i>	12	14	17	
Leguminosae	<i>Crudia reticulata</i>	0	0	2	
Leguminosae	<i>Crudia tenuipes</i>	28	29	27	
Leguminosae	<i>Dialium hydnocarpoides</i>	12	12	10	
Leguminosae	<i>Dialium indum</i>	16	16	17	
Leguminosae	<i>Fordia splendidissima</i> (Blume ex Miq.) J.R.M. Buijsen	520	620	620	*
Leguminosae	<i>Koompassia excelsa</i>	5	8	7	
Leguminosae	<i>Koompassia malaccensis</i>	1	1	1	
Leguminosae	<i>Ormosia calavensis</i>	0	1	2	
Leguminosae	<i>Ormosia macrodisca</i>	1	1	1	
Leguminosae	<i>Parkia singularis</i>	1	1	2	
Leguminosae	<i>Peltophorum racemosum</i>	6	8	7	
Leguminosae	<i>Sindora bruggemanii</i>	2	2	2	
Leguminosae	<i>Sindora irpicina</i>	33	36	36	
Leguminosae	<i>Sympetalandra borneensis</i>	1	1	1	
Liliaceae	<i>Dracaena elliptica</i>	2	2	2	
Linaceae	<i>Ctenolophon parvifolius</i>	4	4	4	
Loganiaceae	<i>Fagraea cuspidata</i>	8	8	7	
Magnoliaceae	<i>Magnolia candollei</i> var. <i>candollei</i>	32	53	49	
Magnoliaceae	<i>Magnolia candollei</i> var. <i>singaporensis</i>	96	97	94	
Magnoliaceae	<i>Magnolia gigantifolia</i>	83	85	73	
Melastomataceae	<i>Melastoma malabathricum</i>	0	0	1	
Melastomataceae	<i>Memecylon costatum</i>	0	2	2	
Melastomataceae	<i>Memecylon excelsum</i>	18	18	13	
Melastomataceae	<i>Memecylon laevigatum</i>	0	0	7	

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Melastomataceae	<i>Memecylon lilacinum</i>	7	7	7
Melastomataceae	<i>Memecylon oleifolium</i>	5	5	4
Melastomataceae	<i>Memecylon paniculatum</i>	57	62	50
Melastomataceae	<i>Memecylon species 1</i>	2	2	1
Melastomataceae	<i>Memecylon species a</i>	1	1	1
Melastomataceae	<i>Pternandra coerulescens</i>	6	7	5
Melastomataceae	<i>Pternandra galeata</i>	73	82	65
Melastomataceae	<i>PYRE SERR</i>	2	2	0
Meliaceae	<i>Aglaia argentea</i>	27	28	23
Meliaceae	<i>Aglaia crassinervia</i>	59	68	53
Meliaceae	<i>Aglaia lawii</i>	1	1	1
Meliaceae	<i>Aglaia leucophylla</i>	0	0	2
Meliaceae	<i>Aglaia macrocarpa</i>	60	60	50
Meliaceae	<i>Aglaia odoratissima</i>	57	59	46
Meliaceae	<i>Aglaia pinnata</i>	0	0	1
Meliaceae	<i>Aglaia rufinervis</i>	17	19	14
Meliaceae	<i>Aglaia silvestris</i>	79	85	79
Meliaceae	<i>Aglaia sp. 10</i>	0	1	1
Meliaceae	<i>Aglaia sp. A</i>	2	2	2
Meliaceae	<i>Aglaia sp. T</i>	1	2	2
Meliaceae	<i>Aglaia sp. Y</i>	2	2	2
Meliaceae	<i>Aglaia species 13</i>	0	1	1
Meliaceae	<i>Aglaia species c</i>	0	1	1
Meliaceae	<i>Aglaia tomentosa</i>	39	43	39
