Ecological studies on Rain Forests at Three Altitudes on Bukit Belalong, Brunei.

A thesis submitted for the degree of
Doctor of Philosophy
at the
University of Stirling

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June 1994 1995

'Bukit Belalong' Boyd and Evans 1992

To Jackie and Lily

CONTENTS

ABSTRACT

Altitudinal zonation of rain forests was investigated on Bukit Belalong (913 m), Brunei. Mean annual rainfall was 4100 mm at 45 m and 5500 mm at 913 m. Mean annual temperatures were 25.7 °C (45 m) and 21.8 °C (913 m).

Three 0.25 ha plots were set up at each of three altitudes. At 200 m and 500 m there was evergreen lowland rain forest and at 850 m there was lower montane rain forest (LMRF). The Dipterocarpaceae had the highest proportion of basal area throughout, but their importance declined in the LMRF where the Fagaceae, Myrtaceae and Lauraceae were increasingly important.

Soils in the LMRF were more organic and had higher concentrations of total nitrogen and phosphorus and the soils from 500 m were the most acid and least base saturated. Rates of nitrogen mineralisation and soil concentrations of inorganic nitrogen did not differ significantly among altitudes.

The rates (t ha^{-1} yr^{-1}) of total small litterfall and leaf litterfall were significantly lower in the LMRF (10.6 and 7.9 at 200 m; 10.5 and 7.9 at 500 m; 8.3 and 6.0 at 850 m). Litterfall nutrient concentrations were similar among altitudes, but smaller quantities of litterfall nutrients were cycled at 850 m. The mass (t ha^{-1}) of the small litter layer was similar throughout (5.2 at 200 m; 6.1 at 500 m; 5.2 at 850 m) but leaf litter k_L values were lower at 850 m (2.4 at 200 m; 2.4 at 500 m; 2.0 at 850 m).

Fine root (<5 mm) mass (t ha^{-1}) in the top 100 cm of soil was 8.3 (200 m); 12.0 (500 m); 10.6 (850 m). Rates (t ha^{-1} yr^{-1}) of fine root growth (estimated by ingrowth bags) were 0.9 (200 m); 2.2 (500 m); 0.5 (850 m).

A bioassay experiment using rice was made at 30 m and 913 m. Nutrients were more limiting in the montane soil, but climate was of overriding importance for rice growth.

It seems that the LMRF is not nutrient limited and the lower temperatures at 850 m are the primary cause of the change in species composition and reduction of stature there.

ACKNOWLEDGEMENTS

I wish to thank the Government of Brunei for permission to work in their country and the Universiti Brunei Darussalam and the Royal Geographical Society for the opportunity to participate in the 1991-92 Brunei Rainforest Project. The RGS bore most of the costs of my stay at Kuala Belalong and I would like to thank the Society and especially the Earl of Cranbrook and Nigel Winser for their support throughout. Catriona and Amanda deserve particular thanks for their efforts in ensuring the smooth running of the project. I would like to thank all of the staff of Kuala Belalong Field Studies Centre, especially Ramlah anak Sapong without whose efforts it would have been impossible to complete the field work.

The Department of Botany and the Environmental Science Unit of Trinity College are thanked for their hospitality during my eight months in Dublin.

I would like to thank all my friends and colleagues (you know who you are) for their help and advice, both practical and impractical, during all stages of the work in Brunei, Dublin and Stirling. Peter Wilkie merits special mention for his work on the bioassay.

Abang Baya Busu collected all the voucher specimens and numerous specialists including Dr G.C. Argent, Professor P.S. Ashton, Dr M.M.J. Van Balgooy, Dr M. Coode, Dr J. Dransfield, Dr D.J. Mabberley, Dr I. Neilsen, Dr M.F. Newman and Dr C.M. Pannell assisted with their identification. I greatly appreciated the expertise of K.M. Kochummen who was able to clarify the most intractable of the taxonomic mysteries.

Financial support for the work came from a two-year Leverhulme Trust Study Abroad Studentship, and I would like to thank Jean Cater who dealt with my numerous requests promptly and efficiently. The Peter Nathan Charitable Trust also supported the field work.

I wish to thank Les and Fionnuala for their permission to use 'Bukit Belalong'.

My supervisor, John Proctor, provided constant inspiration and assistance, and unfailing good humour, even when being force-marched up Bukit Belalong.

CHAPTER 1. ALTITUDINAL ZONATION ON TROPICAL MOUNTAINS

Introduction

In recent years tropical montane forests have been the focus of considerable interest and cloud forests[1] were the subject of a review by Stadtmuller (1987) and a conference held in Puerto Rico in 1993 (Hamilton, Juvik & Scatena 1993). As lowland forests disappear montane forests will contribute an increasing proportion of the remaining rain forests. They are important in watershed protection and the soils can retain and 'store' water, maintaining water supplies to downstream areas during rainless periods. There is a wealth of epiphytes, ferns, herbs and shrubs as well as trees in montane forests and the proportion of endemics can be high.

With increasing altitude on wet tropical mountains there is a reduction in the stature of the trees and leaves are smaller and thicker. Montane forests are divided into Upper Montane Rain Forest (UMRF), at higher altitude, in which the majority of the trees have a low stature (<20 m), and leaves which are predominatly microphylls or leptophylls (Raunkier 1934), and Lower Montane Rain Forest (LMRF) in which the tallest trees reach 35 m or more and the majority of the trees are mesophyllous. These Formations are found throughout the tropics, but the altitude at which they occur varies between mountains. On small, isolated mountains, particularly those close to coasts, the zonation of the vegetation is compressed, and this has been ascribed to a *Massenerhebung* or mass elevation effect (Grubb 1971, 1977; Weaver *et al* 1986). The *Massenerhebung* effect was first recorded in the Alps and is the phenomenon that on large mountains and in the central regions of large mountain ranges the air temperature is higher than it would be at the same altitude on a smaller mountain (Whitmore 1984). In the classical model the extensive surfaces of large mountains are heated

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[1] Montane forests characterised by persistent cloud cover at the vegetation level. See Hamilton *et al* (1993) for complete definition.

by exposure to intense solar radiation which raises the temperature of the surrounding air, and allows plants to extend their altitudinal range. Of the mountain ranges in South East Asia only the central range in New Guinea, and to a lesser extent, the Barisan Range of Sumatra, are likely to be extensive enough to exhibit any mass heating effect (Whitmore 1984). Temperature alone is not the over-riding factor in setting the relatively low limits of montane forests on small, isolated mountains because the lapse rates on such mountains are similar to those of other small mountains.

Brown (1919) recognised that the lower limit of the cloud cap that routinely formed on Mount Maquiling in the Philippines coincided with the transition from tall, large-leaved forests to low, small-leaved forests, and this conclusion has been supported by numerous observations (Weaver *et al* 1986; Stadtmuller 1987; Proctor *et al* 1988). The compression of altitudinal zonation on small isolated mountains is not due to a temperature effect, but is related to the environmental conditions associated with a cloud cap. An alternative name for this phenomenon is the 'coastal proximity zonation effect' (Bush 1986), but cloud forest is not found on all coastal tropical mountains, nor is it restricted to them. It seems that a high atmospheric moisture content rather than a coastal location is the important factor since on Java the cloud forest is more widely distributed in the wetter western parts of the island (Van Steenis 1972).

Within montane forests temperatures are lower than in lowland forests and thus the degree of saturation of a given body of air is higher. Wind speeds are higher and precipitation increases due to the orographic effect and increased horizontal precipitation from fog. Clouds and fog also reduce the intensity of solar radiation. Montane soils are wetter because of the high levels of atmospheric moisture, and acidic, nutrient-poor mor humus, or even peat may form. Thus there is a complex suite of interrelated environmental factors in montane forests and the precise causes of altitudinal zonation of forests generally remain a matter for conjecture (Bruijnzeel & Proctor 1993). No single factor has yet been found that can be applied to all situations, and nor is such a factor likely to be found (Whitmore 1984).

Wind

The greater wind speeds that occur at higher elevations may have considerable effects on vegetation. Isla Margarita, off the coast of Venezuela, is subject to strong north-easterly trade winds for almost the entire year. The wind causes severe stunting of UMRF, which is only 4 m high, on the windward slopes of the mountains (Sugden 1986). The distribution of similar forest on the Serrania de Macuira, Colombia, is also related to the prevailing winds (Dupuy, Santamaria & Cavelier 1993). Lawton (1982) found that in Costa Rican montane forest trees on ridges which are exposed to higher windspeeds than those in gullies have thicker trunks and stouter twigs than similar-sized trees of the same species growing in gullies. Stunting of ridge trees was interpreted as a response to the mechanical stress of winds.

Drought

With increasing altitude leaf thickness tends to be greater and there is an increase in the thickness of the outer epidermal walls and in the incidence of multiple palisade layers and hypodermis (Buckley *et al* 1980). The small, sclerophyllous xeromorphic leaves are superficially similar to the sclerophylls of drought-adapted mediterranean plants and have been called pachyphylls (Grubb 1974). Whitmore (1984) noted the occurrence of the most distinctive, stunted montane forests on ridges, knolls and summits and suggested that as these sites receive water only from precipitation their soils were likely to be more vulnerable to drought than the soils of hillsides and saddles. He discussed the relative importance of drought in the altitudinal zonation of forests on a series of Malaysian mountains and concluded that drought was an important factor on at least some of them. Bruijnzeel (1990) described a stunted, 5 m tall, sclerophyllous forest on Mount Bloomfield in the Philippines, whose occurrence is related to the exceptionally shallow soils and strongly seasonal climate. However, studies on Malayan (Buckley, Corlett & Grubb 1980) and Jamaican (Kapos & Tanner 1985) UMRF trees showed that xeromorphic montane plants were not able to reduce water loss to a greater extent than lowland species. Kapos & Tanner (1985) showed that although Jamaican mor ridge forest had the shortest trees with the most xeromorphic leaves of four sites, water was most consistently available there. Gap (col) forest included the tallest trees with the least xeromorphic leaves, but the lowest soil water potentials were measured there. It should be borne in mind that an absolute measure of the water-efficiency of these forests would require determination of transpiration rates, leaf area index and net assimilation rate.

Though there have been reports of UMRF die-back following a severe drought in Sri Lanka (Werner 1988), Bruijnzeel *et al* (1992) found indirect evidence that a prolonged drought on Gunung Silam, in Sabah had more deleterious effects in lowland than in montane forest. In the lowland forest the litter-layer mass measured in two successive years showed considerable differences, but this was not seen in the montane forest. Just prior to the first sampling in July and August 1983 the area had suffered a long-lasting drought which aparently caused increased litterfall in the forests below the cloud cap. The litter-layer mass was less in 1984 in the lower forests and this was interpreted as a widespread retention of the new leaves which had replaced those affected by drought in 1983 (Bruijnzeel *et al* 1992).

Nutrient limitation

Indications of nutrient limitation in montane forests come from litterfall studies, bioassays in montane soils and fertilisation experiments. Comparison of 62 litterfall studies in tropical forests (Vitousek 1984) showed low nitrogen concentrations in litterfall from montane forests compared with lowland forests, but no clear pattern with phosphorus. Vitousek & Sanford (1986) concluded that whilst lowland forests on oxisol/ultisol soils are rich in nitrogen and may be phosphorus limited, montane forests in general appear to be low in nitrogen and upper montane forests cycle substantially less nitrogen than do lower montane forests. Bruijnzeel & Proctor's (1993) review of litterfall studies at different altitudes on single mountains supported these earlier suggestions: in the five studies with relevant data, litterfall nitrogen concentrations declined with altitude whilst litterfall phosphorus concentrations did not vary consistently.

A bioassay experiment using soils from the Jamaican montane forests (Healey 1989) supported the results of the litterfall (Tanner 1980) and fertilisation studies (see below). Nitrogen and phosphorus addition were found to significantly increase the growth of a grass species in montane soils, and these results agree with a number of agricultural studies on similar soils in the area.

Rates of decomposition and nitrogen mineralisation decline with altitude and it has been suggested that this might cause nutrient limitations (Heaney & Proctor 1989; Marrs *et al* 1988). However, rough estimates by Bruijnzeel *et al* (1992) suggested that atmospheric inputs of nutrients to montane forests might exceed rates of uptake by up to a factor of five to ten. Fertilisation experiments in Jamaican (Tanner *et al* 1990) and Venezuelan (Tanner, Kapos & Franco 1992) montane forests both showed that nitrogen and phosphorus addition can increase girth increments. The response to fertilisation varied among species, and whilst most showed an increase others showed no response or a reduction in mean increment. In the Venezuelan experiment leaf litterfall was significantly increased by addition of nitrogen either singly or in combination with phosphorus, but addition of phosphorus alone had no effect. The nutrients were only added singly in the Jamaican experiment and though an increase in leaf production was inferred for some species it was not found for all.

The responses to added nutrients were slow and the increased growth incorporated a small proportion of these nutrients. The location of the 'missing' nutrients was unclear, but it was suggested that they were either in an unsampled plant fraction, immobilised in the soil or removed by leaching and denitrification. Thus despite evidence of nutrient limitation montane forests appear to be unable to effectively exploit excess supplies of these nutrients. There are not yet any results from fertilisation experiments in lowland forests with which to compare these studies.

Plant-soil interactions

If nutrients are present in adequate quantities why do the trees exhibit signs of limitation? Grubb & Tanner (1976) suggested that the extreme acidity (pH 2.8-3.5) of Jamaican mor ridge soils excluded taller species from the very stunted forests on these soils. Hydrogen-ion toxicity may be an explanation for the exclusion of lowland species from low-stature montane forests at low altitudes on small mountains (Grubb 1989).

Whilst the short-facies LMRF on Gunung Silam has low rates of nutrient uptake, rates of transpiration are also low (Bruijnzeel *et al* 1992). Relatively crude short-term water balance calculations suggested that in the shorter forests transpiration was 24% of the potential Penman evaporation, whilst in taller forest at lower altitude it was 47%. Bruijnzeel *et al* (1992) hypothesised that phenolic compounds leached from litter interfered with ion uptake, transpiration and photosynthesis. The causes of the high concentrations of phenolic compounds in the leaves of trees from the shorter forest are unclear, but may be related to their role as 'filters' that absorb and reduce the UV flux reaching certain plant tissues. UV-B radiation is absorbed by the atmosphere and thus levels are higher at high altitudes. Plants grown at high UV-B levels tend to be small, with small, thick leaves which possess a hypodermis (Flenley 1992). Well-watered plants grown under low levels of light (both conditions common in montane forests) tend to be more sensitive to UV-B radiation than plants grown under constant higher light levels (Bruijnzeel & Proctor 1993). Flenley (1993) has suggested that the presence of stunted forests at low altitudes on coastal mountains may be related to enhanced UV-B radiation due to reflection from the sea. This hypothesis remains untested.

The accumulation of organic matter and the high acidity of UMRF soils can be interpreted as a 'one-sided positive feedback switch' *sensu* Wilson & Agnew (1992). The lignin-rich and phenol-rich leaves of UMRF trees decay slowly (Grubb 1977) and soils thus soils tend to become more organic and more acid, excluding LMRF species which cannot compete under these conditions and reinforcing the boundary between the two formations.

The aims of this study

The study of altitudinal zonation on tropical mountains is complicated by the interaction of climatic, soil and plant variables. The gradual ecotone between lowland forest and LMRF has received less attention than the more dramatic ecotone between LMRF and UMRF and there is a need for work to clarify the reasons for the former.

Bukit Belalong (913 m) is a small mountain c. 50 km from the coast. A cloud cap forms only occasionally at the summit and tall-stature LMRF is found from about 750 m to the summit. The mountain thus serves as a 'baseline' location for work on forest stunting on small tropical mountains. The aims of this study are firstly to comprehensively describe the vegetation and the physical environment on Bukit Belalong and relate the findings to work on other South East Asian mountains, and secondly to investigate the role of the physical environment in the altitudinal zonation of the forests. The study will investigate the relative importance of the direct effects of climate on plant growth and the secondary effects of climate which might restrict nutrient supply and limit growth.

CHAPTER 2. THE PHYSICAL ENVIRONMENT

INTRODUCTION

Negara Brunei Darussalam (Brunei) is an independent Sultanate of 5,765 km^2 on the north-west coast of Borneo (Figure 2.1a). The present study was carried out as part of the 1991-1992 Brunei Rainforest Project, jointly administered by the Universiti Brunei Darussalam and the Royal Geographical Society, London.

The Project was based at the recently completed Kuala Belalong Field Studies Centre (FSC), located on the Belalong River in the Batu Apoi Forest Reserve (4° 32′ N, 115° 10′ E) in the Temburong District of Brunei (Figure 2.1b). The Project area was c. 5,000 ha of the 48,854 ha Reserve and extended from the junction of the Belalong and Temburong Rivers (30 m) to the summit of Bukit Belalong (913 m). None of the Reserve has been logged and human disturbance is limited to small-scale hunting and the collection of some non-wood forest products by local Iban villagers. In March 1991 the Minister of Industry and Primary Resources announced plans for a National Park including the Batu Apoi Forest Reserve which would be about 10% of the total land area of Brunei.

GEOLOGY AND GEOMORPHOLOGY

Bukit Belalong is wholly underlain by sedimentary rocks of the Temburong Formation (Brondijk 1963). The Formation dates from the Middle Oligocene to the Early Miocene (16-30 million years ago) and consists almost entirely of strongly folded, dark grey shales with occasional thin beds of quartzitic sandstone and very rarely thin limestone beds. These rocks were originally assigned to the Setap Shale Formation (Wilford 1961), but Brondijk (1963) discerned the separate Temburong Formation which incorporates the older, more argillaceous succession found in Temburong. The older name is still sometimes used because the distinction between the two Formations has not yet been mapped. There are a few small

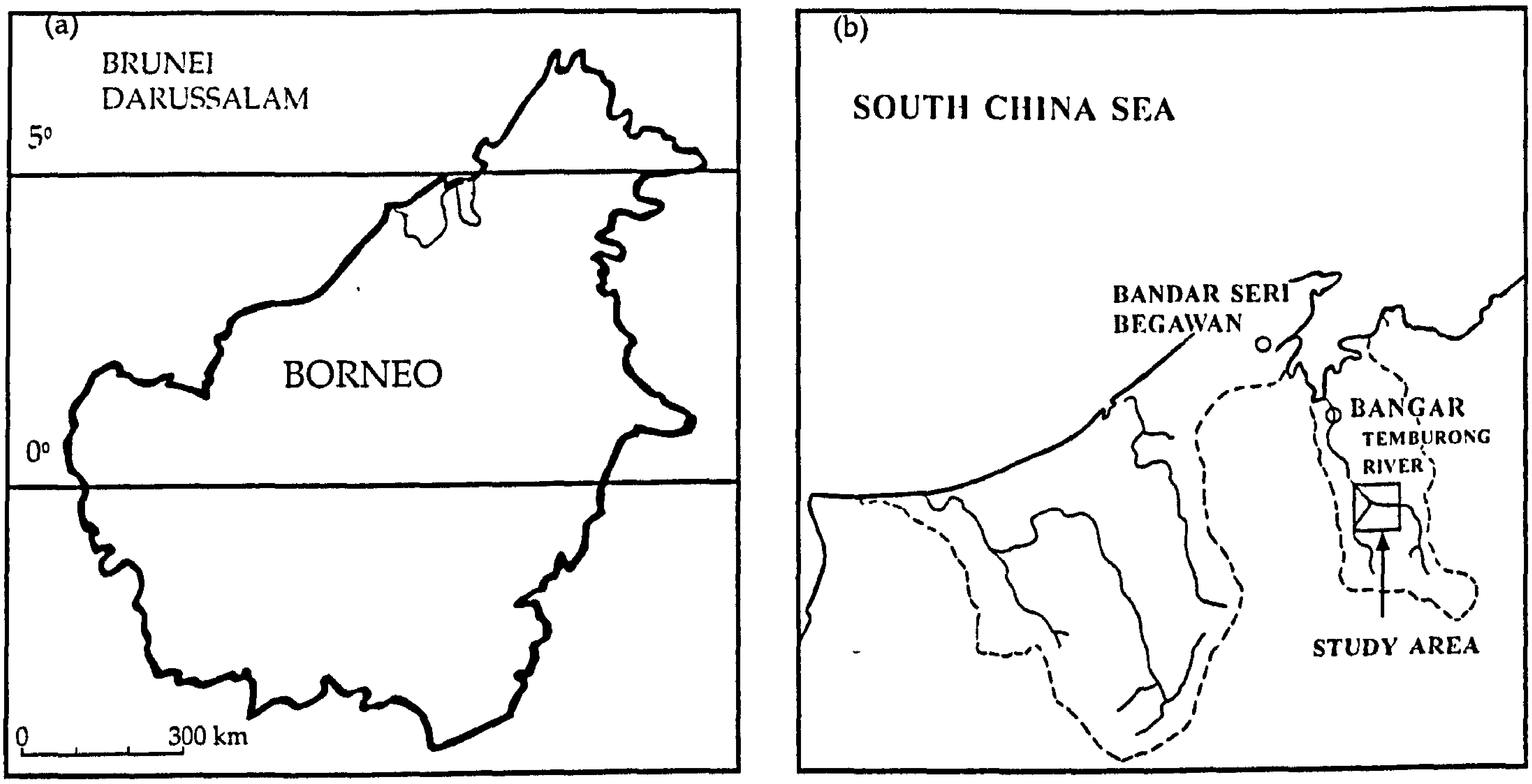


Figure 2.1. (a) The position of Brunei on the north-west coast of Borneo. (b) The location of the study area in the Temburong District of Brunei.

outcrops of sandstone on Bukit Belalong, but none of these occurred near the study plots, which were all located on shale.

Recent tectonic movements have led to rapid uplift of the area (estimated at 0.75 mm yr^{-1}, Dykes 1994) and have resulted in erosion which has produced the rugged topography. Valleys are separated by narrow ridges which are often only a few metres wide with steep slopes that occasionally exceed 60°. Most hillsides bear evidence of landslides of varying sizes.

CLIMATE

Bukit Belalong

An automatic weather station (AWS1) was located near Kuala Belalong (30 m) (Figure 2.2), on a small hillock (45 m) from which the vegetation was cleared, from 18 June 1991 until 22 April 1992. A similar weather station (AWS2) was sited at the summit of Bukit Belalong (913 m) from the 8 of May 1991 to 23 April 1992 (Figure 2.3). The weather stations (manufactured by the Didcot Instrumentation Company, Shaw 1988) used a Kipp solarimeter to measure short wave radiation and a Rimco tipping bucket rain gauge. The net radiometer, anemometer, wind vane and the temperature sensors were designed by the Institute of Hydrology. The air temperature and wet bulb depression were measured by two dry and one wet bulb platinum resistance thermometers housed in a thermal radiation screen. Hourly means from these instruments and daily totals of rainfall and Penman evaporation were recorded by a Campbell Data Logger. Rainfall was also measured daily from 1 February 1991 in a manual rain gauge at the FSC.

The monthly rainfall totals, the number of rain-free days per month and the mean monthly air temperatures are listed for the months during which complete data were collected (Table 2.1) The longest rain-free periods recorded were seven days by AWS1 (24-30 August 1991) and twelve days by AWS2 (9-21 June 1991). The total rainfall for May 1991 to April 1992 is

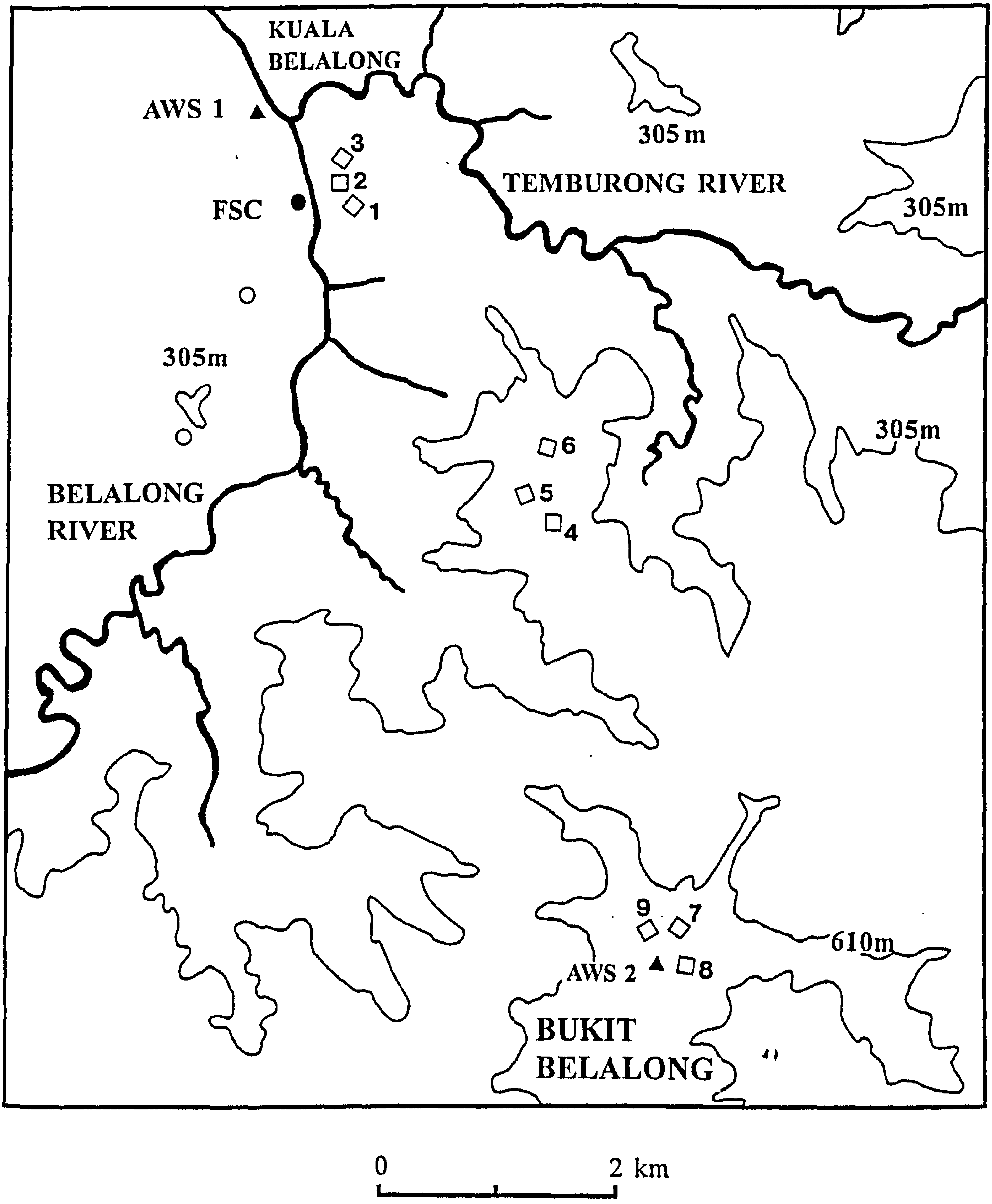


Figure 2.2. The locations of the 50 m x 50 m study plots (1-9), Automatic Weather Stations (AWS1 and AWS2) and Kuala Belalong Field Studies Centre (FSC), Bukit Belalong, Brunei.

Figure 2.3. Automatic weather station (AWS2) at 913 m on the summit of Bukit Belalong, Brunei.

estimated at c. 3200 mm at Kuala Belalong and c. 4300 mm at Bukit Belalong, and its monthly distribution is given in Figure 2.4. Rainfall for the months lacking complete data were estimated from regressions between the monthly totals for the manual rain gauge at KBFSC and the monthly totals at the two AWS's (AWS1 r^2=98.6%, n=9, p=0.000; AWS2 r^2=90.6%, n=10, p=0.000). Most rain falls in intense localised events due to convection cells which form during the afternoon. Rain was uncommon before midday.

Monthly rainfall totals (1973-1992) were obtained from Semabat Agricultural Station, 9 km to the north-west of Kuala Belalong. Mean annual rainfall for these years was 4086 mm, and from May 1991 to April 1992 3200 mm (78% of the mean) was recorded. If it is also assumed that the rainfall at KBFSC during that period was also c. 80% of the annual mean, it is estimated that the mean annual rainfall at Kuala Belalong is c. 4100 mm and at Bukit Belalong c. 5500 mm. Occult precipitation was not measured by the weather stations, but may be important at 913 m (Poulsen & Pendry 1994), and this will be discussed in Chapter 7.

Rainfall tends to be highest in May and December, but seasonality is unpredictable. February and March 1992 were unusually dry and during these months only 45% of their mean rainfall (1973-1992) fell at Semabat. This value is similar to that for February and March 1983, when only 42% of the mean rainfall was recorded. During 1983 a widespread drought had serious impacts on forests throughout Borneo (Ashton 1989), and the data collected for 1991-1992 can be used to investigate the effects of occasional droughts on Bornean forests.

At 45 m mean monthly temperatures were similar from July 1991 to March 1992, but they were more variable at 913 m where the difference between monthly means was up to 2.5 °C (Table 2.1). This is reflected in the more variable mean maximum and minimum temperatures at 913 m (Table 2.2). Diurnal ranges were lower at 913 m. The mean temperatures for July 1991 to May 1992 were 25.7 °C at 45 m and 21.8 °C at 913 m, indicating a lapse rate of 0.45 °C 100 m^{-1}. The daily totals of solar radiation were more variable at 913

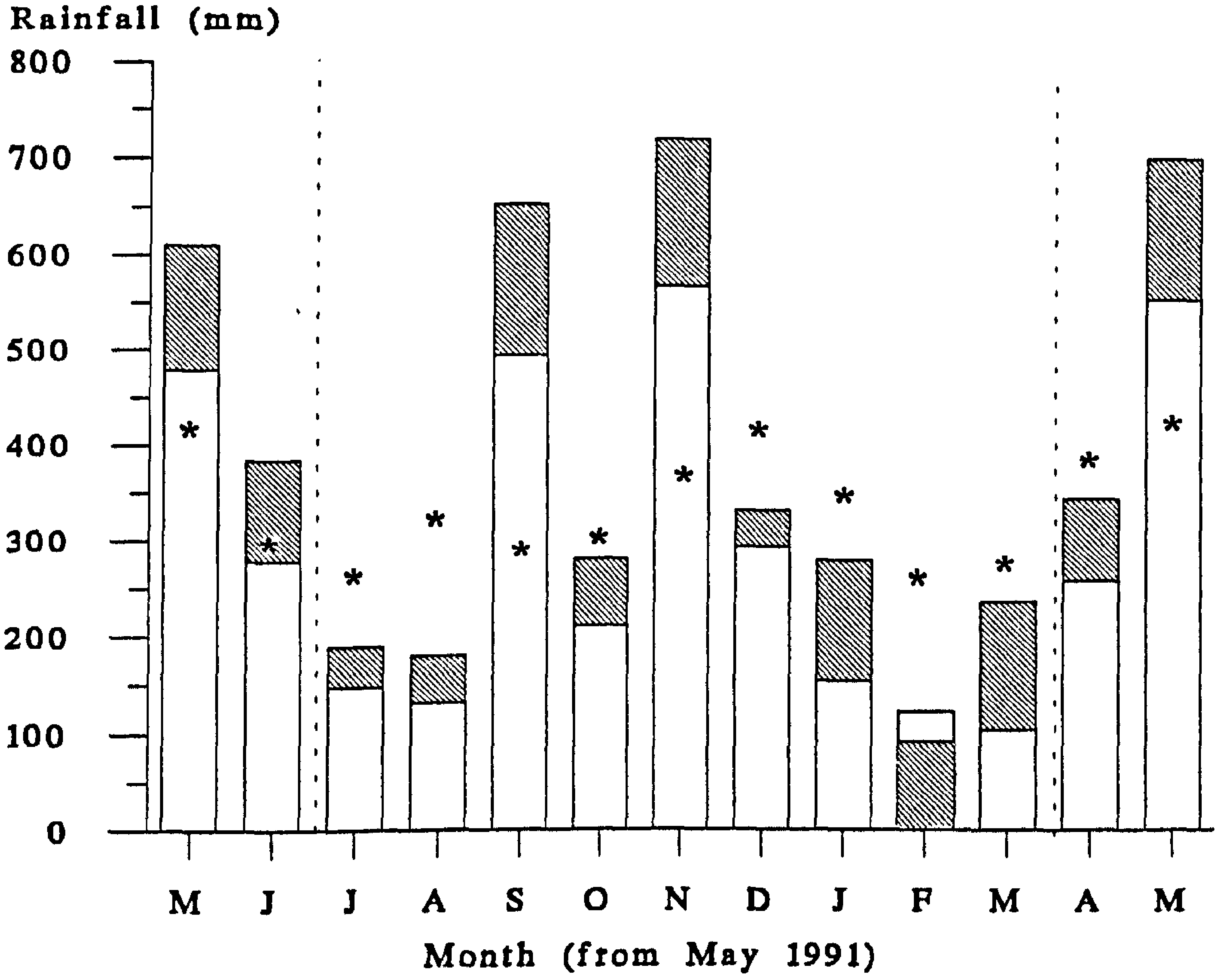


Figure 2.4. Total monthly rainfall at Kuala Belalong (45 m) and Bukit Belalong (913 m) from May 1991 to May 1992. The totals for May and June 1991 and April and May 1992 were estimated from the measurements made by a manual rain gauge at Kuala Belalong Field Studies Centre. The height of the unshaded part of the column represents the rainfall at Kuala Belalong, and the height of the column including the shaded part represents the rainfall at Bukit Belalong, except for February 1992, when more rain was recorded at Kuala Belalong than Bukit Belalong. For this month the total height of the column represents the rainfall at 45 m and the shaded portion the rainfall at 913. '*' represents the mean monthly rainfall (1972-1991) at Semabat Agricultural Station.

Table 2.1. The monthly total rainfall (mm), number of rainless days per month and mean daily temperature (°C) from July 1991 to March 1992 at Kuala Belalong (70 m) and Bukit Belalong (913 m), Brunei.

	Kuala Belalong			Bukit Belalong		
	Rainfall (mm)	Rainless days	Average temperature (°C)	Rainfall (mm)	Rainless days	Average temperature (°C)
July 1991	148.0	17	26.3	190.0	14	23.0
August	131.5	14	25.9	180.5	15	23.1
September	492.5	4	25.6	651.5	3	22.4
October	210.5	9	25.3	278.5	5	21.8
November	564.0	3	25.1	717.0	1	21.4
December	292.0	6	25.4	330.0	5	21.5
January 1992	153.0	14	25.3	277.5	12	20.6
February	121.5	17	25.4	91.5	13	20.6
March	102.5	18	26.9	235.5	15	21.8

Table 2.2. The mean daily maximum and minimum temperatures (°C) and mean daily diurnal range of temperatures from June 1991 to March 1992 at Kuala Belalong (70 m) and Bukit Belalong (913 m), Brunei. The values are the means for each month with the ranges in parentheses.

	Kuala Belalong			Bukit Belalong		
	Maximum temperature (°C)	Minimum temperature (°C)	Diurnal range	Maximum temperature (°C)	Minimum temperature (°C)	Diurnal range
June 1991		-	-	29.7 (22.3-33.1)	20.3 (18.7-21.4)	9.4 (3.4-12.4)
July	33.7 (28.0-36.4)	22.4 (21.0-23.7)	11.0 (6.6-14.0)	29.5 (22.5-33.2)	19.8 (17.9-21.6)	9.7 (4.6-13.3)
August	32.8 (27.4-35.3)	22.3 (20.8-23.8)	10.5 (6.6-14.0)	29.6 (24.5-33.4)	20.0 (18.2-21.7)	9.6 (4.3-12.8)
September	32.8 (28.8-35.4)	22.2 (21.3-23.4)	10.7 (6.7-13.3)	28.6 (24.6-31.9)	19.4 (17.9-21.4)	9.2 (6.2-13.1)
October	31.9 (28.2-34.7)	22.0 (20.7-23.6)	9.9 (6.0-11.9)	27.8 (24.5-30.4)	18.9 (17.5-20.6)	8.9 (5.8-10.7)
November	31.1 (29.0-32.9)	22.2 (21.5-23.2)	9.0 (6.7-11.4)	26.9 (24.0-29.7)	18.8 (18.1-19.6)	8.2 (5.2-10.9)
December	31.0 (26.7-32.6)	22.6 (21.2-24.0)	8.4 (4.0-10.4)	26.7 (23.4-29.5)	18.8 (17.9-19.9)	7.9 (4.9-11.2)
January 1992	30.9 (27.7-34.6)	22.3 (21.0-23.4)	8.5 (4.6-11.3)	25.7 (22.4-27.8)	18.1 (16.9-18.9)	7.6 (4.6-9.9)
February	32.0 (27.7-34.6)	21.9 (19.2-23.4)	10.1 (4.9-13.6)	26.2 (22.9-28.4)	17.6 (15.5-18.8)	8.6 (5.6-11.8)
March	35.0 (30.8-37.1)	22.4 (19.9-24.1)	12.5 (7.2-15.2)	28.5 (24.1-31.3)	18.2 (16.7-19.6)	10.4 (5.8-13.7)

m (Table 2.3), but the averages for July 1991 to March 1992 are very close (15.63 MJ m^{-2} at 45 m and 15.71 MJ m^{-2} at 913 m). The maximum values of insolation were higher at 913 m and the convergence of the means is due to the occasional formation of a cloud cap at the summit. The formation of a cloud cap was infrequent and unpredictable.

Wind speeds were higher at 913 m (Table 2.4), and the mean daily values were 0.47 m s^{-1} at 45 m and 0.89 m s^{-1} at 913 m. Penman open-water evaporation estimates could not be calculated for the entire period because of problems with the net radiometers, and data are only given for those months for which reliable data were collected (Table 2.5). Penman evaporation was more variable at 913 m and both the maximum and minimum daily totals were recorded there. However, the mean daily totals for the six months during which both AWS's functioned were similar.

Comparisons with Gunung Silam

Hydrological observations have been made on Gunung Silam, Sabah (5° N, 119° E), 350 km east of Bukit Belalong, by Proctor *et al* (1988) and Bruijnzeel *et al* (1992). Although Bukit Belalong and Gunung Silam (884 m) are of a similar size and are at about the same latitude there are a number of differences between the climates for the two mountains which have important implications for their vegetation.

Mean annual rainfall on Gunung Silam (2132 mm at 10 m, 1970-1988; estimated to be 2600 mm at 884 m) is low compared with Bukit Belalong, and it is prone to dry spells of a few months which occur at 5-11 yearly intervals in relation to the El Ninõ effect (Bruijnzeel *et al* 1992). Gunung Silam is on the coast (the summit is less than four km from the sea) and typically a cloud cap develops at the summit during late morning and by mid afternoon extends to 650 m before dispersing in the early evening. Occult precipitation within the cloud cap was estimated at 0.4 mm d^{-1} (Bruijnzeel *et al* 1992), or about 9% of ordinary rainfall. Average temperatures are slightly higher on Gunung Silam (27.6 °C at the base and 23.7 °C

Table 2.3. The mean daily solar radiation (MJ m^{-2}) from June 1991 to March 1992 at Kuala Belalong (70 m) and Bukit Belalong (913 m), Brunei. The values are the means for each month with the ranges in parentheses. '-' indicates that data are not available for that month.

	Solar radiation (MJ m^{-2})	
	Kuala Belalong	Bukit Belalong
June 1991	-	17.5 (5.7-25.2)
July	16.3 (9.5-20.4)	17.6 (7.6-24.1)
August	14.6 (8.2-20.5)	16.7 (7.2-24.3)
September	15.0 (7.8-18.6)	15.6 (8.3-22.6)
October	15.0 (7.1-18.6)	15.3 (8.0-21.5)
November	15.4 (9.9-18.9)	14.9 (8.5-21.2)
December	14.6 (9.1-18.3)	13.2 (9.4-18.4)
January 1992	15.1 (9.5-20.2)	13.7 (7.7-19.9)
February	16.2 (8.8-19.1)	15.4 (9.9-24.9)
March	18.5 (12.3-21.8)	19.3 (8.8-24.8)

Table 2.4. The mean wind speed (m s^{-1}) from June 1991 to March 1992 at Kuala Belalong (70 m) and Bukit Belalong (913 m), Brunei. Measurements were made at a height of 2 m in the centre of a cleared area. The values are the means of the average daily wind speed with the ranges in parentheses. '-' indicates that data are not available for that month.

	Mean daily wind speed (m s^{-1})	
	Kuala Belalong	Bukit Belalong
June 1991	-	0.88 (0.46-1.33)
July	0.55 (0.42-0.69)	0.95 (0.56-1.49)
August	0.52 (0.37-0.66)	0.90 (0.63-1.33)
September	0.51 (0.42-0.69)	0.97 (0.60-1.70)
October	0.46 (0.37-0.55)	0.79 (0.33-1.20)
November	0.42 (0.34-0.56)	0.76 (0.37-1.21)
December	0.39 (0.30-0.52)	0.80 (0.38-1.30)
January 1992	0.41 (0.31-0.54)	0.87 (0.58-1.41)
February	0.45 (0.29-0.57)	1.00 (0.65-1.54)
March	0.53 (0.31-0.65)	0.95 (0.63-1.19)

Table 2.5. The mean estimated daily Penman evaporation (mm) from June 1991 to February 1992 at Kuala Belalong (70 m) and Bukit Belalong (913 m), Brunei. The values are the means of the average daily evaporation with the ranges in parentheses. '-' indicates that data are not available for that month (see text).

	Mean Penman evaporation ($mm\ d^{-1}$)	
	Kuala Belalong	Bukit Belalong
June 1991	-	3.58 (1.11-5.47)
July	3.39 (1.80-4.51)	3.53 (1.44-4.92)
August	3.06 (1.64-4.48)	3.38 (1.44-5.18)
September	-	3.19 (1.43-4.75)
October	-	-
November	3.16 (1.96-4.06)	2.80 (1.52-3.87)
December	3.08 (1.79-4.16)	2.57 (1.76-3.85)
January 1992	3.27 (1.88-4.49)	2.69 (1.46-3.92)
February	3.55 (1.72-4.31)	3.03 (1.79-4.65)

at the summit) than at similar altitudes on Bukit Belalong, and the lapse rate (0.35 °C 100 m^{-1} below the cloud cap and 0.17 °C 100 m^{-1} within it) is lower than on Bukit Belalong. The more exposed coastal location of Gunung Silam is reflected in the higher mean daily windspeeds there than on Bukit Belalong (1.5 ms^{-1} at the base and 2.6 ms^{-1} at the summit). Within the cloud cap Penman evaporation rates were about 3.6 mm d^{-1}, compared with 5.1 mm d^{-1} at the base, a reduction of about 30%.

SOILS

Introduction

Soil surveys in tropical forests generally rely on sampling on a single occasion because of the logistical problems of working in remote areas. However, seasonal fluctuations may be important, particularly for nitrogen supply. Touber *et al* (1989) suggested that in the absence of repeated sampling, emphasis should be geared towards analysis of 'topsoil parameters with a permanent character'. A potential problem is that such analyses give no insight into the nutrient dynamics of the soil system. A small pool of plant available nutrients might be supposed to indicate nutrient limitation, but without an indication of rates of turnover of that pool an accurate assessment cannot be made. This section will describe the physical and chemical properties of the soils collected at one sampling time at the three altitudes and will then discuss the results of an experiment to investigate nitrogen dynamics in soils from Bukit Belalong.

Marrs *et al* (1988) found lower rates of nitrogen turnover along an altitudinal transect on Volcán Barva, but also found that amendment with various nutrients affected rates of turnover. The mineralisation experiment therefore tests the effect of added nutrients on rates of nitrogen turnover.

Materials and Methods

Soil sampling

A soil pit was dug from 1 m to 5 m outside each of nine 50 m x 50 m plots which had been set up for the forest description (Chapter 3), at a site which was considered typical of the plot. Each pit was dug to a depth of 1.5 m or less if the bedrock was reached first. The profiles were described using the nomenclature from Hodgson (1974), and Munsell charts (Munsell Color Company 1971) to distinguish the colours. Landon (1992) recommended that samples from many tropical soils without distinct horizons should be collected at fixed depths. The depths selected (0-5 cm, 5-20 cm and 20-100 cm) corresponded roughly to the horizons which were at similar depths in all profiles. Between 5-20 cm and 20-100 cm soil was collected at several depths and bulked to make a single composite sample representative of the depth range.

