Plant-soil nutrient relationships in north Queensland wet tropical rain forests

Thesis submitted by
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in September 1998

for the degree of Doctor of Philosophy
in the Department of Tropical Plant Sciences at the
James Cook University of North Queensland

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ABSTRACT

This study investigated plant-soil nutrient relationships at seven sites in the wet tropical rain forests of north Queensland, Australia. Biomass and nutrient standing stocks were determined for 24-year-old successional vegetation recolonizing a disturbed site (280 m^2). This data was used to generate biomass regressions to estimate above-ground biomass at three undisturbed sites where the influence of soil fertility on fine root dynamics and resource allocation were examined. A further three undisturbed sites were sampled to examine the relationship between fine root biomass and soil fertility.

The dry weight of 150 trees was measured, yielding an above-ground biomass of 53.7 t ha^{-1}. Foliage comprised 7.0%, branches 9.6%, stems 83.0% and reproductive structures 0.4% of the total. The total nutrient standing stocks at the site were 158.8 kg ha^{-1} nitrogen, 7.53 kg ha^{-1} phosphorus, 172.7 kg ha^{-1} potassium, 129.0 kg ha^{-1} calcium, and 43.2 kg ha^{-1} magnesium. Most of the nutrients were contained in the stems of the vegetation. Nutrient concentrations were found to vary within species, between species and between components. Foliage had the highest concentrations of all nutrients and the greatest variability between species. The lowest foliar concentrations were found in the late secondary species, *Darlingia darlingiana,* while the highest were found in the early secondary species. Foliar nutrient concentrations were found to decrease with increasing foliage biomass for *Alphitonia petriei*, however, this trend was not evident for *D. darlingiana.*

Thirteen biomass regressions, based on three allometric models and an exponential model, were tested. Regressions were determined for total above-ground biomass and foliage biomass against diameter at breast height (dbh), alone and in combination with tree height and wood density. The exponential

regressions were found to be unsuitable due to increasing variance with increasing tree size, while all allometric regressions gave highly significant correlations. The equations utilising both dbh and tree height yielded better estimates than equations using dbh or tree height alone. The inclusion of wood density into the regressions did not significantly improve the estimate of biomass. Biasing induced by the logarithmic transformation varied from 11 to 51%.

Estimates of above-ground biomass did not vary substantially at three sites on soils of differing fertility. Fine root biomass was greatest on nutrient-poor sites, and lowest on more fertile sites. However, it is unknown whether this is due to differences in available phosphorus or some other, as yet, undetermined factor. Total fine root biomass in the top 50 cm of soil was found to range from 7.7 to 27.0 t ha^{-1}. The greatest concentration of fine roots at all sites was in the top 10 cm of soil, and this decreased rapidly with depth. Fine root production differed significantly between the sites, with the highest rate of production (3.28 t ha^{-1} y^{-1}) occurring on the nutrient-rich site. Fine root production showed distinct seasonal variations, with peak production occurring during the wet season. Fine root proliferation coincided with increased phosphorus availability at all sites. The results suggest that fine roots may be as important as litterfall in returning nutrients to the soil in tropical forests. Annual nutrient turnover in the top 10 cm of soil by fine roots varied between nutrients and between sites, from 11% of the total magnesium at Mt Spec, to 192% of the phosphorus at Mt Fox.

The results of this study demonstrate the influence of soil fertility on fine root dynamics and resource allocation within tropical rain forests.

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ACKNOWLEDGMENTS

The submission of this thesis would not have been possible without the assistance and support of a number of people. In particular, I wish to thank my supervisor, Dr Robert Congdon, for his assistance in all stages of my work, and especially for his patience when I suspended my studies to undertake employment at the Universiti Brunei Darussalam, and the other breaks I had during the extended gestation period of this thesis. I would also like to express a special thanks to Peter Walsh, Martin Saker, Torres Woolley, Geoff Giles and others too numerous to mention who assisted with the enormous amount of fieldwork and laboratory analysis required for this thesis. A special thanks also goes to my Head of Department at UBD, Dr Joe Charles, and my brother, Bruce Maycock, who have tried to keep me focused on completing this thesis. A special thanks to Dr Peter Brownell for his invaluable advice and excellent company during our many lunch and coffee breaks.

I thank also the Queensland Forest Service for allowing access to the sites used in this study. The research undertaken for this thesis was supported, in part, by several grants from the James Cook University of North Queensland Merit Research Grant scheme.

CHAPTER 1

Introduction

Soil fertility may play an important role in determining floristic diversity and ecosystem dynamics of tropical rain forests (Lamb 1991, Vitousek & Sanford 1986, Webb 1969). While there exists a number of studies examining the relationship between soil fertility and species diversity (Ashton 1964, Gentry & Emmons 1987, Webb 1969, Wright 1992), there is little information on the influence of soil fertility on productivity and resource allocation in rain forests (Vitousek & Sanford 1986). This thesis examines the relationships between soil fertility and the production of rain forests in north east Queensland.

1.1 Influence of soil fertility on rain forests

1.1.1 Influence of soil fertility on floristic diversity

There are two theories addressing the relationship between plant species diversity and soil fertility (Wright 1992). The first predicts an inverse relationship between these factors, with the highest species diversity occurring on low fertility soils. Huston (1979) reasons that low growth rates coupled with environmental fluctuations would prevent competitive exclusion on low fertility soils. Conversely, Tilman (1982) predicts a humped relationship, with low diversity on extremely nutrient-poor soils, a rapid increase in species diversity from the least fertile to relatively fertile soils, followed by a slow decline in species diversity on richer soils. Tilman (1982) argues that nutrient limitations would limit species diversity on extremely nutrient-poor soils, while competitive exclusion would reduce species diversity on richer soils.

The relationship between soil fertility and species richness in tropical forests varies for different life forms, and in different geographic regions (Wright 1992). The biodiversity of terrestrial herbs and understorey shrubs has been found to generally increase with increasing soil fertility (Gentry & Emmons 1987). For tree species, the relationship is more variable. While the floristic complexity of north Queensland wet tropical forests has been found to increase in association with increasing soil fertility (Webb 1969), no relationship between floristic diversity and soil nutrient status has been found for rain forest in northern Borneo or the Neotropics (Ashton 1964, Faber-Langendoen & Gentry 1991).

1.1.2. Influence of soil fertility on ecosystem dynamics

There is little direct evidence that the productivity of tropical rain forests is limited by soil nutrient status, except on extremely infertile soils (Vitousek & Sanford 1986). Soil nutrient status is probably a major determinant of litterfall (Herbohn & Congdon 1993, Spain 1984), with forests on moderately fertile soils returning more litter than those on infertile oxisols (Table 1.1). In contrast, above-ground biomass has been found to be similar over a wide range of soil fertilities (Table 1.1), and basal area increment has been found to be independent of soil nutrient status (Ashton & Hall 1992, Vitousek & Sanford 1986).

There are two theories addressing the relationship between soil fertility and fine root dynamics. The source-sink theory of resource allocation of Bloom *et al.* (1985), predicts that trees growing on infertile sites should allocate a greater proportion of their resources into fine root production, than those growing on fertile sites, as this "investment" in nutrient acquisition should increase growth and/or reproduction. In contrast, others have suggested that the portion of carbon allocated to fine root growth remains relatively constant across fertility gradients, and that fine root turnover rates increase with increasing fertility resulting in lower standing biomass on rich sites (Chapin 1980, Grime 1977, Nadelhoffer *et*

al. 1985). As most studies of root systems in tropical rain forests have, to date, concentrated on root biomass (Edwards & Grubb 1982, Greenland & Kowal 1960, Klinge 1973a, 1973b, 1975, Klinge & Rodrigues 1974), with only recent studies starting to examine fine root productivity (Cavelier 1989, Cuevas & Medina 1988, Green 1992, Pendry 1994, Sanford 1985), there is not enough data available to draw conclusions and the relationship between soil fertility and fine root dynamics remains unclear.

Table 1.1 Litterfall (t ha^{-1} y^{-1}) and biomass (t ha^{-1}) of tropical forests. Data are taken from Vitousek and Sanford (1986). The number of studies included in this analysis is given in parentheses.

	Soil fertility class		
	Moderately Fertile Soils	Infertile Oxisols	Infertile Spodosols
Litterfall (t ha^{-1} y^{-1})	10.5 ± 1.4 (10)	8.8 ± 1.9 (11)	7.4 ± 1.8 (2)
Biomass (t ha^{-1})			
- Above-ground	320 ± 50 (3)	380 ± 60 (5)	130 ± 50 (4)
- Below-ground	18.0 ± 6.8 (2)	43.9 ± 11.6 (2)	77.6 ± 21.5 (5)
- Fine roots (< 6 mm)	5.0 (1)	14.6 (1)	35.6 ± 19.4 (2)

Soil nutrient status is seen as a major factor influencing nutrient cycling patterns in tropical rain forests (Vitousek & Sanford 1986). Two distinct systems of nutrient cycling based upon the nutrient status of the soil have been recognised (Jordan & Herrera 1981). On nutrient-deficient soils, the majority of the nutrients are retained within the biomass and are tightly cycled. This system, referred to as an oligotrophic system, has highly developed nutrient conserving mechanisms and is characterised by low rates of nutrient accession in litterfall (Herbohn & Congdon 1998). This is in contrast to the eutrophic system found in forests on relatively nutrient rich soils, which is a more open system of nutrient cycling. There is less development of nutrient conserving mechanisms and more nutrients are returned to the soil by litterfall within these forests (Brasell *et al.* 1980).

However, the lack of information on the role of fine roots as a pathway of nutrient return to the soil, impedes our understanding of nutrient cycling in tropical rain forests. The data available suggests that, while fine roots only contain a relatively small proportion of the total nutrient stocks within the vegetation at a site, their rapid rate of turnover and moderately high nutrient concentrations suggests that they may be as important as litterfall in returning nutrients to the soil in tropical forests.

1.2 Aims of this study

Our understanding of ecosystem dynamics in the wet tropical rain forests of north Queensland is limited by a lack of information on the influence of soil fertility on productivity, and biomass and nutrient allocation between the above- and below-ground components of the forests (Spain 1991). There are no reliable estimates of above- or below-ground biomass for north Queensland rain forests. Similarly, there are no estimates of nutrient standing stocks within the above- and below-ground portions of the vegetation. While there is some data on above-ground productivity of north Queensland rain forests (Brasell *et al.* 1980, Herbohn & Congdon 1993, Vanclay 1989), there exists no data on the below-ground portion.

This thesis examines plant-soil nutrient relationships in north Queensland wet tropical rain forests. The aims of this study were to examine:

1. the influence of soil fertility on fine root dynamics;
2. the influence of soil fertility on allocation of biomass between the shoot (total above-ground) and fine root systems in forests on soils of differing fertility;

3. nutrient dynamics within fine roots on soils of differing fertility; and
4. seasonal variations in fine root productivity and soil nutrient availability in soils of differing fertility.

The first section of this thesis examines biomass and nutrient stocks within the vegetation at an old log loading ramp on low fertility soil (Chapter 2). The data from this section are used to generate biomass regressions. These regressions are compared to published regressions for tropical rain forests and are utilised to estimate biomass at the three main study sites which have soils of differing fertility (Chapter 3).

Chapter 3 examines the influence of soil fertility on fine root dynamics and the allocation of biomass between the shoot (total above-ground) and fine root systems of forests on soils of differing fertility. This chapter consists of two parts. Firstly, a survey of fine root biomass at six sites in north Queensland examines the relationship between fine root biomass and soil fertility, measured as total nitrogen and available phosphorus. The second part of Chapter 3 examines the influence of soil fertility on fine root dynamics and biomass allocation at the three main study sites.

Fine root nutrient dynamics are examined at the three main study sites in Chapter 4. Fine root biomass and productivity data from Chapter 3 are combined with data on nutrient concentrations to estimate total nutrient standing stocks and annual nutrient allocation to fine roots at each site. Retranslocation of nutrients prior to senescence is also investigated.

Seasonal variations in fine root production and soil nutrient availability at the three main study sites are examined in Chapter 5, using root ingrowth bags and ion exchange resin bags. Changes in fine root production are related to changes in soil nutrient availability, to examine the importance of fine root proliferation at the start of the wet season as a nutrient conserving mechanism.

CHAPTER 2

Biomass, nutrient standing stocks and allometry

2.1 Introduction

Biomass estimates are a prerequisite for studies investigating ecosystem functions, such as nutrient and carbon dynamics (Whittaker *et al.* 1974). These estimates are most precisely determined by the harvesting of the vegetation. This is, however, often not practical or desirable, so other methods are employed.

Regression analysis is the most commonly used alternative approach (Whittaker & Woodell 1968). In this technique a sample of the vegetation is harvested, and a regression equation relating biomass to easily measured tree dimensions is determined (Crow 1978). The regression is then applied to the unharvested vegetation, and the total above-ground biomass estimated.

Various mathematical models have been used for the determination of biomass regressions. The most commonly used models are based on allometric equations (Pastor *et al.* 1984). The constant allometric equation (Model 1),

$$Y = aX^{b}\varepsilon, \qquad [1]$$

is the simplest form of this equation. It relates biomass (Y) to a single independent variable (X). The independent variable may either be a single dimension, usually diameter at breast height (dbh), or a predetermined combination of dbh and height. When dbh and height are combined they are usually in the form $(dbh)^2 \times height$. When available, wood density data is also often incorporated into the regression. In this equation a and b are the regression coefficient and the allometric ratio, respectively, and ε a measure of the error of the regression (Geron & Ruark 1988).

Ovington and Olson (1970) utilised a variation of the constant allometric equation in their study. Their model (Model 2),

$$Y = aX_1^{b_1} X_2^{b_2} \varepsilon, \qquad [2]$$

relates biomass to two independent variables, dbh and height. This equation has the advantage that it allows the relationship between X_1 and X_2 be determined from the data and not a predetermined ratio. This regression has two separate allometric ratios, b_1 and b_2.

The allometric ratios of equations [1] and [2] are constant and do not allow for possible changes in the allometric relationships, with increases in tree size. For some trees, these ratios have been found to decline sharply with increasing size (Geron & Ruark 1988, Ruark *et al.* 1987, Yang *et al.* 1978). The variable allometric model derived by Ruark *et al.* (1987), allows for these changes. This model (Model 3),

$$Y = aX^b e^{cX} \varepsilon, \qquad [3]$$

has an allometric ratio determined by the equation $b + cX$. The estimate of parameter c determines where the allometric ratio is going to increase or decrease with changes in tree size. If it is not significantly different from zero, then the term cX is dropped and equation [3] reduces to equation [1]. This equation has been found to statistically improve the prediction of biomass, particularly foliage biomass estimates (Geron & Ruark 1988, Ruark *et al.* 1987).

The fourth model examined in this study is the exponential model (Model 4),

$$Y = aX^2 \varepsilon, \qquad [4]$$

used by Overman *et al.* (1994).

In temperate forest ecosystems, regressions are usually developed for individual species within a stand (Brand & Smith 1985). This has the advantage that it allows for any error/variation due to interspecific variation in biomass allocation strategies. The high species diversity of tropical forests makes the determination of individual species regressions extremely difficult, and usually in these ecosystems a regression is developed for all the species within a stand (Overman *et al.* 1994). Brown *et al.* (1989) have developed generalised biomass regressions for tropical rain forests. These regressions are based on combined biomass data for a number of tropical forests, and can be used to estimate biomass where a locally derived regression is not available. However, they considered that local biomass regressions, based on the population of interest, are more reliable than these generalised equations. Currently, there are no published biomass regressions for the wet tropical rain forests of north Queensland, so studies examining carbon allocation and nutrient cycling in these forests are limited to the equations of Brown *et al.* (1989). How accurate these equations are in estimating above-ground biomass of north Queensland rain forests has not been tested.

In this study the vegetation recolonising an old log loading ramp was harvested, and the biomass and nutrient stocks within the vegetation determined. The aims of the work described in this Chapter are to:

1. examine biomass and nutrient distribution within the vegetation at this site;
2. derive biomass regressions for this vegetation type; and
3. compare the regressions determined in this study to those of Brown *et al.* (1989) and other published biomass regressions for tropical rain forests.