Meliaceae	<i>Aphanomixis borneensis</i>	2	2	2
Meliaceae	<i>Chisocheton beccarianus</i>	0	0	4
Meliaceae	<i>Chisocheton ceramicus</i>	18	19	18
Meliaceae	<i>Chisocheton patens</i>	1	1	1
Meliaceae	<i>Chisocheton pentandrus</i>	46	49	44
Meliaceae	<i>Chisocheton polyandrus</i>	28	28	26
Meliaceae	<i>Chisocheton sarawakanus</i> Harms	155	169	156
Meliaceae	<i>Chisocheton species 2</i>	1	1	1
Meliaceae	<i>Chisocheton species a</i>	0	2	2
Meliaceae	<i>Chisocheton species b</i>	0	1	1
Meliaceae	<i>Dysoxylum alliaceum</i>	13	15	25
Meliaceae	<i>Dysoxylum cauliflorum</i>	1	1	1
Meliaceae	<i>Dysoxylum cyrtobotryum</i> Miq.	170	182	161
Meliaceae	<i>Dysoxylum grande</i>	0	6	6
Meliaceae	<i>Dysoxylum rigidum</i>	89	101	101
Meliaceae	<i>Dysoxylum rugulosum</i>	28	28	24
Meliaceae	<i>Dysoxylum sp. A</i>	1	1	0
Meliaceae	<i>Dysoxylum sp. D</i>	2	5	6
Meliaceae	<i>Dysoxylum species b</i>	0	1	1
Meliaceae	<i>Lansium domesticum</i>	23	26	23
Meliaceae	<i>Meliaceae species a</i>	1	1	1
Meliaceae	<i>Reinwardtiodendron cinereum</i>	1	1	1
Meliaceae	<i>Reinwardtiodendron dubia</i>	0	0	1
Meliaceae	<i>Reinwardtiodendron humile</i> (Hassk.) D.J. Mabberley	262	281	235
Meliaceae	<i>Walsura pinnata</i>	32	34	35
Meliaceae	<i>Walsura sp. 1</i>	3	3	0
Meliaceae	<i>Walsura sp. 2</i>	1	1	0
Meliaceae	<i>Walsura sp. 3</i>	1	1	0
Meliaceae	<i>Walsura species 4</i>	1	1	1
Monimiaceae	<i>Kibara coriacea</i>	2	2	2
Monimiaceae	<i>Kibara sp.</i>	1	1	1
Monimiaceae	<i>Kibara species a</i>	1	1	1
Moraceae	<i>Artocarpus anisophylla</i>	11	13	12
Moraceae	<i>Artocarpus dadak</i>	1	2	3
Moraceae	<i>Ficus aurata</i>	0	0	2
Moraceae	<i>Ficus c.f. fistulata</i>	1	3	3
Moraceae	<i>Ficus fulva</i>	2	4	5
Moraceae	<i>Ficus glandulifera</i>	0	0	1
Moraceae	<i>Ficus melinocarpa</i>	0	1	1
Moraceae	<i>Ficus midotis</i>	2	2	2
Moraceae	<i>Ficus obscura</i>	0	1	1
Moraceae	<i>Ficus pellucido-punctata</i>	1	1	1
Moraceae	<i>Ficus sp. A</i>	1	1	0
Moraceae	<i>Prainea limpato</i>	2	2	2
Myristicaceae	<i>Gymnacranthera forbesii</i>	1	2	2
Myristicaceae	<i>Horsfieldia splendida</i>	1	1	1
Myristicaceae	<i>Knema conferta</i>	0	0	1
Myristicaceae	<i>Knema elmeri</i>	18	23	24
Myristicaceae	<i>Knema kunstleri</i>	1	1	1

Myristicaceae	<i>Knema latericia</i> Elmer	141	171	171	*
Myristicaceae	<i>Knema latericia</i> ssp. <i>albifolia</i>	0	0	1	
Myristicaceae	<i>Knema laurina</i>	14	17	29	