In addition surface-soil samples were collected at ten random points in each plot using an open-ended, 10 cm x 10 cm stainless steel box inserted into the soil to a depth of 5 cm. Two samples were collected, the first for bulk density determination and the second for the estimation of the nitrogen mineralisation and nitrification rates and other chemical and physical analyses. All soil samples were air dried in the field and returned to Stirling for analyses.

Soil physical and chemical analyses

The bulk-density samples were oven dried at 105 °C and weighed. The degree of stoniness (g stones 100 cm^{-3} sample) was estimated by removing stones (>5 mm along any axis) and weighing. Roots were also separated and weighed (see Chapter 5). Soil bulk density (g soil cm^{-3} sample) was calculated by subtracting the mass of stones and roots from the total mass of the sample.

The samples were ground gently and sieved through a 2-mm mesh. Soil pH was measured on 10-g subsamples mixed with 25 ml of deionised water and left to equilibrate for 2 h. The moisture content of air dried soils was determined by heating subsamples to 105 °C for 16 h, and the same subsamples were used to measure loss-on-ignition by heating to 375 °C for 16 h. Total nitrogen and total phosphorus were measured in 0.2-g subsamples digested in 4.4 ml of a sulphuric acid/hydrogen peroxide mixture with a selenium catalyst (Allen 1989). Nitrogen was measured as ammonia on an FIAStar 5100 flow injection analysis system (Tecator application note AN 50/84 1984). Phosphorus was measured on the FIA system by the ammonium molybdate/ stannous chloride method (Tecator application note AN 60/83 1983). Available phosphorus was extracted from 2.5-g subsamples shaken with 100 ml 2.5 % (v/v) acetic acid and measured on the FIAstar system by the same method. Exchangeable cations were extracted from 5-g subsamples by ten successive additions of 1 M ammonium acetate and measured on a Varian AA-575 atomic absorption spectrophotometer. Potassium and sodium were measured by emission and calcium and magnesium by absorption An air/acetylene flame was used for all elements except calcium for which a nitrous oxide/acetylene flame was used. For total acidity, exchangeable aluminium and hydrogen measurement, 5-g subsamples were leached with ten successive additions of 10 ml of 1 M potassium chloride. A 5 ml aliquot of the extract was titrated against 2.5 mM sodium hydroxide to determine total acidity, and aluminium was measured by titration against 5 mM hydrochloric acid after addition of 1 ml 1 M sodium fluoride; hydrogen was then estimated by subtraction. Cation exchange capacity (CEC) was calculated as the sum of total exchangeable cations plus total acidity. Percentage base saturation was calculated as the proportion of exchangeable cations (excluding aluminium and hydrogen) to CEC. Particle-size analyses were made using the Bouyocos hydrometer method (Allen 1989) on samples from one randomly selected pit at each altitude and three randomly selected surface soil samples from each plot.

Nitrogen mineralisation and nitrification

Surface soils (0-5 cm) were sampled as described above, and the samples to be used for the nitrogen mineralisation and nitrification experiment were treated as follows. The samples were sorted to remove stones, roots and large fragments of organic material (>5 mm along longest axis) and aggregates were crumbled till they were no bigger than 10 mm. Each sample was divided into four fractions which were treated as follows.

Fraction 1, for the determination of initial concentration. The fraction was extracted immediately to determine the ammonium and nitrate/nitrite concentrations. From here on nitrite/nitrate will be referred to simply as nitrate since nitrite concentrations are likely to be low in these soils which do not suffer waterlogging and anaerobic conditions (Tanner 1977). Twenty g (fresh weight) of soil were extracted in 100 ml 1.5 M potassium chloride containing 3 mg l^{-1} mercuric chloride (to prevent bacterial and fungal growth) by stirring by hand for 1 min and allowed to equilibrate for 2 h.

Fraction 2, for the field incubation. About 200 ml of soil were placed in a plastic bag and the top folded down to prevent the entry of water, but to allow gaseous exchange. The bag was then placed at the site of collection and covered with a thin layer of leaf litter. The samples were collected and extracted after 21 d.

Fraction 3, for the laboratory incubation. This fraction was treated the same as fraction 2 except that the soils were incubated under shade at the Field Studies Centre.

Fraction 4, for moisture determination and chemical analyses (see previous section).

In addition, bulk soil samples (c. 3 kg) were collected from the random positions in plots 1-3 and 7-9. The samples were sorted as described above and sieved through a 4.75 mm mesh. Two 20-g subsamples were extracted immediately as described above and ten 50-g subsamples were allocated in pairs to the following nutrient treatments which were all added to the fresh soils in 6 ml of solution or in addition to 6 ml of deionised water:

(a), no nutrient addition, 6 ml deionised water only; (b), 100 mg nitrogen (as ammonium chloride) kg^{-1} soil; (c), 5 mg phosphorus (as sodium dihydrogen phosphate) per kg^{-1} soil; (d), 20 g calcium (as calcium carbonate) per kg^{-1} soil and (e), 20 g calcium (as calcium sulphate) per kg^{-1} soil. The subsamples were incubated under 'laboratory conditions' (see fraction 3 above) for 21 d before extraction.

The extracts were frozen for two months before return to Stirling where they were kept at 2 °C until analysis. The samples could not be analysed for a further eight months because of technical problems. Ammonium was measured on an FIAstar flow injection analysis system (Tecator application note AN 50/84 1984) and nitrate was measured as nitrite after reduction by a cadmium column (Tecator application note AN 62/83 1983).

Results

Physical and chemical descriptions of the soils

A brief description of one soil profile from each altitude is given in Table 2.6 and descriptions of the other six profiles are found in Appendix 1. Soils were at least 1.4 m deep in all pits at 200 m and 500 m, but at 850 m bedrock was reached in two of the plots, at 80 cm in plot 8 and 120 cm in plot 9. At all altitudes the profiles were broadly similar. There were no surface accumulations of organic matter although the loss-on-ignition (LOI) of the samples increased with altitude (Table 2.8). Stones were frequent in all profiles, especially in the pits at 200 m and 850 m and they became much more frequent at depth (Table 2.7). Surface soil bulk densities (corrected for stoniness) were highest at 200 m and lowest at 850 m (Table 2.10), and the samples from 850 m were the stoniest.

Chemical analyses of samples from the soil profiles (Table 2.8) show that the surface layer (0-5 cm) was always more acid and had higher values of LOI and higher concentrations of total nitrogen and phosphorus, acid extractable phosphorus and exchangeable cations than deeper samples. CEC and base saturation also declined with depth in all profiles. Clay content was highest in the 20-100 cm layer at 500 m and 850 m, but highest in the surface

Table 2.6. Profile descriptions from one soil pit at each of three altitudes on Bukit Belalong, Brunei.

Horizon depth (cm)	Description
Plot 1, 200 m.	
O, (4-8)-0	Litter layer. Sharp boundary with mineral soil.
A1, 0-2	Loose, crumbly, organic, granular c. 4 mm. Moderately plastic. Occasional small stones, no mottles. Matrix 7.5 YR 5/4 brown, organic matter 7.5 YR 5/4 dark brown. Regular, clear boundary.
A2, 2-7	Porous, granular 1-4 mm. Very plastic. Occasional small stones, no mottles. 5 YR 5/6 yellowish red. Regular, clear boundary.
B, 7-60	Sticky, granular 8 mm-1 cm. Very plastic. 15-60 cm stones 30%. At 10 cm 5 YR 5/8 yellowish red, >40 cm 5 YR 6/6 reddish yellow.
C, >60	Weathered shale, 80%.
Plot 6, 510 m.	
O, (3-4)-0	Litter layer. Sharp boundary with mineral soil.
A1, 0-(2-6.5)	Dry, crumbly, open, organic. Non plastic. Occasional small stones, no mottles. Matrix 3.5 YR 4/4 dark brown, organic matter 7.5 YR 3/2 dark brown. Clear, wavy boundary.
A2, (2-6.5)-(7-9)	Porous, fine granular 2 mm. Non plastic. Occasional small stones, no mottles. 7.5 YR 4/4 brown. Clear wavy boundary.
B, (7-9)-120	Sticky, granular 2 mm. Very plastic. 40-75 cm, stones 30%; 75-120 cm stones 60%. 7.5 YR 5/8 strong brown.
C, >120	Weathered shale, 80%.
Plot 9, 880 m.	
O, 1-0	Litter layer. Sharp boundary with mineral soil.
A1, 0-9	Porous, crumbly, granular 3 mm. Non plastic. Occasional small stones. Slight mottle 10 YR 5/4 yellowish brown/5 YR 5/6 yellowish red. Matrix 7.5 YR 4/4 yellowish red. Regular, clear boundary.
A2, 9-(21-24)	Porous, sticky, fine granular 5 mm. Moderately plastic. Occasional small stones. 7.5 YR 5/6 strong brown. Irregular, clear boundary.
B, (21-24)-70	Large granular 8-15 mm. Very plastic. 30-70 cm, stones 35%. 7.5 YR 6/8 reddish yellow.
C, >70	Weathered shale, 90%.

Table 2.7. Mean percentage of stones (area of profile face) at a range of depths (5-100 cm) in three soil profiles at each of three altitudes on Bukit Belalong, Brunei.

	200 m		500 m		850 m	
	Depth (cm)	Stones (%)	Depth (cm)	Stones (%)	Depth (cm)	Stones (%)
5-20	5-15	22	5-10	10	5-20	23
	15-20	27	10-20	13		
20-100	20-50	27	20-40	13	20-30	32
	50-62	50	40-75	22	30-40	42
	62-73	67	75-80	47	40-50	48
	73-100	77	80-100	33	50-70	62
					70-80	82
					80-100	88

Table 2.8. Chemical characteristics of soil samples from three soil pits at each of three altitudes on Bukit Belalong, Brunei. Values are the means of three samples at each altitude, with the ranges in parentheses. Concentrations are in oven dried soil (105 °C).

Depth (cm)						Exchangeable cations (mequiv kg^{-1})							
	pH_{H2O}	LOI (%)	N_{Total} (mg g^{-1})	P_{Total} (mg g^{-1})	$P_{Extractable}$ (µg g^{-1})	K	Ca	Mg	Na	Al	H	CEC (mequiv kg^{-1})	BS (%)
200 m													
0-5	3.5 (3.3-3.6)	11.8 (11.7-12.0)	2.43 (1.60-2.98)	0.34 (0.29-0.39)	1.5 (1.1-1.8)	2.34 (2.13-2.46)	1.07 (0.64-1.91)	2.59 (2.32-3.11)	0.55 (0.49-0.58)	80.8 (74.4-86.2)	15.7 (14.9-16.3)	103.0 (96.4-109)	6.3 (5.7-7.3)
5-20	3.6 (3.5-3.7)	7.6 (6.8-8.5)	1.49 (1.21-1.83)	0.29 (0.27-0.31)	0.3 (0.1-0.6	1.52 (1.03-2.37)	0.25 (0.17-0.29)	0.82 (0.72-0.88)	0.45 (0.33-0.59)	69.0 (68.0-70.3)	13.6 (11.8-15.0)	85.6 (83.0-87.0)	3.5 (2.8-4.7)
20-100	3.7 (3.7-3.8)	6.7 (6.1-7.2)	1.15 (1.10-1.23)	0.24 (0.21-0.27)	0.0 (0.0-0.0)	0.99 (0.87-1.20)	0.14 (0.12-0.17)	0.45 (0.39-0.49)	0.40 (0.31-0.51)	66.7 (64.3-69.4)	9.7 (8.4-11.2)	78.3 (77.5-79.8)	2.5 (2.2-2.8)
500 m													
0-5	3.7 (3.4-3.9)	14.1 (11.3-19.2)	3.34 (2.32-5.27)	0.31 (0.27-0.37)	1.3 (0.8-2.3)	2.00 (1.73-2.43)	0.50 (0.43-0.60)	1.96 (1.43-2.65)	0.72 (0.59-0.80)	98.6 (85.0-121)	25.9 (22.6-31.4)	129.6 (113-159)	4.0 (3.8-4.2)
5-20	3.8 (3.7-4.0)	9.0 (7.9-10.0)	1.57 (1.16-1.85)	0.27 (0.26-0.29)	0.2 (0.0-0.3)	0.84 (0.62-1.06)	0.24 (0.23-0.25)	0.73 (0.49-0.93)	0.48 (0.40-0.55)	78.6 (71.9-88.7)	14.5 (12.3-17.8)	95.4 (86.0-109)	2.4 (2.0-2.6)
20-100	3.9 (3.8-4.1)	7.5 (6.8-8.5)	1.26 (0.91-1.56)	0.24 (0.22-0.27)	0.3 (0.0-0.8)	0.70 (0.63-0.82)	0.17 (0.12-0.23)	0.42 (0.36-0.51)	0.42 (0.30-0.58)	63.3 (56.9-68.2)	10.8 (8.0-12.5)	75.8 (70.3-82.2)	2.3 (1.9-2.8)
850 m													
0-5	4.0 (3.9-4.1)	16.6 (12.1-19.0)	3.99 (2.44-4.91)	0.38 (0.23-0.48)	1.2 (0.3-1.7)	2.08 (1.08-2.65)	0.58 (0.35-0.80)	2.10 (0.94-2.98)	0.92 (0.89-0.97)	93.6 (74.3-123)	24.6 (15.7-34.6)	123.8 (96.8-160)	5.0 (2.0-7.0)
5-20	4.3 (4.1-4.5)	10.7 (9.3-13.2)	1.94 (1.37-2.64)	0.31 (0.21-0.37)	0.0 (0.0-0.0)	0.95 (0.69-1.11)	0.21 (0.10-0.29)	0.67 (0.48-0.88)	0.62 (0.54-0.67)	61.1 (41.7-90.7)	13.8 (8.3-23.7)	77.4 (52.4-117)	3.6 (1.7-4.6)
20-100	4.4 (4.2-4.5)	8.8 (6.8-10.7)	1.33 (0.86-1.74)	0.29 (0.18-0.35)	0.2 (0.0-0.4)	0.74 (0.41-1.02)	0.20 (0.10-0.36)	0.50 (0.17-0.91)	0.56 (0.39-0.67)	45.5 (42.3-50.8)	8.2 (3.1-13.5)	55.7 (48.3-65.4)	3.7 (1.6-5.5)

Table 2.9. Particle-size analyses of soil samples from one soil profile at each of three altitudes on Bukit Belalong, Brunei. The texture classes follow the USDA system (USDA 1974): SCL, silty clay loam; SL, silty loam.

Altitude (m)	Depth (cm)	Sand (>50 µm) (%)	Silt (2-50 µm) (%)	Clay (<2 µm) (%)	Texture class
200	0-5	51.2	19.9	28.8	SCL
	5-20	52.8	21.3	25.9	SCL
	20-100	59.7	18.7	21.6	SCL
510	0-5	60.8	25.4	13.9	SL
	5-20	72.9	17.2	9.9	SL
	20-100	64.5	18.0	17.5	SL
870	0-5	54.4	30.0	15.6	SL
	5-20	64.0	22.9	13.1	SL
	20-100	56.6	21.7	21.7	SCL

Table 2.10. Bulk density of soil (g cm^{-3}) (excluding roots and stones >5 mm along the longest axis) and concentration of stones (>5mm) (g 100 cm^{-3} soil) in ten surface soil samples (10 cm x 10 cm area and 5 cm deep) from three plots at three altitudes on Bukit Belalong, Brunei. Values are the means with the ranges in parentheses.

Plot	Bulk density (g cm^{-3})	Stones (g 100 cm^{-3} soil)
1	0.70 (0.43-1.04)	11.14 0.0-52.9)
2	0.55 (0.39-0.81)	4.58 (0.2-28.6)
3	0.61 (0.48-0.79)	10.16 (0.0-29.6)
1-3	0.62	8.62
4	0.42 (0.18-0.64)	0.16 (0.0-0.9)
5	0.39 (0.17-0.65)	1.27 (0.0-10.5)
6	0.55 (0.31-0.85)	2.42 (0.0-12.3)
4-6	0.45	1.28
7	0.43 (0.29-0.61)	15.22 (0.0-40.4)
8	0.36 (0.21-0.47)	21.10 (1.0-31.1)
9	0.41 (0.10-0.74)	2.14 (0.0-11.7)
7-9	0.40	12.82

layer at 200 m (Table 2.9).

Differences in the physical and chemical properties of the surface samples among the three altitudes were tested using the non-parametric Kruskal-Wallis test. Some significant differences ($p<0.05$) were found (Table 2.11): LOI, total nitrogen, exchangeable sodium, aluminium and hydrogen and cation exchange capacity were higher in soils from 850 m compared with those at 200 m. The soils at 500 m were the most acid and had the highest concentrations of extractable phosphorus and exchangeable aluminium and hydrogen, but had the lowest magnesium concentration and base saturation. Calcium concentrations and base saturation were highest in soils from 200 m. In general the soils at 500 m were more similar to those at 850 m than those at 200 m. Samples from 850 m had significantly lower percentages of clay and higher percentages of silt than those from 200 m, whilst the samples from 500 m were intermediate (Table 2.12).

Nitrogen mineralisation and nitrification

Initial concentrations of ammonium and nitrate ions (fraction 1) were similar at all altitudes (Table 2.14), though ammonium concentrations were more variable at 850 m. When expressed on an area basis the highest quantities of both ions were found at 200 m and the lowest quantities at 850 m. Field rates of mineralisation were more variable within each altitude than between altitudes, and in many samples from each altitude ammonium concentrations were found to decline after incubation. Most variation was found at 850 m. Similarly, rates of nitrification did not differ significantly between altitudes and were most variable at 850 m. When expressed on an area basis, rates of mineralisation and nitrification were highest at 200 m and lowest at 500 m. The samples left to incubate in the field suffered considerable disturbance from both pigs and termites and the numbers of replicates were severely reduced, especially at 850 m (Table 2.14).

Rates of mineralisation were higher in samples from all altitudes incubated under laboratory

Table 2.11. Characteristics of surface soil samples (0-5cm) from three plots at each of three altitudes on Bukit Belalong, Brunei. Values are the means of ten samples from each plot, with the ranges in parentheses. All values are expressed as concentrations in oven dried (105 °C) soil. Superscripts with the mean values for each altitude indicate when the differences between altitudes are significant ($p<0.05$, Kruskal-Wallis test, n=30).

Plot						Exchangeable cations (mequiv kg^{-1})							
	pH_{H2O}	LOI (%)	N_{Total} (mg g^{-1})	P_{Total} (mg g^{-1})	$P_{Extractable}$ (µg g^{-1})	K	Ca	Mg	Na	Al	H	CEC (mequiv kg^{-1})	BS (%)
1	4.1 (3.9-4.3)	12.6 (8.5-27.1)	3.39 (1.97-6.69)	0.39 (0.31-0.55)	3.2 (1.4-7.5)	3.24 (1.47-5.60)	4.85 (1.26-15.7)	5.48 (1.91-11.7)	0.70 (0.56-1.13)	67.2 (37.1-84.1)	15.4 (10.0-28.1)	96.9 (72.6-135)	15.1 (6.2-39.2)
2	3.9 (3.8-4.1)	12.8 (8.8-17.9)	3.71 (2.16-5.43)	0.34 (0.24-0.39)	2.7 (0.7-5.6)	2.65 (1.53-4.59)	2.41 (0.61-5.04)	4.34 (1.76-6.53)	0.73 (0.53-0.90)	66.9 (60.0-74.6)	20.1 (16.3-27.4)	97.1 (84.2-118)	10.3 (5.4-16.2)
3	3.9 (3.7-4.0)	14.7 (8.5-24.9)	3.81 (2.32-6.32)	0.39 (0.29-0.51)	3.7 (0.6-9.6)	3.62 (2.06-7.08)	3.85 (0.80-19.4)	7.96 (3.11-19.8)	0.77 (0.58-0.94)	72.9 (52.3-90.9)	18.7 (8.7-29.9)	107.8 (89.5-131)	15.0 (7.3-42.3)
1-3	4.0^{B}	13.4^{A}	3.64^{A}	0.37	3.2^{AB}	3.17	3.71^{B}	5.92^{B}	0.73^{A}	69.0^{A}	18.1^{A}	100.6^{A}	13.5^{C}
4	4.0 (3.7-4.2)	16.8 (11.6-25.4)	3.72 (2.59-5.22)	0.34 (0.26-0.44)	2.9 (1.0-8.1)	2.82 (1.97-3.92)	0.80 (0.66-1.13)	2.10 (1.61-2.95)	1.27 (0.71-4.40)	87.0 (69.2-129)	30.6 (12.9-56.4)	124.6 (89.1-193)	5.9 (3.5-8.6)
5	3.7 (3.4-3.9)	27.0 (16.2-50.2)	6.09 (3.86-11.1)	0.35 (0.28-0.41)	7.3 (2.4-21.7)	3.39 (1.78-5.97)	0.89 (0.51-1.36)	2.70 (1.56-4.47)	1.11 (0.81-1.83)	100.5 (85.9-128)	41.3 (29.5-72.3)	149.9 (128-200)	5.4 (3.4-7.5)
6	3.8 (3.5-4.0)	19.1 (11.8-32.0)	4.06 (2.35-7.84)	0.42 (0.38-0.51)	4.6 (1.4-14.5)	3.53 (2.45-6.21)	1.40 (0.74-2.32)	3.99 (1.98-6.39)	0.95 (0.75-1.24)	107.4 (94.7-133)	28.0 (16.4-45.8)	145.3 (123-189)	6.8 (4.3-10.0)
4-6	3.8^{A}	21.0^{B}	4.62^{AB}	0.37	4.9^{B}	3.25	1.03^{A}	2.93^{A}	1.11^{B}	98.3^{B}	33.3^{C}	140.0^{B}	6.0^{A}
7	4.0 (3.8-4.3)	19.2 (8.6-28.9)	4.70 (1.45-6.68)	0.37 (0.27-0.50)	1.9 (0.0-4.0)	2.69 (1.50-3.73)	1.18 (0.63-1.57)	3.93 (2.11-6.30)	1.16 (0.59-1.93)	72.0 (46.2-99.7)	22.4 (0.8-38.0)	103.4 (57.6-146)	8.9 (6.4-11.6)
8	4.0 (3.7-4.2)	25.2 (16.2-40.4)	7.0 (4.49-10.9)	0.56 (0.42-0.75)	3.8 (1.6-6.3)	3.74 (2.24-6.09)	1.88 (1.00-4.04)	6.11 (2.86-12.4)	1.39 (1.06-1.84)	82.5 (68.1-108)	19.6 (13.0-37.5)	115.2 (93.0-161)	11.2 (7.7-18.3)
9	3.7 (3.3-3.9)	22.1 (13.4-36.7)	5.38 (2.19-8.43)	0.38 (0.25-0.49)	2.3 (0.7-5.2)	2.60 (1.36-4.07)	1.45 (0.66-4.57)	3.62 (1.81-6.49)	1.15 (0.70-1.57)	107.9 (88.8-147)	32.7 (18.0-65.9)	149.4 (118-218)	6.0 (2.7-9.0)
7-9	3.9^{AB}	22.2^{B}	5.69^{B}	0.44	2.7^{A}	3.01	1.51^{A}	4.55^{B}	1.23^{B}	87.5^{B}	24.9^{B}	122.7^{B}	8.7^{B}

Table 2.12. The percentages of particles in three textural classes in mineral soils from surface samples (0-5 cm) at three altitudes on Bukit Belalong, Brunei. Values are the means of nine samples at each altitude with the ranges in parentheses. Significant differences ($p<0.05$, from Kruskal-Wallis test) are indicated by superscripts.

Altitude (m)	Sand (>50 µm) (%)	Silt (2-50 µm) (%)	Clay (<2 µm) (%)
200	49.9 (42.6-60.9)	24.9^{A} (21.8-27.4)	25.2^{B} (12.6-32.2)
500	46.4 (29.2-57.0)	29.7^{AB} (22.7-45.4)	23.9^{AB} (17.5-32.0)
850	45.5 (29.9-59.2)	36.4^{B} (21.4-48.0)	18.1^{A} (12.6-24.1)

Table 2.13. Correlation coefficients with loss-on-ignition for soil nutrient elements, cation exchange capacity and base saturation in surface soil samples (0-5 cm) at three altitudes on Bukit Belalong, Brunei. All correlations are significant at $p<0.001$, except ‡, $p<0.01$; †, $p<0.05$ or *, not significant. n=30 at each altitude.

Altitude (m)	Correlation coefficients										
	N_{Total}	P_{Total}	$P_{Extract.}$	Exchangeable cations						CEC	BS
				K	Ca	Mg	Na	Al	H		
200	0.931	0.813	0.864	0.782	0.716	0.619	0.858	-0.026*	0.349*	0.541‡	0.597‡
500	0.903	0.275*	0.898	0.698	0.085*	0.410†	0.417†	0.374†	0.810	0.679	0.097*
850	0.933	0.674	0.880	0.792	0.662	0.775	0.772	0.576‡	0.630	0.694	0.308*

Table 2.14. Concentrations of ammonium - nitrogen and nitrate/nitrite - nitrogen and rates of mineralisation and nitrification in surface soils (0-5 cm) from three altitudes on Bukit Belalong. The results are expressed on a mass basis and on an area basis. Values are the means ± 95% confidence limits. n=30 for concentrations, and as stated for the incubations.

	N (μg g^{-1})		N (kg ha^{-1})			N (μg g^{-1} 21 d^{-1})		N (kg ha^{-1} 21 d^{-1})	
Altitude (m)	NH_4-N	NO_3-N	NH_4-N	NO_3-N	n	NH_4-N	NO_3-N	NH_3-N	NO_3-N
200	8.4 ±3.2	5.2 ±1.2	2.60	1.61	23	2.1 ±3.5	15.0 ±4.6	0.65	4.65
500	8.1 ±2.0	6.4 ±2.5	1.81	1.43	17	1.8 ±3.4	11.6 ±5.4	0.40	2.60
850	8.8 ±5.2	4.8 ±2.0	1.75	1.08	9	2.1 ±19.8	16.6 ±10.7	0.47	3.72

Table 2.15. Rates of mineralisation and nitrification and net increase in mineral nitrogen (μg N g^{-1} 21 d^{-1}) in surface soils (0-5 cm) from three altitudes on Bukit Belalong incubated for 21 d under identical temperature regimes at Kuala Belalong Field Centre. The values are the means of thirty samples ± 95% confidence limits.

Altitude (m)	Mineralisation (μg NH_4-N g^{-1} 21 d^{-1})	Nitrification (μg NO_3-N g^{-1} 21 d^{-1})	Net mineral nitrogen added (μg N g^{-1} 21 d^{-1})
200	10.1 ±5.1	22.8 ±5.0	33.0 ±7.7
500	14.9 ±5.7	22.1 ±5.2	37.0 ±7.5
850	19.9 ±9.0	42.8 ±11.6	62.7 ±16.8

conditions compared with the same samples incubated in the field (Table 2.15). Mineralisation rates were highest in the soils from 850 m and lowest in those from 200 m, but the differences were not significant (one-way ANOVA). Nitrification rates were similar in soils from 200 m and 500 m, but were significantly higher in soils from 850 m ($p<0.001$, one-way ANOVA). The net rate of nitrogen transformation (mineralisation + nitrification) was also significantly higher in the soils from 850 m ($p=0.001$, one-way ANOVA).

In the nutrient amendment experiment (Table 2.16), mineralisation showed some response to the addition of phosphate (-ve), calcium carbonate (+ve) and calcium sulphate (+ve), but only the response to calcium carbonate was significant ($p=0.001$, Kruskal-Wallis test). Nitrification was inhibited by the addition of ammonium and calcium sulphate though only the response to ammonium was significant ($p<0.01$, Kruskal-Wallis test). In five of the six samples, addition of calcium carbonate also reduced nitrification, but in the soil from plot 9 calcium carbonate increased nitrification and the rate was at least four times that of soils from other plots. Increased nitrification was found in both of the replicate incubations. Net mineralisation was significantly affected only by addition of calcium carbonate ($p<0.001$, Kruskal Wallis test).

Discussion

The soils at all altitudes on Bukit Belalong were identified as orthic acrisols (FAO/UNESCO 1988) or ultisols (USDA 1975). The soils on the slopes were shallow and appear to be actively rejuvenating owing to erosion and landslides. Some deep soils due to the accumulation of debris at the bottom of landslides have been found (A. Dykes personal communication), but these were the exception . The presence of shale fragments throughout the profile is indicative of landslides, and their scarcity in the ridge top soils at 500 m indicate more stable conditions than on the slopes. Ashton (1964) described twenty soil pits at locations south of Kuala Belalong and identified three soil types in the area: yellow clay

Table 2.16. Effect of added nutrients on rates of mineralisation (µg NH_4-N g^{-1} 21 d^{-1}), nitrification (µg NO_3-N g^{-1} 21 d^{-1}) and net mineralisation (NH_4-N+ NO_3-N g^{-1} 21 d^{-1}) in surface soils (0-5 cm) from three altitudes on Bukit Belalong. The values are the means of three samples which were incubated in duplicate, ± 95% confidence limits.

			Mineralisation (µg NH_4 -N g^{-1} 21 d^{-1})		
Altitude (m)	Control	+NH_3	+PO_4	+$CaCO_3$	+$CaSO_4$
200	8.0 ±11.5	92.4 ±339.0	0.2 ±8.2	109.0 ±101.5	43.7 ±18.4
850	16.7 ±10.5	6.1 ±206.5	3.1 ±4.9	158.7 ±138.2	65.8 ±20.3
Mean	12.4 ±6.53	49.3 ±117.0	1.7 ±3.1	133.9 ±53.7	54.7 ±14.7
			Nitrification (µg NO_3-N g^{-1} 21 d^{-1})		
200	33.6 ±16.9	-4.9 ±2.9	37.0 ±20.8	13.2 ±21.9	3.8 ±4.1
850	42.6 ±11.6	-6.8 ±6.5	45.9 ±59.8	52.9 ±112.3	4.7 ±28.3
Mean	38.1 ±7.5	-5.8 ±2.2	41.5 ±17.6	33.0 ±38.1	4.3 ±7.7
			Net mineralisation (µg inorganic N g^{-1} 21 d^{-1})		
200	41.6 ±25.0	87.5 ±340.4	37.2 ±26.5	122.2 ±99.8	47.4 ±15.3
850	59.4 ±1.25	-0.7 ±210.8	49.0 ±64.5	211.6 ±26.2	70.5 ±12.5
Mean	50.5 ±12.2	43.4 ±118.5	43.1 ±19.8	166.9 ±58.4	59.0 ±14.3

latosols on ridges below 650 m, shallow shale lithosols on ridges above 650 m, clay lithosols on hillsides up to at least 750 m. The soils at 200 m and 850 m probably correspond to clay lithosols and those at 500 m to yellow clay latosols. Ashton found a lack of variation in the profiles despite the rugged physiognomy and sharp differentiation between the flat ridge tops and steep upper hillsides. However transects encompassing the full range from ridge top to valley floor revealed differences in pH, texture and soil moisture, with more acid, friable and drier soils towards the ridges. Illuviation of clay to the subsoil was expected (Baillie 1989), but this was not found in the profile at 200 m (Table 2.8). This may be a comparatively young soil with a poorly developed profile and significant inputs of clay minerals weathering from fragments of shale at the surface, or the clay may have been illuvated to the surface layer from further up the slope. The plots at 200 m are roughly midway between the ridge and Belalong river and thus inputs from up-slope may be significant. By contrast the plots at 500 m are close to the ridge top and those at 850 m are not far below the summit and are therefore likely to receive smaller inputs from up-slope. The clay contents of the surface soils, which were taken from widely dispersed points throughout the plots, decreased with altitude, and may indicate either this illuviation effect or reduced weathering at higher altitudes or both. Lower rates of weathering at higher altitudes are to be expected from the reduction in temperature (Young 1976).

Well developed tropical soils have low silt:clay ratios because of leaching (Burnham 1984), so it appears that repeated small scale disturbance on the steep Belalong slopes has prevented the soils from progressing to a deep weathered condition (Baillie & Ashton 1983). Soil organic matter, particularly in the surface layers, supplies most of the cation exchange capacity (CEC) of acid, weathered soils because the clay fraction is dominated by minerals with a low CEC (Sanchez 1976, Young 1976). LOI is considered a reasonable index of soil organic matter, but the correlation is not perfect because of the loss of structural water from minerals and volatilization of some compounds at the high temperatures (Allen 1989).

Nutrient concentrations, CEC and base saturation were regressed against LOI (Table 2.13) and it was found that total nitrogen, extractable phosphorus and exchangeable potassium correlated closely with LOI at all altitudes. It was also expected that close correlations would be found for total phosphorus and extractable calcium, magnesium and sodium, but this was not the case. CEC correlates closely with LOI at 500 m and 850 m but less so at 200 m and this may be because of the greater clay content of these soils, offering other sites for cation exchange.

Bornean lowland forest soils

Comparisons among tropical forest soil analyses are problematic because of the lack of standard methodologies both in sampling and analysis. Landon (1992) discussed sources of error in the preparation and analysis of tropical soils and suggested that the results should be treated as no more than 'order of magnitude' estimates. Surface soil pH in the Belalong samples was similar to that of other Bornean lowland dipterocarp forests (Table 2.17) except for plots from the lower slopes of the ultramafic Gunung Silam where soils were much less acid. LOI in the samples at 200 m was typical of the other studies, but at 500 m LOI was relatively high. Total soil nitrogen at Belalong was within the range of values reported from other Bornean forests, but total phosphorus was relatively high in the Belalong soils. Extractable phosphorus varied considerably between the studies reported in Table 2.17 but this may be due as much to the different extractants used as any real difference between the soils. Bray type, acid-fluoride extractants can be much more vigorous than dilute acid (Allen 1989). Interpretation of these data is difficult because acid extractions (especially the Bray type) may liberate substantial amounts of fixed phosphorus and yield high values in soils which are actually low or deficient in phosphorus (Landon 1992). Concentrations of exchangeable bases and CEC in Belalong soils were within the ranges reported from other studies. The high concentrations of calcium and particularly magnesium in the soils from

Table 2.17. Analyses of surface soil samples from Bornean lowland rain forests. '-' indicates that no data are available.

Location	Sample depth (cm)	n	pH	LOI (%)	Total N (mg g^{-1})	Total P (mg g^{-1})	Extractable P (µg g^{-1})	Exchangeable cations (mequiv kg^{-1})				CEC (mequiv kg^{-1})
								K	Ca	Mg	Na	
Brunei, Belalong, 200 m[1].	0-5	30	4.0	13.4^*	3.6	0.37	3.2^A	3.17	3.71	5.92	0.73	100.6
Brunei, Belalong, 500 m[1].	0-5	30	3.8	21.0^*	4.6	0.37	4.9^A	3.25	1.03	6.11	1.11	140.0
Brunei, Belalong[2].	13	6	4.4	7.1^E	2.9	0.24	-	2.1	1.4	-	-	-
Brunei, Belalong, [3].	0-5	10	3.7	$15.6^\dagger$	3.7	0.42	-	3.4	2.0	8.4	0.2	-
Brunei, Belalong, [3].	0-5	10	4.1	$12.3^\dagger$	-	-	-	-	-	-	-	-
Brunei, Belalong, [3].	0-5	10	4.6	$9.8^\dagger$	2.6	0.27	-	2.2	0.5	1.8	0.3	-
Brunei, Andalau, valley site[2].	0-1	2	3.8	3.3^E	5.1	0.06	-	2.0	2.0	-	-	-
Sabah, Danum[4].	0-8	30	-	$11.4^\dagger$	3.9	0.21	4.2^C	2.38	0.12	0.41	-	-
Sabah, Danum[5].	0-10	160	-	$7.9^\dagger$	-	0.36	9.6^O 4.0^B	2.27	-	3.67	-	-
Sabah, Danum[6].	0-15	72	4.3	6.2^*	1.3	0.28	0.4^A	2.41	3.92	5.40	0.36	154.3
Sabah, Silam, 280 m[9].	0-15	20	5.7	12.5^*	-	-	4.1^A	1.4	77	246	1.0	490
Sabah, Silam, 330 m[9].	0-15	20	5.8	14.2^*	-	-	5.5^A	1.7	23	157	1.3	610
Sabah, Silam, 480 m[9].	0-15	20	6.1	13.0^*	-	-	4.5^A	2.3	42	115	0.6	880
Sarawak, Mulu, Dipterocarp[7].	0-10	25	4.1	19.0^*	5.1	0.12	-	2.5	0.39	1.8	0.59	370
Sarawak, Mulu, Dipterocarp, regosol[8].	0-12	1	4.0	-	2.4	0.12	6^B	1.0	5.2	0.8	0.4	164.0
Sarawak, Mulu, Dipterocarp, podzol 1[8].	0-5	1	-	-	1.9	0.12	$<1^B$	0.8	5.6	<0.1	2.7	98.1
Sarawak, Mulu, Dipterocarp, podzol 2[8].	0-6	1	4.8	-	2.7	0.11	10^B	1.0	5.2	0.7	0.5	140

Notes
Loss on ignition temperature, °C: *, 375-400; †, 550-700; E, estimated from organic carbon value (Allen 1989).
Phosphorus extractants: A, acetic acid; B, Bray type acid/flouride; C, calcium lactate; O, Olsen's reagent.

1, This study; 2, Ashton (1964); 3, Poulsen (1994); 4, Burghouts (1993); 5, D.M. Newbery, personal communication; 6, Green (1992); 7, Proctor *et al* (1983); 8, Tie *et al* (1979); 9, Proctor *et al* (1988).

Gunung Silam are derived from the base-rich ultramafic parent material.

Although the Belalong soils receive constant nutrient inputs from the weathering of the parent material, as well as atmospheric inputs, nutrient concentrations are not noticeably higher than in more stable soils which have deeper weathering fronts such as those at the Danum Valley, Sabah (Green 1992). Nutrient inputs from weathering shale are likely to be small and balanced by losses in an 'open' type nutrient cycling system as described by Baillie (1989) and Burnham (1989). Baillie & Ashton (1983) reported that shallow, relatively unweathered soils are common in lowland forest in north western Borneo and trees often root into a mixture of soil and partially weathered soil.

Tropical montane soils

Soil analyses from montane forests throughout the tropics have been collated in Table 2.18. A number of trends can be discerned in spite of the large range of climatic conditions and parent materials. Soil pH usually falls with altitude, and the most acid soils are generally found under upper montane rain forests (UMRF), though Kitayama (1992) did not find a simple pattern on Gunung Kinabalu. His study suffers from a lack of replication in the soil analyses, and from the complicated changes in lithology on Kinabalu (Burnham 1974). Veneklaas (1990) reported UMRF on soils with a higher pH than soils in a nearby LMRF at a lower altitude.

LOI, and consequently total nitrogen, increase with altitude partly because of reduced decomposition at lower temperatures, but often due to waterlogging in fog-bound UMRF. UMRF is consequently generally found on the most acid, organic, soils which are relatively rich in total nitrogen. Total phosphorus is usually about 1 mg g^{-1}, but extractable phosphorus is much more variable and can be found at comparatively high concentrations in some montane soils (eg Tie *et al* (1979), Edwards & Grubb (1982) and Kitayama (1992); but see earlier discussion of phosphorus extractants). Acid soils generally have high phosphorus

Table 2.18. Analyses of surface soil samples from tropical montane forests. '-' indicates that no data are available.

Location	Altitude (m)	Forest type	Sample depth (cm)	n	pH	LOI (%)	Total N (mg g^{-1})	Total P (mg g^{-1})	Extractable P (µg g^{-1})	Exchangeable cations (mequiv kg^{-1})				CEC (mequiv kg^{-1})
										K	Ca	Mg	Na	
Brunei, Belalong[1].	850	LMRF	0-5	30	3.9	22.2^{*}	5.7	0.4	3^{A}	3.0	1.5	4.6	1.2	123
Colombia, Cordillera Central[2].	2500	LMRF	0-30	-	4.0	-	-	-	-	3	12	8	1	-
	3550	UMRF	0-25	-	4.7	-	9	-	-	3	13	13	2	-
Colombia, Macuira[3].	600	MRF	0-20	2	4.8	4.1^{E}	2.4	-	3^{B}	7	34	28	8	-
Costa Rica, Volcán Barva[4].	1000	LMRF	0-15	25	$4.0^{\#}$	$36.4^{\dagger}$	13	-	1^{T}	2.6	2.1	3.3	2.1	590
	1500	LMRF	0-15	25	$3.8^{\#}$	$47.5^{\dagger}$	19	-	13^{T}	3.0	6.6	6.2	6.3	1007
	2000	LMRF	0-15	25	$3.8^{\#}$	$49.0^{\dagger}$	18	-	5^{T}	1.4	4.2	2.7	1.2	883
	2600	LMRF	0-15	25	$3.6^{\#}$	$37.2^{\dagger}$	19.2	-	56^{T}	2.9	22.5	11.9	1.1	1129
Indonesia, Seram, Gunung Kobipoto[5].	600	LRF-LMRF	0-15	10	5.3	10.3^{E}	-	0.7	5^{B}	3.2	38.5	14.1	-	-
	1000	LMRF	0-15	10	4.8	12.2^{E}	-	0.7	3^{B}	2.1	3.9	4.7	-	-
	1470	UMRF	0-15	10	3.1	63.2^{E}	-	-	19^{B}	13.3	9.1	75.1	-	-
Indonesia, Seram, Gunung Bunaia[5].	1060	LMRF	0-15	10	5.4	9.4^{E}	-	0.9	9^{B}	3.0	87.1	13.3	-	-
	1640	LMRF	0-15	10	5.3	8.8^{E}	-	1.0	6^{B}	3.8	76.2	7.8	-	-
	2100	LMRF-UMRF	0-15	10	4.6	18.9^{E}	-	6.1	46^{B}	6.5	78.8	14.5	-	-
	2400	UMRF	0-15	10	4.1	82.0^{E}	-	-	82^{B}	10.6	236.3	31.7	-	-
Indonesia, Kalimantan, Bukit Raya[6].	900	MRF	0-3	1	5.1	14.8^{E}	-	-	-	-	-	-	-	267
	1750	MRF	0-18	1	-	44.0^{E}	-	-	-	-	-	-	-	1352
Jamaica, Mor Ridge[7].	1500	UMRF	0-10	5	3.0	$96^{\ddagger}$	15.8	-	-	10.0	26.7	102	8.8	-
Mull Ridge.	1500	UMRF	0-10	5	3.6	$73^{\ddagger}$	16.7	-	-	7.4	51.6	20.5	1.9	-
Wet Slope.	1500	UMRF	0-10	5	4.1	$14^{\ddagger}$	3.5	-	-	4.6	118	51.2	2.2	-
Gap.	1500	LMRF	0-10	5	4.3	$21^{\ddagger}$	5.2	-	-	4.8	56.3	15.3	2.4	-
Malaysia, Sabah, Gunung Kinabalu[8].	1400	LMRF	2-37	1	3.5	58^{E}	18.1	-	29^{B}	13.7	2.5	4.5	3.4	915
	1600	LMRF	5-30	1	3.7	69^{E}	14.1	-	15^{B}	10.5	4.6	27.6	4.4	1140

Location	Altitude (m)	Forest type	Sample depth (cm)	n	pH	LOI (%)	Total N (mg g^{-1})	Total P (mg g^{-1})	Extractable P (µg g^{-1})	Exchangeable cations (mequiv kg^{-1})				CEC (mequiv kg^{-1})
										K	Ca	Mg	Na	
	1800	LMRF	2-12	1	4.1	54^{E}	15.8	-	31^{B}	17.6	6.1	24.9	3.7	975
	2000	LMRF	2-7	1	4.9	34^{E}	11.4	-	34^{B}	13.6	152.3	87.3	2.2	468
	2350	UMRF	2-10	1	3.9	60^{E}	19.6	-	37^{B}	11.7	5.1	81.7	2.3	787
	2600	UMRF	2-10	1	3.9	65^{E}	9.8	-	4^{B}	11.7	40.8	72.1	4.2	796
	2800	SARF	3-20	1	4.6	13^{E}	4.5	-	13^{B}	2.6	4.0	2.7	1.0	98
	3000	SARF	1-5	1	5.4	27^{E}	8.3	-	9^{B}	6.3	183.0	24.2	2.0	334
	3200	SARF	5-10	1	3.9	20^{E}	9.1	-	28^{B}	6.8	10.7	10.9	1.8	343
	3400	SARF	2-30	1	4.7	15^{E}	5.6	-	11^{B}	4.0	34.1	4.7	2.1	221
Malaysia, Sabah, Gunung Silam[9].	610	LMRF	0-15	20	6.0	24.0^{*}	-	-	7^{A}	4.2	124	106	1.7	1020
	790	LMRF	0-15	20	5.6	16.7^{*}	-	-	1^{A}	1.7	9	54	0.8	1050
	870	LMRF	0-15	18	4.0	52.0^{*}	-	-	17^{A}	5.3	12	56	4.1	1050
Malaysia, Sarawak, Gunung Mulu[10].	830	LRF-LMRF	0-4	1	4.0	13.5^{E}	5.5	0.3	34^{B}	4.1	2.2	0.1	0.5	134
	1130	LMRF	0-7	1	4.2	8.6^{E}	3.2	0.1	20^{B}	0.8	2.1	3.1	0.9	130
	1310	LMRF	0-15	1	3.9	$42.1^{\dagger}$	7.7	0.3	37^{B}	4.8	1.1	3.0	1.0	454
	1650	LMRF	0-18	1	4.2	$31.1^{\dagger}$	7.8	0.2	2^{B}	3.6	1.1	1.9	0.3	272
	1860	LMRF	0-10	1	4.1	$14.6^{\dagger}$	3.4	0.1	89^{B}	1.1	0.5	1.9	0.5	190
	1930	UMRF	0-15	1	3.4	$98.0^{\dagger}$	18.1	0.4	78^{B}	5.6	0.5	7.2	28.2	738
	2090	UMRF	0-15	1	3.0	$99.4^{\dagger}$	14.0	-	68^{B}	0.3	0.5	0.7	0.5	528
	2370	UMRF	0-30	1	3.2	$98.8^{\dagger}$	11.4	-	38^{B}	2.6	0.6	9.0	2.0	814
New Guinea, Kerigomna[11]. Ridge.	2500	LMRF	0-2	2	6.3	46^{7}	15.4	1.8	38^{B}	14.7	331	104	5.7	-
Valley.	2500	LMRF	0-2	1	5.7	44^{7}	17.1	-	41^{B}	10.5	158	54	5.4	-
Slope.	2500	LMRF	0-2	1	6.6	74^{7}	18.2	1.5	50^{B}	18.0	584	147	6.8	-
U.S.A., Hawai[12]. Old lava.	1220	MRF	-	25	-	61^{E}	-	1.1	15^{B}	11.0	99.8	32.1	-	-

Location	Altitude (m)	Forest type	Sample depth (cm)	n	pH	LOI (%)	Total N (mg g^{-1})	Total P (mg g^{-1})	Extractable P (µg g^{-1})	Exchangeable cations (mequiv kg^{-1})				CEC (mequiv kg^{-1})
										K	Ca	Mg	Na	
	1585	MRF	-	25	-	68^{E}	-	0.8	8^{B}	16.6	210.0	26.3	-	-
New lava.	1220	MRF	-	25	-	67^{E}	-	0.3	18^{B}	21.7	80.8	43.6	-	-
	1675	MRF	-	25	-	14^{E}	-	0.2	6^{B}	7.4	57.5	10.7	-	-
Venezuela, Parque Nacional "Henri Pittier"[13].	1170	MRF	0-7	1	4.0	-	13.3	0.5	-	-	-	-	-	-
	1160	MRF	0-6	1	4.0	-	16.8	0.6	-	-	-	-	-	-
	1680	MRF	0-8	1	4.5	-	12.5	0.4	-	-	-	-	-	-
	1670	MRF	0-5	1	5.2	-	9.7	0.3	-	-	-	-	-	-
Venezuela, Santa Ana[3].	600	MRF	0-12	2	5.5	5.8^{E}	3.9	-	6^{B}	6	67	36.5	8	188
Copey.	600	MRF	0-20	2	5.1	4.2^{E}	2.5	-	6^{B}	1.5	15	20.5	2.5	157
Zumbador.	3100	MRF	0-25	2	3.1	35.4^{E}	9.0	-	30^{B}	5	2	2.5	2	820
Venezuela, Andes Occidentales[14].	2300	LMRF	0-20	13	3.5	9.7^{E}	4.5	0.5	-	4.3	14.6	5.6	1.8	170

Forest types: LMRF, lower montane rain forest; UMRF, upper montane rain forest; SARF, sub-alpine rain forest; MRF, montane forest without sufficient data to apply Whitmore's (1984) classification.

pH measured in water unless otherwise indicated; #, 0.01 M $CaCl_2$.

