Fine Root Dynamics in a Bornean Rain Forest

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

By
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I hereby declare that this thesis has been composed by myself and except where otherwise stated the work contained herein is my own.

James Green

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Abstract

The role of fine root dynamics in the carbon and nutrient cycles of a primary, lowland dipterocarp rain forest in Sabah, Malaysia was investigated. A new method for estimating fine root production was developed which involved the combination of excavation and rhizotron techniques to separately quantify spatial and temporal variability in the root system. The aim was to produce a method that could quantify the simultaneous occurrence of fine root production, mortality and decomposition. The biomass of roots ≤2, >2-≤5, >5-≤10, >10-≤15 mm diameter in the top 1.2 m of the soil was 2830, 3544, 2310, 2157 kg ha^{-1} respectively. Fine root (≤2 mm diameter) production and disappearance were estimated as 4018 and 4843 kg ha^{-1} yr^{-1}. The concentration of acetic acid extractable phosphorus in the soil was very low (0.7 mg kg^{-1} in the top 5 cm) and the C:N ratio high (21). The hypothesis that soil fertility, and in particular phosphorus availability, is the primary factor governing fine root biomass in lowland tropical rain forests was discussed. Fine root production and disappearance rates were expressed in terms of a nutrient flux into and out of fine root biomass. No evidence was found to support the hypotheses that nutrients were retranslocated out of fine roots during senescence or that nitrogen, phosphorus or potassium were potentially limiting to fine root growth. It was suggested that greater synchrony was recorded in rates of fine root growth than has previously been recorded in rates of above-ground litterfall. Fine roots were found to be less important than above-ground litterfall in supplying the soil with organic matter. A new method for quantifying the decomposition rate of fine roots involving the disappearance rate of fine roots on rhizotrons was developed. Fine root decay rates were found to be similar to previously reported rates of leaf decay in the same forest. Fine roots were decomposing on average for 70% of their Persistence.

Chapter 1 General Introduction

There is currently much debate about how critical mineral nutrients are in determining the structure and function of lowland tropical rain forests and how this might affect the response of these forests to large scale disturbance (Grubb 1989, Whitmore 1989, Bruijnzeel 1991, Proctor 1992, Scott *et al.* in press, Thompson *et al.* in press). A model has dominated rain forest ecology which suggests that rain forests on nutrient-poor soils will have; closed and tight nutrient cycles, a large proportion of ecosystem nutrient capital held in plant biomass, high fine root biomass, a root mat, small sclerophyllous leaves, low foliar and litterfall nutrient concentrations and be unproductive (eg Jordan and Herrera 1981, Jordan 1989b). As a growing body of data on rain forest nutrient cycles accumulates it has become clear that this one model is not universally applicable (Proctor 1992).

Processes of fine root turnover are now widely recognised as important components of carbon and nutrient cycles in forest ecosystems (Persson 1980b, Vogt *et al.* 1982, Nadelhoffer *et al.* 1985, Petersen *et al.* 1985, Raich and Nadelhoffer 1989). Studies in a number of temperate and boreal forests have reported fine root production to comprise a significant proportion of ecosystem net primary production (8-85% Fogel 1985, 1991, Santantonio and Hermann 1985), yet there remain few studies of fine root production in tropical rain forests (Jordan and Escalante 1980, Sanford 1985, Cuevas and Medina 1988, Cavelier 1989). The lack of work on forest fine root systems remains largely a reflection of the relative difficulty of observing roots and measuring processes associated with roots rather than the perception of their importance in ecosystem cycles (Vogt *et al.* 1986b).

The efficient uptake of water and mineral nutrients by plants requires both the maintenance of a relatively unprotected interface between plant and soil, and the constant re-exploitation of the soil resource (Kolesnikov 1968, Reynolds 1975, Persson 1983a and b, Fogel 1983, Ulrich *et al.* 1981). Fine roots are, therefore, inherently short lived and their turnover constitutes a potentially important sink for metabolic carbon and mineral nutrients both at the individual plant and ecosystem levels of organisation. A number of methods for estimating fine root production have evolved over the last twenty years, yet all have serious limitations (Fogel 1991).

The sequential soil coring approach to estimating fine root production and turnover has been largely responsible for demonstrating that fine root dynamics in temperate and boreal forests was more important energetically than previously thought. This approach bases the determination of biomass flux, that is, production, mortality and decomposition, on differences between root biomass estimated by soil coring on sequential sampling occasions. At the simplest level, production can be estimated by the difference between observed annual maximum and minimum biomass (Edwards and Harris 1977, Harvey *et al.* 1978). The realization, however, that fine roots often live for considerably less than a year and that frequent fluctuations in fine root biomass often occur, led to the development of more sophisticated methods of calculation. These methods of calculation involve balancing observed changes in live and dead fine root biomass with transfers of biomass from one compartment to another and are often termed 'balancing transfers'. Balancing transfers calculations are all based on a basic relationship of population dynamics (McClaugherty *et al.* 1982, Fairley and Alexander 1985, Fogel 1985, Usher 1985):

$$Biomass_{t+1} = Biomass_t + Production - Mortality$$

The accuracy of balancing transfers estimates has been recognised to be very sensitive to violations of a number of the inherent assumptions:

(a) Singh *et al.* (1984) addressed the questions of sample size and sampling error and highlighted that the calculations rely heavily on the identification of maxima and minima of fine root biomass and are very sensitive to variability in the data. The timing of soil coring to intercept peaks and troughs of fine root biomass is critical (McClaugherty *et al.* 1982, Neill 1992). In recognition of these facts Vogt *et al.* (1986a) suggest that sampling protocols and subsequent calculations of fine root production should be adapted for individual ecosystems.

(b) Production estimates derived by sequential coring methods may be improved substantially if roots are separated into 'live' and 'dead' categories (McClaugherty *et al.* 1982, Santantonio 1979, Alexander and Fairley 1983, Fogel 1991). Common criteria for classifying live fine roots have been; colour, turgidity and integrity of the root apex and cortex (Persson 1983a, Fogel 1983, 1985, Ferrier and Alexander 1985). In practice, however, the classification of the physiological status of fine roots has proved difficult, especially where a mixture of species with differing fine root

morphologies are encountered, or where ectomycorrhizal sheaths mask the physiological status of the host tissue (Fogel 1985, 1991).

(c) Sequential coring methods only record net changes in live and dead fine root biomass between sampling occasions and cannot account for simultaneous production, mortality and decomposition. Failure to account for the simultaneous occurrence of these processes may lead to a substantial underestimation of fine root production (Singh *et al.* 1984, Santantonio and Grace 1987, Neill 1992). The model produced by Kurz and Kimmins (1987) highlights the fact that if fine root biomass is in a steady-state, methods involving sequential coring will yield estimates of zero production, mortality and decomposition. Any temporal overlap in these processes will cause an underestimation of their magnitude, the error becoming greater with increasing overlap. In a steady-state scenario where biomass is constant from one sampling occasion to the next and rates of production, mortality and decomposition are equal, biomass flux may be estimated by combining biomass with an independently measured rate of fine root decay using litter bags (Fairley and Alexander 1985). Where changes in live and/or dead fine root biomass do occur, however, the use of an independently measured fine root decay rate becomes confused.

In-growth bags have provided an alternative, or sometimes complementary method to soil coring for estimating fine root production (Fabiao *et al.* 1985, Persson 1979, 1983a, Steen 1991, Neill 1992). The procedure involves incubating a given volume of root-free soil, or other growth medium, in a mesh bag within the soil and the subsequent sequential harvest of bags to determine the mass of roots contained within. Fine root production can be estimated at the simplest level by summing increments in the mass of roots within the bags (Harris *et al.* 1977, 1980, Persson 1980b). However, as with sequential coring, no in-growth bag method can record simultaneous biomass production and disappearance (Steen 1991, Neill 1992). The main conceptual difficulty with in-growth bag techniques is that analogous unexploited and root-free volumes of soil may rarely be encountered in mature forest ecosystems and may only be realized in the root-throw zone of tree fall gaps (Putz 1983, Sanford 1989a). The technique has certainly been most usefully employed in studies of annual (Hansson and Steen 1984, Hansson and Andren 1986) and young perennial (Fabiao *et al.* 1985, Persson 1980a) crops, where exploitation of a root-free soil is the norm (Neill 1992).

The methodology is, however, supported by the agreement a number of studies have recorded between separate sequential coring and in-growth bag estimates of production in the same ecosystem (Cavelier 1989, Cuevas *et al.* 1991, Neill 1992). Three neotropical studies have used in-growth bags, or allied methodology, to obtain estimates of fine root production in lowland rain forests (Jordan and Escalante 1980, Cuevas and Medina 1988, Cavelier 1989). In-growth bags show great utility in allowing for comparisons between treatments applied to the growth medium (Lund *et al.* 1970, Safford 1974, Steen *et al.* 1984) and have been used to test for potentially limiting nutrients in lowland rain forests in Amazonia (Cuevas and Medina 1988).

Observation methods, which introduce a viewing surface in to the soil, allow a fixed population of roots to be monitored through time. Viewing surfaces have ranged in scale from large walk-in rhizotron facilities to small glass tubes, or mini-rhizotrons (Atkinson and Mackie-Dawson 1991, Mackie-Dawson and Atkinson 1991). Observation methods more readily separate the temporal and spatial variation in a population of fine roots, than other methods commonly used in fine root study (Atkinson 1985). There are, however, often major questions as to how representative the rhizotron population is of roots in bulk soil (Huck and Taylor 1982, van Noordwijk *et al.* 1985, McMichael and Taylor 1987, Vos and Greenwald 1987, Harper *et al.* 1991). A number of studies have found observation surfaces to cause a significant concentration of fine roots and protocols that record the spatial distribution of fine roots need to verify that the spatial distribution of the fine root population is not affected by the observation panel or that it differs to that in bulk soil by a predictable amount (Taylor *et al.* 1970, 1990, Klepper *et al.* 1973, Taylor and Böhm 1976, Atkinson 1985, Meyer and Barrs 1985, Vos and Greenwald 1987). In addition, it needs to be verified that the micro-environment of a root growing against a glass panel in the soil is not significantly different from one growing in bulk soil, or that any difference does not affect the longevity or activity of fine roots on the soil:glass interface.

In ecosystems where a relatively high fine root biomass is maintained relative to short term fluctuations in the biomass, that is in a system that approaches a steady-state, existing methods of estimating fine root production will yield underestimates. A main aim of this project was to develop a new method for estimating fine root production

that could estimate the simultaneous occurrence of fine root biomass production and disappearance. With the sequential coring approach to estimating fine root production the high spatial variability of fine roots in the soil confounds temporal measurements (Atkinson 1985). In the method developed in the current study excavation methods were used to assess the spatial variability of the fine root system and observation methods separately employed to quantify temporal variability.

Although the importance of fine root processes in carbon and nutrient cycles in temperate and boreal forests has been identified, few studies have attempted to measure fine root production in tropical rain forests. The aim of this project was to assess the role of fine root dynamics in the carbon and nutrient cycles of a primary lowland dipterocarp rain forest in Sabah, Malaysia.

Chapter 2 Site, Soils and Vegetation

2.1 Introduction

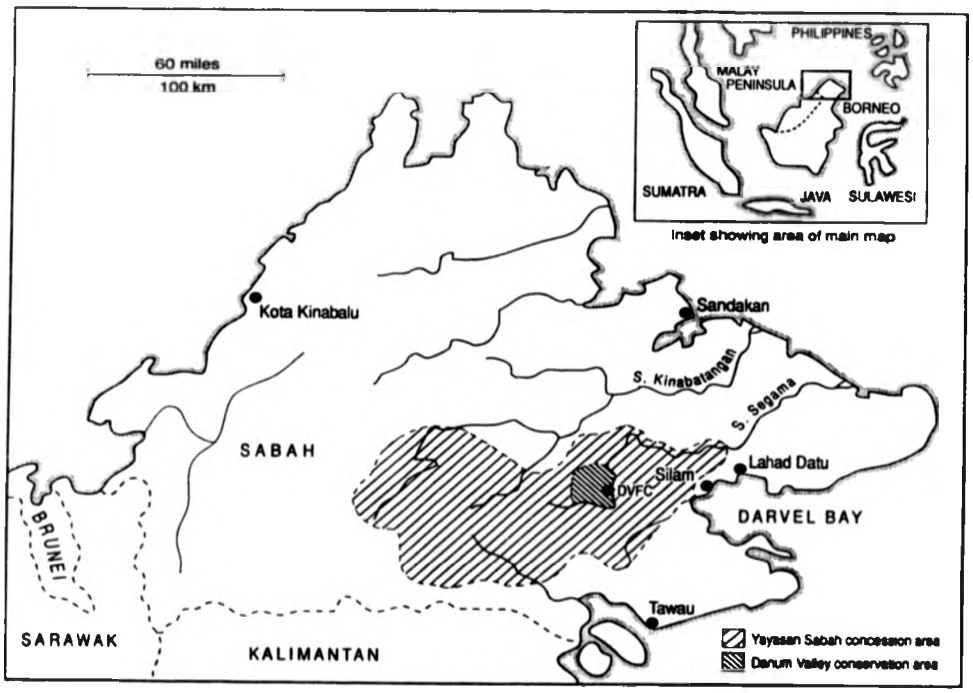
The Malaysian State of Sabah has a land area of 73,371 km^2 and occupies about one tenth of the island of Borneo. Although 45% of the land area is projected to remain as Permanent Forest Reserve, primary lowland evergreen rain forest (*sensu* Whitmore 1984) now occupies less than 6.8% of the land area (Marsh and Greer 1992). The Danum Valley Conservation Area (DVCA) (4°58' N, 117°42'E) comprises 438 km^2 of predominantly lowland forest within the Yayasan Sabah logging concession which was set aside in 1984 (Figure 2.1.1). The DVCA contains what is set to become an increasingly important proportion of the undisturbed lowland dipterocarp forest remaining in Sabah. The conservation area is not yet, however, protected by any legally binding status and its continued existence rests largely on the goodwill of Yayasan Sabah and the Sabah Forestry Department (Marsh and Greer 1992).

The upper Segama River catchment has been uninhabited in recent times (Wright 1975), but coffins and burial jars have been found at three separate locations within the DVCA (Figure 2.4.1). These discoveries raise the possibility that parts of the DVCA have been subject to shifting cultivation in the past. Although there was no systematic search for soil charcoal in this study, cursory examination of soil profiles and cores showed it to be ubiquitous within plots 2 and 3 (Figure 2.4.1) at depths of 30-60 cm. A single radiocarbon test on soil charcoal fragments collected near one of the burial sites dates to 315 ±20 years BP (Marsh and Greer 1992), although the age of the wood when burned was not known. It remains unclear as to whether these charcoal fragments are anthropogenic in origin.

2.2 Physiography and geology

The Ulu Segama highlands, in which the DVCA is situated, comprise an area of rugged and actively eroding terrain that rises to 1093 m at Gunung Danum. The area immediately surrounding the DVFC comprises mostly gently undulating terrain characterised by alternating ridges and deep gullies containing a close dendritic network of ephemeral streams.

Figure 2.1.1 The location of the Danum Valley Field Centre (DVFC) in Sabah, Malaysia.



Three main geological formations have been recognised within the Segama highlands; the Crystalline Basement, Chert-Spillite formation and Kuamut formation (Fitch 1955, Leong 1974, Muhamad *et al.* 1989). The area immediately surrounding the DVFC, and including the research plots (Figure 2.4.1), is occupied by rocks of the lower to upper Miocene Kuamut formation (Leong 1974). The formation is a mixture, or melange, consisting of blocks of sedimentary and volcanic rocks embedded in a matrix of sandstone and mudstone. The melange originates from submarine slumping and the rocks are known collectively as slump breccia. The sedimentary blocks consist of sandstone, radiolarian chert, shale and siltstone, while the volcanic blocks can be divided into three main groups; basalts, tuffs, and agglomerate. The intimate mix of rocks of differing lithology within the melange makes prediction of the parent material of a soil at any particular location problematic.

2.3 Climate

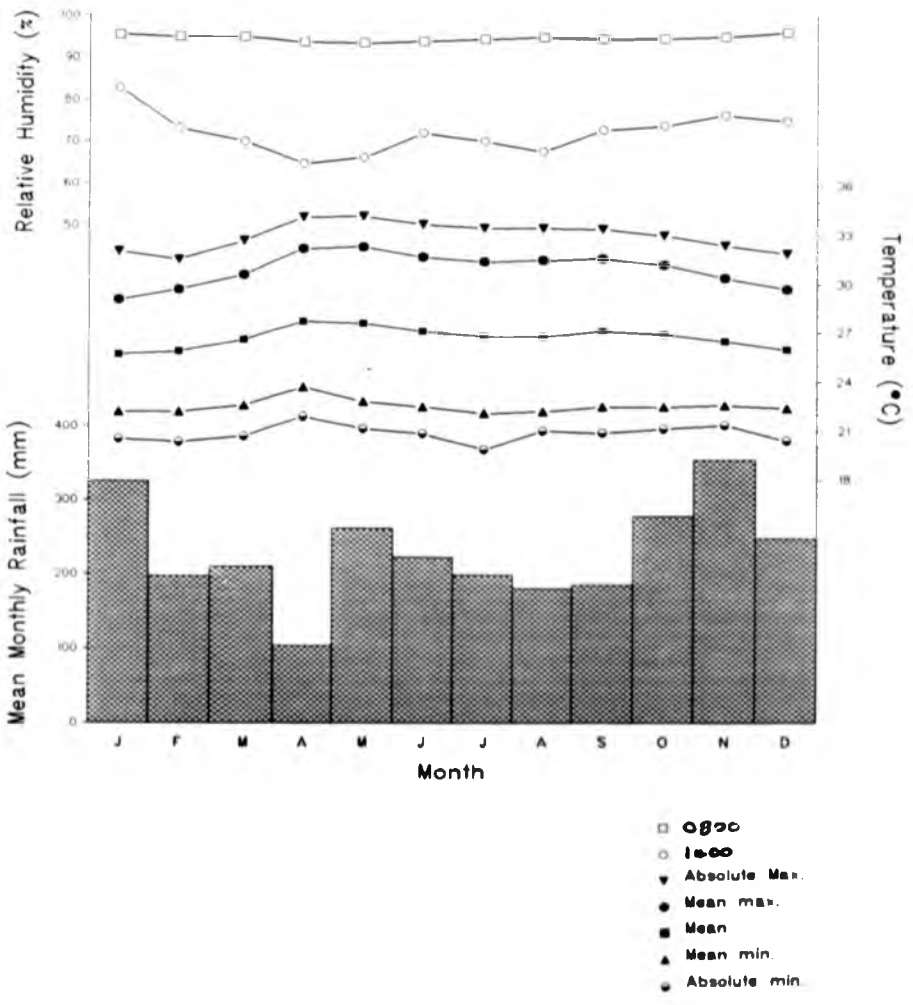
Daily meterological measurements have been taken at DVFC since September 1985. The weather station is located on top of a small grass-covered knoll within a large clearing (about 4 ha) adjacent to the Segama River. The station is about 200 m above sea level and about the same height as the sample plots of this study. Rainfall was recorded with a Casella tilting siphon rainfall recorder. A Stevenson screen (1.2 m from the ground) was used to house maximum, minimum, and wet and dry bulb thermometers. Wet and dry bulb readings were taken at 0800 and 1400 hours. Until the recent penetration of logging roads the Ulu Segama area had remained remote and the nearest weather station with records long enough to show seasonal patterns with some degree of certainty (1971 to present) is Silam camp about 50 km to the east of DVFC and at sea level (Figure 2.1.1).

The climate of the region is greatly influenced by the edge effects of two monsoons; the north-east monsoon in November to March and the south-west monsoon in June and July. The mean annual rainfall for DVFC (September 1985-February 1992) is 2821 mm and measurable rain is received on average in 220 days per year. Figure 2.3.1 shows the mean monthly rainfall pattern. The onset of the monsoons tends to be quite variable, while the general trend for drier periods in the inter-monsoon months of April and August/September appears to be more predictable. The majority of rain falls in the afternoon and evening and is associated with thunder cells whose passage can be quite localised. Rain gauges 2 km apart near DVFC show considerable differences in daily rainfall totals, although annual totals tend to even out.

Brown (1990) collated rainfall data from five sites in south-eastern Sabah and postulated a marked decline in rainfall eastward from the high ground around the Segama and Kuamut rivers towards the coast. It was suggested that the high ground initiates orographic rainfall during the north-east monsoon, when most of the rain falls in eastern Sabah. It is well documented that the east coast of Borneo tends to be drought prone (Beaman *et al.* 1985, Leighton and Wiraman 1986, Walsh unpublished). For four months during 1983 Sabah was affected by a severe drought associated with the El Niño/Southern Oscillation (ENSO) phenomenon in the eastern Pacific (Cane 1983, Philander 1983), during which there were extensive fires in logged forest, which

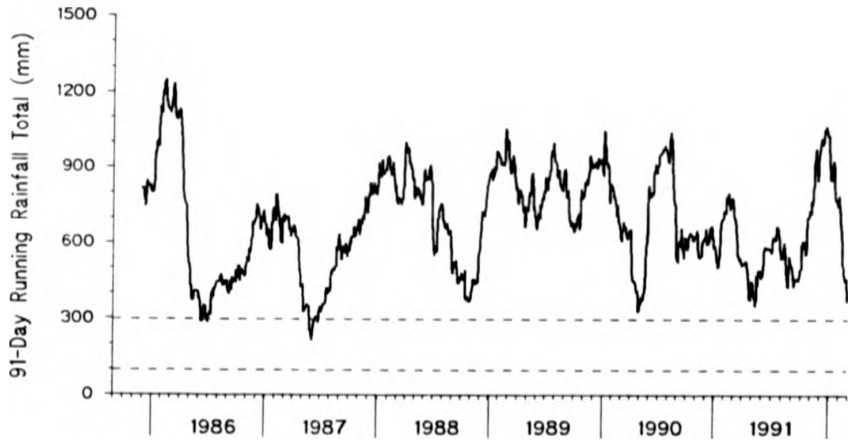
subsequently spread into some areas of primary forest. ESNO episodes are thought to occur cyclically at intervals of 2-10 years (Beaman et al. 1985) and Leighton and Wiraman (1986) matched nine out of ten droughts since 1944 in East Kalimantan with ESNO events.

Figure 2.3.1 Monthly climatic means for the Danum Valley Field Centre, Sabah from September 1985 to February 1992.



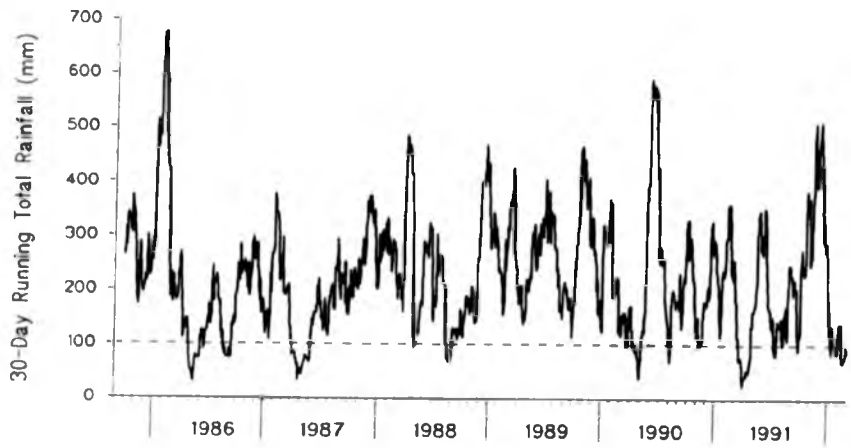
Drought conditions for Sabah have been defined as occurring when total rainfall for any three consecutive months is less than 100 mm (Beaman *et al.* 1985). Figure 2.3.2 shows the 3-month (91-day) running rainfall totals for DVFC. The figure for any one day is the total rainfall that occurred on that and the previous 90 days. No drought of the severity defined by Beaman *et al.* has occurred while meterological records have been kept at DVFC, the lowest 91-day total being 216 mm.

Figure 2.3.2 Three month (91-day) running rainfall totals for the Danum Valley Field Centre, Sabah from September 1985 to February 1992.



Brunig (1969) traced 30-day running rainfall totals for five stations in Sarawak and found that there where periods of 30 days that received less than 100 mm of rain at least once a year in the interior and as often as 3-4 times a year at the coast. Baille (1972, 1976) concluded that vegetation on deeper soils was not subject to moisture-stress during these annual dry periods but that on shallower soils moisture-stress occurred much more frequently. The 30-day running rainfall totals for DVFC (Figure 2.3.3) show that dry periods of this magnitude have occurred on nine occasions since September 1985 and that 275 or 12% of days had received less than 100 mm of rain on that and the previous 29 days. The longest period during which the 30-day rainfall total at DVFC has remained less than 100 mm since September 1985 was 63 days during April-June 1987 and the lowest 30-day rainfall total recorded was 24.4 mm.

Figure 2.3.3 One month (30-Day) running rainfall totals for the Danum Valley Field Centre, Sabah from September 1985 to February 1992.



Mean daily maximum and minimum temperatures at DVFC are 30.9 °C and 22.5 °C. The highest and lowest recorded temperatures are 37 °C and 18 °C, which reflects the freedom from extremes of temperature in a wet equatorial climate. Mean monthly temperature is approximately inversely correlated with rainfall, with the highest temperatures reached in the inter-monsoonal months. Mean relative humidity at 0800 is 94.5% and at 1400 is 72.0%. Consideration must be given to the location of the meterological station when interpreting relative humidity. The relative humidity measured is likely to be considerably lower than at a similar height from the ground under the forest canopy and may more closely resemble the above-canopy environment.

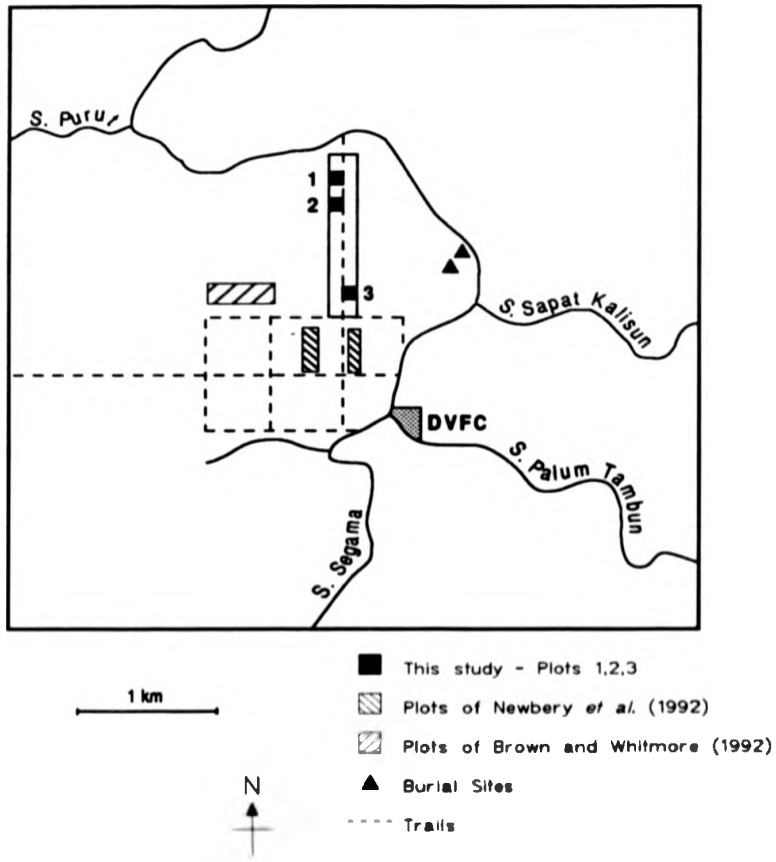
2.4 Research Plots

2.4.1 Plot Selection and Demarcation

A representative rectangular block (1500 m x 200 m) of primary forest was subjectively chosen to be within daily walking distance of the field centre and to exclude the riparian zone of the Segama river (Figure 2.4.1). Within this block three replicate 1 ha plots were selected at random from a possible 30 plots. The boundaries

of each 100 m x 100 m plot was demarcated using a survey tape and compass, without correction for slope. The central 50 m x 50 m of each plot was subdivided into nine subplots (16.7 m x 16.7 m), one of which was eliminated at random (Fig. 2.4.2 a,b,c). The outer boundary of each plot and the corners of each subplot were marked with lengths of PVC pipe driven into the ground to ensure permanency.

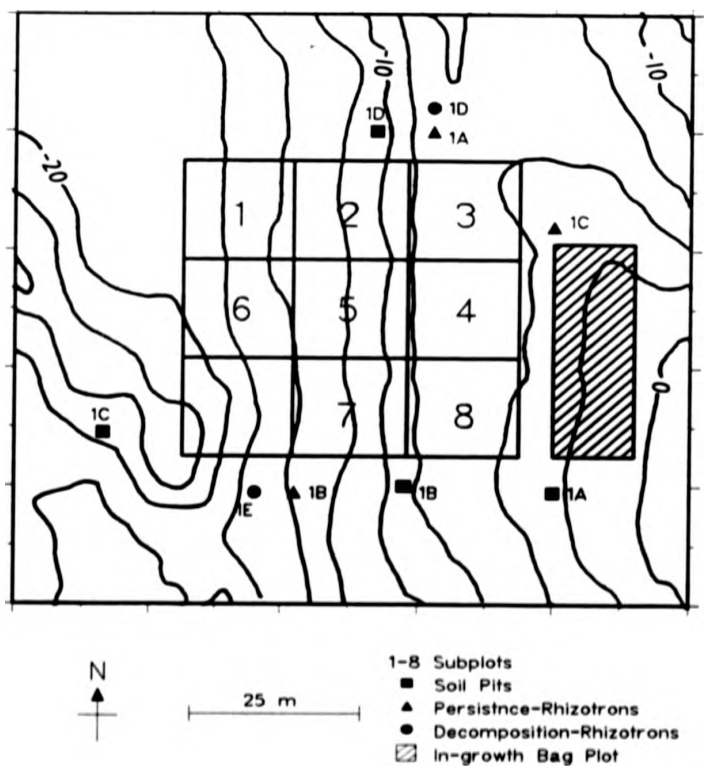
Figure 2.4.1 The location of research plots in relation to the Danum Valley Field Centre.

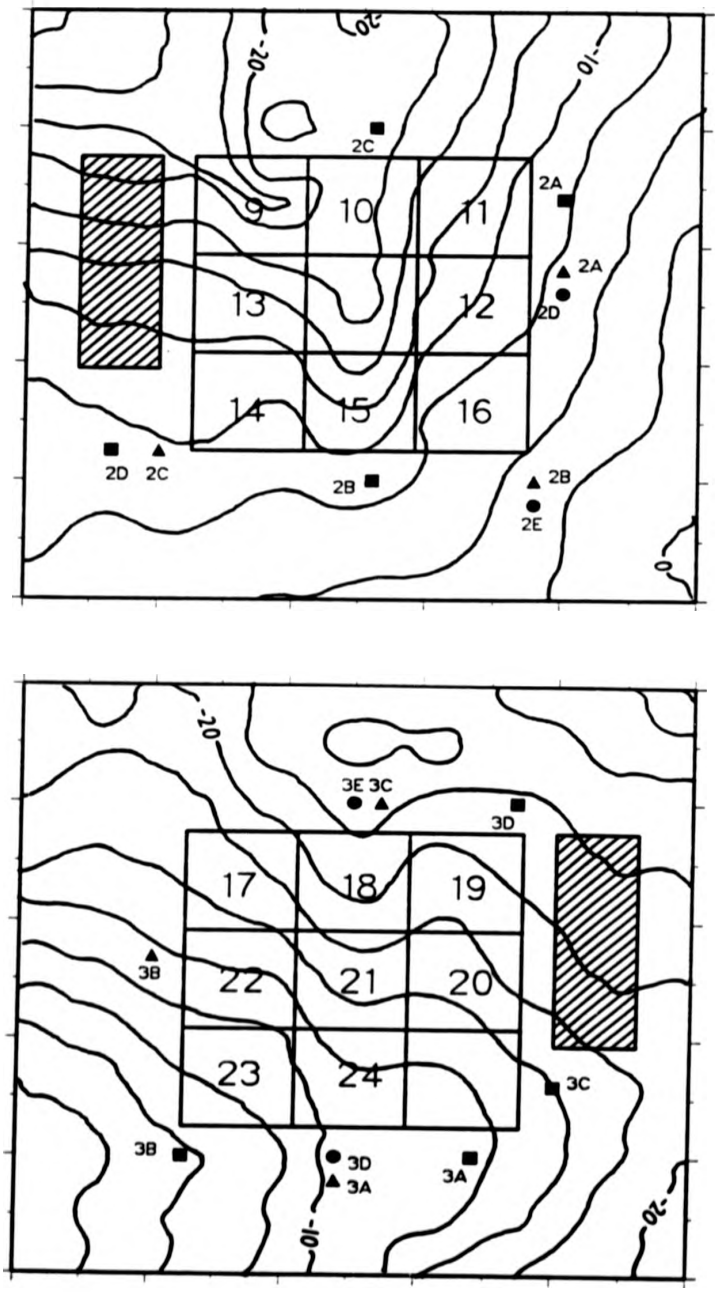


2.4.2 Microtopography of Plots

For the purposes of a survey of microrelief and to aid in vegetation enumeration each plot was further divided into eight 12.5 m wide strips running north to south which were temporarily marked with plastic string. A clinometer strapped to a camera tripod, and a ranging pole, were used to measure the height differences between points to within ±10 cm. Firstly height differences on a base line running east-west along the one side of the plot were measured at 12.5 m intervals and then height differences at 10 m intervals on each line running north. The height of each sample point was expressed relative to a fixed point at the corner of the plot, all plots being about 200 m above sea level. A contour map of each plot was drawn. Figures 2.4.2 a,b and c show the plot boundaries, contours and the location of some of the experimental sampling points.

Figure 2.4.2 Topographic map of Research plots; (a) Plot 1, (b) Plot 2, (c) Plot 3.




-20
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24
3C
3B
3D
3A
3A
-10
-20
N
25 m
1-8 Subplots
Soil Pits
Persisthce-Rhizotrons
Decomposition-Rhizotrons
In-growth Bag Plot

2.5 Soils

2.5.1 Introduction

The soils of the three permanent sample plots form part of the Bang Association (Wright 1975) and are developed mainly on sandstones and mudstones of the Kuamut Formation (Leong 1974). The definite identification of parent material at any particular location is hindered by the presence of blocks of miscellaneous rocks within the sandstone and mudstone matrix of the Kuamut formation. Similar soils near the permanent sample plots have previously been classified under the USDA system as Ultisols (USDA 1975, 1982) or by the FAO system as Orthic Acrisols (FAO/UNESCO 1974, Sinun 1991, Burghouts et al. 1992, Marsh and Greer 1992). The distinguishing feature of Ultisols is a argillic horizon that contains at least 1.2 times as much clay as the topsoil. The argillic horizon of Ultisols typically have a medium to coarse blocky structure with clay coatings on fissure surfaces. Ultisols have, by definition, a low base saturation (<35% in subsoil) and often have high concentrations of exchangeable aluminium (Sanchez 1976, Burnham 1984).