Myristicaceae	<i>Knema membranifolia</i>	3	4	4	
Myristicaceae	<i>Knema oblongata</i>	56	61	62	
Myristicaceae	<i>Knema pallens</i>	2	2	2	
Myristicaceae	<i>Myristica iners</i>	1	1	2	
Myrsinaceae	<i>Ardisia korthalsiana</i>	1	1	1	
Myrsinaceae	<i>Ardisia macrophylla</i>	13	16	16	
Myrsinaceae	<i>Ardisia oxyphylla</i>	1	1	1	
Myrsinaceae	<i>Ardisia sanguinolenta</i> Blume	568	677	699	*
Myrtaceae	<i>Syzygium alcinae</i>	0	3	3	
Myrtaceae	<i>Syzygium castaneum</i>	72	77	59	
Myrtaceae	<i>Syzygium caudatilimba</i>	12	16	16	
Myrtaceae	<i>Syzygium cerasiforme</i>	12	20	17	
Myrtaceae	<i>Syzygium chrysanthum</i>	110	126	121	
Myrtaceae	<i>Syzygium creaghii</i>	22	23	21	
Myrtaceae	<i>Syzygium elopuræ</i> (Ridl.) Merr. & L.M. Perry	134	141	123	*
Myrtaceae	<i>Syzygium heterocladum</i>	35	36	31	
Myrtaceae	<i>Syzygium hirtum</i>	33	37	32	
Myrtaceae	<i>Syzygium lineata</i>	67	76	68	
Myrtaceae	<i>Syzygium malaccense</i>	5	5	6	
Myrtaceae	<i>Syzygium napiformis</i>	1	1	1	
Myrtaceae	<i>Syzygium palawanense</i>	36	40	40	
Myrtaceae	<i>Syzygium</i> sp. C	1	1	0	
Myrtaceae	<i>Syzygium</i> sp. D	30	33	31	
Myrtaceae	<i>Syzygium</i> sp. H	0	1	1	
Myrtaceae	<i>Syzygium</i> sp. L	4	4	4	
Myrtaceae	<i>Syzygium</i> sp. N	2	2	2	
Myrtaceae	<i>Syzygium</i> sp. Q	3	6	6	
Myrtaceae	<i>Syzygium</i> sp. R	0	1	1	
Myrtaceae	<i>Syzygium</i> sp. X	7	7	7	
Myrtaceae	<i>Syzygium</i> species ?	0	1	17	
Myrtaceae	<i>Syzygium</i> species 1	0	1	1	
Myrtaceae	<i>Syzygium</i> species b	17	17	8	
Myrtaceae	<i>Syzygium</i> species j	0	1	1	
Myrtaceae	<i>Syzygium tawaense</i> (Merr.) Masam.	124	137	121	*
Myrtaceae	<i>Syzygium valdevenosum</i>	1	1	1	
Oleaceae	<i>Anacolosa frutescens</i>	1	1	1	
Oleaceae	<i>Ochanostachys amentacea</i>	69	72	64	
Oleaceae	<i>Scorodocarpus borneensis</i>	96	101	91	
Oleaceae	<i>Chionanthus curvicaulus</i>	1	2	2	
Oleaceae	<i>Chionanthus cuspidata</i>	12	12	10	
Oleaceae	<i>Chionanthus longipetalus</i>	8	9	8	
Oleaceae	<i>Chionanthus pluriflorus</i>	0	0	2	
Palmae	<i>Nenga pumila</i> var. <i>pachystachya</i>	2	2	1	
Polygalaceae	<i>Xanthophyllum adenotus</i>	9	10	7	
Polygalaceae	<i>Xanthophyllum affine</i>	59	69	70	
Polygalaceae	<i>Xanthophyllum borneensis</i>	0	1	1	
Polygalaceae	<i>Xanthophyllum flavescens</i>	13	14	13	
Polygalaceae	<i>Xanthophyllum reticulatum</i>	43	45	38	
Polygalaceae	<i>Xanthophyllum</i> species a	1	1	1	
Polygalaceae	<i>Xanthophyllum</i> species b	2	2	2	