Loss-on-ignition temperature, °C: *, 375-400; †, 550 - 800; E, Estimated from organic carbon value (Allen 1989); ?, not specified.

Phosphorus extractants: A, acetic acid; B, Bray type acid/flouride; C, Calcium lactate; O, Olsen's reagent; T, Truog's reagent.

1, This study; 2, Veneklaas (1990) in Bruijnzeel & Proctor (1993); 3, Cavelier, (1988); 4, Payton *et al* (1993); 5, Van Reuler (1987); 6, Grieve *et al* (1990); 7, Tanner (1977); 8, Kitayama (1992); 9, Proctor *et al* (1988); 10, Tie *et al* (1979); 11, Edwards & Grubb (1982); 12, Vitousek *et al* (1988); 13, Zinck (1986); 14, Grimm & Fassbender (1988).

fixation potential (Sanchez 1976) due to iron and aluminium oxides, but this may be reduced in highly organic montane soils which contain low amounts of mineral soil. Concentrations of cations vary considerably depending on the parent material, and no generalisations can be made. Concentrations of total nitrogen and phosphorus and extractable phosphorus in the soils from 850 m on Bukit Belalong are typical for values reported from lower montane forest, but quantities of exchangeable cations are towards the low end of the range.

Soil nutrient reserves

Comparisons of concentrations of nutrients in soil may obscure differences between sites since total quantities of plant available nutrients will depend not only on nutrient concentrations but also on the volume and bulk density of the soil. The estimation of quantities of total nutrients in the upper metre of soil (Table 2.19) is strongly affected by the degree of stoniness, so the data from Table 2.7 were combined with those from Table 2.8 for the estimations. Samples for measurement of the bulk density in the Belalong soil profiles had originally been collected using a 5 cm diameter corer, but it was decided that this method was unreliable because the force required to drive it into stony soils caused excessive compaction. The bulk density of the stone free soil was estimated at 1.0 g cm^{-3} at 5-20 cm depth and 1.2 g cm^{-3} at 20-100 cm from data for an orthic acrisol with few stones at the Danum Valley, Sabah (Green 1992). The quantities of nutrients at a depth of 0-5 cm were calculated from the data in Tables 2.10 and 2.11. In the past, tropical soils were often held to have low reserves of nutrients except in the organic surface horizons (Richards, 1952: Young, 1976), but examination of the nutrient concentrations on a mass basis alone distorts the true picture because of the large volume and high bulk density of the deeper layers compared with the surface horizons. The estimates of nutrients in the Belalong soils (Table 2.19) suggest that at all altitudes substantial quantities are held in the soil below 20 cm and these reserves may be twice the amount in the top 20 cm. Despite generally low nutrient

Table 2.19. Estimated quantities of elements (kg ha^{-1}) in the the upper 1 m of soils at three altitudes on Bukit Belalong.

Altitude (m)	Soil depth (cm)	Loss on ignition (t ha^{-1})	Soil nutrients (kg ha^{-1})								
			$N_{Tot.}$	$P_{Tot.}$	$P_{Extr.}$	$K_{Exch.}$	$Ca_{Exch.}$	$Mg_{Exch.}$	$Na_{Exch.}$	$Al_{Exch.}$	$H_{Exch.}$
200	0-5	37	753	105	0.11	28	7	10	4	225	5
	5-20	87	1701	331	0.33	68	6	12	12	709	16
	20-100	304	5210	1087	1.09	177	14	23	41	2718	45
	0-100	428	7664	1523	1.53	273	27	45	57	3652	66
500	0-5	31	735	68	0.07	17	2	5	2	195	6
	5-20	118	2068	356	0.36	43	7	12	14	931	20
	20-100	547	9185	1750	1.75	197	22	37	73	4155	80
	0-100	696	11988	2174	2.18	257	31	54	89	5281	106
850	0-5	33	798	76	0.08	16	2	5	4	168	5
	5-20	124	2248	391	0.36	94	5	9	17	638	17
	20-100	312	4722	1030	1.03	103	14	21	46	1456	28
	0-100	469	7768	1465	1.47	213	21	35	67	2262	50

concentrations at 500 m, total quantities of all nutrients (on a volume basis), except potassium, are higher there than at the other altitudes because there were fewer stones at 500 m.

Estimates of total nutrient reserves in the upper layers of some lowland and montane rain forest soils (Table 2.20) show that the Belalong soils at all altitudes are fairly nutrient poor. Total nitrogen content of these soils is low and though total phosphorus reserves are similar to those at other sites, extractable phosphorus has the lowest value of all these studies. Quantities of exchangeable cations are also fairly low.

Nitrogen mineralisation and nitrification

There is a problem with the reliability of these results because of the long interval between extraction and analysis. Inorganic nitrogen in aqueous solution may be converted between different forms or lost from solution (Allen 1989). Addition of mercuric chloride, acidification, cold storage or rapid freezing to -20 °C have been recommended (Martin 1968, Allen 1989), but no method of preservation is considered acceptable for long term storage. Despite these problems there was remarkably close agreement between the values for the five initial extractions of the amendment experiment which were extracted in duplicate (one of the initial extractions from plot 9 was lost because of damage in transit). The nitrate values in replicates were close, with replicates of two samples having identical values, two others within 1% and the replicates of the other were within 10%. The ammonium values were less close, with identical values for the replicates of one sample, and the others differing by 1%, 3%, 8% and 24%. The values for both ions were more variable between incubated replicates. The pH of each extract was measured since the equilibrium between ammonium ions and ammonia depends on acidity and in alkali solution tends towards ammonia which may be lost by volatilization. pH values were between 2.9 and 4.0 except for the amendment experiment samples to which calcium carbonate had been added and in these extracts the

Table 2.20. Total nutrients in a range of tropical lowland and montane rain forest soils. '-' indicates that no data are available.

Location	Altitude (m)	Depth (cm)	Soil nutrients (kg ha^{-1})					
			N_{Total}	P_{Total}	$P_{Ext.}$	$K_{Exch.}$	$Ca_{Exch.}$	$Mg_{Exch.}$
Brunei, Belalong[1].	200	0-20	2450	436	0.4	96	13	22
	500	0-20	2800	424	0.4	60	9	17
	850	0-20	3050	435	0.4	110	7	14
Costa Rica, Volcán Barva[2].	100	0-15	3700	840	-	62	200	32
	1000	0-15	8900	950	-	64	27	25
	2000	0-15	10050	700	-	27	42	16
	2600	0-15	12000	690	-	71	280	89
Jamaica[3], Mor ridge.	1500	0-45	9000	-	-	130	30	400
Mull ridge.	1500	0-40	7000	-	-	200	240	150
Wet slope.	1500	0-30	3000	-	-	240	1000	400
Gap.	1500	0-40	9000	-	-	160	300	40
New Guinea[4], Ridge (I)	2500	0-30	19300	-	13.3	288	2280	370
Ridge (II)	2500	0-30	18800	-	13.8	621	4090	887
Valley	2500	0-30	21200	-	16.4	315	2320	431
Slope	2500	0-30	17600	-	20.5	389	6320	1040
Malaysia, Sabah, Danum[5].	200	0-30	1450	650	0.7	190	91	78
Malaysia, Sarawak, Mulu[6].	200	0-30	6000	360	-	96	5	22
U.S.A., Hawai'i[7]. Young lava.	760	-	340	-	10	-	-	-
	1220	-	210	-	7	-	-	-
	1675	-	30	-	1	-	-	-
Old lava.	760	-	530	-	31	-	-	-
	1220	-	1130	-	92	-	-	-
	1585	-	990	-	60	-	-	-

1, This study; 2, Heaney & Proctor (1989); 3, Tanner (1977); 4, Edwards & Grubb (1982); 5, Green (1992); 6, Proctor *et al* (1983); 7, Vitousek, Matson & Turner (1988).

pH's were between 7.3 and 7.6. It is noteworthy that despite the very high pH values in these extracts large amounts ammonium were measured in them. Accepting the problems associated with the long-term storage, the data seem to provide a reasonable index of the rates of nitrogen transformations under different conditions since all the samples were extracted by the same solution and stored under identical conditions.

Studies of nitrogen dynamics in tropical forest soils have reported a wide range of values (Robertson 1989). This can partly be explained by methodological differences, but incubations of a range of soils using the same method have shown a similar range of values (Vitousek & Matson 1988). It is difficult to make comparisons among studies because of differences in incubation temperature. The length of the incubation is also critical since rates of nitrogen transformation are not necessarily linear in short term incubations (Stanford & Smith 1972, Chandler 1985). When assessing nitrogen transformations total net nitrogen mineralisation (the sum of the ammonium and nitrate values) should be considered since all of the nitrate produced must have been ammonium at some point (Robertson 1982). Recorded rates of net nitrogen mineralisation in rain forest soils vary between 4 µg N g^{-1}soil d^{-1} in Jamaican mull ridge soil (Tanner 1977) and net immobilisation of 3.6 µg N g^{-1} soil d^{-1} in a lowland Hawai'ian soil (Vitousek, Matson & Turner 1988). Net immobilisation of nitrogen has been reported from two altitudinal sequences of soils in Hawai'i where soils (dated at 133 and 3100 years old) are developing on lava flows (Vitousek *et al* 1988), but Tanner (1977) also found net immobilisation in soils from his Jamaican slope forest site. Measurements of rates of nitrogen transformation in the field are of more relevance to plant nutrition than indices of soil mineralisation potential under ideal conditions, but the logistical problems have restricted the number of studies (Table 2.21). The estimated values of nitrification and net mineralisation on Bukit Belalong are in the middle of the range of reported values. Low rates were found in montane forests on Volcán Barva (Marrs *et al* 1988) and have been cited as a possible cause of montane forest stunting, but the rates are not as

Table 2.21. Rates of nitrification (µg NO_3-N g^{-1} d^{-1}) and net mineralisation (µg NH_4-N + NO_3-N g^{-1} d^{-1}) in surface soils from tropical rain forests.

Location	Sample depth (cm)	Nitrification (µg NO_3 -N g^{-1} d^{-1})	Net mineralisation (µg NH_3 -N + NO_3 -N g^{-1} d^{-1})
Brunei, Belalong 200 m[1].	5	0.71	0.81
Brunei, Belalong 500 m[1].	5	0.55	0.64
Brunei, Belalong 850 m[1].	5	0.79	0.89
Venezuela, San Carlos, oxisol[2].	10	0.50	0.47
Venezuela, San Carlos, oxisol[2].	10	0.12	0.06
Costa Rica, La Selva, inceptisol[3].		3.43	3.43
Costa Rica, Volcán Barva, 100 m[4].	15	1.55	4.27
Costa Rica, Volcán Barva, 2600 m[4].	15	0.21	0.07

1, This study; 2, Montagnini & Buschbacher (1989); 3, Robertson (1984); 4 Marrs *et al* (1988).

low as those reported from the San Carlos forest on an oxisol (Montagnini & Buschbacher 1989). The dramatic decline in nitrogen mineralisation with altitude on Volcán Barva (even at 1000 m there was a marked reduction compared with 100 m) contrasts with the comparatively high values at the highest altitude on Bukit Belalong.

The increases in rates of mineralisation and nitrification in Belalong soils incubated under laboratory conditions compared with field incubations can best be attributed to the increase in temperature in the Field Centre. This contrasts with the Volcán Barva study (Marrs *et al* 1988) which found that laboratory incubation had no effect on rates. The differences may be due to differences in moisture contents, which ranged from 30% at 200 m and 50% at 850 m on Bukit Belalong, whilst on Volcán Barva they were 40% at 100 m and 80% from about 1000 m. It was concluded that the primary factor limiting mineralisation and nitrification in the Volcán Barva soils was the high moisture content and without improved aeration and structure increase in temperature had no effect.

Fertilisation and nitrogen dynamics

The findings of the amendment experiment contrast with some of the results of Marrs *et al* (1988) who found that addition of ammonium significantly increased nitrification and they concluded that nitrification was partially substrate limited. However Chandler (1985) found that higher ammonium concentrations did not necessarily increase nitrification. Addition of calcium carbonate to the Volcán Barva soils stimulated mineralisation more than addition of calcium sulphate at 100 m and 1000 m though not 2600 m. Nitrification was stimulated more by calcium sulphate than calcium carbonate, but the effects were less dramatic than on mineralisation. Total net mineralisation was higher after incubation with calcium carbonate at 100 m and 1000 m, but higher at 2600 m when calcium sulphate was added. Alleviation of the low pH therefore had a greater effect at the lower altitudes.

Conclusions

At 850 m the soils tended to be more organic and have higher concentrations of total nitrogen and total phosphorus than those from lower altitude. The ridge-top soils at 500 m were the most acid and leached, with the lowest concentrations of exchangeable cations and the lowest base saturation. The soils at 500 m were less stony than those at other altitudes, and total quantities of nutrients were similar amongst the three altitudes and do not indicate lower supply of nutrients at 850 m.

Inorganic nitrogen pools and rates of nitrogen transformations do not differ significantly among altitudes on Bukit Belalong. However, the potential for nitrogen mineralisation, indicated by the rates in laboratory incubations, is highest in the soils from the top plots. The soils from the highest and lowest altitudes generally responded to nutrient addition in a similar way. It is concluded that there is no evidence of a decrease in nitrogen supply with increasing altitude on Bukit Belalong.

Introduction

It has long been recognised that similar altitudinal sequences of rain Forest formations can be distinguished throughout the aseasonal tropics (Richards 1952, Whitmore & Burnham 1969). Typically, evergreen lowland rain forest (LRF) gives way to lower montane rain forest (LMRF) with increasing altitude, and in turn LMRF is replaced by upper montane rain forest (UMRF). However on some small mountains UMRF may be found directly above LRF and a separate LMRF does not occur (Whitmore 1984). The LRF, LMRF, UMRF terminology was introduced by Grubb, Lloyd, Pennington & Whitmore (1963) and their classification is based on that of Richards (1952). Modified versions were produced by Grubb & Tanner (1976) and most recently by Whitmore (1984) and it will therefore be referred to as the 'Whitmore classification'.

The most important characters used to distinguish the Formations are the reduction in leaf size, from the majority of trees having mesophylls in LRF and LMRF to the majority of trees having microphylls in UMRF; the scarcity of large woody climbers in LMRF and UMRF; the abundance of vascular epiphytes in LMRF and the abundance of non-vascular epiphytes in UMRF (Grubb *et al* 1963). The canopy height of LRF is greater than that of LMRF which is taller than UMRF. Emergent trees, buttressing, cauliflory and pinnate leaves are all less frequent in LMRF and UMRF than LRF (Whitmore 1984). This scheme has been widely applied, but this is at least partly due to its use of unquantified terms such as 'rare', 'uncommon' and 'frequent'. Whilst some characters, such as buttressing and leaf size , can be quantified easily, this may be time-consuming for others, particularly abundance of vascular epiphytes. There is no explicit statement as to whether the terms refer to individuals or species, or whether more weight should be given to larger individuals, and there is no indication of the sample plot size or forest growth phase considered. Since leaf size rather than stature is the critical character in this classification, distinctive stunted, bryophyte-rich forests growing in conditions of persistent clouds and fogs may be classified as either LMRF or UMRF. An alternative term, tropical montane cloud forest (TMCF), is used to distinguish such forests from other montane and lowland Formations. A complete definition of this term can be found in Hamilton, Juvik & Scatena (1993).

The aim of this chapter is to provide complete physiognomic and floristic descriptions of the forests at the three altitudes on Bukit Belalong and relate them to forests found on other South East Asian mountains.

Methods

Plot location

Three 50 m x 50 m plots were marked out, without correcting for the slope, in mature forest at each of three altitudes: plots 1-3 at c. 200 m; plots 4-6 at c. 500 m and plots 7-9 at c. 850 m. Some details of the plots are given in Table 3.1. Random plot location was not possible because of the difficult terrain. None of the plots had atypical features and they are treated as statistically independent samples. The plots were divided into twenty-five 10 m x 10 m sub-plots which were used as a sample grid. The plots were surveyed along the sample grid using a clinometer, compass and measuring tape to allow the estimation of the horizontal area.

Forest description

Within each plot the position of each tree and liana (≥10 cm dbh) was measured to the nearest 0.5 m, and each was enumerated and tagged with an aluminium tag and aluminium nail at 140 cm above the ground. Girths were measured 10 cm below the tag except where buttresses, prop roots or damage distorted the trunk, and on these trees girth was measured at 30 cm above the protrusion. A second nail then marked 10 cm above the point of

Table 3.1. Some physical characteristics of the plots on Bukit Belalong, Brunei.

Plot	Altitude (m)	Aspect (°)	Slope (°)	Horizontal area (ha)
1	200	210	23	0.23
2	200	240	25	0.23
3	210	280	26	0.22
4	480	80	16	0.24
5	520	130	21	0.23
6	510	150	30	0.22
7	830	40	33	0.21
8	860	130	35	0.20
9	880	30	30	0.22

measurement. For multiple stemmed trees all trunks ≥10 cm dbh were measured and the points of measurement marked with a nail as described previously. Only the largest trunk was tagged. The presence of buttresses in the size categories ≥50≤200 cm and >200 cm was recorded for each tree.

Voucher specimens for identification were collected from each tree except for those in each plot which were identified as the same by the experienced tree climber (Mr Baya Busu of the Forestry Research Institute, Malaysia). Vouchers were deposited at the herbaria of Brunei (BRUN), Kew (K) and Edinburgh (E). Specialist's groups were identified at Aarhus (Fabaceae), the Arnold Arboretum (Dipterocarpaceae), Kew (Arecaceae, Elaeocarpaceae and Lauraceae) and Oxford (Meliaceae). The rest of the material was identified by myself at Edinburgh, Leiden and Kew. A list of all those who assisted with the identifications is given in the acknowledgements.

The numbers of small trees in the following categories were recorded in three randomly selected 3 m x 3 m quadrats in each plot: seedlings (only the cotyledons or the first pair of true leaves present); saplings < 1 m tall; saplings 1-3 m tall; trees >3 m tall, dbh <5 cm; trees >3 m tall, dbh >5 cm <10 cm. These quadrats were also used to count small woody climbers (<10 cm dbh), palms (including rattans) and bamboos.

In plots one, five and nine the heights of all the trees were measured using a clinometer and in each of these plots a 60 m x 7.5 m strip of representative mature forest was selected for a profile diagram. The size of each crown was estimated by measuring the height to the emergence of the lowest branch and the furthest horizontal projections of the crown in the plane of the diagram. Trees shorter than 6 m were not included in the diagrams.

The plot data were analysed on the Fitopac software developed at the Department of Botany at the University of Campinas, São Paulo, Brazil. This programme collates data on species and family basal area and abundance, and produces matrices suitable for phytosociological analyses. The diversity of the plots was compared using the Shannon diversity index H' which was calculated using the formula:

$$H' = -\sum_{i=1}^{S} P_i \ln P_i$$

where S is the number of species and P_i is the proportion of individuals of the *i*th species (Kent & Coker 1992). The value of the index is slightly reduced since it assumes that all the species from a community are included in the sample, a requirement which is unlikely to be met in a species-rich rain forest.

Classifications of the plots were produced by two contrasting methods; firstly by cluster analysis and secondly using Twinspan. The Morisita index of community similarity (called Morisita's index of overlap by Brower & Zar 1977) refers to the probability that individuals drawn randomly from each of two sampling units will belong to the same species relative to the probability of randomly choosing a pair of specimens of the same species from one of the sampling units. The index is based on Simpson's dominance index (l) which is measured for community 1 by:

$$l_1 = \frac{\sum x_i(x_i - 1)}{N_1(N_1 - 1)}$$

where x_i is the number of individuals of species *i* in community 1 and N_1 is the total number of individuals in community 1 ($\therefore N_1 = \Sigma x_i$). Likewise for community 2,

$$l_2 = \frac{\sum y_i(y_i - 1)}{N_2(N_2 - 1)}$$

where l_2 is the Simpson's Dominance Index, y_i is the abundance of species *i* and $N_2 = \Sigma y_i$, the total number of individuals in community 2. The Morisita Index, I_M, is given by:

$$I_M = \frac{2\sum x_i y_i}{(l_1 + l_2) N_1 N_2}$$

The index can range from 0 (no similarity) to 1 (identical). This index offers a better assessment of similarities between plots than measures such as Jaccard's index or Sørenson's similarity index (Pielou 1984) because it incorporates information on the abundance of each species instead of simple presence or absence data. The Morisita index may be sensitive to the abundance of the commonest species, but this will not be a problem in diverse stands, and it has been considered amongst the most satisfactory of available of indices (Magurran 1988). Fitopac can consider a maximum of 250 species in a cluster analysis so the 'rare' species which were only represented by a single individual in the study were excluded from the analysis and the species list was reduced from 484 to 229. This reduction has negligible effects on the shape of the dendrogram, but will yield higher coefficients of similarity. Twinspan produces a hierarchical classification by identification of differential species and dividing the set of samples into two subsets on the presence of these species in the samples. Further differential species are then identified and the sub-sets sub-divided until no further divisions are possible (Kershaw & Looney 1984). Twinspan is thus a quite different approach to stand classification from the use of cluster analysis. The Twinspan analysis also used the matrix with the reduced species list but the elimination of the 'rare' species has no effect on the analysis since the programme only considers species present in more than one sample.

Results

Physiognomy

Tree density (>10 cm dbh) increased with altitude whilst basal area declined (Table 3.2), though basal area was variable within altitude, especially at 200 m where both the highest

Table 3.2. The density (ha^{-1}) of trees and large woody climbers (<10 cm dbh), the basal area (m^2 ha^{-1}), maximum tree height (m) and the frequency of buttressing (>50<200 cm and >200 cm) in three plots at each of three altitudes on Bukit Belalong, Brunei.

Plot	Density of trees & lianas >10 cm dbh (ha^{-1})	Basal area (m^2 ha^{-1})	Maximum tree height (m)	Percentage of trees with buttresses >50<200 cm	Percentage of trees with buttresses >200 cm
1	513	63.6	60	20.2	10.1
2	496	33.4	-	27.8	10.4
3	527	43.7	-	20.3	11.0
1-3	512	46.9		22.8	10.5
4	638	51.4	-	28.8	10.5
5	670	47.3	45	24.1	8.9
6	682	54.5	-	23.6	10.8
4-6	663	51.1		25.5	10.1
7	843	39.4	-	34.3	3.9
8	765	35.3	-	23.0	4.6
9	786	37.7	33	26.4	5.7
7-9	798	37.5		27.9	4.7

and lowest values of basal area for any plot were recorded (63.6 m^2 ha^{-1} in plot 1 and 33.4 m^2 ha^{-1} in plot 2). Density and basal area were calculated relative to the horizontal area of each plot rather than the area on the ground. Maximum tree height declined with altitude from 60 m at 200 m (*Koompassia excelsa*) to 33 m at 850 m (*Shorea* sp). Though the tallest tree measured at 500 m reached 45 m (*Swintonia acuta*), two individuals of *Shorea pauciflora* in plot 6 were probably taller (c. 50-60 m), but unfortunately the heights of these trees were not measured.

Trees at 850 m differed in their diameter class distribution from those at 200 m and 500 m (Table 3.3), with relatively more trees in the smaller diameter diameter classes at 850 m. The maximum dbh was 161 cm at 200 m (*Shorea laevis*), 114.6 cm at 500 m (*Swintonia acuta*) and 76.1 cm at 850 m (*Shorea parvifolia*). The percentage of trees with small buttresses (<200 cm) increased slightly with altitude (Table 3.2), but the differences were not significant (one way ANOVA on arcsin transformed data). Tall buttresses (>200 cm) were less frequent at 850 m. Fewer small trees (<3 m tall) and seedlings were recorded at 850 m than at the lower altitudes (Table 3.4), though there were more large understorey trees (> 3 m tall, <10 cm dbh) at the higher altitude. Woody climbers (<10 cm and >10 cm dbh) were more frequent at 850 m but differences between altitudes were not significant. Rattans were least abundant at 500 m. Climbing bamboos and small arborescent palms (*Pinanga* species) were only found at 850 m.

The profile diagrams (Figures 3.1-3.3) and photographs (Figures 3.4-3.6) give an overall impression of the forests at each altitude. The most notable differences between the forest at 850 m and those at 200 m and 500 m are the reduction of stature and absence of emergent trees and the comparative evenness of the upper canopy surface.

Floristics

One hundred and sixty-eight taxa of trees and lianas (>10 cm dbh) were recorded from the

Table 3.3. The percentages of trees and lianas (≥10 cm dbh) in a series of diameter classes in three plots at each of three altitudes on Bukit Belalong.

Altitude (m)	Diameter class (cm)									
	10-19.9	20-29.9	30-39.9	40-49.9	50-59.9	60-69.9	70-79.9	80-89.9	90-99.9	≥100
200	50.7	21.0	12.5	5.7	2.8	3.1	1.1	0.8	0.6	1.7
500	56.3	18.6	11.0	4.8	3.3	1.5	2.0	0.7	0.4	1.5
850	63.3	19.0	9.4	4.5	1.9	0.8	1.0	-	-	-

Table 3.4. The densities (m^{-2}) of trees and arborescent palms (<10 cm dbh), woody climbers (> & < 10 cm dbh) and rattans and bamboos at three altitudes on Bukit Belalong, Brunei. Values are the means of three plots in each of which three randomly selected 3 m x 3 m quadrats were described, with the ranges of the plots in parentheses. Statistically significant differences between altitude (from ANOVA on log-transformed data) are indicated by the superscripts.

	Altitude (m)		
	200	500	850
Seedlings (m^{-2})	1.09 (0.59-2.56)	2.30 (1.00-4.67)	0.48 (0.26-1.41)
Trees <1.0 m (m^{-2})	11.36^{b} (10.15-12.81)	5.37^{ab} (3.67-6.96)	2.62^{a} (0.78-4.70)
Trees 1-3 m (m^{-2})	1.10^{b} (0.93-1.44)	0.42^{a} (0.33-0.52)	0.68^{ab} (0.59-0.78)
Trees >3 m, dbh <5cm (m^{-2})	0.09 (0.00-0.19)	0.16 (0.11-0.22)	0.27 (0.26-0.30)
Trees >3 m, dbh >5<10 cm (m^{-2})	0.04 (0.00-0.07)	0.10 (0.04-0.15)	0.09 (0.04-0.11)
Woody climbers dbh <10 cm (m^{-2})	0.16 (0.07-0.30)	0.07 (0.04-0.15)	0.30 (0.15-0.56)
Woody climbers dbh >10 cm (ha^{-1})	2.9 (0.0-4.5)	4.2 (0.0-8.3)	9.5 (5.0-14.3)
Rattans (m^{-2})	0.38 (0.19-0.56)	0.21 (0.19-0.26)	0.42 (0.37-0.52)
Bamboo (m^{-2})	-	-	0.01 (0.00-0.04)
Palms dbh <10 cm (m^{-2})	-	-	0.28 (0.04-0.56)

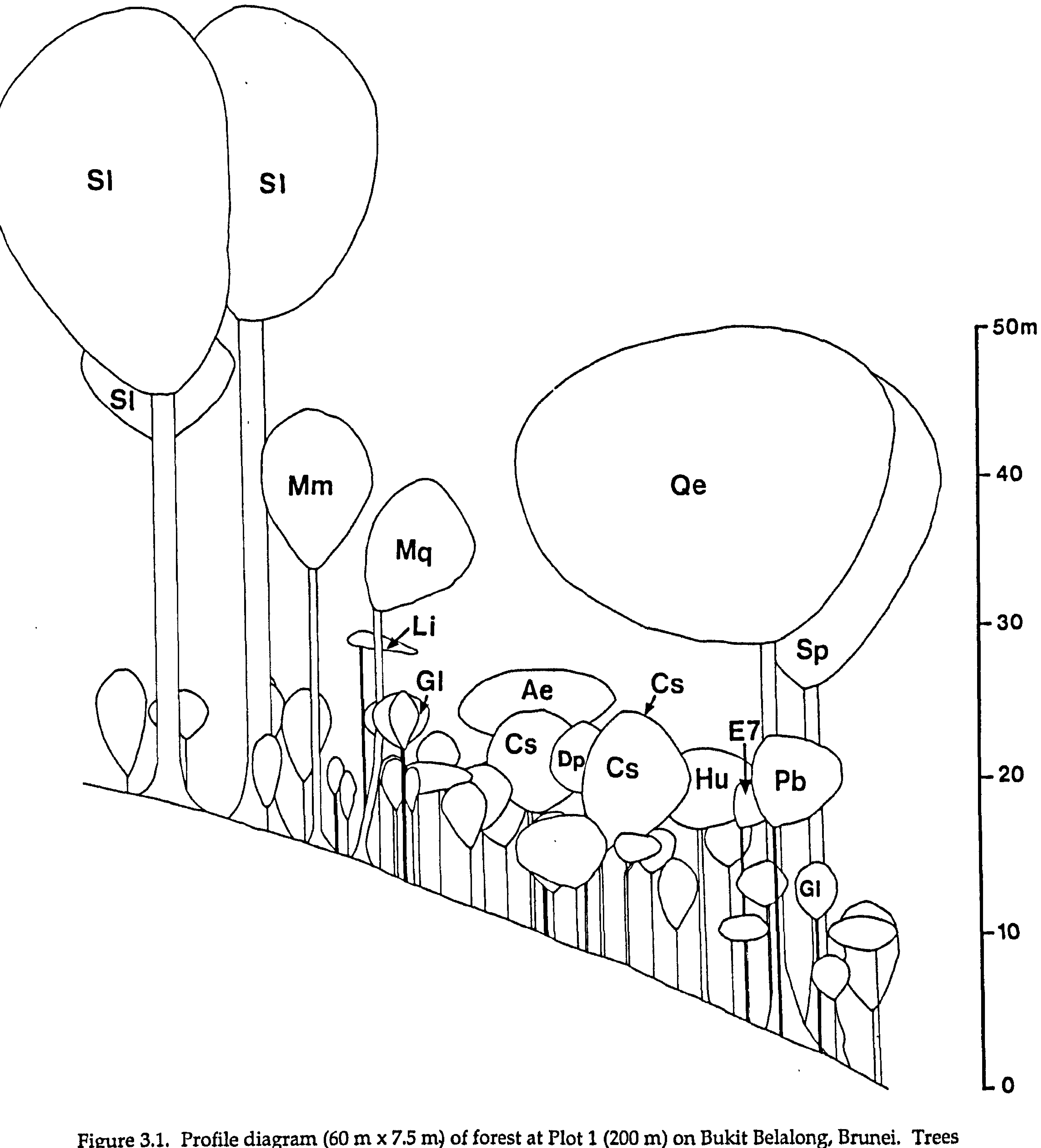


Figure 3.1. Profile diagram (60 m x 7.5 m) of forest at Plot 1 (200 m) on Bukit Belalong, Brunei. Trees less than 6 m are excluded. Symbols for trees over 10 cm dbh: Ae, cf. *Aetoxylon*; Cs, *Casearia* sp.1; Dp, *Dipterocarpus caudiferus*; E7, *Eugenia* sp.7; Gl, *Gluta laxiflora*; Hw, *Hydnocarpus woodii*; Li, *Linociera* sp.1; Mm, *Myristica malaccensis*; Mq, *Mangifera quadrifida*; Pb, *Ptychopyxis bacciformis*; Qe, *Quercus elmeri*; Sp, *Scaphium longiopetalum*.

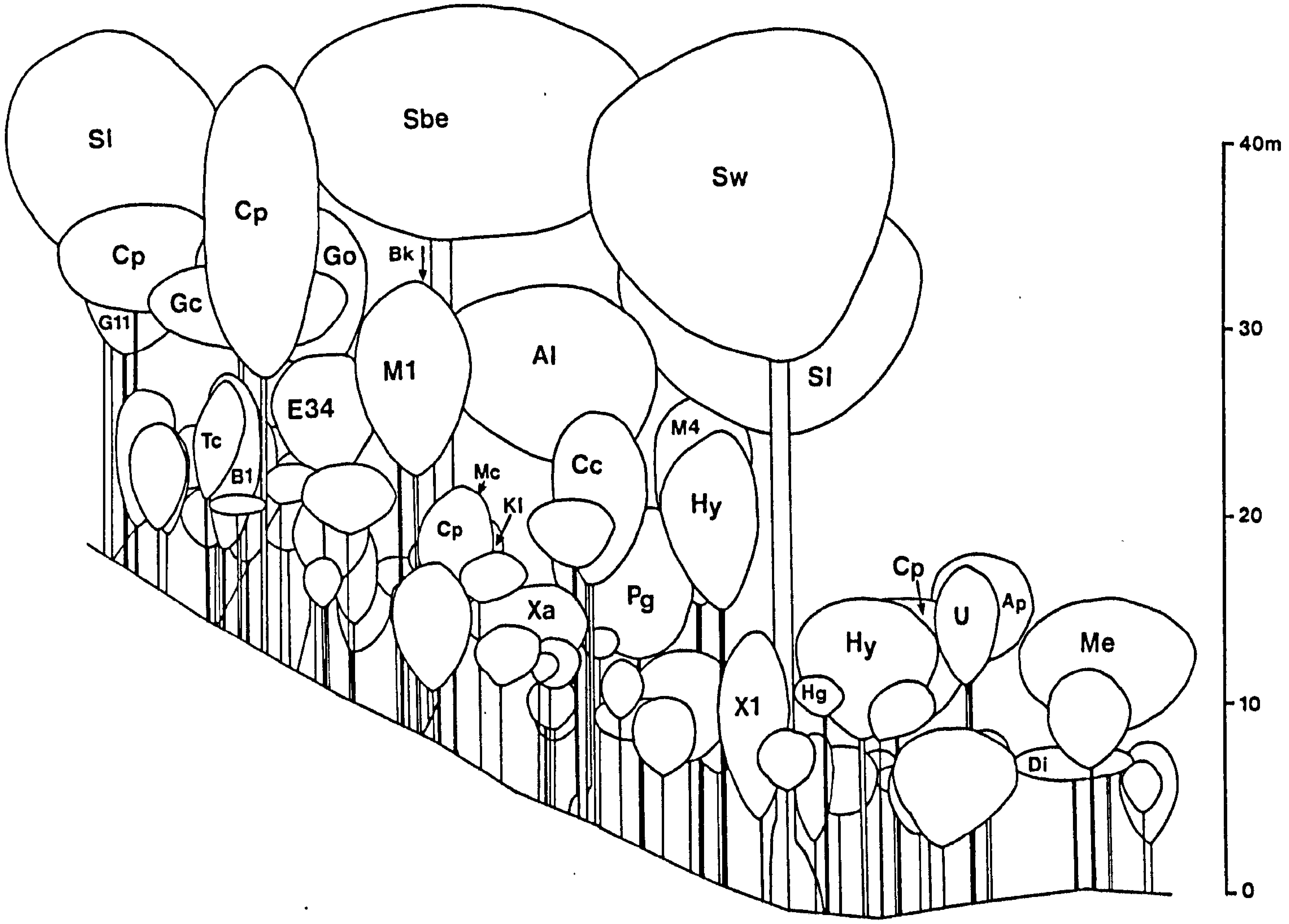


Figure 3.2. Profile diagram (60 m x 7.5 m) of forest at Plot 5 (520 m) on Bukit Belalong, Brunei. Trees less than 6 m are excluded. Symbols for trees over 10 cm dbh: Al, *Anisoptera laevis*; Ap, *Aporusa* species unknown; B1, *Baccaurea* sp.1; Bk, *Blumeodendron kurzii*; Cc, *Canthium confertum*; Cp, *Cinnamomum porrectum*; Di, *Diospyros* species unknown; E34, *Eugenia* sp.34; G11, *Garcinia* sp.11; Gc, *Gymnacranthera contracta*; Go, *Gluta oba*; Hg, *Horsfieldia grandis*; Hy, *Hydnocarpus sumatrana*; Kl, *Knema latericia*; M1, *Madhuca* sp.1; M4, *Madhuca* sp.4; Mc, *Myristica cinnamomea*; Me, *Mesua* species unknown; Pg, *Pimeleodendron griffithianum*; Sbe, *Shorea* cf. *beccariana*; Sl, *Shorea laevis*; Sw, *Swintonia acuta*; Tc, *Teijsmanniodendron coriaceum*; U, Unknown; X1, *Xanthophyllum* sp.1; Xa, *Xanthophyllum affine*.

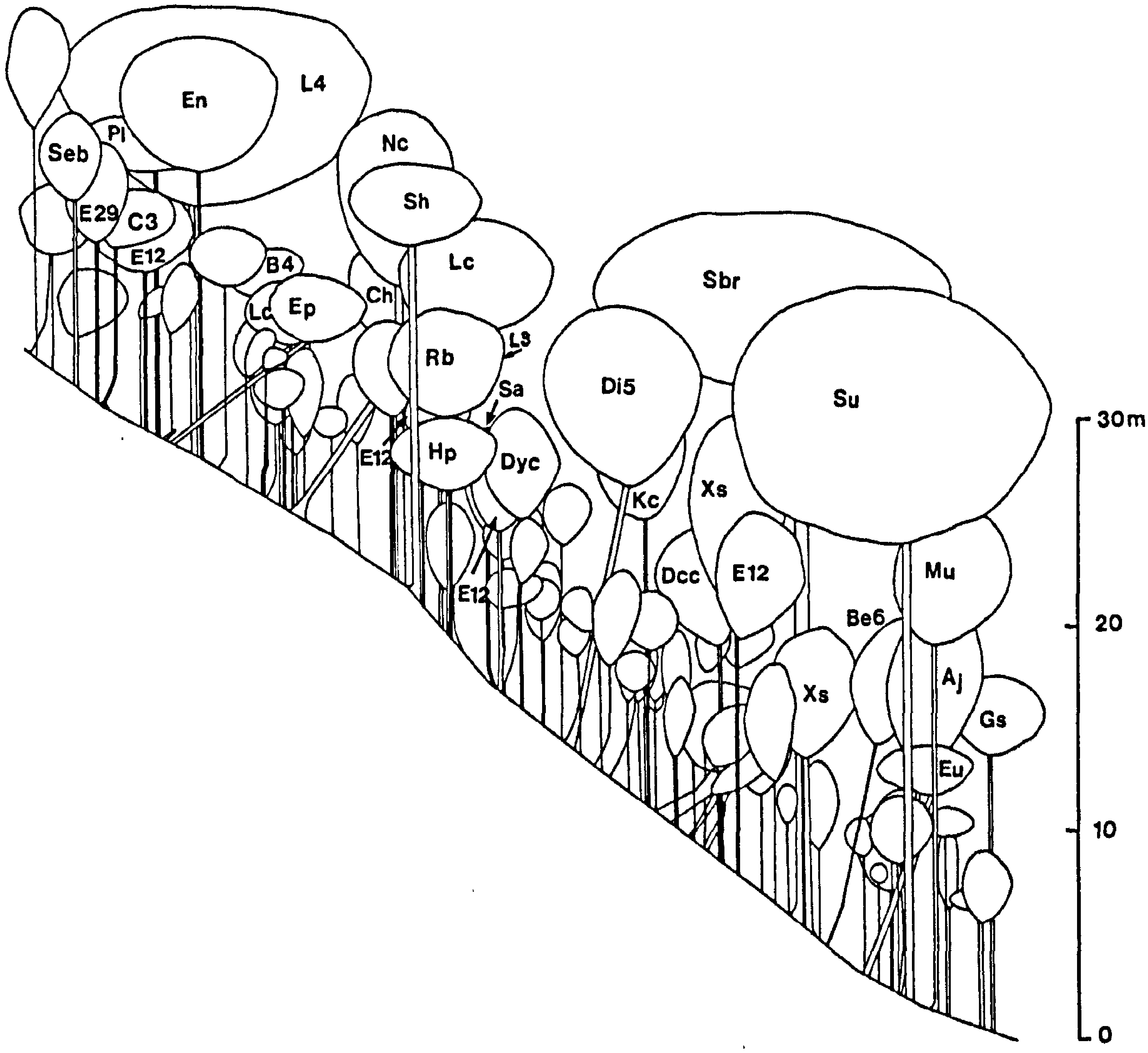


Figure 3.3. Profile diagram (60 m x 7.5 m) of forest at Plot 9 (880 m) on Bukit Belalong, Brunei. Trees less than 6 m are excluded. Symbols for trees over 10 cm dbh: Aj, cf. *Alangium javanicum*; B4, *Baccaurea* sp.4; Be6, *Bielschmeidia* sp.6; C3, *Cryptocarya* sp.3; Ch, *Chionanthus* sp.1; Dcc, *Dacryodes costata;* Di5, *Diospyros* sp.5; Dyc, *Dysoxylum cauliflorum;* E12, *Eugenia* sp.12; E29, *Eugenia* sp.29; En, *Elaeocarpus nitidus;* Ep, *Elaeocarpus palembanicus;* Eu, *Eugenia* species unknown; Gs, *Gironniera subequalis;* Hp, *Horsfieldia polysepherula;* Kc, *Koompassia malaccensis;* L3, *Lithocarpus* sp.3; L4, *Lithocarpus* sp.4; Lc, *Lithocarpus clementianus;* Mu, *Myristicaceae* species unknown; Nc, *Nephelium cuspidatum;* Pl, *Lithocarpus rassa;* Rb, *Ryparosa baccaureodes;* Sh, *Shorea* species unknown 1; Sa, *Symplocos adenophylla;* Sbr, *Shorea* cf. *bracteolata;* Seb, *Semecarpus bunburyanus;* Su, *Shorea* species unknown 2; Xs, *Xanthophyllum stipitatum.*

Figure 3.4. Evergreen lowland rain forest at 200 m on Bukit Belalong, Brunei (Plot 2). The pole is marked at 20-cm intervals.