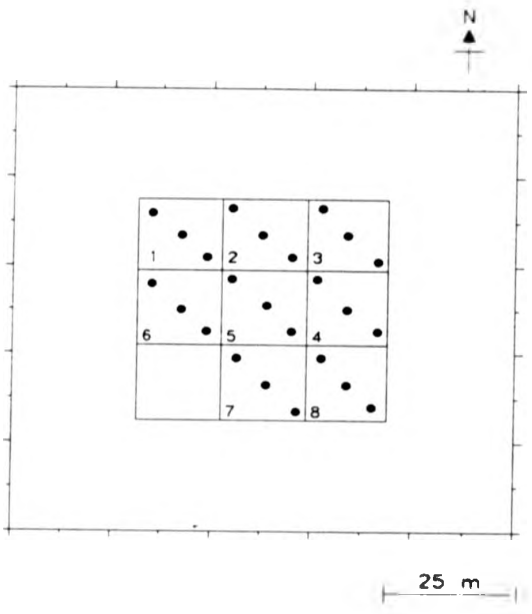
2.5.2 Materials and Methods

Four soil pits were located within each plot on a stratified random basis (Figures 2.4.2a,b,c). The soil profiles were not subjectively positioned as no distinctly different soil types were recognised prior to excavation and also because the pits were used to assess the vertical distribution of root endings. A vertical face was prepared (1 m wide, 1.2 m deep) and a profile description carried out according to the Soil Survey of England and Wales (Hodgson 1974). Rectangular blocks of soil (100 x 100 x 50 mm deep) were cut from each profile face at depths of 5-10, 20-25, 35-40, 50-55, 65-70, 80-85, 95-100 cm using a trowel and retained for analysis. Soil samples of known volume were obtained by driving stainless steel rings (inside diameter 73 mm, depth 50 mm) into the profile at the above depths. The bulk density of these samples was determined by the mass of oven dry soil and its field volume (McIntyre and Loveday 1974).

In addition, three 0-15 cm soil cores were taken from within each of the twenty-four subplots using a cylindrical auger of internal diameter 8 cm in the systematic

arrangement shown in Figure 2.5.1. The litter layer was removed and the core quartered lengthwise, with one quarter being retained at random for analysis.

Figure 2.5.1 The systematic arrangement of cores taken for soil analyses.



Each of the soil samples obtained from pits or cores was broken up, obvious roots removed and air-dried in a fan-ventilated glasshouse (maximum temperature 45 °C). Each sample was pounded to pass a 2 mm sieve and a 250 g subsample retained, by coning and quartering, for analysis (Allen 1989). A subsample (10 g) was ground to 250 μm mesh size in an agate ball mill. Weighed subsamples were oven-dried at 105 °C so that results for the analyses carried out on air-dry soils could be expressed on an oven-dry basis.

A mechanical analysis was carried out on soil samples from two randomly selected pits per plot by a modified hydrometer method (Bouyocos 1927a and b, Day 1965). pH was measured in a mixture of soil in a 1:2 ratio with both water and 0.01 M calcium chloride (McLean 1982). Loss-on-ignition was measured on samples which were heated at 375 °C for 16 hours and again after heating for a further 3 hours at

700 °C (Allen 1989). Total carbon and total nitrogen were determined for ground (250 μm) subsamples with a Carbon-Hydrogen-Nitrogen Elemental Analyzer (Carlo Erba, Model 1106). Total phosphorus was determined on ground subsamples by the method of Smith and Bain (1982) involving fusion with sodium hydroxide in nickel crucibles, followed by water dissolution of the melt and determination of phosphorus as a reduced complex.

Cations were extracted with ammonium acetate at pH 7 (Allen 1989) and analyzed by inductively-coupled-plasma atomic emission spectrometry (ICP-AES, Fisons 3580 B analyzer). Exchange acidity was determined by extraction with neutral barium acetate solution. A back titration of the leachate to pH 7 provides a measure of the exchange acidity of the soil. Effective cation exchange capacity (ECEC) was estimated by the summation of exchangeable cations and exchangeable acidity (Anderson and Ingram 1989, Coleman and Thomas 1967). Percentage base saturation was calculated as total exchangeable bases as a percentage of ECEC (Landon 1984).

2.5.3 Results

A sample profile description is given in Table 2.5.1. The twelve soil pits excavated were superficially very similar. On steeper slopes and stream sides saprolite could be encountered at depths of 0.5-1.2 m. These shallower soils had increasing quantities of weak stones with depth, which often had red coatings (colour typically 10R 5/8).

The variation in soil texture and bulk density with depth in the profile is given in Table 2.5.2. There is a gradual increase in the proportion of clay and in the bulk density down the profile (Figure 2.5.2).

Table 2.5.1 Soil profile description for pit 2A (for location see Figure 2.4.2b).

Depth (cm)	Horizon	Description
-2-0	L	Fresh litter layer. Abrupt boundary with mineral soil.
0-5	Ah	Orange (7.5YR 6/6) sandy clay loam. Rubbed colour bright brown (7.5YR 5/6). Weakly developed medium sub-angular blocky with no mottles or stones. 0.5% very fine to coarse macropores. Slightly sticky and very plastic when wet. Abundant roots. Boundary to next horizon diffuse.
5-55	B_1	Orange (5YR 6/8) clay loam. Moist colour lighter orange (7.5YR 6/6). Massive fine angular blocky with no mottles or stones. 0.1% very fine to coarse macropores. Slightly fluid and very plastic when wet. Common roots. Boundary to next horizon diffuse.
55-120	B_2	Orange (5YR 6/8) clay loam, becoming slightly more orange with depth. Moist colour yellow orange (7.5YR 7/8). Massive fine angular blocky with no mottles or stones. Rare macropores and few roots. Slightly fluid and very plastic when wet.

Figure 2.5.2 The mean particle-size distribution and bulk density of twelve soil profiles (for locations see Figures 2.4.2a-c). Equivalent spherical diameter (mm); sand >0.02, silt 0.02-0.02, clay <0.002.

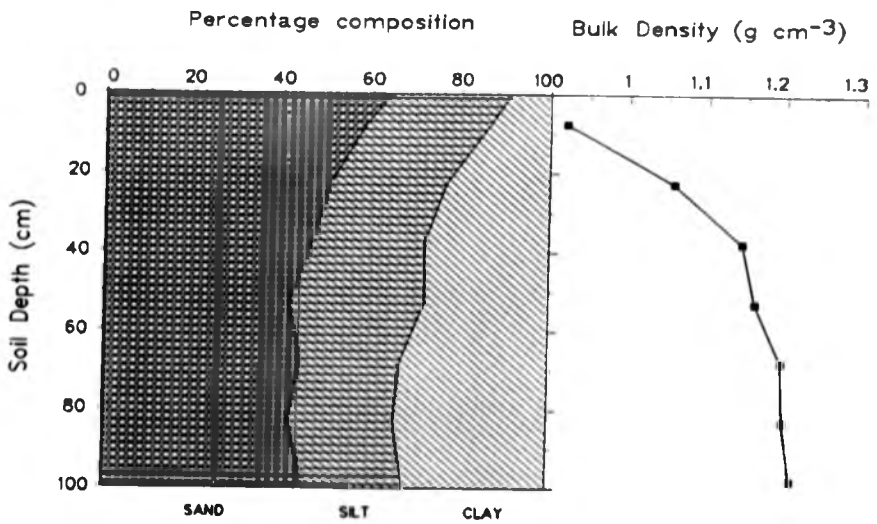


Table 2.5.2 The mean (and ranges) particle size distribution of twelve soil profiles. The textural class according the International system is given.

Soil Depth	International Sand	International Silt	Clay	BSTC Sand	BSTC Silt	Textural Class
(cm)	(>0.02)	(0.02-0.002)	(<0.002)	(>0.06)	(0.06-0.002)	
5-10	58.7 (45-71)	28.0 (20-40)	13.3 (9-22)	40.7 (26-51)	46.0 (35-61)	SL
20-25	50.7 (39-60)	26.1 (19-34)	23.2 (21-27)	35.0 (22-44)	41.8 (34-51)	SCL
35-40	46.5 (35-53)	25.5 (22-32)	28.0 (25-33)	33.0 (22-40)	38.7 (35-45)	SCL
50-55	41.7 (30-50)	30.5 (23-38)	27.8 (12-37)	28.3 (18-38)	43.9 (39-50)	CL
65-70	44.3 (32-50)	22.5 (19-29)	33.2 (29-39)	32.5 (20-39)	34.3 (28-41)	CL
80-85	41.8 (28-50)	23.7 (19-33)	34.5 (30-39)	30.0 (16-40)	35.5 (29-45)	CL
95-100	44.8 (34-59)	22.7 (19-31)	32.5 (22-37)	34.6 (20-51)	32.9 (26-45)	CL

BSTC - British Soil Texture Classification
International - United States Department of Agriculture Classification
SL - Sandy loam
SCL - Sandy clay loam
CL - Clay loam

Table 2.5.3 The means (and ranges) of soil analyses

Sample depth (cm)	n	pH(H_2O)	pH($CaCl_2$)	Loss-on ignition (375°C) (%)	Loss-on ignition (700°C) (%)	Total carbon (%)	Total nitrogen (10^{-3} %)	Total phosphorus (mg $100g^{-1}$)
5-10	12	4.32 (4.13-4.57)	3.70 (3.57-3.81)	4.8 (2.9-7.7)	5.7 (4.1-8.4)	1.36 (0.76-2.01)	75 (15-135)	23.7 (17.4-29.6)
20-25	12	4.42 (4.27-4.53)	3.69 (3.61-3.75)	3.6 (2.5-4.3)	4.4 (3.7-5.0)	0.70 (0.56-0.94)	26 (5-44)	20.0 (16.1-24.4)
35-40	12	4.49 (4.36-4.63)	3.68 (3.61-3.75)	3.5 (2.1-6.4)	4.2 (3.5-4.8)	0.48 (0.40-0.70)	7 (0-29)	18.3 (14.0-22.7)
50-55	12	4.55 (4.42-4.70)	3.69 (3.62-3.79)	3.6 (2.3-7.4)	4.3 (3.6-4.8)	0.41 (0.32-0.72)	2.9 (0-14)	18.9 (12.6-27.5)
65-70	12	4.62 (4.46-4.89)	3.73 (3.66-3.83)	3.5 (2.2-7.5)	4.3 (2.8-5.0)	0.36 (0.19-0.59)	1.1 (0-10)	18.7 (13.5-27.9)
80-85	12	4.64 (4.48-4.87)	3.75 (3.69-3.89)	3.5 (2.2-5.3)	4.7 (2.8-8.7)	0.33 (0.17-0.54)	0.041 (0-0.3)	11.7 (12.6-24.0)
95-100	12	4.71 (4.55-4.95)	3.78 (3.71-3.95)	3.4 (2.1-7.1)	4.6 (2.6-8.4)	0.29 (0.17-0.42)	0.51 (0-4.2)	17.2 (11.3-25.7)
[1]0-15	24	[b]4.25 (4.01-4.51)	[ab]3.64 (3.47-3.90)	†6.5 (4.5-10.0)	†7.9 (6.4-11.2)	†2.45 (1.70-4.30)	[b]125 (52-221)	[b]27.2 (22.2-34.0)
[2]0-15	24	[a]4.38 (4.07-4.58)	[a]3.69 (3.50-3.87)	†6.0 (3.3-10.0)	†7.2 (4.4-11.2)	†2.74 (1.19-4.96)	[b]108 (33-215)	[b]26.7 (16.1-35.8)
[3]0-15	24	[b]4.22 (3.94-4.43)	[b]3.61 (3.49-3.71)	†6.2 (4.5-10.6)	†7.9 (5.8-12.0)	†2.67 (1.73-5.34)	[a]164 (108-263)	[a]30.2 (23.1-38.8)

1 - Plot 1
2 - Plot 2
3 - Plot 3
† - P >0.05 (not significant)
a,b,c - non-significant ranges of Duncan's multiple range test (P <0.05)

Table 2.5.3 (continued)

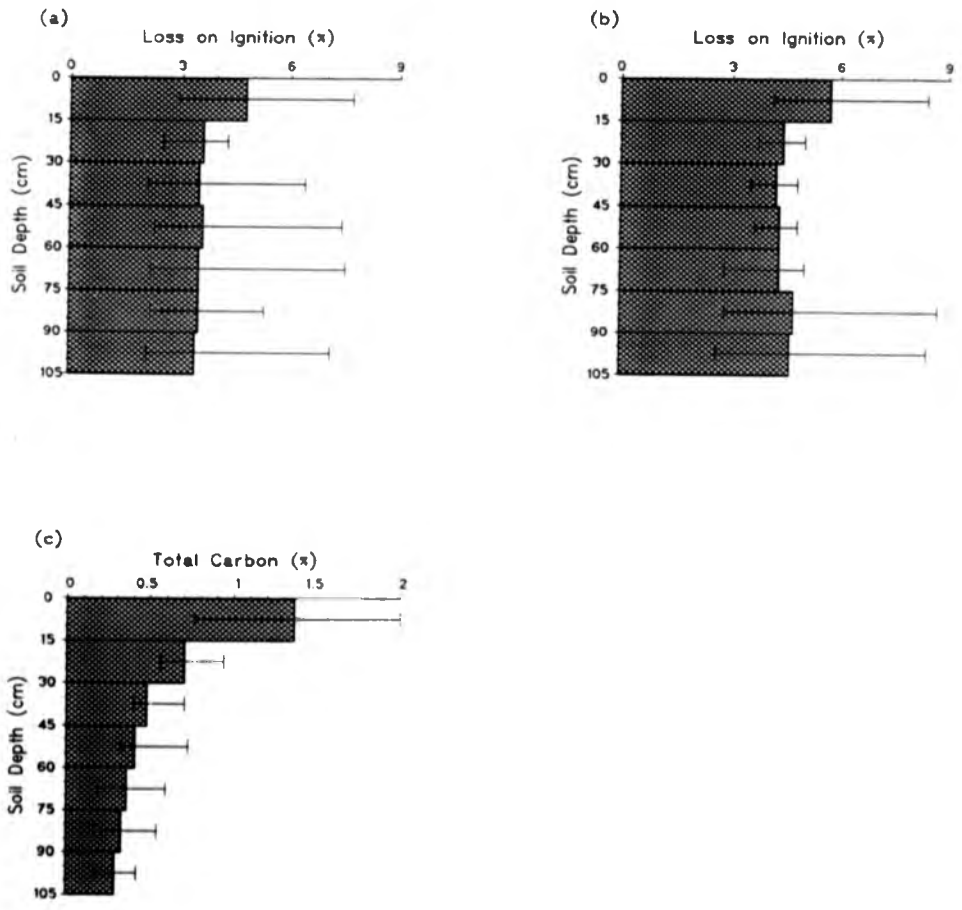
Sample Depth cm	Extractable phosphorus (mg kg^{-1})		Exchangeable calcium (m-equivs $100g^{-1}$)		Exchangeable magnesium (m-equivs $100g^{-1}$)		Exchangeable potassium (m-equivs $100g^{-1}$)		Exchangeable sodium (m-equivs $100g^{-1}$)	
5-10	0.25	(0.15-0.39)	0.203	(0.05-1.07)	0.238	(0.10-0.49)	0.171	(0.11-0.25)	**0.043**	**(0.02-0.18)**
20-25	0.24	(0.10-0.37)	0.110	(0.03-0.49)	0.195	(0.06-0.61)	0.158	(0.11-0.24)	**0.036**	**(0.02-0.11)**
35-40	0.29	(0.12-).64)	0.056	(0.03-0.16)	0.187	(0.05-0.61)	0.160	(0.11-0.24)	**0.035**	**(0.02-0.10)**
50-55	0.37	(0.17-0.82)	0.043	(0.03-0.11)	0.163	(0.04-0.56)	0.160	(0.12-0.23)	**0.036**	**(0.02-0.12)**
65-70	0.38	(0.23-0.92)	0.036	(0.02-0.10)	0.127	(0.03-0.40)	0.153	(0.10-0.20)	**0.032**	**(0.02-0.06)**
80-85	0.41	(0.24-1.12)	0.038	(0.02-0.08)	0.112	(0.03-0.33)	0.168	(0.12-0.23)	**0.039**	**(0.02-0.11)**
95-100	0.44	(0.20-1.20)	0.036	(0.02-0.08)	0.096	(0.03-0.32)	0.158	(0.10-0.28)	**0.047**	**(0.01-0.24)**
[1]0-15	0.34	(0.24-0.68)	†0.531	(0.13-3.74)	†0.498	(0.21-0.99)	†0.214	(0.13-0.43)	[ab]**0.035**	**(0.03-0.04)**
[2]0-15	0.37	(0.18-0.63)	†0.397	(0.06-3.88)	†0.541	(0.15-1.89)	†0.258	(0.12-0.47)	[b]**0.033**	**(0.02-0.06)**
[3]0-15	0.48	(0.33-).67)	†0.248	(0.10-0.49)	†0.581	(0.2-3.51)	†0.250	(0.14-0.40)	[a]**0.040**	**(0.03-0.08)**

Table 2.5.3 (continued)

Soil Depth	Exchangeable acidity		Effective cation exchange capacity		Base saturation percentage		C:N Ratio	
cm	(m-equivs $100g^{-1}$)		(m-equivs $100g^{-1}$)		(%)			
5-10	11.0	(7.6-13.9)	11.7	(8.2-14.8)	5.7	(3.3-12.6)	21	(14.8-49.8)
20-25	10.6	(7.3-13.3)	11.1	(7.6-14.7)	4.4	(2.2-9.3)	44	(15.7-123.9)
35-40	10.9	(7.6-14.7)	11.4	(7.9-15.7)	3.8	(2.0-6.6)		
50-55	11.2	(7.3-14.7)	11.6	(7.6-15.6)	3.4	(1.8-6.0)		
65-70	10.8	(4.2-14.3)	11.1	(4.4-15.0)	3.1	(1.7-4.7)		
80-85	10.8	(4.7-14.3)	11.1	(4.9-14.9)	3.3	(1.7-4.7)		
95-100	9.8	(4.2-12.1)	10.2	(4.4-12.4)	3.4	(1.7-5.3)		
[1]0-15	[a]14.9	(13.1-19.7)	[a]16.2	(14.3-20.8)	[†]7.8	(4.0-27.3)	[b]21	(14.4-32.6)
[2]0-15	[b]13.0	(9.6-19.5)	[b]14.2	(10.1-20.8)	[†]8.1	(3.0-28.9)	[a]28	(14.4-48.8)
[3]0-15	[a]14.8	(12.1-21.4)	[a]15.9	(13.0-22.0)	[†]7.1	(2.5-24.2)	[c]16	(12.7-24.6)

The means and ranges of soil analyses are given in Table 2.5.3. Analysis of variance was used to test for differences in soil analyses of 0-15 cm core samples between plots and significant differences were indicated by a Duncan's multiple range test ($P<0.05$).

Figures 2.5.3 The mean and ranges from twelve soil profiles of; (a) loss-on-ignition at 375 °C, (b) loss-on-ignition at 700 °C, (c) total carbon.



The means and ranges of soil analyses are given in Table 2.5.3. Analysis of variance was used to test for differences in soil analyses of 0-15 cm core samples between plots and significant differences were indicated by a Duncan's multiple range test ($P<0.05$).

Figures 2.5.3 The mean and ranges from twelve soil profiles of; (a) loss-on-ignition at 375 °C, (b) loss-on-ignition at 700 °C, (c) total carbon.

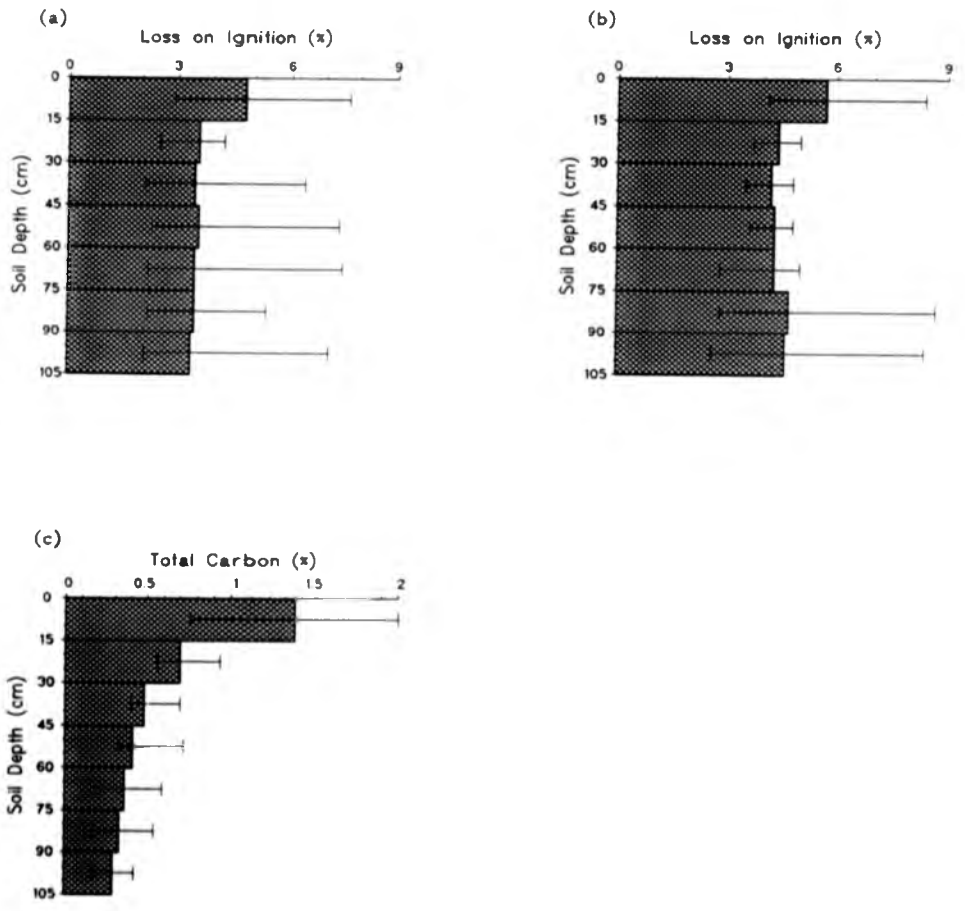
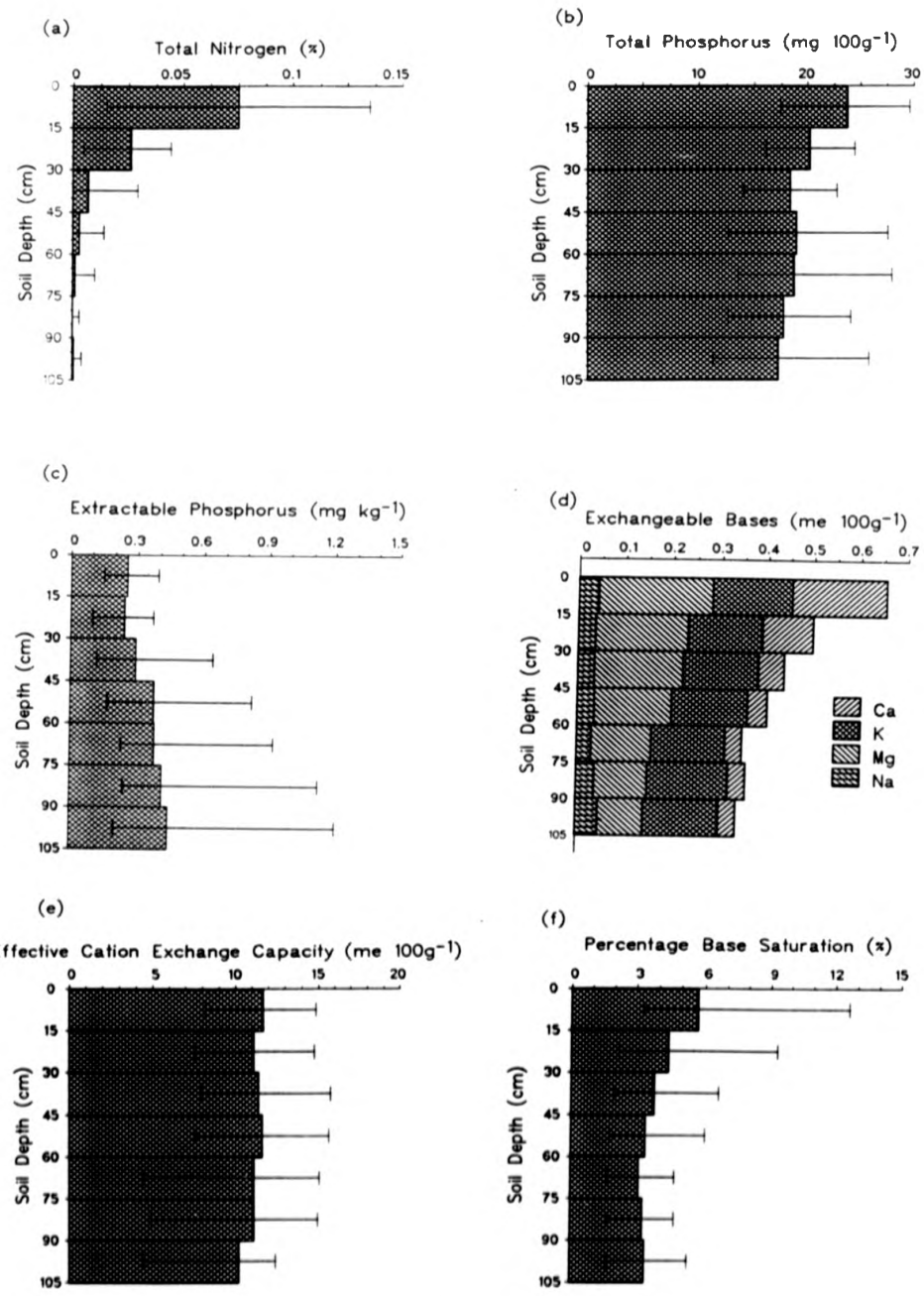


Figure 2.5.4 The mean and ranges of soil analyses from twelve soil profiles; (a) total nitrogen, (b) total phosphorus, (c) acetic acid extractable phosphorus, (d) exchangeable base cations, (e) effective cation exchange capacity, (f) percentage base saturation.



Soil organic matter contains the principal cation exchange sites in acid tropical soils and is generally recognised as a major pool of phosphorus and nitrogen in the soil (Proctor 1983, Sanchez 1976, Young 1976). Loss-on-ignition and total carbon are useful measures of soil organic matter. Table 2.5.4 gives correlation coefficients and level of significance (t-test) of linear correlations between soil analyses and total carbon and loss-on-ignition.

Table 2.5.4 Correlation coefficients of linear regressions between total carbon and loss-on-ignition, and soil analyses (n = 156, all values significant at P<0.001 except † P<0.01 and ‡ P>0.05 (not significant)

	Total C	Loss-on-ignition (375°C)	Loss-on-ignition (700°C)
Total C	-	-	-
Loss-on-ignition (375°C)	0.919	-	-
Loss-on-ignition (700 °C)	0.885	0.937	-
Total N	0.920	0.851	0.818
Total P	0.812	0.788	0.854
Extractable P	0.251†	0.406	0.522
Exchangeable K	0.631	0.607	0.599
Exchangeable Ca	0.402	0.390	0.365
Exchangeable Mg	0.488	0.443	0.467
Exchangeable Na	0.031‡	0.061‡	0.049‡
Exchangeable acidity	0.750	0.781	0.861
Effective cation exchange capacity	0.797	0.818	0.888
Base saturation	0.478	0.434	0.421

† P<0.01
‡ P>0.05 (not significant)

Percent total carbon values were consistently much lower than loss-on-ignition and remain much less than half the loss-on-ignition values when a conversion factor of 1.72 (Landon 1984) was used to express total carbon in terms of percent organic matter. This suggests that loss-on-ignition removed a considerable portion of the soil other than organic matter. Loss-on-ignition and total carbon were, however, correlated

(r=0.85, P<0.001, n=156) and there were no significant differences between plots in these measures of soil organic matter.

Plot 3 had a significantly larger percentage of total nitrogen and, total and acetic acid extractable phosphorus in the top 15 cm of the soil than plots 1 and 2, and the lowest mean C:N ratio. Nitrogen was shown to be highly correlated with soil organic matter and although total phosphorus exhibited a less pronounced decrease with depth (Figures 2.5.4a and b), it is still highly correlated with loss-on-ignition and total carbon (Table 2.5.4). Acetic acid extractable phosphorus is much less strongly correlated with soil organic matter than is total phosphorus.

Because the acetic acid extractable phosphorus measured was very low, twenty-four 0-15 cm soil samples were also analyzed for extractable phosphorus by a second method involving anion exchange resin (Somasiri and Edwards 1992). It has been suggested that phosphate extraction using an anion exchange resin is more analogous to withdrawal by plant roots than other single extraction methods (Amer *et al.* 1955, van Raij *et al.* 1986, Reith *et al.* 1987). Phosphorus extraction by the two methods was significantly correlated (r=0.65, P<0.001, n=24), with the anion resin extracting on average 22% less phosphorus. The anion resin extraction therefore supports the use of the acetic acid method and suggests that pool of plant-available phosphorus in the Danum soils was not significantly underestimated by this method.

Fig. 2.5.4d shows the relative quantities of exchangeable calcium, magnesium, potassium and sodium with depth in the soil. The availability of calcium declined most rapidly with depth. There were no significant differences between plots in the amount of exchangeable calcium, potassium or magnesium in the top 15 cm of soil. Calcium, potassium and magnesium were shown to be significantly correlated with soil organic matter while sodium was not correlated (Table 2.5.4). Plot 2 exhibits significantly lower exchangeable acidity than either of plots 1 or 2 and hence also a lower effective cation exchange capacity, however, there were no significant differences between plots in terms of percentage base saturation. ECEC was highly correlated with loss-on-ignition and total carbon suggesting that cation exchange sites were dominated by organic matter (Table 2.5.4).

Some analytical results from Table 2.5.3 are expressed on a mass per hectare basis for

both 15-cm soil horizons and the total in the top 1 m of soil (Table 2.5.5). Mass per hectare was calculated using mean bulk density for each horizon (Table 2.5.2). The estimates of total soil nutrient mass should be taken as approximate indicators only.

Table 2.5.5 Estimates of the mass per hectare of soil nutrients in 15-cm horizons and in the top 1 m in three plots at Danum Valley.

Soil Depth	LOI 700°C	Total C	Total N	Total P	Extr. P	Exch. K	Exch. Ca	Exch. Mg	Exch. Na
cm	t ha^{-1}	t ha^{-1}	kg ha^{-1}	kg ha^{-1}	kg ha^{-1}	kg ha^{-1}	kg ha^{-1}	kg ha^{-1}	kg ha^{-1}
0-15	79	19	1035	327	0.35	92	56	40	14
15-30	70	11	413	321	0.38	98	35	38	13
30-45	72	8	120	313	0.50	107	19	39	14
45-60	75	7	50	329	0.64	109	15	35	14
60-75	77	6	20	337	0.68	108	13	28	13
75-90	78	5	1	292	0.68	108	13	23	15
90-105	69	4	8	258	0.66	93	11	18	16
0-100	496	60	1644	2091	3.67	684	158	213	94

2.5.4 Discussion

The soils of the three forest plots were generally deep except on steep slopes and stream sides. The percentage of clay and the bulk density increased with depth, as has previously been reported for Bornean soils under dipterocarp forest (Ballie 1989). The increase in clay with depth, weakly developed blocky structure, and lack of clay cutans on ped surfaces suggests that the B horizon is no longer actively weathering and that little further profile differentiation is taking place (Young 1976). These suppositions are supported by the strong correlation between soil nutrients and organic matter which suggest that the majority of soil nutrients are made available through organic matter and are cycled in the top layers of the soil.

Results of chemical analyses for a range of soils under lowland evergreen rain forest have been collated by Proctor *et al.* (1983a) and Thompson *et al.* (in press). It is a common misnomer that all rain forests are supported on fragile soils low in

available nutrients and the wide range of the soil analyses published to date warn against making such generalisations. Both the lack of standard analytical methodology and the variation of sampling depth pose problems when attempting to compare between rain forest sites. The steep decline in most nutrients with depth measured in the Danum forest demonstrates how selection of sampling depth may greatly influence overall results. Notwithstanding the problems in comparing results of soil analyses, the following comparisons with the data compiled by Proctor *et al.* (1983a) and Thompson *et al.* (in press) are suggested.

Highly weathered, acid tropical soils are known to often exhibit phosphorus deficiency as a result of fixation as aluminium or iron phosphates (Sanchez 1976). The acetic acid extractable phosphorus measured in the Danum soils was very low and below that recorded in any of the compiled rain forest sites. Values for total phosphorus, however, are similar to those reported for a range of dipterocarp forests and are considerably higher than those reported for a number of neotropical sites. The extractable phosphorus pool in the Danum soil represents only 0.14% of the total phosphorus pool in the top 15 cm. Although the concentration of plant-available phosphorus in the Danum soil appears very low, it is important to consider that there was no measure of the turnover rate of this pool. That is, there was no indication of the potential flux of phosphorus between 'fixed' and 'plant-available' pools.

A limitation of the soil sampling procedure employed was that the top 5 cm of the soil was not individually sampled. This horizon is potentially the most biologically active portion of the soil (Burnham 1989). However, the soil cores represent a mix of soil between 0 and 15 cm (Section 2.5.2) and using the concentrations recorded at 5-10 cm and 20-25 cm it is possible to estimate the mean concentration of soil nutrients in the top 5 cm of the soil. In contrast to concentrations of total N and P and exchangeable K, Ca and Mg, the concentration of acetic acid extractable phosphorus tended to increase with depth (Figure 2.5.4c). However, estimating the concentration of acetic acid extractable phosphorus in the top 5 cm of the soil, by the concentration recorded in 0-15 cm samples, suggested that the concentration in top 5 cm was 0.7 mg kg^{-1}, higher than in the horizons immediately below.

The value of 0.7 mg kg^{-1} is still very low and only comparable with samples from 0-

15 cm in a Paleudult (Ultisol) from Amazonian Ecuador (Koming *et al.* 1992) and from below 20 cm in a Paleudult from Maracá island, Brazil (Thompson *et al.* in press). Burghouts *et al.* (1992) and Korthals (1990) measured easily soluble phosphorus in 0-3 cm and 3-8 cm layers of the soil in the plots of Newbery *et al.* (1992) at Danum (Figure 2.4.1). Using the Bray and Kurtz method (0.1 M hydrochloric acid and ammonium fluoride extraction, Bray and Kurtz 1945, Jackson 1958) they recorded a concentration of phosphorus about ten times larger than that recorded in the current study (9.4 and 6.4 mg kg^{-1} in 0-3 cm and 3-8 cm layers), while the concentration of total phosphorus they recorded was lower (156 and 138 mg kg^{-1}). The higher concentrations of extractable phosphorus recorded may have been a function of the more vigourous extractant used. Also using the Bray and Kurtz method, Acres *et al.* (1975) reported values for easily extractable phosphorus from a range of ten Orthic Acrisols across Sabah. The range of values in the top 3 cm of the soil was 1-19 mg kg^{-1} and in the horizon immediately below 3 cm the range was trace-4 mg kg^{-1}. Comparing the values recorded by Burghouts *et al.* (1992) with those of Acres *et al.*, it does not appear that the Danum soils were particulary deficient in extractable phosphorus compared to other Orthic Acrisols in Sabah. The use of an acetic acid extraction to estimate plant-available phosphorus, however, was supported by values obtained by the anion exchange resin extraction.

The percentage of total carbon measured in the Danum soils was close to the median value of the range reported in other dipterocarp forests, although towards the upper end of the range of neotropical sites. Loss-on-ignition values were higher than those reported for a sandy topsoil in Brazil (7.7% vs. 3.9%, Thompson *et al.* in press). Total nitrogen is towards the lower end of the range of reported values and the mean C:N ratio of the Danum soils is relatively high.