The development of biomass regressions for north Queensland rain forests will allow for the non-destructive determination of above-ground biomass, as in the following Chapter, at other sites where other aspects of resource allocation are being examined.

2.2 Study site

This study was conducted in the tropical rain forest of the Mt Spec State Forest, Queensland, Australia (19° 00' S, 146° 11' E). This forest became part of the Wet Tropics World Heritage Area in 1988 (Mosley 1990). The study site, a regenerating gap of approximately 900 m^2, was created in 1963/64 by the construction of a log loading ramp as part of a selective logging operation. The site was cleared in 1987 for the installation of a rain gauge, and the opportunity was taken to examine biomass and nutrient distribution within the tree species as such opportunities are rare, with almost all of these forests now protected in conservation reserves.

The site is situated in upland tropical rain forest between Mt Spec and the township of Paluma, at an altitude of 880 m (Figure 2.1). A detailed description of the site (plot 5) is given in Congdon and Herbohn (1993). The region has a monsoonal climate with hot wet summers and mild dry winters. Mean annual rainfall is 2630 mm, based on rainfall data from the Paluma meteorological substation. The majority of the rain falls between the months of November and April (Congdon & Herbohn 1993). Monthly mean minimum and maximum temperatures range from 9.6°C (July) to 26.6°C (March) (Congdon & Herbohn 1993). Tracey (1982), has classified the vegetation in this area as simple notophyll vine forest.

The soil at the study site is a shallow red earth underlain by granite (Coventry *pers. comm.*). The soil is strongly acidic and relatively infertile (Congdon & Herbohn 1993). Soil compaction, resulting from the construction of the loading ramp, was still evident 25 years after logging, with soil bulk density being 45% higher than the surrounding undisturbed forest (Maycock & Congdon 1992).

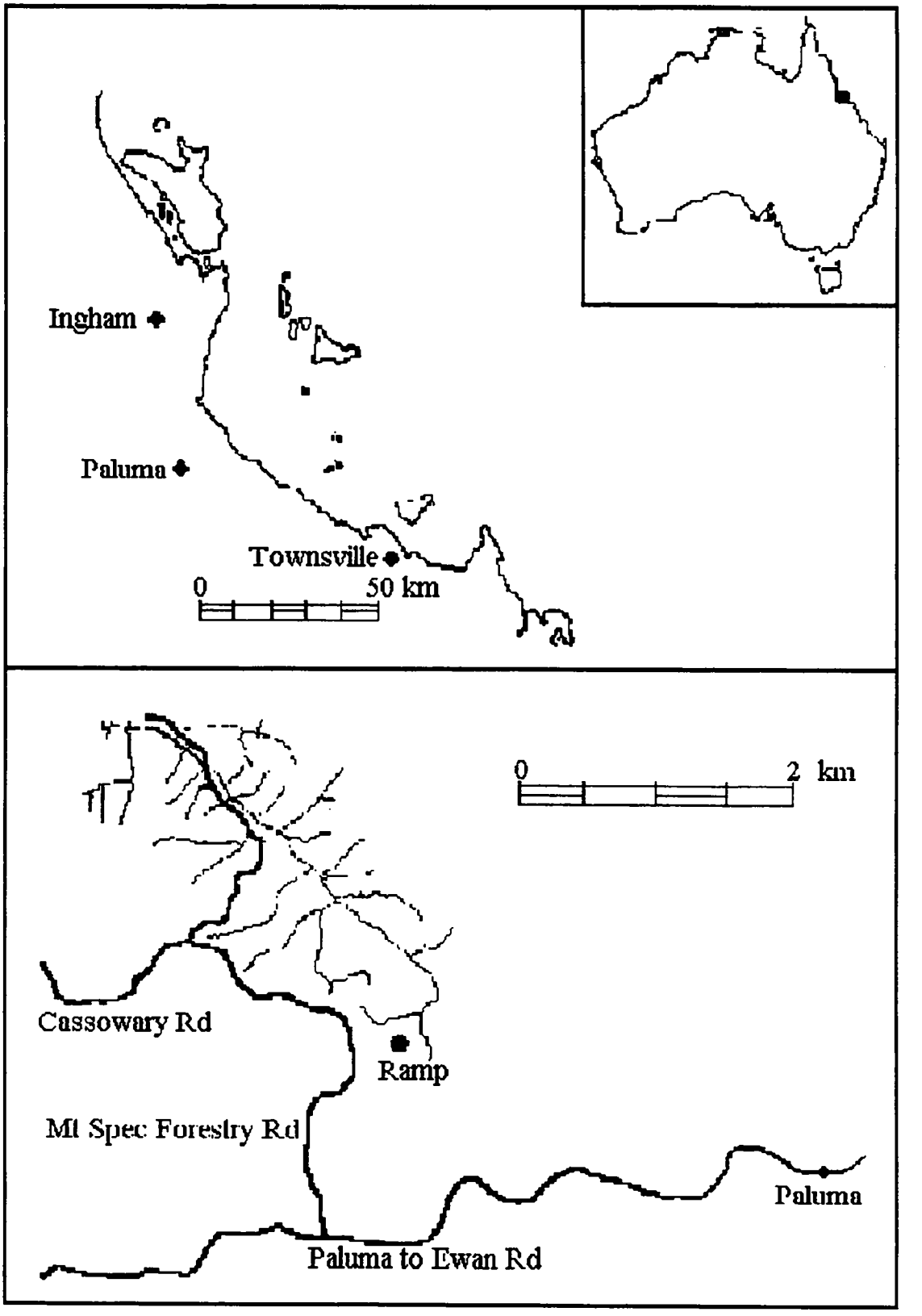


Figure 2.1 The location of the study site (ramp) near Paluma.

2.3 Methods

2.3.1 Biomass harvest

Above-ground biomass was determined by harvesting all trees over 1.3 m in height from an area of 280 m^2, representing about one-third of the ramp site (Maycock & Congdon 1992). Diameter at breast height (dbh) was measured before harvest, whilst heights were measured following felling. The leaves, branches, stems and reproductive material (flowers and fruit) were separated for each tree and their total fresh weight measured in the field. Subsamples of each component were taken and dried to constant weight at 80°C. The number and size of the sub-samples taken were dependent on the size of each tree. A single sub-sample of stem was taken for trees below 3 m height. Two sub-samples were taken, from the base and top of the bole, for trees between 3 and 5 m. Trees over 5 m were sampled from three places - at the base, mid-bole and from the top. All foliage was taken for trees below 3 m, whilst random sub-samples of not less than 5% were taken for taller trees. The total dry weight of each tree was calculated by multiplying the dry weight : fresh weight ratio by the fresh weight of the component and then summing the weights of each component.

Wood densities were determined for all species on duplicate oven-dried samples using the immersion method (Browning 1967). Radial cross sections of the samples were used to account for any variation in wood density across the radial axis of the tree (Wiemann & Williamson 1989).

2.3.2 Nutrient determinations

Plant material collected for dry weight determination was used to determine nutrient concentrations. The foliage, branch and reproductive materials were ground to 2 mm using a hammer mill (Janke & Kunkel GMBH & Co), and a sub-sample retained for analysis. A single bole sample was analysed for trees below

3 m height. Samples from the base and top of the bole were analysed for trees between 3 and 5 m, while samples from the base, mid-bole and the top were analysed for trees over 5 m. This was to allow for any vertical variations in nutrient concentrations within the trunk (Grubb & Edwards 1982). Radial cross sections were taken from the stems and large branches to account for differences in nutrient concentrations between young and old wood (Grubb & Edwards 1982). These sub-samples were reduced to wood shavings using an electric planer, and the shavings were then ground to 2 mm using the micro-hammer mill.

Duplicate samples of the plant material were digested using a block digester and the selenium-sulphuric acid-hydrogen peroxide digestion mixture as outlined in Allen (1974). Nitrogen and phosphorus concentrations in the digests were determined by the colorimetric procedures presented in Anderson and Ingram (1989). Calcium and magnesium concentrations were determined by atomic absorption spectrophotometry, while potassium was determined by flame photometry.

Nutrient standing stocks for each tree were calculated by multiplying the nutrient concentration for each vegetation component by its biomass. For large trees where several bole samples were taken, the average concentration was used. The nutrient stocks in each tree were then summed to give total standing stocks for the site, and for the most abundant species.

2.3.3 Regression analysis

2.3.3a Total and foliage biomass regressions for all species combined

Thirteen regressions, based on the three allometric models and the exponential model of Overman *et al.* (1994), were applied to the total and foliage biomass data (Table 2.1).

Table 2.1 Biomass regressions applied to the ramp site biomass data. Dbh is the diameter at breast height of the tree; hgt the height of the tree; wd the wood density; a the regression coefficient; b_1, b_2 and c the allometric ratios.

Model #	Regression	Equation
1	a	Biomass = $a(\text{dbh})^b$
	b	Biomass = $a(\text{hgt})^b$
	c	Biomass = $a((\text{dbh})^2\ \text{hgt})^b$
	d	Biomass = $a((\text{dbh})^2\ \text{hgt wd})^b$
2	a	Biomass = $a(\text{dbh})^{b_1}\ (\text{hgt})^{b_2}$
3	a	Biomass = $a(\text{dbh})^b\ e^{c(\text{dbh})}$
	b	Biomass = $a(\text{hgt})^b\ e^{c(\text{hgt})}$
	c	Biomass = $a((\text{dbh})^2\text{hgt})^b\ e^{c((\text{dbh})^2\text{hgt})}$
	d	Biomass = $a((\text{dbh})^2\text{hgt wd})^b\ e^{c((\text{dbh})^2\text{hgt wd})}$
4	a	Biomass = $a(\text{dbh})^2$
	b	Biomass = $a(\text{hgt})^2$
	c	Biomass = $a((\text{dbh})^2\ \text{hgt})$
	d	Biomass = $a((\text{dbh})^2\ \text{hgt wd})$

The three allometric models are non-linear, with the exception of when their allometric ratios, b, b_1 and b_2, and $b + c\text{X}$, equal one. While statistical procedures to fit non-linear models are available (Gillespie & Cunia 1989), their parameter estimates can be unstable for small sample sizes and are complex and difficult to compute (Ruark *et al.* 1987). To overcome this, the data were logarithmically transformed and the regressions determined by the ordinary least square procedure, using the statistical package - SYSTAT 5.05 for Windows (SPSS Inc.). The logarithmic transformations convert the regressions into simple linear equations of the form,

Model [1] $$\log \text{Y} = \hat{a} + b \log \text{X} + \xi, \qquad [5]$$

Model [2] $$\log Y = \hat{a} + b_1 \log X_1 + b_2 \log X_2 + \xi, \text{ and} \quad [6]$$

Model [3] $$\log Y = \hat{a} + b \log X + cX + \xi. \quad [7]$$

In these equations log a and log ε have been simplified to $\hat{a}$ and ξ, respectively.

While these transformations make the equations easier to fit, they induce a biasing and should be used with caution (Zar 1984). While the untransformed equations are mathematically equivalent to the transformed equations, they are not statistically equivalent for the least squares solutions (Zar 1968), introducing this bias. The least squares procedure fits a regression by minimising the sum of squares of the residuals of the dependent variable (Y).That is:

$$\sum_{i=1}^{n} (Y_i - \hat{Y}_i)^2 \quad [8]$$

is minimised for all n observations, where Y_i is the ith observed value of Y and $\hat{Y}_i$ is the ith predicted value of Y (Zar 1968). For the log transformed equation it is,

$$\sum_{i=1}^{n} (\log Y_i - \log\hat{Y}_i)^2 \quad [9]$$

that is being minimised, which is not the same as equation [8] (Zar 1968). As a result, logarithmic transformation should only be used when data is log normally distributed or when there is heteroscedasticity, increasing variance in the data with increasing size, in the variance of Y at any value of X (LaBarbera 1989, Zar 1984).. The biasing induced by these transformations arises when the predicted values of Y are converted to untransformed units by taking the antilog of the predicted value. In most cases the biasing introduced is often very small, generally 10% or less. However, if the range of X is large, biasing can be of the order of 10 to 20% for uncorrected estimates (Baskerville 1972). The biasing induced by the transformation was accounted for by the

maximum likelihood method (Baskerville 1972). While there are several possible statistical methods to account for the biasing (Beauchamp & Olson 1973, Finney 1941), this method is the easiest to use and most widely applied in biomass studies. It has been found that, for large sample sizes, the estimates of the correction factor of this method did not differ significantly from those of the others, and due to its ease of computation, it is the preferred method of use (Lee 1982). This method eliminates the bias by multiplying the final result by a correction factor. The correction factor (CF) is calculated by the formula,

$$CF = e^{\left[\frac{(SEE)^2}{2}\right]}, \qquad [10]$$

where SEE is the standard error of estimate of the regression (Sprugel 1983). The standard error of the estimate is calculated from the formula,

$$SEE = \sqrt{\frac{\sum_{i=1}^{n} (\ln Y_i - \ln \hat{Y}_i)^2}{n - 2}}, \qquad [11]$$

where $\ln Y_i$ is the natural log of the ith observed value of Y, $\ln \hat{Y}_i$ is the natural log of the ith predicted value of Y, and n the number of samples. The denominator for this equation varies with the number of parameters being estimated. In equations [1] and [3] where two parameters are being fitted, the denominator is n - 2, while for equation [2] where there are three parameters, the denominator is n - 3 (Sprugel 1983).

The exponential model, Model 4 (Table 2.1), was fitted to the untransformed data by the ordinary least square procedure, using SYSTAT 5.05 for Windows (SPSS inc.).

Comparison of the regressions was based on three important considerations; 1) the statistical correctness of the regression, 2) the accuracy of the estimates, and

3) the practicality of the model (Overman *et al.* 1994). The significance of the regressions and regression coefficients were tested by an F-test and a t-test, respectively. The coefficients of determination (R^2) for the regressions were calculated, and these were corrected for the number of variables included in the model (Draper & Smith 1981). These statistics formed the bases for selecting the best models.

There are, however, problems with relying solely on R^2 to select the best regression. R^2 values give more weighting to observations with large magnitudes and the maximal attainable R^2 can be different between models (Draper & Smith 1981, Overman *et al.* 1994). Numerous other statistics have been used to compare biomass regressions, with little standardisation of the statistics used between different studies. Schlaegel (1981) advocates reporting a number of statistics to allow for the comparison of biomass models. In this study the following statistics were determined for each regression: index of fit; standard error of the estimate; mean percentage error; mean residual; and percentage coefficient of variation of the regression.

The index of fit (FI) is analogous to R^2 (Brand & Smith 1985, Schlaegel 1981). It measures the amount of sample variation, in original units, which is accounted for by the regression equation relative to the total sample variation (Brown *et al.* 1989). It is used when a transformation is made on the dependent variable Y and is calculated by the formula,

$$FI = 1 - \left[\frac{\sum_{i=1}^{n} (Y_i - \hat{Y}_i)^2}{\sum_{i=1}^{n} (Y_i - \bar{Y})^2} \right], \qquad [12]$$

where Y_i are the observed values of the dependant variable, $\hat{Y}_i$ are the

predicted values for Y and $\bar{Y}$ is the mean of the observed dependent variables.

The standard error of the estimate (E) was determined by the formula,

$$E = \sqrt{\frac{\sum_{i=1}^{n} (Y_i - \hat{Y}_i)^2}{n - 2}} \quad . \qquad [13]$$

Mean percentage standard error (%SE) was calculated by the formula,

$$\%SE = \left(\frac{100}{n} \right) \times \sum_{i=1}^{n} \frac{(Y_i - \hat{Y}_i)}{\hat{Y}_i} \quad . \qquad [14]$$

The mean residual (RES) was calculated by the formula,

$$RES = \frac{\sum_{i=1}^{n} (Y_i - \hat{Y}_i)}{n} \quad , \qquad [15]$$

while, the percentage coefficient of variation (CV) of the regressions was determined by the equation,

$$CV = 100 \times \frac{\sqrt{\frac{\sum_{i=1}^{n} (Y_i - \hat{Y}_i)^2}{n - 2}}}{\bar{Y}} \quad . \qquad [16]$$

The standard error of the estimate and index of fit were determined from the logarithmic transformed data, while the mean residual and percentage standard error were determined on the untransformed data.