Polygalaceae	<i>Xanthophyllum vitellinum</i>	137	138	130	
Proteaceae	<i>Helicia pterygota</i>	8	8	5	
Proteaceae	<i>Helicia robusta</i>	17	18	15	
Proteaceae	<i>Heliciopsis artocarpoides</i>	9	12	10	
Rhamnaceae	<i>Ziziphus angustifolius</i>	1	1	1	
Rhizophoraceae	<i>Anisophyllea corneri</i>	16	16	15	
Rhizophoraceae	<i>Carallia brachiata</i>	5	6	5	
Rubiaceae	<i>Canthium confertum</i>	2	2	2	
Rubiaceae	<i>Canthium</i> species a	3	3	2	
Rubiaceae	<i>Cowiea borneensis</i>	16	16	14	
Rubiaceae	<i>Diplospora</i> sp. A	6	6	4	
Rubiaceae	<i>Gardenia tubifera</i>	1	1	1	
Rubiaceae	<i>Ixora blumei</i>	0	0	1	
Rubiaceae	<i>Maschalocorymbus corymbosus</i> (Blume) Bremek.	403	463	375	*
Rubiaceae	<i>Pleiocarpidia enneandra</i>	3	4	3	
Rubiaceae	<i>Pleiocarpidia sandakanica</i>	0	0	2	
Rubiaceae	<i>Porterandia anisophylla</i>	2	2	2	
Rubiaceae	<i>Praravinia suberosa</i>	11	12	10	
Rubiaceae	<i>Prismatomeris beccariana</i>	4	5	5	
Rubiaceae	<i>Prismatomeris tetrandra</i>	0	0	1	

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Rubiaceae	<i>Rothmannia merrillii</i>	0	1	1	
Rubiaceae	<i>Rothmannia species a</i>	16	18	17	
Rubiaceae	<i>Tarenna sp.</i>	0	1	1	
Rubiaceae	<i>Timonius borneensis</i>	1	1	1	
Rubiaceae	<i>Timonius species ?</i>	1	1	1	
Rubiaceae	<i>Urophyllum glabrum</i>	40	56	39	
Rubiaceae	<i>Urophyllum griffithianum</i>	0	0	4	
Rubiaceae	<i>Urophyllum woodii</i>	73	81	60	
Rutaceae	<i>Melicope incana</i>	0	0	1	
Rutaceae	<i>Melicope lunu-ankenda</i>	1	2	2	
Rutaceae	<i>Melicope species b</i>	4	4	3	
Sabiaceae	<i>Meliosma sumatrana</i>	15	15	15	
Santalaceae	<i>Santalaceae species a</i>	1	1	1	
Santalaceae	<i>Scleropyrum wallichianum</i>	1	1	1	
Sapindaceae	<i>Dimocarpus longan ssp. malesianus</i>	1	1	1	
Sapindaceae	<i>Guioa pterorhachis</i>	0	1	1	
Sapindaceae	<i>Lepisanthes amoena</i>	2	2	2	
Sapindaceae	<i>Mischocarpus pentapetalus</i>	11	19	21	
Sapindaceae	<i>Nephelium lappaceum</i>	3	3	3	
Sapindaceae	<i>Nephelium ramboutan-ake</i>	67	73	67	
Sapotaceae	<i>Madhuca dubardii</i>	0	0	1	
Sapotaceae	<i>Madhuca elmeri</i>	23	27	29	
Sapotaceae	<i>Madhuca korthalsii</i> H.J. Lam	508	568	568	*
Sapotaceae	<i>Madhuca malaccensis</i>	2	3	3	
Sapotaceae	<i>Madhuca mindanaensis</i>	5	5	5	
Sapotaceae	<i>Madhuca sp. D</i>	1	1	1	
Sapotaceae	<i>Palaquium beccarianum</i>	4	4	4	
Sapotaceae	<i>Palaquium ericalyx</i>	1	1	2	