Exchangeable bases are all within the range reported for other sites, with magnesium being the dominant base cation in the Danum soils. The percentage base saturation is low, as can be seen by the comparison with a lowland forest site on Maracá island, Brazil (7.5% vs. 54.6%).

Overall the picture is of a soil in which the majority of nutrients are associated with organic matter and are cycled in the top layers of the soil. The soil pool of available

phosphorus is small and the C:N ratio high, but otherwise the soil does not appear to be particulary deficient in essential nutrients when compared with other rain forest sites.

2.6 Vegetation

2.6.1 Introduction

Lowland dipterocarp forest has been defined as a type of forest within the tropical lowland evergreen rain forest formation (Whitmore 1984) and is characterised by the dominance of trees in the family Dipterocarpaceae in the canopy and emergent strata. The greatest dominance of Dipterocarpaceae (76 % of tree basal area) has been recorded in Seram, Maluku Province, Indonesia (I.D.Edwards and J.Proctor unpublished). Dipterocarpaceae reach their greatest diversity, however, in Borneo, with 10 genera and about 267 species described to date (Whitmore 1984). The forests of eastern Sabah have previously been distinguished from other areas of Borneo and the Malay Peninsula by the fewer species of dipterocarp in a given area (Fox 1972, Whitmore 1984, Campbell 1990). Whitmore (1984) further distinguishes forests around Darvel Bay by the dominance of *Parashorea malaanonan* Bl. (Fox 1972). Proctor *et al.* (1988), however, recorded no *Parashorea* species on a ridge on Gunung Silam (Figure 2.1.1) above 280 m, but all of the forests below 250 m in the Silam area have been heavily logged.

A full enumeration of all trees ≥10 cm girth at breast height (gbh) has been carried out (Campbell 1990, Newbery *et al.* 1992) for two 4 ha primary forest plots about 0.5-1.5 km south of the plots in the current study (Figure 2.4.1). The completeness of the taxonomic identification, the relatively small minimum girth of trees included and the relatively large sample areas allow for good quantitative ecological description and comparison with other sites. It was not attempted to repeat the detail of this work in the current study, but to give enough information to characterize the forest in the plots in which the root study was made. Comparison with the plots of Newbery *et al.* (1992) is of interest in quantifying the variation in lowland dipterocarp forest over a small area.

2.6.2 Materials and methods

Each of the three forest plots was further subdivided into a grid of 80 subplots, each 12.5 m by 10 m, to aid in the enumeration of the vegetation. The grid was laid out by compass and tape and temporarily marked with string. The diameter at breast height (dbh, 1.3 m) of all trees and lianes (≥ 10 cm dbh) was measured to within 1 mm with a steel tape. Where a buttress or other protrusion occurred on the stem at 1.3 m, dbh was measured 30 cm above the protrusion. Where a tree had multiple stems each stem was measured separately but the tree was recorded as one individual. The position of each tree was recorded to the nearest 0.5 m southing and easting relative to the corner of each plot. The presence or absence of buttresses greater than 0.5 m or 2 m in height was recorded. Each tree was marked with an individually numbered aluminium tag.

Tree identification was undertaken by E.J.F. Campbell-Gasis. As far as possible botanical specimens were collected from each tree. The majority of specimens consisted of infertile material. Specimens were collected using pruning poles or by a tree climber. Large canopy and emergent trees that could not be readily climbed or reached from an adjacent tree were identified by a combination of matching fallen leaves to those in the crown using binoculars, and by utilizing bark characteristics. The identification of voucher specimens was confirmed at the Sabah Forest Department herbarium in Sandakan (Figure 2.1.1).

A transect (60 m x 7.5 m) of forest in plot 2 was subjectively chosen for a profile diagram of trees over 6 m high. Tree height and depth of crown were measured using a Haga gauge and crown widths estimated by eye using a tape laid on the ground.

2.6.3 Results

Forest Structure

The profile diagram (Figure 2.6.1) gives a general impression of the vertical structure of the forest. The mean density of trees (≥ 10 cm dbh) for the three plots was 423 ha^{-1}. The basal area of plots 1, 2 and 3 was 22.7, 24.2 and 18.8 m^2 ha^{-1} respectively (mean 21.9 m^2 ha^{-1}). 21.6 % of trees (≥ 10 cm dbh) had buttresses greater than 0.5 m

high and 4.3% greater than 2 m high. 10.2% of buttresses greater than 0.5 m in height were classed as flying buttresses. 2.0% of individuals ≥ 10 cm dbh were lianes, and lianes made up 0.6% of the overall basal area of stems ≥ 10 cm dbh.

Floristics

A total of 182 taxa were identified in the 3 hectares. 158 (86.8%) of the taxa were to the level of species, 15 (8.2%) to genus, and 8 (4.4%) to the family only level. 1181 (93.1%) individuals were identified to species, 26 (2.05%) to genera only, 21 (1.7%) to family only, and 41 (3.2%) individuals remained unidentified. Individuals identified only to genus or family, and those that remained unidentified, were not separated into different taxa. The fact that 88 (6.9 %) individuals were not identified to species needs to be taken into account when considering the following analyses. Species:area curves were not plotted for this reason.

Of the 47 families recognised the Lauraceae were the most species rich with 19 species in 8 genera, followed by Euphorbiaceae with 16 species in 8 genera and Annonaceae and Meliaceae with 13 species in 7 and 6 genera respectively. Plot 1 contained 102 taxa, plot 2 119 taxa and plot 3 104 taxa. 51 taxa were common to all three plots.

Euphorbiaceae were the most abundant family with 190 individuals in 3 ha, followed by Dipterocarpaceae with 169 individuals and Meliaceae with 144 individuals (Table 2.6.1). Table 2.6.2 shows the percentage basal area contributed by each family and it can be seen that although overall Dipterocarpaceae ranked second in terms of number of individuals they contribute by far the largest basal area (45.9% overall). Euphorbiaceae, the most abundant family, rank fifth in terms of overall basal area (5.0 %). Interestingly, Leguminosae contributed only 26 individuals ≥10 cm dbh in 3 ha (basal area 0.38 m^2 ha^{-1}), 38% of which were lianes.

Figure 2.6.1 Profile diagram (60 m x 7.5 m) of forest in plot 2 Danum Valley, Sabah. Trees less than 6 m high are excluded. Symbols for trees over 10 cm dbh: Ae *Alangium ebenaceum* (Clarke) Harms.; Bs *Baccaurea stipulata* J J Sm.; Dc *Dysoxylon cyrtobotryum* Miq.; Dn *Diospyros nitidia* Merr.; Fs *Fordia splendidissima* (Miq.) Buij.; Ge *Glochidion* cf. *elmeri* Merr.; Lf *Litsea fenestrata* Gamb.; Ln *Lithocarpus nieuwenhuisii* (V.Seem.) A Camus; Mr *Microcos reticulata* Ridl.; Nf *Neoscortechinia forbesii* (Hk f.) Pax + Hoffm.; Pc *Phaeanthus crassipetalus* Becc.; Sj *Shorea johorensis* Foxw.; Sl *Shorea leprosula* Miq.; Ua Unknown A; Sp *Shorea parvifolia* Dyer.; Ao *Alseodaphne oblaceolata* (Merr.) Kosterm..

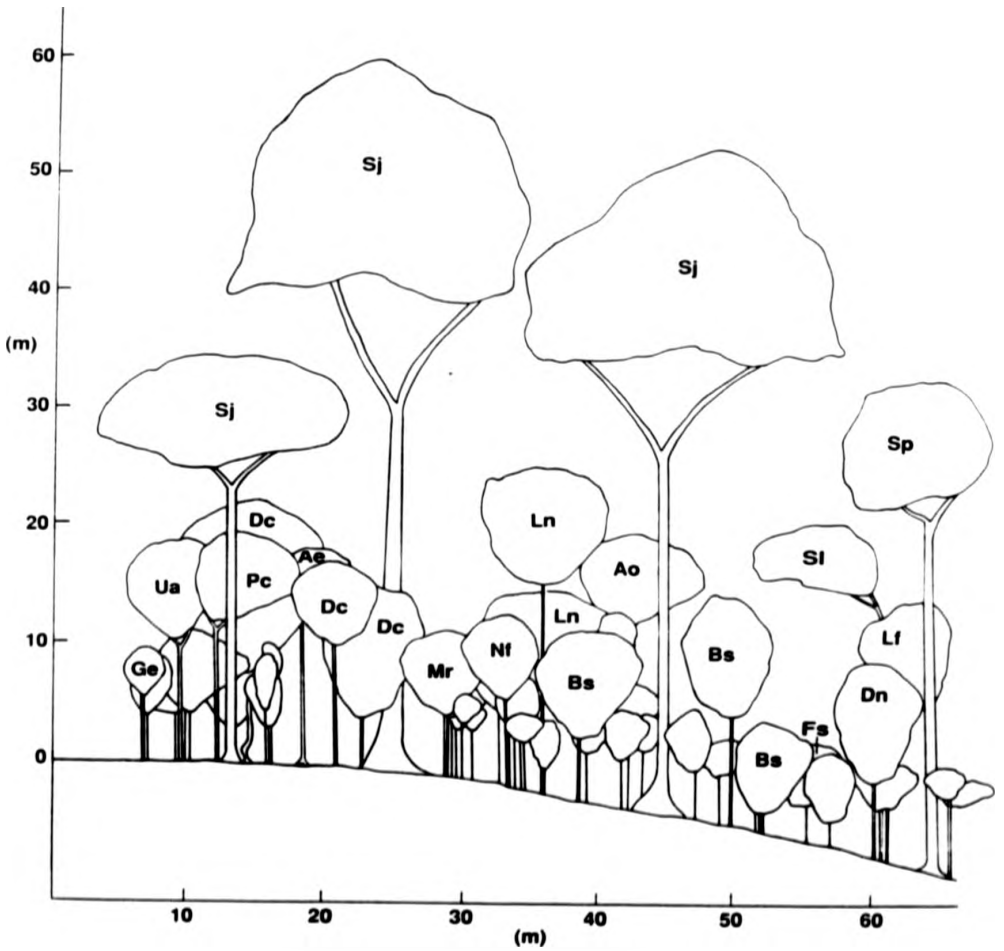


Table 2.6.1 The percentage contribution of each family to tree (≥10 cm dbh) density in three plots in Danum Valley, Sabah. Rank in parentheses, equal ranks underlined.

Family	Plot 1		Plot 2		Plot 3	
Alangiaceae	0.9	(18)	0.4	(28)	-	
Anacardiaceae	-		-		0.8	(16)
Annonaceae	7.0	(4)	5.2	(6)	6.1	(6)
Apocynaceae	-		-		0.3	(26)
Burseraceae	2.6	(10)	0.9	(20)	2.5	(11)
Celastraceae	0.2	(27)	-		-	
Chrysobalanaceae	1.2	(14)	0.4	(28)	-	
Clusiaceae	0.5	(25)	-		-	
Combretaceae	0.2	(27)	0.4	(28)	0.3	(26)
Dilleniaceae	0.9	(18)	0.7	(25)	0.6	(22)
Dipterocarpaceae	12.3	(2)	11.7	(2)	17.1	(1)
Ebenaceae	0.7	(21)	2.0	(12)	1.7	(13)
Euphorbiaceae	22.6	(1)	11.1	(3)	11.6	(3)
Fagaceae	0.7	(21)	4.4	(7)	2.8	(10)
Flacourtiaceae	6.1	(5)	0.9	(20)	1.4	(14)
Gonystylaceae	0.5	(25)	0.2	(32)	-	
Guttiferae	0.2	(27)	-		-	
Icacinaceae	0.2	(27)	-		-	
Lauraceae	5.4	(6)	8.5	(5)	10.5	(4)
Lecythidaceae	1.4	(13)	1.1	(19)	0.8	(16)
Leguminosae	1.6	(12)	3.5	(9)	0.8	(16)
Loganiaceae	0.7	(21)	-		0.3	(26)
Magnoliaceae	-		1.5	(15)	1.1	(15)
Mastixiaceae	-		0.9	(20)	0.3	(26)
Melastomataceae	1.2	(14)	1.5	(15)	0.6	(22)
Meliaceae	11.9	(3)	10.7	(4)	12.1	(2)
Meliosmaceae	-		0.2	(32)	-	
Moraceae	1.2	(14)	0.2	(32)	0.3	(26)
Myristicaceae	1.9	(11)	0.7	(25)	1.9	(12)
Myrsinaceae	-		-		0.3	(26)
Myrtaceae	4.7	(7)	4.4	(7)	3.9	(8)
Olacaceae	0.2	(27)	1.7	(13)	0.8	(16)
Oleaceae	0.2	(27)	1.5	(15)	0.8	(16)
Proteaceae	0.2	(27)	0.9	(20)	0.6	(22)
Rhizophoraceae	0.2	(27)	-		-	
Rosaceae	-		0.2	(32)	-	
Rubiaceae	-		0.7	(25)	0.3	(26)
Rutaceae	0.2	(27)	0.2	(32)	-	
Sapindaceae	0.2	(27)	1.5	(15)	0.8	(16)
Sapotaceae	0.7	(21)	2.6	(10)	4.7	(7)
Sterculiaceae	-		-		0.3	(26)
Symplocaceae	-		0.2	(32)	-	
Tiliaceae	4.4	(9)	13.7	(1)	10.5	(4)
Trigoniaceae	-		0.4	(28)	-	
Ulmaceae	0.2	(27)	0.2	(32)	-	
Verbenaceae	1.2	(14)	0.9	(20)	-	
Xanthophyllaceae	0.9	(18)	1.7	(13)	0.6	(22)
Unidentified	4.7	(7)	2.17	(11)	3.0	(9)

Table 2.6.2 The percentage contribution of each family to tree (≥10 cm dbh) basal area in three plots in Danum Valley, Sabah. Rank in parentheses.

Family	Plot 1	Plot 2	Plot 3
Alangiaceae	1.05 (16)	0.41 (25)	-
Anacardiaceae	-	-	0.26 (20)
Annonaceae	3.63 (8)	2.30 (9)	3.05 (7)
Apocynaceae	-	-	0.09 (31)
Burseraceae	1.05 (15)	1.86 (10)	0.70 (13)
Celastraceae	0.05 (35)	-	-
Chrysobalanaceae	6.25 (4)	0.51 (23)	-
Clusiaceae	0.12 (30)	-	-
Combretaceae	0.11 (31)	0.54 (22)	0.25 (21)
Dilleniaceae	0.70 (19)	0.12 (31)	0.20 (24)
Dipterocarpaceae	39.54 (1)	46.60 (1)	55.43 (1)
Ebenaceae	0.16 (29)	1.57 (12)	1.23 (12)
Euphorbiaceae	8.17 (3)	3.22 (8)	3.40 (6)
Fagaceae	1.36 (13)	4.07 (6)	5.47 (5)
Flacourtiaceae	1.57 (12)	0.21 (29)	0.38 (18)
Gonystylaceae	0.33 (24)	0.07 (35)	-
Guttiferae	0.04 (36)	-	-
Icacinaceae	0.23 (26)	-	-
Lauraceae	4.71 (6)	5.38 (3)	5.75 (3)
Lecythidaceae	1.13 (14)	0.94 (16)	0.34 (19)
Leguminosae	0.44 (23)	4.25 (5)	0.24 (22)
Loganiaceae	0.21 (28)	-	0.10 (29)
Magnoliaceae	-	0.54 (21)	0.65 (14)
Mastixiaceae	-	0.69 (19)	0.05 (33)
Melastomataceae	0.46 (21)	0.42 (24)	0.17 (25)
Meliaceae	8.79 (2)	4.99 (4)	5.55 (4)
Meliosmaceae	-	0.08 (33)	-
Moraceae	1.78 (11)	0.08 (34)	0.12 (28)
Myristicaceae	0.56 (20)	0.15 (30)	1.47 (11)
Myrsinaceae	-	-	0.07 (32)
Myrtaceae	5.07 (5)	3.49 (7)	2.35 (9)
Olacaceae	0.21 (27)	1.29 (13)	0.45 (17)
Oleaceae	0.06 (34)	0.66 (20)	0.22 (23)
Proteaceae	0.06 (33)	0.34 (27)	0.16 (26)
Rhizophoraceae	0.09 (32)	-	-
Rosaceae	-	0.28 (28)	-
Rubiaceae	-	0.34 (26)	0.13 (27)
Rutaceae	0.04 (37)	0.07 (36)	-
Sapindaceae	0.29 (25)	0.88 (17)	0.50 (16)
Sapotaceae	0.77 (17)	1.77 (11)	2.42 (8)
Sterculiaceae	-	-	0.57 (15)
Symplocaceae	-	0.05 (38)	-
Tiliaceae	3.76 (7)	8.43 (2)	6.08 (2)
Trigoniaceae	-	0.09 (32)	-
Ulmaceae	0.44 (22)	0.05 (37)	-
Verbenaceae	2.77 (10)	0.83 (18)	-
Xanthophyllaceae	0.72 (18)	1.19 (15)	0.10 (30)
Unidentified	3.29 (9)	1.22 (14)	2.06 (10)

The most common species is *Mallotus wrayi* King ex Hk.f. (Euphorbiaceae) with 91 individuals in 3 ha followed by, *Pentace laxiflora* Merr. (Tiliaceae, 69 individuals), *Shorea johorensis* Foxw. (Dipterocarpaceae, 64 individuals), *Dysoxylon cyrtobotryum* Miq. (Meliaceae, 45 individuals), *Parashorea malaanonan* Bl. (Dipterocarpaceae, 44 individuals) and *Baccaurea stipulata* J J Sm. (Euphorbiaceae, 43 individuals). These six species stand out as being the most abundant with the next most common species being represented by 30 individuals.

2.6.4 Discussion

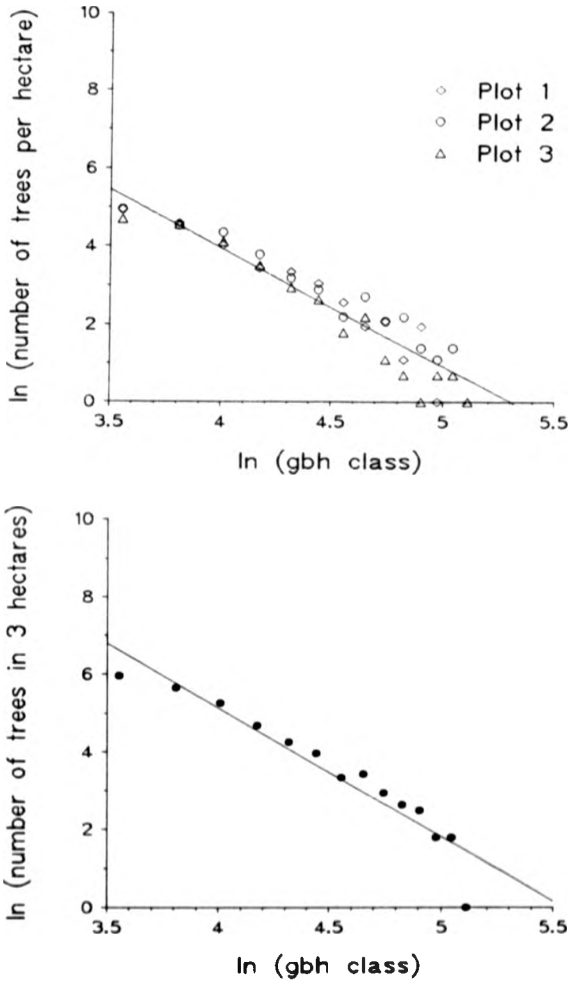
Forest Structure

Newbery *et al.* (1992) compiled the basal area and density of trees from nine sites in Borneo and two from Peninsular Malaysia. The mean density of trees in the three plots in current study is 79% of the mean for other sites but similar to that of two previous studies at Danum Valley (Kamarudin 1986, Campbell 1990, Newbery *et al.* 1992). The mean basal area in the current study was only 61% of the mean of the other nine sites and is the lowest basal area of the compiled primary lowland dipterocarp forest studies. No survey of tree fall gaps was carried out in the current study, but the fact that the basal area is lower than the two other enumerated plots at Danum Valley supports the visual impression of a relatively high number of recent large tree falls in the three plots randomly selected for this study.

Buttressing was less frequent than that reported for a lowland rain forest on ultrabasic rocks in Sabah (Proctor *et al.* 1988) and for a site in Costa Rica (Heaney and Proctor 1990), but more frequent than that reported for a lowland Amazonian forest (Thompson *et al.* in press).

Newbery *et al.* (1992) plotted natural log frequency distributions for trees in 10 cm gbh classes from 30-170 cm gbh. Fluctuations in the number of trees within the 90-160 cm gbh classes were shown to have been significantly correlated between the two plots of Newbery *et al.*. It was postulated that these fluctuations might record releases in canopy tree growth caused by abnormally high mortality of emergents on two (or three) occasions in the past. Were such releases of tree growth caused by widespread

Figure 2.6.2 Frequency distributions of trees in increasing gbh classes; 31.4-170 cm with 10 cm intervals. (a) Per plot; common line; ln(N) = -3.02.ln(gbh)+16.03, r^2 = 0.90. (b) All plots (3 ha); common line; ln(N) = -3.31.ln(gbh)+18.35, r^2 = 0.91.



catastrophic events, such as drought, it might be expected that similar fluctuations be recorded in plots 1, 2 and/or 3 in the current study which were only 0.5-1.5 km away. Figure 2.6.2a shows that there was no correlation between plots 1, 2 and 3 in the fluctuations of ln number of trees about the common line in 90-160 cm gbh classes, in the current study. In addition, the patterns of fluctuation for individual plots and the sum of all plots (Figure 2.6.2b) do not fit the pattern found by Newbery *et al.* (1992). No evidence was found to support the hypothesis that catastrophic events in the past have caused releases in tree growth over an area that includes both the plots of

Newbery *et al.* and the plots in the current study.

Floristics

Newbery *et al.* (1992) compared the species richness of their Danum plots with six sites in Borneo and Peninsular Malaysia. Using the same plot area and size class of trees they found the Danum plots to be mostly less species rich, with only 60% of the species richness (trees ≥ 30 cm gbh) compared with other statistically reliable values. Newbery *et al.* (1992) also compared the percentage contributions of the principal families in their Danum plots with six other sites in north-east and east Borneo. The Danum forest was distinctive in having a relatively high proportion of Euphorbiaceae, Meliaceae and Lauraceae. The proportion of dipterocarps was intermediate and most similar to sites at Andalau in Brunei (Aston 1964) and Mulu in Sarawak (Proctor *et al.* 1983a). In the plots of the current study Euphorbiaceae and Dipterocarpaceae were less dominant in terms of tree density compared with the plots of Newbery *et al.* (15.0% vs. 20.6% and 13.3% vs. 16.2% respectively), with Meliaceae and Tiliaceae contributing a relatively larger proportion of stems (11.3% vs. 7.5% and 9.4% vs. 4.4% respectively).

Newbery *et al.* (1992) concluded their plots to be no more similar to other sites in Sabah than those outside Sabah in north and east Borneo. It is noteworthy that although the plots in the current study were more similar to those of Newbery *et al.* than those elsewhere, there were important differences in the family composition even though the plots were only 0.5-1.5 km away from each other. It should be noted however, that the percentage contributions of families to tree density, in the current study, may be affected by the fact that 6.9 % of individuals were not identified to species and also that Newbery *et al.* (1992) demonstrated that 3 ha is an insufficient area to sample rare species.

In conclusion it can be stated that the 3 ha enumerated in the current study are more similar, in many respects, to other plots enumerated at Danum than to other sites in Borneo and Peninsular Malaysia, but differ significantly from the plots of Newbery *et al.* (1992) in having a lower basal area and a relatively high representation of Meliaceae and Tiliaceae.

Chapter 3 Fine Root Biomass

3.1 Introduction

Part of the lore of tropical rain forest ecology in the past has been that the majority of nutrients in the ecosystem are held in above-ground biomass and that nutrient cycles are closed and tight (Richards 1952, Jordan and Herrera 1981, Jordan 1989b). Although intuitively appealing ideas, these generalizations have been shown to be oversimplifications and largely incorrect now that more data have accumulated (Proctor 1983, 1987, 1992, Whitmore 1989). Allied to the concept of closed and tight nutrient cycles in tropical rain forests has been the hypothesis that fine root biomass is an inverse function of site fertility (Gower 1987, Kellman 1990). Stark and Jordan (1978) demonstrated the efficiency of root mats in Amazonian *tierra firme* forest on oxisols to absorb nutrients; <0.1% of ^{32}P and ^{45}Ca in a solution sprinkled on the surface of the root mat leached through to the mineral soil, and no detectable radioactivity leached through when applied in the form of labelled leaves (Jordan and Stark 1978, Jordan and Herrera 1981). Herrera *et al.* (1978b) demonstrated that mycorrhizal fungi are one of the pathways by which ^{32}P was transferred from decomposing leaf to root. In an ecosystem where mineral nutrients are limiting it might be expected that investment in a large fine root system would incur ecological advantage to the individual plant.

The hypothesis that fine root biomass is largely a function of site fertility has been given added credence by studies that have reported fine root biomass to decrease following stand fertilization (eg Alexander and Fairley 1983, Gill and Lavender 1983, Freidman-Thomas 1986, Cavelier 1989, Gower and Vitousek 1989). Experiments have frequently demonstrated that a typical plant response to nutrient stress is an increase in the root:shoot dry mass ratio, although absolute fine root mass may be higher in more vigorous, fertilized plants (eg Troughton 1977, Ericsson 1981, Robinson 1986, Adams *et al.* 1989, Millard and Neilsen 1989, Mackie-Dawson *et al.* submitted).

Fine root biomass in the Danum forest was estimated by a combination of excavation techniques and compared to values reported for other rain forest sites. The concordance of the Danum forest with the hypothesis that fine root biomass is a function of site fertility was evaluated. The relationship between the spatial

distribution of fine roots and soil nutrients, and the seasonality in fluctuations in fine root biomass, were investigated.

3.2 Materials and Methods

Fine root biomass was estimated by a combination of two root excavation techniques between June 1990 and September 1991. Counts of root endings on profile walls were used to quantify the vertical distribution of roots to a depth of 1.2 m. Horizontal variability in the fine root system was quantified by intensive soil coring in the top 0.15 m of the soil.

In the current study fine roots were defined as ≤2 mm diameter. This diameter category was an attempt to separate two physiological classes of roots; ephemeral, fleshy fine roots and those that had become secondarily thickened. However, a wide variety of different root morphologies were encountered in the Danum forest and fleshy roots >2 mm diameter and woody roots ≤2 mm diameter were encountered. The diameter category was selected to give the minimum overlap between the two physiological classes in the population of fine roots encountered in the Danum forest, as well as to allow for comparisons with previous studies. It was recognised that a large proportion of the fine roots in the Danum forest were mycorrhizal. However, a systematic survey of mycorrhizae was outside the scope of the current study.

Profile wall method

The profile wall method involved the excavation of a soil pit and the preparation of a smooth, vertical soil face 1 m by 1.2 m deep. Metal pins marked with 10 mm graduations were pushed into the soil face so their ends were flush with the soil. Ten millimetres of soil was carefully removed from the profile face with a variety of small tools, the pins acting as a guideline as to how much soil to remove. A counting frame (50 cm x 50 cm) divided into squares of 25 cm^2 was pinned against the profile (Böhm 1979) and the number of 'root endings' per square recorded. Root endings in this sense may either be a true apex of an intact root or a root severed in the preparation of a smooth working face. Roots were categorised as greater or less than 2 mm diameter using a gauge of that diameter. Roots growing through the litter above the

soil were included with those in the top 5-cm horizon. A total of twelve pits, four per plot located on a stratified random basis (Figures 2.4.2a,b,c), were excavated at regular intervals between May 1990 and December 1991. Root endings on each profile wall were counted on a single occasion immediately following excavation.

Auger method

The auger consisted of a cylindrical tube, internal diameter 8 cm and length 15 cm, with a serrated cutting edge. Cores are forced out of the auger by a spring loaded plunger, operated with a handle on the side of the auger (Schuurman and Goedewaagen 1971).

At intervals of about three months, three 15-cm deep cores were taken within each of the twenty-four subplots (Figure 2.4.2a,b,c). Cores were randomly located on a 1 m grid, no intersection being sampled more than once. Where a core could not be taken owing to the presence of a tree, fallen trunk, large root, stone, or other factor, the core was taken as close to the random point as possible. It is recognised that this may lead to a slight overestimation in root biomass. It could not be assumed, however, that there were no roots at a particular point just because the auger could not be driven in.

Roots were separated from the soil in each core by a combination of washing techniques. Each core was placed in a mesh (250 μm) bag and suspended from a bridge into the Segama river (Figure 2.4.1) for between 4-12 hours depending on the river level and flow. The fraction remaining in the mesh bag was further washed over a sieve (250 μm) and the roots were carefully extracted by hand. Tap water for the sieve washing was drawn from the Palum Tambun stream (Figure 2.4.1). The removal of the bulk of the soil by initially washing cores in the river considerably hastened the overall washing procedure and allowed for greater replication in the soil coring. The effect of the river washing compared with the standard technique of washing over a sieve on the nutrient content of fine roots was tested (Section 5.2.1).

Roots were not sorted into 'live' and 'dead' categories by the commonly used criteria of intactness, friability, turgidity, colour and integrity of root apex (Fairly 1983, Fogel

and Hunt 1979, 1983, McClaugherty *et al.* 1982, Chapter 1). The wide range of fine root morphologies encountered in the Danum forest and in particular the large proportion of ectomycorrhizae (eg many Dipterocarpaceae and Fagaceae), in which the host tissue is masked by a fungal sheath, made recognition made the physiological status of fine roots unreliable. All roots that were reasonably intact and clearly distinguishable from other plant debris were included in the estimates of root mass. Roots were sorted into the diameter categories; ≤2 mm, >2-≤5 mm, >5-≤10 mm, >10-≤15 mm using a gauge of metal rods of these diameters. Root samples were dried to constant mass at 80 °C, weighed to ±0.1 mg and retained for chemical analysis.

Relationship of total length on dry mass for samples of fine roots

In order to be able to express a mass of roots in a given volume of soil in terms of root length density a relationship was sought between the dry mass and total fresh length of roots in samples of roots ≤2 mm diameter. One randomly located soil core was taken per subplot and the fine roots separated as previously described. The root samples were bulked together and then divided into a range of different sized samples. The total length of each sample was measured using a root length scanner (Commonwealth Aircraft Corporation Ltd., Melbourne, Australia). Each sample was then dried to a constant mass at 80 °C and weighed to ±0.1 mg.

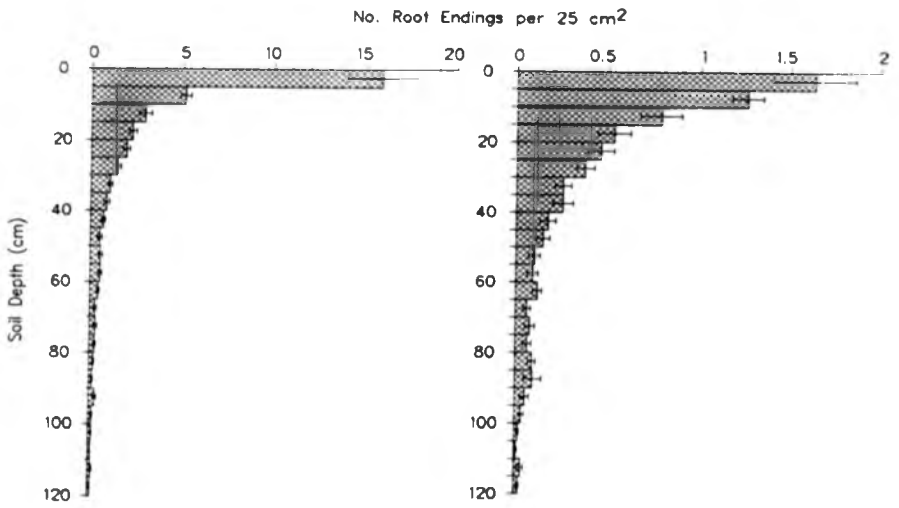
3.3 Results

3.3.1 Variability in Root Mass

Vertical distribution

For each of twelve profile walls a mean number of root endings per 25 cm^2 was calculated for 5-cm soil horizons to a depth of 1.2 m. As grid squares within each pit are not independent, *pits* was used as the sampling unit for calculating the mean vertical distribution of roots and standard errors. Figure 3.3.1a and b show the mean vertical distribution of root endings in two categories: ≤2 mm diameter and >2 mm diameter.

Figure 3.3.1 The mean (± S.E.) number of root endings per 25 cm^2 in twelve soil profiles with; (a) Fine roots ≤2 mm diameter, (b) roots >2 mm diameter. (note axes in (a) and (b) are not equal.



The count of root endings on profile walls was used to estimate the percentage of roots between 15 cm and 120 cm depth that were not sampled by the (15-cm) soil cores. If fluctuations in the root mass were greatest in the top layers of the soil, then it might be anticipated that the absolute number of root endings below 15 cm would exhibit less variation between profile walls than their percentage of the total roots in each profile. Table 3.3.1 shows, however, that for roots both ≤2 mm and >2 mm diameter, the mean percentage of roots below 15 cm depth in each pit was less variable than their actual numbers. Therefore, the mean percentage of roots below 15 cm was used to estimate fine root biomass to a depth of 120 cm.

Table 3.3.1 The mean count of root endings below 15 cm and the mean count as a percentage of the roots in the whole profile. Standard deviations in parentheses and standard deviation as a percentage of the mean given.

Root diameter (mm)	Count below 15 cm as % of whole profile	S.D. as % of the Mean	Count below 15 cm	S.D. as % of the mean
≤2	33.9 (10.1)	29.7	244.3 (96.5)	39.5
>2	43.9 (10.8)	24.5	60.3 (34.9)	57.9

Variability in root mass between plots and sampling occasions

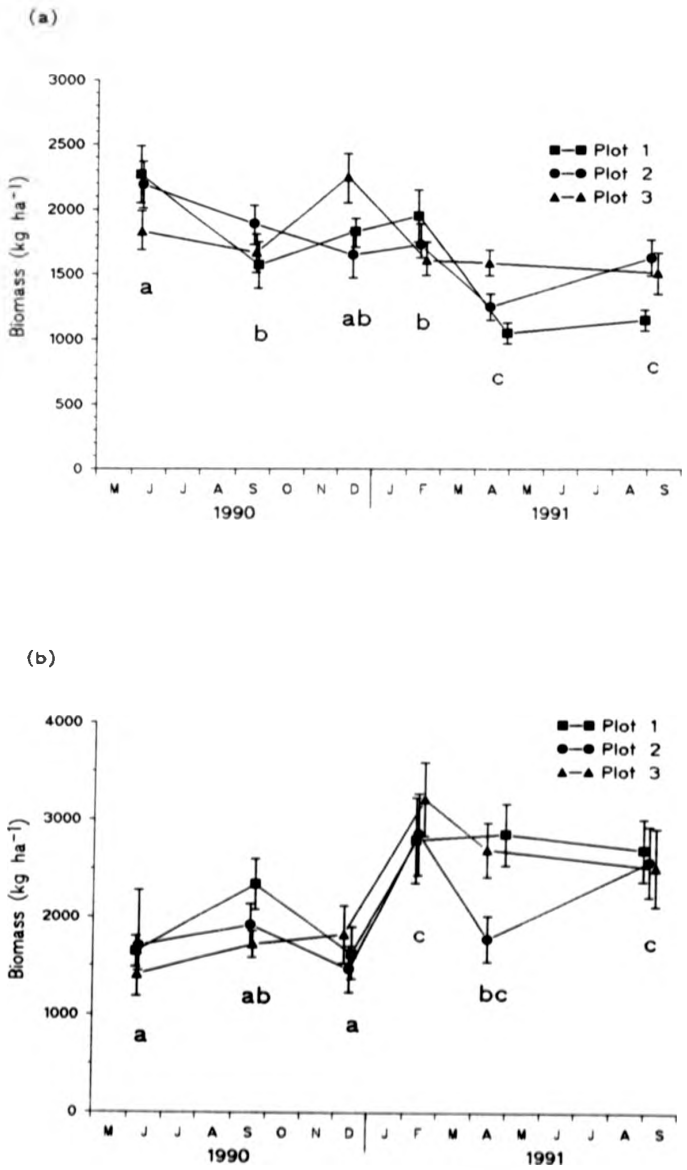
Table 3.3.2 gives the mean dry mass of roots per soil core in each of the diameter categories ≤2, >2-≤5, >5-≤10 and >10-≤15 mm. An analysis of variance with plots and sampling occasion as factors showed no significant difference in the mass of roots between plots for any of the root diameter categories. Categories >5-≤10 mm and >10-≤15 mm also showed no significant differences between sampling occasions, but, for categories ≤2 mm and >2-≤5 mm sampling occasion was significant ($P<0.001$). Duncan's multiple range test ($P<0.05$) was used to indicate significantly different sampling occasion means (Figure 3.3.2a and b).