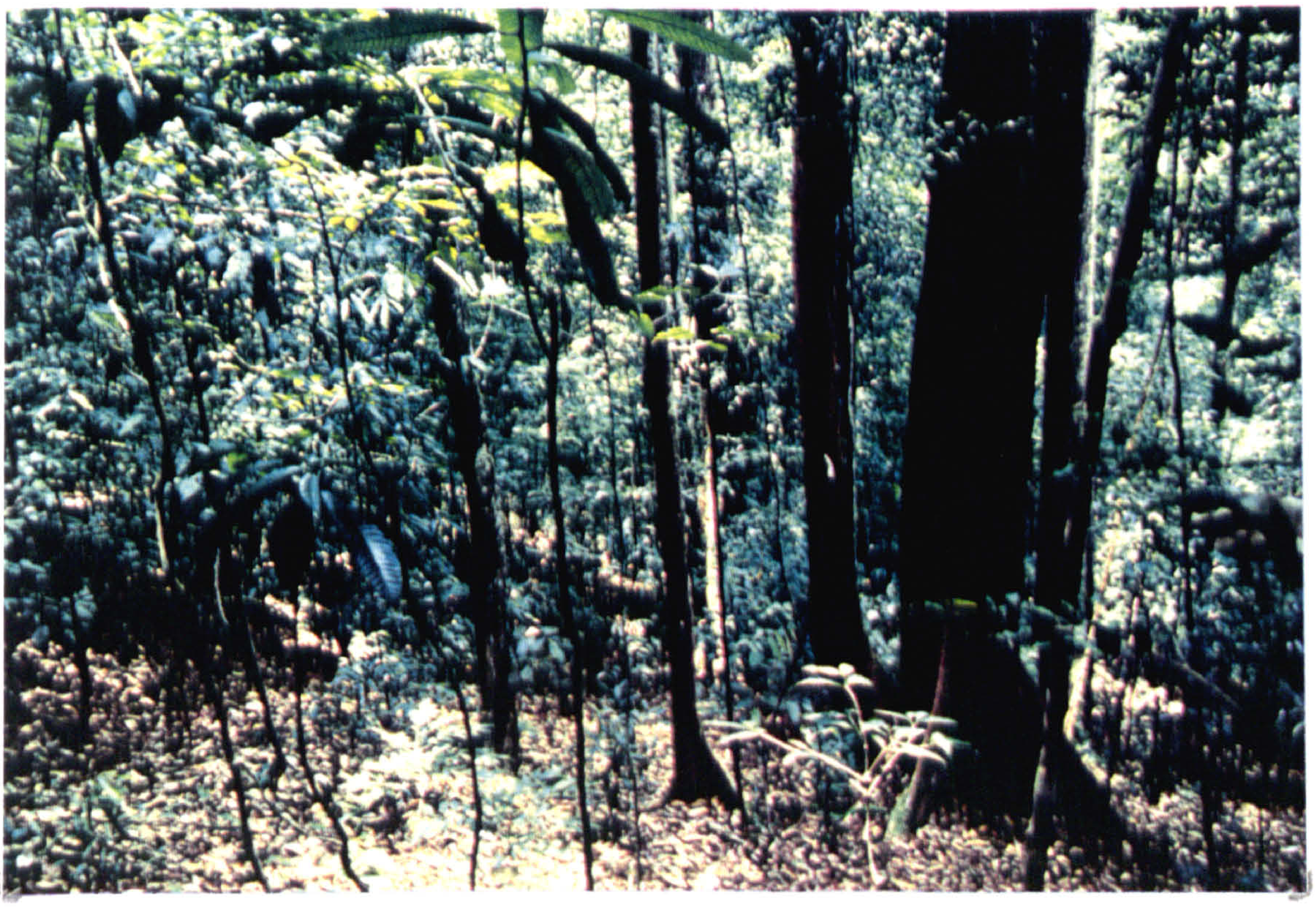


Figure 3.5. Evergreen lowland rain forest at 500 m on Bukit Belalong, Brunei (Plot 6).

Figure 3.6. Lower montane rain forest at 500 m on Bukit Belalong, Brunei (Plot 9). The pole is marked at 20-cm intervals.

plots at 200 m, 194 at 500 m and 223 at 850 m; 33 families were present at 200 m, 36 at 500 m and 47 at 850 m. One hundred and sixty-one taxa, 33% of the total, were recorded only at 850 m, but 28% of the LMRF taxa (62) were also found at lower altitudes. Sixteen species were present at both 200 m and 850 m. The Shannon indices tended to be higher in the plots at 850 m, especially when the tree families were considered (Table 3.5). However, the high species richness and diversity of the 850 m plots are largely a function of the high density of trees at that altitude since the ratio of number of species : number of individuals is highest at 200 m.

The Dipterocarpaceae contributed the highest proportion of basal area of trees (>10 cm dbh) at all altitudes, but it was less important at 850 m (Table 3.6) and in plot 8 it contributed only 8.9% of the basal area and was ranked fourth (after the Myrtaceae, Fagaceae and Anacardiaceae). The Clusiaceae, Fagaceae, Lauraceae and Myrtaceae had higher proportions of basal area at 850 m than at the lower altitudes and these four families were also more diverse at 850 m (Table 3.6) whilst the Dipterocarpaceae and Flacourtiaceae were more diverse at the lower altitudes. Fourteen families were recorded only at 850 m, whilst five families were restricted to the lower altitudes.

Species-area curves were drawn for each plot (Fig 3.7) and each altitude (Fig.3.8). The horizontal area of each sub-plot was not calculated separately, but estimated as 1/25 of the horizontal area of the whole plot. It is accepted that this may cause some distortion of the curves from the more uneven plots. None of the single-plot species-area curves show any indication of levelling off and the slopes of the curves for all the plots at each altitude are only slightly shallower at the maximum area. Extrapolation of these curves to 1 ha suggest that there are likely to be c. 210 species ha^{-1} at 200 m, c. 230 species ha^{-1} at 500 m and c. 250 species ha^{-1} at 850 m.

The dendrogram produced by cluster analysis of the tree species using Morisita's index (Figure 3.9) show that the plots at each altitude are more similar to the other plots at the

Table 3.5. The numbers of species and families of trees (>10 cm dbh), the Shannon indices of diversity for species and families and the ratio between the number of species and the number of individuals in three 50 m x 50 m plots at each of three altitudes on Bukit Belalong, Brunei.

Plot	Number of species	Number of families	Shannon Diversity Index		Species: individuals ratio
			Species	Families	
1	69	24	3.98	2.58	0.58
2	76	26	4.18	2.90	0.67
3	83	29	4.30	2.96	0.72
1-3	168	33	4.78	2.95	0.48
4	98	30	4.38	2.89	0.64
5	90	27	4.32	2.89	0.58
6	76	27	3.97	2.51	0.51
4-6	194	36	4.87	2.93	0.42
7	121	34	4.66	3.16	0.68
8	91	36	4.29	3.18	0.59
9	96	33	4.30	3.11	0.55
7-9	223	47	5.07	3.28	0.44

Table 3.6. The percentage contribution of each family to tree and liana (≥10 cm dbh) basal area at three altitudes on Bukit Belalong, Brunei. The values are the means from three plots at each altitude, with the ranges in parentheses. '-' indicates that the family was not recorded in the plots at that altitude.

Family	Altitude (m)		
	200	500	850
Alangiaceae	0.1 (0.0-0.5)	0.1 (0.0-0.3)	0.1 (0.0-0.4)
Anacardiaceae	3.3 (2.3-5.1)	7.1 (4.1-13.2)	6.9 (5.6-9.7)
Annonaceae	2.8 (0.0-5.0)	0.1 (0.0-0.2)	0.3 (0.0-0.9)
Apocynaceae	-	1.3 (0.1-2.6)	-
Arecacae	-	-	1.0 (0.0-2.4)
Bombacaceae	-	0.5 (0.1-1.2)	0.1 (0.0-0.2)
Boraginaceae	-	-	0.2 (0.0-0.5)
Burseraceae	2.5 (0.7-5.9)	3.7 (2.8-5.0)	2.1 (0.4-3.4)
Celastraceae	-	0.1 (0.0-0.3)	0.04 (0.0-0.1)
Clusiaceae	0.7 (0.0-3.2)	2.0 (1.1-2.6)	5.1 (2.3-9.7)
Cornaceae	-	-	0.1 (0.0-0.3)
Crypteroniaceae	0.5 (0.0-2.0)	-	0.04 (0.0-0.1)
Dipterocarpaceae	45.5 (37.4-51.5)	51.9 (36.7-59.1)	23.0 (8.9-29.9)
Ebenaceae	0.9 (0.6-1.5)	0.5 (0.2-1.0)	0.6 (0.0-1.4)
Elaeocarpaceae	-	-	3.1 (0.0-7.2)
Euphorbiaceae	6.4 (4.1-12.6)	6.0 (2.9-10.7)	4.5 (3.7-4.2)
Fabaceae	5.9 (0.9-1.5)	2.5 (0.5-5.1)	4.3 (1.4-7.5)
Fagaceae	2.4 (0.0-5.2)	0.03 (0.0-0.08)	9.8 (7.7-13.6)
Flacourtiaceae	5.1 (4.1-7.4)	1.9 (1.0-2.5)	0.7 (0.5-0.8)
Hypericaceae	-	-	1.0 (0.0-2.9)
Icacinaceae	0.3 (0.0-1.3)	1.2 (0.1-1.9)	-
Lauraceae	1.8 (0.0-4.8)	2.0 (0.0-5.0)	6.1 (4.8-7.2)
Lecythicidaceae	1.3 (0.4-2.7)	0.1 (0.0-0.2)	-
Linaceae	-	-	0.1 (0.0-0.3)
Loganiaceae	-	0.1 (0.0-0.3)	-
Magnoliaceae	-	-	1.0 (0.0-2.1)
Melastomataceae	0.3 (0.0-0.7)	0.1 (0.0-0.2)	0.6 (0.3-0.9)
Meliaceae	1.2 (0.9-1.5)	0.3 (0.0-0.6)	3.2 (0.6-5.9)
Moraceae	1.8 (0.2-4.3)	0.7 (0.0-1.9)	1.9 (0.4-5.0)
Myristicaceae	1.5 (0.2-2.5)	2.8 (2.4-3.4)	1.1 (0.6-1.9)
Myrsinaceae	-	-	0.1 (0.0-0.2)
Myrtaceae	3.2 (0.3-6.7)	4.3 (3.6-5.0)	9.9 (6.0-14.0)

Family	Altitude (m)		
	200	500	850
Olacaceae	1.1 (0.1-2.2)	0.6 (0.3-0.7)	1.0 (0.0-2.2)
Oleaeceae	-	0.5 (0.2-0.8)	0.8 (0.5-1.3)
Opiliaceae	-	-	0.1 (0.0-0.2)
Oxalidaceae	0.4 (0.0-1.3)	-	-
Podocarpaceae	-	-	0.2 (0.0-0.8)
Polygalaceae	2.2 (0.7-4.8)	2.3 (0.6-3.9)	2.1 (0.0-5.5)
Proteacae	-	-	0.1 (0.0-0.2)
Rhizophoraceae	0.1 (0.0-0.3)	0.5 (0.1-1.1)	0.2 (0.0-0.4)
Rosaceae	1.0 (0.4-2.0)	0.3 (0.0-0.9)	0.3 (0.1-0.5)
Rubiaceae	0.2 (0.0-0.4)	0.2 (0.0-0.3)	0.9 (0.7-1.3)
Rutaceae	-	-	0.1 (0.0-0.2)
Sapindaceae	0.3 (0.2-0.4)	0.6 (0.1-1.6)	1.6 (1.3-2.1)
Sapotaceae	0.8 (0.2-1.4)	1.0 (0.3-2.1)	0.8 (0.0-1.8)
Simaroubaceae	-	0.03 (0.0-0.09)	-
Sterculiaceae	4.0 (0.1-8.0)	1.8 (0.0-5.1)	1.4 (1.0-1.8)
Symplocaceae	-	-	0.1 (0.0-0.2)
Theaceae	-	-	1.1 (0.7-1.3)
Thymeleaceae	0.4 (0.2-0.9)	0.8 (0.0-1.6)	0.2 (0.1-0.2)
Tiliaceae	0.3 (0.1-0.8)	-	0.3 (0.0-0.5)
Ulmaceae	0.6 (0.0-1.9)	0.5 (0.0-1.4)	0.9 (0.4-1.6)
Verbenaceae	0.1 (0.0-0.2)	0.3 (0.2-0.4)	0.5 (0.1-0.7)
Family unknown, trees	0.9 (0.0-2.6)	1.3 (0.0-2.1)	0.3 (0.1-0.4)
Family unknown, lianas	0.2 (0.0-0.4)	0.1 (0.0-0.4)	0.4 (0.0-0.9)

Table 3.7. The species-richness of tree and liana (>10 cm dbh) families at three altitudes on Bukit Belalong, Brunei. The values are the total numbers of species recorded at each altitude, with the ranges of the numbers of species in the individual plots in parentheses. '-' indicates that the family was not recorded in the plots at that altitude.

Family	Altitude (m)		
	200	500	850
Alangiaceae	1 (0-1)	1 (0-1)	1 (0-1)
Anacardiaceae	8 (3-5)	10 (3-6)	12 (4-7)
Annonaceae	4 (2-3)	3 (0-2)	3 (0-2)
Apocynaceae	-	3 (1-1)	-
Arecacae	-	-	1 (0-1)
Bombacaceae	-	2 (1-2)	1 (0-1)
Boraginaceae	-	-	1 (0-1)
Burseraceae	10 (3-6)	10 (3-6)	6 (2-6)
Celastraceae	-	1 (0-1)	1 (0-1)
Clusiaceae	4 (0-4)	8 (1-4)	14 (4-9)
Cornaceae	-	-	1 (0-1)
Crypteroniaceae	1 (0-1)	-	1 (0-1)
Dipterocarpaceae	24 (12-14)	31 (12-18)	14 (2-12)
Ebenaceae	6 (3-4)	5 (1-3)	2 (0-2)
Elaeocarpaceae	-	-	5 (0-4)
Euphorbiaceae	14 (4-8)	15 (5-11)	15 (7-8)
Fabaceae	6 (1-3)	4 (1-2)	5 (2-3)
Fagaceae	1 (0-1)	1 (0-1)	9 (5-5)
Flacourtiaceae	7 (3-6)	5 (2-3)	4 (1-2)
Hypericaceae	-	-	1 (0-1)
Icacinaceae	1 (0-1)	2 (1-1)	-
Lauraceae	7 (0-5)	5 (0-4)	28 (8-13)
Lecythicidaceae	3 (1-2)	2 (0-2)	-
Linaceae	-	-	1 (0-1)
Loganiaceae	-	1 (0-1)	-
Magnoliaceae	-	-	1 (0-1)
Melastomataceae	2 (0-1)	1 (0-1)	3 (1-2)
Meliaceae	5 (1-2)	3 (0-2)	8 (2-7)
Moraceae	3 (1-3)	4 (0-4)	3 (2-3)
Myristicaceae	6 (2-4)	12 (5-6)	8 (3-5)
Myrsinaceae	-	-	1 (0-1)

Family	Altitude (m)		
	200	500	850
Myrtaceae	7 (2-6)	16 (6-9)	21 (8-9)
Olacaceae	2 (1-2)	2 (1-2)	2 (0-2)
Oleaeceae	-	2 (1-2)	2 (1-2)
Opiliaceae	-	-	1 (0-1)
Oxalidaceae	1 (0-1)	-	-
Podocarpaceae	-	-	1 (0-1)
Polygalaceae	11 (2-5)	10 (4-10)	1 (0-1)
Proteacae	-	-	1 (0-1)
Rhizophoraceae	1 (0-1)	1 (1-1)	1 (0-1)
Rosaceae	3 (1-1)	2 (0-2)	4 (1-3)
Rubiaceae	4 (0-3)	3 (0-2)	6 (2-3)
Rutaceae	-	-	2 (0-1)
Sapindaceae	4 (1-2)	5 (1-3)	3 (1-2)
Sapotaceae	5 (2-3)	5 (1-3)	4 (0-3)
Simaroubaceae	-	1 (0-1)	-
Sterculiaceae	4 (1-3)	2 (0-2)	3 (1-2)
Symplocaceae	-	-	1 (0-1)
Theaceae	-	-	4 (3-3)
Thymeleaceae	4 (1-2)	5 (0-3)	2 (1-1)
Tiliaceae	2 (1-1)	-	3 (0-2)
Ulmaceae	1 (0-1)	2 (0-2)	1 (1-1)
Verbenaceae	1 (0-1)	1 (1-1)	2 (1-2)

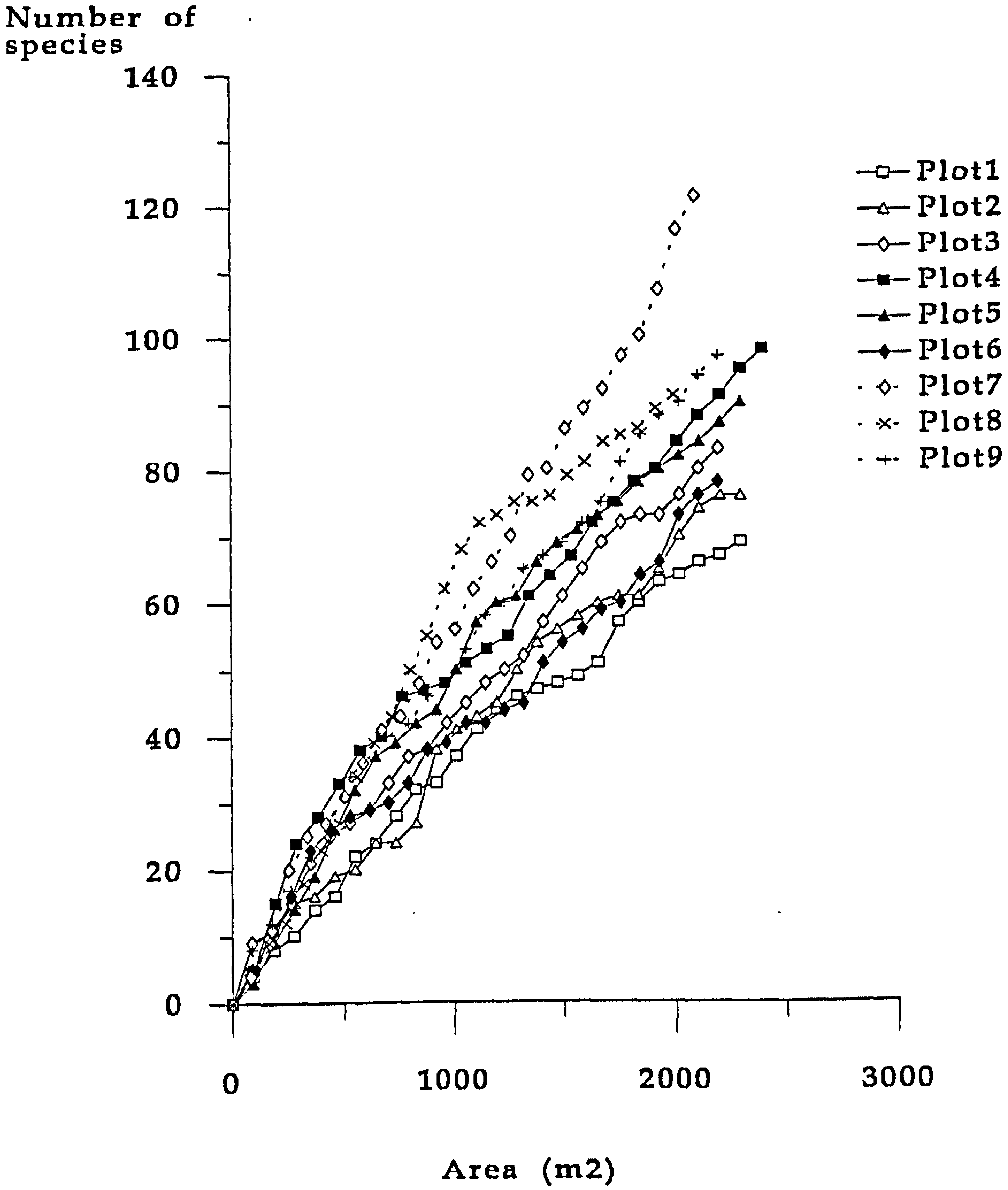


Figure 3.7. Species-area curves for trees and lianas (≥10 cm dbh) in nine 0.25 ha plots on Bukit Belalong, Brunei. Plots 1-3 are at 200 m, 4-6 at 500 m and 7-9 at 850 m. Each curve follows the order of enumeration of 10 m x 10 m sub-plots.

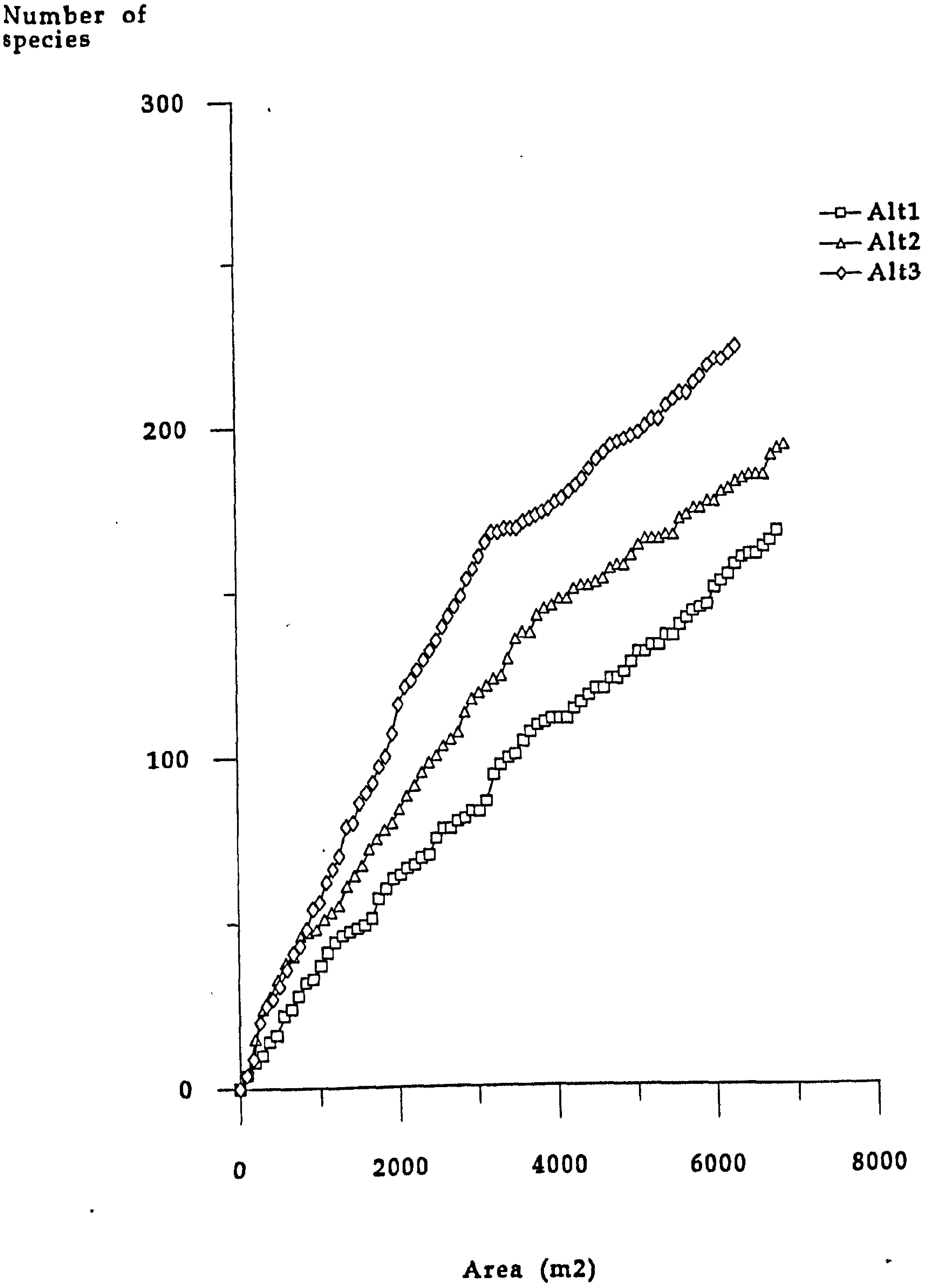
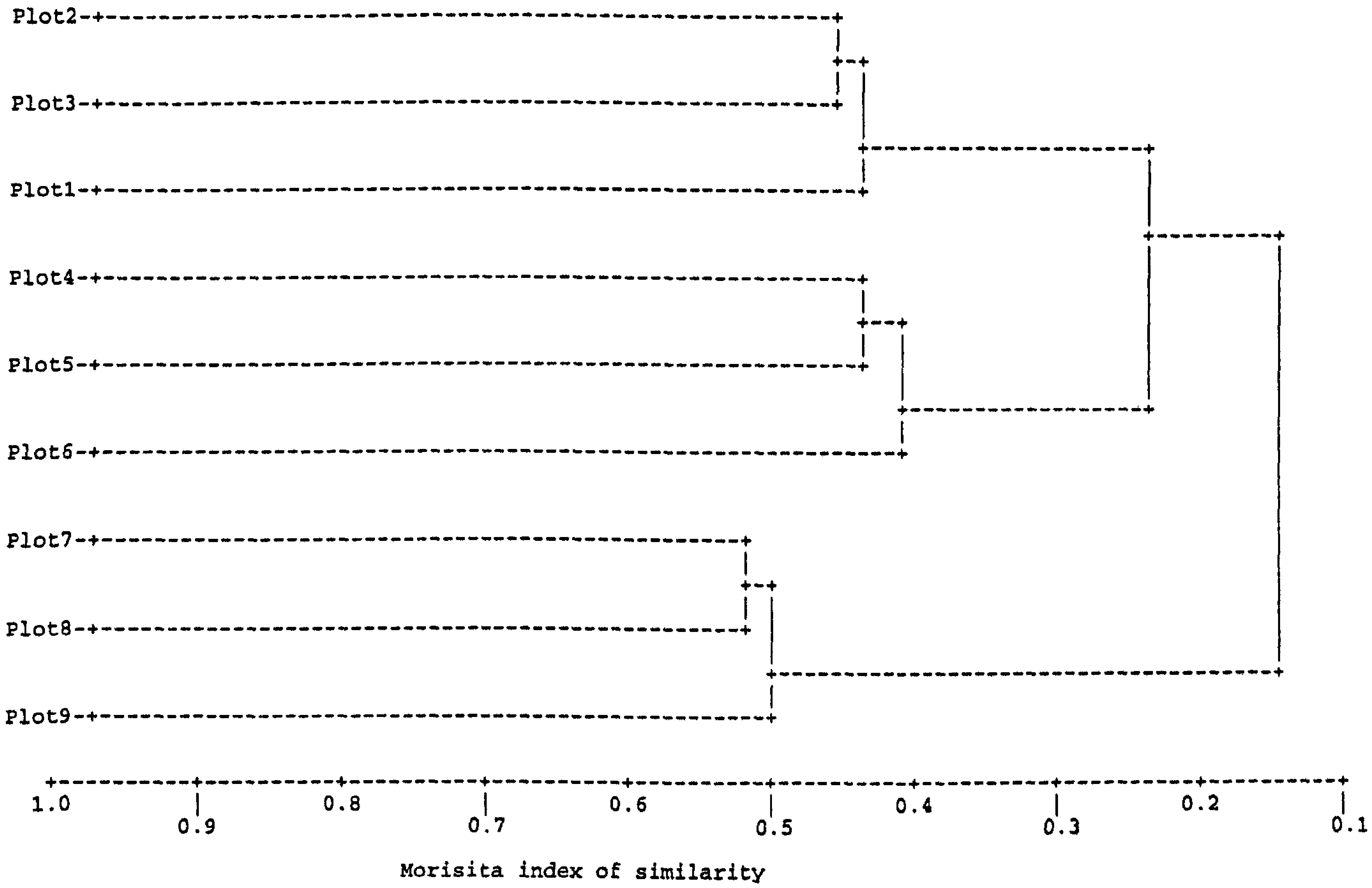


Figure 3.8. Species-area curves for trees and lianas (≥10 cm dbh) at 200 m (Alt 1), 500 m (Alt 2) and 850 m (Alt 3) on Bukit Belalong, Brunei. At each altitude there were three independent 0.25 ha plots, which are treated as a single plot 0.75 ha plot. Each curve follows the order of enumeration of 10 m x 10 m sub-plots.

Figure 3.9. Dendrogram of similarities between three plots at each of three altitudes on Bukit Belalong, Brunei. The classification uses the Morisita index (modified by Horn) and group centred clustereing.



same altitude than the plots at other altitudes and the plots at 850 m are distinct from those at 200 m and 500 m. The Twinspan analysis agrees very closely with the cluster analysis (Table 3.8). The first division separates the 850 m plots as a single unit and the second divides the 200 m plots from those at 500 m. The plots at 850 m are more closely related to those at 500 m than those at 200 m. Of the forty commonest species *Mallotus penangianus* and *Lithocarpus clemantianus* were found in all the plots at 850 m but not at lower altitudes and they can be considered indicator species for the community at 850 m. Likewise *Xanthophyllum* sp.1 is an indicator species for the forest at 500 m and *Casearia* sp.1 and *Hydnocarpus woodii* indicators for the lowest altitude forest. *Elateriospermum tapos* and *Shorea pauciflora* were found in all of the plots at 200 m and 500 m, but none of the plots at 850 m. Five species of the forty commonest species were found at all altitudes and of these *Baccuarea* sp.1 was present in all the plots except plot 2.

The distribution of rattan species in the plots (Table 3.9) also reflect the differences between altitudes. Of the twenty species identified (four seedlings could only be identified to the level of genus) nine were restricted to 200 m and seven restricted to 850 m. Only one species, *Calamus javensis*, was found at both 200 m and 850 m, but it was not recorded at 500 m where rattan diversity was lowest.

Discussion

The forests at 200 m and 500 m are tropical evergreen lowland rain forest (*sensu* Whitmore 1984). The forest at 850 m is considered to be a tall stature lower montane forest for the following reasons: compared with the low altitude forests that at 850 m has increased density, reduced stature and a paucity of emergents; lower frequency and basal area of the Dipterocarpaceae and complete absence of species of large dipterocarps which are important components of the lowland forest (eg *Dipterocarpus* spp., *Dryobalanops* spp., *Shorea laevis*, *Shorea pauciflora*); increased basal area and diversity of families typical of montane

Table 3.8. Classification derived from a Twinspan analysis of the distribution and abundance of trees (>10 cm dbh) in three plots at each of three altitudes on Bukit Belalong, Brunei. 'Rare' species (ie those found only once in the study) were excluded from the analysis, and the table lists the forty commonest species. Abundance in each plot is indicated as follows: -, absent from that plot; 1, 1 individual; 2, 2-3 individuals; 3, 4-5 individuals; 4, 6-10 individuals; 5, 11 or more individuals. The first division separates plots 7-9 (LMRF) from 1-6 (LRF), and the second division separates the plots at 200 m (1-3) from those at 500 m (4-6).

```
                                  Plot
                                123456789
Mangifera cf. quadrifida        212--1---
Xylopia malayana                2221-----
Shorea cf. faguetiana           123-11---
Diospyros sp.1                  221--1---
Casearia sp.1                   342------
Hydnocarpus woodii              423------
Ryparosa kostermansii           3221-----
Shorea laevis                   22-22----
Shorea leprosula                -3-31----
Shorea pauciflora               321314---
Dipterocarpus caudatus          -114-----
Elateriospermum tapos           322325---
Gluta wallichii                 --1212---
Gonocaryum minus                -2--44---
Xanthophyllum sp.1              ---421---
Teijsmanniodendron coriaceum    -1-222---
Shorea amplexicaulis            ----351--
Hydnocarpus kunstleri           ---2331--
Dacryodes rugosa                1--2-31--
Artocarpus lowii                112---11-
Baccaurea sp.1                  11-222111
Semecarpus bunburyanus          1--12--12
Eugenia sp.3                    ---21-3--
Xanthophyllum stipitatum        -1-12--13
Horsfieldia polysepherula       ---11-121
Eugenia ochneocarpa             ---11--31
Girroniera subequalis           ---2-1221
Shorea parvifolia               2-----2-2
Bielschmeidia sp.6              -11-1-211
Artocarpus odoratissimus        -2-1--232
Parashorea parvifolia           ----1-242
Shorea cf. curtisii             ----1-3-4
Vatica dulitensis               ------2-4
Mallotus penangianus            ------332
Lithocarpus clementianus        ------222
Artocarpus nitidus              ---1---32
Eugenia sp.11                   -------25
Eugenia sp.28                   ----1--23
Chionanthus cf. curvicarpus     ---1--322
Xerospermum noronhianum         ----1-142

                                000000111
                                000111
```

Table 3.9. The number of rattans in three randomly selected 3 m x 3 m quadrats from three plots at each of three altitudes on Bukit Belalong, Brunei.

	Plot								
Species	1	2	3	4	5	6	7	8	9
Calamus sordidus J.Dransf.		1							
Calamus pogocanthus Becc. ex. H.Winkl.		1							
Calamus flabellatus Becc.			1						
Calamus praetermissus J.Dransf.			1						
Calamus javensis Bl.		2						1	
Calamus comptus J.Dransf.							3		2
Calamus aff. *semoi* Becc.								1	2
Calamus zonatus Becc.									1
Calamus laevigatus var. *mucronatus* (Becc.) J.Dransf.								1	1
Calamus muricatus Becc.								1	
Calamus sp. 1	1								
Calamus sp. 2									2
Ceratolobus subangulatus (Miq.) Becc.					1		1	1	2
Ceratolobus concolor Bl.			1						
Korthalsia rostrata Bl.	1			1	1				
Korthalsia hispida Becc.			1						
Korthalsia debilis Bl.								1	
Daemonorops sparsiflora Becc.	1								
Daemonorops korthalsii Bl.	1								
Daemonorops pericanthia Miq.		2	2						
Daemonorops oxycarpa Becc.			1			1			
Daemonorops longipes (Griff.) Mart.								2	2
Daemonorops sp. 1					1	1			
Daemonorops sp. 2									1

communities (Myrtaceae, Fagaceae, Lauraceae and Clusiaceae). None of these factors considered separately are strikingly different between the low and high altitude forests, but when considered together they do indicate the distinctness of the forest at 850 m (Whitmore 1984).

A study of the herbaceous ground vegetation (including ferns) in the Bukit Belalong plots (Poulsen & Pendry 1994, see Appendix 3) also revealed clear differences between the LRF and LMRF. Herb abundance and diversity were much higher in the LMRF and 57 species from a total of 121 were restricted to it. Vascular epiphytes were not quantified.

However, there are discrepancies between the forest at 850 m and the Whitmore definition of LMRF. In this scheme pinnate leaves are 'rare' but at 850 m there are members of the Meliaceae, Burseraceae, Fabaceae and Sapindaceae which have pinnate leaves. Cauliflory is also considered 'rare' in LMRF in the Whitmore classification, but the single cauliflorous species found in this study, *Dysoxylum cauliflorum* (Meliaceae), was restricted to 850 m. According to the Whitmore scheme buttresses are 'uncommon' and 'small' in LMRF, and whilst at 850 m there are indeed fewer large buttresses (>200 cm), the opposite is true for small buttresses (>50<200 cm). This may be due to confusion over precisely what constitutes a buttress. Though most workers would claim to be able to recognise a buttress easily, it is not always obvious in the intermediates between trees with tall, thin buttresses and unbuttressed trees with fluted trunks. In this study a buttresss was defined as 'a continuous longitudinal projection of the surface of the bole which distorts the cross-sectional shape from circular or oval, which is most pronounced at the base and which progressively merges with the bulk of the trunk with increasing height'. This definition certainly included some trees which others might have considered to have fluted trunks, and as this intermediate morphology is particularly prevalent in the Myrtaceae which is most abundant at 850 m the degree of buttressing, *sensu* Whitmore, may have been over estimated.

In the Whitmore classification large woody climbers are 'often abundant' in LRF and there are 'ususally none' in LMRF. The abundance of large woody climbers is very variable in LRF, and though Ashton (1964a) stated that they were not a prominent feature of Bornean dipterocarp forests, at Danum 2% of individuals (≥ 10 cm dbh) were lianas (Green 1992), and none was recorded in dipterocarp forest at Mulu (Proctor *et al* 1983a). On Bukit Belalong lianas were 0.6% of individuals ≥10 cm dbh at 200 m, 0.6% at 500 m and 1.2% at 850 m. Liana distribution is highly clumped and as abundance may be related to previous large scale disturbance which is no longer readily apparent (Campbell & Newbery 1992) it may not be a good character with which to distinguish forest formations.

Grubb (1974) rejected the use of stature in forest classification because of the great variation within each formation and the considerable overlap between formations. This is undoubtedly the case at the regional level, but in a transect on a single mountain the stature of a stand can be very useful for its classification. For example, the LMRF forests at the summit of Gunung Silam described by Proctor *et al* (1988) are readily distinguished from LMRF at lower altitude by their reduced height.

Martin (1977) described an altitudinal sequence of forests on Gunung Mulu (2378 m), 70 km south-west of Bukit Belalong, and the lower montane forests he describes between 820 m and 1180 m show some similarities with the LMRF on Bukit Belalong. The Gunung Mulu plots are located along a ridge system and some differences might be expected between them and the Belalong LMRF plots which are located on slopes. Grubb & Tanner (1976) noted the influence of topography on upper montane forest structure and floristics in Jamaica, though Edwards (1977) found no such differences in lower montane forest in New Guinea. Ashton (1964a) enumerated fifty 0.4 ha plots in the Belalong area, ranging from the banks of the Belalong river south of Kuala Belalong to ridge-tops at 650 m north of Bukit Belalong. In his ordination the slope and ridge plots clustered separately, but clustering was tighter in the ridge samples because of the greater variability of the slopes which were uneven and include small spurs and hollows. At low altitudes (up to 500 m) ridge forest was denser than on slopes and had taller trees and higher basal area, whilst at the higher altitudes the slopes supported taller forest than the ridges. Profile diagrams from the ridges at 550 m and 650 m showed clear differences, with smaller, twisted trees with more irregular crowns at 650 m. Leaf size tended to be reduced on the higher ridge-tops. These ridge-top forests are also less species-rich than those at lower altitude, but some low altitude species (eg *Shorea laevis*) were found there, though they did not grow as tall at 650 m as they did at 550 m. These narrow ridges have shallow soils which were described as shale lithosols by Ashton and the differences between the forests seem to be due more to the edaphic conditions than an altitudinal effect.

Martin (1977) described the ridges on Gunung Mulu as very narrow, sometimes only 4 m wide, with steep sides in excess of 35°. Aerial surveys indicated that trees in the valleys had larger crowns (and were probably taller) than those on the ridges, and it is likely that this is also the case on Bukit Belalong, though no trees were measured outside the plots.

The lower-altitude facies of LMRF on Gunung Mulu was termed 'FGM' (Martin 1977) because of the high basal area of the Fagaceae, Guttiferae and Myrtaceae, but at the lowest site in this forest type (820 m) the Dipterocarpaceae had the highest basal area (18.5%). In the next plot (900 m) the basal area of the Dipterocarpaceae was reduced to 7.4% and above this their importance declined rapidly and they were not recorded above 1310 m. The LMRF from 1310-1580 m was designated LMRF (SGM) because of the importance of the Sapotaceae, Guttiferae and Myrtaceae in these plots, and the highest LMRF, 1860 m, was called FPGM because the Fagaceae, Podocarpaceae, Guttiferae and Myrtaceae were the most important families. The LMRF on Bukit Belalong can be considered analagous to the LMRF (FGM) on Gunung Mulu (despite the differences the location of the former plots on slopes and the latter on ridge-tops), because the changes in family composition between the LRF and LMRF on Bukit Belalong are similar to those found on Gunung Mulu. However, the Clusiaceae (Guttiferae) are less important on Bukit Belalong than on Gunung Mulu and the Lauraceae more important. The paucity of dipterocarps in plot 8 on Bukit Belalong (8.9 % of basal area compared with a mean of 29.0 % in plots 7 and 9) may be related to the steepness of that plot. Ashton (1964a) suggested that dipterocarps achieve their greatest abundance on level, well-drained soils.

Whilst several lowland species are found in the LMRF on Bukit Belalong this not unexpected in South East Asian LMRF (Whitmore 1984), and there are a number of common species which are indicative of the montane nature of this community. *Vatica dulitensis* (7.3% of basal area at 850 m) is characteristic of communities at 700-1350 m in Temburong (Ashton 1964b) and *Parashorea parvifolia* (3.1% of basal area) is frequent between 1000 and 1350 m in the area (Ashton 1964b). Unfortunately the third common LMRF dipterocarp (3.8% of basal area at 850 m) has not been identified. *Mallotus penangianus,* one of the indicator species of forest at 850 m on Bukit Belalong, is common between 1020 m and 1080 m on Gunung Mulu and was not recorded at lower altitudes. The other Belalong LMRF indicator species identified by Twinspan, *Lithocarpus clementianus,* was not recorded from Mulu. However it is quite possible that the same species did occur in both studies but was not been recognised as the same because of the difficulty of naming sterile Fagaceae. It is equally possible (and this applies to all the species comparisons between mountains) that a species was present, but did not occur in the sample plots. The presence of *Nageia wallichiana* (Podocarpaceae) in plot 8 on Bukit Belalong is noteworthy since the family was not recorded below 1310 m on Gunung Mulu.

The canopy heights of LMRF on Bukit Belalong and LMRF (FGM) on Gunung Mulu are similar, but density of trees and species-area curves cannot be compared since Martin used progressively smaller girth classes (33-10 cm gbh) in the higher altitude forests with smaller trees. No other physiognomic measures were made on Gunung Mulu.

The forests at 500 m on Bukit Belalong are more similar in density to those described by Martin (1977) and Proctor *et al* (1983a) from 200 m on Gunung Mulu (Proctor *et al* extended

Martin's 200 m plot from 0.4 ha to 1 ha) than are those at 200 m on Bukit Belalong. This is probably due to their ridge-top position of the Mulu plot, which is also indicated by the occurrence of the ridge-top species *Dryobalanops beccarrii* and not *D. lanceolata* which is found on low slopes (Ashton 1964b). The percentage of Dipterocarpaceae in all of these plots is high, but the Euphorbiaceae are less important in the Mulu forests than those at Belalong. Proctor *et al* (1983a) recorded c. 210 species ha^{-1} at 200 m which is similar to the estimated values for the forests at 200 m and 500 m in this study and the 231 species ha^{-1} in the 1 ha plot set up on the other side of the Belalong valley by a team from Aarhus University (Poulsen, Neilsen, Tan & Balslev 1994). Ashton (1964a) estimated that there were 90 species ha^{-1} in plots near my plots at 200 m, and the large difference is almost certainly due to inadequate identification of the non-dipterocarp species.