The final method used to examine the suitability of the regressions was to apply them to the individual diameter and height data for all the trees at the ramp site. The predicted biomass values were then compared to the observed values to examine how closely the regressions determined the biomass of this dataset.

2.3.3b Comparison with published biomass regressions

The standard technique for comparing regressions is to use an analysis of covariance (Zar 1984), which requires access to the original tree data for both regressions (Campbell *et al.* 1985). Ovington and Olson's (1970) dataset for a lower montane rain forest was the only one which could be found in the literature. However, their regressions, based on Model 2, have two independent variables, and cannot be compared by this technique. To overcome this problem, simple allometric regressions were determined for Ovington and Olson's (1970) dataset, using the procedure outlined above. An analysis of covariance was then conducted to compare the two sets of regressions.

While it is not possible to compare statistically the regressions of Brown *et al.* (1989) to those generated for the ramp site, it is possible to compare how accurately the different regressions estimate biomass at the ramp site and the site of Ovington and Olson (1970). To examine this, the regressions were applied to diameter and height data for both datasets and the biomass of individual trees estimated; these were then compared to the actual biomass. For comparsion, the regressions of Crow (1978), Martinse-Yrizar *et al.* (1992), Ogawa *et al.* (1965) and Overman *et al.* (1994) were also applied to the two datasets.

Biomass regressions, based on Model 1, were determined for all trees at the ramp site greater than 5 cm diameter as part of this comparative analysis. These regressions were also applied to both datasets.

2.4 Results

2.4.1 Biomass

A total of 150 trees, representing 17 families and 23 species, were present in the 280 m^2 sample area (Table 2.2). Regeneration was dominated by the early secondary species *Alphitonia petriei* and *Polyscias australiana*, and the late secondary species *Cardwellia sublimis*, forming a continuous canopy. Saplings of *Darlingia darlingiana*, *Alangium villosum* and *Solanum viridifolium* were common under the canopy. The maximum tree height, diameter at breast height and the total basal area at the site were 17 m, 28.4 cm and 17.5 $m^2\ ha^{-1}$, respectively.

The total above-ground biomass for the ramp site was 53.7 $t\ ha^{-1}$ with foliage comprising 7.0% of the total biomass, branches 9.6%, reproductive structures 0.4%, and stems 83.0% (Table 2.3). The majority of the trees harvested (73.3%) were below 5 cm dbh, but these contributed only 6.5% of the biomass. Trees between 10 and 15 cm dbh accounted for 37.2% of the total biomass, comprising 34.0% of the foliage, 33.6% of the branches, 37.9% of the stems and 22.5% of the reproductive material. The majority of the reproductive material was found on trees between 15 and 20 cm diameter.

The eight most abundant species accounted for 98% of the total biomass, but only 80% of the number of individuals harvested (Table 2.4). The early secondary species *Alphitonia petriei* and *Polyscias australiana*, and the late secondary species *Cardwellia sublimis*, accounted for 83.2% of the total biomass. *Darlingia darlingiana* accounted for 41.4% of the total number of trees harvested (Table 2.4).

Table 2.2 Species, number of individuals, successional status and wood densities (dry weight to dry volume) for the trees harvested at the ramp site. Successional status is based on Hyland and Whiffin (1993).

Species	Number of individuals	Wood density ($g\ cm^{-3}$)	Successional status
Acacia melanoxylon R.Br.	4	0.47 ± 0.01	Early secondary
Alangium villosum (Blume) Wangerin	8	0.61 ± 0.01	Early secondary
Alphitonia petriei Braid & C.T. White	23	0.50 ± 0.01	Early secondary
Archirhodomyrtus beckleri (F. Muell.) A.J. Scott	3	0.77 ± 0.02	Early secondary
Brackenridgea nitida A. Gray	1	0.56	Primary
Caldcluvia australiensis (Schltr.) Hoogl.	1	0.39	Primary
Cardwellia sublimis F. Muell.	9	0.51 ± 0.01	Late secondary
Darlingia darlingiana (F. Muell.) L. Johnson	62	0.76 ± 0.01	Late secondary
Elaeocarpus angustifolius Blume	1	0.66	Late secondary
Elaeocarpus elliffii B. Hyland & Coode	1	0.41	Primary
Ficus leptoclada Benth.	1	0.68	Late secondary
Litsea leefeana (F. Muell.) Merr.	4	0.50 ± 0.02	Late secondary
Melicope broadbentiana Bailey	2	0.73 ± 0.01	Early secondary
Mischocarpus lachnocarpus (F. Muell.) Radlk.	1	0.83	Primary
Polyscias australiana (F. Muell.) Philipson	5	0.45 ± 0.02	Early secondary
Rhodamnia costata A.J. Scott	1	0.78	Primary
Solanum viridifolium Dunal	10	0.56 ± 0.01	Early secondary
Symplocos cochinchinensis (Lour.) S. Moore	3	0.57 ± 0.05	Early secondary
Synoum glandulosum (Smith) Adr. Juss.	3	0.61 ± 0.01	Primary
Syzygium endophloium B. Hyland	1	0.59	Primary
Syzygium sp.	1	0.80	
Timonius timon (Sprengel) Merr.	1	0.59	Early secondary
Unknowns	4	N/A	

Table 2.3 Above-ground biomass (dry weight) for the ramp site. The percentage each component and dbh size class contributes to the total is given in parentheses.

DBH Size Class (cm)	Biomass					Number of individuals per ha .
	Foliage	Branches	Stems	Reproductive	Total	
			($t\ ha^{-1}$)			
<5	0.49	0.43	2.6	0.001	3.55	3929
	(13.1)	(8.4)	(5.9)	(0.3)	(6.5)	(73.3)
5 to <10	0.63	1.01	8.0	0.013	9.65	750
	(16.9)	(19.6)	(17.9)	(6.0)	(18.0)	(14.0)
10 to <15	1.27	1.73	16.9	0.047	20.95	429
	(34.0)	(33.6)	(37.9)	(22.5)	(37.2)	(8.0)
15 to <20	0.51	0.88	8.4	0.115	9.85	143
	(13.5)	(17.2)	(18.7)	(54.8)	(18.3)	(2.7)
20 to <25	0.47	0.73	4.2	0.012	5.45	71
	(12.5)	(14.2)	(9.5)	(5.7)	(10.2)	(1.3)
>25	0.38	0.36	4.5	0.022	5.25	35
	(10.0)	(7.0)	(10.1)	(10.5)	(9.8)	(0.7)
Total	3.75	5.14	44.6	0.210	53.7	5357
	(7.0)	(9.6)	(83.0)	(0.4)	(100.0)	(100.0)

Table 2.4 Most abundant species at the ramp site, expressed as a percentage of each component, total biomass and number of individuals.

Species	Biomass (%)					Individuals (%)
	Foliage	Branches	Stems	Reproductive	Total	
A. petriei	19.2	48	52.8	89.2	50.2	15.4
P. australiana	19.4	9.1	13.5	10.6	13.5	3.4
A. melanoxylon	1.8	3.2	2.5	0	2.5	2.6
A. villosum	0.4	0.2	0.1	0	0.1	5.4
S. viridifolium	0.2	0.5	0.1	0.1	0.2	6.0
C. sublimis	35.4	21	18	0	19.4	6.0
D. darlingiana	19	14.3	11.4	0	12.1	41.4
% of total	95.4	96.3	98.4	99.9	98	80.0

Wood densities ranged from 0.39 to 0.83 g cm^{-3} with the most abundant early secondary species, *A. petriei* and *P. australiana,* generally possessing lower wood densities than the primary and late secondary species (Table 2.2).

2.4.2 Nutrient standing stocks

Most of the nutrients within the vegetation at the ramp site were contained in the stems and branches; these accounted for over 65% of the total standing stocks (Table 2.5). The total nitrogen standing stock for the ramp site was 158.8 kg ha^{-1}. Total nutrient standing stocks for the other nutrients were phosphorus 7.53 kg ha^{-1}, potassium 172.7 kg ha^{-1}, calcium 129 kg ha^{-1} and magnesium 43.2 kg ha^{-1}. The percentage of the total nutrient standing stock contained in each component of vegetation varied between nutrients; the foliage contributed 33% of the nitrogen at the site, but only 17% of the potassium, although the foliage only makes up 7% of the biomass at the site (Table 2.5).

Table 2.5 Total nutrient standing stocks (kg ha^{-1}) at the ramp site, with the percentage that each component contributes to the total in parentheses.

	Nutrient (kg ha^{-1})					
	Nitrogen	Phosphorus	Potassium	Calcium	Magnesium	Biomass
Foliage	52.4	2.19	28.4	21.3	8.2	
	(33.0)	(29.0)	(17.0)	(17.5)	(19.0)	(7.0)
Branches	28.9	1.65	40.5	16.1	7.0	
	(18.0)	(21.0)	(23.0)	(12.0)	(16.0)	(9.6)
Stems	74.9	3.55	102.1	90.9	27.6	
	(47.0)	(47.0)	(59.0)	(70.0)	(64.0)	(83)
Reproductive	2.6	0.24	1.7	0.7	0.4	
	(2.0)	(3.0)	(1.0)	(0.5)	(1.0)	(0.4)
TOTAL	158.8	7.53	172.7	129.0	43.2	

Of all the species at the site, *A. petriei* contained the greatest quantity of all nutrients. Forty-five percent of the total nitrogen, 44% of the phosphorus, 46% of the potassium, 56% of the calcium and 40% of the magnesium were contained in *Alphitonia* trees (Figure 2.2). The foliage of *Alphitonia* contained approximately 9% of the total nitrogen and phosphorus standing stocks, with a similar quantity contained in the foliage of *Polyscias australiana.* Eighteen percent of the total magnesium at the site was contained in the stems of *C. sublimis.*

The foliage and reproductive material had the highest nutrient concentrations (Table 2.6), with potassium also being high in the branches. Foliage nutrient concentrations varied considerably between species (Figure 2.3), for example, nitrogen concentrations ranged from 11.6 to 36.5 mg g^{-1} (Table 2.6). The highest nitrogen concentrations were found in the leaves of the early secondary species *Solanum viridifolium*, with the lowest in the late secondary species *Darlingia darlingiana. S. viridifolium* also possessed the highest foliage phosphorus and potassium concentrations, 1.4 and 29.1 mg g^{-1}, respectively. The highest calcium concentrations were found in *Alangium villosum* and highest magnesium in *Synoum glandulosum.* In general, the early secondary species tended to have higher foliage nutrient concentrations than the late secondary species.

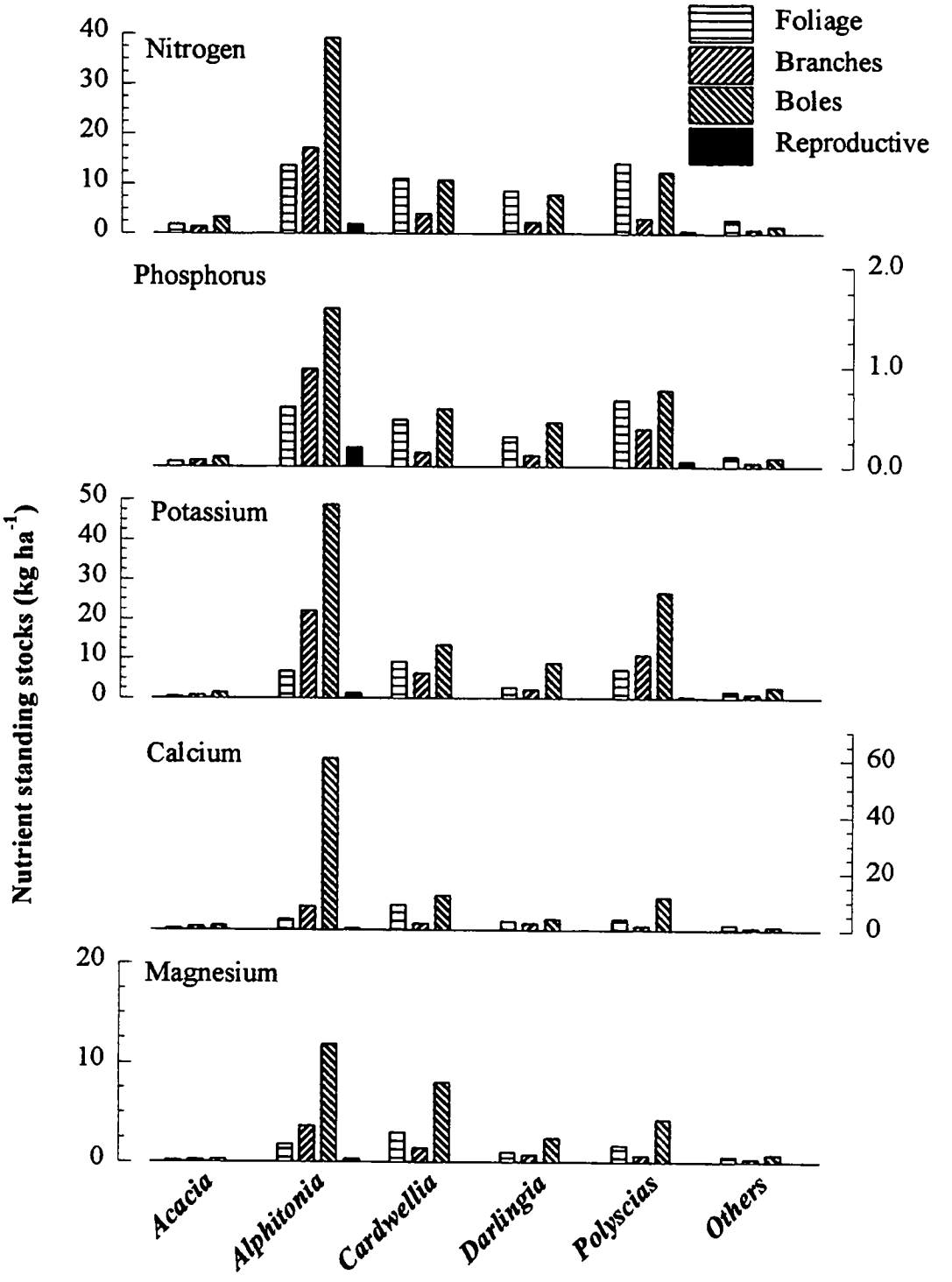


Figure 2.2 Nutrient standing stocks (kg ha^{-1}) for species comprising more than 2% of the total biomass.

Table 2.6 Mean and range of nutrient concentrations (mg g^{-1}) for the vegetation recolonising the ramp site.

	Nutrient concentrations (mg g^{-1})				
	Nitrogen	Phosphorus	Potassium	Calcium	Magnesium
Foliage (n = 150)					
- mean	17.7	0.70	9.7	7.1	2.6
- maximum	36.5	1.40	29.1	21.0	6.2
- minimum	11.6	0.42	4.4	3.5	1.5
Fruit (n = 11)					
- mean	9.6	0.94	3.9	3.2	1.8
- maximum	11.9	0.95	10.1	4.2	2.3
- minimum	9.4	0.61	3.7	2.8	1.5
Flowers (n =8)					
- mean	17.6	1.50	14.8	3.4	2.3
- maximum	39.7	2.70	39.6	6.4	5.8
- minimum	20.9	1.80	18.7	3.1	2.1
Branches (n =86)					
- mean	5.6	0.33	8.1	4.7	1.6
- maximum	11.0	0.64	16.8	9.3	2.2
- minimum	1.8	0.10	1.3	0.9	0.7
Stems (n =150)					
- mean	2.9	0.18	4.7	2.3	0.8
- maximum	7.1	0.39	10.7	5.3	2.9
- minimum	1.1	0.05	1.3	0.5	0.3

The ratios of foliage phosphorus to nitrogen were fairly constant between species (Table 2.7), ranging between 0.31 and 0.46. Ratios of potassium, calcium and magnesium to nitrogen showed greater variability between species. *Symplocos cochinchinensis* possessed K, Ca and Mg to N ratios that were between two to three times higher than the site mean, while *Acacia melanoxylon* had lower ratios than the site mean for all nutrients. Nutrient ratios in the late secondary species *Cardwellia sublimis* and *D. darlingiana* were similar to the site means for most nutrients.