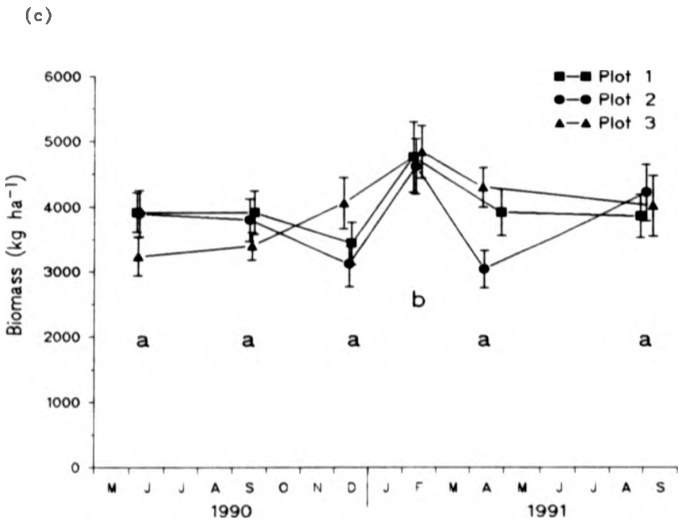
Table 3.3.2 Mean mass of roots in soil cores (8 cm diameter) in the top 15 cm of the soil (n = 432)

Diameter category (mm)	≤2	>2-≤5	>5-≤10	>10-≤15
Mean mass (g)	0.856	1.112	0.724	0.677
Standard error	0.041	0.038	0.056	0.093

There was a general trend for decreasing biomass of roots ≤2 mm diameter between June 1990 and September 1991 and an increase in the biomass of roots >2-≤5 mm diameter. Although all plots generally followed these trends, there was significant interaction in the analyses of variance between plot and sampling occasion. Figure 3.3.2c shows that the biomass of roots ≤5 mm in diameter remained more constant than either of the categories ≤2 mm or >2-≤5 mm, with only one sampling occasion mean (February 1991) being significantly different from the others ($P<0.05$). This would suggest that an increasing proportion of the fine roots were persisting, becoming secondary thickened and hence moving into the larger size class during this period. The individual history of roots that made up the biomass is however not known.

Figure 3.3.2 The mean (± S.E.) biomass of roots on six sampling occasions between June 1990 and September 1991; (a) fine roots ≤2 mm diameter, (b) roots >2-≤5 mm diameter, (c) all roots ≤5 mm diameter.





Fine root biomass

In combining data from the profile wall and auger methods to produce estimates of root biomass to a depth of 1.2 m it was assumed that the count of root endings on a profile wall was directly proportional to the mass of roots per unit volume of soil in a given horizon on the profile wall. This should be a reasonable assumption where roots are orientated randomly or if orientation is equally biased between horizons. The mean percentage of root endings encountered between 0.15 m and 1.2 m on profile walls was used to convert the mean biomass of roots in the top 0.15 m to an estimate of that in the top 1.2 m (Table 3.3.3).

Table 3.3.3 Mean root biomass in the top 15 cm and top 120 cm of the soil in four diameter classes. The cumulative biomass in increasing diameter classes also given. (All values kg ha^{-1})

Soil Depth (cm)	Diameter Category (mm)	≤2	>2-≤5	>5-≤10	>10-≤15
0-15	Mean biomass	1704	2212	1442	1346
	(95% C.I.)	(75)	(147)	(218)	(363)
	Cumulative biomass		3916	5358	6704
0-120	Mean biomass	2830	3544	2310	2157
	(95% C.I.)	(125)	(235)	(349)	(582)
	Cumulative biomass		6374	8684	10841

3.3.2 Fine Root Length Density

Figure 3.3.3 shows a regression of total fresh length on dry mass for samples of fine roots in a range of sample sizes (r^2 = 0.827, n = 30, P<0.001). It was assumed, as previously stated, that the count of root endings on a profile wall was directly proportional to the dry mass of root per unit volume of soil from that horizon. The regression equation relating dry mass to total fresh length for roots ≤2 mm diameter was used to express the biomass of roots in the top 15 cm of the soil in terms of root length density. The mean fine root length density in the top 15 cm of the soil was estimated as 2.4 cm cm^{-3}.

As the mean vertical distribution of root endings in profile pits was related to root mass, and fine root mass was related to fine root length density, Figure 3.3.1a can be redrawn with new axes indicating estimated fine root length density (Figure 3.3.4). Figure 3.3.4 should be taken as only an approximate indication of root length density as number of root endings was only calibrated relative to fine root biomass, and hence root length density, at one depth (0-15 cm). The mean fine root length density in the top 1.2 m of soil was estimated as 0.6 cm cm^{-3}.

Figure 3.3.3 A regression of total fresh length on dry mass for samples of fine (≤2 mm diameter) roots; n = 30, total fresh length = 21.27.(dry mass)+0.068, r^2 = 0.83.

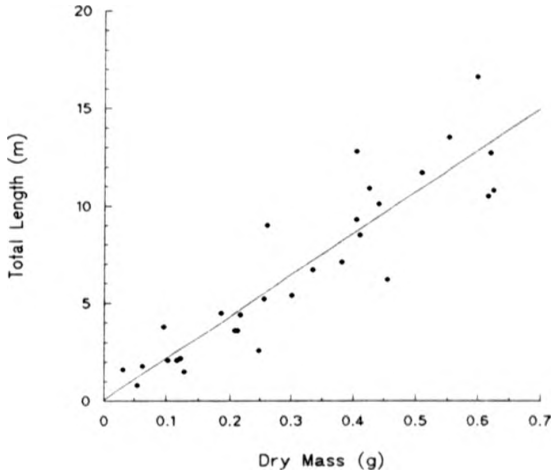
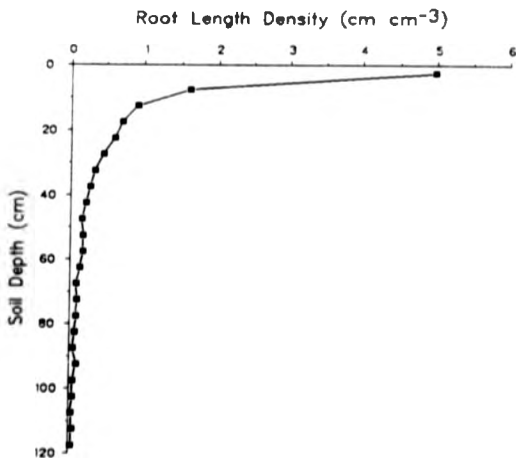


Figure 3.3.4 Estimated mean root length density in twelve soil profiles.



3.3.3 Fine Root Distribution in Relation to Soil Characteristics

Table 3.3.4 gives the results of correlations between mean root count per 25 cm^2 in 5-cm soil horizons on profile walls and various soil parameters measured on samples collected from these horizons (n = 84). Fine root distribution was strongly correlated with total nitrogen and total phosphorus, exchangeable calcium and organic matter, although this does not necessarily imply an association between these factors. Extractable phosphorus exhibited a weak inverse correlation with root distribution. Effective cation exchange capacity was not correlated, although the percentage base saturation was significantly correlated with root distribution. It is possible that a proportion of the soil nutrient concentration measured may have been contributed by root fragments that passed through the sieve prior to soil analyses. This would serve to increase the correlation recorded between the distribution of fine roots and soil nutrients.

Table 3.3.4 Correlation coefficients and level of significance for linear regressions between mean count of root endings per 25 cm^2 and soil analyses (n=84).

	r	P
Total N	0.849	***
Total P	0.441	***
Extractable P	-0.296	**
Exchangeable Ca	0.420	***
Exchangeable Mg	0.212	n.s.
Exchangeable K	0.086	n.s.
Exchangeable Na	0.040	n.s.
Exchangeable Acidity	0.086	n.s.
Effective Cation Exchange Capacity	0.121	n.s.
Base Saturation	0.418	***
Total C	0.870	***
Loss On Ignition (375°C)	0.460	***
Loss On Ignition (700°C)	0.225	*

Where
n.s. P > 0.05 (not significant)
* P = 0.05-0.01
** P = 0.01-0.001
*** P < 0.001

3.4 Discussion

3.4.1 Comparison of Fine Root Biomass with other Tropical Rain Forests

Comparisons of fine root biomass estimates between forests are confounded by the wide range of fine root diameter classes and soil depths that have been used. Fine root biomass data for a range of rain forest sites are compiled in Table 3.4.1. The biomass estimates for the Danum forest for roots ≤2 mm and ≤5 mm are both towards the lower end of the range of previous studies. The biomass recorded in the Danum forest is of comparable magnitude to that reported for lowland (Arboleda soil series, Gower 1987) and pre-montane (Raich 1980, Berish and Ewel 1988, Sanford 1989a) sites in Costa Rica. The relatively low values for fine root biomass recorded in the Danum forest are in contrast to the high values reported for Amazonian *tierra firme* forest on deeply-weathered oxisols, where a thick root mat develops above the mineral soil. (Klinge 1973,1975, Stark and Spratt 1977, Jordan and Escalante 1980, Sanford 1985). The root mat described by Sanford (1985) in *tierra firme* forest was, on average, 25 cm thick and contained 57% of the total biomass of roots <1 mm diameter. However, there was no root mat in a *tierra firme* forest at the limit of the range of the biome on Maracá island, Brazil (Thompson *et al.* in press) and fine root biomass was lower than reported for *tierra firme* forests on oxisols in Venezuela. In the Danum forest, although fine roots could be found growing through fresh litter above the mineral soil, and growing invasively into fallen stems, there was no development of a root mat.

Table 3.4.1 Fine root biomass estimates from a range of tropical rain forests.

Country	Forest Type	Soil Depth (cm)	Diameter Class (mm)	Fine Root Biomass (t ha^{-1})	Reference
	Evergreen forests				
Venezuela	*Tierra firme*	0-50	<1	10.7	Sanford (1985, 1989b)
		0-50	<2	14.3	
		0-50	<5	21.6	
	Caatinga	0-50	<1	13.3	
		0-50	<2	18.7	
		0-50	<5	28.0	
	Bana	0-50	<1	12.5	
		0-50	<2	16.1	
		0-50	<5	25.0	
Venezuela	*Tierra firme*	0-50	<6	56.0	Jordan & Escalante (1980)

Table 3.4.1 (continued)

Country	Forest Type	Soil Depth (cm)	Diameter Class (mm)	Fine Root Biomass (t ha^{-1})	Reference
Venezuela	*Tierra firme*	0-50	<6	31.9	Stark & Spratt (1977)
Venezuela	*Caatinga*	0-40	<6	62.1	Klinge & Herrera (1978)
Brazil	*Tierra firme*	0-40	<1	5.0	Klinge (1973,1975)
		0-40	<2	8.4	
		0-40	<3	10.5	
		0-40	<6	15.3	
	Campina	0-40	<1	3.6	
		0-40	<2	5.6	
		0-40	<3	7.3	
		0-40	<6	11.2	
Brazil	*Tierra firme*	0-100	<5	11.2	Thompson *et al.*(In Press)
Costa Rica	Eutrophic (River series)	0-50	≤5	3.7	Gower (1987)
	Oligotrophic (Arboleda series)	0-50	≤5	6.6	
Costa Rica	Pre-montane	0-15	<2	1.4	Sanford (1989a)
		0-15	<5	2.3	
Costa Rica	Pre-montane	0-85	<1	2.0	Berish (1982)
		0-85	<2	3.4	
		0-85	<5	6.4	
Costa Rica	Pre-montane	0-50	<2	2.9	Raich (1980)
Costa Rica	Pre-montane	0-25	<2	1.4	Berish & Ewel (1988)
New Guinea	Montane	0-25	<5	4.0	Edwards & Grubb (1977)
Hawaii	Montane	0-30	<1	2.6	Gower & Vitousek (1989)
		0-30	<2	3.4	
	Semi-evergreen				
Panama	Lowland	0-25	<1	1.4	Cavelier (1989)
		0-25	<2	2.8	
		0-25	<5	9.5	
	Montane	0-25	<1	2.0	
		0-25	<2	4.0	
		0-25	<5	9.5	
Ghana	Upper slope	0-50	<2	4.0	Lawson *et al.*(1970)
	Middle slope	0-50	<2	10.4	
	Bottom slope	0-50	<2	4.0	
Ghana	Lowland	0-30	<6	3.5	Greenland & Kowal (1960)
Malaysia	Lowland dipterocarp	0-15	≤2	1.7	This study
		0-15	≤5	3.9	
		0-120	≤2	2.8	
		0-120	≤5	6.4	

3.4.2 Nutrient Availability and Fine Root biomass

It has been postulated that fine root biomass in forest ecosystems is largely governed by an inverse relationship to nutrient availability (Gower 1987, Kellman 1990). Source-Sink theory (Bloom *et al.* 1985) suggests that trees should allocate more energy to roots on infertile sites as the investment in nutrient acquisition would yield increased growth and/or reproduction on a nutrient-limited site. Direct evidence of nutrient limitation in lowland rain forests is, however, lacking (Proctor 1992).

Nitrogen is often considered to be the most limiting mineral nutrient in temperate forest ecosystems. An inverse relationship between nitrogen availability and fine root biomass in temperate evergreen forests has been substantiated by a number of studies (Grier *et al.* 1981, Keyes and Grier 1981, Vogt *et al.* 1983a, 1985, Linder and Rook 1984, Nadelhoffer *et al.* 1985). The hypothesis that nitrogen availability governs fine root biomass is further supported by studies that recorded a significant decrease in fine root biomass following nitrogen fertilization (eg Alexander and Fairley 1983, Gill and Lavender 1983, Friedman-Thomas 1986, Ahlström *et al.* 1988).

Vitousek and Sanford (1986) grouped thirteen root biomass studies in tropical moist forests according to site fertility and concluded that overall root biomass appeared to be greatest on relatively infertile sites. Gower (1987), more specifically, sought a relationship between the nutrient content of litterfall and fine root biomass for eight lowland rain forest sites. No correlation was found between the nitrogen content of litterfall and fine root biomass, but phosphorus (r^2=0.63, P<0.05) and calcium (r^2=0.55, P<0.05) showed significant inverse relationships. He suggested that phosphorus and/or calcium availability appear to govern fine root biomass in lowland tropical ecosystems in much the same manner as nitrogen governs fine root biomass in temperate evergreen ecosystems. In contrast, Sanford (1985) found no correlation between nutrient availability and fine root biomass in a soil nutrient catena through three Amazonian forest types. The most nutrient rich site, *tierra firme* forest on oxisols, supported the largest fine root biomass and surface root mat. Sanford suggested, however, that the correlation between nutrient status and fine root biomass may have been confounded by seasonal flooding and/or moisture stress due to a widely fluctuating water table outwith the *tierra firme* forest.

As data on the nutrient content of litterfall in the Danum forest are not yet available it is not possible to directly compare the Danum forest with the relationships between litterfall nutrients and fine root biomass produced by Gower (1987). However, a notable feature of the Danum forest was the relatively low extractable phosphorus measured in the soil (0.40 mg kg^{-1} in the top 15 cm of the soil, Section 2.5.3). The Danum forest would appear to be inconsistent with the model of Gower (1987) in that a relatively low fine root biomass (Table 3.4.1) is maintained on a site relatively low in available soil phosphorus. In *tierra firme* forest recently described on Maracá island, Brazil on soils very low in total phosphorus (0-10 cm 61 mg kg^{-1}) and exchangeable calcium (0-10 cm 2.3 m-equivs kg^{-1}), fine root biomass, although higher than in the Danum forest, was considerably lower than that reported for a number of *tierra firme* forests on oxisols in Venezuela (Thompson *et al.* in press, Table 3.4.1). The Maracá forest did not display a number of other features commonly held to be adaptive features of rain forest on oligotrophic soils (Scott *et al.* in press). Thompson *et al.* suggest that the absence of a root mat might be explained by the lack of strong leaching under the seasonal climate of Maracá, or that root mats in other forests may be a response to poor aeration and/or toxins found in seasonally waterlogged soils or spodosols. It is noteworthy, however, that the Maracá soils were not particularly deficient in available phosphorus (0-10 cm 5.1 mg kg^{-1}). Both the Danum and Maracá forests seasonally experienced relatively dry periods not found in the Venezuelan oxisol sites possessing root mats, where no monthly rainfall total was less than 150 mm (Thompson *et al.* in press)

3.4.3 Fine Root Biomass Distribution and Soil Nutrients

It has been suggested that the surface concentration of fine roots observed in many tropical rain forests is governed by the inflow of nutrients in litterfall (Odum 1970). The Danum soils exhibit a steep decline in most nutrients with depth (Figure 2.5.4 and Sinun 1991). The significant correlations between total nitrogen and phosphorus and exchangeable potassium, calcium and magnesium with total carbon and loss on ignition values (Table 2.5.3) suggests that the bulk of soil nutrients are associated with organic matter in the soil. The evidence would seem to suggest that a large proportion of soil nutrients in the Danum soil are made available through the decomposition of plant litter and are cycled in the top layers of the soil.

The distribution of fine roots in the Danum forest was shown to be significantly correlated with organic matter, total nitrogen and phosphorus, and exchangeable calcium, but not correlated with exchangeable potassium or magnesium (Table 3.3.4). Similarly, in a semi-evergreen lowland forest in Panama, fine root biomass (<2 mm) was shown to be strongly correlated with the concentration of carbon, nitrogen and calcium in the soil profile (Cavelier 1989); nitrogen and calcium concentration accounted for 99.7% of the distribution of roots <1 mm diameter in the top 25 cm of the soil. In contrast, Stark and Spratt (1977) found no correlation between root distribution and the concentration of individual cations in an Amazonian forest on oxisols. A notable feature of the soil nutrient and fine root distribution in the Danum forest was that acetic acid extractable phosphorus increased with depth in the soil profile and was negatively correlated with fine root biomass. It is possible, however, that the pool of plant-available phosphorus in the soil was rapidly depleted by the concentration of fine roots. It is difficult, however, to separate the effects of specific nutrients by these methods. Although soil nutrient distribution is implicated in governing fine root distribution specific associations are probably best investigated by in-growth bag methods which supply localised nutrient-rich sources.

3.4.4 Seasonal Fluctuations in Fine Root Biomass

A wide variety of patterns in the fluctuation of fine root biomass have been reported for temperate and boreal forest ecosystems and it may not be surprising that forests with diverse climates, species and soils exhibit no common pattern. In the Danum forest the lowest mean fine root biomass coincided with a relatively dry period in April 1991 (Section 4.3.3). In a semi-deciduous lowland forest in Panama fine root (<2 mm diameter) biomass peaked at the beginning of (April/May), and during (September) the wet season and remained at a relatively low level during the dry season (Cavelier 1989). Similarly, in a lowland rain forest in Costa Rica dry season biomass of roots <1 mm diameter was half of that measured in the wet season (Sanford 1987). Both of these previous results for tropical rain forests are broadly in agreement with the results for Danum in that fine root biomass was found to be lowest during relatively dry periods.

Chapter 4 Fine Root Temporal Distribution

4.1 Introduction

4.1.1 Fine Root Persistence and Rates of Production and Disappearance

Some of the limitations of existing methods for estimating fine root production have been outlined in Chapter 1. It was also reported that sequential excavation methods show particular utility in recording the spatial distribution of fine roots, while observation methods allow measurement of the temporal variation in a fixed sample of the root system (Atkinson 1985). A new method for estimating fine root production was developed in the current study, which involved the combination of excavation and observation techniques in an attempt to separately quantify spatial and temporal variability of the fine root system. The method is superficially similar to that used by Sanford (1985, 1989b) in Amazonian *tierra firme* forest, who estimated fine root production by combining the monthly percentage mortality of fine roots on small plexi-glass windows with fine root biomass from soil cores. The problems of adequately separating fine roots into 'live' and 'dead' categories in the Danum forest have been discussed previously (Chapter 1, Section 3.2). Similarly, recognition of the point of physiological death, in a population of fine roots displaying a wide range of surface morphologies, behind a glass observation panel was not feasible. Fine root appearance and disappearance, however, were readily monitored and a new term fine root *Persistence* is introduced in preference to the use of *Longevity* or *Mortality*.

Estimates of fine root production and disappearance for the Danum forest were compared to estimates produced by various methods for other forests. It was shown that estimates of fine root production and disappearance calculated by the new method will improve as the fine root biomass approaches a steady-state.

4.1.2 Fine Root Decomposition

Two commonly used comparative measures of decomposition are litterfall:standing crop quotients (k_L values) and the rate of mass loss from material enclosed in mesh bags (Swift *et al.* 1979). It is a widely held belief that plant litter decomposes more rapidly in the humid tropics than in temperate zones, and that this results in tropical rain forest soils low in organic matter and the majority of the ecosystem nutrient

capital being held in plant biomass (Anderson *et al.* 1983, Proctor 1987, Jordan 1989b). However, the assumptions of a simple latitudinal gradient of decomposition have been largely refuted, with decomposition rates being shown to be dependant on a complex of factors involving: the nature of the decomposer community, the characteristics of the organic matter (resource quality), and the physicochemical environment (Meentemeyer 1978, Anderson and Swift 1983, Berg *et al.* 1984, Jordan 1989a). It has been demonstrated that there is considerable overlap in both the ranges of k_L values and the rates of mass loss from leaves in litterbags, between temperate and tropical forests reported in the literature (Anderson and Swift 1983, Proctor 1987). Jordan (1989a) concludes, however, the generalization that process rates are higher in the tropics is true, if sites of comparable soil fertility and water balance are compared.

A method involving the disappearance rate of excised roots in rhizotrons was used in this study to produce estimates comparable to both k_L values and the rate of mass loss from litterbags. Decomposition rates for fine roots can thus be compared with leaf decomposition rates for the Danum forest and other sites. A decomposition assay, analogous to the standard cotton strip method (Latter and Howson 1977, Harrison *et al.* 1988), was used to test whether decomposition was more rapid behind glass observation panels than in bulk soil. The average *Persistence* of excised fine roots was compared to the average *Persistence* of live fine roots still attached to the rest of the plant and thereby tentative estimates of mean fine root *Longevity* produced.

4.1.3 Seasonal Periodicity of Fine Root Growth and Soil Moisture

An advantage of the methodology introduced in this Chapter was that neither the spatial distribution nor the seasonal periodicity of fine root activity on observation surfaces was directly included in the calculation of fine root production. This freed the estimates from a number of the criticisms commonly levelled at rhizotron methods, that the population of roots visible on observation surfaces is not representative of the population in bulk soil (Huck and Taylor 1982, Atkinson 1985, McMichael and Taylor 1987, Vos and Greenwald 1987, Taylor *et al.* 1990, Cheng *et al.* 1991, Harper *et al.* 1991). It was assumed that the Persistence of roots on the glass soil interface was representative of the Persistence of roots in the bulk soil but not that the distribution

or timing of that activity was necessarily representative of the whole fine root population. However, seasonal periodicity in rates of root appearance and disappearance are of interest in quantifying the degree of seasonality below-ground in the Danum forest as well as the extent of any correlation of this activity with environmental variables and above-ground activity.

4.2 Materials and Methods

4.2.1 Fine Root Persistence and Rates of Net Primary Production and Disappearance

The rhizotron

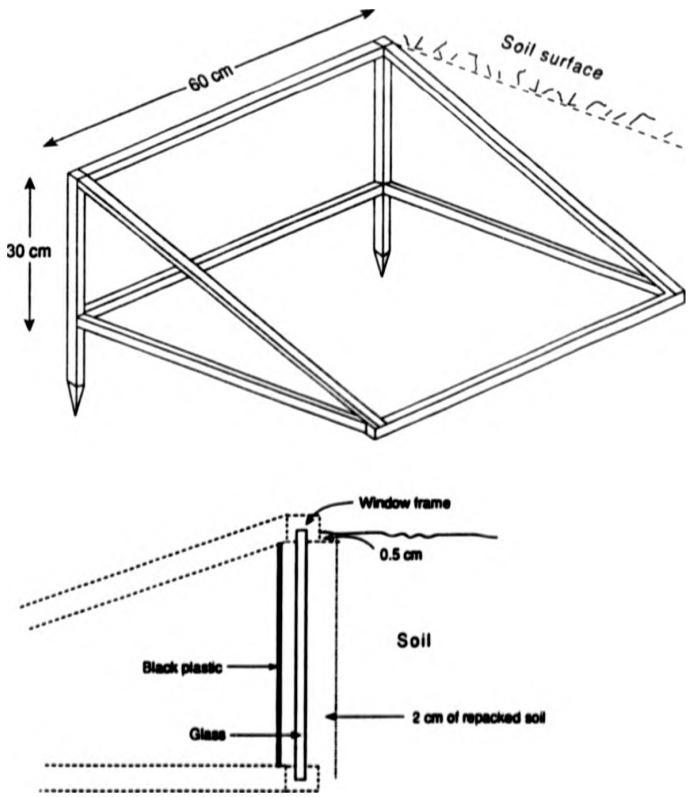
A simple rhizotron was designed which consisted of a wooden frame supporting a vertical glass observation window (Figure 4.2.1). The design was similar to that used by Asamoah (1984). Features of the rhizotron were designed to ensure that the glass was held rigidly throughout the experiment and that no light could enter the rhizotron except while measurements were being taken.

In order to install the rhizotron a hole 0.6 m x 0.6 m x 0.3 m deep with vertical sides was excavated. Soil removed in 5-cm depth increments was kept separate so that it could be used to repack the soil behind the glass face in layers that mimicked those present in the bulk soil. The soil was crushed by hand and obvious roots were removed. In excavating the pit particular care was taken not to disturb the observation face and to ensure that the face was not left smeared by the spade. The rhizotron was placed into the pit and gently hammered into place leaving a gap of about 2 cm between the glass and the prepared profile. Soil was carefully packed around the sides of the rhizotron so that the frame was held rigidly in the soil. The profile face was then built up in 5-cm increments, being packed with a wooden dowel to restore the original bulk density of the soil and to ensure an intimate contact between the soil and glass.

The in-filled soil was built up level with the surrounding soil which was about 0.5 cm above the top of the glass; this ensured that light could not leak into the rhizotron and be piped down the glass. Roots growing in the top 0.5 cm and 'superficially' above the mineral soil surface can not, therefore, be observed in the rhizotron. A sheet of

thick black plastic was pined against the observation side of the glass face so that light was excluded between observations. Pearson (1974) established that plant roots of different species differ in their response to light leaks in rhizotrons and Levan *et al.* (1987) found the root length density of soybean (*Glycine max* L. Merr) measured in mini-rhizotrons with deliberate light leaks to be only 20% of that in shielded rhizotrons. Huck and Taylor (1982) conclude, however, that short periods of illumination during measurement of roots are unlikely to have an effect on root growth. In the current study each rhizotron was exposed to light for about half an hour once each week.

Figure 4.2.1 Sketch of rhizotron showing general structure and a cross-section of the soil:glass interface.



Experimental design

Three rhizotrons were installed per plot; located on a stratified random basis and orientated with the observation window at right angles to the prevailing slope of the ground (Figures 2.4.2a-c). After installation each rhizotron was left for two months to allow for the soil to settle, for invasion of soil fauna, and for root activity against the glass to have reached some sort of equilibrium rather than be purely invasive. The activity of roots visible against the rhizotron glass was monitored at about weekly intervals between 7 December 1990 and 7 December 1991 using the following method of recording.

On the first sampling occasion a clear acetate sheet was pinned against the rhizotron glass. The profile was illuminated with a spotlight and a magnifying glass was used, where necessary, to view roots. All roots (≤2 mm diameter) that were visible on the profile were directly traced onto the acetate sheet with an indelible pen. Each root was individually assigned a number which identified the sampling occasion when the root was first present. On subsequent visits to the rhizotron the acetate sheet was again pinned on the observation panel and aligned as before. Any new root growth that had occurred in the intervening period was traced on the acetate sheet and marked with a number indicating the first date present. Any root that was no longer visible, or recognisable as a root, whether this was due to gradual decomposition, herbivory, or any other factor, was marked with a second number which corresponded to the sampling occasion that the root was first absent. Thus, changes in the population of roots present behind the rhizotron glass were recorded with weekly resolution.

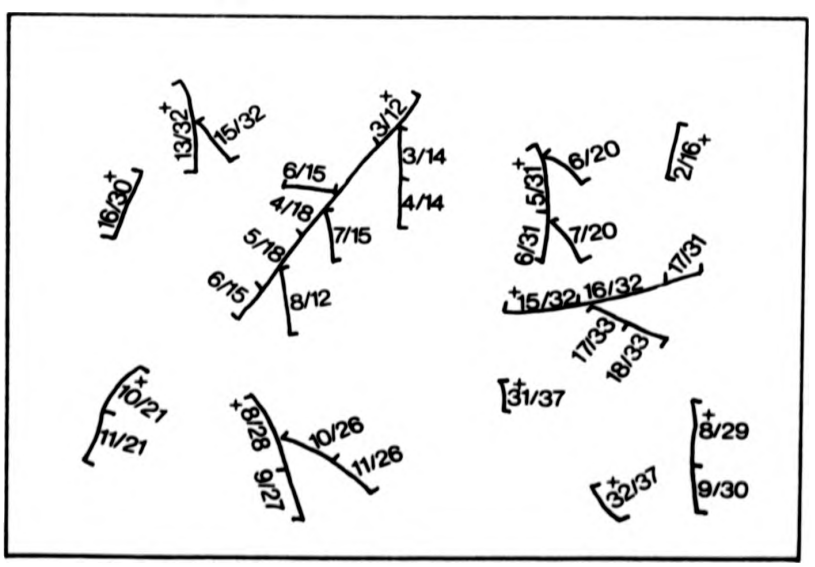
On completion of observations on rhizotrons in the field, the length of individual roots traced onto the acetate sheet was measured, to ±1 mm, using a digitizing tablet (Calcomp 200 series) and Apple IIe computer with 'Vids Linear Measurement' software (Micro Measurements Ltd., Essex, U.K.). Root length data from each rhizotron were grouped within Persistence categories defined by appearance and disappearance dates.

Calculation of fine root Persistence

The individual Persistence of a fine root is defined here as, the length of time from when a root first appears on the rhizotron profile to the first date when it is no longer visible or recognisable as a root. Conceptually this period may include a live stage, a stage of active senescence, and a decomposition stage, which may, or may not, be temporally separate. The rhizotron tracings yield information on a population of roots whose individual Persistence is known to within twice the sampling interval.

The mean Persistence of a population of fine roots is defined here as a mean of the Persistences of individual roots as recorded on rhizotrons. Three different estimates of mean Persistence were calculated: (a) Mean Persistence-(length) (*PsL*) utilized the sum of root lengths in each Persistence category; (b) Mean Persistence-(count) (*PsC*) utilized the number of roots in each Persistence category; (c) First Point of Contact Persistence-(count) (*PsF*) utilized only the number of first points of contact of roots with the rhizotron glass within each Persistence category. *PsF* was used to test for bias in the *PsL* and *PsC* estimates caused by roots tracking along the observation panel. Figure 4.2.2 illustrates the selection of first points of contact from a schematic rhizotron tracing. The following section outlines the calculation of *PsL*. *PsC* and *PsF* were calculated by simply substituting root number for length in these calculations.

Figure 4.2.2 A schematic section of a rhizotron tracing. The first number indicates the sampling occasion the root was first present and the second number the sampling occasion when first absent. + indicates selected as first point of contact.



Persistence categories

The length of individual roots (±1 mm) measured on the rhizotron tracings were grouped within Persistence categories defined by dates of appearance and disappearance. In the following notation a Persistence category (L) is recognised by two subscripts. The first subscript (i) corresponds to the sampling occasion roots in that category were first present and the second subscript (j) to the sampling occasion roots in that category were first absent. That is, Persistence category $L_{i,j}$ contains lengths of roots that were first present in sample i and first absent in sample j.

Roots that were present in sample 1 may have been initiated at any time before sample 1. These roots were grouped within Persistence categories where the first subscript i=1. Roots that were first present in sample 2 were initiated between samples 1 and 2. These roots are grouped within Persistence categories where i=2. If the rhizotrons were sampled on t occasions then roots that were first present in the last sample were grouped within a category where i=t.

Roots that were first absent in sample 2 were grouped within a Persistence category where the second subscript j=2. Roots first absent in the last of t samples were grouped within Persistence categories where j=t. Roots that were still present in the last sample t were grouped within categories where j is a notional sample $t+1$.

If for example a rhizotron was sampled on 4 occasions there are 10 possible Persistence categories. The possible categories are:

$L_{1,2}$ $L_{1,3}$ $L_{1,4}$ $L_{1,5}$ $L_{2,3}$ $L_{2,4}$ $L_{2,5}$ $L_{3,4}$ $L_{3,5}$ $L_{4,5}$

Any root monitored will fall into only one of these categories. Therefore, the total length of root monitored on the rhizotron during the 4 sampling occasions is the same as the sum of root lengths in these Persistence categories. The sum of all possible Persistence categories for t sampling occasions can be expressed more compactly by:

$$\text{Total length} = \sum_{i=1}^{t} \sum_{j=i+1}^{t+1} L_{i,j}$$

Time between samples

The time in days (Persistence time) between any two samples *i* and *j* is denoted in the following equations as $S_{i,j}$. $S_{i,j}$ was calculated as the time in days from the day midway between samples *i* and *i-1* to the day midway between samples *j* and *j-1*. This assumes that roots that were first recorded present in sample *i* were on average actually initiated midway between samples *i* and *i-1*. Similarly roots that were first recorded absent in sample *j* were assumed to have actually become absent, on average, midway between samples *j* and *j-1*. These assumptions become important when sampling intervals are not equal.

In summary, the length of individual roots were grouped within Persistence categories denoted by $L_{i,j}$, while the time between samples *i* and *j* was denoted by $S_{i,j}$.

Calculation of mean Persistence

The basic equation used for calculating mean Persistence-(length) (*PsL*) of roots was:

$$(a) \qquad PsL = \frac{\sum length\ (L) \times Persistence\ time\ (S)}{\sum length\ (L)}$$

Not all roots recorded on rhizotrons during a given sampling period will have been monitored for their entire Persistence. Some assumptions need to be made about roots that only coincided with the sampling period for a part of their Persistence. In order to take this into account the possible Persistence categories are grouped into 4 distinct Classes. Each Class is treated differently in the calculation of overall mean Persistence.