The Dipterocarpaceae are at their most diverse in Borneo (Ashton 1982) and by tropical standards their taxonomy has been thoroughly studied because of their commercial value. Despite this background and Ashton's extensive collections in the Belalong area there may be two undescribed dipterocarp species (one *Vatica*, one *Hopea*) in the Belalong LMRF plots (P.S. Ashton, personal communication). Confirmation of the taxonomic status of these trees will depend on the collection of fertile material. Tree families of lesser economic importance have not been studied in such detail, but make a large contribution to the species-richness of the Belalong forests. Ashton (1989) discussed the relative diversity of the Dipterocarpaceae and Euphorbiaceae in Borneo and the identification of new species in these families since Merrill's (1921) enumeration. Since then the combined efforts of the forestry departments of Sarawak, Sabah, Brunei and Indonesia have raised the number of dipterocarp species from 102 to 267, an increase of 162%. In the same period the species total for the Euphorbiaceae, which are generally small understorey trees of little economic importance, increased 106%, from 165 to 340. The latter figure can be compared with the current total of 371 species of Euphorbiaceae in the flora of the Malaya Peninsula where the total number of spermatophyte species is thought to be c. 7,500 (Whitmore 1973), whilst the estimated total number of spermatophytes in Borneo is between ten and fifteen thousand (Ashton 1989).

Altitudinal zonation in South East Asia

Quantitative descriptions of altitudinal zonation in Malaysia and the Philippines are also available for Gunung Kinabalu, 4101 m (Kitayama 1992), Gunung Jerai, 1200 m (Kochummen 1982), Mount Maquiling, 1055 m (Brown 1919) and Gunung Silam, 884 m (Proctor *et al* 1988). These mountains cover a wide range of situations. Two, Gunung Silam in Sabah and Gunung Jerai in West Malaysia, are isolated coastal mountains, whilst the others are all inland. Mount Maquiling (also called Mount Makiling) is an isolated volcanic peak on Luzon, in the Philippines and Gunung Kinabalu, Sabah, like Gunung Mulu, is a large mountain in the midst of a range of smaller mountains. The accounts from these contrasting mountains illustrate the altitudinal range of occurrence of the different montane formations and this is summarised in Table 3.10.

Montane forest is found at particularly low altitudes on the coastal mountains, and though Mount Maquiling is an inland mountain its isolated position in a low area results in a frequent cloud cap which causes depression of the altitudinal zonation. Bukit Belalong is the highest peak in an area consisting of rugged hills and ridges up to 700 m and is therefore not a particularly isolated peak. This lack of isolation ensures that there is no compression of altitudinal zonation relative to the much higher Gunung Mulu. The highest limits of LRF in the region are found on Gunung Kinabalu (1200 m), but further afield LRF can be found at 1500 m on the largest mountains in New Guinea (Whitmore 1984). The range of occurrence of montane forests on these mountains exemplifies variation in altitudinal zonation on tropical mountains and the importance of a cloud cap in depressing the limits of the Formations.

The Dipterocarpaceae extend from the LRF into the lower parts of LMRF on all these

Table 3.10. The altitudinal distribution of lowland rain forest (LRF), lower montane rain forest (LMRF) and upper montane rain forest (UMRF), and the highest recorded occurrence of dipterocarps on selected mountains in South East Asia.

	Summit altitude (m)	Maximum altitude for dipterocarps (m)	Altitudinal limits of forest formation (m)		
			LRF	LMRF	UMRF
Gunung Silam[1]	884	700	280-540	610-884	-
Bukit Belalong[2]	913	880	60-750	750-913	-
Mount Maquiling[3]	1055	600	200-600	600-900	900-1055
Gunung Jerai[4]	1200	870	150-210	480-1140	1140-1200
Gunung Mulu[5]	2376	1350	220-700	820-1860	1930-2070
Gunung Kinabalu[6,7]	4101	2000	600-1200	1400-2000	2350-2600

1, Proctor *et al* (1988); 2, This study; 3, Brown 1919; 4, Kochummen (1982); 5, Martin (1977); 6, Wood & Meijer (1964); 7, Kitayama (1992).

mountains, though the precise limits of zonation on Gunung Jerai are rather unclear. Symington (1943) classified mountain vegetation in Malaya into Lowland Dipterocarp Forest (0-300 m), Hill Dipterocarp Forest (300-750 m), Upper Dipterocarp Forest (750-1200 m), Montane Oak-Laurel forest (1200-1500 m) and Montane Ericaceous Forest (>1500 m). It was however accepted that the altitudinal limits of these Formations were variable and were lower on coastal hills and isolated mountains. The first two formations in this sequence are equivalent to LRF, the second two to LMRF and the Ericaceous Forest is UMRF (Whitmore 1984). Hill Dipterocarp Forest is distinguished from Lowland Dipterocarp Forest by the presence of *Shorea curtisii* and Upper Dipterocarp Forest is distinguished from Hill Dipterocarp Forest by the presence of *S. platyclados* and *S. ovata*. Burgess (1969) disputed the division of LRF into two formations because he considered *S. curtisii*-dominated forests to be an edaphic climax of LRF found on ridges and spurs. It should be noted that *S. curtisii* is much less frequent in Bornean dipterocarp forests and has not been found above 400 m in Brunei (Ashton 1964b).

Kochummen (1982) found *S. curtisii* from 150 m to 750 m on Gunung Jerai and *S. ovata* from 480 m to 780 m and could not distinguish the Hill and Upper Dipterocarp forests and thus the boundary between LRF and LMRF is unclear. The status of the 'Montane Myrtaceous Forest' in the Whitmore classification is not clear, but it may be analagous to the stunted LMRF found at the highest altitudes on Gunung Silam. In the absence of data on leaf sizes it is not possible to decide whether the myrtaceous forest on Gunung Jerai is LMRF or UMRF *sensu* Whitmore.

Analogues of Symington's Montane Oak-Laurel Forest can be found on Mount Maquiling (*Quercus-Neolitsea* association), Gunung Mulu (LMRF-FGM) and Gunung Kinabalu (LMRF), but not on Gunung Silam or Gunung Jerai. On the coastal mountains the Fagaceae and Lauraceae are relatively unimportant at higher altitude and the Myrtaceae are much more abundant than on the inland mountains. It may be that the altitudinal compression on coastal mountains favours the Myrtaceae, and leads to differences between inland upper LMRF and coastal upper LMRF. Grubb (1974) noted that on the largest mountains in New Guinea few species are found in more than two formations, whereas on smaller mountains more species are able to persist in three or more formations. On Java the woody and herbaceous flora of forests on high mountains are distinct from those of low altitude forests (Van Steenis 1972). For example, *Albizia lopantha* is found between 1100 m and 3100 m, but is only found on mountains at least 2500 m high, and is not recorded from those with a lower summit (Van Steenis 1972).

Apart from Proctor *et al* (1988) all of the studies discussed derived their classification primarily from the floristic data and the physiognomic differences between the forests were discussed in relation to this classification. The physiognomic differences between LRF and LMRF may be comparatively slight, and it may be necessary to use floristic data to clarify the affinities of low altitude LMRF, as was the case on Bukit Belalong.

Conclusions

The forest around the summit of Bukit Belalong is a lower montane rain forest and is similar floristically and structurally to forests at a similar altitude on Gunung Mulu. It is concluded that in the absence of a cloud cap on Bukit Belalong there is no compression of the zonation as has been observed on small coastal mountains, such as Gunung Silam.

CHAPTER 4. THE PRODUCTION AND DISAPPEARANCE OF LITTER

Introduction

Litterfall studies have been widely used to investigate production and nutrient cycling in lowland and montane tropical forests. Nutrient use efficiency, defined as the amount of organic matter fixed per unit of nutrient taken up, can be increased by either fixing more carbon per unit of nutrient, or reabsorbing more nutrients from senescing tissues. The latter has been described as 'within-stand cycling' (Vitousek 1984). Efficient within-stand nutrient cycling indicates that nutrients may be limiting primary production, while inefficient cycling suggests that the trees are not limited by nutrient supply. In practice it is extremely difficult to measure the pools and fluxes of nutrients in a complex ecosystem such as a tropical forest and less satisfactory measures have been employed (reviewed by Grubb 1989). A commonly used estimation of nutrient-use efficiency is the ratio between the dry mass of litterfall and its nutrient content. Forests on fertile soils tend to produce more litter with higher nutrient concentrations than forests on less fertile sites (Vitousek & Sanford 1986). Analysis of litterfall is more appropriate to investigations of nutrient limitation than the analysis of fresh leaves because litterfall integrates the effects of nutrient and energy reabsorption during leaf senescence (Grubb 1977).

Reduced rates of decomposition in montane forests have been suggested as a cause of restricted nutrient supply (Edwards & Grubb 1977; Marrs *et al* 1988; Heaney & Proctor 1989) which reduces their production relative to lowland forests. This chapter describes a litterfall study and two measures of litter decomposition on Bukit Belalong.

Materials and methods

Small litterfall was collected from 8 May 1991 to 8 May 1992 in plots 1-6 and 7 May 1991 to 7 May 1992 in plots 7-9. The litter traps consisted of baskets made of perforated metal sheeting, with a horizontal area of 40 cm x 40 cm, mounted on poles 1.2 m above the ground. There were thirteen litter traps placed in a restricted random design in each plot. It was difficult to collect litterfall at regular intervals because of the remoteness of the sites, but collections were usually at 14-20 day intervals. Two collections (9-10 December 1991 and 5-6 April 1992) were after 12 days and two other collections were after 36 days (26-27 June 1991) and 39 days (17-18 January 1992).

The litter traps were emptied into cotton bags and the litter was air dried within two days of collection. Alternate collections (eleven out of nineteen) were sorted into four fractions, following the recommendations of Proctor (1983): leaves (including stipules), small wood (twigs with diameter <2 cm, and bark fragments smaller than 2 cm along their longest dimension), reproductive parts and trash (any plant fragments with a longest dimension smaller than 2 mm and faeces, insect bodies and resin). The sorted samples were weighed and combined to give bulked samples of the litterfall fractions for each collection from each plot. The bulked samples were ground and a 20-g sub-sample dried at 105 °C before chemical analysis. When the total mass of the bulked sample was less than 20 g the entire sample was oven dried. Unsorted collections were oven dried at 105 °C and weighed.

Litter was collected from the litter layer in each plot during 22 August to 20 September 1991 and again between 3 and 23 March 1992. Collections were made at random points in ten sub-plots chosen randomly from those which did not contain a litter trap. Disturbance of the litter layer on the steeper slopes was unavoidable, so care was taken not to enter these sub-plots unnecessarily. The same sampling pattern was used for all the plots. At each point all the small litter was removed from a 50 cm x 50 cm quadrat and the slope was measured so that a correction could be made for the reduction in horizontal area because of the slope. The litter was sorted and dried as above, except that the trash fraction was discarded because of the difficulty in distinguishing small litter fragments from soil organic matter.

A decomposition-bag experiment was set up to make an additional measure of decomposition. It was not possible to obtain sufficiently large quantities of freshly fallen leaves from two species, so at a site at c. 200 m altitude mature, fully expanded leaves were collected from five individuals of *Ixora* sp (Rubiaceae), and five-pole sized individuals of *Shorea laevis*. *Ixora* sp. is a conspicuous understorey shrub which is common at low altitudes and *Shorea laevis* is an emergent dipterocarp which is found up to at least 650 m on Bukit Belalong. The leaves were air dried and c. 2 g was weighed accurately into 15 cm x 15 cm bags made of plastic netting with 2 mm mesh. No large holes were made in the mesh. Fifteen bags of leaves of each species were pegged out at random points in each plot. After 100 d the bags were collected and air dried to halt decomposition. The air dried leaves were oven dried at 105 °C for 24 h and weighed. Duplicate samples of leaves of each species were kept for chemical analysis of undecomposed material, and they were analysed by the following techniques which were also used for analysis of the litter.

0.4 g of each sub-sample was digested in 4.4 ml of a sulphuric acid/hydrogen peroxide mixture with a selenium catalyst (Moore & Chapman 1986). Samples were digested at 100 °C for 20 min, followed by 2 h at 370 °C. Analyses for potassium and magnesium were made by atomic absorption spectrophotometry on a Perkin Elmer 3100 AAS using an air/acetylene flame and 1% lanthanum chloride was added to the samples for magnesium analysis to act as a releasing agent (Allen 1989). Calcium was measured by atomic absorption spectrophotometry on an Instrumentation Laboratory 257 Spectrophotometer with a nitrous oxide/acetylene flame with potassium chloride added at 1000 mg l^{-1} as an ionisation buffer (Allen 1989). Phosphorus was measured manually on the digests on a Pye Unicam SP6-350 spectrophotometer by the ascorbic acid/molybdenum blue method (Allen 1989). Nitrogen was determined as ammonium in the digests on a Tecator FIAstar 5000 flow injection analysis system using Tecator ammonium indicator (5000-0295).

It was not practicable to analyse all the samples in duplicate so the precision of the method was tested by analysing five replicates of eight samples. The results were always within 10%

of the mean and usually within 5%. A foliar standard supplied by E.V.J. Tanner was also analysed and the results obtained agreed closely with the supplied values for nitrogen (-3% of supplied value), calcium (-4%) and magnesium (+3%), but the results for phosphorus (-14%) and for potassium (+15%) agreed less well.

The data were analysed on Minitab. Log transformation was applied to the litterfall rate data, but not to the nutrient element concentration data which were found to be normally distributed. The percentage mass losses in the decomposition bags were arcsine transformed before analysis.

Results

Litterfall and litter layer mass

The estimated mean annual rate of total litterfall was 10.6 t ha^{-1} yr^{-1} at 200 m, 10.5 t ha^{-1} yr^{-1} at 500 m and 8.3 t ha^{-1} yr^{-1} at 850 m (Table 4.1). The reduction at 850 m was significant (two-way ANOVA, $p<0.05$). The corresponding rates of leaf litterfall were 7.9 t ha^{-1}, 7.9 t ha^{-1} and 6.0 t ha^{-1} and the value for 850 m was also significantly lower (two-way ANOVA, $p<0.05$). The rates for small wood, flowers and fruits and trash litterfall did not differ significantly between altitudes. The proportions of litter in each of the four fractions was similar at all altitudes. At 850 m there were no significant differences between plots in rates of litterfall for any fraction, but at both 200 m and 850 m some significant differences were found. The masses of the litterfall fractions for each litter trap in the eight collections which were not sorted (from a total of nineteen) were estimated by multiplying the mean proportion of each fraction in the preceding and following collections (both sorted) by the total mass of litter in the litter trap in the unsorted collection.

Total small litterfall was unevenly distributed through the year and a large peak was found at all altitudes during April and May 1992 (Figure 4.1). Leaf litterfall (Figure 4.2) corresponded closely to total litterfall at 200 m and 500 m plots, but followed it less closely

Table 4.1. Estimated rate of small litterfall (t ha^{-1} yr^{-1}) in each of three plots at three altitudes on Bukit Belalong, Brunei. The values are the means ±95% confidence limits based on nineteen collections over 366 d from thirteen litter traps (area 0.16 m^2) in each plot and the means ± 95% confidence limits for all thirty-nine litter traps at each altitude. Eleven of the collections were sorted into the four fractions and the values for the fractions are extrapolations over the whole collection period. Where differences are significant ($p<0.05$, from two-way ANOVA on log transformed data) this is indicated by letters (a-b for differences between plots at each altitude and x-y for differences between altitudes).

Plot	Rate of litterfall (t ha^{-1} yr^{-1})				
	Leaves	Small wood (<2cm diameter)	Flowers & fruits	Trash	Total
1	7.63 ±0.99 ab	1.86 ±0.65	0.54 ±0.18	0.49 ±0.12 ab	10.53 ±1.48
2	7.44 ±0.43 a	2.05 ±1.59	0.39 ±0.15	0.33 ±0.06 a	10.21 ±1.82
3	8.69 ±0.80 b	1.55 ±0.52	0.51 ±0.31	0.51 ±0.10 b	11.27 ±1.09
1-3	7.88 ±0.44 y	1.76 ±0.57	0.47 ±0.12	0.44 ±0.06	10.56 ±0.80 y
4	7.94 ±0.68 b	1.85 ±0.52	0.47 ±0.16 ab	0.36 ±0.07	10.61 ±0.64 b
5	6.79 ±0.62 a	1.18 ±0.36	0.76 ±0.37 b	0.48 ±0.11	9.21 ±0.86 a
6	8.81 ±0.76 b	1.71 ±1.04	0.36 ±0.10 a	0.53 ±0.20	11.41 ±1.65 b
4-6	7.89 ±0.46 y	1.60 ±0.40	0.53 ±0.14	0.46 ±0.08	10.48 ±0.69 y
7	5.86 ±0.44	1.09 ±0.31	0.54 ±0.23	0.36 ±0.08	7.85 ±0.61
8	6.00 ±0.82	1.38 ±0.55	0.73 ±0.70	0.53 ±0.29	8.63 ±1.50
9	6.17 ±0.98	1.48 ±0.44	0.41 ±0.13	0.32 ±0.07	8.39 ±1.27
7-9	6.02 ±0.41 x	1.32 ±0.24	0.53 ±0.22	0.40 ±0.10	8.26 ±0.63 x

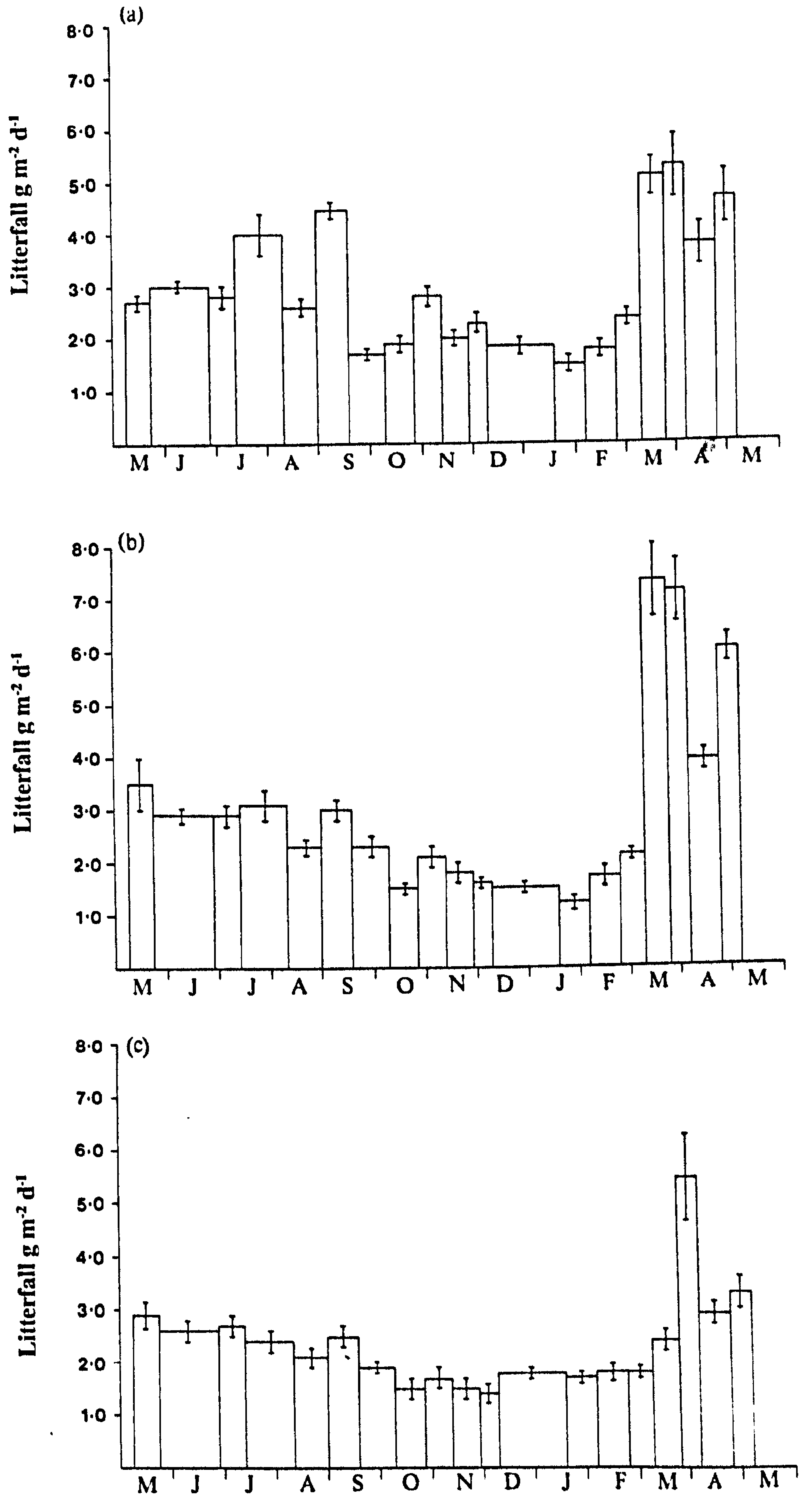


Figure 4.1. Total small litterfall (g m^{-2} d^{-1}) from May 1991 to May 1992 at (a) 200 m, (b) 500 m and (c) 850 m on Bukit Belalong, Brunei. The error bars are the 95% confidence intervals.

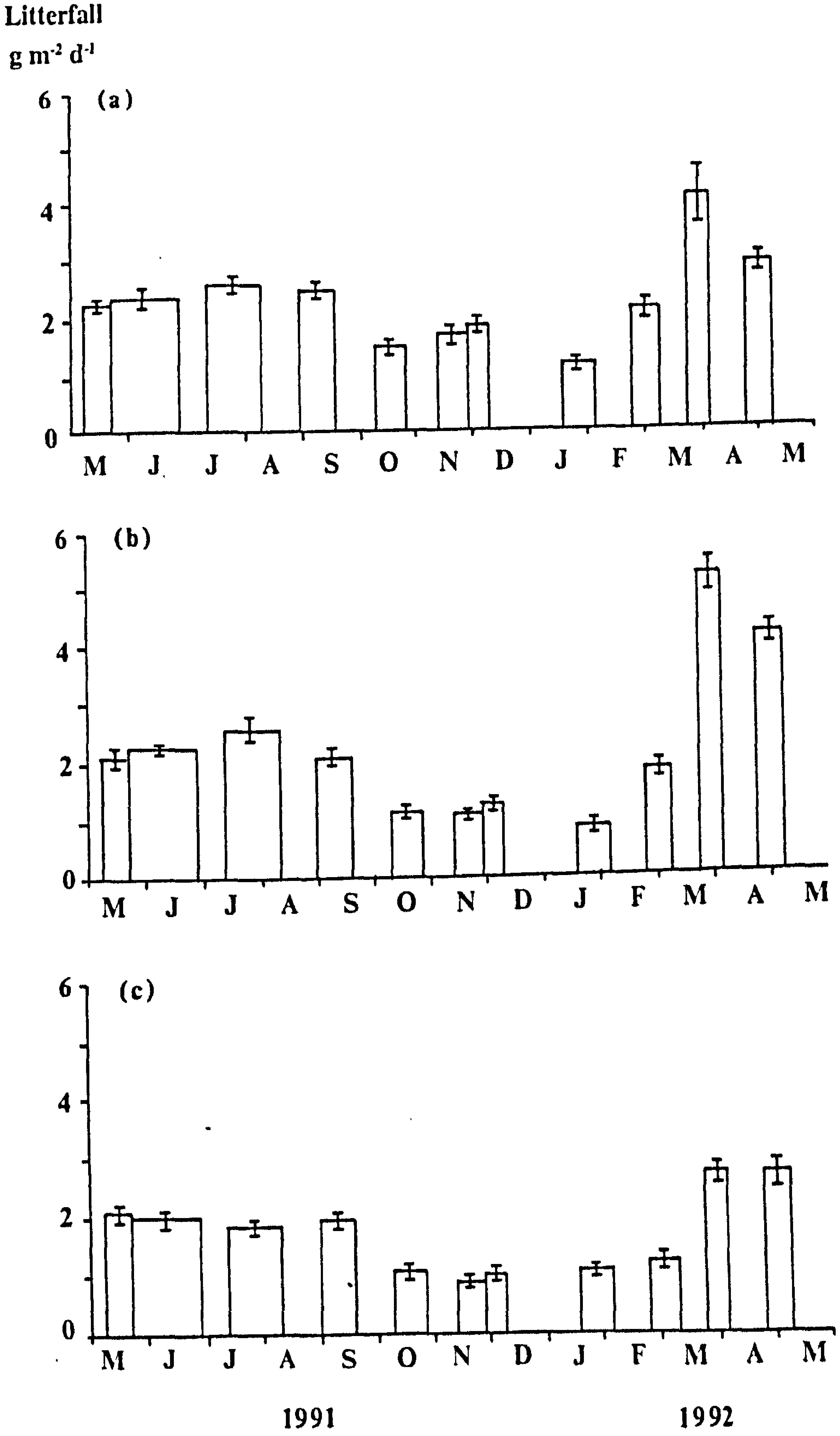


Figure 4.2. Leaf litterfall (g m^{-2} d^{-1}) from May 1991 to May 1992 at (a) 200 m, (b) 500 m and (c) 850 m on Bukit Belalong, Brunei. Eleven collections out of a total of nineteen were sorted. The error bars are the 95% confidence intervals.

at 850 m where the April peak in total litterfall was greatly increased by the collection of a single *Castanopsis spinosa* fruit which comprised 37% of the mass of litter collected from plot 8 at that sampling time. The maximum rates of leaf litterfall, in April 1992, were 1.85 times higher than the mean annual rate at 200 m, 2.35 times higher at 500 m and 1.65 times higher at 850 m.

In May 1992 there was a peak in reproductive parts litterfall at 200 m and 500 m (Figure 4.3), because of a mass flowering of forest trees, including dipterocarps, whereas the April peak at 850 m was due to a single fruit, as noted above.

Table 4.2 gives the masses of the small litter layer on two occasions in each plot and the data are summarised in Table 4.3. The mean total mass of the small litter layer is estimated at 5.17 t ha^{-1} at 200 m, 6.10 t ha^{-1} at 500 m and 5.16 t ha^{-1} at 850 m. The mass of the leaf litter layer was similar at all altitudes and the high total mass of small litter at 500 m is due to the high mass of small wood litter. Values of the litter decomposition quotient, k_L (annual input of small litter/litter layer mass) are given in Table 4.4. There was a general trend towards lower k_L at higher altitudes, but this was only significant for small wood and flowers and fruits.

Nutrients in the litterfall and litter layer

Table 4.5 shows the mean concentrations of nutrient elements in the small litterfall. High concentrations of nitrogen and phosphorus were found in the reproductive and trash fractions compared with leaves and small wood. Potassium was highest in reproductive parts and lowest in small wood. Calcium and magnesium did not show a consistent pattern among litterfall fractions. Significant differences in litterfall nutrient concentrations were found among plots at each altitude and among altitudes. When altitudinal differences in nutrient concentration were significant the highest values were always found at 200 m and the lowest values were mostly found at 500 m. The largest differences found were among

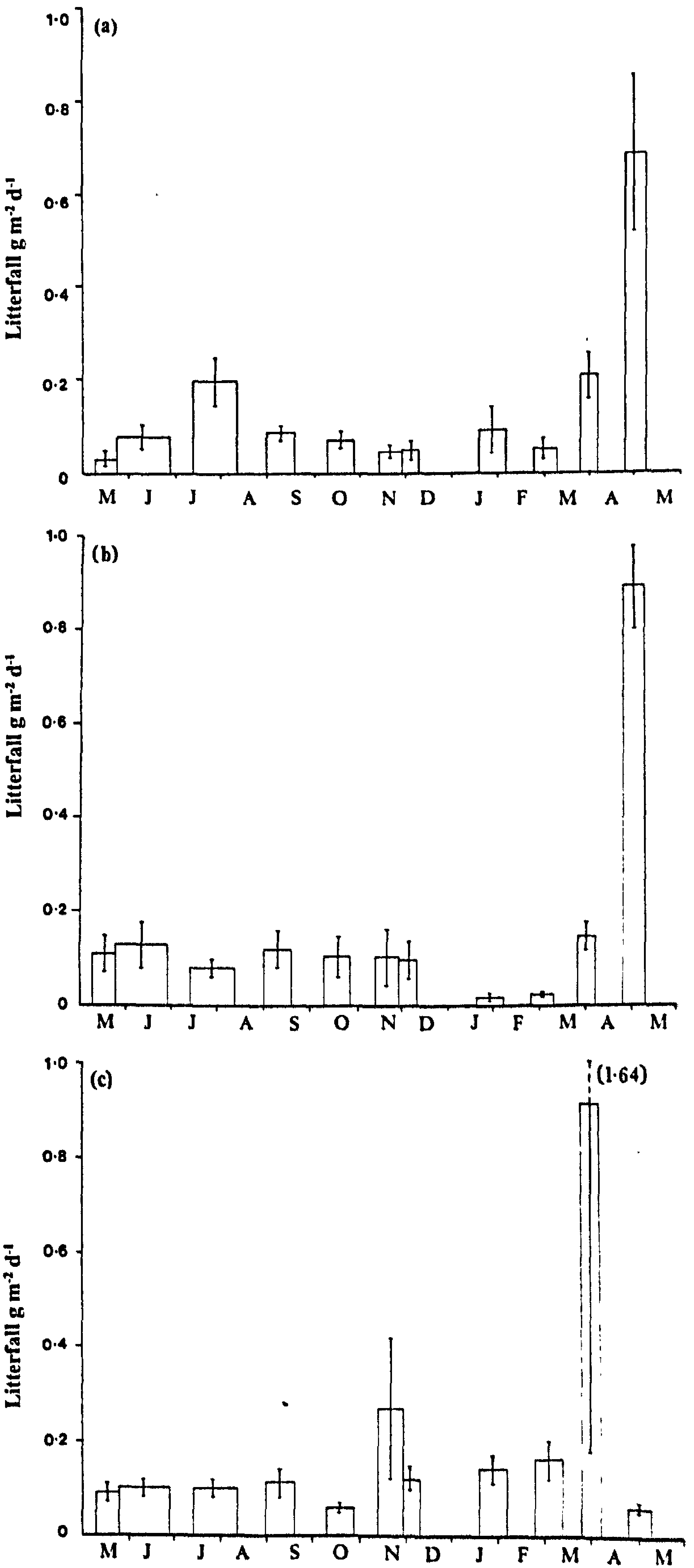


Figure 4.3. Reproductive parts litterfall (g m^{-2} d^{-1}) from May 1991 to May 1992 at (a) 200 m, (b) 500 m and (c) 850 m on Bukit Belalong, Brunei. Eleven collections out of a total of nineteen were sorted. The error bars are the 95% confidence intervals.

Table 4.2. Estimated mass (t ha^{-1}) of small litter layer at two sampling times in three plots at each of three altitudes on Bukit Belalong, Brunei. Values are the means ±95% confidence limits of ten 0.25 m^2 quadrats per plot and all 30 quadrats at each altitude.

Plot	Collection date	Small litter layer (t ha^{-1})			
	Collection 1	Leaves	Small wood (<2cm diameter)	Flowers & fruits	Total
1	4 Sep 1991	4.24 ±0.72	1.71 ±0.77	0.09 ±0.08	6.05 ±0.75
2	4 Sep 1991	4.23 ±0.60	2.17 ±0.56	0.05 ±0.05	6.45 ±0.86
3	4 Sep 1991	4.22 ±0.72	1.53 ±0.51	0.05 ±0.05	5.80 ±0.98
1-3		4.23 ±0.34	1.81 ±0.33	0.06 ±0.03	6.10 ±0.45
4	20 Sep 1991	3.67 ±0.52	2.89 ±0.82	0.04 ±0.03	6.59 ±0.78
5	20 Sep 1991	3.97 ±0.87	2.92 ±2.04	0.03 ±0.03	6.92 ±2.77
6	19 Sep 1991	3.84 ±0.90	3.25 ±1.18	0.03 ±0.03	7.12 ±1.71
4-6		3.82 ±0.40	3.02 ±0.73	0.03 ±0.01	6.88 ±0.98
7	22 Aug 1991	4.25 ±1.58	1.10 ±0.47	0.51 ±0.71	5.86 ±1.74
8	28 Aug 1991	3.38 ±0.87	1.89 ±1.22	0.28 ±0.22	5.55 ±1.75
9	23 Aug 1991	3.89 ±0.88	1.64 ±0.61	0.23 ±0.18	5.76 ±1.12
7-9		3.84 ±0.60	1.54 ±0.44	0.34 ±0.23	5.72 ±0.79
	Collection 2				
1	3 Mar 1992	2.36 ±0.43	2.29 ±1.21	0.03 ±0.06	4.68 ±1.38
2	3 Mar 1992	2.28 ±0.43	1.48 ±0.77	0.03 ±0.03	3.80 ±0.92
3	4 Mar 1992	2.22 ±0.29	1.97 ±1.03	0.05 ±0.04	4.24 ±1.12
1-3		2.29 ±0.20	1.94 ±0.53	0.04 ±0.02	4.24 ±0.60
4	19 Mar 1992	2.77 ±0.27	2.53 ±0.98	0.02 ±0.03	5.33 ±0.99
5	19 Mar 1992	2.57 ±0.29	2.67 ±0.78	0.07 ±0.07	5.31 ±0.85
6	8 Mar 1992	2.50 ±0.75	2.83 ±1.28	0.01 ±0.01	5.33 ±1.96
4-6		2.61 ±0.25	2.67 ±0.52	0.03 ±0.03	5.32 ±0.68
7	23 Mar 1992	2.28 ±0.51	2.10 ±1.07	0.24 ±0.18	4.63 ±1.32
8	22 Mar 1992	2.23 ±0.43	1.04 ±0.33	0.17 ±0.19	3.44 ±0.42
9	9&21 Mar 1992*	2.46 ±0.78	3.18 ±2.22	0.09 ±0.03	5.72 ±2.49
7-9		2.33 ±0.30	2.11 ±0.80	0.17 ±0.08	4.60 ±0.90

* Half of the second collection from plot 9 was made on the 9 March 1992 and half on 21 March.

Table 4.3. Summary of small litter layer mass (t ha^{-1}) in three plots at each of three altitudes on Bukit Belalong, Brunei. Values are the means of the data in table 4.3.

Plot	Small litter layer (t ha^{-1})			
	Leaves	Small wood (<2cm diameter)	Flowers & fruits	Total
1	3.30	2.30	0.06	5.37
2	3.26	1.83	0.04	5.13
3	3.22	1.75	0.05	5.02
1-3	3.26	1.96	0.05	5.17
4	3.22	2.71	0.03	5.96
5	3.27	2.80	0.05	6.12
6	3.17	3.04	0.02	6.23
4-6	3.22	2.85	0.03	6.10
7	3.27	1.60	0.38	5.25
8	2.81	1.47	0.23	4.50
9	3.18	2.41	0.16	5.74
7-9	3.09	1.83	0.26	5.16

Table 4.4. The values of the decomposition quotient k_L (mean annual mass of litterfall/mean mass of small litter layer) for three plots at each of three altitudes on Bukit Belalong, Brunei. Where the mean values are significantly different ($p<0.05$, from ANOVA) between altitudes this is indicated by superscripts.

Plot	Decomposition quotient (k_L)			
	Leaves	Small wood (<2cm diameter)	Flowers & fruits	Total
1	2.31	0.81	9.00	1.87
2	2.28	1.12	9.75	1.93
3	2.70	0.89	10.20	2.14
1-3	2.43	0.94^{b}	9.65^{b}	1.96
4	2.47	0.68	15.67	1.72
5	2.08	0.42	15.20	1.43
6	2.78	0.56	18.00	1.76
4-6	2.44	0.55^{a}	16.29^{c}	1.64
7	1.79	0.68	1.42	1.43
8	2.13	0.94	3.17	1.80
9	1.94	0.61	2.56	1.40
7-9	1.95	0.74^{a}	2.38^{a}	1.52

Table 4.5. The mean concentrations (mg g^{-1}) of nitrogen, phosphorus, potassium, calcium and magnesium in the small litterfall collected from three plots at each of three altitudes on Bukit Belalong, Brunei. The values are the means of the data for each plot and each altitude ±95% confidence limits. n=eleven for the means of each plot and n=33 for the means at each altitude. Where differences were significant ($p<0.05$, from two-way ANOVA) this is indicated by letters (a-c for differences between plots at each altitude, x-z for differences between altitudes).

Plot	Mineral element concentration (mg g^{-1})				
	Nitrogen	Phosphorus	Potassium	Calcium	Magnesium
Leaves					
1	10.67 ±0.46 a	0.309 ±0.018	5.62 ±1.25	7.54 ±0.87 c	2.76 ±0.37
2	12.52 ±0.54 b	0.340 ±0.018	6.33 ±0.91	5.93 ±0.45 b	3.04 ±0.24
3	10.99 ±0.70 a	0.328 ±0.030	6.36 ±0.74	4.20 ±0.21 a	3.08 ±0.17
1-3	11.40 ±0.41	0.325 ±0.013 y	6.10 ±0.52	5.89 ±0.57 y	2.96 ±0.15 z
4	10.20 ±0.31 a	0.245 ±0.017	5.61 ±0.76	1.86 ±0.15 a	1.56 ±0.10 a
5	10.82 ±0.31 b	0.243 ±0.017	5.64 ±0.84	2.13 ±0.15 b	1.59 ±0.08 a
6	10.77 ±0.45 b	0.271 ±0.029	6.35 ±0.66	1.98 ±0.15 ab	2.35 ±0.13 b
4-6	10.60 ±0.21	0.253 ±0.012 x	5.86 ±0.41	1.99 ±0.09 x	1.83 ±0.14 x
7	11.58 ±0.44 b	0.353 ±0.034 b	5.64 ±0.75 b	1.99 ±0.11 a	2.08 ±0.20 a
8	10.54 ±0.31 a	0.328 ±0.023 ab	4.77 ±0.56 ab	2.60 ±0.34 b	3.05 ±0.32 b
9	11.71 ±0.45 b	0.292 ±0.020 a	4.14 ±0.49 a	1.69 ±0.06 a	2.32 ±0.03 a
7-9	11.27 ±0.28	0.324 ±0.016 y	4.85 ±0.38	2.09 ±0.17 x	2.48 ±0.19 y
Small wood					
1	7.32 ±0.62	0.201 ±0.024	3.09 ±0.64	9.51 ±1.29 c	3.38 ±0.33 b
2	8.41 ±1.35	0.251 ±0.066	4.18 ±1.02	7.09 ±1.53 b	2.27 ±0.40 a
3	7.92 ±0.65	0.220 ±0.031	3.70 ±0.68	4.33 ±0.23 a	2.43 ±0.23 a
1-3	7.88 ±0.50	0.224 ±0.024 y	3.66 ±0.44 y	6.97 ±0.96 y	2.69 ±0.24 y
4	6.65 ±0.54 a	0.154 ±0.025	2.67 ±0.41	1.71 ±0.21 a	1.19 ±0.19 a
5	8.00 ±0.62 b	0.183 ±0.033	2.88 ±0.53	2.11 ±0.29 b	1.62 ±0.14 b
6	6.81 ±0.80 a	0.162 ±0.023	2.56 ±0.74	1.78 ±0.20 a	1.53 ±0.27 b
4-6	7.15 ±0.40	0.166 ±0.015 x	2.70 ±0.30 x	1.86 ±0.14 x	1.44 ±0.12 x
7	7.36 ±1.03	0.223 ±0.037	2.49 ±0.48	1.85 ±0.19 b	1.57 ±0.20 b
8	7.46 ±0.64	0.190 ±0.026	2.24 ±0.59	2.10 ±0.33 b	1.53 ±0.27 b
9	8.09 ±0.54	0.220 ±0.048	2.40 ±0.41	1.40 ±0.18 a	1.11 ±0.10 a
7-9	7.64 ±0.41	0.211 ±0.020 y	2.38 ±0.26 x	1.78 ±0.16 x	1.40 ±0.13 x

Table 4.5 continued.

Plot	Mineral element concentration (mg g^{-1})				
	Nitrogen	Phosphorus	Potassium	Calcium	Magnesium
Flowers & fruits					
1	16.40 ±3.53	1.013 ±0.248	6.02 ±1.39	6.30 ±1.30 b	2.81 ±0.52
2	18.31 ±2.53	0.959 ±0.099	7.14 ±2.64	3.98 ±0.90 a	2.47 ±0.39
3	18.53 ±3.48	1.100 ±0.170	8.62 ±0.96	3.77 ±1.35 a	2.68 ±0.49
1-3	17.75 ±1.68 y	1.024 ±0.096 y	7.26 ±1.00	4.68 ±0.74 y	2.66 ±0.25 y
4	14.70 ±2.39	0.785 ±0.150	6.47 ±1.16	1.75 ±0.30 a	1.72 ±0.27 a
5	16.01 ±1.74	0.860 ±0.127	5.71 ±0.92	2.44 ±0.42 b	2.22 ±0.40 b
6	17.26 ±2.52	0.991 ±0.169	6.98 ±0.90	1.73 ±0.17 a	2.16 ±0.27 b
4-6	15.99 ±1.21 xy	0.879 ±0.082 y	6.39 ±0.55	1.97 ±0.20 x	2.03 ±0.18 x
7	14.02 ±1.43	0.769 ±0.105	6.28 ±0.86 b	1.54 ±0.29	1.83 ±0.24 ab
8	13.82 ±3.36	0.740 ±0.127	7.05 ±1.74 b	1.23 ±0.33	2.17 ±0.42 b
9	13.26 ±1.47	0.672 ±0.125	4.00 ±0.78 a	1.28 ±0.26	1.63 ±0.18 a
7-9	13.70 ±1.17 x	0.727 ±0.070 x	5.78 ±0.77	1.35 ±0.16 x	1.88 ±0.17 x
Trash					
1	20.98 ±1.14	0.888 ±0.125	3.45 ±0.52	6.36 ±0.33 b	1.96 ±0.29
2	20.67 ±1.41	0.835 ±0.088	3.78 ±0.55	5.77 ±1.21 b	2.35 ±0.27
3	20.70 ±2.09	0.820 ±0.099	3.96 ±0.68	4.33 ±0.48 a	2.17 ±0.22
1-3	20.78 ±0.82 y	0.848 ±0.055 y	3.73 ±0.31	5.49 ±0.50 y	2.16 ±0.15 z
4	18.08 ±1.47	0.693 ±0.130	3.12 ±0.65	2.12 ±0.38	1.13 ±0.25
5	15.61 ±2.06	0.606 ±0.143	3.12 ±0.50	2.45 ±0.61	1.21 ±0.25
6	17.88 ±1.99	0.604 ±0.146	3.22 ±0.83	1.91 ±0.80	1.32 ±0.32
4-6	17.19 ±1.03 x	0.634 ±0.073 x	3.15 ±0.34	2.16 ±0.33 x	1.22 ±0.14 x
7	19.24 ±0.92	0.793 ±0.067	3.74 ±0.44 b	2.16 ±0.43	1.55 ±0.15
8	17.81 ±1.11	0.768 ±0.106	3.00 ±0.51 a	2.51 ±0.58	1.69 ±0.19
9	17.36 ±1.57	0.694 ±0.071	2.92 ±0.31 a	1.79 ±0.44	1.48 ±0.12
7-9	18.14 ±0.69 x	0.751 ±0.045 y	3.22 ±0.26	2.15 ±0.27 x	1.58 ±0.09 y

calcium concentrations with high concentrations in all fractions from 200 m and particularly in samples from plot 1, where concentrations of calcium in the soil were particularly high (Chapter 2). Litterfall from 500 m had the lowest concentrations of phosphorus except for the reproductive parts fraction in which the lowest concentrations were in litter from 850 m. The values in Table 4.5 were multiplied by the annual litterfall rates (Table 4.1) to make an estimate of the annual addition of nutrient elements to the forest floor via the small litterfall (Table 4.6). Leaves were by far the most important pathway for small litterfall nutrient accession. The quantities of elements returned to the forest floor were greatest at 200 m and least at 850 m and the values for the 500 m plots were more similar to those at 850 m than the plots at 200 m except for potassium which was significantly lower at 850 m.