Sapotaceae	<i>Palaquium sp. A</i>	1	1	1	
Sapotaceae	<i>Payena acuminata</i>	13	13	12	
Sapotaceae	<i>Pouteria malaccensis</i>	1	1	1	
Sapotaceae	<i>Pouteria species b</i>	0	1	1	
Sapotaceae	<i>Sapotaceae indet</i>	1	1	1	
Saxifragaceae	<i>Polyosma mutabilis</i>	34	40	29	
Simaroubaceae	<i>Eurycoma longifolia</i>	62	68	67	
Simaroubaceae	<i>Irvingia malayana</i>	2	2	2	
Sterculiaceae	<i>Heritiera simplicifolia</i>	0	0	1	
Sterculiaceae	<i>Scaphium macropodium</i>	53	68	67	
Sterculiaceae	<i>Sterculia rubiginosa</i>	4	5	4	
Symplocaceae	<i>Symplocos FASC</i>	1	1	0	
Symplocaceae	<i>Symplocos odoratissima</i>	1	1	1	
Symplocaceae	<i>Symplocos odoratissima v. wenzelii</i>	0	0	1	
Theaceae	<i>Pyrenaria kunstleri</i>	1	1	1	
Theaceae	<i>Pyrenaria serrata</i>	1	1	1	
Theaceae	<i>Pyrenaria serrata v. masocarpa</i>	2	2	2	
Theaceae	<i>Schima species 1</i>	4	4	1	
Thymelaeaceae	<i>Aquilaria malaccensis</i>	1	1	1	
Thymelaeaceae	<i>Gonystylus forbesii</i>	1	1	1	
Thymelaeaceae	<i>Gonystylus keithii</i> Airy Shaw	121	136	137	*
Thymelaeaceae	<i>Phaleria capitata</i>	1	1	2	
Thymelaeaceae	<i>Phaleria perrottetiana</i>	3	3	1	
Tiliaceae	<i>Brownlowia peltata</i>	10	10	10	
Tiliaceae	<i>Microcos antidesmifolia</i>	26	29	26	
Tiliaceae	<i>Microcos crassifolia</i>	36	38	31	
Tiliaceae	<i>Microcos elmeri</i>	21	24	21	
Tiliaceae	<i>Microcos hirsute</i>	0	3	7	
Tiliaceae	<i>Microcos latistipulata</i>	0	1	1	
Tiliaceae	<i>Microcos reticulate</i>	56	64	57	
Tiliaceae	<i>Microcos species ?</i>	0	1	1	
Tiliaceae	<i>Pentace laxiflora</i> Merr.	240	267	243	*
Trigoniaceae	<i>Trigoniastrum hypoleucum</i>	46	47	46	
Ulmaceae	<i>Gironniera celtidifolia</i>	27	28	24	
Ulmaceae	<i>Gironniera nervosa</i>	41	65	78	
Various	Broken trees (2001 on visit by Madani)	0	0	1	
Various	Dead LATE (1996)	10	10	0	
Various	Dead trees (1996 on revisit)	0	3	3	
Various	Dead trees (1996 early)	23	23	1	
Various	Dead trees (2001 on visit by Madani)	0	0	1	
Various	Missing trees (1996)	2	4	2	
Various	<i>SPEC 11</i>	1	1	0	
Various	<i>SPEC 18</i>	1	1	0	
Various	<i>SPEC 23</i>	1	1	0	
Various	<i>SPEC 9</i>	1	1	0	

Various	<i>Species B</i>	1	1	1
Verbenaceae	<i>Callicarpa involucrata</i>	1	1	1
Verbenaceae	<i>Callicarpa pentandra</i>	1	1	1
Verbenaceae	<i>Geunsia hexandra</i>	0	1	2
Verbenaceae	<i>Teijsmanniodendron bogoriense</i>	27	27	26
Verbenaceae	<i>Teijsmanniodendron holophyllum</i>	35	37	39