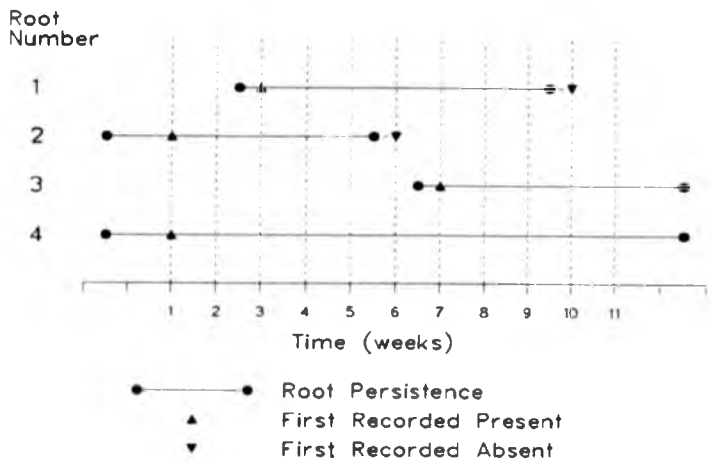
Class 1 roots have both appeared and disappeared within the sampling period.

Class 2 roots were already present in the first sample but disappeared within the sampling period.

Class 3 roots first appeared within the sampling period but were still present in the last sample.

Class 4 roots were present in the first sample and still present in the last sample.

Figure 4.2.2a. A rhizotron was sampled at weekly intervals for eleven weeks. The Persistence of 4 roots is indicated by the horizontal lines. Roots number 1, 2, 3 and 4 fall into Persistence category Classes 1, 2, 3 and 4 respectively. Note that no indication of root length is given.



Class 1 Persistence categories

Class 1 includes Persistence categories containing roots which have both appeared and disappeared within the sampling period. Class 1 is represented by root number 1 in Figure 4.2.2a which has both appeared and disappeared within the sampling period of 11 weeks. Root number 1 would be placed within a Persistence category $L_{3,10}$. Its entire Persistence has been monitored and we can be confident of its Persistence to within 2 sampling intervals (in this example 2 weeks). If the rhizotrons where sampled on t occasions the possible Persistence categories within Class 1 are:

Class 1 $L_{i,j}$ $2 \le i < j \le t$

Applying the basic equation (a), the mean Persistence of Class 1 roots can be estimated by:

$$(b) \qquad PsL_{class\ 1} = \frac{\sum_{i=2}^{t-1} \sum_{j=i+1}^{t} L_{i,j} \cdot S_{i,j}}{\sum_{i=2}^{t-1} \sum_{j=i+1}^{t} L_{i,j}}$$

Class 2 and 3 Persistence categories

Class 2 includes roots that were already present in the first sample but disappeared within the sampling period. Class 2 roots may have appeared at any time before the first sample. Class 2 is demonstrated by root number 2 in Figure 4.2.2a. Root number 2 would be placed within a Persistence category $L_{1,6}$. If the rhizotrons were sampled on t occasions the possible Persistence categories within Class 2 are:

Class 2 $\qquad L_{1,j} \quad 2 \leq j \leq t$

Class 3 includes roots that first appeared during the sampling period but where still present in the last sample. Class 3 is demonstrated by root number 3 in Figure 4.2.2a. Roots that are still present in the last sample were grouped within Persistence categories where the second subscript (j) was a notional sample $t+1$. Root number 3 in Figure 4.2.2a would therefore be placed within a Persistence category $L_{7,12}$. If the rhizotrons were sampled on t occasions the possible Persistence categories within Class 3 are:

Class 3 $\qquad L_{i,t+1} \quad 2 \leq i \leq t$

Roots in Classes 2 and 3 have only been monitored for a part of their total Persistence. If these roots were ignored it would be likely to cause an underestimation of overall mean Persistence of the fine root population. The longer the sampling period relative to the mean Persistence, the smaller the proportion of Class 2 and 3 roots there are likely to be.

It was assumed in these calculations that roots in Classes 2 and 3 were in fact monitored for half of their total Persistence. Given a scenario where both the

Persistence and the rate of appearance of roots was constant, the assumption that Class 2 and 3 roots have been monitored for half of their total Persistence will yield an estimate of mean Persistence close to the true value.

Applying equation (a) and assuming that roots have been monitored for half of their Persistence, the mean Persistence of roots within Class 2 can be estimated by:

$$(c) \qquad PsL_{Class\ 2} = \frac{2 \sum_{j=2}^{t} L_{1,j} \cdot S_{1,j}}{\sum_{j=2}^{t} L_{1,j}}$$

Similarly, the mean Persistence of roots within Class 3 can be estimated by:

$$(d) \qquad PsL_{Class\ 3} = \frac{2 \sum_{i=2}^{t} L_{i,t+1} \cdot S_{i,t+1}}{\sum_{i=2}^{t} L_{i,t+1}}$$

Class 4 Persistence category

Class 4 includes roots that were already present in the first sample and were still present in the last sample. This Class comprises a single Persistence category $L_{1,t+1}$. This Class is demonstrated by root number 4 in Figure 4.2.2a. Root number 4 would be placed within a Persistence category $L_{1,12}$. Roots in Class 4 comprise a proportion of the roots ≤2 mm diameter sampled in the biomass cores and cannot be ignored when calculating overall mean Persistence for the purposes of estimating fine root production. It is assumed in these calculations that Class 4 roots are a permanent proportion of the fine root population that neither appears or disappears. The estimate of mean Persistence is increased by the proportion; length of Class 4 roots:total root length.

Class 4 roots are taken into account by the following equation:

$$(e) \qquad PsL = \left[1 + \frac{length\ Class\ 4}{total\ length} \right] \times PsL_{Classes\ 1,2,3}$$

Working equations

Combining equations (b), (c) and (d) gives a working equation for calculating the mean Persistence-(length) of roots in Classes 1, 2 and 3:

$$1. \qquad PsL_{Classes\ 1,2,3} = \frac{\sum_{i=2}^{t-1} \sum_{j=i+1}^{t} L_{i,j} \cdot S_{i,j} + 2\sum_{j=2}^{t} L_{1,j} \cdot S_{1,j} + 2\sum_{i=2}^{t} L_{i,t+1} \cdot S_{i,t+1}}{\sum_{i=1}^{t} \sum_{j=i+1}^{t+1} L_{i,j} - L_{1,t+1}}$$

Taking into account Class 4 roots, overall mean Persistence-(length) is calculated by:

$$2. \qquad PsL = \left[1 + \frac{L_{1,t+1}}{\sum_{i=1}^{t} \sum_{j=i+1}^{t+1} L_{i,j}} \right] \cdot PsL_{Classes\ 1,2,3}$$

In practice, root length data were arranged within Persistence categories on a PC spreadsheet program. Equations (1) and (2) may then be readily solved.

Note that the explanation above outlines the calculation of Mean Persistence-(length) or *PsL*. This utilizes the length of root in each Persistence category and the basic equation (a). The same working equations were used to calculate two further estimates of Persistence, namely Mean Persistence-(count) or *PsC*, and first point of contact Persistence-(count) or *PsF* (page 59). Both of these estimates utilize the number of roots (or count) in each Persistence category rather than the length of roots. The estimates were calculated by simply substituting the number of roots, for the length of roots, in the working equations (1) and (2).

Calculation of fine root net primary production and disappearance

Many studies that have attempted to estimate fine root Net Primary Production (NPP) by demographic methods have based their calculations on a basic relationship adapted from population dynamics (McClaugherty et al. 1982, Fairley and Alexander 1985, Usher 1985, Chapter 1):

$$B_{t+1}^{(live)} = B_t^{(live)} + Production - Mortality$$

where $B^{(live)}$ = biomass of live roots at t and $t+1$.

As has been previously explained fine roots were not sorted into live and dead categories in this study. This was primarily due to the difficulty of adequately recognising physiological death by external characteristics in a population of roots of many species and morphologies. In particular the high proportion of ectomycorrhizae in the population, in which the host tissue is shielded by a fungal sheath, made recognition of 'live' and 'dead' roots problematic (Fogel 1983). Where live and dead roots are not assigned separate categories and are both included in the estimates of fine root biomass, only the boundary between dead roots and soil organic matter needs

to be recognised. Where a biomass containing both live and dead roots is being considered it is equally true that:

$$3. \quad B_{t+1}^{(live+dead)} = B_t^{(live+dead)} + Production - Disappearance$$

Where biomass has remained constant from time t to $t+1$ it follows that Production and Disappearance are equal. If an area of climax vegetation that is in a quasi-steady-state, is sampled over a large enough area of the vegetation for a long enough time scale biomass might be expected to remain constant (Kershaw 1973). In the steady-state scenario it follows that inputs to the system must equal losses. With this state of affairs the estimation of production and disappearance is greatly facilitated by the ability to apply the expression:

$$Root\ Production = \frac{Maximum\ Root\ Biomass}{Turnover\ Time} \qquad (Chapman\ 1986)$$

where turnover time was defined as the time required for the decomposition of a weight of organic matter equal to the weight of root biomass. It would seem however that with this definition of root turnover the above expression is only strictly true for dead root biomass. The expression is directly analogous to that commonly used to calculate litter turnover coefficients (k_l) from above-ground litterfall and litter 'standing crop' measurements (Swift *et al.* 1979). The expression can be refined to:

$$Production = Mortality = \frac{Biomass^{(live)}}{Mean\ Longevity}$$

where *Mean Longevity* is the average time from initiation to 'death' for the population of fine roots.

As has already been stated satisfactory recognition of the point of physiological death of a root behind a glass observation panel was not a feasible proposition in the Danum forest. In the steady-state scenario it is also true that:

$$4. \quad Production = Disappearance = \frac{Biomass^{(live+dead)}}{Mean\ Persistence}$$

Mean fine root Persistence has already been defined and is preferred to the term '*turnover time*' which appears ambiguous in the literature, as the confusion with the definition of Chapman (1986) demonstrates. Note that the above equation assumes steady-state conditions.

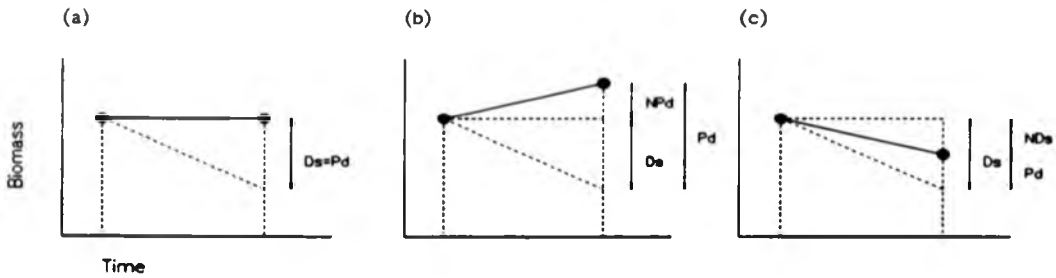
Biomass and Persistence can be independently estimated for the same population of roots by the auger and rhizotron methods respectively. The great advantage of this method of calculation is that it exploits the utility of the auger method for measuring spatial distribution of roots and the rhizotron method only for looking at temporal distribution (Chapter 1). It is assumed in this method that where the measurements of Biomass and Persistence were taken in different time periods the Persistence is constant through the composite time period. That is, the mean Persistence is assumed to be an inherent quality of the plant roots and their soil environment. This assumption is likely to be more acceptable the more aseasonal the climate. As has been previously discussed the estimate of Persistence will be more accurate the longer the sampling period over which rhizotrons were monitored (Section 4.2.1).

Where biomass is not constant between t and $t+1$ only the net production relative to disappearance is known. The absolute magnitude of the production and the disappearance that made up the net change are not known. A net increase in biomass, for example, could be due to an increase in production, a decrease in disappearance, or any combination of these two factors. As the fine root Persistence is assumed to be a constant and inherent quality of the roots and the soil environment, if the age structure of the population of fine roots was known in addition to the net change in biomass, then Disappearance and hence Production could be accurately estimated. In this study the rhizotrons were used to provide a large enough sample of the fine root population to adequately estimate fine root Persistence but the sample was not large enough to adequately reflect the true age structure of the whole population of roots. That is, the rhizotrons tend to intercept 'cells' of root activity (*sensu* Reynolds 1975). Although it is assumed that the individual Persistence of roots in a particular cell is representative of the Persistence of the roots in the whole population, the timing of activity in that cell can not be expected to reflect activity in the whole population. In a less species-rich vegetation in a more seasonal climate it might be more reasonable to assume that rhizotrons better reflect the periodicity of root activity in the whole

population.

The two main assumptions in the following calculations are that mean Persistence is constant and that the age structure of the fine root population remains even, despite fluctuations in biomass. Given this, Disappearance between samples *i* and *i+1* is a function of the biomass at *i* dependant on the constant *PsL*. Figure 4.2.3 illustrates the calculation of Disappearance (*Ds*) and Production (*Pd*) rates in three possible scenarios; (a) biomass remains constant, (b) biomass increases, (c) biomass decreases.

Figure 4.2.3 To illustrate the calculation of mean fine root production (*Pd*) and disappearance (*Ds*) assuming constant Persistence and an even aged structure in the population; (a) biomass constant between *t* and *t+1*, (b) biomass increases, (c) biomass decreases.



Where:

Ds = Mass Disappearance

NDs = Net Mass Disappearance

Pd = Mass Production

NPd = Net Mass Production

Applying Equation 4 it follows that the rate of Disappearance (kg ha^{-1} day^{-1}) for the period between biomass samples *i* and *i+1* can be estimated by:

$$Ds_{i,i+1} = \frac{B_i}{PsL}$$

where:

B_i = Fine root biomass in sample *i* (kg ha^{-1})

PsL = Mean Persistence estimate (days)

Applying Equation 3 it follows that the rate of fine root Production (kg ha^{-1} day^{-1})

between samples i and $i+1$ can be estimated by:

$$Pd_{ii+1} = \frac{B_{i+1} - B_i + (Ds_{ii+1} \cdot S_{ii+1})}{S_{ii+1}}$$

where:

S_{ii+1} = time between samples i and $i+1$ (days)

Overall Production (Pd) and Disappearance (Ds) for t sampling occasions was calculated by a weighted-mean, where:

Pd_{ii+1} = Mean Production between i and $i+1$ (kg ha^{-1} day^{-1})

Ds_{ii+1} = Mean Disappearance between i and $i+1$ (kg ha^{-1} day^{-1})

S_{ii+1} = Time between i and $i+1$ (days)

$$\text{Weighted Mean } Pd = \frac{\sum_{i=1}^{t} Pd_{ii+1} \cdot S_{ii+1}}{S_{1t}}$$

$$\text{Weighted Mean } Ds = \frac{\sum_{i=1}^{t} Ds_{ii+1} \cdot S_{ii+1}}{S_{1t}}$$

This method of calculation might be expected to show particular utility in systems where a relatively large root biomass is always maintained irrespective of significant fluctuations in the biomass. Methods that only utilize net changes in the biomass with tend to underestimate the true throughput of matter in the fine root system as they do not take account of the simultaneous occurrence of production and disappearance.

4.2.2 Fine root Decomposition

An additional set of rhizotrons was used to investigate fine root decomposition by a method that is directly comparable to that used to calculate fine root Persistence. The Decomposition-rhizotrons were identical to the Persistence-rhizotrons in all respects except that excised roots (Ferrier and Alexander 1985) were placed behind the observation panel during installation.

Two Decomposition-rhizotrons were installed per plot adjacent to existing Persistence-rhizotrons. In order to obtain live excised fine roots ten randomly located soil cores were taken for each rhizotron. Each core was broken open and roots were extracted unwashed, by hand in the field. The unwashed, live ≤2 mm diameter roots were carefully separated and cut into 10-30 mm sections or 'sprigs' of roots (the criteria for separating live roots being the same as those discussed in Section 3.2) During the repacking of soil behind the rhizotron glass (as in Section 4.2.1) the excised roots were placed against the rhizotron glass at a density similar to that of the population of roots commonly encountered on the Persistence-rhizotrons. Again, care was taken to mimic the original bulk density of the soil and also to ensure an intimate contact between excised root, soil and glass.

Once the rhizotron was installed a clear acetate sheet was placed against the observation panel and all visible sections of excised root were traced directly onto the acetate. On each subsequent visit to the rhizotron the acetate sheet was aligned on the observation panel and roots no longer visible, or clearly recognisable as roots, were recorded by marking the tracing of the root with a number corresponding to the sampling occasion. As with the recording of root Persistence, no attempt was made to attribute cause to the disappearance, be it gradual decomposition, herbivory, or being obscured by new root growth. New root growth into the Decomposition-rhizotrons was not recorded. The decomposition rhizotrons were monitored at about weekly intervals until none of the excised roots remained.

Calculation of mean decomposition time

The length of each root on the tracings was measured in the same way as for the Persistence-rhizotrons. For each individual root length time from excision to disappearance is known to within one sampling interval. With this information an estimate of the mean time from excision to disappearance behind the rhizotron glass, or a Mean Decomposition time can be produced, where:

l_j = length of root excised in sample 1 that was first absent in sample j.

S_j = time between date of excision (sample 1) and the date midway between sample j and j-1 ($1<j\leq t$).

Mean Decomposition time (Dc) in days can be estimated by:

$$Dc = \frac{\sum_{j=2}^{t} l_{1j} \cdot s_{1j}}{\sum_{j=2}^{t} l_{1j}}$$

The Decomposition estimate has an advantage over the Persistence estimate in that the entire history of all roots from the date of excision is known.

Filter paper decomposition assay

Filter papers were used as a index of decomposition in a method analogous to that using cotton strips (Latter and Howson 1977, Harrison *et al.* 1988), to test the hypothesis that decomposition was more rapid behind the rhizotron observation panels than in the bulk soil.

Whatman No.42 filter papers were dried at 80 °C and weighed to ±1 mg. During the repacking of soil behind the observation panel in the Decomposition-rhizotrons, one filter paper was placed against the glass at 2-8 cm depth and another at 22-28 cm depth. A further two filter papers were placed, at each of these depths in the soil, 2-3 m away from the observation panel in bulk soil. A spade was used to cut a slot in the soil at each location in the bulk soil which could be pushed closed once the filter paper had been inserted at the correct depth. The position of each filter paper in the bulk soil was marked with a numbered peg.

The decomposition of the filter papers in each rhizotron was monitored at weekly intervals with acetate tracings in the same manner as excised roots. On the first sampling occasion when none of the filter paper remained visible behind the rhizotron glass the corresponding filter papers in the bulk soil were carefully excavated. Any paper that remained was carefully brushed free of soil, dried to constant mass at 80 °C, and weighed to ±1 mg.

The experimental design was such that decomposition more rapid behind the observation panel than in the bulk soil could be tested for, but, no information could be gained as to whether decomposition is less rapid behind the glass than in the bulk

soil. The limitations of this design were due to the fact that the only clearly recognisable point in the visual assessment of decomposition of filter papers behind the rhizotron observation panel was the first occasion when no filter paper remained. Had additional rhizotrons been installed, on which no other measurements were being taken, then filter papers could have been sequentially harvested from both rhizotron and bulk soil, and the rate of percentage mass loss compared.

4.2.3 Seasonal Periodicity in Root Growth and Soil Water Availability

Calculation of rates of fine root appearance and disappearance

The rate of new root appearance and root disappearance in the Persistence-rhizotrons can be used as an indicator of periodicity in root activity. We can estimate a Root Appearance Rate (*RAR*) and Root Disappearance Rate (*RDR*) (in terms of length per rhizotron per day) for sampling occasions 2 to t by:

$$RAR_i = \frac{l_i}{S_{ii-1}}$$

$$RDR_j = \frac{L_j}{S_{jj-1}}$$

where:

l_i = length of root first present in sample i

S_{ii-1} = time between sample i and i-1

l_j = length of root first absent in sample j

S_{jj-1} = time between sample j and j-1

Weekly gravimetric water content measurements

One randomly located 8 cm diameter soil core was taken from each of subplots 3,5,7,11,12,14,19,21,23 (Figure 2.4.2a-c) at about weekly intervals between December 1990 and December 1991. No point on a 1 m grid was sampled twice. A subsample of approximately 100 g was cut from each core at depths 5-10 cm, 15-20 cm and 25-30 cm and sealed in a plastic bag. The water content of each sample was determined

by measuring the mass of water lost upon drying the sample in an oven at 105 °C to constant mass (Gardner 1965, Reynolds 1970).

Moisture-release curves

Tension table and pressure cell apparatus (Richards 1965, Marshall and Holmes 1979) were used to determine the relationship between soil water content and matric potential for a set of undisturbed soil cores. The cores were collected with stainless steel rings (inside diameter 7.3 cm, depth 5.0 cm, volume ≈210 cm^3) from positions and depths located according to the weekly sampling scheme for gravimetric water content described above. Each undisturbed core was refrigerated at 5 °C until measurement, to inhibit soil faunal activity.

Cores were equilibrated on tension tables at suctions of 1, 5 and 10 kPa and duplicate subsamples in pressure cells at 50, 200 and 1500 kPa. Undisturbed cores were subsampled by taking two smaller (inside diameter 2.8 cm, depth 1.5 cm, volume ≈9.25 cm^3) cores one from the upper and one from the lower surface. Duplicate subsamples were equilibrated in separate pressure cells. Cores were said to have equilibrated when their mass differed by less than 1 g on consecutive days. Thus, moisture-release characteristic curves could be plotted and the relationship used to express gravimetric water content in terms of matric potential.

4.3 Results

4.3.1 Fine Root Persistence and Rates of Production and Disappearance

Fine root Persistence

Estimates of mean fine root Persistence calculated by Equation 2 for each rhizotron are given in Table 4.3.1. It cannot be assumed that the Persistence of individual roots within each rhizotron are independent and therefore confidence limits for the Persistence estimates are calculated using *rhizotrons* as the sampling unit. The overall Persistence-(length) (PsL) estimate with 95% confidence intervals is 195 ±34 days. Figure 4.3.1. shows the distribution of the data that were used to calculate *PsL*.

Table 4.3.1 Estimates of fine root Persistence-(length) (*PsL*), Persistence-(count) (*PsC*) and first point of contact Persistence-(count) (*PsF*).

Rhizotron	n	*PsL* (days)	*PsC* (days)	n	*PsF* (days)
1A	529	156	152	228	150
1B	192	157	140	120	119
2A	385	215	195	169	189
2B	374	195	180	173	154
2C	224	191	184	96	155
3A	407	263	254	167	239
3C	449	186	183	236	179
ALL	2573	195(14)	183(14)	1189	169(13)

Figure 4.3.1 The frequency distribution of total fine root length in 10-day Persistence categories from seven rhizotrons. Mean Persistence-(length) (*PsL*) = 195 days.

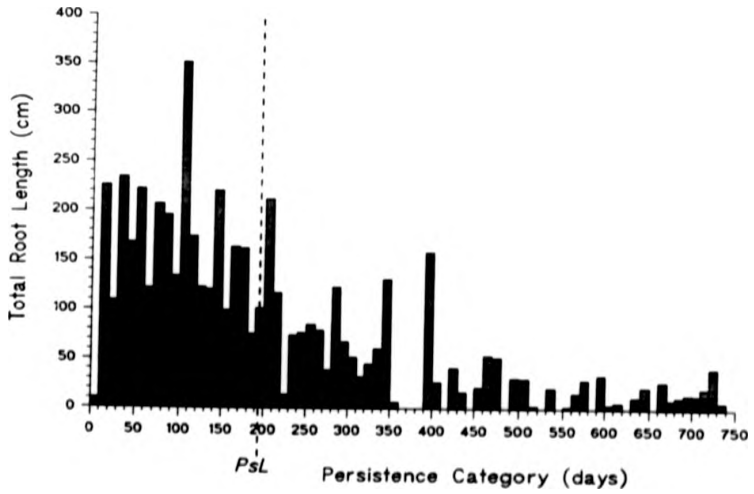
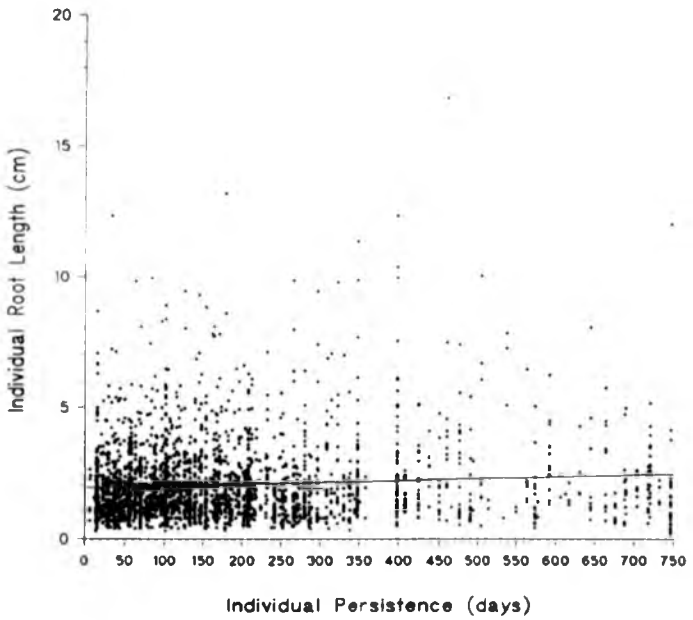


Figure 4.3.2 shows the relationship between Persistence and Length for all roots included in the *PsL* estimate. Although the linear correlation is significant because of the large number of sample points (n = 2523, r = 0.075, P<0.001) the trend for increasing Persistence with root length can be seen to be slight (slope=0.0007). That

longer roots do not tend to Persist longer is further supported by the fact that *PsC* calculated by summing root counts is not significantly different to *PsL* calculated by summing root lengths (Student's t-test P>0.05, Table 4.3.1). Figure 4.3.3 shows the distribution of the data used to calculate *PsC* and when compared to the distribution used to calculate *PsL* (Figure 4.3.1) it can be seen that the patterns are very similar.

Figure 4.3.2 A regression of length on Persistence of individual fine roots from seven rhizotrons; n = 2523, length = 0.0007.Persistence+1.95, r = 0.075, P<0.001.

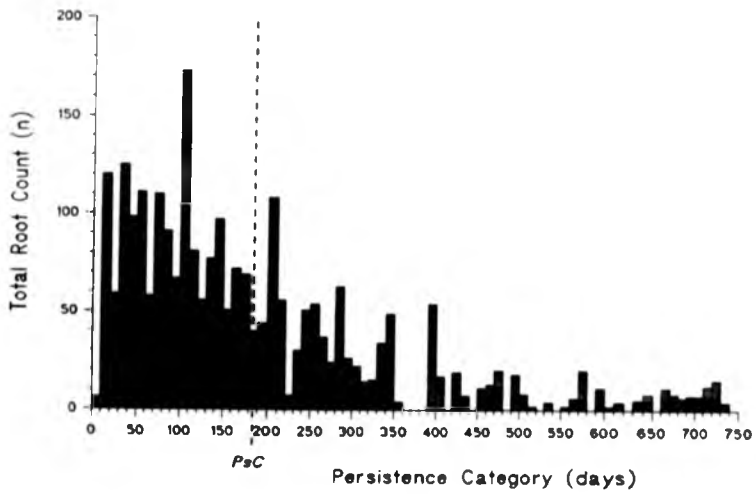


The data do not support the idea that short lateral roots are considerably more ephemeral than longer roots, and suggests that roots cannot be separated into physiological classes by their length. These conclusions, however, only hold if roots track along the glass window. If the visible length of root is not correlated with its true total length then this will serve to confound the relationship.

On intercepting the glass panel an actively growing root apex may either terminate its extension, turn away from the glass or track along the glass (Harper *et al.*1991). Roots were frequently observed to track along the glass in this study and in others (Taylor

and Böhm 1976, Huck and Taylor 1982, Mackie-Dawson *et al.* 1989). The ability of a rhizotron observation surface to alter the spatial distribution of a root system was the primary reason that rhizotrons were not used to measure root spatial distribution in this study (Section 4.2.1). Where roots track along glass, the population of roots visible in the rhizotron will be biased towards later orders of branching (Fitter 1985, 1987, Rose 1983) than the population present in any instantaneous cross section of bulk soil. If the rhizotron population is biased towards later orders of branching, this may in turn bias the estimates of fine root Persistence.

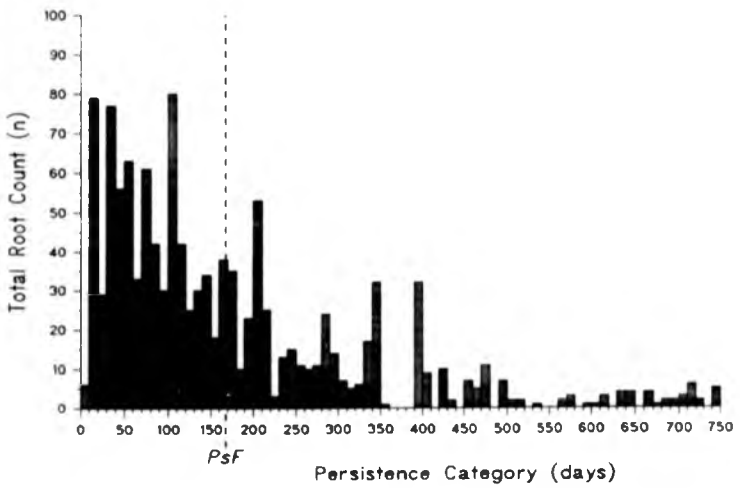
Figure 4.3.3 The frequency distribution of number of roots in 10-day Persistence categories from seven rhizotrons. Mean Persistence-(count) (Psc) = 183 days.



If we assume that the *first point of contact* of all roots with the rhizotron glass occurs in a random manner, we can test for bias in the *PsL* estimate by comparing the *PsC* estimate with *PsF*. The *PsF* estimate is not significantly different from *PsC* (Student's t-test P>0.05). Figure 4.3.4 shows the distribution of the data used to calculate *PsF* and it can be seen that although the total number of roots included in the *PsF* estimate was much lower than in *PsC* (1189 vs. 2523) the distributions of the data used to calculate the two estimates remain very similar. There was no evidence of bias in the *PsL* estimate due to root tracking, and the use of *PsL* in the calculation of fine root

Production (*Pd*) and Disappearance (*Ds*) is thus supported.

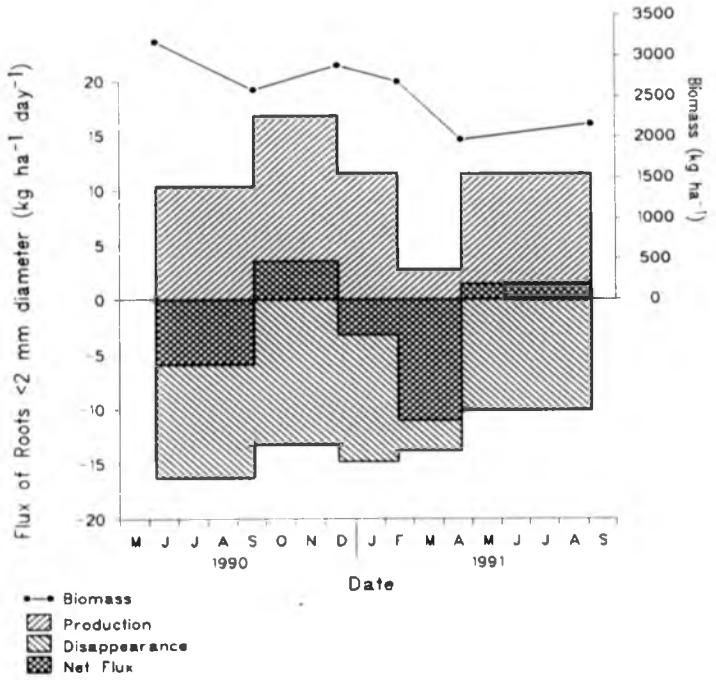
Figure 4.3.4 The frequency distribution of first points of contact roots in 10-day Persistence categories from seven rhizotrons. Mean first point of contact Persistence-(count) (*PsF*) = 169 days.



Fine root net primary production and disappearance

Overall estimates of fine root Production (*Pd*) and Disappearance (*Ds*) between June 1990 and September 1991, calculated by the method outlined in Section 4.2.1, were 4018 and 4843 kg ha^{-1} $year^{-1}$ respectively. Figure 4.3.5 illustrates the fluctuations in the rates of *Pd* and *Ds* and the biomass of fine roots.

Figure 4.3.5 Estimates of fine root biomass (mean for all plots) and rates of production and disappearance between June 1990 and September 1991.



4.3.2 Fine Root Decomposition

Estimates of mean Decomposition Time (*Dc*) for each rhizotron are given in Table 4.3.2. The all-rhizotron mean *Dc* with 95% confidence intervals is 133 ±12 days.

If it is assumed that decomposition processes occur only after fine root death and that excision induces death, then *PsL* minus *Dc* provides a tentative estimate of mean fine root longevity. Using this model in which life and decomposition are temporally separate phenomena, mean fine root longevity in the Danum forest was 62 days and fine roots were decomposing on average for 70% of their Persistence. If the frequency distributions of the data used to estimate Persistence and Decomposition are compared, however, (Figures 4.3.1 and 4.3.6) an anomaly is found. Figure 4.3.6 shows that a relatively small proportion (11%) of the total root length had disappeared before 100

days on the Decomposition-rhizotrons. Whereas, Figure 4.3.1 shows that on the Persistence-rhizotrons the total individual Persistence of a much larger proportion (31%) of all roots was less than 100 days. This would seem to suggest that it is not valid to simply subtract *Dc* from *PsL* to estimate longevity and that the model of temporally separate life and decomposition is not supported. However, the discrepancy between the two methods could be explained by a number of factors, which are discussed in Section 4.4.2.

Table 4.3.2 Estimates of mean fine root decomposition time (*Dc*).

Rhizotron	*Dc* (days)
1D	132
1E	141
2D	140
2E	107
3D	141
3E	140
All	133 (5.1)

Figure 4.3.6 The frequency distribution of length of fine roots in 10-day decomposition categories from six decomposition-rhizotrons. *Dc* = 133 days.