Nutrient concentrations in the small litter layer followed a similar pattern to concentrations in fine litterfall, with the highest concentrations at 200 m (Table 4.7). The mineral element quotients, k_E, (annual input of element in litterfall/quantity of element in small litter layer) were generally highest at 200 m and lowest at 850 m, except for calcium for which the opposite trend was found (Table 4.8). The values of k_E were higher than the corresponding decomposition quotients, k_L, except for calcium in plots 1, 2 and 3 and nitrogen in plots 1 and 8. However the overall values for nitrogen k_E at each altitude were similar to or higher than the corresponding k_L values.

Nitrogen and phosphorus concentrations were higher in the *Shorea laevis* leaves than in the *Ixora* leaves, calcium and magnesium concentrations were similar, but the potassium concentration was much higher in the *Ixora* leaves (Table 4.9). There were no significant differences (two-way ANOVA) in weight loss among the altitudes (Table 4.10), but weight loss was significantly greater in the *Shorea laevis* leaves. The species x altitude interaction was not significant.

Discussion

Table 4.6. The estimated masses of nitrogen, phosphorus, potassium, calcium and magnesium (kg ha^{-1} yr^{-1}) returned to the forest floor in the small litterfall in three plots at each of three altitudes on Bukit Belalong, Brunei. The values are the means of the data for each altitude with the ranges in parentheses. n=3 for each mean. Significant differences ($p<0.05$, from one-way ANOVA) between altitudes are indicated by letters.

Altitude	Mass of element in litterfall kg ha^{-1} yr^{-1}				
	Nitrogen	Phosphorus	Potassium	Calcium	Magnesium
Leaves					
1	90.02 y (81.41-95.50)	2.58 (2.36-2.85)	48.41 y (42.88-55.27)	46.05 y (36.50-57.53)	23.48 (21.06-26.77)
2	83.11 xy (73.47-94.88)	1.99 (1.65-2.39)	46.26 y (38.30-55.94)	15.56 x (14.46-17.44)	14.63 (10.80-20.70)
3	67.78 x (63.24-72.25)	1.95 (1.80-2.07)	29.07 x (25.54-33.05)	12.56 x (10.43-15.60)	14.93 (12.19-18.30)
Small wood					
1	14.38 (12.28-17.24)	0.41 (0.34-0.51)	6.68 y (5.74-8.57)	12.98 y (6.71-17.69)	4.90 y (3.77-6.29)
2	11.13 (9.44-12.30)	0.26 (0.22-0.28)	4.24 xy (3.40-4.94)	2.90 x (2.49-3.16)	2.24 x (1.91-2.62)
3	10.10 (8.02-11.97)	0.28 (0.24-0.33)	3.12 x (2.71-3.55)	2.33 x (2.02-2.90)	1.82 x (1.64-2.11)
Flowers & fruits					
1	8.48 (7.14-9.45)	0.49 (0.37-0.56)	3.48 (2.78-4.40)	2.29 (1.55-3.40)	1.28 (0.96-0.52)
2	8.43 (6.21-12.17)	0.46 (0.36-0.65)	3.30 (2.51-4.34)	1.10 (0.62-1.85)	1.09 (0.78-1.69)
3	7.70 (5.44-10.09)	0.41 (0.28-0.54)	3.39 (1.64-5.15)	1.75 (0.52-0.90)	1.08 (0.67-1.58)
Trash					
1	9.22 (6.82-10.56)	0.38 (0.28-0.44)	1.65 (1.25-2.02)	2.41 y (1.90-3.12)	0.95 (0.78-1.11)
2	7.83 (6.51-9.48)	0.29 (0.25-0.32)	1.44 (1.12-1.71)	0.98 x (0.76-1.18)	0.56 (0.41-0.70)
3	7.31 (5.56-9.44)	0.30 (0.22-0.41)	1.29 (0.93-1.59)	0.89 x (0.57-1.33)	0.64 (0.47-0.90)
Total					
1	122.1 y (114.2-127.8)	3.86 y (3.69-4.17)	60.23 y (53.57-67.42)	63.73 y (47.34-81.74)	30.61 y (29.01-33.01)
2	110.5 xy (102.6-122.2)	3.00 x (2.81-3.34)	55.24 y (47.53-64.54)	20.54 x (19.52-22.12)	18.53 x (14.98-24.80)
3	92.89 x (90.38-95.22)	2.94 x (2.62-3.18)	36.87 x (31.67-40.50)	16.54 x (13.60-20.73)	18.48 x (15.45-22.89)

Table 4.7. The mean concentrations of nitrogen, phosphorus, potassium, calcium and magnesium (mg g^{-1}) in the small litter layer in three plots at each of three altitudes on Bukit Belalong, Brunei. The values are the means of two collections in each plot and the means ±95% confidence limits for all six values at each altitude.

Plot	Concentration of element (mg g^{-1})				
	Nitrogen	Phosphorus	Potassium	Calcium	Magnesium
Leaves					
1	12.51	0.365	5.07	7.98	2.36
2	13.11	0.390	4.84	7.38	2.44
3	12.24	0.360	5.68	6.14	2.72
1-3	12.62 ±1.84	0.372 ±0.030	5.20 ±0.77	7.16 ±0.90	2.51 ±0.19
4	11.12	0.260	3.73	2.26	1.51
5	12.89	0.290	3.44	2.28	1.52
6	12.18	0.310	4.10	2.00	1.63
4-6	12.06 ±1.13	0.287 ±0.043	3.75 ±0.60	2.18 ±0.18	1.55 ±0.14
7	12.86	0.355	5.41	2.04	1.48
8	13.36	0.365	3.52	2.47	2.92
9	13.32	0.270	2.60	1.45	1.62
7-9	13.18 ±0.88	0.330 ±0.057	3.84 ±1.44	1.98 ±0.51	2.00 ±0.79
Small wood					
1	8.04	0.180	2.02	9.43	2.59
2	8.55	0.200	2.75	5.93	1.69
3	8.08	0.190	3.06	5.95	1.87
1-3	8.22 ±0.49	0.190 ±0.023	2.61 ±.60	7.10 ±1.94	2.05 ±0.46
4	6.90	0.170	1.23	1.82	1.07
5	6.30	0.115	1.07	1.65	0.97
6	6.42	0.180	2.32	1.55	1.30
4-6	6.54 ±0.33	0.155 ±0.036	1.54 ±0.65	1.67 ±0.16	1.11 ±0.17
7	8.24	0.195	2.16	1.31	1.08
8	7.76	0.190	1.09	2.03	1.74
9	6.59	0.100	0.92	0.86	0.76
7-9	7.53 ±1.8	0.162 ±.055	1.39 ±0.67	1.40 ±.60	1.19 ±0.47

Table 4.7. continued.

Plot	Concentration of element (mg g^{-1})				
	Nitrogen	Phosphorus	Potassium	Calcium	Magnesium
Flowers & fruits					
1	8.15	0.365	8.11	4.36	1.40
2	10.85	0.495	5.76	3.60	2.12
3	10.92	0.695	9.14	4.09	3.02
1-3	9.97 ±2.79	0.518 ±0.190	7.67 ±2.99	4.01 ±1.34	2.18 ±1.27
4	6.97	0.405	7.31	0.62	0.88
5	11.49	0.440	2.41	1.56	1.19
6	9.48	0.425	4.15	1.76	1.34
4-6	9.31 ±2.15	0.423 ±0.017	4.62 ±3.33	1.31 ±0.63	1.13 ±0.33
7	6.16	0.455	3.69	0.81	0.80
8	6.23	0.285	2.50	0.69	1.10
9	6.44	0.265	2.14	0.65	0.54
7-9	6.27 ±1.11	0.335 ±0.163	2.77 ±0.97	0.72 ±0.10	0.81 ±0.28

Table 4.8. The values of the mineral element quotient, k_E (annual input of element in litterfall/ mean standing crop in small litter layer) for nitrogen, phosphorus, potassium, calcium and magnesium and the decomposition quotient, k_L (annual small litterfall/ litter layer mass) in three plots at each of three altitudes and the mean value at each altitude on Bukit Belalong, Brunei.

Plot	Mineral element quotient (k_E)					k_L
	Nitrogen	Phosphorus	Potassium	Calcium	Magnesium	
1	1.72	2.00	2.37	1.63	2.09	1.87
2	2.00	2.06	2.78	1.72	2.54	1.93
3	2.17	2.46	2.71	1.49	2.62	2.14
1-3	1.95	2.16	2.61	1.64	2.41	1.96
4	1.83	1.98	3.37	1.53	1.98	1.72
5	1.58	1.95	3.20	1.55	1.86	1.43
6	1.93	1.96	3.12	1.90	2.63	1.76
4-6	1.78	1.97	3.24	1.65	2.19	1.64
7	1.45	1.66	1.74	1.60	2.17	1.43
8	1.66	2.02	3.05	1.92	2.00	1.80
9	1.51	2.10	2.84	1.92	2.35	1.40
7-9	1.52	1.88	2.35	1.76	2.08	1.52

Table 4.9. The concentrations (mg g^{-1} dry matter) of nitrogen, phosphorus, potassium, calcium and magnesium in mature leaves of *Shorea laevis* and *Ixora* sp. collected on Bukit Belalong, Brunei. The values are the means of two analyses. Variation between the two analyses were always within 5%.

	Nutrient concentration (mg g^{-1})				
	N	P	K	Ca	Mg
Shorea laevis	16.8	0.64	4.2	6.0	2.0
Ixora sp.	12.0	0.47	13.6	5.4	3.3

Table 4.10. The percentage loss of dry weight of *Shorea laevis* and *Ixora* sp.leaves in decomposition bags at three altitudes on Bukit Belalong, Brunei. The values are the means ± 95% confidence limits.

	Shorea laevis		*Ixora* sp.	
Altitude	n	% loss	n	% loss
200	30	46.3 ±5.4	32	37.5 ±2.4
500	31	51.1 ±7.9	41	34.8 ±2.5
850	26	47.1 ±4.7	25	32.8 ±1.8

Rates of litterfall

The litterfall rates at 200 m and 500 m are high compared with other South East Asian lowland forests (Table 4.11), but are within the range of values reported. The litterfall rate at 850 m is the highest yet found in any montane forest (Table 4.12) in which measurements have been made for a full year (the study on Gunung Mulu reported in Proctor *et al* 1983c lasted only sixteen weeks).

Plant production might be expected to be higher at intermediate elevations (Janzen 1973) for the following reasons: dry spells are rarer and trees are not defoliated; cloudy conditions in the middle of the day ameliorate the harsh conditions that produce a midday photosynthetic depression; reduced decomposition buffers nutrient release and reduces leaching (Terborgh 1977). On Bukit Belalong there is no evidence of increased net primary production (nor larger insect communities; N. Maudsley, personal communication) at intermediate elevations. No other litterfall study at a range of altitudes on a single mountain has used replicated plots so elevated production at intermediate altitude has never been satisfactorily demonstrated.

Increased rates of litterfall following dry weather, as in this study, are commonly reported (Bruijnzeel 1984, Edwards 1977, Gong & Ong 1983 and Proctor *et al* 1989), but in other studies peak litterfall has been found in the middle of the dry season (Scott *et al* 1992) or wet season (Proctor *et al* 1983; Tanner *et al* 1992), whilst in the high altitude montane forests in the Colombian Andes, litterfall peaks were related not to rainfall but to hail storms (Veneklaas 1992). The largest increases in leaf litterfall at the time of the April peak were recorded in the plots at 500 m which are all situated close to the crest of a ridge. A similar effect was reported from New Guinea where lower montane forest ridge sites also had a more seasonal pattern of litterfall than sites on slopes or in a valley (Edwards 1977). By contrast, Tanner (1980) found no difference in litterfall seasonality between ridge and slope sites in Jamaican montane forests. Though January to March are generally the driest months in Brunei, the rainfall for these months in 1992 was exceptionally low and may have caused more litterfall,

Table 4.11. Small litterfall (t ha^{-1} yr^{-1}), altitude and rainfall in South East Asian lowland rain forests. '-' indicates that no data are available.

			Litterfall (t ha^{-1} yr^{-1})					
Location	Altitude (m)	Rainfall (mm)	Total	Leaves	Wood	Flowers & fruits	Trash	Forest type
Brunei, Belalong[1].	200	4100	10.6	7.9	1.8	0.5	0.4	LRF
	500	4100	10.5	7.9	1.6	0.5	0.5	LRF
Malaya, Pasoh[2].	100	2100	8.9	6.4	1.5	0.3	0.4	LRF
Malaya, Pasoh[3].	100	2100	9.2	6.8	-	-	-	LRF
Malaya, Pasoh[4].	100	2100	10.6	6.3	-	-	-	LRF
Malaya, Penang[5].	70-130	3400	7.5	5.4	-	-	-	LRF (coastal ridge)
Sabah, Danum[6].	120-150	2500	11.5	6.6	2.3	0.4	2.2	LRF
Sabah, Silam[7].	280	2100	6.5	3.9	1.5	0.2	1.0	LRF on ultrabasic
	330	2100	7.4	4.5	1.9	0.2	0.8	LRF on ultrabasic
	480	2100	5.2	3.4	0.8	0.2	0.8	LRF on ultrabasic
Sarawak, Mulu[8].	50	5000	11.5	6.6	2.4	0.4	2.1	LRF (alluvial)
	200	5000	8.9	5.4	2.1	0.3	1.1	LRF
	200	5000	9.2	5.6	2.2	0.3	1.1	Heath forest
	300	5000	12.0	7.3	3.0	0.1	1.6	Forest on limestone
	500	5100	10.9	6.7	2.3	0.5	1.4	LRF
Sumatra, Ketambe[9]. (site 5)	350	4000	11.0	7.3	-	-	-	LRF
(site 9)	350	4000	11.5	6.7	-	-	-	LRF
(site 13)	350	4000	9.8	6.5	-	-	-	LRF
(site 17)	450	4000	8.1	5.3	-	-	-	LRF

1, This study; 2, Lim (1978); 3, Gong (1972); 4, Ong *et al* (1980); 5, Gong & Ong (1983); 6, Burghouts (1993); 7, Proctor *et al* (1989); 8, Proctor *et al* (1983b); 9, Van Schaik & Mirmanto (1985).

Table 4.12. Small litterfall ($t\ ha^{-1}\ yr^{-1}$), altitude, rainfall and mean canopy height in tropical montane rain forests. '*' indicates that the value is for 'non-woody litter' and '-' that no data are available.

Location	Altitude	Rainfall	Litterfall ($t\ ha^{-1}\ yr^{-1}$)					Canopy height	Forest type
	(m)	(mm)	Total	Leaves	Wood	Flowers & fruits	Trash	(m)	
Brunei, Belalong[1].	850	5000	8.3	6.0	1.3	0.5	0.4	25-30	LMRF
Java, Cibodas[2].	1600	3460	6.0	4.5	1.1	0.4	-		LMRF
Java, Pringombo[3].	650	4600	6.8	5.4	-	-	-		LMRF
New Guinea, Kerigomna,[4].	2500	4000	7.3	6.4*	1.0	-	-	27-33	LMRF
Sabah, Silam[5].	610	c. 2500	5.6	4.1	0.9	0.1	0.5	20-25	LMRF on ultrabasic
	790	c. 2700	5.5	3.7	0.9	0.1	0.8	10-15	LMRF " "
	870	2700	4.8	3.3	0.9	0.1	0.5	10-12	LMRF " " (stunted)
Sarawak, Mulu[6].	1310	5600	11.0	5.7	3.2	0.4	1.7	9-15	UMRF
	1860	5700	3.6	2.3	0.6	0.1	0.6	6-13	UMRF
Colombia, Cordillera Central[7].	2550	2100	7.0	4.6	1.1	0.7	0.5	25	LMRF
	3370	1500	4.3	2.8	0.8	0.3	0.2	22	UMRF
Costa Rica, Volcán Barva[8].	100	c. 4000	9.0	7.6*	1.4	-	-		LRF
	1000	c. 5000	6.6	5.5*	1.1	-	-	30-35	LMRF
	2000	c. 3400	5.8	4.8*	1.0	-	-	20-25	LMRF
	2600	c. 3300	5.3	4.6*	0.7	-	-	20-23	LMRF
Costa Rica, Monteverde[9].	1500	2300	7.0	4.8	0.9	0.7	0.6	15-30	LMRF
Jamaica, Blue Mountains[10].	1500	2200	6.6	4.9*	1.5	-	-	5-7	UMRF (mor ridge)
	1500	2200	5.7	5.5*	0.2	-	-	8-13	UMRF (mull ridge)
	1500	2200	5.6	4.4*	1.2	-	-	8-13	UMRF (slope)
	1500	2200	6.5	5.5*	0.9	-	-	12-16	LMRF (col)

Location	Altitude (m)	Rainfall (mm)	Litterfall (t ha^{-1} yr^{-1})					Canopy height (m)	Forest type
			Total	Leaves	Wood	Flowers & fruits	Trash		
Panama, Gigante peninsula[11].	60	2600	11.8	-	-	-	-	30-35	LRF
Panama, Cordillera Central[11].	1200	3900	7.3	-	-	-	-	10-15	LMRF
Puerto Rico, Luquillo[12].	1000	5000	3.1	2.4	0.3	-	0.4	5	UMRF
Venezuela,Andes Occidentales[13].	2300	1500	7.0	3.4	2.5	1.1	-	-	LMRF
Venezuela, Sierra Nevada[14].	2500	2500	4.3	-	-	-	-	10	UMRF

1, This study; 2, Yamada (1976); 3, Bruijnzeel (1984); 4, Edwards (1977); 5, Proctor *et al* (1989); 6, Proctor *et al* (1983c); 7, Veneklaas (1992); 8, Heaney & Proctor (1989); 9, Nadkarni & Matelson (1992); 10, Tanner (1980); 11, Cavelier (1989); 12, Weaver *et al* (1986); 13, Grimm & Fassbender (1981b); 14, Tanner *et al* (1992).

particularly at 500 m. During the peak period of leaf loss several large trees were deciduous, which is not usually seen in the Belalong forests (D. Edwards, personal communication), but widespread defoliation of the forest did not occur.

Some litterfall studies lasting for longer than two years at the same site have found considerable variation in the litterfall rates among years: the greatest difference is a 1.9-fold difference found by Blasco and Tassy (1975) in an Indian montane forest.

The peak in flower and fruit litterfall in the low and mid plots during April 1992 was due to a mass flowering of the forest involving both dipterocarps and also many non-dipterocarp trees. Peak dipterocarp flowering following dry weather has been recorded from several lowland forests (Ashton *et al* 1988; Burgess 1972; Ng 1977; Toy *et al* 1992 and Whitmore 1984). Ng (1977) suggested that the stimulus to flowering is not the lack of rain during a dry spell, but the increase in solar radiation that is associated with clear weather. Though dipterocarps are present in the top plots no peak of flowering was recorded there despite the higher solar radiation during that period.

Decomposition

Rates of decomposition are regulated by three groups of variables: the physicochemical environment, the resource quality and the nature of the animals and micro-organisms which comprise the decomposer community. Their efects have been ranked in the order macroclimate> microclimate> resource quality> organisms (Anderson & Swift 1983). Resource quality (i.e. chemical composition of litterfall) varies only slightly between the altitudes on Bukit Belalong and microclimatic conditions will be the most important factor in determining rates of decomposition.

Of the available methods, k_L values are the most frequently used to compare litter disappearance between different forests (Anderson & Swift 1983), but they need to be evaluated critically. The calculation of k_L assumes that the litter layer is in equilibrium, but

k_L is prone to distortion because it combines the rate of litterfall and the litter layer mass which are both subject to annual and seasonal variation, so if either is markedly atypical, k_L will be unreliable. For example, Proctor *et al* (1989) did not report k_L from Gunung Silam because the calculated values were very low following the severe drought of January to April 1983. The drought apparently caused considerable premature leaf loss prior to sampling, resulting in a very high litter-layer mass during the time of the study when the rate of litterfall was low because susceptible leaves had already been shed.

k_L calculations assume the simple exponential disappearance of litter in which the absolute rate of decomposition decreases linearly as decay proceeds. Soluble components and easily degraded compounds such as starches and proteins are rapidly utilised, while more recalcitrant substances such as cellulose and tannins are lost at slower rates. This may be unrealistic and the double exponential decay model has been proposed as a more explicit statement of the two-step nature of decomposition. In it, litter is assumed to consist of a labile and a non-labile fraction, which each have a separate k (Wieder & Lang 1982).

The k_L values for flowers and fruits (Table 4.4) at 200 m and 500 m are high, and indicate turnover times as low as nineteen days. Whilst the resource quality of the reproductive fraction of litter in the LMRF is lower because of the more frequent woody fruits from trees of the Fagaceae, the large differences in quotients can be considered an artefact of the sampling programme. A large part of the flower and fruit fall in the LRF occurred after the litter layer mass was measured for the second time and thus was not included in the denominator of the calculation of k_L. More frequent sampling of the litter layer would be necessary to make an accurate estimate of k_L for this rapidly decomposing fraction whose input is unevenly distributed both temporally and spatially. The values for litter layer mass and k_L in the LRF are typical for lowland forests (Table 4.13), but the values at 850 m are high for montane forests and are only exceeded in the lower montane forest at 1000 m on Volcán Barva.

Table 4.13. The mass of the small litter layer and the decomposition quotient k_L in South East Asian primary lowland rain forests and montane rain forests throughout the tropics. '-' indicates that no data are available.

Location	Altitude (m)	Rainfall (mm)	Mass of litter layer (t ha^{-1})		k_L Total litter	k_L Leaf litter
			Total	Leaves		
Brunei, Belalong[1].	200	4100	5.2	3.3	2.0	2.4
	500	4100	6.1	3.2	1.6	2.4
	850	5000	5.2	3.1	1.5	2.0
Malaya, Penang[2].	70-130	3400	4.9	3.1	1.5	1.7
New Guinea, Kerigomna[3].	2500	4000	6.5	5.5	1.1	1.2
Sabah, Danum[4].	120-150	2500	-	2.4	-	2.7
Sabah, Silam[5].	280	2100	-	7.2	-	0.5
	330	2100	-	7.8	-	0.6
	480	2100	-	4.0	-	1.1
	610	c. 2500	-	6.3	-	0.7
	790	c. 2700	-	4.4	-	1.3
	870	2700	-	2.6	-	1.3
Sarawak, Mulu[6]. (a)	50	5000	5.5	3.8	1.7	1.7
(b)	200	5000	5.9	3.2	1.3	1.7
(c)	200	5000	6.1	3.9	1.3	1.4
(d)	300	5000	7.1	4.2	1.5	1.7
Costa Rica, Monteverde[7].	1500	2300	10.1	7.2	0.7	1.5
Costa Rica, Volcán Barva[8].	100	5000	3.5	2.3	2.5	3.3
	1000	5000	4.2	2.4	1.6	2.3
	2000	3400	5.2	3.3	1.1	1.5
	2600	3300	6.3	3.7	0.8	1.2
Jamaica, Blue Mountains[9]. (e)	1550	2200	-	11.1	-	0.4
(f)	1550	2200	-	11.7	-	0.5
(g)	1550	2200	-	10.3	-	0.4
(h)	1550	2200	-	8.1	-	0.7
Puerto Rico, Luquillo[10].	1000	5000	4.34	-	0.7	-

1, This study; 2, Gong & Ong (1983); 3, Edwards (1977); 4, Burghouts (1992); 5, Proctor *et al* (1989); 6, Proctor *et al* (1983) [(a) alluvial forest; (b) dipterocarp forest; (c) heath forest; (d) forest over limestone]; 7, Nadkarni & Matelson (1992); 8, Heaney & Proctor (1989); 9, Tanner (1981) [(e) mor ridge; (f) mull ridge; (g) wet slope; (h) col]; 10, Weaver *et al* (1986).

The high mineral element quotients, k_E, compared with corresponding values of k_L suggest that there was no net immobilisation of any nutrient in the litter except possibly for calcium at 200 m. It is accepted that comparisons of k_E calculations are also sensitive to distortion, but nonetheless comparisons with k_L values can be informative.

The decomposition bag technique suffers from a number of artefactual problems, due to the unnatural moisture regime within the bag, differential exclusion of fauna and the alteration of animal/microbial interactions (Anderson & Swift 1983). Despite these problems the technique is commonly used to compare the effects of species, sites and experimental manipulations on decomposition.

The results of the decomposition bag experiment do not entirely agree with the pattern of reduced decomposition in the LMRF derived from the measurement of k_L. Leaves of *Ixora* sp. tended to decompose more slowly at 850 m than 200 m and 500 m, but the differences were not significant, and no altitudinal pattern was found for the *Shorea* leaves. These results may be atypical for the Belalong forests because of the very dry period at low altitudes from January to March 1992. Tanner (1981) showed that leaf litter decomposition rates in Jamaican montane forests were higher in the wet season, but were also higher when the rainfall in the wet season was more evenly distributed. Thus it may be that the rates of decomposition were reduced more in the lowland plots than the montane plots because of the greater number of rain-free days at low altitude (Chapter 2), and the expected differences between the altitudes were not found. The higher rate of decomposition of *Shorea laevis* leaves may be due to higher nitrogen or phosphorus concentrations or both.

The effects of altitude and precipitation on decomposition have been quantified by Vitousek & Turner (1994) in a series of experiments on Mauna Loa, Hawai'i. Hawai'ian forests are unusual because of the monodominance of the tree, *Metrosideros polymorpha* (Myrtaceae), which is found in a broad range of environments from sea level to the tree line. Precipitation is dependent on aspect because of the north-easterly trade winds, and varies from c. 6000 mm

yr^{-1} on the windward side to less than 500 mm yr^{-1} on the north-west flank. Tethered (rather than bagged) *M. polymorpha* leaves, birch wood dowels and filter papers were used to measure decomposition at sites from 70 m to 2410 m on the wet east side of Mauna Loa and at two sites at 700 m on the dry north-west flank. Sites were selected on young (c. 100 years old) and old (c. 3000 years old) lava flows to test the effect of soil development on decomposition. Decomposition was reduced at higher altitudes and in the drier sites, and was correlated with substrate quality, especially phosphorus concentration. No correlation was found for nitrogen concentration. Decomposition was faster on the old flows, due to either to greater nutrient availability on the older soils or moister conditions under the less open canopy of the older forest. Temperature data from each site were used to calculate Q_{10} values (the proportional increase in decomposition for a 10 °C rise in temperature), but as precipitation is not constant over the transect (1200 to 6000 mm yr^{-1}) moisture also affects this value. The Q_{10} values for leaves were 4.0 on young lava flows and 6.2 on old flows and for wood they were 5.6 and 11.0. The Q_{10} value for Volcán Barva was calculated to be 1.9, whilst that for Bukit Belalong (using k_L for leaf litter) is 4.3.

Litterfall nutrients

The litterfall nutrient concentrations at 200 m and 500 m are typical of lowland tropical forests (Table 4.14), and likewise the litterfall nutrient concentrations at 850 m are within the ranges of values found in other lower montane forests. However, litterfall calcium concentrations at 500 m and 850 m are amongst the lowest values reported. The annual rate and seasonal distribution of litterfall at 500 m corresponded closely to those at 200 m, but the litterfall nutrient concentrations at 500 m were similar to, or lower than those at 850 m. There is no simple pattern of declining nutrient concentrations associated with reduced stature forest at higher altitudes, except for potassium though even for that element differences were only significant for small wood litterfall.

Table 4.14. The concentrations (mg g^{-1}) of nitrogen, phosphorus, potassium, calcium and magnesium in leaf litterfall from South East Asian lowland rain forests and montane rain forests throughout the tropics.

Location	Forest type	Mineral element concentration (mg g^{-1})				
		N	P	K	Ca	Mg
Brunei, Belalong[1].	LRF (200 m)	11.4	0.33	6.1	5.9	3.0
	LRF (500 m)	10.6	0.25	5.9	2.0	1.8
	LMRF	11.3	0.32	4.9	2.1	2.5
Java, Pringombo[2].	LMRF	11.2	0.55	4.8	21.6	3.9
Malaya, Pasoh[3].	LRF	11.5	0.30	3.8	7.0	2.2
New Guinea, Kerigomna[4].	LMRF	11.3	0.59	4.6	13.1	2.9
Sabah, Silam[5].	LRF (280 m)	12.6	0.26	1.4	7.5	4.0
	LRF (330 m)	10.8	0.19	1.0	6.3	3.4
	LRF (480 m)	11.2	0.19	1.6	9.1	1.7
	LMRF (610 m)	10.5	0.17	2.6	10.7	4.8
	LMRF (790 m)	10.5	0.17	1.0	6.8	3.3
	LMRF (870 m)	8.3	0.20	0.9	5.8	3.0
Sarawak, Mulu[6].	LRF (alluvial)	9.0	0.27	2.6	24	2.0
	LRF (200 m)	9.5	0.11	4.5	1.5	1.1
	LRF (500 m)	10.0	0.17	4.3	5.1	1.2
	Heath forest	5.7	0.14	2.3	8.9	1.6
	Limestone forest	12	0.38	1.6	31	3.3
Sarawak, Mulu[7].	LMRF (1310 m)	8.1	0.21	3.7	1.9	2.8
	UMRF (1860 m)	7.4	0.26	1.8	1.9	1.0
Colombia, Cordillera Central[8].	LMRF	11.1	0.74	8.9	-	-
	UMRF	7.8	0.40	3.5	-	-
Costa Rica, Monteverde[9].	LMRF	15	0.8	1.2	19.1	2.7
Costa Rica, Volcán Barva[10].	LRF (100 m)	14	0.54	2.0	8.3	1.7
	LMRF (1000 m)	11	0.45	1.4	7.2	1.9
	LMRF (2000 m)	9.0	0.54	2.2	11	1.9
	LMRF (2600 m)	6.8	0.53	3.0	10.4	2.3
Jamaica, Blue Mountains[11].	UMRF (Mor)	6.0	0.18	2.3	5.8	3.3
	UMRF (Mull)	8.4	0.25	5.9	9.1	3.2
	UMRF (Slope)	6.6	0.39	4.1	10.1	4.2
	LMRF (Col)	9.3	0.38	5.9	9.5	2.8
Puerto Rico, Luquillo[12].	UMRF	7.7	0.24	1.4	5.3	2.4
Venezuela, Andes Occidentales[13].	LMRF (2300 m)	12	0.62	5.7	7.3	2.6

1, This study; 2, Bruijnzeel (1984); 3, Lim (1978); 4, Edwards (1982); 5, Proctor *et al* (1989); 6, Proctor *et al* (1983b); 7, Proctor *et al* (1983c); 8, Veneklaas (1991); 9, Nadkarni & Matelson (1992); 10, Heaney & Proctor (1989); 11, Tanner (1980); 12, Weaver *et al* (1986); 13, Grimm & Fassbender (1981b).

Whilst montane forests throughout the tropics share many common features which distinguish them from lowland forests (see Chapter 3) comparisons between litterfall studies that are widely separated geographically and temporally are problematic because of the unrelated species (and indeed families) involved and because of the possibility of large fluctuations in litterfall from year to year. The most valuable studies are therefore those which simultaneously examine litterfall in a series of forests at different altitudes on a single mountain (i.e. the studies from Gunung Mulu, Gunung Silam, Volcán Barva and the Colombian Andes). All these studies indicate reduced nitrogen concentrations in leaf litterfall in upper montane forest and low-stature lower montane forest compared with lowland forest and tall-stature lower montane forest. Leaf litterfall potassium concentrations also generally decrease with altitude, though on Volcán Barva a slight increase was found. Phosphorus concentrations in litterfall on these mountains show no overall trend, and calcium and magnesium also vary between altitudes without any consistent pattern.

Nitrogen cycling in litterfall and concentrations of nitrogen in leaf litterfall are greater in LRF than UMRF. Lower montane forests are intermediate between the two, and tend to have lower rates of litterfall than lowland forests, but similar nitrogen concentrations.

Quantities of mineral nutrients cycled in litterfall are lower in montane forests than lowland forests (Table 4.15), and the rates of nutrient input in the small litterfall of the Belalong forests were generally high or about the middle of the ranges of equivalent forests. The rate of addition of magnesium at 200 m was high and the rates of potassium addition at 200 m and 500 m were the highest of any of the lowland forests, even after allowing for possible overestimation of potassium concentrations. The rate of nitrogen addition at 850 m was very high for lower montane forests, but rates of calcium addition were low there and at 500 m.

Replication in litterfall studies

There have been numerous litterfall studies in tropical forests (Proctor, 1984), but many of

Table 4.15. The rates of addition (kg ha^{-1} yr^{-1}) of nitrogen, phosphorus, potassium, calcium and magnesium in leaf litterfall from South East Asian lowland rain forests and montane rain forests throughout the tropics.

Location	Forest type	Rate of mineral element accession (kg ha^{-1} yr^{-1})				
		N	P	K	Ca	Mg
Brunei, Belalong [1].	LRF (200 m)	122	3.9	60	64	31
	LRF (500 m)	110	3.0	55	21	19
	LMRF	92	2.9	37	17	19
Java, Pringombo[2].	LMRF	-	3.7	35	144	25
Malaya, Pasoh[3].	LRF (1972)	119	3.2	37	82	21
	(1973)	81	2.3	26	57	16
New Guinea, Kerigomna[4].	LMRF	91	5.1	28	95	19
Sabah, Silam[5].	LRF (280 m)	85	1.5	9	56	25
	LRF (330 m)	76	1.6	7	46	23
	LRF (480 m)	60	1.8	8	47	8
	LMRF (610 m)	60	1.2	13	59	24
	LMRF (790 m)	60	1.1	5	38	16
	LMRF (870 m)	42	1.1	5	27	13
Sarawak, Mulu[6].	LRF (alluvial)	111	4.1	26	286	20
	LRF (200 m)	81	1.2	33	13	9
	Heath forest	55	1.6	18	83	12
	Limestone forest	140	4.5	16	370	33
Colombia, Cordillera Central[7].	LMRF	82	6.1	59	-	-
	UMRF	34	1.9	14	-	-
Costa Rica, Monteverde[8].	LMRF	93	5.5	12	115	15
Costa Rica, Volcán Barva[9].	LRF (100 m)	110	4.5	17	72	15
	LMRF (1000 m)	65	2.6	9	45	12
	LMRF (2000 m)	46	2.7	12	61	10
	LMRF (2600 m)	34	2.6	15	52	11
Jamaica, Blue Mountains[10].	UMRF (Mor)	39	1.3	15	34	19
	UMRF (Mull)	50	1.5	39	50	17
	UMRF (Slope)	35	2.1	21	54	21
	LMRF (Col)	59	2.4	34	55	17
Puerto Rico, Luquillo[11].	UMRF	24	0.7	4	16	8
Venezuala, Andes Occidentales[12].	LMRF (2300 m)	69	4.0	33	43	14

1, This study; 2, Bruinzeel (1984); 3, Lim (1978): 4, Edwards (1982); 5, Proctor *et al* (1989); 6, Proctor *et al* (1983b); 7, Veneklaas (1991); 8, Nadkarni & Matelson (1992); 9, Heaney & Proctor (1989); 10, Tanner (1980); 11, Weaver *et al* (1986); 12, Grimm & Fassbender (1981b).

the early studies were seriously flawed and it is difficult to make comparisons between them. Proctor (1983) suggested guidelines to ensure that future studies might produce results that would be more comparable. One of his main recommendations was that sufficient litter traps should be used to give 95% confidence limits which are within 10% of the mean for all fractions and total litterfall. In Table 4.16 the 95% confidence limits of the Belalong litterfall data are expressed as percentages of the means. It can be seen that the thirteen traps in each plot were generally sufficient only for a reasonable estimate of leaf litterfall and all thirty-nine traps at each altitude were needed to reduce the confidence limits to less than 10% of the mean for total litterfall. However, even using thirty-nine traps at each altitude the confidence limits of small wood, reproductive parts and trash litterfall still exceeded 10% of the mean and it is unrealistic to expect enough traps to be deployed to achieve this goal.

Since Proctor's (1983) recommendations experimental designs have become more rigorous, but this study and those of Tanner *et al* (1992) and Scott *et al* (1992) demonstrate the need for replication of plots. In species-rich tropical forests, plots in the same forest type are likely to have quite different specific compositions which may, in turn, cause differences in the nutrient cycling and production. Tables 4.1 and 4.5 show that different conclusions might be drawn if unreplicated plots had been studied. If, for example, plots 3, 5 and 9 were the only plots used to determine rates of litterfall (Table 4.1) it would be concluded that the rates of leaf and total litterfall did not differ significantly between 500 m and 850 m, but were significantly higher at 200 m. There were significant differences in rates of litterfall between plots at the same altitudes, and leaf litterfall in plot 5 was significantly lower than in plot 6 even though the confidence limits for each plot met Proctor's (1983) guidelines.

In view of the differences in specific composition between plots, it is unsurprising that there were differences in mineral element concentrations at the same altitude (Table 4.5). Significant differences in leaf litterfall nutrient concentrations between plots were found at at least one altitude for each of the elements studied, and leaf nitrogen and calcium were the

Table 4.16. The 95% confidence intervals of rates of litterfall expressed as percentages of the mean for four litterfall fractions and total litterfall from three plots at each of three altitudes on Bukit Belalong, Brunei.

Plot	95% confidence interval as percentage of mean				
	Leaves	Small wood	Flowers & fruits	Trash	Total
1	13	35	33	24	14
2	6	78	38	18	18
3	9	33	61	20	10
1-3	6	32	26	14	8
4	9	28	34	19	6
5	9	31	49	23	9
6	9	61	28	38	14
4-6	6	25	26	17	7
7	8	28	43	22	8
8	14	40	96	55	17
9	16	30	32	22	15
7-9	7	18	42	25	8

most variable. The data from plots 1, 4 and 9 examined in isolation would yield the conclusion that concentrations of leaf litterfall nitrogen were significantly higher in the montane forest than in the lowland forests.

Plot replication allows analysis of the significance of differences in annual nutrient addition between the three altitudes on Bukit Belalong (Table 4.6). Comparison of the ranges of nutrient addition at each altitude shows that without replicated plots the differences might be either overlooked or greatly exaggerated.

Scott *et al* (1992) measured litterfall in three plots in lowland forest in Brazil. Though no significant differences were found among rates of litterfall in the three plots, there were significant differences in litterfall nutrient concentrations among the plots. Calcium and magnesium were the most variable elements, as in the Belalong forests, and this may be because supply of these elements is not restricted and efficiency of use is not adaptive. The differences would therefore be a result of the different tree species present in the plots. Comparison of nutrient concentrations in the fresh leaves and leaf litter of six common species in the plots indicated that nitrogen, phosphorus and potassium were retranslocated prior to abscission in all species (albeit at very variable rates), but calcium and magnesium were more variable, with some species retranslocating these elements whilst others were net accumulators.

The four-year fertilisation experiment in Venezuelan UMRF described by Tanner *et al* (1992) used replicated study plots to test the effects of nitrogen and phosphorus addition. Addition of both nutrients together, but not singly, were found to significantly increase litterfall and trunk growth during the fourth year of the experiment. These conclusions could not have been drawn without the use of replicated plots.

On other tropical mountains such as Gunung Silam and Volcán Barva replication of the plots at each altitude rather than reliance on single study sites might have clarified some of the altitudinal trends. Tanner (1980) demonstrated that litterfall and nutrient cycling varied among forest types at a single altitude in Jamaica, but replication of the plots would have indicated the significance of the differences between the forest types. The variation from year to year is such that, if possible, litterfall measurements should be made for at least two years. Annual variations in rates of litterfall are not necessarily fluctuations about a mean value. Litterfall declined progressively over the four years of the Venezuelan fertilisation experiment described by Tanner *et al* (1992). No firm conclusions were drawn concerning the causes of this decline, but it was suggested that it might represent either a decline in the forest or some change in its successional status.

Conclusions

Rates of litterfall production are high in the forests on Bukit Belalong compared with similar forests, but the high rates in the lowland forests may be due in part to the low rainfall for January - March 1992. The montane forest has higher rates of litterfall than any previously measured in a montane forest. The mass of the small litter layer was similar at all altitudes, but the rate of decomposition, measured by the decomposition quotients, was lower at 850 m. The decomposition bag experiment did not indicate lower rates at 850 m, but this may have been because of the unusually dry conditions at low altitudes. Nutrient concentrations in litterfall were similar to those elsewhere, though calcium concentrations at 500 m and 850 m were low. Large quantities of nutrients are cycled in the litterfall, except for calcium at 500 m and 850 m, and there was no indication of nutrient immobilisation in litter except calcium at 200 m.

The annual rate of litterfall and its temporal distribution were very similar at 200 m and 500 m, but this is not the case for litterfall nutrient concentrations, since concentrations at 500 m are similar to or lower than those at 850 m. If nutrient limitation were important in reducing the production and stature of the lower montane forest it might be expected that litterfall nutrient concentrations would be lowest in that forest and it is therefore concluded that the litterfall study gives no evidence of nutrient limitation as a cause of the reduction in stature in the LMRF on Bukit Belalong.

Introduction

Root systems remain the most poorly known part of tropical forest ecosystems (Berish & Ewell 1988; Sanford 1989b; Whitmore 1990). They are notoriously difficult to sample (Whitmore 1984; Proctor 1987; Sanford 1989a) and there are no methods that directly assess fine root production in undisturbed soils (Mackie-Dawson & Atkinson 1991; Hendricks *et al* 1993).

Roots are only able to absorb water and nutrients during the early phase of development after elongation behind the root cap, before suberisation when the development of secondary thickening renders the root surface impermeable. Fine roots make most of the length of a root system (Persson 1980) and their importance to nutrient cycling outweighs their relatively small contribution to total root biomass (Sanford 1989a).

Fine roots are generally defined as being ≤2 mm diameter, but in this study many thicker roots did not show signs of woodiness, so the upper limit of fine roots was increased to ≤5 mm. It is accepted that some small woody roots will be included by this definition.

Fine roots can be studied by a range of techniques depending on the information required, but all methods cause some disturbance. Soil profiles can be used to describe the vertical distribution of roots and Mackie-Dawson & Atkinson (1991) have suggested that this method may have a more favourable ratio of information gained to labour expended compared with other methods. This is doubly true in most ecological studies since pits are usually dug to describe the soils. Soil coring methods provide data on root biomass in the upper layers of the soil and are frequently used to estimate production by calculating differences in biomass at sequential sampling times. The calculations require estimates of biomass and necromass at each sampling time to estimate mortality, but their use in aseasonal environments is problematic since an ecosystem with constant production and mortality will yield zero net changes. Root ingrowth bags are used to assess root responses to different treatments (Steen 1991) and sometimes for production estimates. Direct observation of living roots in rhizotrons and mini-rhizotrons can be used to assess root distribution, periodicity of growth, longevity, turnover and survival times and to compare the effects of specific treatments. Installation of the window disturbs the soil environment and conditions immediately behind it may differ from those in undisturbed soil, but Fogel (1991) suggested that direct observation techniques may be the best for studying roots in an ecosystem context.

This study uses a combination of profile descriptions, soil coring and ingrowth bags to assess fine root mass and production at three altitudes on Bukit Belalong.

Methods

The vertical distribution of fine roots (≤5 mm diameter) was quantified in the top metre of each of the nine soil profiles (Chapter 2). The face of the pit was prepared by picking away a few mm of soil to expose the cut ends of roots and a 50 cm x 50 cm wooden frame was positioned against it (Figure 5.1). The frame was divided into one hundred 25-cm^2 squares and within each of the squares the number of root endings was counted (Mackie-Dawson & Atkinson 1991). Any roots growing amongst the litter above the mineral soil were included in the top 5 cm.

In each plot ten surface-soil samples (10 cm x 10 cm x 5 cm deep) were collected to estimate bulk density (Chapter 2), and these samples were also used to estimate fine root biomass. After oven drying overnight at 105 °C the roots were separated and weighed separately. The roots were not washed, but the dry soil was easily brushed off.

Fine root production and response to added nutrients was examined using the ingrowth bag technique (Steen 1991, Green 1992). Cylindrical bags (made of loosely woven polypropylene with a 2-mm mesh) 20 cm long and 7 cm in diameter were filled with horticultural Perlite (expanded volcanic rock which provides an medium onto which nutrients can be adsorbed).