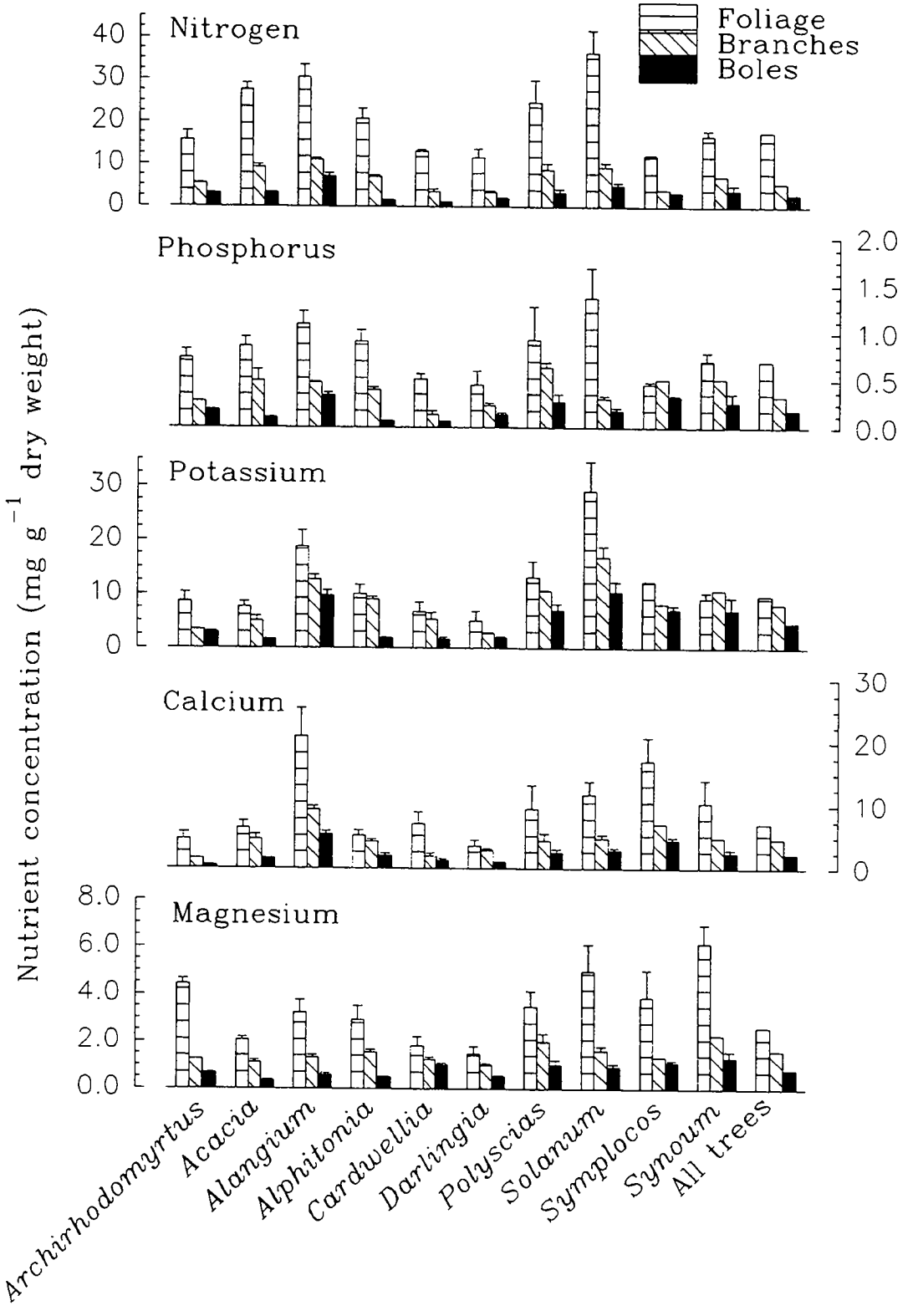


Figure 2.3 Nutrient concentrations (mg g^{-1}) in the foliage, branches and boles of the most abundant species at the ramp site. Bars indicate standard errors.

Mean foliage nutrient concentrations varied between individual trees of some species. Foliage nitrogen in *Alphitonia* varied between 16.2 and 25.6 mg g^{-1}, and decreased significantly with increasing foliage biomass ($P < 0.05$, Figure 2.4). This relationship was also found to occur for foliage phosphorus and magnesium concentrations in *Alphitonia*. *Darlingia* did not show any significant relationships between foliage nutrient concentrations and biomass (Figure 2.5). No other species harvested from the ramp site possessed enough individuals, or covered a wide enough range of sizes, to allow further investigation of this relationship.

Table 2.7 Ratios of mean foliage nutrient concentrations to foliage nitrogen concentration for all trees harvested and the most abundant species.

Species	Foliage nutrient to foliage nitrogen ratio			
	Phosphorus	Potassium	Calcium	Magnesium
All trees	0.040	0.55	0.40	0.15
Archirhodomyrtus	0.046	0.55	0.29	0.28
Acacia	0.031	0.27	0.23	0.08
Alangium	0.036	0.61	0.69	0.10
Alphitonia	0.043	0.48	0.25	0.14
Cardwellia	0.038	0.51	0.54	0.14
Darlingia	0.039	0.43	0.30	0.13
Polyscias	0.037	0.53	0.38	0.14
Solanum	0.037	0.80	0.32	0.14
Symplocos	0.037	1.01	1.40	0.31
Synoum	0.042	0.55	0.62	0.37

Nutrient concentrations were lower in the stems and branches, than those found in the foliage (Table 2.6). Species that had high foliage nutrient concentrations tended to also possess relatively high concentrations in their stems and branches (Figure 2.3). Concentrations of nitrogen, phosphorus and magnesium were higher at the top of the trunk of *Alphitonia*, than at the base (Table 2.8). Trunk potassium and calcium concentrations were similar throughout, however.

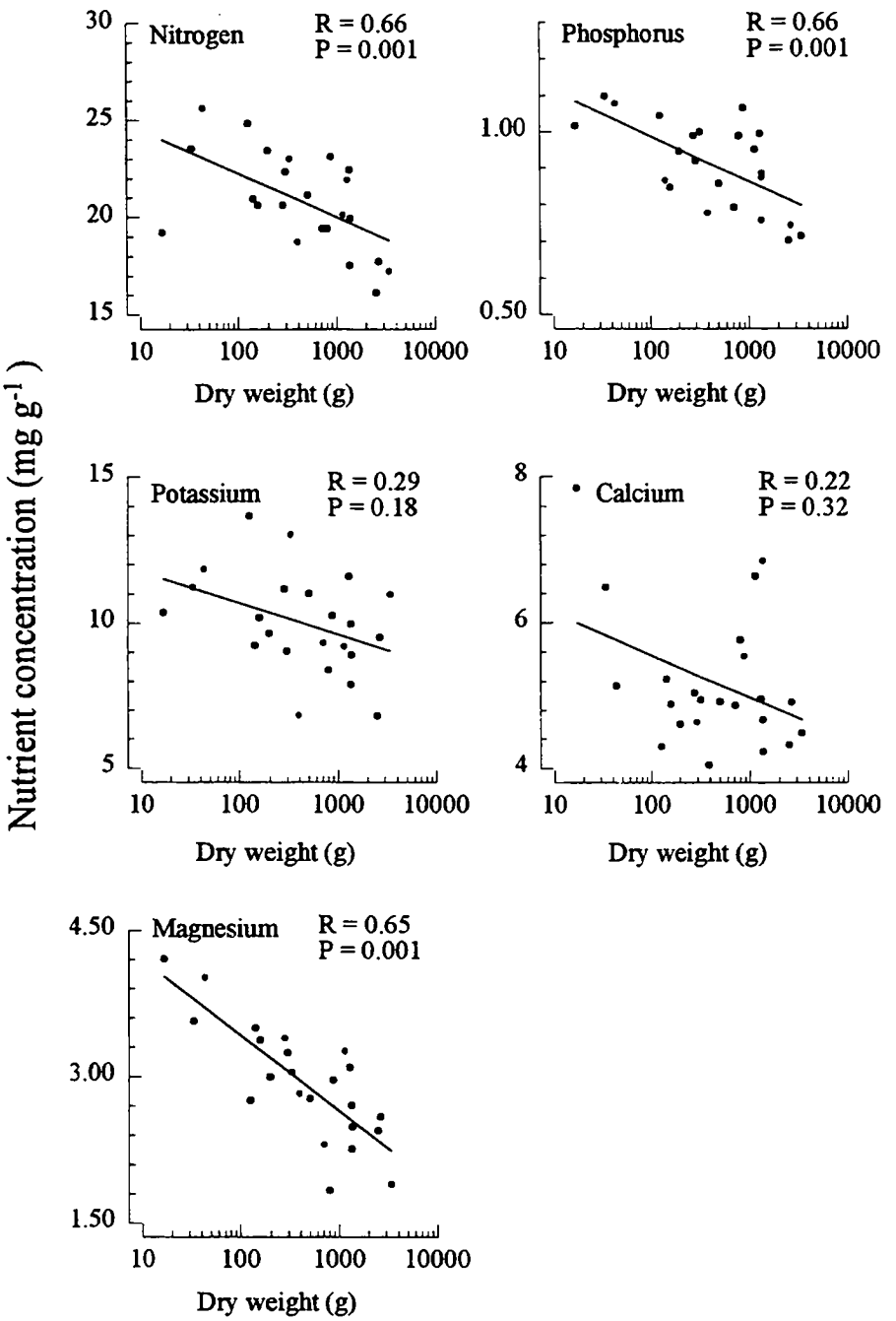


Figure 2.4 Foliage nutrient concentrations (mg g^{-1}) versus foliage biomass (g) for *Alphitonia petriei* harvested from the ramp site.

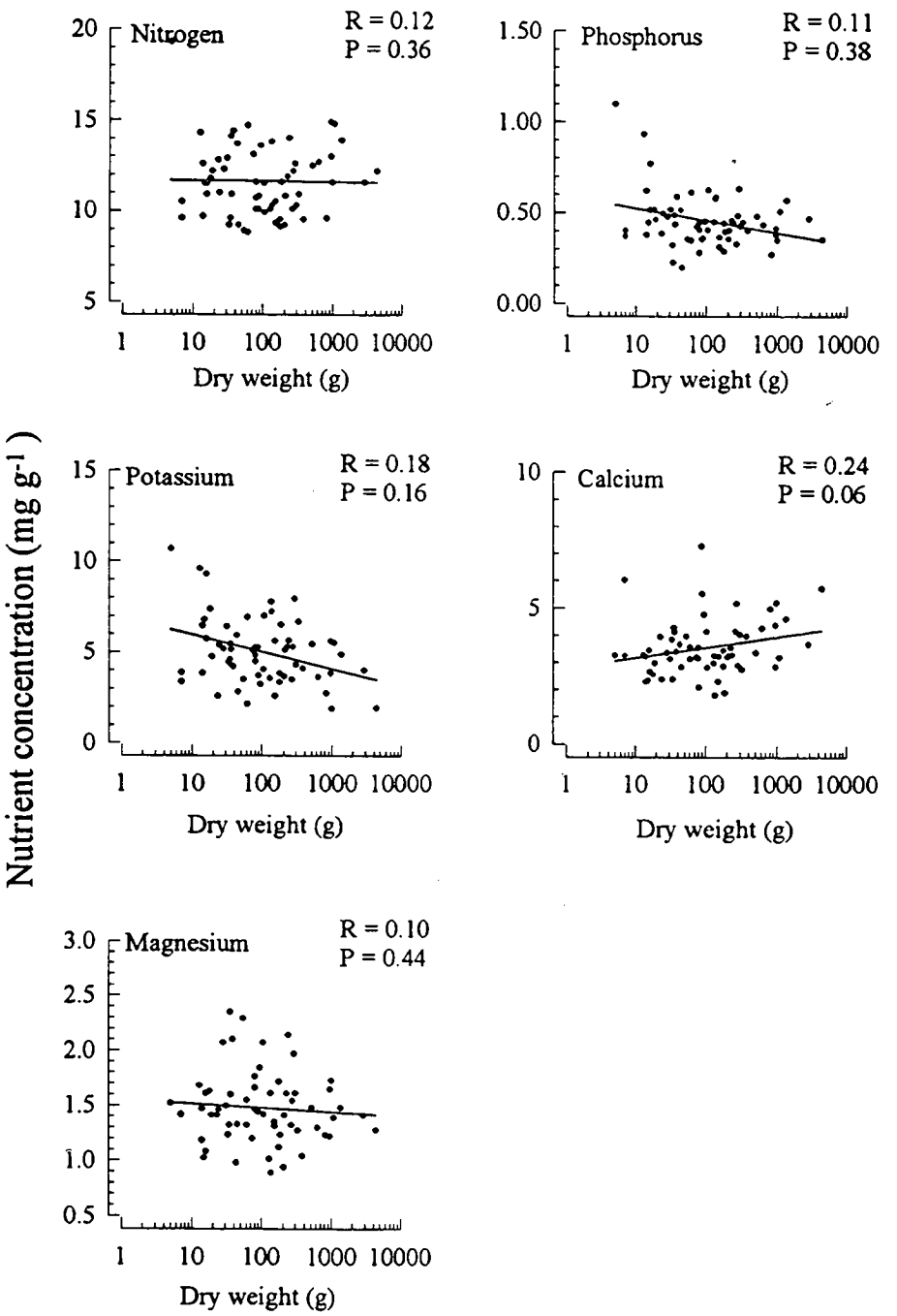


Figure 2.5 Foliage nutrient concentrations (mg g^{-1}) versus foliage biomass (g) for *Darlingia darlingiana* harvested from the ramp site.

Table 2.8 Nutrient concentrations (mg g^{-1}) at the base, middle and top of the boles of *Alphitonia petriei*.

Section	Nitrogen	Phosphorus	Potassium	Calcium	Magnesium
Base (n = 23)	1.35 ± 0.13	0.06 ± 0.01	2.05 ± 0.19	2.09 ± 0.39	0.45 ± 0.02
Middle (n = 15)	1.41 ± 0.11	0.06 ± 0.01	1.80 ± 0.12	2.17 ± 0.32	0.46 ± 0.02
Top (n = 23)	2.04 ± 0.22	0.08 ± 0.01	2.00 ± 0.18	2.11 ± 0.46	0.60 ± 0.04

Reproductive material was only found on three species, with *Alphitonia* being the only species that had both fruit and flowers. Flowers had higher concentration of nutrients, than the fruits (Table 2.6). The nutrient concentrations in the flowers of *Alphitonia* were comparable to the concentrations of most nutrients within the leaves (Table 2.6).

2.4.3 Allometry

2.4.3a Total above-ground biomass

All of the regressions were statistically significant (Table 2.9). However, the variance of the biomass data increased with increasing tree size (Figure 2.6), therefore not satisfying the assumptions of the least squares procedure for the regressions of Model 4. The coefficients of the regressions were significant with the exception of regression 3c. The coefficient of determination, R^2, varied between regressions. The simple and variable allometric regressions (Models 1 & 3) had values between 0.93 and 0.95; Model 4 had the lowest values, ranging from 0.78 to 0.89, and; Model 2 had the highest R^2 of 0.96.

All of the regressions had very high coefficients of variation (CV). They ranged from 76 % for regression 1c to 180 % for regression 3a. The mean percentage standard errors (%SE) were relatively constant for Models 1 to 3, but were highly variable for Model 4.