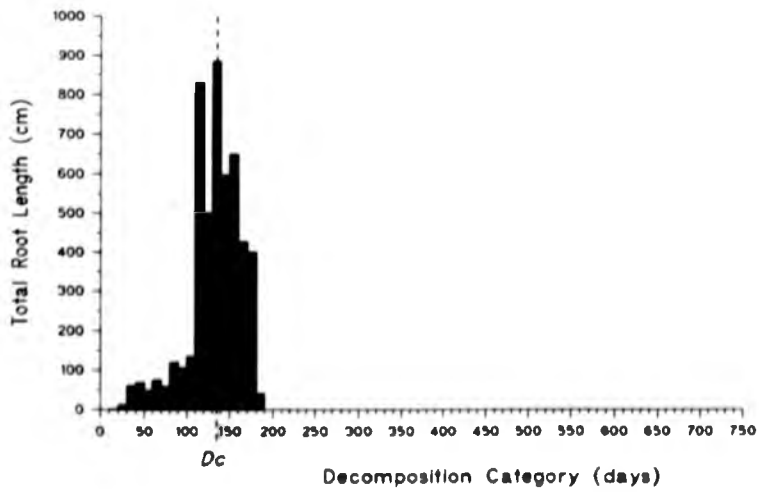
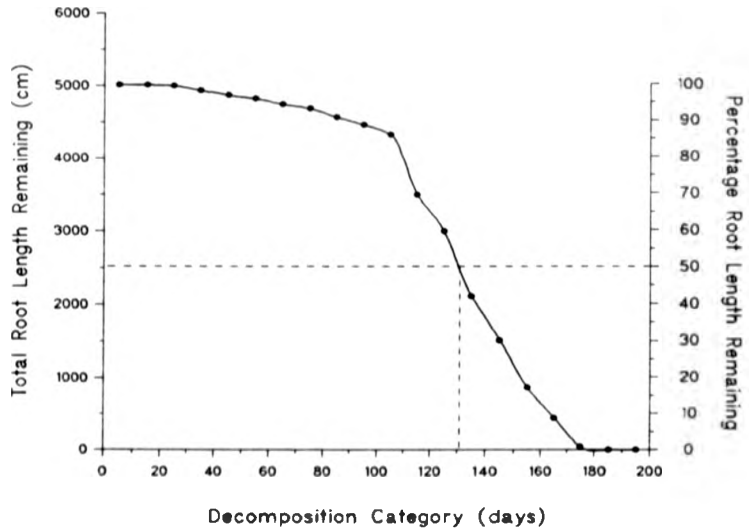


Figure 4.3.7 shows the decomposition data plotted in terms of the total length of root remaining with time. Fifty per-cent of the original root length remained after 130 days, a value close to the *Dc* estimate of 133 days. The point at which 50% of the original root length remained is equivalent to the median of the decomposition data presented in the frequency distribution in Figure 4.3.5. The mean (*Dc)* and median (50% remaining) are not equal because the distribution of the decomposition data was skewed.

Figure 4.3.7 The total length, and percentage of initial length, of excised fine root remaining with time (10-day decomposition categories) in six decomposition-rhizotrons. Fifty per-cent of the initial fine root length remained after 130 days.



Litterfall/standing crop quotients (k_L) have commonly been used to characterize decomposition rates in forest ecosystems (Swift *et al.* 1979), where the litter standing crop is assumed to be in a steady-state and k_L is equivalent to the reciprocal of turnover time. With currently available data k_L values provide the only basis on which geographical patterns of litter decay can be compared throughout the humid tropics (Anderson and Swift 1983). The reciprocal of fine root *Dc* expressed in years may be considered as equivalent to k_L values for above-ground litter. Expressing *Dc* in these

terms k_R=2.7 . k_R may be used to compare fine root decomposition in the Danum forest with k_L values for above-ground litter reported for adjacent plots and other lowland rain forests.

A second widely-used comparative measurement of litter decomposition is the loss of mass of material enclosed in mesh bags (Swift *et al.* 1979). No one model of exponential decay adequately describes the various patterns of decomposition reported for litterbag studies and hence there is no common factor by which to compare decay rates between sites (Weider and Lang 1982). Anderson and Swift (1983) assumed a linear pattern of weight losses with time, which although an over-simplification of the true course of decomposition (Anderson *et al.* 1983, Figure 4.3.6), allowed for comparison of decay rates between sites in terms of percent per year. For comparative purposes the length of root disappearing in Decomposition-rhizotrons may be thought of as analogous to the loss of weight from litter bags. A linear model was fitted to the total length of root remaining with time (Figure 4.3.7, r = -0.93, n = 20, P<0.001) which indicated 100% fine root disappearance in 202 days or an equivalent turnover rate of 181 % yr^{-1}.

Filter paper decomposition assay

Filter papers placed in bulk soil were excavated on the first sampling occasion that corresponding papers in the Decomposition-rhizotrons were no longer visible. Remains of only one filter paper was recovered from bulk soil in these excavations, the other twenty-three papers having fully decomposed. The weight of the filter paper recovered was 15% of that when buried. There was no evidence to support the hypothesis that decomposition was more rapid behind the rhizotron glass than in bulk soil.

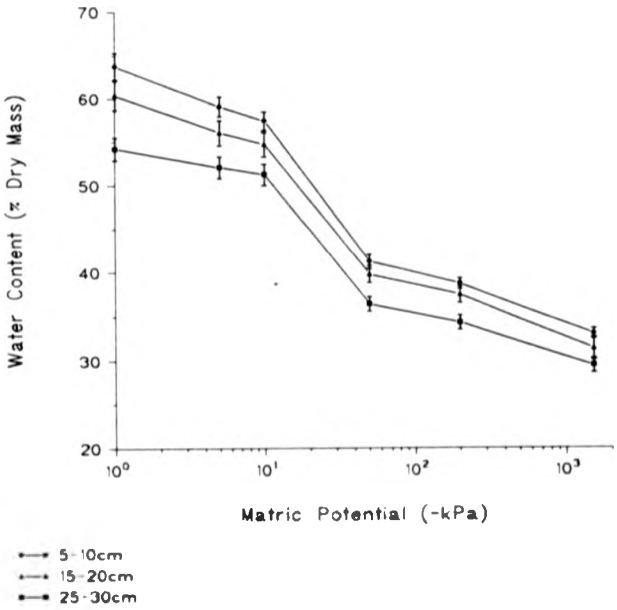
4.3.3 Seasonal Periodicity of Root Growth and Soil Moisture

Moisture-release curves

Undisturbed cores taken from three depths in the soil were equilibrated on tension table and pressure plate apparatus and moisture-release curves were plotted (Figure 4.3.8). The replicates from each depth were in close agreement and the standard errors were small. Moisture content was calculated on a mass basis rather than the more

commonly used volumetric method as the relationships were used to express weekly gravimetric soil moisture data (per-cent dry mass) in terms of matric potential. It can be seen that at a given percentage moisture content, matric potential will be greater in the surface layers of the soil.

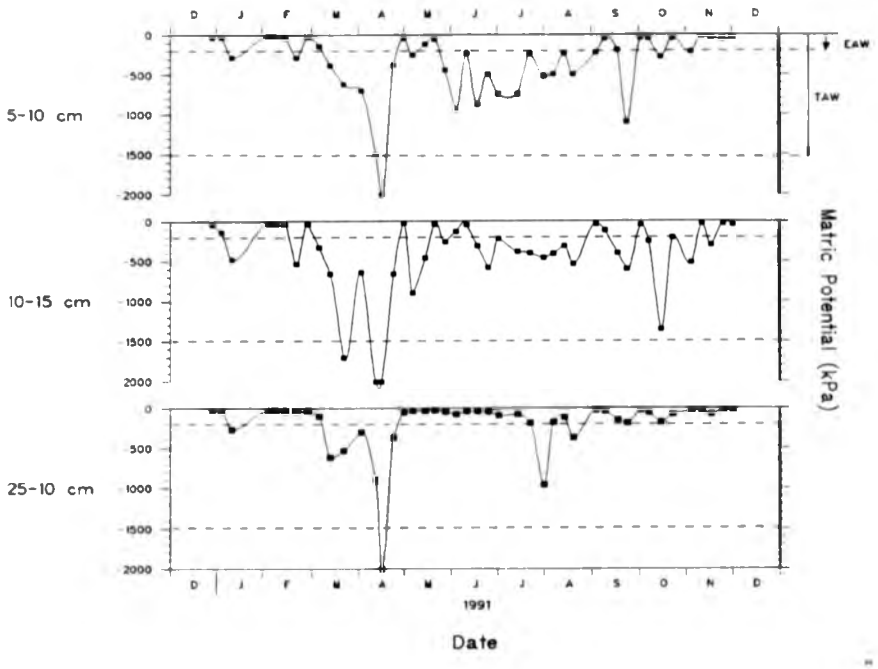
Figure 4.3.8 Mean (± S.E.) moisture-release characteristics for three depths in the soil. (n = 9 at -1, -5 and -10 kPa, n = 18 at -50, -200 and -1500 kPa).



Seasonal Variation of Soil Moisture at Three Depths in the Soil

Weekly gravimetric soil moisture content data (per-cent dry mass) was converted manually to matric potential using the moisture-release curves. For the majority of December 1990 to December 1991 the total moisture content remained higher in the 5-10 cm layer than in the horizons below. When these data are expressed in terms of matric potential, however, it can be seen that water availability tends to increase down the profile (Figure 4.3.9)

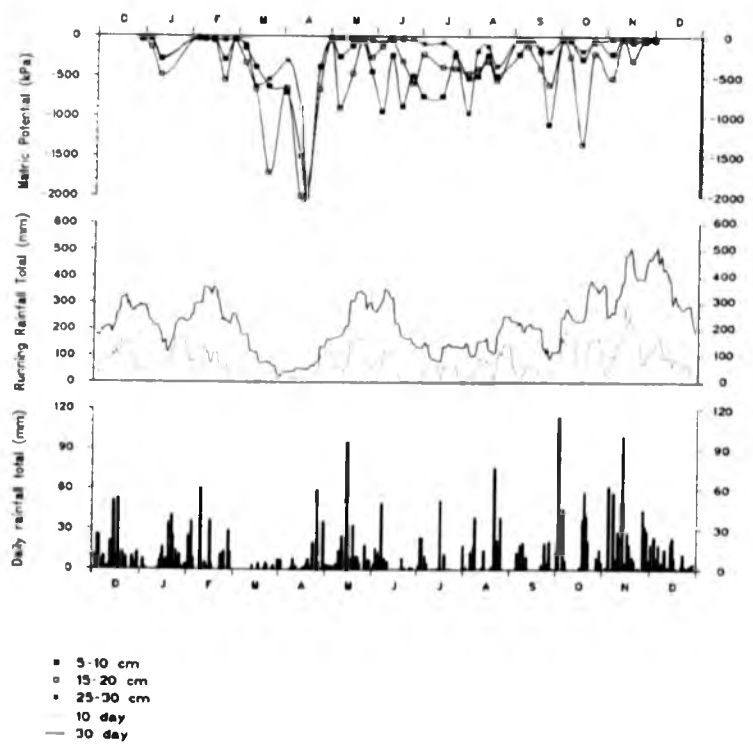
Figure 4.3.9 Mean matric potential at three depths in the soil between December 1990 and December 1991, (n = 9).



Easily available water is often considered to be water held between field capacity (-5 kPa) and -200 kPa (Hall *et al.* 1977) and to be equivalent to removing all water from pores greater than 1.5 μm in diameter (Ball and Hunter 1980). Similarly, total available water is often taken to be water held between field capacity and the permanent wilting point (-1500 kPa), equivalent to the removal of all water from pores greater than 0.2 μm, although many plants with drought tolerance can extract water from soil below this tension (Marshall and Holmes 1979). In the 5-10 cm layer in the Danum soils easily available water was available for only 46% of the year from December 1990 to December 1991, while it was available for 78% of the year at 25-30 cm. Figure 4.3.9 clearly demonstrates that fluctuations in the matric potential were greatest in the top layers of the soil. The horizon with most widely fluctuating soil moisture contains the highest concentration of fine roots (Figure 3.3.1) and fine roots may be implicated in the soil drying.

Figure 4.3.10 shows soil matric potential with 10-day and 30-day running rainfall totals from December 1990 to December 1991. At all three soil depths matric potential was significantly correlated with both 10-day and 30-day running rainfall totals for the meterological station at DVFC, 1-2 km from the research plots (Table 4.3.3, Figure 2.4.1).

Figure 4.3.10 Daily rainfall totals, 10-day and 30-day running rainfall totals, and mean matric potential at three depths in the soil (n = 9) between December 1990 and December 1991.



The matric potential at all soil depths was more closely correlated with 30-day running totals than with 10-day totals. This suggests that rainfall in the preceding month is more important to current soil moisture than that in the preceding 10 days and that soil matric potential did not respond rapidly to fluctuations in rainfall input in the Danum forest. The degree of correlation of matric potential with rainfall decreases down the soil profile.

Table 4.3.3 Results of linear regressions between soil matric potential and 10-day and 30-day running rainfall totals (n = 44).

Soil depth (cm)	No. of days in running total	r	P	Significance level
5-10	10	0.47	1.2×10^{-3}	**
	30	0.60	2.0×10^{-5}	***
15-20	10	0.41	6.1×10^{-3}	**
	30	0.55	1.1×10^{-4}	***
25-30	10	0.30	4.9×10^{-2}	*
	30	0.44	2.8×10^{-3}	**

* P<0.05-0.01
** P<0.01-0.001
*** P<0.001

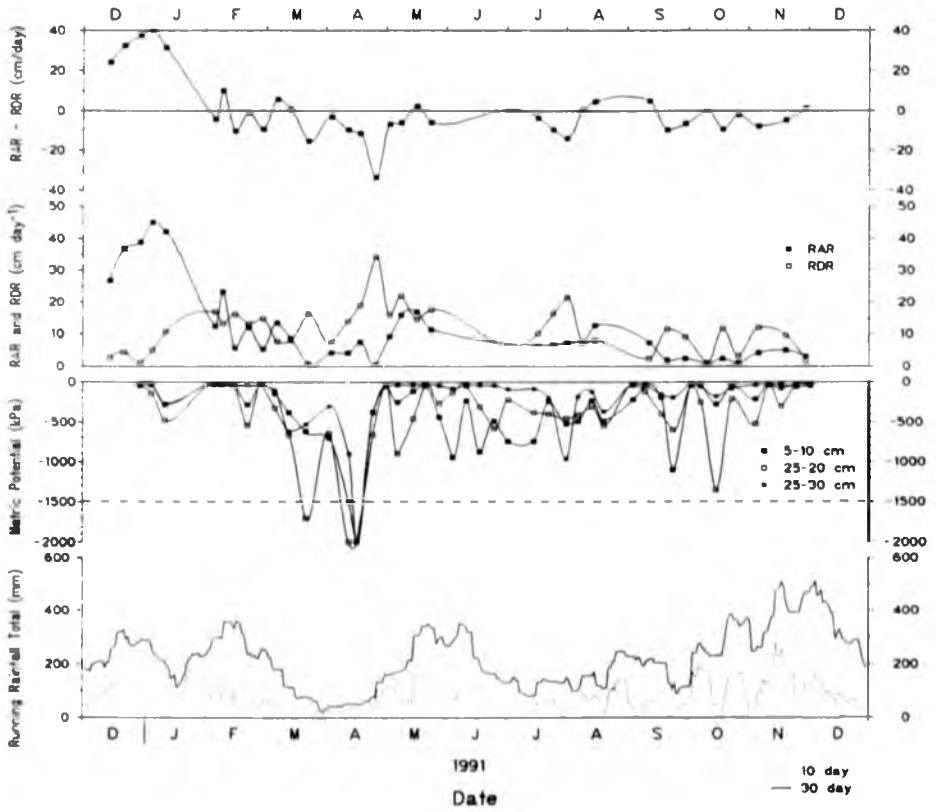
Seasonal periodicity of root growth and soil moisture content

Persistence rhizotrons were left to settle for two months before any measurements of root initiation or disappearance were made (Section 4.2.1). Figure 4.3.11 shows that at the beginning of sampling Root Appearance Rate (*RAR*) was high and Root Disappearance Rate (*RDR*) low. *RAR* and *RDR* did not meet until two months into the period of measurement. Root growth into a rhizotron might have been initially high after installation because of the stimulation of fine root growth by severing larger roots, or perhaps because the soil repacked behind the observation panel provided a preferential, root-free environment for fine root growth. The pattern of *RAR* and *RDR* in Figure 4.3.11 suggests that root growth in the rhizotrons did not equilibrate in terms of root appearance and disappearance until four months after installation.

In terms of the calculation of fine root Production (*Pd*) and Disappearance (*Ds*) rates (Section 4.3.1), the initial lack of a normal age structure in the rhizotron fine root population is unlikely to have biased estimates. *RAR* and *RDR* were not used directly in calculating *Pd* or *Ds*. The assumption used in the calculation method (4.2.1) was that the Persistence of fine roots intercepted by rhizotrons was representative of the Persistence of roots in the ecosystem as a whole, but that the timing of that activity was not necessarily representative. The small number of rhizotrons used may only reflect discrete cells of activity (Reynolds 1975) and temporal changes in root mass were better estimated by the more rigorous soil core sampling (Section 3.2).

Nonetheless, the *RAR* and *RDR* estimates are of interest in relating root activity to environmental variables over a short scale.

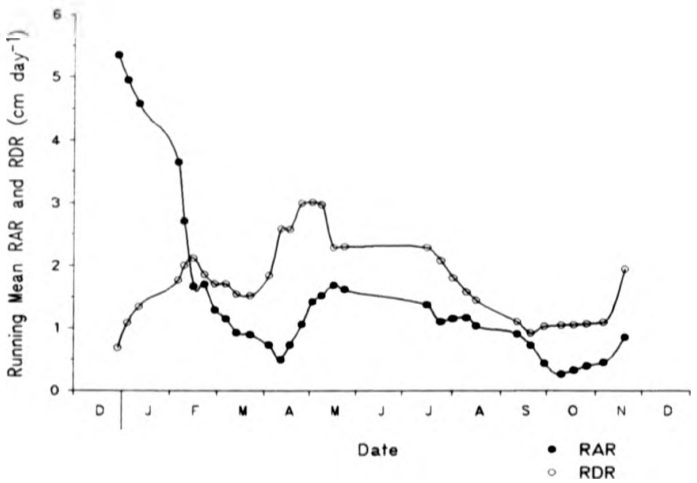
Figure 4.3.11 10-day and 30-day running rainfall totals for DVFC; mean matric potential at three depths in the soil (n = 9); and root appearance rate (RAR), root disappearance rate (RDR) and RAR minus RDR for seven rhizotrons; between December 1990 and December 1991.



Correlations were sought between *RAR*, *RDR*, *RAR minus RDR*, and 10-day and 30-day running rainfall totals. No significant linear correlations were recorded. Although root activity and rainfall are not linearly correlated it can be seen in Figure 4.3.11 that peaks of root disappearance coincided with inter-monsoonal dry periods in April and August 1991. In addition the lowest *RAR* coincided with the lowest soil moisture

content in April. *RAR-RDR* indicates the net change of root length on rhizotrons between sampling occasions. Two large net decreases in root length on the Persistence-rhizotrons coincided with the dry inter-monsoonal months. The patterns of RAR and RDR are more clearly seen when plotted as running means (five sampling occasions for all rhizotrons) which serve to even out short-term fluctuations (Figure 4.3.12).

Figure 4.3.12 Five-sampling occasion running mean root appearance rate (RAR) and root disappearance rate (RDR) for seven rhizotrons.



4.4 Discussion

4.4.1 Fine Root Persistence and Net Primary Production

Mean fine root persistence

Observation methods allow fine root systems to be studied in demographic terms. The change in size of any live population is ultimately controlled by birth and death rates (Olson 1964). All plant organs have a life history in which they pass from birth to death and/or disappearance from the live population (Harper *et al.* 1991). The application of demographic methods to root systems, however, poses a number of problems. Roots branch and ramify, may maintain active meristems, and are not

unitary organs in the same sense as leaves. A cohort of fine roots may have members of various ages and physiological states. In addition, individuals may pass out of the current population not only by death and/or disappearance but by becoming secondarily thickened and moving into a conceptually separate population.

To apply demographic reasoning to root observation methods it is necessary that the history of individual roots is monitored. More frequently in previous studies the approach has been to record only net changes in root length against a given area of glass. Individual monitoring requires that roots can be located and recognised from one sampling occasion to the next. Mini-rhizotron technologies have been developed whereby video or still photographic images of areas of glass inside a tube can be taken and hence roots monitored through time (Smucker *et al.* 1987, Taylor *et al.* 1990, Atkinson and Mackie-Dawson 1991). The main advantages of the acetate tracing method used in this study are that: (a) observations can be made without the aid of a viewing device; (b) fine roots are readily identified by their previous position and orientation on the tracing; (c) as the current tracing contains information on the previous state of the root comparisons between sampling occasions are inherently carried out while in the field, and therefore subsequent analysis does not involve the comparison of photographic images or drawings. The relative ease with which measurements can be taken means that a large number of roots can be sampled in a given time. These small rhizotrons, moreover, maintain the advantage over large rhizotron facilities in that a large number of points can be sampled in an ecosystem thereby improving replication and statistical validity. It would seem that both within and between rhizotron replication can be maximised by this method.

A method analogous to the drawing method used in this study for recording root length could be used in conjunction with mini-rhizotrons, although it would require that the viewing device is supported thus freeing the observers hands to make a drawing. A method using 22 mm diameter tubes, borescope and tripod was attempted in this study but was not pursued because of the low productivity in terms of the number of roots that could be monitored, as well as the frequent disturbance of the mini-rhizotron tubes: The soil around the tubes was frequently colonized by an ant species, while many tubes were destroyed by larger unidentified animals.

A main assumption in the methodology outlined here for calculating mean fine root Persistence is that the Persistence of roots against the rhizotron glass was not significantly different from that of roots in bulk soil. It was not assumed that the spatial distribution of fine roots, or the periodicity of root growth, against the rhizotron, was necessarily representative of that in bulk soil. The method is, therefore, free from the criticisms commonly levelled at methods which estimate fine root length density from rhizotrons (McMichael and Taylor 1987, Vos and Greenwald 1987, Harper *et al.* 1991) which assume the window does not influence the structure, density or periodicity of the root system compared to that in bulk soil, and that roots are visible in the rhizotron up to a given distance from the glass (Atkinson 1985, Atkinson and Mackie-Dawson 1991, Mackie-Dawson and Atkinson 1991). An initial concern was that the rhizotron served to concentrate the soil arthropod community behind the observation panel thus hastening the disappearance of fine roots compared to the situation in bulk soil. The filter paper decomposition assay, however, provided no evidence that decomposition was more rapid behind the rhizotron glass than in the bulk soil.

Mean Persistence of fine roots (≤2 mm) in the Danum forest was estimated as 195 ±14 days (standard error). It is important to consider that the grouping of all roots ≤2 mm diameter includes not only roots from a wide range of species, but also roots in two main physiological categories. That is, ephemeral, fleshy roots involved primarily in water and nutrient uptake and roots that were destined to become secondarily thickened and part of the structural framework of the root system (Hermann 1977). In the calculations outlined in this chapter it is important that both categories are included in the Mean Persistence estimate since both represented in the biomass of roots ≤2 mm diameter. In addition, Persistence was defined as the length of time from initiation to disappearance. This means that the estimate of mean Persistence of roots in the Danum forest is difficult to compare with previous estimates of fine root longevity. For example, fine roots of field grown apple (*Malus pumila* Mill.) turned brown, on average, four weeks after initiation and 20-25% of new roots survived to become components of the woody root system (Head 1966, Atkinson 1985). No estimate of the percentage of fine roots that become part of the permanent woody root system are available by the methods used in the current study. Mackie-Dawson and Atkinson (1991) reported that the measurements of survival in apple roots were

relatively constant and therefore relatively small populations could be used to determine root longevity. These findings support the methodology adopted in the current study. Harper *et al.* (1991) used a novel approach to root system demography by utilizing a particular growth habit of white clover (*Trifolium repens*). All new roots in white clover are developed from nodes that also support leaves. By monitoring the development of leaves in the field it was possible to determine the age structure of the root population of subsequently harvested plants. They found the mean age of roots in clover plants to be significantly correlated with season. However, this does not necessarily infer that the mean Persistence of clover roots was also varied significantly through the season as the variation in the mean age structure of the clover plants could be a function of fluctuating production rates of fine roots which have a subsequent constant mean Persistence.

Fine Root Net Primary Production and Disappearance

The importance of including fine root production in ecosystem-level carbon and nutrient budgets has been well documented in temperate and boreal forests (Persson 1979, 1983a and b, McClaugherty *et al.* 1982, Vogt *et al.* 1982, 1987, Fogel 1985, 1991, Nadelhoffer *et al.* 1985, Petersen *et al.* 1985), but few studies have attempted to estimate fine root production in tropical rain forests. The results of four previous rain forest studies are compiled in Table 4.4.1. The estimate of fine root production for the Danum forest is within the range, but lower than the mean (5.7 t ha^{-1} yr^{-1}), of that reported for the other sites. It is important, however, to take account of the methodologies employed in estimating fine root production and the soil depth to which estimates correspond.

It is perhaps more useful to compare estimates of fine root production with other parameters in the same ecosystem than to compare absolute values between sites. In the Danum forest the fine root production to leaf litterfall ratio was 0.61 and the ratio to total small litterfall 0.34. This suggests that fine root turnover was less important than above-ground small litter production in supplying organic matter to the soil system in the Danum forest. This is in contrast to the situation reported for a number of other forests in which fine root production was greater than or equivalent to above-ground litterfall (eg Persson 1978, 1979, Fogel and Hunt 1979, Ågren *et al.* 1980,

Table 4.4.1 Fine root production estimates in lowland tropical rain forests.

Country	Forest Type	Methodology	Soil Depth (cm)	Fine Root Diameter (mm)	Fine Root Production (t ha^{-1} yr^{-1})	Leaf Litterfall (t ha^{-1} yr^{-1})	Reference
Venezuela	*Tierra firme* on oxisol	Growth into pits, litter bags and through screens	40	n.g.[a]	2.01	5.72[d]	Jordan & Escalante (1980)
Venezuela	*Tierra firme* on oxisol	In-growth bag (soil) and surface litter bag	10	<2	2.47	5.72[d]	Sanford (1985,1989b)
		Soil coring and plexi-glass windows	10	<2	15.36[b]		5.72[d]
Venezuela	*Tierra firme* on oxisol	In-growth bag (vermiculite)	10	n.g.[a]	11.20	5.72[d]	Cuevas & Medina (1983,1988)
Panama	Semi-evergreen	Sequential coring	25	<2	1.15-4.12[c]	7.80[e]	Cavelier (1989)
		In-growth bag (soil)	25	<2	3.70	7.80[e]	
Malaysia	Dipterocarp on ultisol	Profile walls, sequential coring and rhizotrons	120	≤2	4.02	6.60[f]	This study

a All in-growth roots
b 39.0 t ha^{-1} yr^{-1} in whole profile
c Dependent on calculation method. Extrapolated from 10 cm depth assuming production proportional to biomass
d Jordan & Herrera (1981) - litterfall for San Carlos *tierra firme* forest
e Small litter not separated into fractions. Value for leaves 60% of total small litter based on two similar lowland forests on Barro Colorado Island (Leigh 1975, Leigh & Windsor 1982)
f Burghouts *et al.* (1992) - total small litterfall = 11.5 t ha^{-1} yr^{-1}

Harris *et al.* 1980, Grier *et al.* 1981, Nadelhoffer *et al.* 1985, Sanford 1985, Commeau and Kimmins 1989, Cuevas *et al.* 1991).

In rain forests, high values of fine root production have been reported by Sanford (1985, 1989b) and Cuevas and Medina (1983, 1988) for *tierra firme* forest at San Carlos de Rio Negro, Venezuela. One of the methods employed by Sanford is superficially similar to that employed in this study and involves the combination of root biomass from soil coring and root mortality measured on plexi-glass windows. The average monthly mortality of roots on the windows was 26 per-cent, which is equivalent to a fine root turnover rate of 3.1 times per year. The mean Persistence of fine roots in the Danum forest (195 days) suggests an equivalent turnover rate of 1.9 times per year. In Sanford's study a high fine root biomass (Table 3.4.1), a large proportion of which consisted of root mat, has combined with a rapid turnover rate, to yield large estimates of fine root production; reported to comprise about 70% of net primary production in the San Carlos forest. The measurement of percentage mortality by Sanford's method would appear to be heavily dependent on the assumption that the age structure of the population of fine roots observed on the plexi-glass windows was normal with respect to that in bulk soil. It is not clear whether high rates of fine root mortality could have been due, in part, to death of roots which appeared during an initial flush of new root growth onto the windows shortly after installation, as was recorded in the current study. In addition, soil was excavated from one side of each window in order to make the monthly observations and it is not clear as to how this level of disturbance might affect subsequent survival of fine roots. Sanford (1985) does not include details of his rhizotron design.

Cuevas and Medina (1983, 1988) recorded considerably higher values of fine root production in the root mat and top 10 cm of the soil than Jordan and Escalante (1980) who used analogous in-growth methods on an adjacent site (Table 4.4.1). They suggested a possible explanation for the discrepancy between the two studies was the intrinsic variability in depth and perhaps vigour of the root mat depending on the proximity of trees to the experimental points. Sanford (1987b) reported thicker root mats near tree stems in *tierra firme* forest. The use of the in-growth bag method to estimate fine root production is supported, however, by the agreement that Cavelier (1989) recorded between separate in-growth bag and sequential coring methods in

semi-evergreen rain forest in Panama.

In accord with previous discussion in the literature Cavelier (1989) found sequential coring methods of estimating fine root production to be highly dependent on the method of calculation used (Chapter 1). Four methods yielded the following results for fine root production in the top 10 cm of the soil (t ha^{-1}): (a) summing all positive increments in biomass, 2.8; (b) using all changes in live and dead biomass and the decision matrix of Fairley and Alexander (1985), 2.78; (c) summing only statistically significant ($P<0.05$) increments in biomass, 0.83; (d) using only statistically significant changes in live and dead biomass and the decision matrix of Fairley and Alexander (1985), 0.78. The debate as to which method of calculation provides the best estimate of fine root production with sequential coring techniques remains unresolved (Fogel 1991, Neill 1992).

Sequential coring methods, even when allied with 'balancing transfers' calculations such as those of Fairley and Alexander (1985), only record net changes in live and dead fine root biomass and cannot reflect simultaneous changes in fine root production, mortality and disappearance. In the steady-state scenario where live and dead biomass are constant, all such methods will yield zero production, mortality and disappearance. Were a true steady-state scenario encountered, production, mortality and disappearance rates could be accurately estimated by combining sequential live and dead biomass measurements with an independently measured rate of root decay using litter bags. Where changes in live and/or dead fine root biomass do occur, however, the application of an independently measured fine root decay rate becomes confounded (Chapter 1).

Sequential coring and balancing transfers calculations would appear to be most applicable for ecosystems where fine root appearance, death and disappearance tend not to occur simultaneously and therefore these processes are reflected by net changes in the live and dead fine root biomass. In contrast, the estimates calculated by the method outlined in the current study (Section 4.2.1) will improve the closer the system approaches to steady-state; that is, where a large fine root biomass is maintained relative to the fluctuations in the biomass. The methodology allows for the calculation of simultaneous production and disappearance. The selection of the most appropriate

method for estimating fine root production in forest ecosystems should be based on existing knowledge of criteria such as the degree of seasonal and inter/intra-specific synchrony in the ecosystem under study.

4.4.2 Fine Root Decomposition

An anomaly was found when comparing the frequency distributions of *PsL* and *Dc* (Figures 4.3.1. and 4.3.5.). By 100 days only 11% of the excised fine roots in the Decomposition-rhizotrons had disappeared whereas the total Persistence of 31% of fine roots in the Persistence-rhizotrons was less than 100 days. The discrepancy between the two methods might be explained by a number of factors:

(a) The assumption that roots that are present on the first sampling occasion or are still present on the last sampling occasion (categories l_{1j} and l_{ii+1}) have been monitored for, on average, half of their existence, may yield some very short individual Persistences. The large number of short Persistences may seem anomalous when the frequency distributions of *PsL* and *Dc* are compared. It is important to note however, that this was unlikely to bias the estimate of *PsL* as the same number of roots will have their Persistence underestimated as overestimated. In a scenario where new root appearance occurs at a constant rate the assumption that l_{1j} and l_{ii+1} roots have been monitored for half of their Persistence will yield an estimate of *PsL* identical to that if all roots had been monitored for all of their Persistence.

(b) A possible empirical explanation for the apparent incompatibility of the *PsL* and *Dc* distributions is that following installation of the Decomposition-rhizotrons the soil decomposer community took some time to re-establish itself. About 2 cm of soil behind the rhizotron glass was sorted free of roots and subsequently repacked on the first sampling occasion. In contrast, the Persistence-rhizotrons were left to settle for two months prior to the first recorded observations.

(c) A third explanation for these results could be that the decomposition of roots that are still attached to the rest of the plant is more rapid than roots that have become severed. It has been suggested that a common mycorrhizal-mycelial network might be involved in the transport of material away from senescent fine roots (Read *et al.* 1985,

Newman 1988, Newman and Eason 1989). This might serve to reduce *Dc* for fine roots that maintain live mycorrhizal links during decomposition. However, if such a hyphal pathway involved net nutrient transfer, or if there was significant retranslocation of nutrients out of senescent fine roots to other parts of the plant (Nambiar 1987) the reduction in the resource quality (Swift et al. 1979) for decomposer organisms might be expected to lead to an increase in *Dc* compared with roots that have been severed from the plant. An intact, common mycorrhizal-mycelial network could potentially be involved in the transport of decomposition products in the Persistence-rhizotrons, but the excision process inherent in the Decomposition-rhizotron technique would have destroyed any such links.

Burghouts *et al.* (1992) recorded a decay rate (k_L) value for leaf litter in the plots of Newbery *et al.* (1992) at Danum (Figure 2.4.1) of 2.7, a value identical to the fine root decay rate (k_R) estimated by Decomposition-rhizotrons in the current study. This suggests that fine root and leaf decay rates were similar in the Danum forest.

Anderson and Swift (1983) compiled k_L quotients for fourteen lowland rain forest sites. They reported some evidence of regionality in k_L values, with k_L values in west African forests generally being greater than in south-east Asia and the neotropics. Gross climatic characteristics did not appear to function as the primary variable in controlling decay rates, with resource quality and particular groups of soil fauna providing large contributory factors. Leaf litter consistently turned over more rapidly than total small litter. k_L values for leaf litter in lowland forests ranged between 1.1 and 3.6. k_L values exist for other lowland dipterocarp forests at Pasoh, Peninsular Malaysia, 3.6 (Ogawa 1978, Yoda 1978); Mulu, Sarawak, 1.7 (Anderson *et al.* 1983); and Penang, Peninsula Malaysia, 1.1 (Gong and Ong 1983). k_R and k_L values for the Danum forest are within the range of values reported for other dipterocarp forests and towards the upper end of the range of lowland rain forests worldwide.

To enable the length of root disappearing in the decomposition rhizotrons to be compared with the results of previous litter bag studies a linear model was fitted to the total length of root remaining with time (Section 4.3.2). The equivalent turnover rate of 181 % yr^{-1} is within the range of annual percentage weight loss from leaves reported for seven lowland rain forest sites (35-538 % yr^{-1}, Anderson and Swift 1983,

Anderson *et al.* 1983), although it was considerably higher than that reported for mixed species, freshly fallen leaf litter weight loss in lowland dipterocarp forest at Mulu, Sarawak (50 % yr^{-1} Anderson *et al.* 1983).

4.4.3 Seasonal Periodicity of Root Growth and Soil Moisture

The rate of fine root Appearance (*RAR*) on the Persistence-rhizotrons was initially high, and the rate of root Disappearance (*RDR*) low (Figure 4.3.11). Values of RAR and RDR did not become equivalent until four months after the rhizotrons were installed, suggesting that root growth was predominantly invasive in nature until this time. This may be an important consideration for fine root observation studies whose methodology assumes that the age structure of the population of fine roots on soil:glass interfaces is representative of the root population in bulk soil.