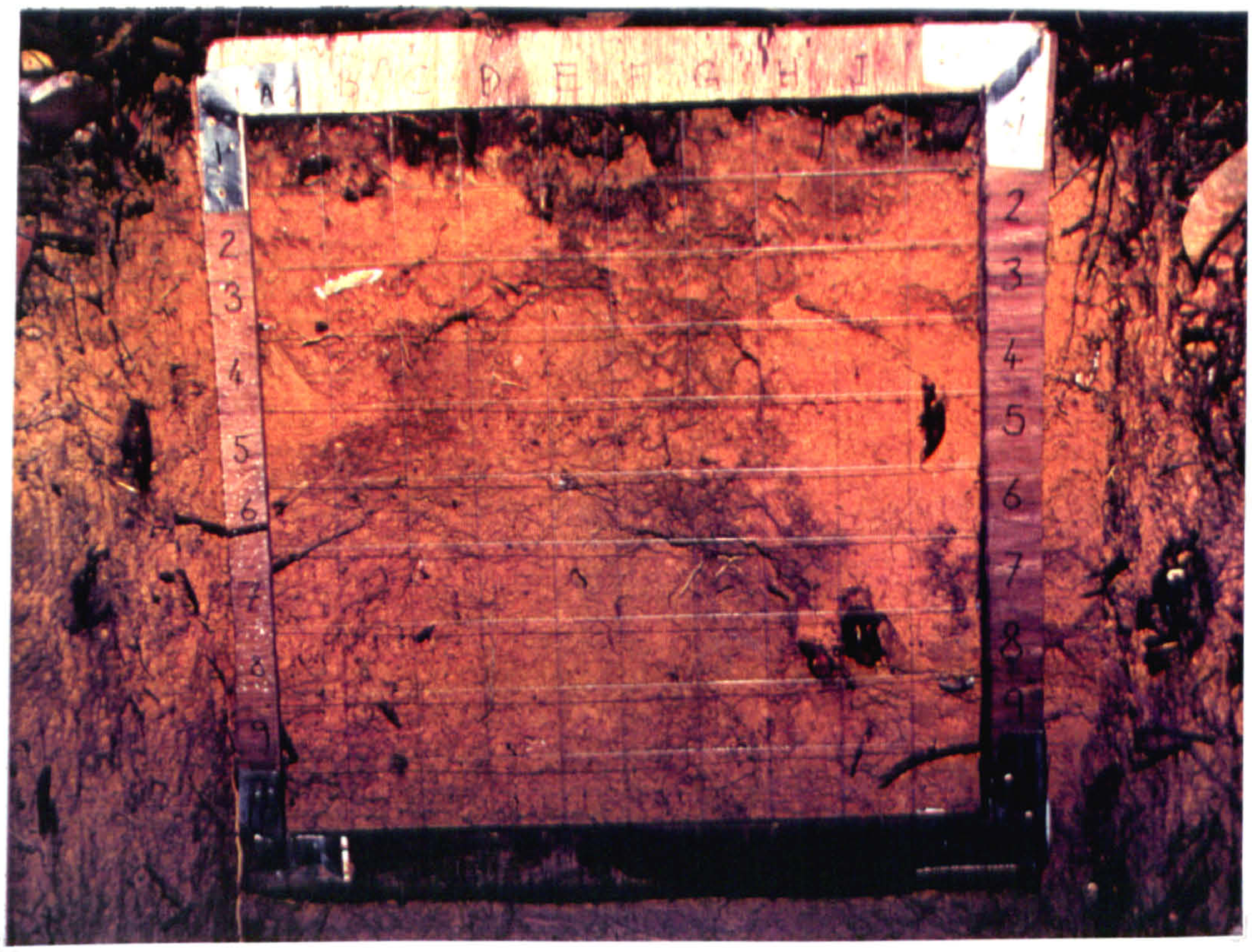


Figure 5.1. The root counting frame in soil pit at Plot 4 (480 m).

Perlite is a suitable substrate for this type of experiment because roots are easily sorted from it. Solutions of 0.1 M ammonium chloride, 0.1 M sodium dihydrogen phosphate (Cuevas & Medina 1988) and 0.1 M potassium chloride and a combined treatment of all three were made up in stream water and the bags were soaked in the solution for 48 h. A control treatment used Perlite which had been soaked in stream water only.

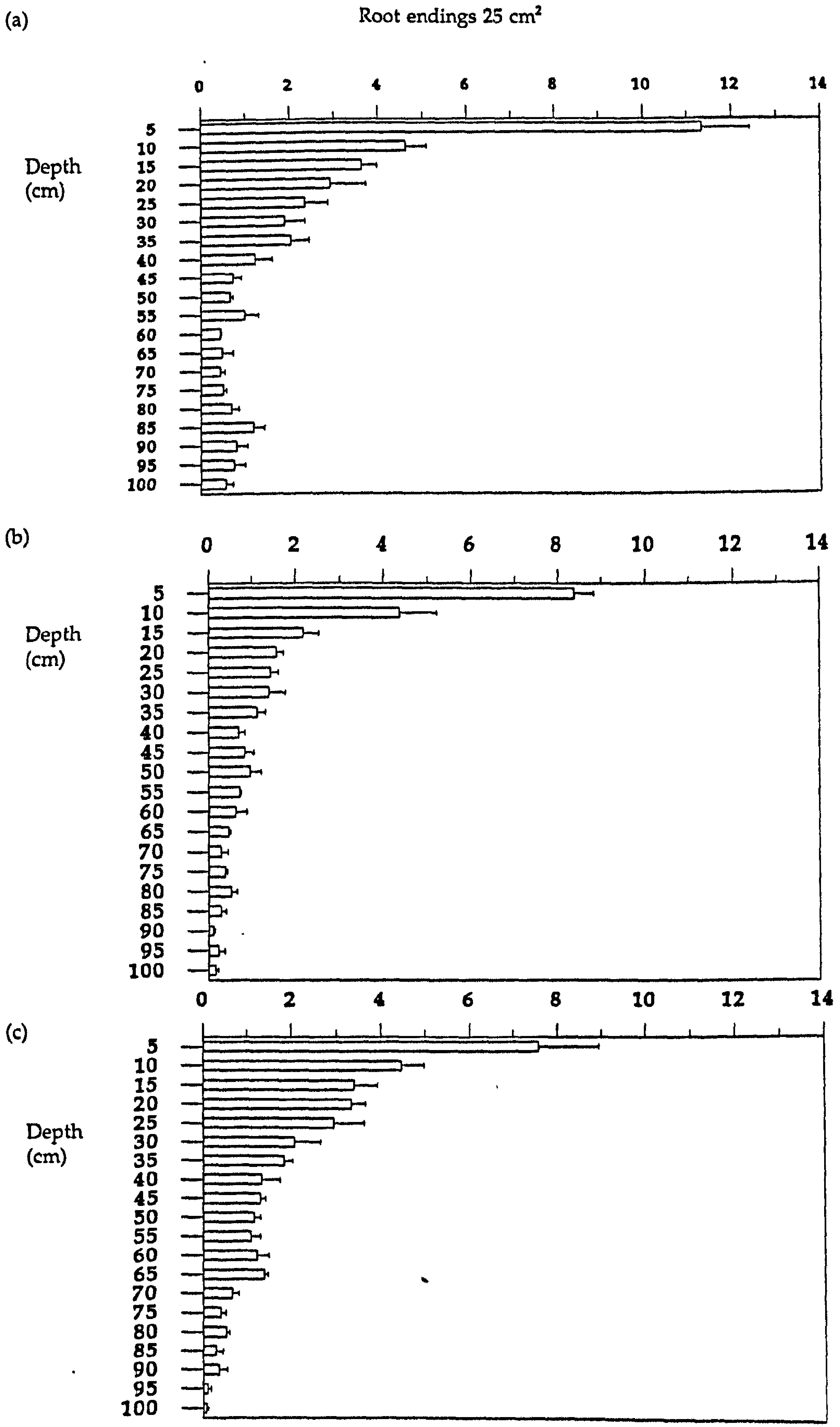
Sub-plots which were not used for litter collection (Chapter 4) were selected for the ingrowth bag experiment to minimise any effect of disturbance in the vicinity of the bags. In each sub-plot the bags were located at random points along a horizontal line but the points were reselected if they were closer than 50 cm so that it was unlikely that nutrients leached from one bag could affect another. Each bag was placed in a 20-cm deep hole which was excavated with a 7-cm diameter Edelman auger. The tops of the bags were flush with the surface of the mineral soil.

There were four replicate bags per plot but at 850 m these were supplemented by four additional bags per plot. J.J. Green (personal communication) observed loss of ingrowth bags from predation by wild pigs (*Sus barbitus* Muller) in a similar experiment in the Danum Valley, Sabah. There was evidence of much pig activity near the 850 m plots, and the extra bags were added to offset possible losses of replicates. After eight months the bags were recovered and the roots were separated from the Perlite, dried and weighed. No roots >5 mm were found in the bags.

Results

Fine roots were concentrated in the top 10 cm of the soil profiles at all altitudes (Figure 5.2). The 25 cm^3 sampling squares are not statistically independent so the standard errors were calculated using the mean values from the 5-cm deep layers in the three pits at each altitude. The mean mass of roots in the surface samples differed significantly between all three altitudes ($p<0.05$, one-way ANOVA), with the highest values at 500 m and the lowest values

Figure 5.2. The mean (±S.E.) number of root endings per 25 cm² in three soil profiles at each altitude on Bukit Belalong, Brunei. (a) 200 m; (b) 500 m; (c) 850 m.



at 200 m (Table 5.1). The values between the plots at each altitude did not differ significantly except between plots 5 (8.73 g 500 cm^{-3}) and 6 (4.68 g 500 cm^{-3}) ($p<0.01$, one way anova). The relationship between the number of root endings in the 0-5 cm layer and the mass of roots in the surface soil samples was used to estimate the biomass in the profiles from 5-100 cm (Table 5.2). This calculation depends on the assumptions that at all depths roots are either randomly orientated or orientated in the same plane and that the size distribution of roots in each 5-cm horizon was the same. A value of 0.18 g per root ending in each 10 cm x 10 cm x 5 cm deep layer was used for all plots (mean number of root endings at 0-5 cm / mean mass of roots in 500 cm^{-3} surface sample). This value is derived from the data from the plots at 200 m only, as it was considered that at 500 m and 850 m the relationship between the count of root endings at 0-5 cm and root mass (from the surface samples) was not representative of the relationship in the mineral soils below 5 cm depth. At 500 m and 850 m there were many thick (3-4 mm diameter), non-woody roots in the top 5 cm, but at 200 m such roots were uncommon, and at all altitudes they rarely occured below 5 cm. Another factor that complicates the relationship at the higher altitudes was the difficulty in preparing a uniform face for the root count in the crumbly organic layers, but this was not a problem below 5 cm in any pit, so the estimates of root numbers in the deeper layers are considered to be valid. The differences in root mass between altitudes are mainly due to differences in surface root concentrations.

The mass of roots in the ingrowth bags at 500 m was significantly higher than at 200 m and 850 m ($p<0.001$, general linear model anova), and there was no significant difference between masses at these two altitudes. No significant differences were found at any altitude among fertiliser treatments.

Table 5.1. Mean mass (g) of fine roots (<5 mm diameter) in surface soil samples (10 cm x 10 cm x 5 cm deep) at three altitudes on Bukit Belalong, Brunei. Values are the means of thirty samples ±95% confidence limits.

	Altitude (m)		
	200	500	850
Mass of roots (g)	2.17 ±0.65	6.50 ±1.16	4.00 ±1.12

Table 5.2. Estimated mass (t ha^{-1}) of fine roots (<5 mm diameter) in the top 100 cm of soil and percentage of fine root biomass in the top 5 cm of soil at three altitudes on Bukit Belalong, Brunei. The values are the means of three plots with the ranges in parentheses.

	Altitude (m)		
	200	500	850
Root mass (t ha^{-1})	8.3 (7.3-8.8)	12.0 (10.2-15.4)	10.6 (9.4-13.2)
% of mass in 0-5 cm	26.3 (21.7-34.1)	54.3 (46.2-58.8)	37.5 (33.3-47.0)

Table 5.3. Mean mass (g) of fine roots (<5 mm diameter) in mesh ingrowth bags incubated for 8 months at three altitudes on Bukit Belalong, Brunei. The bags were treated with N, P, K, NPK or a control treatment of no fertiliser. The values are the means ± 95% confidence limits with the number of replicates in parentheses.

	Altitude (m)		
Treatment	200	500	850
Control	0.274 ±0.214 (7)	0.612 ±0.384 (11)	0.123 ±0.063 (15)
+N	0.265 ±0.257 (8)	0.440 ±0.297 (10)	0.107 ±0.052 (16)
+P	0.175 ±0.102 (12)	0.411 ±0.235 (10)	0.123 ±0.051 (15)
+K	0.277 ±0.134 (11)	0.742 ±0.491 (8)	0.133 ±0.058 (15)
+NPK	0.190 ±0.071 (11)	0.568 ±0.326 (10)	0.130 ±0.058 (14)
All bags	0.236 ±0.057 (49)	0.555 ±0.136 (49)	0.123 ±0.023 (75)

Discussion

Fine root mass

The higher root density in the uppermost soil layers is typical of rain forests (Odum 1970, Whitmore 1984, Cavelier 1992). It has been suggested that root systems are generally more superficial in montane forests than lowland forests (Lyford 1969, Cavelier 1989), possibly as a response to anaerobic conditions in wet soils, but there are no quantitative studies on which to base this generalisation. At Belalong no simple altitudinal sequence was observed, since the highest concentration of surface roots was at 500 m (Table 5.2) and there was some overlap between the values at 200 m and 850 m.

There are few studies with which to compare the Belalong data, and comparisons with other studies are complicated by the lack of standard sampling techniques, depths and root sizes. Studies from rain forests have found root masses ranging from 3.0 to 100 t ha^{-1} (Vogt *et al* 1985), but the highest values are from South American forests with dense root mats growing on spodosols. It is possible that the nutrient cycling in these forests is distinct from other rain forests (Vitousek & Sanford 1986, Gower 1987), so comparisons of root biomass are here restricted to lowland studies from South East Asia and montane forests throughout the tropics (Table 5.4). The estimates of root mass (<5 mm) at all altitudes at Belalong are the highest recorded for South East Asia (but comparisons with the Pasoh data are unclear because roots up to 10 mm diameter were lumped together into a single category, Yoda 1978). Higher values have been recorded for Amazonian *tierra firme* forests (lowland evergreen forests not on spodosols); eg 56.0 t ha^{-1} (Jordan & Escalente 1980), 31.9 t ha^{-1} (Stark & Spratt 1977). The studies in Table 5.4 do not demonstrate a consistent relationship between altitude and root mass, and no such relationship was found in this study. Whilst the Belalong values are high they are none the less likely to be an underestimate since Fogel (1983) found that wet sieving of soils produced 40% more fine roots (<2.5 mm) than hand sorting, and Mackie-Dawson & Atkinson (1991) describe an automated system using

Table 5.4. Mass of roots (live and dead) (t ha^{-1}) in some tropical lowland and montane rain forests.

Location	Altitude (m)	Forest type	Depth (cm)	Root diameter (mm)	Root mass (t ha^{-1})
Brunei, Belalong[1].	200	LRF	100	<5	8.3
Brunei, Belalong[1].	500	LRF	100	<5	12.0
Brunei, Belalong[1].	850	LMRF	100	<5	10.6
Malaysia, Pasoh[2].	100	LRF	100	<10	20.5
Malaysia, Danum[3].	200	LRF	120	<5	6.4
Malaysia, Danum[3].	200	LRF	120	<10	8.7
Malaysia, Danum[3].	200	LRF	120	<15	10.8
New Guinea, Kerigomna[4].	2500	LMRF	25	<5	4.0
New Guinea, Kerigomna[4].	2500	LRF	25	<30	13.5
Hawaii, Hawaii Volcanoes National Park[5].	1150	MRF	30	<2	8.0
Jamaica, Blue Mountains[6].	1500	UMRF	50	<20	11.2
Panama, Gigante Peninsula[7].	60	LRF	25	<5	5.0
Panama, Cordillera Central[7].	1200	LMRF	25	<5	6.6

1, This study; 2, Yoda (1978); 3, Green (1992); 4, Edwards & Grubb (1977); 5, Gower & Vitousek (1989); 6, Tanner (1980); 7, Cavelier, (1989).

pressurised water and air flotation which separated out 15-25% more roots than wet sieving by hand.

Fine root production

Studies on root production in South East Asian forests consist solely of Green's (1992) intensive investigation of fine root dynamics at the Danum Valley, Sabah. He used a complex method combining examination of numerous soil profiles and an extensive soil coring programme to estimate root mass and observations of fine root dynamics in a series of rhizotrons (Mackie-Dawson & Atkinson 1991) to estimate fine root production and turnover over one year. Annual fine root production at Danum was estimated at 6.60 t ha^{-1} $year^{-1}$. Ingrowth bags were used to examine fine root response to local nutrient sources, but the data were not used to calculate production. Estimates of fine root production (t ha^{-1} yr^{-1}) at Danum and Belalong were made by extrapolation of the data from the control treatments in the ingrowth bag experiments (Table 5.5).

Mesh ingrowth bag techniques have been used to estimate fine root production in studies of many boreal and temperate systems (eg Persson 1983, Steen 1985, Fabião *et al* 1985, Steen 1991) and some tropical forest ecosystems (Table 5.5). The estimate of root production at 500 m at Belalong is similar to values reported from Danum (Green 1992) and *tierra firme* forest at San Carlos, Venezuela (Sanford 1985). The rate measured at 200 m is very close to that found by J. Proctor (unpublished) in two plots in lowland evergreen forest at Barito Ulu, Kalimantan. The estimated rate of root growth at 850 m on Belalong is the lowest yet recorded in any tropical rain forest, and Cavelier (1989) also found lower rates of fine root growth in a montane forest compared with a lowland forest in Panama. No comparison was made between rates of root growth in soil and Perlite at Belalong, and whilst Green (1992) found that rates were similar at the Danum valley, J. Proctor (unpublished) found that rates of root growth were significantly higher in ingrowth bags containing soils than in bags

Table 5.5. Root production (t ha^{-1} year^{-1}) in tropical rain forests measured by variations on the mesh ingrowth bag method and methods using sequential coring and observation.

Location	Forest type	Depth (cm)	Root diameter (mm)	Root production (t ha^{-1} year^{-1})	
				Ingrowth method	Other method
Brunei, Belalong[1].	LRF	20	<5	0.92 P	-
Brunei, Belalong[1].	LRF	20	<5	2.16 P	-
Brunei, Belalong[1].	LMRF	20	<5	0.48 P	-
Indonesia, Barito Ulu[2].	LRF (1)	20	-	0.96 P	-
Indonesia, Barito Ulu[2].	LRF (1)	20	-	5.02 S	-
Indonesia, Barito Ulu[2].	LRF (2)	20	-	0.90 P	-
Indonesia, Barito Ulu[2].	LRF (2)	20	-	1.82 S	-
Indonesia, Barito Ulu[2].	Heath	20	-	0.87 P	-
Indonesia, Barito Ulu[2].	Heath	20	-	2.28 S	-
Malaysia, Danum[3].	LRF	30	-	2.63 P	6.6* (0-120 cm)
Malaysia, Danum[3].	LRF	30	-	2.12 S	6.6* (0-120 cm)
Panama, Gigante Peninsula[4].	Semi-deciduous	25	<2	3.70 S	1.1-3.0† (0-10 cm)
Panama, Cordillera Central[4].	LMRF	25	<2	1.14 S	0.8-3.3† (0-10 cm)
Venezuela, San Carlos[5].	*Tierra firme*	10	<2	2.47 S	15.4* (0-10 cm)
Venezuela, San Carlos[6].	*Tierra firme*	10	-	11.17 V	-
Venezuela, San Carlos[6].	*Caatinga*	10	-	1.20 V	-
Venezuela, San Carlos[6].	*Bana*	10	-	2.35 V	-

Ingrowth substrate: S, soil; P, Perlite; V, vermiculite.
Other method of estimation: *, sequential coring and observation; †, sequential coring only, with various methods of calculation.

1, This study; 2, J.Proctor, unpublished; 3, Green (1992); 4, Cavelier, (1989); 5, Sanford (1985); 6, Cuevas & Medina (1988).

containing Perlite, whether fertilised or unfertilised. The relevance of these conflicting results to the Belalong data is unclear. When estimating production it is important to consider an incubation period shorter than the time taken to reach saturation, defined as attainment of stand root biomass levels in the ingrowth bags. Saturation was not achieved after eight months in this study nor at Danum (Green 1992) nor a Panamanian montane forest (Cavelier 1989), but it was reached after five months in the Panamanian lowland forest. Cuevas & Medina (1988) did not measure the standing root biomass at San Carlos and based their calculations on time when maximum root density was reached (90 d in *tierra firme*). The ingrowth method can give very different results to more intensive methods (Sanford 1985, Green 1992). However Cavelier (1989) measured similar rates using the ingrowth method and a soil coring method.

The ingrowth technique is best suited to estimates of fine root production by crops or plantation trees which are exploiting regions of root-free soils or comparison of experimental treatments in stable ecosystems (Steen 1985), and calculations are more complicated when the objective is to obtain absolute estimates of root production in established stands (Steen 1991). Production estimates ideally require measures of the masses of live and dead roots and rates of root decomposition (Fogel 1991, Steen 1991), but none of the tropical ingrowth bag studies have attempted to do this. Persson (1983) described techniques for distinguishing live and dead roots based on external appearance, and though they may be practicable in boreal forests where few species are present, they are less suitable for species-rich tropical forests where there is likely to be a wider range of root morphologies. Gower (1987) described a method of staining root sections for starch granules, which are only present in live tissues, but this is only practicable for small sample sizes.

Incubation time may be important since a study of a temperate perennial grassland showed that long-term incubations (2-12 months) yielded higher estimates than short-term incubations (1 month). The latter gave results comparable with soil coring methods (Steen 1985).

The ingrowth bag method suffers from artefactual problems due to pruning of roots during excavation of the hole, altered drainage and differential compaction in the bag. The technique cannot quantify very rapid turnover of fine roots which has been found to be as little as 3 weeks in temperate deciduous trees (Mackie-Dawson & Atkinson 1991). A volume of completely root-free soil is unlikely to occur naturally in a dry-land forest ecosystem except as a result of landslides or tree falls, so root competition will be an important factor not addressed by this method. Steen (1991) recommended inserting the mesh bag empty into the excavated hole and packing it with soil *in situ*. This is more time consuming than using ready-made bags but has the advantage of creating a closer fit with the soil surface. Growth across an air gap into loosely fitting ingrowth bags may be easier for drought-resistant roots adapted to grow on litter above the mineral soil surface. Cuevas & Medina (1988) measured higher rates of root growth in cylinders of vermiculite buried in the mineral soil than in those placed in the root mat of the San Carlos forests, but the latter were invaded more rapidly and it cannot be ruled out that some of the growth in the buried cylinders was due to roots from the root mat. Root growth into the cylinders was most rapid in the *tierra firme* forest which has a better developed root mat than nearby *caatinga* and *bana* heath-type forests (Cuevas & Medina 1988). Thus it may be that the higher rates of root growth at 500 m on Belalong are a reflection of the ability of superficial roots to invade the bags rather than a true measure of root production.

The budget approach (Hendricks *et al* 1993) offers an alternative method for estimating fine root production and it has been used in some temperate and boreal ecosystems. The method assumes reliable measurements of nitrogen flux into and out of the available soil pool and requires accurate determination of the partition between woody biomass and above ground litter. These assumptions have not yet been met in any species-rich tropical stand.

Response of fine roots to nutrients

Nitrogen limitation of boreal and temperate forest ecosystems is widely accepted (Gower 1987, Hendricks *et al* 1993) and many studies have found that fine roots respond to nitrogen fertilisation (reviewed by Hendricks *et al* 1993). Response to limiting nutrients depends on application methods; if the whole stand is fertilised, total root biomass would be expected to be lower, whilst localised sources such as a fertilised ingrowth bag would promote root growth at that site. Drew *et al* (1973) and Drew (1975) demonstrated proliferation of *Hordeum vulgare* roots in zones of enrichment by nitrate, ammonium and phosphate (though not potassium). Tropical studies are at a much earlier stage, and the few studies so far have shown a variety of responses. Gower & Vitousek (1989) found that root biomass decreased in a nitrogen-fertilised Hawaiian montane forest. Cuevas & Medina (1988) showed that root growth was stimulated in phosphorus-enriched and calcium-enriched ingrowth cylinders in *tierra firme* forest, whilst in *caatinga* roots responded only to nitrogen and in *bana* to nitrogen and phosphorus. In a Panamanian semi-deciduous forest addition of a combined nitrogen and phosphorus treatment removed seasonal variation in fine root biomass, but there was no effect in LMRF (Cavelier 1989). Fine roots did not respond to nitrogen, phosphorus and potassium enriched ingrowth bags in LRF at Danum (Green 1992) and though rates of fertilisation were low compared with those used by Cuevas & Medina (1988) the study at Belalong found no response at any altitude to Perlite fertilised at the higher rates. J. Proctor (unpublished) carried out a similar experiment using Perlite-filled ingrowth bags fertilised with urea and rock phosphate in evergreen lowland forest and heath forest at Barito Ulu. Addition of nitrogen at twice the Belalong rate did not elicit any additional root growth, but addition of phosphorus at about one fifth of the Belalong rate promoted root growth in one dipterocarp plot.

Gower (1987) hypothesized that root biomass in tropical forests is inversely related to phosphorus and calcium availability based on the significant inverse correlation between the mass of these elements in litterfall and fine root biomass. No relationship was found with nitrogen, though it has been demonstrated in temperate studies (Gower 1987). However, Green (1992) and Thompson *et al* (1992) showed that lowland rain forest with low root biomass and no root mat can occur on soils with low phosphorus concentrations.

Conclusions

Fine roots in the Belalong forests are concentrated in the upper layers of the soil at all altitudes, but the proportion of superficial fine roots and fine root mass and production were greatest at the middle altitude. There are a number of problems with the ingrowth bag method used to estimate production and the rates are low compared with other methods. Fertilisation of ingrowth bags with nitrogen, phosphorus and potassium did not affect fine root growth at any altitude.

CHAPTER 6. A BIOASSAY EXPERIMENT TO INVESTIGATE THE EFFECTS OF NUTRIENT ADDITION ON THE GROWTH OF RICE AT TWO ALTITUDES.

Introduction

There have been few experimental studies of nutrient limitation in tropical forests despite the considerable interest in their nutrient cycling. Bioassay experiments can be a useful tool to investigate the nutrient status of soils, since extrapolation of soil-based measurements of nutrient availability to indicate nutrient limitation of plants is not straightforward (Denslow, Vitousek & Schultz 1987).

The choice of bioassay species is critical since plant species respond to nutrient addition in different ways. Mitchell & Chandler (1939) (summarised in Grubb 1989), described nutrient addition experiments in temperate woodland stands on soils of differing nutrient status. It was found that trees on 'less fertile', base-poor soils responded less to fertilisation than trees on 'more fertile', base-rich soils. Denslow *et al* (1987) used seven local species to investigate nutrient limitations in a Costa Rican lowland rain forest. The fast-growing herb, *Phytolacca rivinoides*, which does not grow under mature forest, proved to be much more sensitive to nutrient concentrations than the other six species which were shrubs found either in gaps or under the closed canopy. Hill rice, *Oryza sativa* L., is a suitable plant for a bioassay because seeds can be easily obtained in large quantities, it is a reliable germinator, as a fast-growing crop plant it has a high nutrient requirement and as it is a small plant a compact experiment with a high degree of replication can be set up easily and cheaply. Hewitt (1950) found that hill rice was a more suitable species than tomato for a fertility test of Jamaican soils because it was not affected by eelworms which damaged the latter and reduced their vigour. The use of a monocotyledenous crop plant in a model of nutrient limitation in 60 m tall rain forest might initially seem curious, but it is no less realistic than the conventional extractants used to estimate 'available' soil nutrients.

The environmental conditions of bioassays examining altitudinal zonation require careful consideration. Tanner (1977) and Heaney (1988) used bioassays to investigate nutrient limitations to growth in montane soils, but carried out their experiments at lowland sites with very different conditions from those at the sites from which the soils originated. Though Tanner (1977) found evidence for phosphorus limitation in Jamaican montane forest soils there was no indication that growth was limited by shortage of any other mineral nutrient. Heaney (1988) observed higher rates of growth in montane forest soils from Volcán Barva than in lowland soils, but both of these results can be attributed to increased rates of mineralisation due to disturbance in the collection and preparation of the soils and the higher temperatures at the site of the bioassay. Healey (1989) carried out another bioassay using the Jamaican montane forest soils, but set up the experiment at a similar altitude to the forest and he was able to demonstrate nitrogen and phosphorus limitation.

Bioassays can also be used to indicate toxic soil conditions. Smith (1994) used soils from old secondary forest and stunted (<20 m) heath forest in Kalimantan and demonstrated extreme toxicity in the heath forest soils. Rice seeds germinated and grew well in secondary forest soils, but in the very acid heath forest soils (pH 2.7) they developed a small shoot but no root. NPK fertilisation did not increase growth unless $CaCO_3$ was added to raise the pH. Ambak, Abu Bakar & Tadano (1991) demonstrated toxicity to maize and tomatoes grown in organic peat swamp soils.

Materials and Methods

A total of about 6 kg of surface soil (0-5 cm) was collected from six positions randomly selected just outside plots 3 (lowland soil, LS) and 9 (montane soil, MS). The soil was sorted to remove stones, roots and recognisable fragments of organic matter (>5 mm along any dimension), crumbled by hand to give aggregates no larger than 10 mm and thoroughly mixed. The soils were stored for up to 5 d before the experiment was set up.

The two sites for the replicated experiment were an open space in the middle of Kuala Belalong Field Studies Centre (30 m) and the summit of Bukit Belalong (913 m) (Figure 6.1). At each site 500 ml of LS was placed in each of forty-eight 14-cm diameter plant pot and 500 ml of MS was placed in each of a further forty-eight pots. Seeds of hill rice *Oryza sativa* L. were obtained from local farmers and in each pot seven pre-germinated seeds were planted at a depth of 3 cm. The number of plants in each pot was reduced to five as the shoots emerged. Seven fertiliser treatments were added to the soils and at each site there were six replicates of each treatment. Nitrogen was added as 0.1 g $Na NO_3$, phosphorus as 0.05 g NaH_2PO_4 and potassium as 0.1 g KCl. There were four combined treatments of NP, NK, PK and NPK added at the same rates, and all treatments were added in 10 ml of water from the nearest stream. There was a control treatment of stream water only. The nitrogen and phosphorus fertilisation rates were adapted from Healey (1989), but reduced by 50% because of the shorter growing time and were equivalent to 38 kg N ha^{-1} and 22 kg P ha^{-1} at 10-cm depth. The rate of potassium fertilisation was equivalent to 118 kg K ha^{-1}.

The pots were laid out in six blocks containing one replicate of each treatment, with the pots independently randomised within in each block. The pots were rerandomised after 7 d at 913 m and after 8 d and 11 d at 30 m. The bioassay at 913 m was set up 2 d after that at 30 m. The plants were watered with water from the stream as required. After 14 d the plants were harvested; the soil was washed from their roots and the plants were air dried.

At each site the bioassay was set up on a table with a green plastic 2-mm mesh screen to protect from flying insects and with metal sheeting on the legs to exclude rats and mice. It is accepted that the netting will have reduced the photosynthetically available radiation available to the plants and may also have affected the red:far red ratio of the light.

Climatic data for the period of the experiment were obtained from the weather stations at Kuala Belalong and Bukit Belalong.

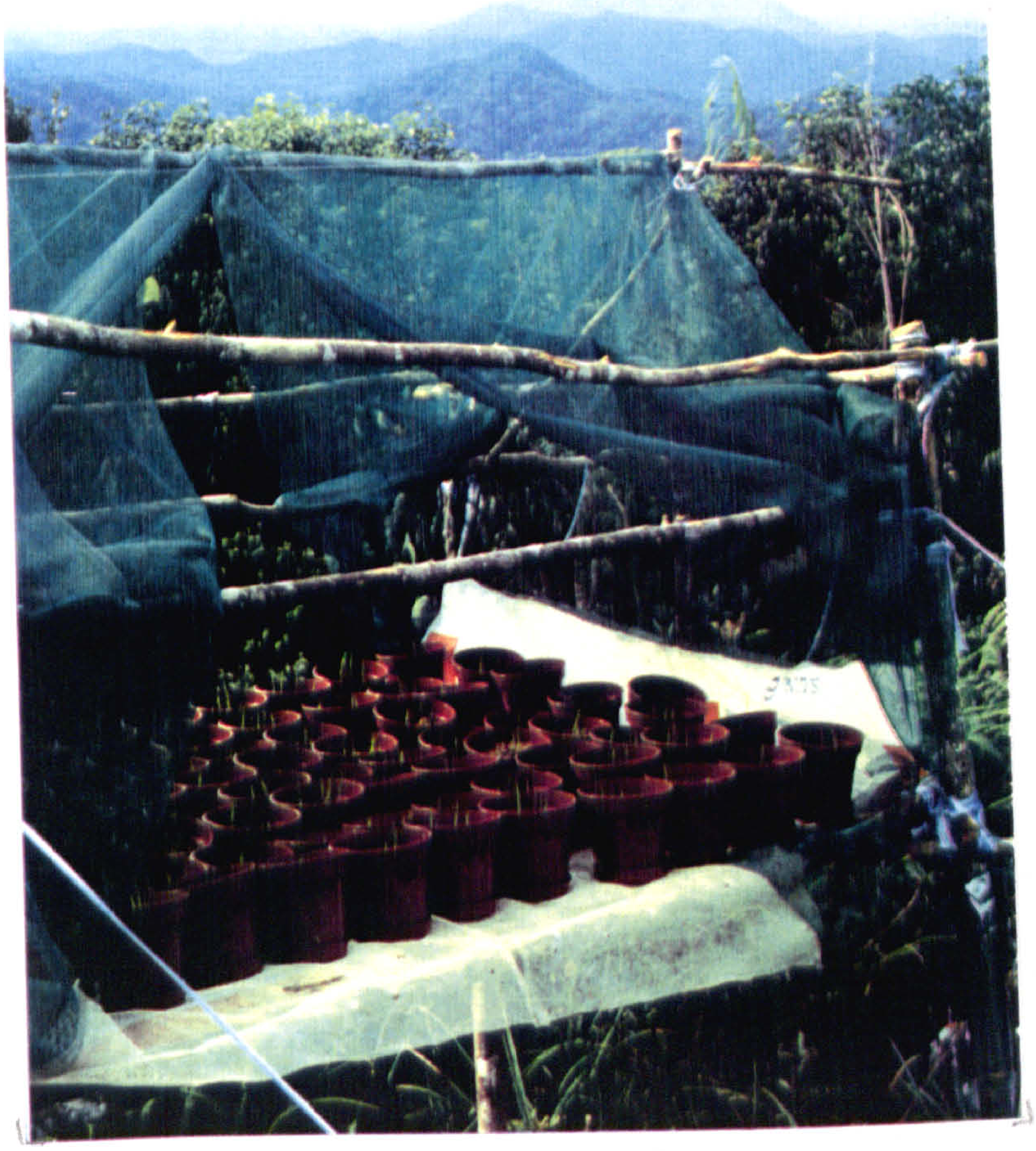


Figure 6.1. The bioassay experiment at the summit (913 m) of Bukit Belalong, Brunei.

Results

Climatic data for this period are summarised in Figure 6.2. Maximum and minimum daily temperatures (Figure 6.2a) were higher at 30 m and the mean difference was 3.13 °C for maxima and 1.95 °C for minima. Solar radiation was generally higher at 913 m (Figure 6.2b) and the mean values were 14.47 MJ m^{-2} at 30 m and 17.03 MJ m^{-2} at 913 m. The Penman open-water evaporation estimates followed a similar pattern to solar radiation and the total values were 51.5 mm at 30 m and 58.2 mm at 913 m (Figure 6.2c).

The altitude at which the experiment was carried out had large effects on the growth of the rice seedlings, but the effects were different in the two soils (Table 6.1). In LS plants, grown at 913 m had reduced shoot heights (but not shoot mass) and increased root mass and total mass compared with plants grown at 30 m. Plants grown in MS at 913 m had reduced shoot height and shoot mass compared with their equivalents at 30 m. In both soil types plants at 913 m had higher root:shoot ratios and shoot mass: height ratios. It is not known whether the differences in the latter ratio are due to an increase in leaf area or leaf thickness at 913 m.

The growth of rice seedlings at each altitude depended upon the soil type in which they were grown, and at 913 m significant differences were found between growth in the two soil types in all the variables measured. At both altitudes MS plants were shorter, with lower shoot mass, but at 913 m root mass and total mass were also significantly lower in the MS plants, and thus the differences between the soils can be considered to be accentuated at the higher altitude.

Significant differences between growth in the two soils and the altitudes were also found amongst seedlings which had been given a complete NPK fertilisation. There were large differences between seedlings grown at 30 m and 913 m in both soil types (Tables 6.1b (1) and 6.2b (1)). Fertilisation of MS accentuated the differences between plants grown at 30 m and 913 m, except for shoot mass which was significantly reduced at 913 m in unfertilised

Figure 6.2. (a) Maximum (closed symbols) and minimum (open symbols) daily temperatures (°C); (b) Daily totals of solar radiation (MJ m^{-2}); (c) Daily Penman evaporation estimates (mm) at 45 m (solid lines) and 913 m (dashed lines) on Bukit Belalong, Brunei.

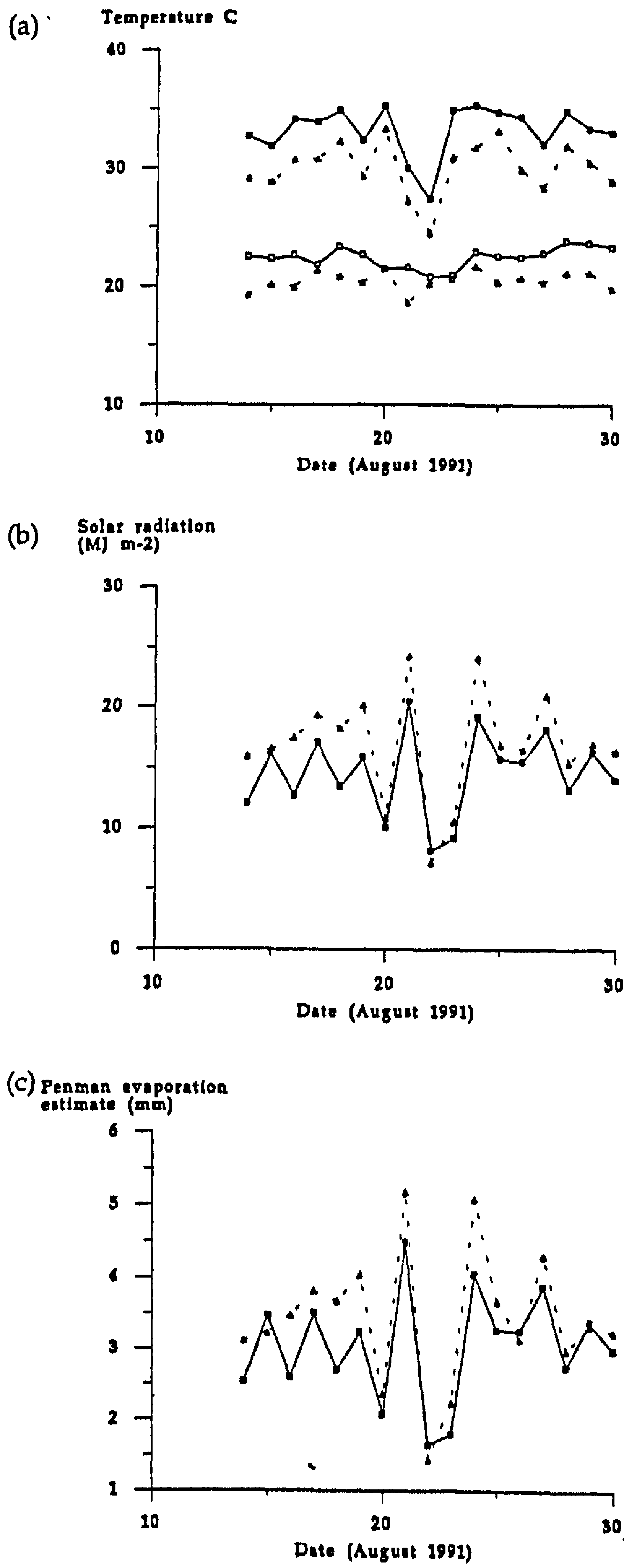


Table 6.1a. Measures of rice seedling growth in unfertilised soils from 200 m (LS) and 880 m (MS) in experiments at 30 m and 913 m. The values are the averages of the values for five seedlings in each of six replicate pots.

Soil type	Altitude (m)	Plant mass (mg)	Shoot height (mm)	Shoot mass (mg)	Shoot mass : height ratio (mg mm^{-1})	Root mass (mg)	Root : shoot ratio
LS	30	65.0	270.3	48.8	0.18	16.2	0.33
LS	913	120.4	110.7	54.7	0.49	65.7	1.20
MS	30	55.8	192.2	40.8	0.21	15.0	0.37
MS	913	54.6	72.0	30.3	0.42	24.3	0.80

Table 6.1b. Significant differences between the values in Table 6.1a (T-test). (1) The effect of altitude for each soil type and (2) The effect of soil type at each altitude. *, $p<0.05$; **, $p<0.01$; ***, $p<0.001$.

Soil type	Altitude (m)	Plant mass (mg)	Shoot height (mm)	Shoot mass (mg)	Shoot mass : height ratio (mg mm^{-1})	Root mass (mg)	Root : shoot ratio
(1)							
LS	30 & 913	***	***		***	***	***
MS	30 & 913		***	**	***		*
(2)							
LS & MS	30		***	*	*		
LS & MS	913	***	***	***	*	***	*

Table 6.2a. Measures of rice seedling growth in NPK-fertilised soils from 200 m (LS) and 880 m (MS) in experiments at 30 m and 913 m. The values are the averages of the means of five seedlings in each of six replicate pots.

Soil type	Altitude (m)	Plant mass (mg)	Shoot height (mm)	Shoot mass (mg)	Shoot mass : height ratio (mg mm^{-1})	Root mass (mg)	Root : shoot ratio
LS	30	76.8	310.2	61.8	0.20	15.0	0.24
LS	913	115.2	128.0	59.7	0.47	55.5	0.93
MS	30	62.0	246.7	49.7	0.20	12.3	0.25
MS	913	85.5	101.0	46.5	0.46	39.0	0.84

Table 6.2b. Significant differences between the values in Table 6.2a (T-test). (1) The effect of altitude for each soil type and (2) The effect of soil type at each altitude. *, $p<0.05$; **, $p<0.01$; ***, $p<0.001$.

Soil type	Altitude (m)	Plant mass (mg)	Shoot height (mm)	Shoot mass (mg)	Shoot mass : height ratio (mg mm^{-1})	Root mass (mg)	Root : shoot ratio
(1)							
LS	30 & 913	***	***		***	***	***
MS	30 & 913	**	***		***	***	***
(2)							
LS & MS	30	*	**	*			
LS & MS	913	***	***	**		*	

soil, but not in fertilised soil. Fertilisation tended to reduce the number of significant differences between plants grown in LS and MS at each altitude (Table 6.1b (2) and 6.2b (2)), but all measures of growth indicate that even with the complete fertilisation treatment production was lower in MS than LS at both altitudes.

A further test was made of the effect of each nutrient by comparing the growth of all seedlings (in each soil and altitude permutation) to which the nutrient was added (both alone and in combination) with those to which the nutrient had not been supplied. This method of testing the effects of fertilisation was considered superior because of the increase in replication compared with tests of individual treatments (n=24 versus n=6). The results of the individual tests (Appendix 4) do not conflict with those of the combined tests.

Nutrient addition had few effects on seedlings grown in LS at either altitude (Table 6.3), but had more effects on seedlings grown in MS. Added nitrogen reduced the root:shoot ratio in LS seedlings at 913 m, but had no other effects on the LS seedlings at that altitude and, none on LS seedlings at 30 m. By contrast fertilisation with nitrogen increased total plant mass in MS seedlings at 913 m and increased shoot height and shoot mass of MS seedlings at both altitudes. At 30 m nitrogen addition decreased root mass and root:shoot ratio, but at 913 m root mass was increased.