Estimates of above-ground biomass varied between the regressions (Table 2.9). Model 1 slightly underestimated the total biomass for the site, with the exception of regression 1a where the estimate was almost identical. The degree of underestimation ranged from 4.5% for regression 1c to 10.8% for regression 1d. Model 2 also underestimated biomass. Model 3 overestimated biomass with the estimates being between 2.9% and 23.6% greater. The greatest variations in estimates were found for Model 4. Regression 4b substantially overestimated site biomass (+22.9%), while the other three regressions underestimated site biomass (from -11.9% to -38.5%). The biasing introduced by the log-transformation of Models 1, 2 and 3 was between 11% and 18%.

Similar trends were exhibited in graphs of the predicted above-ground biomass for individual trees plotted against harvested biomass, for the regressions of Models 1, 2 and 3. The regressions slightly overestimated the biomass of small trees and underestimated the biomass of large trees (Figure 2.7). Model 4 was very variable; regression 4a gave the best fit, and showed a similar trend to the regressions of Models 1, 2, and 3. Regression 4b markedly overestimated at small tree size and underestimated the biomass of trees over 10 kg (Figure 2.7). Regressions 4c and 4d underestimated biomass, particularly for small trees.

Table 2.9 Parameters of regressions for total above-ground biomass of all species combined, harvested from the ramp site. a, b_1, b_2 and c are as defined in Table 2.1; R^2 is the coefficient of determination; P(reg) is the significance of the regression; P(con) is the significance of the constant; $P(X_1)$ and $P(X_2)$ are the significance of the coefficients; CF is the correction factor; CV is the coefficient of variation; %SE is the mean percentage standard error; RES is the mean residual; E the standard error of the estimate; and Biomass is the predicted biomass (kg ha^{-1}) determined by the regression for the site. The actual biomass measured was 53700 kg ha^{-1}.

	Regression model												
	1a	1b	1c	1d	2a	3a	3b	3c	3d	4a	4b	4c	4d
a	166.8	12.5	82.5	109.9	35.2	163.9	17.0	84.2	113.6	212.0	245.0	13.3	30.3
b_1	2.078	3.027	0.786	0.813	0.906	1.892	2.397	0.7743	0.786	-	-	-	-
b_2	-	-	-	-	1.77	-	-	-	-	-	-	-	-
c	-	-	-	-	-	0.044	0.109	3.35×10^{-5}	1.58×10^{-4}	-	-	-	-
R^2	0.93	0.94	0.95	0.95	0.96	0.93	0.95	0.95	0.95	0.89	0.78	0.84	0.83
P(reg)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
P(con)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-	-	-	-
$P(X_1)$	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
$P(X_2)$	-	-	-	-	0.00	0.03	0.00	0.30	0.04	-	-	-	-
CF	1.18	1.15	1.13	1.14	1.11	1.18	1.14	1.13	1.13	-	-	-	-
CV	85	119	76	96	85	180	113	98	117	81	115	96	100
%SE	18	14.3	12.5	13.6	10.1	16.8	13.2	12.3	13	-0.57	-63.9	331.0	191.0
RES	1540	2220	1590	2140	1790	-490	660	890	900	1200	-2300	2700	1920
E	8520	11980	7600	9580	8470	18060	11300	9860	11750	8130	11560	9670	10030
Biomass	53800	48100	51200	47900	49000	66400	57200	55400	55300	47300	66000	33000	43400

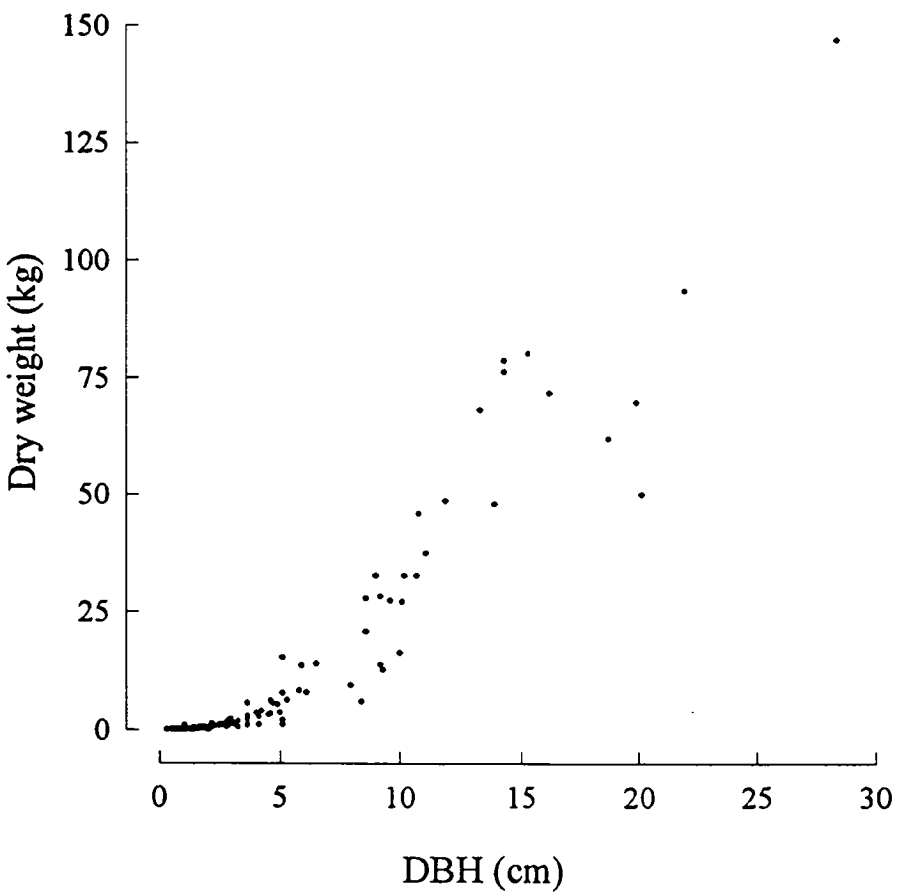


Figure 2.6 Relationship between dbh and total above-ground biomass (dry weight) for 150 trees harvested from 24-year-old regenerating rain forest on an old log loading ramp site, near Mt Spec, north Queensland.

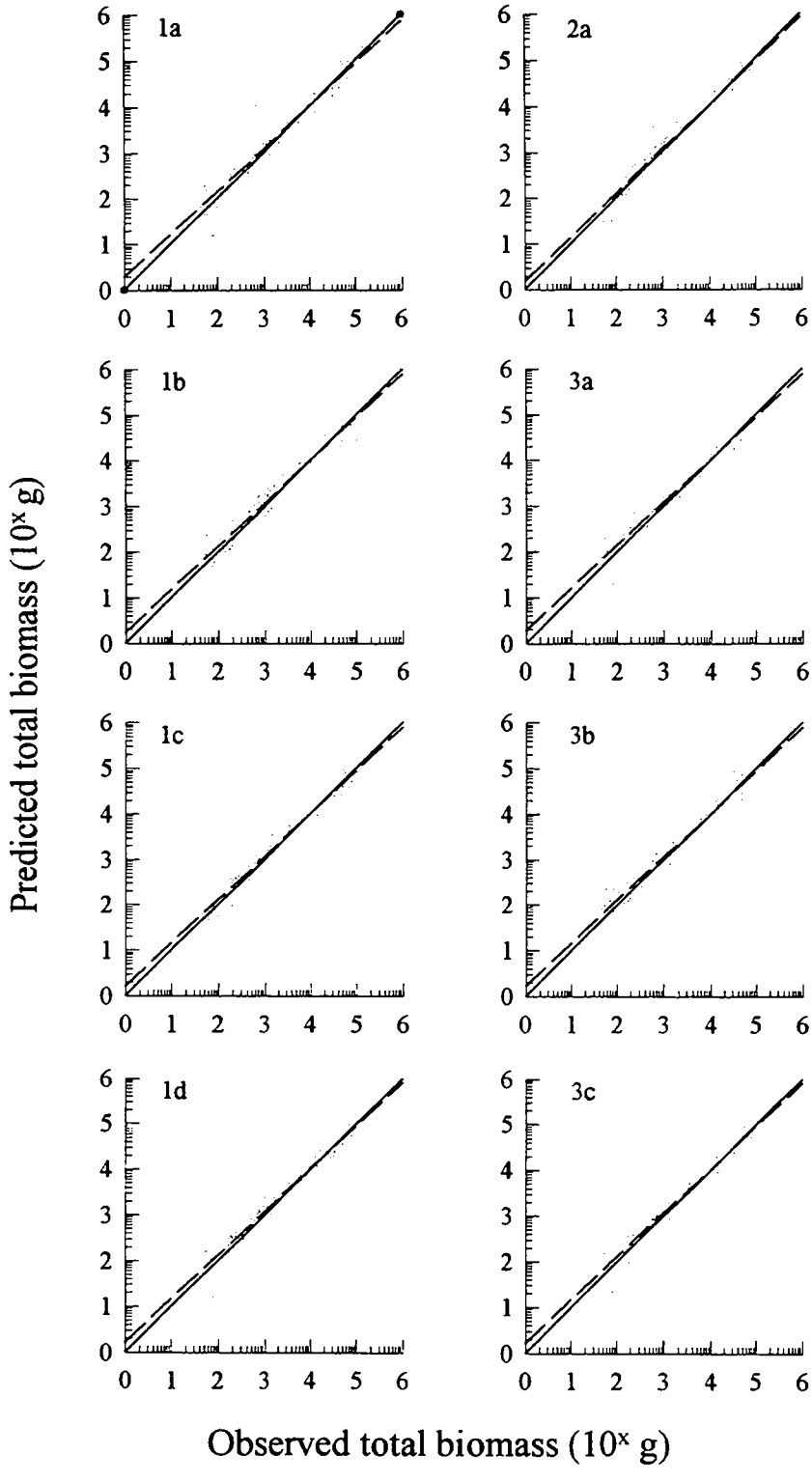


Figure 2.7 Comparison of observed to predicted total above-ground biomass for individual trees using biomass regressions described in Table 2.1. The dashed line is the calculated regression line.

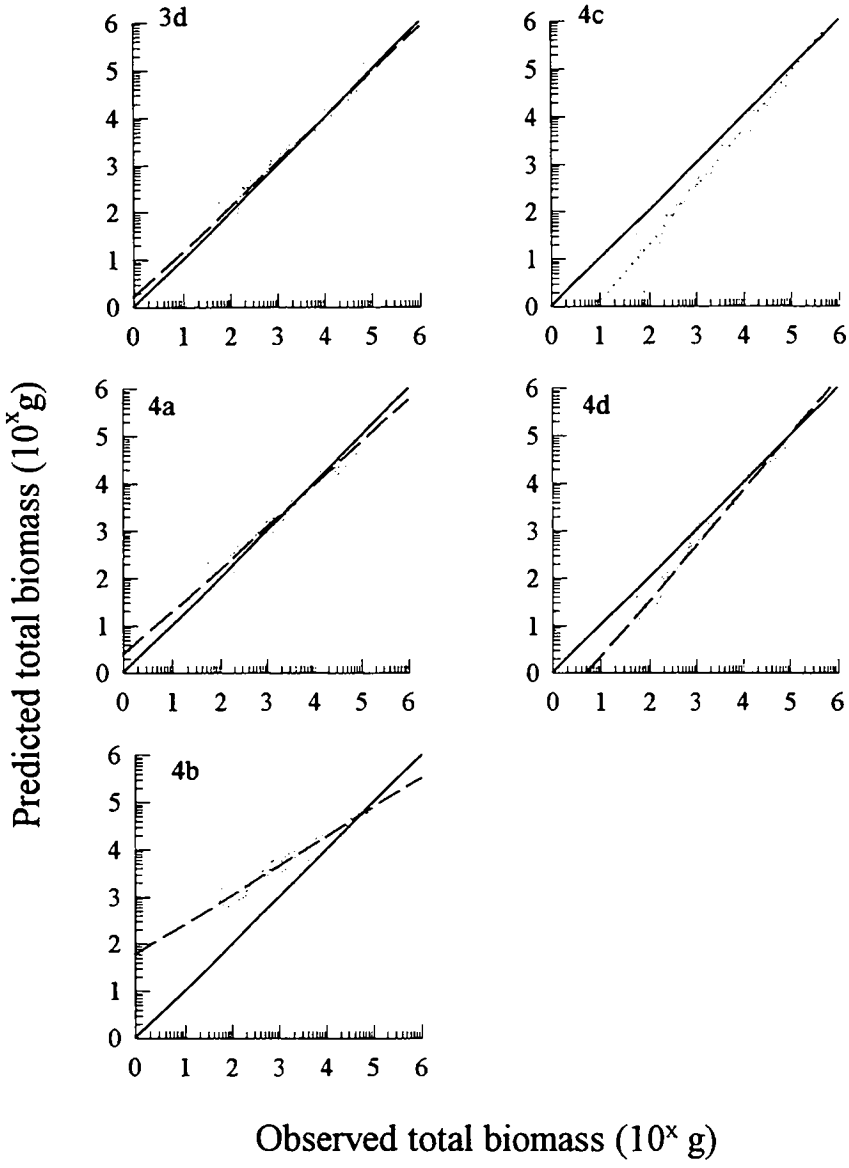


Figure 2.7 continued

2.4.3b Foliage biomass

All regressions of dbh, height and wood density against foliage biomass were significant, however, the regression coefficients of regressions 2a, 3b, 3c and 3d were not significant (Table 2.10). The R^2 values of the foliage biomass regressions were much lower than those for total biomass, ranging from 0.42 to 0.77. The R^2 values of Models 1, 2 and 3 had a similar range, while those of Model 4 were more variable. The coefficients of variation were very high, ranging from 162% to 228%. The range of mean standard errors of estimates was similar for Models 1 to 3, ranging between 37% to 49%. Model 4 had a wider range, varying from -27% to 1430%. There was substantial biasing induced by the logarithmic transformation, from 43% to 51%.

Models 1 and 2 underestimated foliage biomass, by between 13.6% and 17.6%. Estimates for Model 3 varied from a 10.9% underestimate by regression 3b to a 5.8% overestimation by regression 3a. Model 4 showed the greatest variation with estimates varying from a 3.2% overestimate by regression 4b to a 30.4% underestimate by regression 4c.

The regressions for Models 1 to 3 tended to overestimate biomass at small tree sizes and underestimate foliage biomass for the larger trees (Figure 2.8). There was more variation in the regressions of Model 4; where regression 4b showed a similar pattern to the regressions of Models 1 to 3; regression 4a consistently underestimated foliage biomass over a range of tree sizes; and, 4c and 4d showed substantial underestimation at small tree sizes, but this decreased with increasing tree size.

Table 2.10 Foliage biomass regressions for the combined species harvested from the ramp site. a, b_1, b_2 and c are as defined in Table 2.1; R^2 is the coefficient of determination; P(reg) is the significance of the regression; P(con) is the significance of the constant; $P(X_1)$ and $P(X_2)$ are the significance of the coefficients; CF is the correction factor; CV is the coefficient of variation; %SE is the mean percentage standard error; RES is the mean residual; E the standard error of the estimate; and Biomass is the predicted biomass (kg ha^{-1}) determined by the regression for the site. The actual foliage biomass was 3750 kg ha^{-1}.