No simple linear correlation was found between RAR, RDR and rainfall running totals (Section 4.3.3). It was shown, however, that the highest value of RDR and the lowest value of RAR coincided with the dry inter-monsoonal period in April 1991 (Figure 4.3.11). Soil moisture would appear to be the dominant influence controlling fine root activity for at least part of the year in the Danum forest, although causality cannot be inferred. Fine root biomass and production have been variously related to environmental variables, such as water and nutrient availability, and the growth of the above-ground biomass in previous studies (Cavelier 1989). Few studies, however, have directly evaluated root activity and specific environmental conditions simultaneously in forest ecosystems. Studies in temperate forests, for instance, have found it difficult to separate the effects of rainfall, soil temperature and shoot activity on fine root dynamics (Lyr and Hoffmann 1967, Roberts 1976, Santantonio and Hermann 1985). Santantonio and Hermann (1985) found changes in fine root activity in natural stands of Douglas Fir in north-west USA to be generally explained by seasonal changes in rainfall and soil temperature. They found the decrease in fine root counts in soil cores to coincide with summer droughts and with low temperatures in winter, and increases to coincide with either, rainfall after dry periods or with soil warming in spring. Deans (1979) reported interaction between the effects of soil temperature and moisture on the rate of fine root growth in plantations of Sitka Spruce in the U.K.. Santantonio and Hermann (1985), however, conclude that soil moisture and temperature alone do not

provide an adequate basis for predicting seasonal patterns of fine root growth in temperate forests but that neither can they be predicted on the basis of shoot growth. Fine root growth in temperate forests appeared to be governed by a complex interaction of endogenous and exogenous factors.

In the Danum forest seasonal variation in soil temperatures under mature phases of forest were minimal (Brown 1990) and soil temperature may reasonably be eliminated as a potential factor affecting root activity in areas where the forest canopy is intact. Above-ground activity at the community-level in dipterocarp forests in controlled by a complex series of individual phenologies (Medway 1972, Ng 1984, Whitmore 1984). The Danum forest as a whole was basically evergreen, although within this overall classification some tree species were deciduous, which may (for example *Koompassia excelsa* (Becc.) Taub.) or may not exhibit synchrony in leaf shedding between individuals. Burghouts *et al.* (submitted) have attempted to separate the seasonal contributions of different species to leaf litterfall in the plots of Newbery *et al.* (1992) in the Danum forest. Many emergent and upper canopy tree species were found to shed their leaves throughout the year, but with distinct peaks once, or several times per year. Some species displayed synchrony in leaf litterfall (for example *Shorea johorensis* Foxw. and *Shorea pauciflora* King), while other species alternated between individuals in their pattern of leaf litterfall (for example *Shorea argentifolia* Sym.). Burghouts *et al.* report that the majority of species are of the 'periodic growth, leaf exchanging type' (Longman and Jenik 1979, Ng 1984) and add a new flush of leaves more or less simultaneously with shedding the previous generation. A relatively low number of large emergent and canopy trees were found to periodically dominate leaf litterfall locally and the species composition of leaf litterfall showed large variability throughout the year. Importantly, Burghouts *et al.* (1992) have previously demonstrated that overall patterns of litterfall and litter disappearance rates were not related to the pattern of rainfall in the Danum forest. Although individual species may be synchronous in their leaf shedding, at the community-level the various patterns of leaf fall tend to even out (Burghouts *et al.* submitted) and Burghouts et al. (1992) reported that the spatial variability of the litterfall, collected monthly from 30 traps, was greater than the temporal variation.

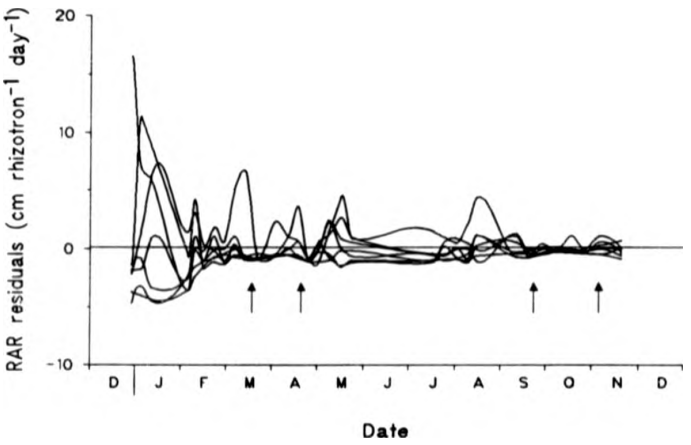
In terms of seasonality in reproductive effort, dipterocarps as a family are known to

exhibit infrequent and gregarious (mast) fruiting at periods of about 2-7 years (Wood 1956, Burgess 1972, Fox 1972, Ng 1977, 1981, Whitmore 1984). A mast fruiting of dipterocarps occurred in the DVFC area in August/September 1990. Other species in lowland dipterocarp forest, however, flower and fruit continuously, while others still, fruit periodically but at regular intervals of a year or less (for example many *Ficus* species, Whitmore 1984). It can be seen that patterns of above-ground activity in dipterocarp forest are difficult to evaluate, and hence to relate to below-ground activity at the community level of organisation.

Although synchrony of leaf litter between individuals has been demonstrated within some species in the Danum forest, the various patterns between species served to even out litterfall at the community-level (Burghouts *et al.* submitted) and the community-level pattern was found not to be correlated with rainfall (Burghouts *et al.* 1992). Fine roots were not separated by species in the current study and therefore it was not possible to discern whether synchrony between individuals of particular species in leaf litter was reciprocated in rates of fine root appearance and disappearance on rhizotrons. Figure 4.4.1 shows the Root Appearance Rate (RAR) residuals for seven rhizotrons: The RAR on each rhizotron for each sampling date was subtracted from the (five sampling occasion) running mean for all rhizotrons. It would appear that the greatest synchrony in RAR between rhizotrons occurred between the two pairs of arrows in Figure 4.4.1, dates that coincide with the dry period in April 1991 and immediately follow the dry period in September 1991. Rhizotron 3C which showed peaks of RAR in both periods marked in Figure 4.4.1 and rhizotron 1B which showed a peak in the first period were both positioned towards the bottom of slopes (Figures 2.4.2a and c) and were noted to remain considerably more moist during these periods than other rhizotrons. It would appear that the rhizotrons displayed some synchrony in their RAR during dry periods. It should be noted also, that the lowest fine root biomass was recorded in April 1991 (Section 3.4.4). It is cautiously suggested that below-ground activity at the community-level in the Danum forest was more synchronous at certain times of the year than was above-ground activity. This is likely to be true where patterns of fine root activity are controlled to a larger extent by gross exogenous factors. Using a similar argument, Ng (1984) claimed leaf shedding behaviour in dipterocarp forest in peninsular Malaysia to be a genotypic characteristic, more than being triggered by climatic events or nutrient status, because of the low

level of synchronisation among individuals. That synchrony in below-ground activity was not reciprocated in above-ground patterns in the Danum forest may indicate that the level of stress induced on individual plants during dry periods was low.

Figure 4.4.1 Root appearance rate residuals for seven rhizotrons between December 1990 and December 1991. Calculated as: RAR on each rhizotron, on each date subtracted from the five-sampling occasion running RAR mean for all rhizotrons.



In semi-evergreen forest in Panama, Cavelier (1989) found peaks of fine root biomass to occur at the beginning of (April/May) and during (September) the wet season. These peaks in fine root biomass coincided with peaks of leaf production of deciduous trees in May and June and evergreen trees in September. It was suggested that the peaks could be in response to water and/or nutrient availability. In mature *tierra firme* forest in Venezuela fine root biomass peaked during November/December at the end of the wet season (Sanford 1985). In contrast to the semi-evergreen forest in Panama, fine root production in the Venezuelan forest was lowest at the time of peak leaf initiation. In lowland rain forest in Costa Rica dry season biomass of roots <1 mm diameter was half of wet season biomass (Sanford 1987). All three rain forest studies have recorded lower fine root biomass in dry compared to wet seasons. The pattern of ***RAR minus RDR*** (Figure 4.3.11) may be thought of as a relative measure of the change in fine root biomass over a short time scale. The maximum net reduction in

the length of root visible in the Persistence-rhizotrons coincided with the dry period in April 1991. In the Danum forest, as in the three previous rain forest studies presented, soil moisture appears to be a major factor influencing fine root activity for at least part of the year.

Chapter 5 Fine Roots and Mineral Nutrients

5.1 Introduction

High rates of fine root production and turnover have been reported for a number of forest ecosystems (Chapter 1, Section 4.4.1). As the concentrations of nutrients in fine roots are often comparable with those in leaves (Kimmins and Hawkes 1978, Meier *et al.* 1985, Vitousek and Sanford 1986, Cuevas and Medina 1988), the flux of nutrients required for fine root production, and the subsequent release of nutrients from the fine root biomass, are potentially important pathways in ecosystem-level nutrient budgets (McClaugherty *et al.* 1982, Nadelhoffer *et al.* 1985). The main objectives of this section of the study were: (a) to determine the concentration of nutrients in the fine root biomass and how this varied throughout the period of sampling; (b) to estimate the mass of nutrients tied up in the fine root biomass; (c) to produce estimates of the flux of nutrients into and out of the fine root biomass; (d) to seek evidence in support of the hypothesis that nutrients are retranslocated out of fine roots prior to root death; (e) to investigate whether N, P, or K were potentially limiting to fine root growth in the Danum forest.

5.1.1 Fine Root Nutrient Content

Nutrient requirement of fine root production and losses to the soil system

Nutrient requirement is generally viewed as the quantity of nutrients annually incorporated into biomass production (Switzer and Nelson 1972, Cole and Rapp 1981). The nutrient requirement for fine root production may be met either by internal redistribution in the plant or by uptake from the soil. Fine root nutrient requirement can be estimated by combining estimates of dry mass production (Section 4.3.1) and nutrient concentration (Section 5.3.1) (Meier *et al.* 1985). In the following section the nutrient requirement for biomass production is termed flux into fine root biomass.

Conceptually there are two pathways by which nutrients may leave the fine root biomass. Losses from the plant through processes such as decomposition, shedding, sloughing, herbivory, leaching and exudation (Fogel 1983, 1985, 1991, Newman 1985) can be grouped as losses to the soil system. Alternatively nutrients may be translocated internally to other parts of the plant prior to root death. In the following

calculations it is assumed that retranslocation of nutrients out of fine roots during senescence is negligible and evidence in support of this assumption is given.

If it is assumed that nutrients are not retranslocated, estimates of the flux of nutrients annually lost to the soil system from the fine root biomass can be calculated by combining the estimates of fine root disappearance (Section 4.3.1) and fine root nutrient concentration. Movement of nutrients from the plant to the soil system is not intended to necessarily infer plant availability or availability to any other group of organisms in the soil. In the following section nutrient fluxes into and out of the fine root biomass are calculated.

5.1.2 Nutrient Retranslocation out of Fine Roots During Senescence

A fundamental assumption used in the calculation of the annual flux of nutrients out of fine root biomass to the soil system (Section 5.2.1) was that the nutrient content of the current fine root biomass would eventually move entirely to the soil system. This assumes that nutrient retranslocation out of fine roots to other parts of the plant did not occur during senescence. The assumption has been used in previous studies when estimates of nutrient loss from fine roots have been calculated (eg van Praag *et al.* 1988, Vitousek and Sanford 1986). As this assumption has a potentially significant influence on the magnitude of the estimates of fluxes into and out of the fine root biomass, evidence was sought to support a hypothesis that nutrient retranslocation was occurring during fine root senescence in the Danum forest.

Retranslocation of nutrients out of leaves prior to abscission has been well documented (Switzer and Nelson 1972, Woodwell 1974, Cole and Rapp 1981, Luxmore *et al.* 1981, Ostman and Weaver 1982, Ryan and Bormann 1982). In addition a number of studies have recorded larger quantities of nutrient scavenging from leaves in forest stands on nutrient-poor substrates than those on more nutrient-rich substrates (Stachurski and Zimka 1975, Vitousek 1982, 1984, Boerner 1984). That an analogous nutrient conservation mechanism might be present in fine roots is an attractive concept but the evidence of such a process in roots remains equivocal.

Meier *et al.* (1985) reported that in *Abies amabilis* (Doug.) Forb. stands internal

redistribution within below-ground components contributed between 40-50% of the annual requirement of nitrogen for fine root production, and between 45-70% of the requirement of phosphorus . Fairley (1983) used a model of nitrogen cycling in 38-year-old Sitka spruce (*Picea sitchensis* Bong. Carr), based on sequential sampling of live and dead fine roots, to predict a withdrawal of nitrogen from dying roots of about 21%. Ferrier and Alexander (1991) droughted part of the root system of Sitka spruce seedlings, and estimated that 23% of the nitrogen present prior to water stress being imposed was retranslocated out of droughted fine roots. Some studies however, have failed to find evidence of nutrient retranslocation in fine roots. Two studies in temperate north American forests suggested that retranslocation of nitrogen from senescent fine roots was small (McClaugherty *et al.* 1982, Nadelhoffer *et al.* 1985). Nambiar (1987) found no evidence of nutrient retranslocation out of fine roots in Australian *Pinus radiata* D. Don plantations. He reported that monthly variations in the nutrient content of fine roots were small and showed no seasonal pattern, and that nutrient concentrations and calcium:mobile nutrient ratios were not significantly different between live and dead fine roots. The results for fine roots were in contrast to those for green and senescent *P.radiata* needles, in which nutrient retranslocation was clearly indicated using the same criteria.

Retranslocation from a set of leaves can be measured directly by sequentially examining the changes in nutrient content of leaves initiated at the same time (Fife and Nambiar 1982). A leaf is a determinate organ but there is no unitary root in the same sense (Harper *et al.* 1991). Roots branch and ramify and a cohort of roots may have members of various ages and physiological states from live to dead and decomposing (Section 4.4.1). However, with observation methods such as rhizotrons the date of initiation of individual lengths of fine root can be monitored. On completion of the observations, if the rhizotron is carefully dismantled, lengths of fine roots of known age can be collected. Thereby, evidence of nutrient retranlocation can be sought by methodology directly analogous to that commonly used for leaves.

If appreciable net retranslocation of nutrients out of fine roots prior to senescence was occurring, older fine roots might be expected to show consistent trends in one or more of the following; (a) lower nutrient concentrations, (b) lower nutrient mass per unit length of fine root, (c) higher calcium:mobile nutrient ratios.

(a) For the purposes of identifying nutrient retranslocation in fine roots, concentrations of nutrients calculated on a mass basis can be misleading. Meier *et al.* (1985) have shown the specific gravity of senescent fine roots (<2 mm diameter) of *Abies amabilis* to be 40-60% of that of live fine roots. Simultaneous decreases in root mass with nutrient content during senescence may mask significant net retranslocation. In leaves, although mass has been shown to decrease during senescence, decreases in nutrient concentration have frequently still been evident and have provided qualitative evidence of retranslocation (Ostman and Weaver 1982).

(b) In order to quantify foliar retranslocation the mass of nutrient per unit leaf area (Leaf Area Index) has previously been used as an alternative to nutrient concentrations (Stacharski and Zimka 1975, Medina 1984, Vitousek and Sanford 1986). An analogous method for fine roots would be to express nutrient content per unit volume of fine root. Measurement of fine root volume, however, is problematic: assuming that roots are cylindrical can lead to errors; the diameter of a fine root often changes along its length; and root diameter has also been shown to fluctuate depending on the moisture status of the root and the surrounding soil; Huck *et al.* (1970) demonstrated that fine roots of cotton (*Gossypium hirsutum* L.) plants shrunk by up to 60% of their maximum diameter on dry sunny days. Root length however, is readily measured and nutrient mass per unit length of fine root could be used to assess retranslocation.

(c) Calcium is generally recognised to be relatively immobile in plants and not to be transported in the phloem (Epstein 1972, Ostman and Weaver 1982, Nambiar 1987). Calcium:mobile nutrient concentration ratios can therefore be used as useful indicators of mobile nutrient translocation.

In this study individual fine roots in a number of age classes were collected by dismantling the Persistence-rhizotrons. Trends in; nutrient concentration, nutrient mass per unit length of root, and calcium:mobile nutrient quotients, with root age since initiation, were investigated. Evidence was sought in support of the hypothesis that nutrients are retranslocated out of fine roots during senescence.

5.1.3 The Response of Fine Root Growth to Localised Sources of Nitrogen, Phosphorus and Potassium.

The heterogeneous nature of soil with respect to organic matter, microbial activity and nutrient availability is well known (Brady 1984, Miles 1985). An association between fine roots and soil organic matter has been reported in a number of forest ecosystems (Damman 1971, Kimmins and Hawkes 1978, Jordan and Escalante 1980, St John 1983, Harper *et al.* 1991). In some tropical rain forests fine roots are concentrated in organic layers above the mineral soil and may invade and proliferate inside decomposing logs (Jordan and Escalante 1980). In the Danum forest number of fine root endings was positively correlated with organic matter, total nitrogen and phosphorus and exchangeable calcium pools in the soil (Table 3.3.4).

St John (1983) and St John *et al.* (1983) investigated the mechanism by which fine roots are able to proliferate in localised nutrient sources. They demonstrated that the concentration of fine roots and mycorrhizal hyphae in localized patches of organic matter in Amazonian *tierra firme* forest was brought about by random encounters of roots with organic matter and a subsequent change in the growth habit of roots to produce large numbers of short laterals. Alternative hypotheses that the proliferation of roots and mycorrhizal hyphae in patches of organic matter was brought about by negative geotropism, or an inhibitory factor such as aluminium toxicity or flooding, or by an active tropism for nutrients (Stark 1971) were tested and rejected. Laboratory experiments support the hypothesis of St John that proliferation of short lateral roots occurs in nutrient-rich zones. Drew *et al.* (1973) and Drew (1975) reported modification of root form in the seminal root system of barley in localised high concentrations of nitrate, ammonium and phosphate, although they found no effects with localised concentrations of potassium.

In-growth bag methods (Lund *et al.* 1970, Steen 1983, 1984, 1985, 1991) in which a root-free volume of soil or other medium is placed in the soil, utilize the plasticity of the plant root system in being able to preferentially modify its growth habit depending on the quality of the substrate. Sequentially harvested in-growth bags has been used as a method to estimate fine root production in several forest ecosystems (Persson 1979, Fabiao *et al.* 1985, Cuevas and Medina 1983, 1988, Cavelier 1989). In mature

forest ecosystems, however, root-free volumes of soil such as those within in-growth bags may be rare and only encountered in the root-throw zone of fallen stems (Putz 1983, Sanford 1989a, Chapter 1). In-growth bag methods of estimating fine root production may therefore, be viewed as estimating potential maxima for root growth (Cavelier 1989). A further limitation of this technique is that the rate of root proliferation within an in-growth bag is likely to be largely a factor of the quality of the in-growth medium compared to the surrounding soil environment. In the method of Cavelier (1989) for example, soil was dried, crushed and sieved free of roots prior to being placed in the in-growth bag. The effect of this pre-treatment on subsequent nutrient mineralization and microbial activity within the in-growth bag is unknown.

In-growth bag methods are particularly useful in allowing for comparisons within a specific site between treatments applied to the in-growth medium (Lund et al. 1970, Steen *et al.* 1984, Böhm 1979). In the experiment described in this section separate in-growth bags were filled with Perlite imbibed with solutions of NO_3^-, NH_4^+, $H_2PO_4^-$ and K^+ ions. If these nutrients were potentially limiting in the Danum forest a fine root growth response might be expected. In-growth bags were not used to produce estimates of fine root production.

5.2 Materials and Methods

5.2.1. Nutrient Content of Root Biomass

Dried root material collected by the auger method (Section 3.2) was bulked for each subplot for each sampling occasion. Each sample was milled to pass a mesh size of 0.5 mm. A 250 mg subsample was wet-ashed in a mix of sulphuric acid and hydrogen peroxide with a selenium catalyst (Allen 1989). Analyses for nitrogen were carried out by flow-injection analysis (FIA) (Star 5010 analyzer) and for phosphorus, potassium, calcium, magnesium and sodium by inductively-coupled-plasma atomic emission spectrometry (ICP-AES, Fisons 3580 B analyzer).

A standard tropical foliage material (supplied by E.V.J. Tanner, Cambridge University) was analyzed with batches of root samples so that results could be compared with those from other laboratories working with tropical plant material. Results of the analysis of the standard foliar material by six laboratories are given in Table 5.2.1.

Results for nitrogen, phosphorus and potassium in this study are within 10% of the mean of the other laboratories. The results for calcium and sodium however are outside the range of that found by other laboratories (Ca; 0.52, range 0.21-0.29, Na; 0.12, range 0.002-0.01, per-cent dry weight).

Table 5.2.1 Chemical analysis of a standard foliar material by a range of laboratories. (all values % dry weight)

	Stirling Thompson & Proctor	Ross	Camus U.S.A.	ITE Merlewood	Cambridge	This study
N	1.07	0.918	0.882	1.06	1.109	1.112
P	0.0495	0.030	0.0517	0.053	0.046	0.0496
K	0.3301	0.2776	0.337	-	0.3269	0.338
Mg	0.477	0.271	0.477	-	-	0.279
Ca	0.281	0.219	0.286	-	-	0.524
Na	0.0039	0.0115	0.0024	-	-	0.123
Al	-	-	-	-	-	0.275

Initially washing roots free of soil by hanging cores in mesh bags in the Segama river greatly speeded up the overall washing and sorting process and allowed for greater replication in the auger method (Section 3.2). A concern was, however, that the river washing might affect the nutrient content of roots compared to the more commonly used method of washing roots over a sieve. The effect of river washing on the nutrient content of fine roots was therefore tested. On each of four sampling occasions a set of sixteen 15-cm randomly positioned soil cores were taken. Each core was halved longitudinally. One half was washed entirely over sieves and the other half washed by a combination of river and sieve as previously described. Each root sample was dried to constant mass at 80 °C, ground and analyzed by the standard methods previously described. Where necessary two samples of the same treatment were bulked together to give a sample of 250 mg of dry root material for analysis.

A two-way analysis of variance was used to test for significant differences between washing techniques and sampling occasion. There was no significant differences in the concentration of nitrogen, phosphorus, potassium, magnesium, or aluminium between river and sieve washed samples ($P>0.05$, $df = 47$). The concentration of sodium was significantly lower in the river washed samples ($P<0.001$, overall means, 0.20 and 0.13

per-cent dry weight), while the concentration of calcium was significantly higher in the river washed samples ($P<0.05$, overall means, 0.45 and 0.53 per-cent dry weight). The discrepancy found in the concentrations of sodium and calcium measured in the standard foliar material compared to other laboratories and the significant effect of the washing technique on these elements urges caution in the interpretation of the results of calcium and sodium concentration in fine roots. An additional problem was that calcium was used as a reference element in part of the investigation into nutrient retranslocation during fine root senescence.

The mass of nutrient held in the fine root biomass was calculated as the product of mean biomass and mean nutrient concentration for each sampling occasion (Nadelhoffer *et al.* 1985).

Nutrient flux into and out of fine root biomass

Fine root production rates were calculated for five intervals between June 1990 and September 1991 (Section 4.3.1). Mean fine root dry mass production can be combined with mean nutrient concentration of the biomass for each interval to yield estimates of the nutrient requirement of fine root production, or nutrient fluxes into the fine root biomass. Similarly fine root dry mass disappearance rates and mean nutrient concentration can be combined to yield estimates of the rate at which nutrients are made available to the soil system or nutrient fluxes out of the fine root biomass. The rate of the flux into and out of the fine root biomass (kg ha^{-1} yr^{-1}) for each nutrient between sampling occasions i and $i+1$ can be estimated by:

$$Flux^{in} = Pd_{ii+1} \cdot C_{i+1}$$

$$Flux^{out} = Ds_{ii+1} \cdot C_{i}$$

where:

Pd = Dry Mass Production (kg ha^{-1} yr^{-1})

Ds = Dry Mass Disappearance (kg ha^{-1} yr^{-1})

C = Mean Nutrient Concentration (% dry mass)

Overall means of the rates of nutrient flux into and out of the fine root biomass between June 1990 and September 1991 were calculated as weighted-means. For t

sampling occasions:

$$\text{Weighted mean } Flux^{in} = \frac{\sum_{i=1}^{t} Flux_{ii+1}^{in} \cdot S_{ii+1}}{S_{1t}}$$

$$\text{Weighted mean } Flux^{out} = \frac{\sum_{i=1}^{t} Flux_{ii+1}^{out} \cdot S_{ii+1}}{S_{1t}}$$

where:

S_{ii+1} = Number of days between sampling occasions i and $i+1$

5.2.2 Nutrient Retranslocation out of Fine Roots During Senescence

The Persistence-rhizotrons were dismantled once observations were completed (Section 4.2.1) and individual fine roots were collected from behind the observation panel: The appropriate tracing was pinned against the glass panel and the glass carefully loosened so that lengths of root could be cut from the exposed soil face. Each length of root was individually labelled according to its date of initiation.

Lengths of root were washed free of soil by holding in forceps and swilling in a beaker of water. The sample was laid flat in a plastic bag and each root traced onto an acetate sheet. The total length of each tracing was measured using Apple IIe length measurement apparatus (Section 4.2.1). Root samples were dried at 80 °C for 24 hours.

Each length of root was cut up using a razor blade and a 4-6 mg subsample taken. Where necessary roots from the same rhizotron with a common appearance date were bulked to provide a sample of 4-6 mg. The root material was wet-ashed in a scaled-down version of the sulphuric acid, hydrogen peroxide and selenium digestion (Allen 1989) in which the final dilution volume was 20 ml (Gupta 1987). The digests were analyzed for nitrogen by FIA analysis, using a range of standards from 1-10 mg l^{-1} nitrogen. Analysis for phosphorus, potassium, calcium, magnesium and sodium was carried out by ICP-AES spectrometry.

The micro-digestion technique was initially tested by comparing the results for nitrogen of ten 5 mg subsamples of a standard foliar material by micro-digestion, with ten 250 mg subsamples digested by the standard method of Allen (1989). The percentage nitrogen measured in the micro-digests was within 5% of that measured in the standard digestion.

5.2.3 Ingrowth Bag Technique

Cylindrical mesh bags (30 cm x 8 cm diameter) were made from plastic woven material with a pore size of 5 mm. An auger was used to remove a soil core of the same size as the mesh bag to be inserted. A PVC pipe (outside diameter 7.8 cm) was placed inside the mesh bag and then both inserted into the hole created by the removal of the soil core. Growth medium was poured into the pipe in layers and compacted with a wooden dowel while the pipe was gradually withdrawn. The growth medium was built up until level with the surrounding mineral soil.

In-growth media

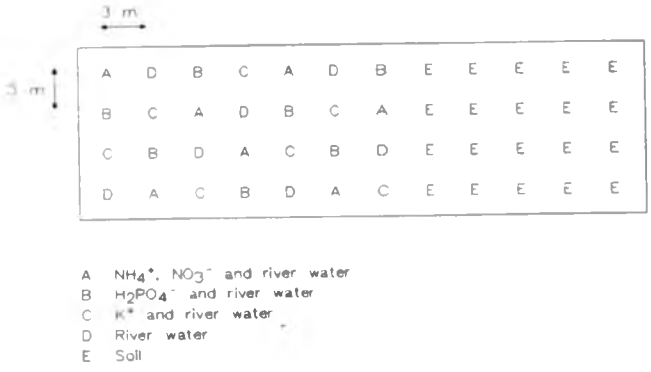
Nutrient treatments were applied to horticultural Perlite. Perlite provides an inert medium onto which nutrients can be absorbed but remain available to plant roots. Nutrient solutions A, B and C were made up containing 5 m-equivs. l^{-1} of NH_4^+ and NO_3^- (ammonium nitrate), $H_2PO_4^-$ (sodium di-hydrogen ortho-phosphate), and K^+ (potassium chloride) ions respectively. For each of the three nutrient treatments 15 l of the respective nutrient solution was thoroughly mixed with 100 l of perlite. The perlite was spread on trays and dried at 40 °C in a drying room. Before being placed into mesh bags the perlite was rehydrated with river water from the Sungai Palum Tambun (Figure 2.4.1). The Perlite control treatment (D) consisted of fresh perlite hydrated with 15 l of river water.

A second control treatment (E) consisting of soil filled in-growth bags was used. 15-cm soil cores were cut into 5 cm sections. Each soil section was crumbed by hand and obvious roots removed. Soil was returned to its original location in 5-cm increments, with care being taken to approximate the original bulk density of the soil.

Seven replicates of each Perlite treatment and twenty soil filled bags were arranged on a 3 m grid (Figure 5.2.1) within a subjectively chosen rectangular block within each plot (Figure 2.4.2a-c). All bags were incubated for 8 months before harvesting,

although the soil treatment was installed 3 months later than other bags. On harvesting, a sharp knife was used to cut around the mesh bag before it was carefully excavated. All roots were separated from Perlite or soil without water, sorted into diameter classes ≤2 mm and >2 mm, then rinsed in water, dried at 80 °C and weighed to ±1 mg.

Figure 5.2.1 The arrangement of in-growth bag treatments within a subjectively chosen block within each plot (see Figure 2.4.2a-c for location).



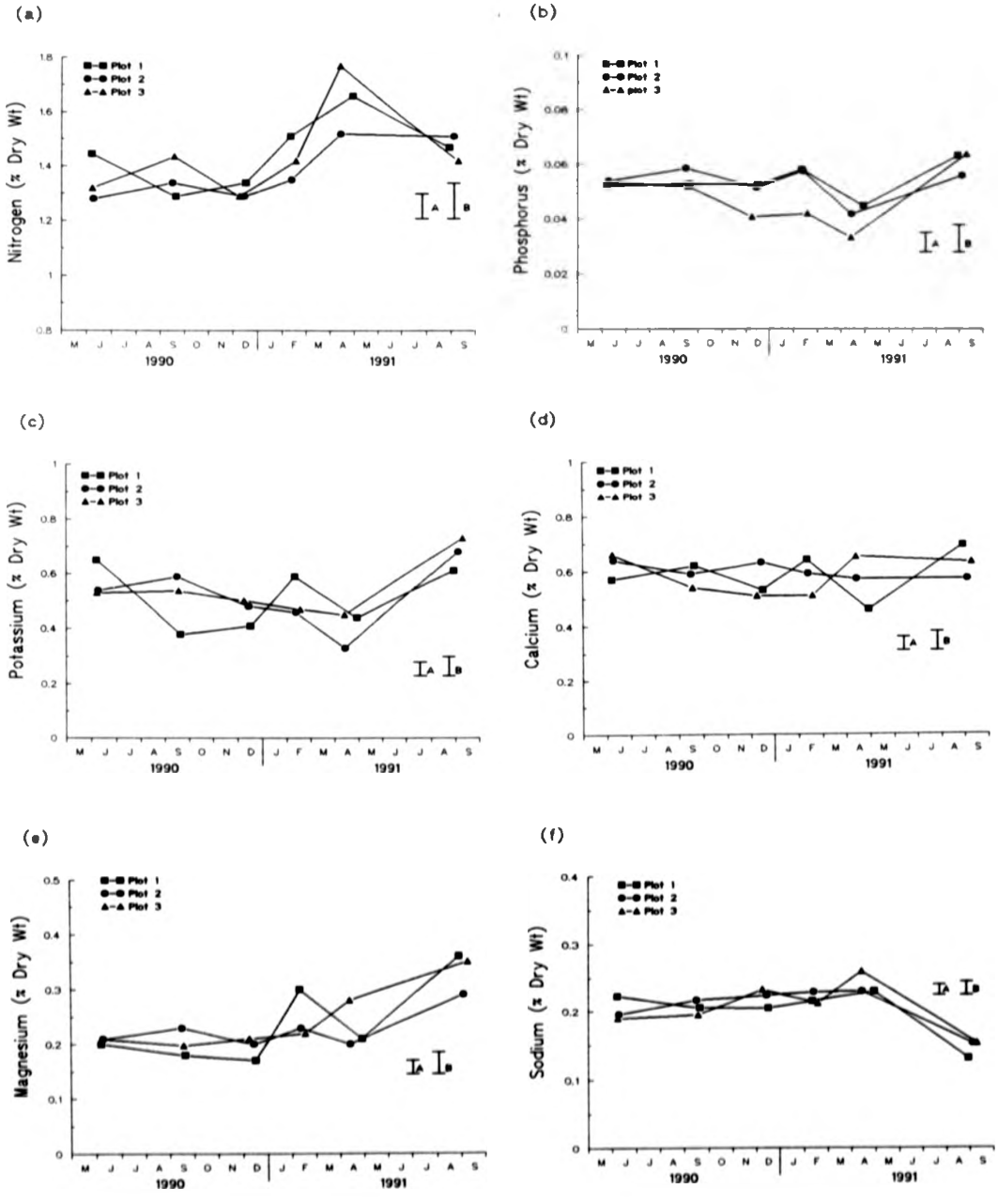
5.3 Results

5.3.1 Nutrient Content of Fine Root Biomass

Nutrient Concentrations

Figures 5.3.1a-f show the mean concentrations of N, P, K, Ca, Mg and Na in roots ≤2 mm diameter from 24 soil cores from each of three plots on six sampling occasions. Two way analysis of variance was used to assess the effect of, and interaction between, sampling occasion and plot. The least significant differences (P=0.05) between plots and sampling occasion means are indicated in Figure 5.3.1. Sampling occasion was significant for all nutrients other than calcium (N, K, Mg, Na $P<0.001$, P $P<0.01$), indicating significant fluctuations in the concentration of nutrients over time. Effects of plot were not significant for P, K, Ca, Mg or Na but were significant for N ($P<0.05$). A Duncan's multiple range test showed the N concentration of fine roots to be significantly lower in Plot 2 ($P<0.05$). The mean concentration of total

Figure 5.3.1 The mean concentration of nutrients in fine (≤2 mm diameter) roots from three plots on six sampling occasions (n = 24). The least significant difference between plot means (A) sampling occasion means (B) are indicated. (a) nitrogen, (b) phosphorus, (c) potassium, (d) calcium, (e) magnesium, (f) sodium.



nitrogen recorded in 0-15 cm of the soil in plot 2 was lower than plots 1 and 2, although not significantly lower than plot 1 ($P>0.05$, Table 2.5.3). There were significant effects of interaction between sampling occasion and plot for K, Ca and Mg (K $P<0.01$, Ca, Mg $P<0.05$). The changes in nutrient concentration in fine roots over the sampling period do not appear to follow any patterns of annual seasonality. The overall means of nutrient concentration are given in Table 5.3.1.

Table 5.3.1 Mean concentrations of nutrients in fine (≤2 mm diameter) roots (n = 143, standard errors in parentheses) and estimates of the mass of nutrients held in fine roots in the top 120 cm of the soil.

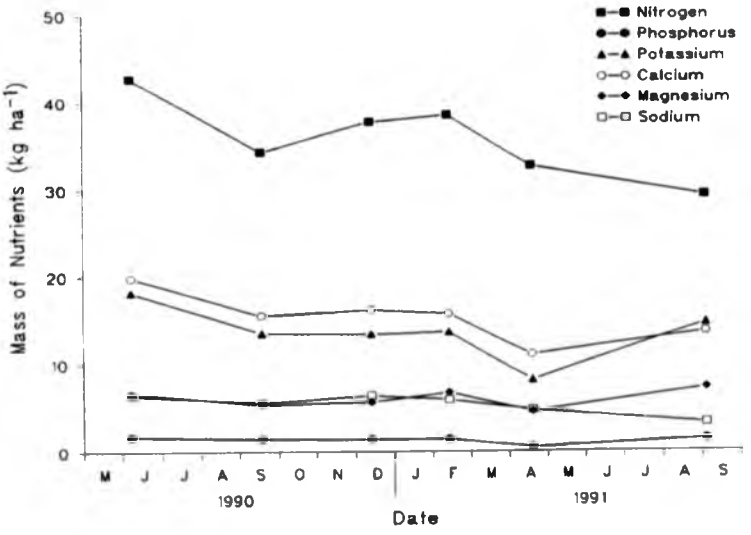
	N	P	K	Ca	Mg	Na
Concentration % dry mass	1.41 (0.022)	0.052 (0.0014)	0.52 (0.013)	0.59 (0.011)	0.24 (0.0070)	0.21 (0.0038)
Content kg ha^{-1}	35.9	1.3	13.6	15.3	6.0	5.4

Nutrient mass in fine root biomass

The nutrient mass held in the fine root biomass for each of the six sampling occasions was calculated as the product of mean biomass and mean nutrient concentration (Figure 5.3.2). Overall means of the nutrient content of fine root biomass are given in Table 5.3.1.