Phosphorus addition had slight effects, and the only significant differences were an increase in shoot mass (and consequently total mass) in LS seedlings at 30 m, and a decrease in MS seedling root mass and root:shoot ratio at 30 m. Phosphorus fertilisation had no effect on growth in either soil at 913 m. Potassium addition increased shoot height in LS seedlings at 913 m, but otherwise had no effects on growth in that soil type. In MS seedlings potassium fertilisation increased shoot height and shoot mass and total plant mass at both altitudes but had no effect on root growth.

Table 6.3. The effect of nutrient addition on growth of rice seedlings: (a) plant dry mass, (b) shoot height, (c) shoot mass, (d) root mass and (e) root:shoot ratio. The plants were grown in soil collected from 200 m (LS) and 880 m (MS) on Bukit Belalong and the experiment was carried out at Kuala Belalong Field Studies Centre (30 m) and the summit of Bukit Belalong (913 m). The values used are the averages of the means of five seedlings in twenty-four pots with the nutrient added and twenty-four without. Significant differences (T-test) between the averages for growth with and without the nutrient were tested separately for each altitude and soil type. *, $p<0.05$; **, $p<0.01$; ***, $p<0.001$).

(a)

Altitude (m)	Soil type	Plant mass (mg)					
		-N	+N	-P	+P	-K	+K
30	LS	65.4	70.6	64.5	71.5*	67.7	68.3
30	MS	57.2	60.0	59.9	57.3	55.5	61.7**
913	LS	116.1	115.1	111.5	119.7	117.8	113.4
913	MS	62.5	77.1**	69.8	69.7	62.7	76.9**

(b)

		Shoot height (mm)					
30	LS	262.5	281.5	261.5	278.9	264.2	279.8
30	MS	212.8	238.6**	228.1	223.3	208.2	243.2***
913	LS	116.3	122.4	117.9	120.7	115.3	123.4*
913	MS	82.5	93.6*	89.1	87.0	77.4	98.7***

(c)

		Shoot mass (mg)					
30	LS	50.3	55.5	48.8	57.0**	51.7	54.1
30	MS	43.3	48.3**	45.8	45.7	43.4	48.2**
913	LS	54.4	58.5	55.5	57.4	56.7	56.2
913	MS	35.0	41.3**	37.9	38.3	33.5	42.8***

Table 6.3. continued.

(d)

Altitude (m)	Soil type	Root mass (mg)					
		-N	+N	-P	+P	-K	+K
30	LS	15.1	15.1	15.7	14.5	16.0	14.2
			*		**		
30	MS	13.9	11.8	14.1	11.6	12.2	13.5
913	LS	61.7	56.7	56.0	62.3	61.1	57.2
			**				
913	MS	27.5	35.8	31.9	31.4	29.3	34.1

(e)

		Root : shoot ratio					
		-N	+N	-P	+P	-K	+K
30	LS	0.31	0.28	0.32	0.26	0.32	0.27
			**		*		
30	MS	0.31	0.25	0.30	0.26	0.27	0.28
			*				
913	LS	1.15	0.98	1.03	1.10	1.08	1.04
913	MS	0.78	0.87	0.83	0.81	0.86	0.78

Discussion

The primary factor affecting growth is the microclimate of the experiment, which can be related both to the climate at each altitude (as measured by the weather stations) and specific effects due to the site of the bioassay. At 913 m the climate was consistently cooler, but the Penman evaporation was generally higher and consequently plants at 913 m were more likely to be water stressed. The amount of light received by the plants was greater at 913 m, but the differences were larger than indicated by Figure 6.1c because the weather stations were both sited on cleared summits with good exposure in all directions (especially at 913 m). At 913 m the bioassay table was located beside the AWS, and was in full sunlight from 6 am till 6 pm, but the Field Studies Centre (30 m) is situated at the bottom of a steep valley and direct sunlight only reached the table there between c. 8 am and c. 4 pm. There was also some shading from trees at some times of the day. It should be noted that the insolation during the bioassay was atypical since mean daily totals of solar radiation measured for eight months by the weather stations were very similar (Chapter 2).

The dramatically higher root mass and root:shoot ratio in all plants in both soils at 913 m indicates that a climatic factor affecting all plants is responsible. Water stress was more likely at 913 m (indicated by Penman evaporation estimate, fig 6.1c) and the development of a larger root system may be a response to the increased transpiration under these conditions (Nye & Tinker 1977, Baker 1984). It is unclear why the LS seedlings should have had a higher root:shoot ratio than MS seedlings at 913 m.

There were clear differences in seedling growth between the two soil types at both altitudes, but there was no evidence of the soil toxicity found in heath forest and peat swamp soils (Ambak, Abu Bakar & Tadano 1984; Smith 1994). There were more differences between growth in the two soils at 913 m than at 30 m and these differences were also found with NPK fertilised seedlings, so factors other than a low supply of these nutrients in MS must also have been important. Soils at 200 m were more clay-rich and less organic than those from the higher altitude, and because the pots were filled by volume rather than weight plants grown in MS had less soil (by mass) to exploit. The physical differences between the soils may also have affected their water retention capacities and the greater differences between growth in the two soil types at 913 m may be a reflection of the drier environment there. The use of intact soil cores would have made the results easier to apply to growth in the undisturbed forests, and the mixing and sorting of the soils would almost certainly have had some effects on nitrogen and phosphorus mineralisation. If soil cores were to be used, the degree of replication would need to be increased because of the heterogenous nature of the Belalong surface soils (Chapter 2).

Seedlings in the two soils responded differently to fertilisation. Nitrogen and potassium were apparently limiting in MS and in general phosphorus had little effect, but this may be because of the short duration of the experiment since longer term bioassays have indicated phosphorus limitation in both lowland (Denslow *et al* 1987) and montane (Tanner 1977, Healey 1989) soils. It is possible that in the short term the larger root systems in the plants at 913 m allowed more efficient exploitation of available phosphorus, but if the experiment had been allowed to proceed for longer, phosphorus might eventually have limited growth in this crop plant.

The largest total dry weight was found in seedlings grown in LS at 913 m, but there was no assessment of the stage of development of the seedlings. The ultimate measure of a plants ability to survive could be considered to be the amount of viable seed produced. Some surplus seedlings were planted on the summit of Bukit Belalong, and they flowered and set seed, but many of the husks were empty. The local farmers from whom the rice seeds had been obtained considered that lower yields would be expected from rice grown at this altitude.

Conclusions

Altitude had a profound effect on the growth of rice seedlings in both soils and this was probably due to the lower temperatures and possibly greater water stress at 913 m. The experiment may not have lasted long enough to demonstrate nutrient limitation of growth in the lowland soils, but it did indicate reduced supply of nitrogen and potassium in the montane soil. The role of phosphorus is unclear and evidence of phosphorus limitation might have been found if the experiment had been allowed to proceed for longer. Growth of rice seedlings in the montane soil was never as high as in lowland soil, even with complete fertilisation and it may be that the physical properties of the lowland soil may have been more suitable for rice.

Altitudinal zonation on Bukit Belalong

The altitude of the ecotone from LRF to LMRF is similar on both Bukit Belalong and Gunung Mulu and appears to be typical for inland mountains in this region, which are up to 2500 m high. Although there are important floristic differences between the LRF and LMRF on Bukit Belalong sixteen species of tree were found to occur at both the lowest and the highest altitude. This, and the rather gradual physiognomic changes from LRF to LMRF, suggests that the physical environment does not change dramatically between the lowest and the highest altitude.

Wind

At 4° 30′ N Brunei is situated in the region of the equatorial trough between the north-east and south-east tradewind systems. Mean wind speeds at this latitude are of the order of 0.5-1.5 m s^{-1} (Riehl 1979). Severe tropical storms occur outside the zone 5° N to 5° S (Lockwood 1974) so Brunei does not suffer from their effects. Mean wind speeds at the summit of Bukit Belalong (0.89 m s^{-1}) are higher than at Kuala Belalong (0.47 m s^{-1}), but are lower than at 12 m on the seaward side of Gunung Silam (1.5 m s^{-1}) (Proctor *et al* 1988). At this altitude on Gunung Silam tall lowland forest would have existed before felling. At no site on Bukit Belalong was there any indication that wind had shaped the canopy, and differences in wind speeds are discounted as cause of altitudinal zonation on Bukit Belalong.

Drought

Soils in the LMRF are shallower and stonier and frequently on steeper slopes than soils in the LRF and might be more prone to drought. The highest daily total Penman evaporation was recorded at 913 m (5.47 mm), but mean evaporation was lower there (3.00 mm d^{-1}) than at Kuala Belalong (3.25 mm d^{-1}) and there are several other lines of evidence that suggest that at least in the surface soils drought is less important in the LMRF than in the LRF. The profusion of ground herbs (Appendix 3) and bole bryophytes in the LMRF are indications that within the forest relative humidity and surface soil moisture are higher than in the LRF. The soil surface in the LMRF was never observed to dry out as much as in the LRF, and herbs were never observed to wilt in the LMRF, though they did so on several occasions in the LRF after a few dry days.

Monthly rainfall totals were higher at 913 m than 45 m except for February 1992, but during that month rainfall was distributed more evenly at the higher altitude, and there were fewer rainless days there. Occult precipitation was not measured, but on several evenings in March 1992, whilst camping at Bukit Belalong, fog was observed to deposit moisture on vegetation at the summit and on some mornings heavy dew formed. Neither fog nor dew appeared to be important at lower altitudes.

The total rainfall at Semabat for January - March 1992 (386.7 mm) was lower than for the same period in 1983 (504.7 mm) when Borneo suffered a widespread drought. It may therefore be that the conditions experienced at Belalong during early 1992 were exceptionally dry.

Following this dry period, widespread shedding of leaves in the LRF caused large peaks in leaf litterfall in April and May 1992, especially at 500 m where the plots were located near a ridge top. The large litterfall peak was not seen in the LMRF.

Fine root production (measured in the top 20 cm of soil by ingrowth bags) was comparatively low at 200 m and 850 m, but less so at 500 m. The higher rates of root production in the forest at 500 m were interpreted as a greater ability of drought-resistant surface roots to invade the bags. Low rates of production at the other altitudes may be related to the dry period at the beginning of 1992, since Green (1992) found that rates of fine root production were lowest during dry periods. Forests on ridges at 500 m may be more likely to suffer droughts than the other forests studied and the different root morphology (p136) may be a response to this.

Decomposition, mineralisation and nutrient limitation

The higher loss-on-ignition and total nitrogen in the LMRF soils suggest that decomposition is slowed at high altitude, as has been found on other tropical mountains (Grubb (1977); Proctor *et al* (1988); Grieve *et al* (1990). The decomposition quotients (k_L) indicate a tendency towards slower decomposition of litter in the LMRF, but there was some overlap in values. The results of the decomposition bag experiment are equivocal, with slower decomposition of *Ixora* leaves in LMRF, whilst there was no difference in decomposition of *Shorea* leaves among the altitudes. Decomposition is related to resource quality (Anderson & Swift 1983), and the more nutrient-rich *Shorea* (Table 4.9) leaves decomposed significantly faster at all altitudes. Nutrient concentrations in the fresh leaves were much higher than those measured in litterfall (Table 4.5), and the concentrations in *Ixora* were more similar to those in the litterfall.

The rice bioassay yielded some evidence of greater nutrient limitation in the LMRF soils than in the LRF soils, but emphasized the overwhelming importance of climate on rice growth. The LMRF cycles smaller quantities of litterfall nutrients than the LRF, but this is almost certainly due to the lower litterfall mass. Litterfall nutrient concentrations and the total quantities of nutrients cycled were high compared with other montane forests.

The mineralisation experiment did not show low supplies of inorganic nitrogen or reduced rates of mineralisation in the LMRF, but it is accepted that there were problems with the analyses. Marrs *et al* (1988) found that high soil moisture content and poor aeration were the primary factors limiting rates of nitrogen turnover at higher altitudes on Volcán Barva. Though there were no measurements of soil moisture the comparatively slight increase in LOI with altitude indicate that the soils do not become waterlogged in the absence of a cloud cap, and waterlogging was never observed during numerous visits to the sites. The mineral element quotients (k_E) were higher than the k_L values indicating that there was no net immobilisation of nutrients in decomposing litter.

Fresh litter samples from Bukit Belalong were analysed for phenolic compounds by Bruijnzeel *et al* (1992). The concentrations measured were low compared with litter from other mountains. Concentrations were highest in litter from 200 m and the lowest in litter from 500 m, so there is no indication that phenolics affect processes in the LMRF.

It is concluded that lower temperatures in the LMRF slightly reduced rates of nutrient turnover and possibly nutrient supply in the LMRF soils, but it is unlikely that the reductions influence plant growth.

Temperature and photosynthesis

Since the LMRF on Bukit Belalong is not adversely affected by wind, drought or nutrient limitation compared with the LRF it is concluded that the replacement of LRF by LMRF is due to the lower temperatures at the higher altitude. Burgess (1972) suggested that the change from LRF to LMRF was primarily due to reduced temperature, and Grubb (1974) concluded that temperature sets the uppermost limit for each of the Formations on tropical mountains, with frequently cloudy conditions lowering the limits.

Temperature affects metabolic processes by way of its influence on the reaction kinetics of chemical events and on the effectiveness of the various enzymes involved (Larcher 1980). Dark respiration increases exponentially with increased temperature, and the balance between it and gross photosynthesis defines a species' optimum temperature. For each species there are 'cardinal temperatures', a range about a genetically fixed norm (Larcher 1980), outside which a species' competitive capacity is reduced. Van Steenis (1972) proposed that plants can be classified as megatherms, adapted to the high temperatures of low altitudes and low latitudes; mesotherms in the cool conditions of mid altitudes and latitudes and microtherms found at high altitudes and latitudes. Such broad categories are an oversimplification. Some species of coastal heath forests in Brunei are also found in UMRF at 1850 m on Gunung Pagon (Ashton 1964a), though most of the species from each forest type are restricted to it. Likewise several species in this study were found to grow at all altitudes, but some of the more common species were recorded only at a single altitude (Appendix 2).

Friend & Woodward's (1990) review of mountain plant ecophysiology suggested that throughout the world the decline in plant stature can be related to the differences between air temperature and leaf temperature. The aerodynamic boundary layer conductance (and therefore energy transfer) increases with plant height so low vegetation maintains higher leaf temperatures than tall vegetation. The differences can be large and one study at 2040 m in the Snowy Mountains of Australia found differences of up to 30 °C between the temperatures of leaves on a small tree and a moss cushion (Korner & Cochrane 1983).

This model is based on temperate studies and though it may be relevant to low temperature conditions at high altitudes on tropical mountains it is not applicable to the situation at lower altitudes. Kapos & Tanner (1985) showed that the leaf temperature of low stature, Jamaican UMRF trees closely followed the air temperature. The upright leaves of UMRF trees have a high albedo (Whitmore 1984) which would tend to minimise leaf temperature increases. Although local effects of topography are important, mean wind speeds tend to be lower on tropical than temperate mountains (eg 2 m s^{-1} at 4250 m on Mt. Jaya, New Guinea and 23 m s^{-1} at 1915 m on Mt. Washington, USA; Friend & Woodward 1990). Thus tropical montane vegetation is not coupled so closely to the atmosphere as temperate montane vegetation and dwarfing would less important in maintaining high leaf temperatures.

The reduction of air pressure with increasing altitude lowers the partial pressure (but not the mole fraction) of CO_2 and studies on temperate plants have shown different photosynthetic responses in high-altitude ecotypes (reviewed by Friend & Woodward 1990). This has not yet been studied in tropical species, but it may be important in defining altitudinal limits for some species. It would be interesting to compare the photosynthesis of ecotypes of the heath forest species on Gunung Pagon with examples from the lowland heath forests, and to repeat the work using low and high altitude ecotypes from Bukit Belalong.

Conclusions

A complicating factor in most studies on single mountains is that the processes which created the mountain (eg volcanism, intrusion of granitic rocks, differential weathering of rock types) cause it to have non-uniform lithology. Bukit Belalong is unusual in having the same lithology and similar soils (orthic acrisols) from the base to the summit.

The occurrence of a cloud cap on a mountain coincides with dramatic change from LMRF to UMRF, but the high humidity associated with the cloud cap can have noticeable effects on the LMRF immediately below it (Whitmore 1984). Mountains which do not develop a cloud cap and have uniform lithology are the most suitable situation in which to study the differences between LRF and LMRF because temperature is the only factor which changes with altitude.

It is concluded that on Bukit Belalong reduced temperatures at increased altitude alter the competitive balance between species and lead to the broad ecotone between LRF and LMRF.

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Appendix 1. Profile Descriptions.

Horizon depth (cm)	Description
Plot 2, 200 m.	
O, 4-0	Litter layer. Sharp boundary with mineral soil.
A, 0-3.5	Porous, granular, 2-4 mm. No mottles. Slightly plastic. 7.5 YR 5/4 brown - 7.5 YR 5/6 strong brown. Abrupt, smooth boundary.
B, 3.5-50	Less porous, granular 4 mm. Moderately plastic. 7.5 YR 6/8 reddish yellow. Gradual, smooth boundary.
C, >50	Sticky, granular 4 mm. Moderately plastic. 7.5 YR reddish yellow. Weathered shale 70% to 100 cm, but only 10% from 100 to 160 cm. Bed rock not reached.
Pit 3, 210 m.	
O, (2-3)-0	Litter layer. Sharp boundary with mineral soil.
A, 0-4	Granular 5 mm. Moderately plastic. 7.5 YR 5/4 brown. Smooth clear boundary.
B, 4-70	Granular 8 mm. Moderately plastic. 7.5 YR 6/6 reddish yellow - 5 YR 6/6 reddish yellow. Diffuse, smooth boundary.
C, >70	Moderately plastic. 7.5 YR 6/6 reddish yellow. Weathered shale 80%.
Plot 4, 480 m.	
O, (2-3)-0	Litter layer. Sharp boundary with mineral soil.
A1, 0-2	Porous, fine granular 2 mm. Slightly plastic. 5 YR 3/4 dark reddish brown. Smooth, abrupt boundary.
A2, 2-4.5	Less porous. Peds 1.5 cm, breaking into 2-3 mm granules. Slightly plastic. 7.5 YR 4/4 dark brown. Smooth abrupt boundary.
B, 4.5-130	Sticky. Peds 1-2 cm, breaking into 4-8 mm granules. Moderately plastic. 10 YR 5/6 yellowish brown - 10 YR 5/8 yellowish brown - 7.5 YR 5/8 strong brown. Smooth gradual boundary.
C, >130	Weathered shale 80%.
Plot 5 520 m.	
O, (2-3)-0	Litter layer. Sharp boundary with mineral soil.
A1, 0-4	Very open and organic. Fine granular 1-2 mm. Slightly plastic. Matrix 7.5 YR 5/6 strong brown; organic matter 7.5 YR 4/4 brown/dark brown. Smooth abrupt boundary.

A2, 4-10	Granular 2-4 mm. Slightly plastic. 10 YR 5/6 yellowish brown - 10 YR 4/4 dark yellowish brown. Smooth abrupt boundary.
B, 10-105	Granular 4 mm. Moderately plastic. 10 YR 5/8 yellowish brown. Smooth, gradual boundary.
C, >105	Weathered shale 80%.
Plot 7, 840 m.	
O, (1-2)-0	Litter layer. Sharp boundary with mineral soil.
A, 0-6	Porous, granular 8 mm. Moderately plastic. 5 YR 5/8 yellowish red. Smooth abrupt boundary.
B, 6-40	Slightly sticky, granular 8 mm. Moderately plastic. 5 YR 5/8 - 5 YR 5/6 yellowish red. Smooth, gradual boundary.
C, >40	Sticky, granular 3-5 mm. Moderately plastic. 5 YR 6/8 yellowish red. Weathered shale 70%.
Plot 8, 870 m.	
O, 1-0	Litter layer. Sharp boundary with mineral soil.
A, 0-25	Very open and crumbly, granular 3 mm. Slightly plastic. 10 YR 5/4 yellowish brown. Smooth, clear boundary.
B, 25-50	Open, granular 5 mm. Slightly plastic. 7.5 YR 6/6 reddish yellow - 7.5 YR 5/6 strong brown. Smooth gradual boundary.
C, 50-80	Granular 5 mm. Moderately plastic. 7.5 YR 6/6 reddish yellow. Weathered shale 80% to 80 cm and continuous below.

Appendix 2.

The tree and liana species (≥10 cm dbh) and the number of individuals in each plot on Bukit Belalong, Brunei.

Species	Number of individuals per plot								
	1	2	3	4	5	6	7	8	9
Alangiaceae									
Alangium javanicum (Bl.) Wang			1	2			1		
Anacardiaceae									
Buchanania sessiflora Bl.								1	
Gluta aptera (King) Ding Hou									1
Gluta laxiflora Ridl.	2		4						
Gluta macrocarpa (Engl.) Ding Hou				1				1	
Gluta oba (Merr.) Ding Hou					1				
Gluta wallichii (Hk.f.) Hou			1	2	1	2			
Mangifera cf. quadrifida Jack	3	1	3			1			
Melanochyla bullata Hou							1		
Melanochyla caesia (Bl.) Hou							2	1	1
cf. Melanochyla castaneifolia Hou					3				
Melanochyla densiflora King								2	
Melanochyla fulvinervis (Bl.) Hou					1		2	1	
Melanochyla minutiflora Hou							1		
Melanochyla sp.1							1		
Parishia maingayi Hook.f.	1								
Semecarpus bunburyanus Gibbs	1			1	3			1	2
Semecarpus glaucus Engl.		1	2						
Swintonia acuta Engl.					1		1	1	2
Swintonia glauca Engl.			1			2			
Swintonia sp.1							1		
Anacardiaceae genus unknown sp.1			1						
Anacardiaceae genus unknown sp.2				1					
Annonaceae									
Goniothalamus sp.1				1					
Monocarpia marginalis (Scheff.) Sinclair						1			
Polyalthia cauliflora Hk.f & Th.							1		
Polyalthia sp.1	1								
Polyalthia sp.2							1		
Sageraea lanceolata Miq.	3	2							
Xylopia malayana Hk.f. & Th.	2	2	2	1					
Xylopia sp.1			1						
Annonaceae genus unknown sp.1					1				
Apocynaceae									
Dyera costulata (Miq.) Hk.f.						1			
Apocynaceae genus unknown sp.1					1				
Apocynaceae genus unknown sp.2				1					
Arecaceae									
Eugeissona utilis							1	4	
Bombacaceae									
Durio cf. *carinatus* Mast.				1	1	1			
Durio cf. *graveolens* Becc.				1					
Durio lanceolata Mast.								1	
Boraginaceae									
Pteleocarpa lamponga (Miq.) Bakh.									1
Burseraceae									
Canarium apertum Lam					1				

Species	Number of individuals per plot								
	1	2	3	4	5	6	7	8	9
Canarium caudatum King.							1		
Canarium denticulatum Bl.			1						
Canarium dichotomum (Bl.) Miq.			1						
Canarium kinabaluensis Leenh.	1		1						
Canarium littorale Bl.						1			
Canarium pilosum Bennett					1	1	1		
Dacryodes costata (Bennett) Lam		1		1			1		1
Dacryodes laxa (Bennett) Lam	1		1		1				
Dacryodes longifolia (King.) H.J.L.						3	2	1	
Dacryodes macrocarpa var. *patentinervum* (King.) Lam							1	1	1
Dacryodes rostrata (Bl.) Lam			1						
Dacryodes rugosa (Bl.) Lam	1			2		4	1		
Santiria apiculata Bennett						1			
Santiria griffithii (Hk.f.) Engl.			1						
Santiria megaphylla Kalkm.		1							
Triomma malaccensis Hk.f.	1	1		1		1			
Burseraceae genus unknown sp.1					1				
Celastraceae									
Bhesa paniculata Arn.					1				
Lophopetalum sp.1									1
Clusiaceae									
Calophyllum sp.1								1	
Calophyllum sp.2				1					
Calophyllum sp.3							1		
Calophyllum sp.4						1	1		
Garcinia sp.1							3		2
Garcinia sp.2							1		1
Garcinia sp.3							1		
Garcinia sp.4									1
Garcinia sp.5								1	
Garcinia sp.6				1					
Garcinia sp.7									4
Garcinia sp.8		1	1						
Garcinia sp.9					1				
Garcinia sp.10				2					
Garcinia sp.11					1		1		
Garcinia sp.12							1	1	
Garcinia sp.13		1							
Garcinia sp.14					2				
Garcinia sp.15							1		
Garcinia sp.16		1							
Khayea grandis King								2	
Khayea sp.1					1				
Khayea sp.2		2							
Mesua sp.1							1		
Cornaceae									
Mastixia cuspidata Bl.								1	
Crypteroniaceae									
Crypteronia griffithii Clarke		2						1	
Dipterocarpaceae									
Anisoptera costata Korth.						1			
Anisoptera laevis Ridl.		1		1	2				
Dipterocarpus caudatus ssp. *penangianus* (Foxw.) Ash.		1	1	6					
Dipterocarpus caudiferus Merr.	2								
Dipterocarpus sp.1				1					
Dryobalanops beccarrii Dyer				2	1				

Species	Number of individuals per plot								
	1	2	3	4	5	6	7	8	9
Dryobalanops lanceolata Burck	5	1	3						
Hopea cf. griffithii Kurz									1
Hopea cf. dryobalanoides Miq.		2							
Parashorea parvifolia Wyatt-Smith ex Ashton					1		2	6	2
Parashorea smythiesii Wyatt-Smith ex Ashton			2						
Shorea agamii ssp. *agamii* Ashton				1		4	1		
Shorea amplexicaulis Ashton					5	13	1		
Shorea cf. andulensis Ashton				1					
Shorea atrinervosa Sym.	1	1				3			
Shorea cf. beccariana Burck				1	1				
Shorea cf. bracteolata Dyer									1
Shorea cf. curtisii Dyer ex King					1		4		7
Shorea cf. exelliptica Meijer					1				
Shorea cf. faguetiana Heim	1	2	4		1	1			
Shorea faguetioides Ashton		1	1	1		1			
Shorea falciferoides ssp. *glaucescens* (Meijer) Ashton	1								
Shorea cf. *fallax* Meijer							3		
Shorea ferruginea Dyer ex Brandis						1			
Shorea cf. *flaviflora* Wood ex Ashton	2								
Shorea laevis Ridl.	2	3		3	3				
Shorea leprosula Miq.		5		5	1				
Shorea macroptera ssp. *macropterifolia* Ashton			2						
Shorea maxwelliana King			1						
Shorea cf. *obscura* Meijer				1	1	3			
Shorea cf. *ovalis* (Korth.) Bl.							1		
Shorea parvifolia Dyer	2						2		2
Shorea parvistipulata Heim	1	1	1			3			
Shorea cf. *patoiensis* Ashton	1								
Shorea pauciflora King	4	2	1	5	1	7			
Shorea pinanga Scheff.				3					
Shorea rubra Ashton					1				
Shorea cf. *scaberrima* Burck		1	1	1	1				
Shorea superba Sym.			1						
Shorea sp.1				1					
Shorea sp.2					1				
Shorea sp.3						1			
Vatica cf. *albiramis* Sloot.							1		
Vatica dulitensis Sym.							3		7
Vatica cf. *endertii* Sloot.							2	2	
Vatica micrantha Sloot.	1	1	2						
Vatica oblongifolia ssp. *oblongifolia* Hk.f.	1			4					
Vatica odorata ssp. *mindanensis* (Foxw.) Ashton		1		1			1		
Vatica vinosa Ashton					1	2			
Dipterocarpaceae genus unknown sp.1				1					
Dipterocarpaceae genus unknown sp.2							2		
Ebenaceae									
Diospyros sp.1	3	2				1			
Diospyros sp.2		1	1		2	1			
Diospyros sp.3	1								
Diospyros sp.4	1		1						
Diospyros sp.5							2		1
Diospyros sp.6									1
Diospyros sp.7					1				
Diospyros sp.8					2				
Diospyros sp.9				1					
Diospyros sp.10			1						
Diospyros sp.11		1							
Elaeocarpaceae									
Elaeocarpus clementis Merr.							1		

Species	Number of individuals per plot								
	1	2	3	4	5	6	7	8	9
Elaeocarpus nitidus Jack									6
Elaeocarpus palembanicus (Miq.)							1		1
Elaeocarpus pedunculatus Wall. ex Mast.							1		
Elaeocarpus stipularis Bl.							2		1
Euphorbiaceae									
Antidesma sp.1		2							
Antidesma sp.2		1			1				
Antidesma sp.3				1					
Antidesma sp.4							1		
Aporusa benthamiana Hk.f.		1			1			1	
Aporusa cf. *confusa* Gage						1			
Aporusa sp.1						1			
Aporusa sp.2							1		
Baccaurea latifolia King ex Hk.f.						1			
Baccaurea sp.1	1	1		2	3	3	1	1	1
Baccaurea sp.2									1
Baccaurea sp.3									1
Baccaurea sp.4								1	1
Blumeodendron cf. *bullatum* Airy Shaw								1	
Blumeodendron concolor Gage									1
Blumeodendron kurzii (Hk.f.) J.J.Sym.					1	3			
Cleistanthus baramicus Jabl.							2		
Cleistanthus sp.1								1	1
Elateriospermum tapos Bl.	5	2	2	4	3	11			
Glochidion sp.1									1
Koilodepas laevigatum Airy Shaw	8		1						
Macaranga anceps Airy Shaw							5	1	
Macaranga hullettii King ex Hk.f.						1			
Macaranga lowii King ex Hk.f.	1		1						
Mallotus eucastus Airy Shaw					2				
Mallotus cf. *griffithianus* (M.A.) Hk.f.	2								
Mallotus laevigatus (M.A.) Airy Shaw		1							
Mallotus penangensis M.A.							4	4	2
Mallotus wrayii King ex Hk.f.				1	3	1			
Mallotus sp.1	1								
Mallotus sp.2							1	7	
Neoscortechnia kingii (Hk.f.) Pax & Hoffm.			1						
Pimeleodendron griffithianum Benth.		1			2	2			
Ptychopyxis bacciformis Croizart	2	5							
Euphorbiaceae genus unknown sp.1	1				1	1			
Euphorbiaceae genus unknown sp.2				1					
Euphorbiaceae genus unknown sp.3		1							
Euphorbiaceae genus unknown sp.4						3			
Fabaceae									
Albizia splendens Miq.						1	1		
Crudia cf. *caudata* Prain									2
Crudia sp.1	1								
Crudia sp.2					1				
Dialium cf. *indum* L.							1		
Dialium sp.1							3	3	
Dialium sp.2			1						
Dialium sp.3		1							
Intsia palembanica Miq.			1						
Koompassia excelsa (Becc.) Taubert	1								
Koompassia malaccensis Maing. ex Benth.			1	1				1	3
Sindora sp.1				2	2				

Species	Number of individuals per plot 1	2	3	4	5	6	7	8	9
Fagaceae									
Castanopsis megacarpa Gamble								1	
Lithocarpus clementianus (King ex Hk.f.) Camus							2	3	3
Lithocarpus gracilis (Koerth.) Soepadmo							4		1
Lithocarpus niewenhuissii (van Seemen) Camus							1	1	
Lithocarpus rassa (Miq.) Rehd.									3
Lithocarpus sp.1						1			
Lithocarpus sp.2							1		
Lithocarpus sp.3							1		2
Lithocarpus sp.4								2	1
Lithocarpus sp.5								1	
Quercus elmeri Merr.	1								
Flacourtiaceae									
Casearia elliptifolia Merr.		1							
Casearia sp.1	5	6	2						
Hydnocarpus elmeri Merr.			2						
Hydnocarpus cf. *heterophylla* Bl.			2						
Hydnocarpus kunstleri (King) Warb.				2	5	4	1		
Hydnocarpus sumatrana (Miq.) Koord.				1	3				
Hydnocarpus woodii Merr.	7	2	4						
Hydnocarpus sp.1						3		1	
Ryparosa cf. *acuminata* Merr.								1	
Ryparosa baccaureoides Sleum.			2		1				3
Ryparosa kostermansii Sleum.	4	3	3	1					
Hypericaceae									
Cratoxylon arborescens (Vahl) Bl.									3
Icacinaceae									
Gonocaryum minus Sleum.		2			6	9			
Stemonurus scorpioides Becc.				1					
Lauraceae									
Actinodaphne sp.1								2	
Alseodaphne sp.1									1
Alseodaphne sp.2								1	
Alseodaphne sp.3							1		
Alseodaphne sp.4								1	
Alseodaphne sp.5							1		
Bielschmeidia wallichiana Kosterm.							1		
Bielschmeidia sp.1		2							
Bielschmeidia sp.2							1		
Bielschmeidia sp.3									1
Bielschmeidia sp.4							1		
Bielschmeidia sp.5							1		
Bielschmeidia sp.6		1	1		1		2	1	1
Bielschmeidia sp.7			1						
Bielschmeidia sp.8		1							
Cinnamomum porrectum (Roxb.) Kosterm.					4				
Cinnamomum sp.1									1
Cryptocarya sp.1									1
Cryptocarya sp.2					1		1	2	
Cryptocarya sp.3							1		3
Cryptocarya sp.4									1
Dehaasia sp.1			1						
Dehaasia sp.2				1	4				
Endiandra sp.1				1				1	
Lindera sp.1									1
Litsea cf. *castanea* Hk.f.									2
Litsea grandis Hk.f.									1

Species	Number of individuals per plot								
	1	2	3	4	5	6	7	8	9
Litsea sessilis (Bl.) Boerl.									1
Litsea sp.1			1						
Litsea sp.2							1		
Litsea sp.3							1		
Nothaphoebe sp.1			1					2	1
Persea sp.1								1	
Phoebe sp.1									1
Lauraceae genus unknown sp.1							2		
Lauraceae genus unknown sp.2							1		
Lecythicidaceae									
Barringtonia lanceolata (Ridl.) Payens		3	1						
Barringtonia racemosa (L.) Sring			1						
Barringtonia sp.1	1								
Barringtonia sp.2				1					
Barringtonia sp.3				1					
Linaceae									
Ctenolophum parvifolius Oliv.								1	
Loganiaceae									
Fagraea fragrans Roxb.					1				
Magnoliaceae									
Aromadendron nutans Dandy								1	4
Melastomataceae									
Memecylon sp.1								1	
Memecylon sp.2									1
Pternandra coerulescens Jack			1	1		1			
Pternandra echinata Jack	1						2		2
Meliaceae									
Aglaia aspera (Teijsm. & Binn.)					2				1
Aglaia exstipulata (Griff.) Theobald		1					1	2	
Aglaia lawii (Wight) Saldanha ex Ramamoorthy			1						
Aglaia leptantha Miq.							1		
Aglaia leucophylla King		1							
Aglaia simplicifolia (Bedd.) Harms			1						
Aphanamixis sp.1							1	1	
Dysoxylum cauliflorum Hiern							2	1	2
Dysoxylum cyrtobotryum Miq.							2		
Dysoxylum cf. *densiflorum* (Bl.) Miq.							2	2	
Dysoxylum cf. *excelsum* Bl.						1			
Dysoxylum rugulosum King						2			
Sandoricum sp.1								1	
Walsura pinnata Hassk.	1								
Moraceae									
Artocarpus dadah Miq.				1					
Artocarpus integer var. *sylvestris* Corner		1	1	1					
Artocarpus lowii King	1	1	2				1	1	
Artocarpus odoratissimus Blanco		2		1			2	4	2
Artocarpus nitidus Trec.				1				4	2
Myristicaceae									
Gymnacranthera contracta Warb.				1	2				
Horsfieldia grandis (Hk.f.) Warb.					1				
Horsfieldia cf.*polysepherula* (Hk.f. emend. King) Sinc.				1	1		1	2	1
Knema cinerea (Poir.) Warb.						1	1		

Species	Number of individuals per plot								
	1	2	3	4	5	6	7	8	9
Knema elmeri Merr.	1		3						
Knema furfuracea (Hk.f. & Th.) Warb.		1	1	3		1			
Knema cf. *glauca* (Bl.) Warb.								1	
Knema glaucescens Jack							1		
Knema latericia Elmer					1				
Knema latifolia Warb.				1		1			
Knema stenophylla (Warb.) Sinclair					1				
Myristica cinnamomea King			1		2				1
Myristica guatteriifolia D.C.				2					
Myristica iners Bl.					1	1	1		
Myristica malaccensis Hk.f.	1					3	1	1	
Myristica maxima Warb.		1				1			
Myristicaceae genus unknown sp.1			1						
Myrsinaceae									
Ardisia sp.1								1	
Myrtaceae									
Eugenia ochneocarpa Merr.				1	1			5	1
Eugenia sp.1	1	1	1						
Eugenia sp.2			1			1			
Eugenia sp.3						2			
Eugenia sp.4				3	1		4		
Eugenia sp.5				2		2			
Eugenia sp.6								1	
Eugenia sp.7	1	2							
Eugenia sp.8				1		2			
Eugenia sp.9							1		
Eugenia sp.10								1	
Eugenia sp.11									4
Eugenia sp.12								3	13
Eugenia sp.13							2		
Eugenia sp.14									1
Eugenia sp.15				1		1			1
Eugenia sp.16									1
Eugenia sp.17							1		
Eugenia sp.18									1
Eugenia sp.19								1	
Eugenia sp.20							1		
Eugenia sp.21	1			1					
Eugenia sp.22					2	1			
Eugenia sp.23	1								
Eugenia sp.24								1	
Eugenia sp.25					1				
Eugenia sp.26							1		
Eugenia sp.27	1	2							
Eugenia sp.28				2					
Eugenia sp.29					1			3	4
Eugenia sp.30							1		
Eugenia sp.31						1	1	4	1
Eugenia sp.32	1								
Eugenia sp.33								1	
Eugenia sp.34					2				
Eugenia sp.35						1			
Eugenia sp.36						1			
Olacaceae									
Anacolosa fructescens Bl.							1		
Ochanostachys amantacea Mast.				1	1	1	1	2	
Scorodocarpus borneensis Becc.		3	1						
Strombosia ceylanica Gardn.	1		2	1					

Species	Number of individuals per plot								
	1	2	3	4	5	6	7	8	9
Oleaceae									
Chionanthus cf. *curvicarpus* Kiew				1			4	2	2
Chionanthus sp.1									3
Olea javanica (Bl.) Knobl.				1	3	1			
Opiliaceae									
Champereia manillana (Bl.) Merr.							1		
Oxalidaceae									
Sarotheca sp.1			1						
Podocarpaceae									
Nageia wallichiana (Presl.) O.K.								1	
Polygalaceae									
Xanthophyllum affine Korth.	1				5	1			
Xanthophyllum amoemum Chad.			1		1				
Xanthophyllum cf. *borneense* Miq.					1				
Xanthophyllum ellipticum Korth.					1				
Xanthophyllum eurhynchium Miq.	4								
Xanthophyllum ferrugineum Meijden		1							
Xanthophyllum griffithii Hk.f.			1	5	1	1			
Xanthophyllum neglectum Meijden			1						
Xanthophyllum resupinatum Meijden			2						
Xanthophyllum schizocarpon Chad.				2	1	1			
Xanthophyllum scortechinii King					1				
Xanthophyllum stipitatum Benn.		1		1	2			1	4
Xanthophyllum vitellinum (Bl.) Dietr.	1								
Xanthophyllum sp.1				8	3	1			
Xanthophyllum sp.2				1	2				
Xanthophyllum sp.3			2						
Xanthophyllum sp.4	1								
Proteaceae									
Helicia excelsa (Roxb.) Bl.							1		
Rosaceae									
Atuna excelsa (Jack) Kosterm.				1					
Atuna racemosa Rafin.								1	
Kostermanthus heteropetalus (Scort. ex King) Prance				1					
Licania splendens (Korth.) Prance			1						
Maranthes corymbosa Bl.			1						
Parinari sp.1		1							
Prunus arborea var. *stipulacea* (King.) Kalkm.								1	
Prunus cf. *becarrii* (Ridl.) Kalkm.							2	1	
Prunus spicata Kalkm.	1								
Rubiaceae									
Canthium cf. *arborescens*	1	1							
Canthium confertum Korth.					1				
Gardeniopsis longifolia Miq.		1							
Nauclea maingayi Hk.f.		1							
Nauclea sp.1								1	
Porterandia anisophyllea (Jack ex Roxb.) Ridl.	1			1					
Psydrax sp.1				1					
Rothmannia sp.1							1		1
Timonius cf. *flavescens* (Jack) Barber							1		
Timonius cf. *wallichianus* (Korth.) Val.								3	
Rubiaceae genus unknown sp.1							1		

Species	Number of individuals per plot								
	1	2	3	4	5	6	7	8	9
Rutaceae									
Euodia cf. *punctata* Merr.									1
Macleurodendron porteri (Hk.f.) Hartley								1	
Sapindaceae									
Nephelium cuspidatum Hiern.						1			
Nephelium lappaceum L.									1
Xerospermum noronhianum Bl.					1		1	7	2
Sapindaceae genus unknown sp.1	1			1					
Sapindaceae genus unknown sp.2		1							
Sapindaceae genus unknown sp.3			1	1			2		
Sapindaceae genus unknown sp.4				1					
Sapindaceae genus unknown sp.5			1						
Sapotaceae									
Ganua palembanica Miq.					1				
Madhuca sp.1			1						
Madhuca sp.2		1	1						
Madhuca sp.3							4		
Madhuca sp.4					5				
Madhuca sp.5									1
Palaquium sp.1	1								
Palaquium sp.2					2				
Palaquium sp.3	1	2							
Palaquium sp.4			1						
Palaquium cf. *calophyllum* (T. & B.) Pierre						1			
Payena cf. *endertii* Lam							1		2
Payena sp.1				1					
Payena sp.2							1		
Simaroubaceae									
Irvingia malayana Benn.						1			
Sterculiaceae									
Heritiera cf. *sumatrana* (Miq.) Kosterm.	1						2		
Scaphium affine Ridl.	1	1							
Scaphium longiopetalum Kost.	2								
Scaphium parvifolium Ridl.						1		4	2
Sterculia scortechinii King			1						
Symplocaceae									
Symplocos adenophylla Wall. ex Don.							1		
Theaceae									
Adinandra acuminata Korth.							2	1	1
Adinandra cordifolia Ridl.							3	1	1
Schima wallichii (DC.) Korth.							1		1
Ternstroemia magnifica Stapf.								1	
Thymeleaceae									
?*Aetoxylon*	1			1					
Aquilaria beccariana Van Tiegh.								1	
Aquilaria malaccensis Lamk.				1					
Aquilaria microcarpa Baill.		1				1			
Gonystylus borneensis (Tiegh.) Gilg.		1					1		1
Gonystylus forbesii Gilg.				1					
Gonystylus spectabilis Airy Shaw			1			1			
Tiliaceae									
Grewia omphocarpa Miq.								1	
Microcos cinnamomifolium Burret	1		3				1		

Species	Number of individuals per plot								
	1	2	3	4	5	6	7	8	9
Microcos cf. *elmeri* Merr.		1							
Microcos florida Miq.								1	
Tiliaceae genus unknown sp.1					2	1	1		2
Ulmaceae									
Girroniera nervosa Planch.			1	2					
Girroniera subequalis Planch.				2		1	2	2	1
Verbenaceae									
Teijsmanniodendron bogoriense Koorders							1	1	1
Teijsmanniodendron coriaceum (C.B.Clarke) Kosterm.		1		3	2	3			
Vitex cf. *vestita* Wall.									1
Unknown lianas									
Liana, Family unknown sp.1		1							
Liana, Family unknown sp.2			1						
Liana, Family unknown sp.3				1					
Liana, Family unknown sp.4				1					
Liana, Family unknown sp.5							1		
Liana, Family unknown sp.6							1		
Liana, Family unknown sp.7							1		
Liana, Family unknown sp.8									1
Unknown trees									
Family unknown sp.1	1								
Family unknown sp.2		1							
Family unknown sp.3			1						
Family unknown sp.4				1					
Family unknown sp.5				2					
Family unknown sp.6				1					
Family unknown sp.7				1					
Family unknown sp.8				1					
Family unknown sp.9				1					
Family unknown sp.10					1				
Family unknown sp.11									
Family unknown sp.12							1		
Family unknown sp.13								1	
Family unknown sp.14									1
Family unknown sp.15									1

Appendix 3. Poulsen, A.D. & Pendry, C.A. Altitudinal zonation of ground herbs on Bukit Belalong, Brunei, Borneo. submitted to 'Biodiversity and Conservation', May 1994.

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