	Regression model												
	1a	1b	1c	1d	2a	3a	3b	3c	3d	4a	4b	4c	4d
a	34.19	5.67	20.80	25.46	19.03	33.31	6.63	21.89	26.42	14.63	14.39	0.89	1.87
b_1	1.498	2.131	0.563	0.584	1.056	1.236	1.818	0.534	0.554	-	-	-	-
b_2	-	-	-	-	0.667	-	-	-	-	-	-	-	-
c	-	-	-	-	-	0.062	0.054	8.31×10^{-5}	1.76×10^{-5}	-	-	-	-
R^2	0.76	0.73	0.77	0.77	0.76	0.76	0.73	0.77	0.77	0.69	0.42	0.59	0.50
P(reg)	0	0	0	0	0	0	0	0	0	0	0	0	0
P(con)	0	0	0	0	0	0	0	0	0	-	-	-	-
$P(X_1)$	0	0	0	0	0	0	0	0	0	0	0	0	0
$P(X_2)$	-	-	-	-	0.06	0.04	0.34	0.13	0.18	-	-	-	-
CF	1.45	1.51	1.44	1.43	1.44	1.44	1.51	1.43	1.43	-	-	-	-
CV	193	228	202	212	203	170	225	184	204	162	213	180	198
%SE	39.1	48.8	38.2	39.6	38.2	37.0	48.1	37.5	38.4	140.0	-27.0	1430.0	1020.0
RES	280	310	280	300	290	180	290	220	250	90	-20	210	199
E	1350	1600	1410	1480	1420	1190	1570	1280	1430	1130	1490	1250	1380
Biomass	3240	3150	3190	3090	3190	3970	3340	3690	3430	3260	3870	2610	2680

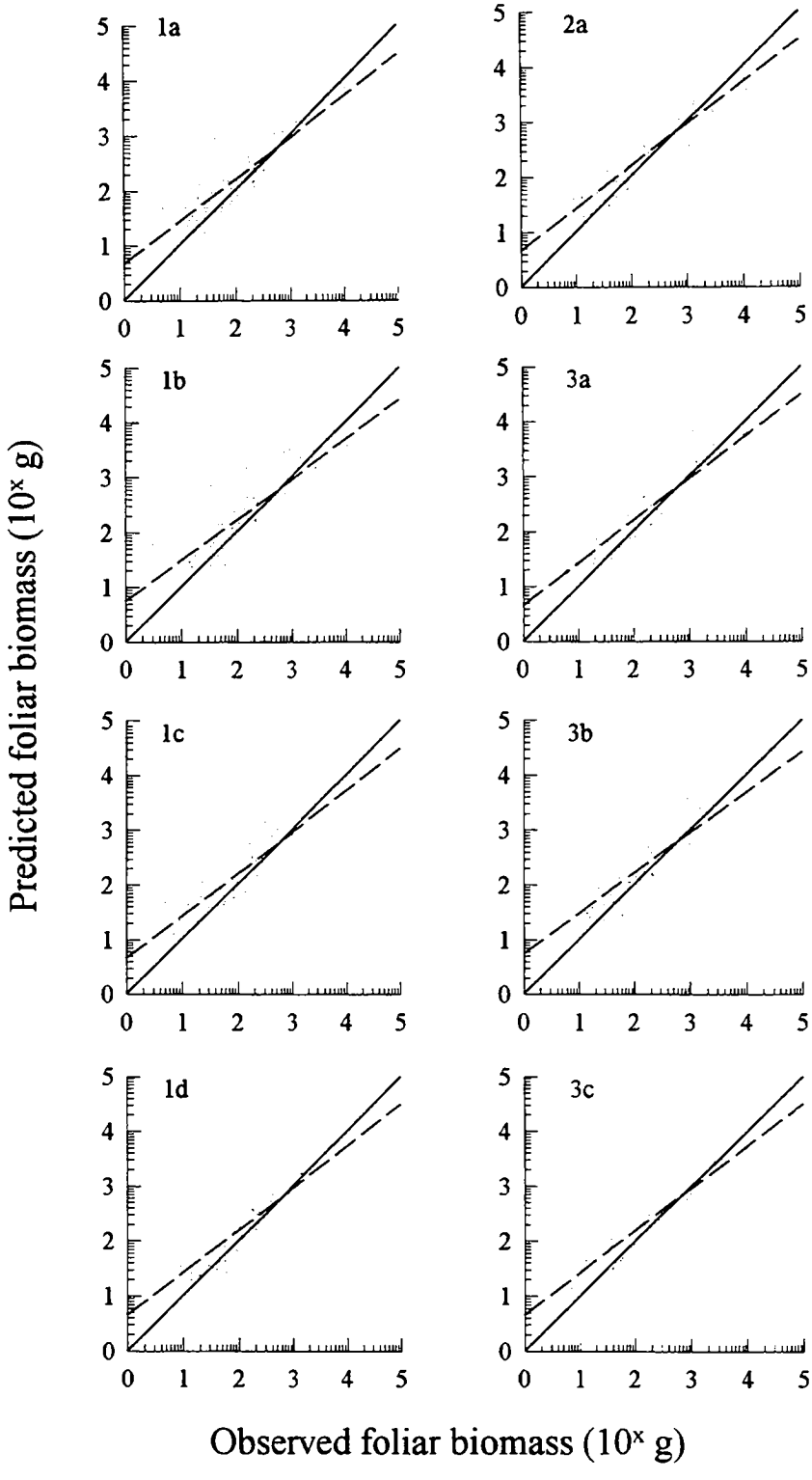


Figure 2.8 Comparison of observed to predicted foliage biomass for individual trees using the allometric regressions described in Table 2.1. The dashed line is the calculated regression line.

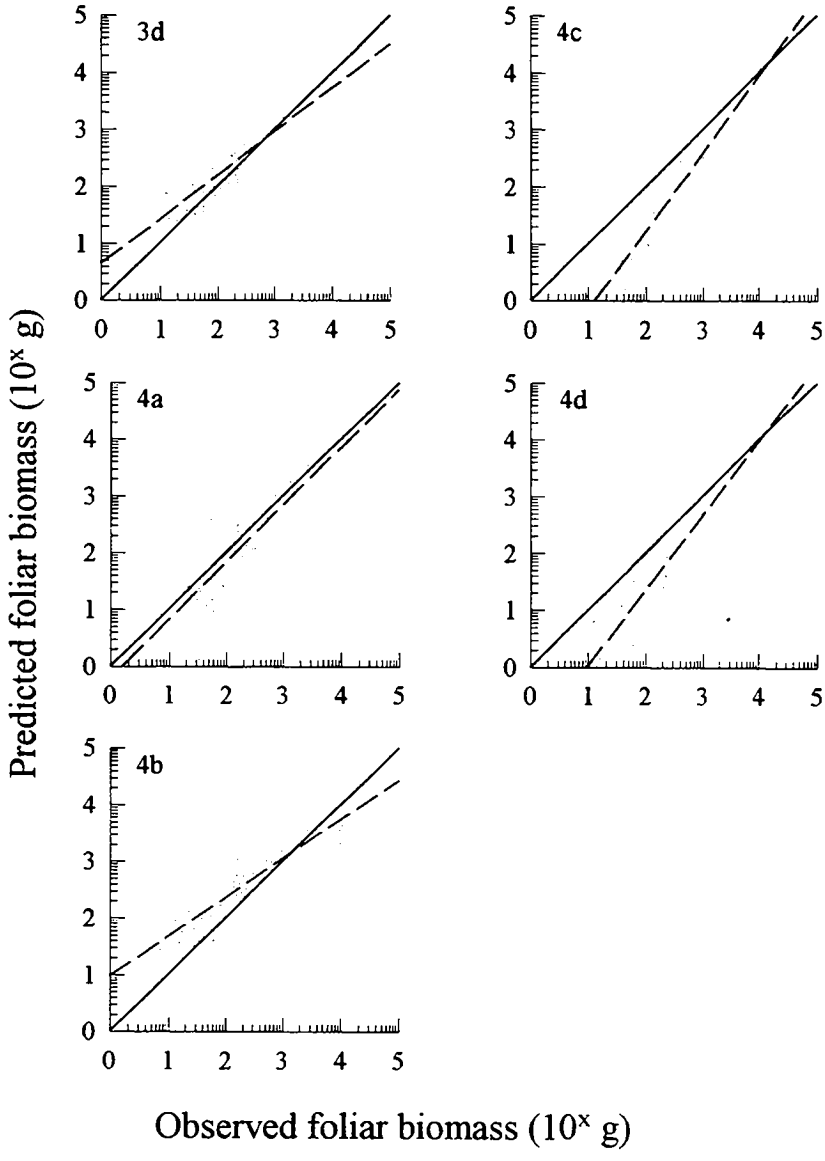


Figure 2.8 continued

2.4.3c Comparison with published biomass regressions

The allometric ratios for the ramp site vegetation were not significantly different from those determined for the Puerto Rican rain forest examined by Ovington and Olson (1970) (Table 2.11), however, the regression coefficients were significantly different. A plot of above-ground biomass to tree diameter using the data of Ovington and Olson (1970) and the ramp site, shows that for a given diameter the Puerto Rican trees have a greater biomass (Figure 2.9a). This was not due to differences in the height of the trees, as the trees at the ramp site were taller for a given diameter (Figure 2.9b).

Table 2.11 Comparison of above-ground biomass regression coefficients using an analysis of covariance, for the ramp site and the Ovington and Olson (1970) data sets. a and b are as defined in Table 2.1, R^2 is the coefficient of determination for the regression and P(b) and P(a) indicate the significance of the allometric ratio and regression coefficient, respectively.

Regression	a	b	R^2	P(b)	P(a)	Data sets
$Y = a(dbh)^b$	210	2.107	0.94	0.65	0.02	Ovington & Olson (1970)
	167	2.078	0.93			This study
$Y = a((dbh)^2*hgt)^b$	102	0.801	0.96	0.54	0.01	Ovington & Olson (1970)
	83	0.786	0.95			This study

The estimates of above-ground biomass at the ramp site, determined using various published biomass regressions, ranged from 47.8 to 110.7 t ha^{-1}, as compared to an actual harvested biomass of approximately 53.7 t ha^{-1} (Table 2.12). The generalised biomass regressions of Brown *et al.* (1989) substantially overestimated biomass, by between 44 and 105%. The biomass regressions determined by Overman *et al.* (1994) showed a similar range of overestimation. The biomass regressions of Martinse-Yrizar *et al.* (1992) gave estimates closest to the ramp site's actual biomass. The biomass regressions determined for the trees greater than 5 cm diameter at the ramp site slightly overestimated biomass, by between 12 and 15%.

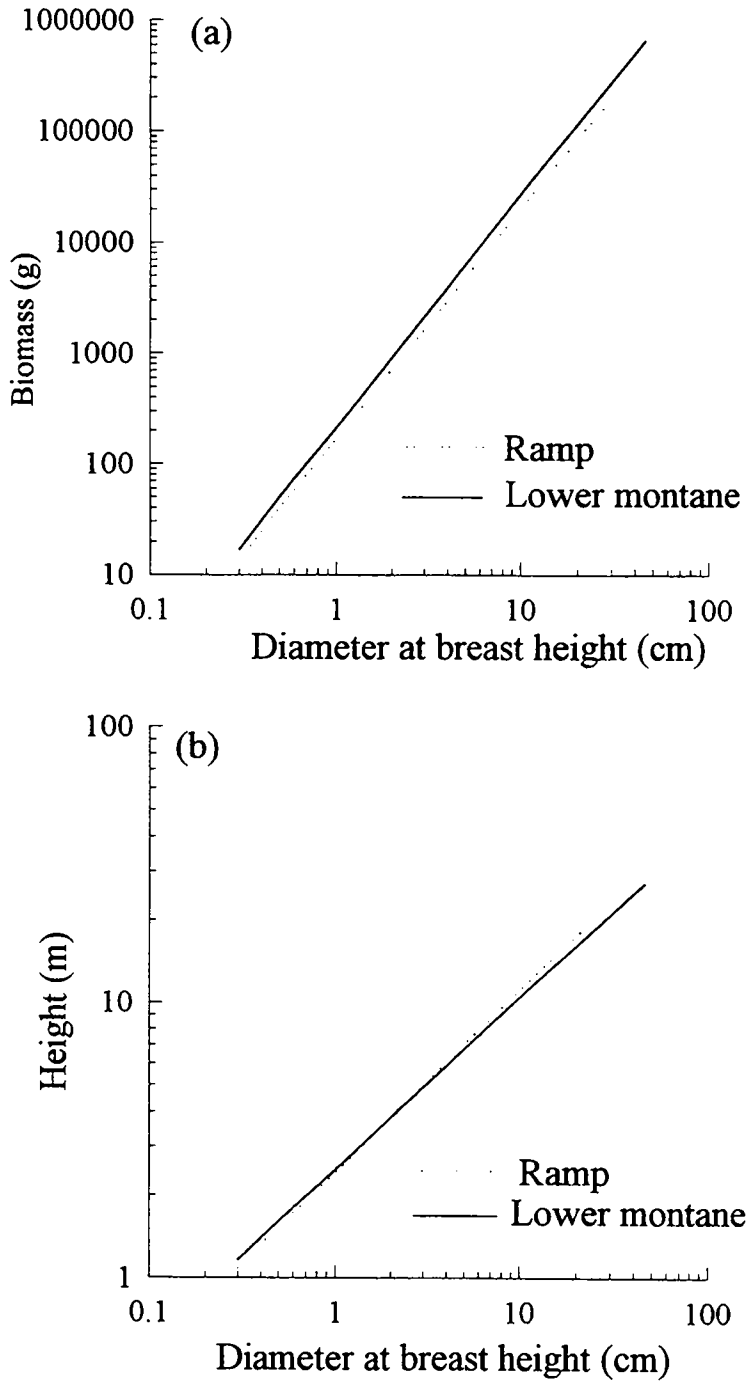


Figure 2.9 A comparison of allometric relationships between trees at the ramp site and the lower montane rain forest site of Ovington and Olson (1970), showing the relationship between (a) diameter at breast height (dbh) and total above-ground biomass, and (b) dbh to tree height.

Most of the biomass regressions, generated from the combined trees harvested in this study, underestimated the biomass in the Puerto Rican Lower Montane Forest of Ovington and Olson (1970), by between 30 and 70% (Table 2.12). These regressions slightly overestimated biomass at small tree size, but substantially underestimated biomass of the large trees (Figure 2.10). Regression 3a overestimated biomass by 70%. The regression based on only those trees greater than 5 cm in diameter gave the best estimates, with estimates being only 13 and 19% lower than the harvested biomass (Table 2.12).

The generalised equations of Brown *et al.* (1989) gave varied estimates (Table 2.12). Equation 1 determined for moist tropical forests overestimated biomass by 55%, while equation 3 for wet tropical forests yielded an estimate approximately 7% greater than the actual harvested biomass. Both of these equations underestimated the biomass of small trees, but overestimated that of large ones (Figure 2.10).

The regressions of Crow (1978), Martinse-Yrizar *et al.* (1992) and Ogawa *et al.* (1965) all underestimated biomass at the ramp site, with estimates being between 10 and 20% lower. The regression of Overman *et al.* (1994) substantially overestimated biomass (Table 2.12).

Table 2.12 A comparison of biomass estimates, using the regressions determined in this study and various published biomass regressions, for the ramp site and the Puerto Rican Lower Montane forest examined by Ovington and Olson (1970). a, b_1, b_2 and c are as defined in Table 2.1.