Figure 5.3.2 is useful in indicating the relative masses of nutrients held in fine root biomass. There was a drop in the estimated mass of all nutrients between samplings in February and March/April 1992. This period included the dry months of March and April 1991. The lowest root biomass was measured in April 1991 this coincided with the highest N concentration and the lowest P and K concentration of fine roots.

Figure 5.3.2 Estimated mass of nutrients held in fine (≤2 mm diameter) root biomass in the top 120 cm of the soil on six sampling occasions between June 1990 and September 1991.



Nutrient flux into and out of fine root biomass

Figures 5.3.3a-f show the estimated flux of N, P, K, Ca, Mg, Na into and out of the fine root biomass between June 1990 and September 1991. The net flux of nutrients between sampling occasions are indicated.

The long time interval (about 3 months) between each sampling occasion means that the patterns of change are of little use in indicating seasonal patterns. However, the largest net flux out of the fine root biomass occurred for all nutrients between sampling occasion 4 and 5, a period that included the dry March and April of 1991 (Section 4.3.3).

The overall (weighted-mean) values of nutrient flux are given in Table 5.3.2. There was an overall net flow of all nutrients out of the fine root biomass between June 1990 and September 1991.

Figure 5.3.3 The estimated nutrient fluxes into and out of fine (≤2 mm diameter) root biomass between June 1990 and September 1991. Net fluxes and the estimated mass of nutrients held in fine roots in the top 120 cm are indicated. (a) nitrogen, (b) phosphorus, (c) potassium, (d) calcium, (e) magnesium, (f) calcium.

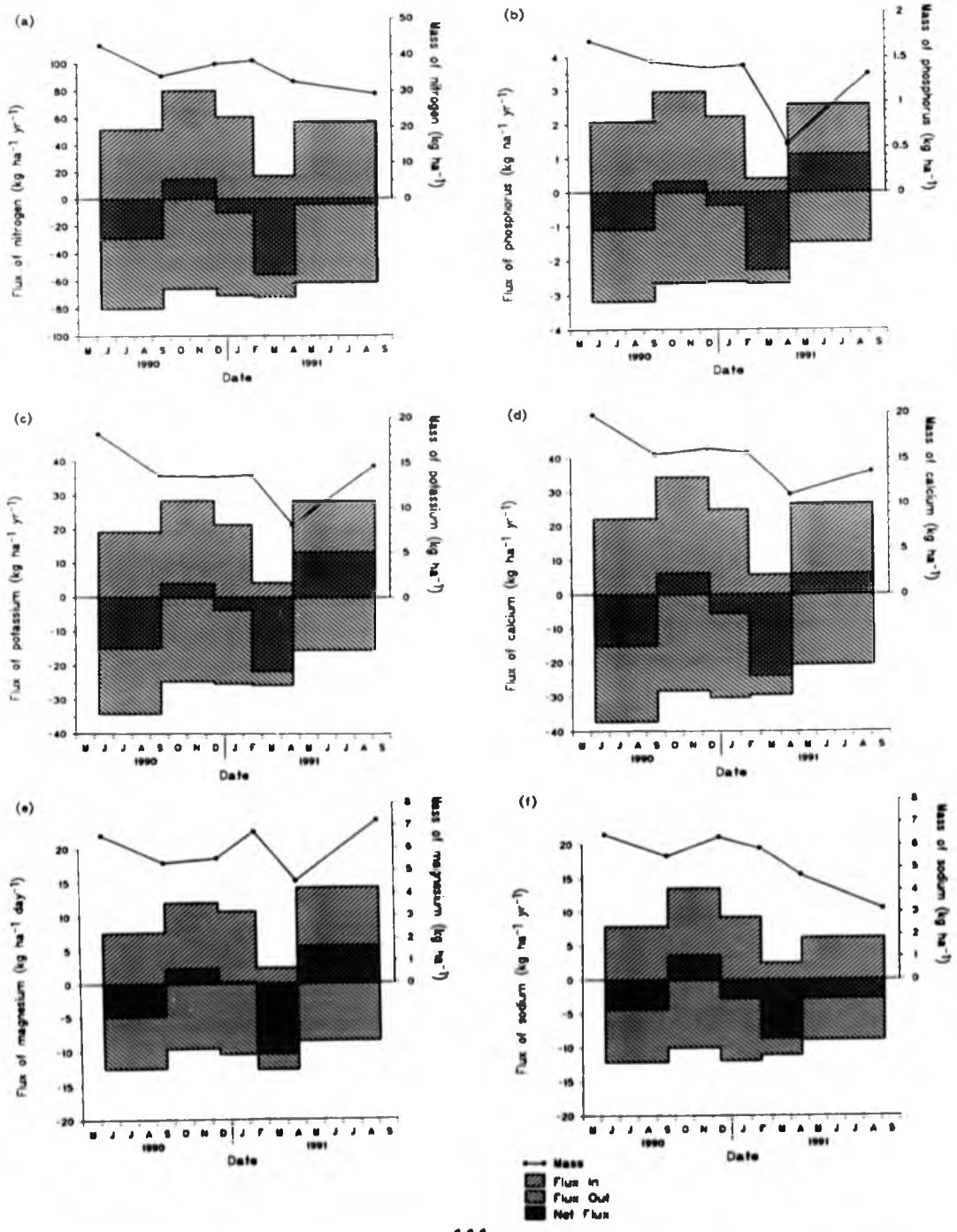


Table 5.3.2 Weighted mean flux of nutrients into and out of fine root biomass between June 1990 and September 1991 (all values kg ha^{-1} yr^{-1})

	N	P	K	Ca	Mg	Na
Flux in	54.8	2.17	21.9	23.7	10.0	7.8
Flux out	69.1	2.40	24.1	28.4	10.5	10.5
Net flux	-14.4	-0.23	-2.2	-4.7	-0.5	-2.7

5.3.2 Nutrient Retranslocation out of Fine Roots During Senescence

A total of forty-nine fine root samples were analyzed in the age classes 1, 5, 10, 20, 25, 30 and 35 weeks since initiation. Results for each nutrient were plotted as percent concentration, mass per unit root length and calcium:mobile nutrient quotient. No patterns with fine root age were discernible on these graphs and no further samples were analyzed. No evidence was found in support of the hypothesis that nutrients are retranslocated out of fine roots prior to senescence.

5.3.3 Response of Fine Root Growth to Localised Sources of Nitrogen, Phosphorus and Potassium.

Of 144 in-growth bags installed only 70 remained undisturbed and could be harvested. This appeared to be due mainly to the digging of bearded pig (*Sus barbicus*). Table 5.3.3 shows the mean mass of roots (g m^{-3}) for each treatment for bags which remained undisturbed. Analysis of variance showed no significant differences between treatments or plots. No evidence was found that nitrogen, phosphorus or potassium fertilization stimulated fine root growth.

Table 5.3.3 The mean (±S.E.) mass of fine roots in in-growth bags (in g m^{-3})

Treatment		No. installed	No. harvested	Root ingrowth (g m^{-3})
NH_4^+,NO_3^- and river water	A	21	9	225 (84)
$H_2PO_4^-$ and river water	B	21	7	458 (180)
K^+ and river water	C	21	7	325 (74)
River water	D	21	7	584 (113)
Soil	E	60	40	471 (67)

5.4 Discussion

5.4.1 Nutrient Content of Fine Root Biomass

Nutrient concentrations

Concentrations of nutrients in the fine root biomass were shown to vary significantly with time during the sampling period from June 1990 to September 1991. No previous tropical rain forest study has sequentially measured fine root nutrient concentrations. A number of studies in temperate forests, however, have reported seasonal fluctuations in the nutrient concentration of fine roots. McClaugherty *et al.* (1982) reported significant seasonal fluctuations in the concentration of nitrogen in fine roots for both broadleaved and coniferous forest in Massachusetts, USA, with the highest values recorded in spring. McKay and Malcolm (1988) failed to find significant fluctuations in the concentration of nitrogen and phosphorus with sampling time in Sitka spruce and Scots pine plantations in Scotland, although fluctuations in potassium were significant. The potassium fluctuations showed a bimodal pattern with peaks in spring and autumn. The fluctuations in N, P, K and Ca concentration recorded by Nambiar (1987) in Australian *Pinus radiata* were significant but showed no clear seasonal trends. Nadelhoffer *et al.* (1985) however, found no significant fluctuations in the nitrogen concentration of fine roots in a number of mixed species stands in Wisconsin, USA. There appear to be no consistent trends in the fluctuations of nutrient concentration in fine roots between the different sites reported in the literature. The results for the Danum forest help to confirm that it can not be assumed that the concentration of nutrients in forest fine root biomass will remain constant throughout the year.

Few tropical rain forest studies have measured nutrient concentrations in fine roots. The data that do exist are from a wide range of forest and soil types (Table 5.4.1). Between-site comparisons are further confounded by the different size classifications for fine roots employed. Concentrations of N, P and K are often higher in non-woody than woody roots (Kimmins and Hawkes 1978, Meier *et al.* 1985, Vitousek and Sanford 1986, McKay and Malcolm 1988, van Praag *et al.* 1988). For example, a diameter class of <6 mm will undoubtedly contain a large proportion secondarily thickened roots and the concentrations of N, P and K might be expected to be lower than in a size class of ≤2 mm.

Table 5.4.1 Nutrient concentrations in fine roots from a range of tropical rain forests.

Country	Forest Type	Root Diameter (mm)	N	P	K	Ca	Mg	Na	N:P Ratio	Reference
Venezuela	*Tierra Firme*	†	2.30	0.11	0.67	0.21	0.26	-	20.9	Cuevas & Medina (1988)
	Tall *Caatinga*	†	1.04	0.095	0.83	0.30	0.39	-	10.9	
	Low *Bana*	†	0.84	0.051	1.22	0.35	0.37	-	16.5	
Venezuela	*Tierra Firme*	<2	2.23	0.073	-	-	-	-	30.5	Vitousek & Sanford (1986)
Brazil	On Latosols	<6	1.00	0.014	0.069	0.11	0.062	0.079	71.4	Klinge (1973,1975)
Venezuela	*Caatinga* on Spodosol	<6	0.67	0.057	0.29	0.16	0.14	-	11.8	Herrera (1979)
Brazil	*Campina* on Spodosol	<6	1.07	0.031	0.11	0.12	0.15	0.18	34.5	Klinge (1975)
		<2	1.19	0.029	0.088	0.062	0.10	0.13	41.0	
Ghana	Semi-evergreen	<6.4	1.36	0.08	0.56	0.88	0.10	-	17.0	Greenland & Kowal (1960)
New Guinea	Montane	<5	0.75	0.036	0.39	0.71	0.61	-	20.8	Edwards & Grubb (1982)
Venezuela	Montane	<5	0.64	0.037	0.24	0.44	0.10	-	17.3	Grimm & Fassbender (1981)
			1.20	0.054	0.41	0.31	0.22	0.14	27.6	Mean
			0.64	0.014	0.069	0.062	0.062	0.079	10.9	Minimum
			2.30	0.11	1.22	0.88	0.61	0.18	71.4	Maximum
Malaysia	Dipterocarp on ultisol	≤2	1.41	0.052	0.52	0.59	0.24	0.21	27.1	This study

† all in-growth roots

Notwithstanding the problems in comparing results, the average concentrations of N, P, K, Ca and Mg in fine roots recorded in the Danum forest are all close to the means of the values for other sites. The concentration of sodium in fine roots has been less frequently reported than the major essential nutrients. The average sodium concentration in the Danum forest is higher than that reported in two previous studies.

Concentrations of nutrients in fine roots are reportedly often comparable to those in

foliage (Kimmins and Hawkes 1978, Meier *et al.* 1985). Table 5.4.2. gives the mean and range of foliar nutrient concentrations from twenty-six rain forest sites (Vitousek and Sanford 1986, Thompson *et al.* in press). The average concentrations of N, P, K, Ca and Mg in fine roots from a range of rain forest sites are all close to, but slightly lower than, the average concentrations in foliage (Tables 5.4.1 and 5.4.2). Taking into account the large proportion of woody roots included in a number of the studies it would seem reasonable to suggest that fine root and foliar nutrient concentrations over a range of rain forest sites are similar. Vitousek and Sanford (1986) grouped published foliar nutrient concentration data from 25 rain forest sites according to site fertility and found concentrations of all the major nutrients in leaves to be significantly correlated with site fertility. Assuming that fine roots might equally indicate nutrient deficiency the concentrations of nutrients measured in fine roots do not suggest any particular nutrient deficiency in the Danum forest. However, the use of nutrient concentrations in litterfall as an indicator of site fertility has recently been called into question by work on Maracá island, Brazil, where relatively high foliar nutrient concentrations were recorded from forest on very nutrient-poor sandy soils (Proctor 1992, Thompson *et al.* in press, Scott *et al.* in press).

Table 5.4.2 Mean and ranges of foliar nutrient concentrations from a range tropical rain forests (from Vitousek and Sanford 1986 and Thompson *et al.* in press).

	N	P	K	Ca	Mg	N:P
n	25	26	26	26	26	25
Mean	1.46	0.082	0.78	0.81	0.28	20.1
Minimum	0.61	0.02	0.35	0.11	0.10	7.6
Maximum	2.54	0.15	1.92	2.29	0.88	43.5

N/P concentration quotients in foliage have been used as an ecological indicator of phosphorus supply (Medina *et al.* 1990) and it would seem reasonable to use fine root N/P quotients in the same way. The average N/P quotient in fine roots from Danum is close to the mean value for other rain forest sites (Table 5.4.1). This would suggest that phosphorus supply in the Danum forest is intermediate compared to the other sites. Yet the extractable phosphorus measured in the Danum soil was the lowest reported for any of the compiled rain forest sites (Section 2.5.4). Soil total phosphorus was not particulary low, however, and we have no indication of the potential rate of

mobilization of phosphorus from this pool (Section 2.5.4). Thompson *et al.* (in press) reported high variability in foliar N/P quotients and suggested that the quotient may be of limited value as an indicator of phosphorus supply.

Nutrient mass held in fine root biomass

Comparisons of the mass of nutrients held in fine root biomass between rain forest sites is particularly hindered by the different size categories used to define fine roots. Two previous studies that used a category of <2 mm are available for comparison (Table 5.4.3). The amount of nitrogen held in fine roots in the Danum forest was considerably lower than the two previous studies from Amazonia. This is largely a function of the higher fine root biomass of these sites (16.1 and 14.3 versus 2.8 t ha^{-1}) as the nitrogen concentrations were similar (Table 5.4.1). A large proportion of the fine root biomass of these two Amazonian sites consisted of a root mat developed on the soil surface, a feature poorly developed in the Danum forest. The concentrations of P, K and Ca in the fine roots of the *campina* forest on Spodosols described by Klinge (1973, 1975) were towards the lower end of the range of other rain forest studies (Table 5.4.1) and hence the overall mass of these nutrients held in the fine root biomass are more comparable with the Danum forest.

Table 5.4.3 Estimated mass of nutrients held in roots ≤2 mm diameter in three lowland tropical rain forests (all values kg ha^{-1}).

Country	Forest type	N	P	K	Ca	Mg	Na	Reference
Brazil	*Campina* on spodosols	137	2.4	6.6	5.1	8.6	9.7	Klinge (1973,1975)
Venezuela	*Tierra firme* on oxisols	†319	†10.4	-	-	-	-	Sanford (1985),Vitousek & Sanford (1986)
Malaysia	Dipterocarp on ultisols	36	1.3	13.6	15.3	6.0	5.4	This study

† Calculated using biomass data from Sanford (1985) and concentration data from Vitousek & Sanford (1986)

Given the potential importance of fine roots as a nutrient pool in forest ecosystems it is interesting to compare the mass of nutrients held in the fine root biomass with the amount of nutrients present in the soil. Table 5.4.4 shows the mass of nutrients in fine roots as a percentage of that measured in the soil to a depth of 1 m. The pool of

phosphorus in fine roots is one third of the size of the acetic acid extractable phosphorus pool measured. Again, we do not have, however, any measure of the potential flux of phosphorus from the total to the acetic acid extractable pool (Section 2.5.4). The amount of nutrients in fine roots is less than 10% of the pool of total nitrogen and phosphorus and exchangeable bases measured in the soil.

Table 5.4.4 Mass of nutrients held in fine (≤2 mm diameter) roots as a percentage of the soil pool in the top 1 m of the soil in three plots in Danum Valley.

	Total N	Total P	Extr. P	Exch. K	Exch. Ca	Exch. Mg	Exch.Na
Soil Pool (kg ha^{-1})	1644	2091	3.7	684	158	213	94
	N	P		K	Ca	Mg	Na
Fine root content (kg ha^{-1})	35.9	1.3	-	13.6	15.3	6.0	5.4
Fine root content as % of soil pool	2.2	0.062	35.1	2.0	9.7	2.8	5.7

Nutrient fluxes into and out of fine root biomass

Few studies have estimated the cost of fine root production and disappearance in terms of mineral nutrients. The studies which do exist used widely differing methods to assess the importance of fine root turnover in ecosystem-level nutrient budgets. These estimates can broadly be grouped into either; the requirement of nutrients for fine root dry matter production, or the amount of nutrients relinquished to the soil system by root death. Estimates of these fluxes into and out of the fine root biomass for a range of tropical and temperate-zone forests are given in Table 5.4.5.

Cuevas and Medina (1988) calculated fine root production in the root mat and top 10 cm of the soil in three Amazonian forests by sequential harvesting of in-growth bags. They also reported nutrient concentrations of fine roots in the unfertilized bags and the product of these two was used here to produce estimates of the nutrient requirement of fine root production or flux into the fine root biomass. Similarly, Vitousek and Sanford (1986) used the product of fine root dry matter production, calculated by a combination of sequential coring and observations on plexi-glass

Table 5.4.5 Estimates of nutrient fluxes into and out of fine root biomass in tropical and temperate-zone studies (all values kg ha^{-1} yr^{-1}).

Country	Forest type	Root diameter (mm)	Flux direction	N	P	K	Ca	Mg	Na	Reference
	Tropical									
Venezuela	*Tierra firme* on oxisol	a	In	256.9	12.29	74.8	23.5	29.0	-	‡Cuevas & Medina (1988)
	Tall *Caatinga*	a	In	12.48	1.14	9.96	3.6	4.68	-	
	Low *Bana*	a	In	19.74	1.20	28.7	8.23	8.7	-	
Venezuela	*Tierra firme* on oxisol	<2	Out	343	11.0	-	-	-	-	Sanford (1985), Vitousek & Sanford (1986)
Malaysia	Dipterocarp	≤2	In	54.8	2.17	21.9	23.7	10.0	7.8	This study
			Out	69.1	2.40	24.1	28.4	10.5	10.5	
	Temperate									
Belgium	Beech	<5	In	15.1	0.96	0.83	13.28	1.75	1.32	van Praag *et al.* (1988)
			Out	11.67	0.70	0.38	13.12	1.44	0.86	
	Spruce	<5	In	17.0	1.46	0.43	16.39	1.59	0.79	
			Out	18.34	1.51	0.41	36.10	3.19	1.14	
Scotland	Sitka spruce	<2	In	†21-80	†3-13	†10-32	-	-	-	McKay & Malcolm (1988)
	Sitka spruce and Scots pine	<2	In	†13-51	†2-8	†5-8	-	-	-	
U.S.A.	*Abies amabilis*	<5	In	73.0	14.21	-	-	-	-	Meier *et al.* (1985)
U.S.A.	Hardwoods	<3	In	†73-184	-	-	-	-	-	McClaugherty *et al.* (1982)
	Plantations	<3	In	†44-122	-	-	-	-	-	
U.S.A.	Range of 9 sites	≤3	In	20-79	-	-	-	-	-	Nadelhoffer *et al.* (1985)

a All in-growth roots

† Dependent on sequential coring calculation method

‡ Calculated here from in-growth bag production estimates and concentration of nutrients in unfertilized bags

windows (Sanford 1985), and nitrogen and phosphorus concentrations to estimate what they termed the amount of nutrients annually added to the soil by fine root turnover.

Both of the previous tropical studies indicate a large turnover of nitrogen and phosphorus in the fine roots of *tierra firme* forest on oxisols compared with that calculated for the Danum forest. Although nitrogen and phosphorus concentrations were higher in *tierra firme* than in the Danum forest the greater turnover of nutrients is largely a product of the higher fine root dry mass production in these forests. Both of the *tierra firme* estimates were only for the top 10 cm of the soil and so will be underestimates of the fine root nutrient fluxes occurring in the whole rooting zone.

In the *tierra firme* and Danum forests the ratio of the fluxes of N:P was considerably higher than in the temperate studies. This would appear to indicate a relatively low availability of phosphorus in these tropical rain forest sites.

The magnitude of nitrogen turnover in the Danum forest was most similar to the range of eleven sites in Wisonsin and Massachussetts USA (McClaugherty *et al.* 1982, Nadelhoffer *et al.* 1985), where the dry mass production estimates of roots ≤3 mm diameter were similar to those for roots ≤2 mm diameter in the Danum forest. The estimates of Meier *et al.* (1985) although superficially similar are for roots ≤5 mm diameter and calculated from the product of a higher dry mass production than in the Danum forest and a much lower nitrogen concentration in the larger diameter roots. The estimates of McKay and Malcolm (1988) are for the top 5 cm of the soil only.

Estimates of the nutrient pools and fluxes associated with fine roots are most useful when other parts of nutrient budget for the same ecosystem are known. It is hoped that data on the annual flux of nutrients in above-ground litterfall will soon be available for the plots of Newbery *et al.* (1992) at Danum (T.B.A. Burghouts pers. comm.).

5.4.2 Nutrient Retranslocation out of Fine Roots during Senescence

The fine roots harvested from the Persistence-rhizotrons showed no consistent trends with root age in terms of nutrient concentrations, nutrient mass per unit length of fine root, or calcium:mobile nutrient ratios. No evidence was found to support the

hypothesis that nutrients are retranslocated out of fine roots prior to, or during senescence in the Danum forest. The methodology was directly analogous to that often used to indicate and quantify foliar retranslocation (Fife and Nambiar 1982, Nambiar 1987). Patterns of nutrient retranslocation in the fine roots of the Danum forest may however, have been confounded by inter-specific variation and lack of seasonality in the system. Temperate foliar studies which employed similar methodology had the advantage that leaves are more readily sorted by species than are roots, and in deciduous forests net nutrient transfers at the plant level may be more readily measured than where a continual process of sloughing and renewal is taking place. Nambiar (1987), using similar methodology to that employed in this study, also found no evidence of nutrient retranslocation out of fine roots in *Pinus radiata* plantations, while needles clearly displayed retranslocation.

Evidence in favour of a fine root nutrient retranslocation mechanism has been provided by Ferrier and Alexander (1991) who recorded a significant reduction in the total nitrogen content in droughted parts of root systems of Sitka spruce seedlings. They rejected the possibility that the reduction in the nitrogen content of fine roots was due to loss to the substrate as this would have required an unrealistically high rate of nitrogen uptake in the undroughted part of the root system to account for the nitrogen content of the rest of the seedling. Root death in this study however, was imposed by an external factor, moisture stress. Little is known of the physiology of fine root death and whether or not roots go through a programmed sequence of aging analogous to that in leaves or whether death is normally caused by an external factor (Ferrier and Alexander 1991, Fogel 1991).

Meier *et al.* (1985) based their estimates of fine root nitrogen and phosphorus retranslocation in *Abies amabilis* on the difference between the nitrogen and phosphorus concentration in live and senescent fine roots. Senescent roots were selected according to the criterion that the cortex had begun to soften or deteriorate. The lower specific gravity of senescent fine roots was also taken into account when nutrient contents were calculated. Similarly, Fairley (1983) used the difference between the nitrogen content of live and dead fine root biomass in Sitka spruce to indicate nutrient retranslocation. There appears to be no direct evidence in either of these studies that nutrients were in fact retranslocated within the plant and not lost to

the soil system.

The physiology of fine root senescence in perennial plants and particularly possible mechanisms for nutrient retranslocation prior to root death, deserves greater attention.

5.4.3 The Response of Fine Root Growth to Localised Sources of Nitrogen Phosphorus and Potassium.

Localised fertilization with separately applied, high nitrogen, phosphorus and potassium treatments did not significantly stimulate fine root in-growth in the Danum forest. The method was adapted from that of Cuevas and Medina (1983, 1988) who used nutrient enriched Vermiculite (imbibed for 48 hours in 0.1 M solutions) in-growth bags to test for potentially limiting nutrients in a range of Amazonian forests. They found no significant effects of nutrient treatment in the top 10 cm of the mineral soil. In the surface root mat, however, fine root in-growth was significantly stimulated by phosphorus (potassium hydrogen phosphate) and calcium (calcium chloride) in *tierra firme* forest, by nitrogen (ammonium chloride) in the tall *caatinga* and by nitrogen and phosphorus in low *bana*. Although Cuevas and Medina conclude that the significant response recorded in the potassium hydrogen phosphate treatments in *tierra firme* and low *bana* forests was due to phosphorus it can not be ruled out that the effects were in fact a response to potassium.

Cavelier (1989) used in-growth bags to estimate fine root production in both unfertilized and N-P fertilized plots in lowland semi-evergreen forest in Panama. No statistically significant differences between root ingrowth in fertilized and unfertilized plots were recorded. However, fine root ingrowth in the control plots peaked in the rainy season but no peak was observed in the N-P fertilized plots. In this study soil nutrient status was ameliorated at the stand level which is conceptually very different from providing localised nutrient-rich sources in an otherwise undisturbed system. It has already been discussed that a number of studies have recorded a decrease in fine root biomass following fertilization at the stand level (Sections 3.1 and 3.4.2). That Cavelier (1989) recorded no wet season root in-growth peaks in N-P fertilized plots would be consistent with the hypothesis that fine root biomass and production are generally higher on oligotrophic compared to eutrophic sites (Section 3.4.2, Gower

1987).

Drew (1975) demonstrated the proliferation of short lateral roots of barley (*Hordeum vulgare* cv. Proctor) in zones high in nitrate, ammonium and phosphate, but failed to record any such modification of fine root growth with localized sources of potassium ions. The lack of a root growth response to localised application of potassium in in-growth bag studies should be interpreted with caution until the potential for potassium to cause modification of plant root growth has been substantiated by laboratory experiments.

Chapter 6 General Discussion and Further Work

"Root/mycorrhiza studies have reached a critical juncture. The practical limit of the soil coring approach for improving our basic knowledge of root production and turnover has been reached" (Fogel 1991). There do not appear to be revolutionary new methods for measuring fine root processes on the horizon at the present time. However, the currently available methods can be improved to give better estimates of fine root production. In particular, existing methods of measuring fine root processes can be separately employed to quantify different aspects of the same fine root population and subsequently combined in new ways. This approach was taken in the current study and a new method for estimating fine root production was developed that employed excavation methods to measure spatial variability and observation methods to measure temporal variability (Section 4.2.1). The main aim of this approach was to quantify the simultaneous occurrence of fine root production and disappearance and to produce a method particularly applicable to mature forest ecosystems in which fine root biomass approaches a steady-state.

The fine (≤2 mm diameter) root biomass of the Danum forest was found to be relatively low compared with a number of previously described lowland rain forests (Section 3.4.1). There was no development of a root mat at Danum, unlike some of the well documented *tierra firme* forests of Amazonia (Klinge 1973, 1975, Stark and Spratt 1977, Jordan and Escalante 1980). The maintenance of a high fine root biomass and root mat have frequently been put forward as an adaptive feature of tropical rain forest on oligotrophic sites. Although the Danum soils may not be classed overall as oligotrophic, they were found to have both very low levels of extractable phosphorus and a high C:N ratio (Section 2.5.4). On this limited evidence the Danum forest would appear to be inconsistent with the model put forward by Gower (1987) that phosphorus availability is the primary factor governing fine root biomass in lowland tropical rain forests.

Both high rates of fine root disappearance and low rates of fine root appearance were found to coincide with relatively dry periods at Danum (Section 4.3.3). Fine root activity appeared to be more synchronous between rhizotrons during dry periods and it was suggested that such a pattern might be expected when the primary factor

controlling activity was external in origin (Section 4.4.3). No similar synchrony was found in overall levels of above-ground litterfall by Burghouts *et al.* (1992 and submitted). That the effects of relatively dry periods at Danum on fine root appearance and disappearance were not reciprocated in patterns of above-ground litterfall may indicate that the level of stress, on the whole plant, induced by the dry periods was relatively low. The lowest fine root biomass recorded in the current study coincided with a dry period in April 1991. A lower fine root biomass in relatively dry compared to wet seasons has been reported for other 'perhumid' lowland rain forests in Venezuela (Sanford 1985) and Costa Rica (Sanford 1987, Section 3.4.4). The dry period that the current study coincided with in April 1991 did not appear to be exceptional and similar periods of low rainfall have occurred in all but one year at Danum since 1985 (Figures 2.3.2 and 2.3.3). It may be that soil moisture replaces soil fertility as the primary factor governing fine root biomass and the production of a root mat in lowland rain forests which seasonally experience relatively dry periods. Much of the previous work of fine root systems in tropical rain forests has been descriptive in nature and has tended to measure roots in isolation. Future studies should attempt to describe below-ground activity while concurrently recording environmental variables and above-ground phenology.

Some very high estimates of fine root production have been reported for evergreen forests in both the boreal (eg 73% of ecosystem net primary production (NPP) in Douglas Fir forests in the USA, Fogel and Hunt 1983) and tropical zone (eg 70% of NPP in *tierra firme* forest in Venezuela, Sanford 1985). The ratio of fine root dry mass production, estimated in the current study, to above-ground litterfall, measured by Burghouts *et al.* (1992) in adjacent plots, suggested that the proportion of NPP allocated to fine root production in the Danum forest appeared to be considerably lower than that estimated in a number of other forests (fine root production:leaf litter = 0.61, fine root production:total small above ground litter = 0.34, Section 4.4.1). Fine roots appear to be less important than above-ground litter in supplying the soil with organic matter in the Danum forest.

Fine root dry mass production (*Pd*) and disappearance (*Ds*) estimates were expressed in terms of a flux of nutrients into and out of the fine root biomass (Section 5.3.1). These estimates will become more useful when data on the nutrient flux in above-

ground litterfall become available for adjacent plots at Danum (Section 5.4.1). A considerable body of data is accumulating on aspects of the nutrient cycle in the Danum forest and future studies at Danum may wish to work towards completing an ecosystem-level nutrient budget for primary forest. The production of such a model for primary forest could provide important base line information in attempting to predict how forest productivity might respond to the intensive timber extraction that is occurring in a large proportion of the lowland dipterocarp forests of Sabah.

It has previously been postulated that fine roots possess a nutrient conservation mechanism, analogous to that in leaves, which allows nutrients to be retranslocated to other parts of the plant during senescence and prior to abscission (eg Nambiar 1987). If such a nutrient conservation mechanism was present in plants it could have an important influence on estimates of the contribution of fine roots in ecosystem-level nutrient cycles (Section 5.4.2). The micro-digestion of individual fine roots of known age in the current study produced no clear patterns, with root age, of nutrient concentration, mass of nutrient per unit length of root, or calcium:mobile nutrient ratios (Section 5.3.2). No evidence was found in the current study to support the hypothesis that nutrients are retranslocated to other parts of the plant prior to root death (Section 5.4.2). The factors that cause the main absorbing organs of plants to be ephemeral deserves greater attention in future work. In particular, it needs to be determined whether fine roots go through an active process of senescence, analogous to that in leaves, or whether there ultimate death is normally caused by an external factor. Whether fine roots possess a nutrient retranslocation mechanism as part of an active senescence needs to be specifically investigated, perhaps using radioactive tracers.

The incubation of localised nutrient-rich sources provided no evidence in support the hypothesis that nitrogen (NH_4^+, NO_3^-), phosphorus ($H_2PO_4^-$), or potassium (K^+) were potentially limiting to fine root growth in the Danum forest (Section 5.3.3). However, the replication in this experiment was reduced by the destruction of a large proportion of the in-growth bags. At present there is no direct evidence of nutrient limitation in lowland rain forests (Proctor 1992). Methods such as the in-growth technique may provide initial pointers as to which nutrients are potentially limiting to plant growth in lowland rain forests, but nutrient limitation will have to be verified by fertilization

experiments at the stand-level. Girth increment data have shown tree growth to be limited by nitrogen and phosphorus in montane forests in Hawaii and Jamaica (Gerrish and Bridge 1984, Vitousek *et al.* 1987, Tanner *et al.* 1990), but there is no such data available for lowland rain forests. This is a great need for further work on the response of lowland rain forests to nutrient additions.

Fine root decomposition was investigated using rhizotron methodology directly comparable to that used to estimate fine root production and disappearance. Comparison of the two methods suggested that, on average, fine roots in the Danum forest were decomposing for about 70% of their Persistence (Section 4.3.2). A filter paper decomposition assay provided no evidence that decomposition occurred more rapidly behind a glass plate than in bulk soil. Few studies have attempted to characterize the micro-environment of the soil:glass interface in rhizotrons and mini-rhizotrons. The effect of any differences in the soil:glass micro-environment compared to bulk soil on the activity of fine roots, and in particular on individual Persistence, deserves greater attention. The decomposition rate constant (k) was estimated for fine roots in the Danum forest by a new rhizotron method (Section 4.3.2) and was found to be similar to the estimate of k for leaf litter decomposition reported by Burghouts *et al.* (1992) for adjacent plots. The rate of leaf and fine root decomposition in the Danum forest was within the range reported for three other dipterocarp forests and towards the upper end of the range reported for a number of lowland rain forests worldwide (Section 4.4.2).

Fine root growth in Persistence-rhizotrons did not equilibrate in terms of rates of fine root appearance and disappearance until four months after installation (Section 4.3.3). This may be an important consideration for studies that employ observation methods for studying fine roots in mature forest ecosystems, particulary where the periodicity of fine root appearance and disappearance is being monitored. It suggests that a considerable 'settling in' period is required in glass wall observation methods.

The distribution of tree girth sizes in plots 1, 2, and 3 gave no evidence in support of the hypothesis of that catastrophic events in the past, such as drought, have caused releases in tree growth, over an area that included both the plots in the current study and those of Newbery *et al.* (1992) (Section 2.6.4). Evidence that primary lowland rain

forests are not immune from burning, however, is accumulating (Beaman *et al.* 1985, Sanford *et al.* 1985, Leighton and Wiraman 1986, Woods 1989) and a detailed study of the soil charcoal found to be ubiquitous in the Danum soils is warranted.

Lowland tropical rain forests are rapidly disappearing and vast tracts of undisturbed lowland rain forest in south-east Asia are already a thing of the past (Whitmore 1989). As large areas of natural forest are brought into commercial timber production a sound knowledge of their carbon and mineral nutrient cycles will be essential if their viability as productive, semi-natural stands, with many associated benefits, is to be sustained. As more data accumulates on rain forest nutrient cycles it has become clear that the prevailing model of how rain forest structure and function is determined by mineral nutrition, largely established in a limited number of Amazonian forests, needs to be re-evaluated.

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