Model #	Regression	Regression parameters				Estimates (t ha^{-1})		Source
		a	b_1	b_2	c	Ramp	Lower Montane	
1	$Y = a(dbh)^2\ hgt)^{b}_1$	44	0.972	-	-	110.7	452	Brown *et al.* (1989)
2	$Y = a((dbh)^2\ hgt\ WD)^{b}_1$	90	0.952	-	-	94.2	-	
3	$Y = a((dbh)^2\ hgt)^{b}_1$	37	0.944	-	-	76.8	309	
1	$Y = a((dbh)^2)^{b}_1$	291	1.000	-	-	63.5	231	Martinse-Yrizar *et al.* (1992)
2	$Y = a((dbh)^2)^{b}_1 (WD)^{b}_2$	355	0.997	-	-	47.8	-	
3	$Y = a((dbh)^2)^{b}_1 (hgt)^{b}_2 (WD)^{c}$	171	0.901	0.565	0.572	64.6	-	
	$Y = a((dbh)^2\ hgt)^{b}_1$	40	0.933	-	-	68.2	260	Ogawa *et al.* (1965)
1	$Y = a((dbh)^2)^{b}_1$	128	1.256	-	-	110.3	534	Overman *et al.* (1994)
2	$Y = a((dbh)^2\ hgt\ WD)^{b}_1$	56	0.990	-	-	74.6	-	
3	$Y = a((dbh)^2\ WD)^{b}_1$	304	1.229	-	-	94.2	-	
4	$Y = a((dbh)^2\ hgt)^{b}_1$	29	1.002	-	-	85.7	375	
5	$Y = a((dbh)^2)^{b}_1 (WD)^{b}_2$	266	1.239	1.106	-	95.0	-	
	$Y = a((dbh)^2\ hgt)^{b}_1$	27	0.972	-	-	63.5	262	Crow (1978)

Table 2.12 *Continued.*

Model #	Regression	Regression parameters				Estimates (t ha^{-1})		Source
		a	b_1	b_2	c	Ramp	Lower Montane	
1a	$Y = a(dbh)^{b}_{1}$	210	2.107	-	-	70.7	267	From Ovington & Olson
1b	$Y = a(hgt)^{b}_{1}$	15.7	3.094	-	-	84.3	168	(1970) data
1c	$Y = a((dbh)^2\ hgt)^{b}_{1}$	102	0.801	-	-	71.4	230	
2	$Y = a(dbh)^{b}_{1}\ (hgt)^{b}_{2}$	117	1.701	0.649	-	71.4	238	
3a	$Y = a(dbh)^{b}_{1}\ e^{c(dbh)}$	221	1.812	-	0.05	75.8	515	
3b	$Y = a(hgt)^{b}_{1}\ e^{c(hgt)}$	39	1.514	-	0.256	111.7	322	
1a	$Y = a(dbh)^{b}_{1}$	167	2.078	-	-	53.9	200	This study (all trees)
1b	$Y = a(hgt)^{b}_{1}$	12.5	3.027	-	-	47.8	97	
1c	$Y = a((dbh)^2\ hgt)^{b}_{1}$	83	0.786	-	-	51.4	157	
2	$Y = a(dbh)^{b}_{1}\ (hgt)^{b}_{2}$	35	1.77	0.906	-	48.9	178	
3a	$Y = a(dbh)^{b}_{1}\ e^{c(dbh)}$	164	1.892	-	0.044	66.0	431	
3b	$Y = a(hgt)^{b}_{1}\ e^{c(hgt)}$	17	2.397	-	0.109	57.1	129	
1a	$Y = a(dbh)^{b}_{1}$	142	2.199	-	-	60.3	252	This study (trees greater than
1c	$Y = a((dbh)^2\ hgt)^{b}_{1}$	36	0.916	-	-	61.4	235	5 cm dbh)
		Biomass harvested				53.7	289	

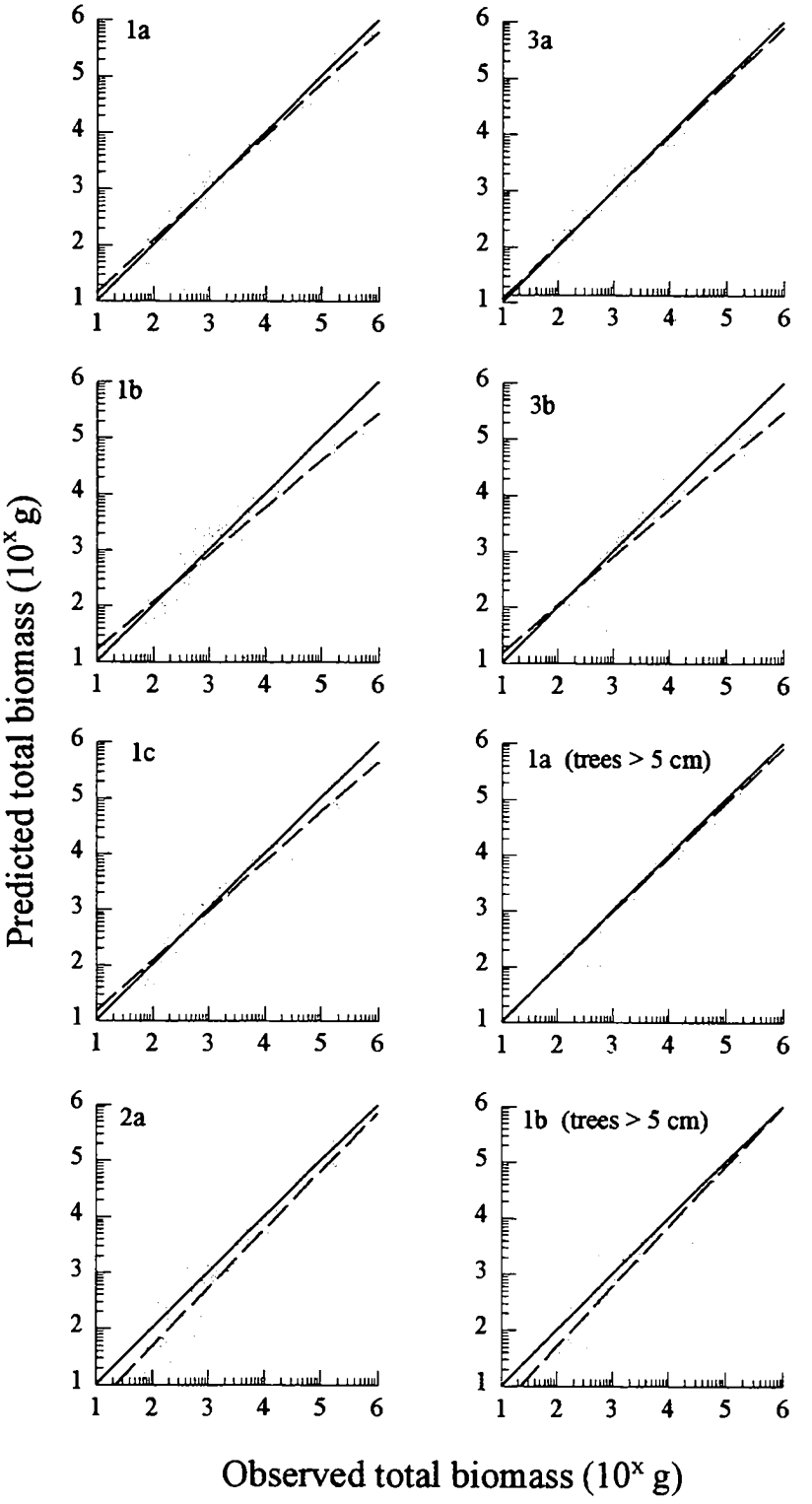


Figure 2.10 Comparison of observed to predicted biomass for individual trees from Ovington and Olson's (1970) study using the biomass regressions described in Table 2.14. The dashed line is the calculated regression line.

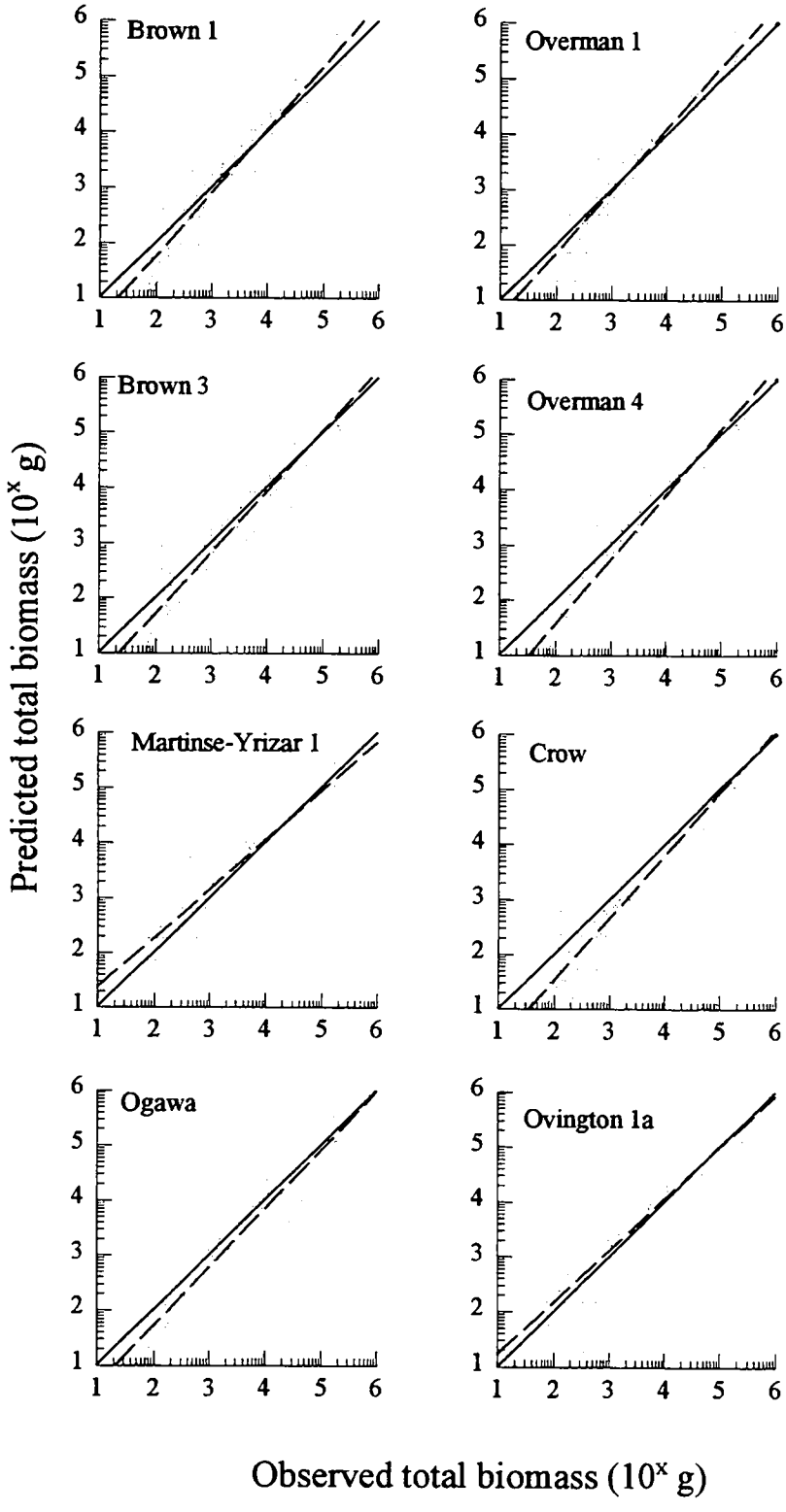


Figure 2.10 continued

2.5 Discussion

2.5.1 Biomass

The above-ground biomass of the ramp site is amongst the lowest published values for similar aged secondary rain forests, with most 20-year-old sites having between 61.5 and 147.6 t ha^{-1} (Table 2.13). The data presented in Table 2.13 covers a range of rain forest types subject to different environmental conditions, but most show a rapid accumulation of biomass, with 50 t ha^{-1} produced within 4 to 14 years. The total basal area, maximum tree height and stem density of the ramp site were also substantially lower than those found for another disturbed site within 500 m of the ramp site (plot 2, Congdon & Herbohn 1993).

Previous studies of biomass accumulation in secondary rain forest have concentrated on sites recolonised after shifting cultivation or other disturbances of similar intensity (Tables 2.13). These disturbances are generally of moderate severity, because whilst the original vegetation is removed, the topsoil is usually not degraded (Jordan 1985). Conversely, the construction of the loading ramp involved the removal of the vegetation, and some removal, disturbance and compaction of the topsoil. A 45% greater soil bulk density was still evident 25 years after logging at the ramp site compared to the surrounding undisturbed forest (Maycock & Congdon 1992). This compaction was caused by the heavy machinery used in selective logging operations to extract and transport the logs (Malmer & Grip 1990, Queensland Department of Forestry 1981).

The disturbance and compaction of the soil at the ramp site caused changes in soil physical properties that may reduce a plant's ability to recolonise the site, restrict the air supply to plant roots causing a build-up of toxic products, make plants more susceptible to waterlogging, and limit the uptake of nutrients. These

changes include increases in the mechanical resistance to penetration of the soil, decreases in air-filled porosity, and decreases in soil permeability (Landon 1984). The effects of soil compaction have been found to decrease the chance of successful tree establishment and to reduce growth rates by up to 30% (Calais & Kirkpatrick 1983, Gayoso & Iroumé 1991, Wert & Thomas 1981). These changes can limit nutrient uptake by plants in a number of ways. Firstly, increases in mechanical resistance have been found to inhibit root elongation, thus reducing the volume of soil available to the plants for nutrient uptake (Bennie 1992, Grant 1993). Secondly, a decrease in the air-filled porosity reduces the rates of diffusion of oxygen through the soil profile, limiting respiration associated with root growth and nutrient uptake (Grant 1993). Finally, decreases in soil permeability reduce the rate of mass flow and nutrient diffusion within the soil (Jungk 1992). Fine roots take up water and nutrients from the rhizosphere, creating localized gradients in soil water potential and nutrient concentration in the ambient solution. These localized depletions are replenished by the movement of water and nutrients across these gradients by mass flow and diffusion (Jungk 1992).

As well as soil compaction, the removal of the topsoil during the construction and operation of the loading ramp could have influenced seedling establishment and growth rates. Mechanical timber extraction has been found to cause some losses of organic carbon and plant nutrients (Gillman *et al.* 1985). Kjeldahl N, available P and cation exchange capacity were all found to be lower at the ramp site compared to a tree-fall gap (Congdon & Herbohn 1993). This decreased nutrient availability may have contributed to a suppression of growth rates and a decrease in seedling survivorship.

Table 2.13 Above-ground biomass and basal area recorded for secondary rain forests and some nearby undisturbed rain forests. Above-ground biomass for plot 2 of Congdon and Herbohn (1993) was calculated using biomass regression 1a.

Location	Forest type	Rainfall (mm)	Latitude	Age (yr)	Biomass (t ha^{-1})	Basal area (m^2 ha^{-1})	Source
Australia	Wet tropical	2630	19°S	24	53.7	17.5	This study
				24	120	43.1	Congdon & Herbohn (1993)
				Undisturbed	-	92.2	
				Undisturbed	-	121.3	
Colombia	Wet tropical	~4000	2°N	2	15.8	-	Golley *et al.*(1976)
				4	49.4	-	
	Moist tropical	3500	2°N	12	81.8	17.3	Saldarriaga *et al.* (1988)
				20	97.6	18.7	
				35	108	20.1	
				40	159	23	
				60	197	31	
				60	138	24.7	
				80	134	22.3	
				Undisturbed	271	37	
India	Moist sub-tropical	2200	26°N	1	5.0	-	Toky & Ramakrishnan (1983)
				5	23.3	-	
				10	57.5	-	
				15	103.7	-	
				20	147.6	-	
Mexico	Wet Tropical	3640	17°N	0.8	4.7	-	Williams-Linera (1983)
				7	43.5	-	
Panama	Moist tropical	~2000	2°N	2	13	-	Ewel (1971)
				4	38	-	
				6	42.8	-	

Table 2.13 *continued.*

Location	Forest type	Rainfall (mm)	Latitude	Age (y)	Biomass (t ha^{-1})	Basal area (m^2 ha^{-1})	Source
Venezuela	Moist tropical	~3500	2°N	1	7.1	0.5	Uhl (1987)
				2	12.8	1.8	
				3	20	4	
				4	28.6	5.7	
				5	33.9	7	
	Moist tropical	~3500	2°N	9	43.9	11.2	Saldarriaga *et al.* (1988)
				11	52.9	11.5	
				14	53.4	11.1	
				20	83.3	17.5	
				20	61.5	14.5	
				20	63.8	17.1	
				30	53.8	11.7	
				35	109	19.6	
				60	116	17.7	
				80	178	26.4	
				80	144	23.9	
				80	142	23.2	
				Undisturbed	262	35.6	

Regeneration following slashing-and-burning of rain forest occurs from germination, from the existing seed banks and seeds transported to the area, and by vegetative propagation from the remains of the original vegetation (Stocker 1981). Removal of the topsoil by ramp construction would cause a reduction/removal of the existing seed bank, causing regeneration to be more dependent on the transportation of seeds to the area. Regeneration from seeds is limited by low seed production in most years, a high level of consumption by animals, and a limited period of seed viability (Stocker 1981). The abundance of *Cardwellia sublimis, Darlingia darlingiana* and *Alphitonia petriei* at the ramp site is possibly related to *C. sublimis* and *D. darlingiana* possessing wind-dispersed seeds and having possible seed trees nearby in the surrounding undisturbed forest, while *A. petriei* produce large quantities of seeds that are viable for extended periods and readily dispersed by birds.

2.5.2 Nutrients

There are limited data on nutrient concentrations and distribution within Australian tropical rain forests (Beadle & White 1968, Grubb 1977). Mean foliage nutrient concentrations have been reported for an Australian montane primary rain forest, also on soils derived from granite (Grubb 1977). The montane vegetation had lower foliage nitrogen, phosphorus, potassium and calcium concentrations than that of the secondary vegetation of the ramp site, while foliage magnesium was higher for the montane rain forest (Table 2.14). The phosphorus to nitrogen and potassium to nitrogen ratios for the montane forest were similar to the values for the ramp site (Table 2.14). The differences in mean foliage nutrient concentrations between the sites could be due to the different species composition or differences in the soil fertility.

Table 2.14 Mean foliage nutrient concentrations and ratios for Australian rain forests.

Forest type	No. of species	Concentrations (mg g^{-1})					Ratios		Source
		N	P	K	Ca	Mg	P:N	K:N	
Tropical									
- undisturbed	26	11.1	0.5	6.2	6.5	3.6	0.043	0.56	Grubb (1977)
- disturbed	23	17.7	0.7	9.7	7.1	2.6	0.040	0.55	This study
Sub-tropical									
- undisturbed	45	17.2	1.0	10.2	9.6	3.8	0.059	0.59	Lambert &
- disturbed	14	33.2	1.7	19.6	11.5	3.8	0.051	0.59	Turner (1986)

There is considerable variation in foliage nutrient concentrations within different species (Golley *et al.* 1980a,b, Grubb & Edwards 1982, Jordan 1977, Lambert & Turner 1986, Ovington & Olson 1970). These variations reflect differences in nutrient uptake and use-efficiencies, and storage strategies between the species. At the ramp site the lowest foliage nutrient concentrations were found in the late secondary species, *D. darlingiana* and *C. sublimis,* and the highest in the pioneer species (Figure 2.3). Bazzaz (1991) also found higher foliage nutrient contents, and higher uptake rates and faster foliage turnover in pioneer species.

Differences in soil fertility are known to cause variations in the mean nutrient concentrations of individual tissues (Vitousek & Sanford 1986). The mean foliage nutrient concentrations reported for a disturbed sub-tropical rain forest, on soils derived from basalt, were greater than those found in this study (Lambert & Turner 1986). Foliage nitrogen, phosphorus and potassium were approximately twice the concentrations found in this study (Table 2.14). These differences are probably, at least in part, due to differences in the soils at the two study sites. In Lambert and Turner's (1986) study, the soil was a deep, well-structured red clay loam kraznozem. The soil was relatively fertile, with total nitrogen and phosphorus concentrations of 0.89% and 1360 μg g^{-1}, respectively.

In contrast, the soil at Mt Spec is a red earth, derived from granitic parent material (Isbell *et al* 1968). The soil was highly acidic and relatively infertile, with total nitrogen and phosphorus concentrations of 0.31% and 126 $\mu g\ g^{-1}$, respectively (Congdon & Herbohn 1993).

Within a single species, variations in site soil fertility usually result in only slight differences in nutrient concentrations (Vitousek & Sanford 1986). Unfortunately due to the species richness of tropical forests and few studies examining foliage nutrient concentrations, little comparable data exists for Australian rain forests. Three species were common to this study and Lambert and Turner's (1986) study, these being *Acacia melanoxylon, Alangium villosum* and *Synoum glandulosum*. This allows for a limited comparison of the influence of differences in soil fertility on foliage nutrient concentrations (Table 2.15). Foliage nitrogen concentrations were similar in both studies, despite the large differences in soil total nitrogen concentration. Foliage phosphorus concentrations were at least 50% higher on the basaltic soil, reflecting the higher concentrations of available phosphorus in this soil type. The trends for potassium, calcium and magnesium are less clear, with some species showing higher foliage nutrient concentrations on the basaltic soils and others similar or lower concentrations. This lack of clear trends for these elements could be due to problems associated with foliage nutrient analysis. While foliage nutrient analysis can be a good indicator of the nutrient status of a tree, it is influenced by leaf age, shading and position in the crown (Drechsel & Zech 1991, Grubb 1977, van den Driessche 1974). These variables cause difficulties in diagnostic foliage nutrient analysis, particularly for very mobile elements and when there is an interaction between elements (Grubb 1977).

Table 2.15 Comparison of foliage nutrient concentrations in species common to the granitic soils of this study and the basaltic soils of Lambert and Turner (1986).

Species	Concentrations (mg g^{-1})					Source
	N	P	K	Ca	Mg	
Acacia melanoxylon	25.0	1.5	1.2	3.1	1.9	Lambert & Turner (1986)
	27.2	0.8	7.6	6.4	2.0	This study
Allangium villosum	30.5	1.6	7.7	13.3	7.0	Lambert & Turner (1986)
	30.5	1.0	18.7	20.9	3.2	This study
Synoum glandulosum	15.9	1.1	10.5	10.8	4.1	Lambert & Turner (1986)
	16.7	0.7	9.2	10.4	6.2	This study

In this study, the mean foliage nutrient content of *Alphitonia petriei* was found to decrease with increasing foliage biomass (Figure 2.4). This trend could possibly represent changes in nutrient-use efficiencies or increases in proportions of structural materials with increasing tree size. However, this trend was not evident in the late secondary species *Darlingia darlingiana* (Figure 2.5), and no other species harvested from the ramp site possessed enough individuals, or covered a wide enough range of sizes to allow for further investigation. Willams-Linera (1983) found that foliage nutrient concentrations were roughly two times higher in ten-month-old stands of secondary vegetation compared to seven-year-old stands. In contrast, Grubb and Edwards (1982) found no significant differences in the concentrations of nutrients between the leaves of large trees, small trees, saplings and seedlings of the same species, in a primary montane rain forest in New Guinea.

Nutrient concentrations in other plant components have not been analysed as often as in leaves, so comparisons between sites and species is difficult (Vitousek & Sanford 1986). While some studies have found a significant correlation between foliage nutrient concentrations and concentrations in the other components (Tanner 1977), other studies have found that they are not

always correlated (Grubb & Edwards 1982). This study found that high concentrations of nutrients in foliage were generally associated with high concentrations in other parts of the tree (Figure 2.3).

Nitrogen, phosphorus and magnesium concentrations were greater in bole samples taken from the top, rather than from the base of *Alphitonia* (Table 2.8). These differences in concentrations are probably the result of changing proportions of bark, young wood and old wood within the sample (Grubb & Edwards 1982). These vertical variations were not evident for potassium and calcium.

A rapid accumulation of nutrients has been found within secondary vegetation recolonizing sites after shifting cultivation (Fölster *et al.* 1976, Saldarriaga 1986, Toky & Ramakrishnan 1983, Willams-Linera 1983). These studies also found a rapid accumulation of biomass, with up to 100 t ha^{-1} being accumulated within the first 15 years. This was not the case at the ramp site, where the total nutrient standing stocks in the vegetation were low (Table 2.5). These low nutrient standing stocks are partly a result of the reduced rate of regeneration at the ramp site, with only 53.7 t ha^{-1} of above-ground biomass being accumulated in the first 25 years (Table 2.3).

As well as having low total nutrient standing stocks, the ramp site had substantially lower nitrogen, phosphorus and calcium contents, per tonne of biomass, compared to other published studies (Table 2.16). Nitrogen and phosphorus contents were approximately 110% and 370% greater, at a site examined by Williams-Linera (1983). The total above-ground biomass for this site was similar to the ramp site, being approximately 43.5 t ha^{-1}, as compared to 53.7 t ha^{-1} at the ramp site. These differences in nutrient content do not

appear to be due to differences in soil nutrient status, as both soil Kjeldahl nitrogen levels and available phosphorus were greater at the ramp site (Table 2.16). Other possible explanations for the reduced nutrient content per tonne of biomass at the ramp site are that there are differences in uptake and use-efficiencies, and storage strategies, between the species at the ramp site and the other studies; and the uptake of nutrients by the plants at the ramp site was limited by the severe soil disturbance and compaction.

2.5.3 Allometry

From the regression analysis, above-ground biomass was found to be closely correlated with dbh and height, which suggests that biomass can be confidently estimated from these measurements at other sites with similar species composition and growth conditions. The equations utilising both dbh and tree height yielded better estimates than the equations using dbh or tree height alone. The accuracy of the regression was improved by incorporating these two variables as two separate independent variables, rather than combined as a single variable. However, while the inclusion of tree height data can increase the precision and accuracy of the biomass estimates, the accuracy of these measurements is critical (Cunia 1987). Errors in height estimates can cause a significant loss in accuracy of the regressions (Brown *et al.* 1989). Surprisingly, the inclusion of wood density in the regression equations did not significantly improve the estimation of biomass.

Table 2.16 Above-ground biomass, mean nutrient content per tonne of biomass, soil Kjeldahl nitrogen and available phosphorus for secondary rain forests. Mean nutrient content = total above-ground nutrient standing stock / above-ground biomass.

Location	Age	Biomass	Biomass nutrient content					Soil nutrient content		Source
	(y)	(t ha^{-1})	N	P	K ($kg\ t^{-1}$)	Ca	Mg	Kjeldahl - N (%)	Available - P ($\mu g\ g^{-1}$)	
Australia	24	53.7	2.9	0.14	3.2	2.4	1.0	0.34	10.7	This study
Mexico	0.8	4.7	15	1.07	42.0	9.2	3.8	0.17	2.5	Williams-Linera (1983)
	7	43.5	6.2	0.66	7.9	4.3	1.1	0.20	5.8	
Ghana	50	217	5.9	0.39	3.0	7.2	1.0	0.20	8.4	Greenland & Kowal (1960)
Zaire	18	122	3.6	0.54	3.2	-	-	-	-	Bartholomew *et al.* (1953)

Logarithmic transformations are commonly employed in determining biomass regressions. These transformations are necessary, as the biomass data often has increasing conditional variance with increasing tree size (Brown *et al.* 1989, Gillespie & Cunia 1989, Smith 1980). This heteroscedasticity in the biomass data was found to occur at the ramp site, justifying the use of the transformations. Logarithmic transformations have been found to induce a bias, when the data are converted back into untransformed units (Baskerville 1972, Beauchamp & Olson 1973). The importance of determining correction factors for this bias has been discussed by a number of authors (Baskerville 1972, Brown *et al.* 1989, Ruark *et al.* 1987), however, they are often neglected. The bias induced by the transformation was found to vary between components and regressions in this study. The degree of bias varied from 11% to 51%, highlighting the importance of determining correction factors for these regressions.

In this study the inclusion of the variable allometric ratio in the regressions did not improve the accuracy of the total above-ground biomass regressions. However, the foliage biomass regression, using dbh only, was found to show slight improvement. Previous studies have found that the inclusion of the allometric ratio into the model can statistically improve the prediction of biomass, particularly for foliage biomass estimates (Geron & Ruark 1988, Ruark *et al.* 1987). These studies found that the variable allometric model allowed for initially large allometric ratios that declined linearly with increasing stem diameter, however, none of the regressions determined for the ramp site exhibited this trend. The previous studies examined a wider range of diameters than were found at the ramp site.

2.5.4 Comparison with published biomass regressions

Few studies have compared biomass regressions for tropical rainforests. Crow (1978) compared regressions for the lower montane forest examined by Ovington and Olson (1970) with the data of Ogawa *et al.* (1965) for a Thailand forest. Using an analysis of covariance on logarithmically transformed data, he found that there was no significant difference between the stem biomass and branch biomass regressions for the two sites. The comparison, however, was based on a select subsample of the trees harvested and excluded tree species which showed any substantial difference in tree architecture.

The differences, found in the present study, between the regressions for the ramp site and the lower montane forest were probably not due to differences in tree height, as the ramp site trees were taller for a given dbh. This difference in stem allometry could be related to the successional status of the vegetation. The ramp site was dominated by early secondary species. These species have been found to have thinner stems than late successional species for a given height (Claussen & Maycock 1995).

The differences between regressions could also be due to either variations in wood densities or differences in tree architecture and branching patterns. Previous studies have shown that wood densities vary considerably between species, with pioneer species tending to have lower wood densities than primary or secondary species (Wiemann & Williamson 1989), as was also found in this study.

Few of the published biomass regressions examined were found to be suitable for estimating biomass at the ramp site, as most were found to overestimate biomass. The exception to this was the regression of Martinse-Yrizar *et al.*

(1992), which were derived for a tropical deciduous forest in Jalisco, Mexico.

Whether the regressions determined in this study may also be applicable to a broader range of sites is uncertain. Overman *et al.* (1994) found that regression equations for 17-year-old successional and mature Amazon forests were not significantly different, and that the inclusion of large trees (dbh >45 cm) was not necessary to improve the accuracy of the regressions. All of the regressions determined in the present study were found to substantially underestimate the biomass using Ovington and Olson's (1970) dataset. However, few of the published biomass regressions were found to give accurate estimates for their site. The closest estimates obtained from the ramp site regressions, were based only on trees greater than 5 cm diameter, which were found to give a better estimate for the larger trees (Figure 2.10).

Selection of the "best" model for estimation of biomass at other sites is dependant on what data is available for that site, and the quality of the data. Regressions incorporating the greatest number of variables are the most appropriate, as these can allow for changes in diameter : tree height relations and wood densities between and within species. Regression 1d is the most appropriate of the regressions incorporating all three variables. It is unlikely, however, that wood density data will be available for many sites. Regressions 1c and 2a are the best of the two variable regressions, with little difference between them. However, as the accuracy of tree height data can be very variable, these regressions should only be used when the collection of the height data fulfils the recommendations of Romesburg and Mohai (1990).

How accurately, either the regressions determined in this study, or previously published regressions, would estimate biomass at other sites in north

Queensland is unknown. While it is relatively easy, in ecosystems with low biodiversity, to test and calibrate a biomass regression generated at one site and applied to another using the selective harvest technique as outlined by Campbell *et al.* (1985), the high species diversity, variations in tree architectures and wood densities in tropical forests reduces the effectiveness of this technique.

In conclusion, while the regressions determined in this study may be applied to other sites in north Queensland, the estimates obtained must be viewed with caution, as differences in species composition, tree architecture and stem allometry may result in significant errors in biomass estimates. However, this is a feature common to all biomass regressions, not just the regressions determined in this study. The inclusion of the Mt Spec State Forest into the Wet Tropics World Heritage Area means that it is not possible to either test the accuracy of these regressions or to expand the dataset to include a greater variety of species or a greater range of tree sizes. Opportunities to test the biomass regressions generated in this study are limited, as most of Australia's tropical rain forest is now protected in the World Heritage Area. However, opportunities will arise when newly planted plantations of rainforest trees are harvested.

CHAPTER 3
Fine root dynamics and soil fertility

3.1 Introduction

The nutrient status of the soil is seen as a major factor influencing the productivity of north Queensland rain forests (Gillman 1976, Webb 1969). Phosphorus is suspected of being the major nutrient limiting the productivity of rain forests growing on soils of low fertility (Gillman *et al.* 1985). Plant-available phosphorus is a relatively small proportion of the total soil phosphorus (Saker 1994). The majority of phosphorus exists in the soil in a variety of organic and inorganic forms which are unavailable to plants (Dalal 1977, Tate 1985). The quantity of available phosphorus in rain forest soils is dependent upon the total level of soil phosphorus, the rate of chemical breakdown of the insoluble inorganic phosphorus complexes, and the rate of mineralisation of organic phosphorus compounds (Tarafdar & Claassen 1988). Levels of total soil phosphorus are, in part, determined by the type of soil parent material (Murtha 1986). In general, soils derived from basaltic parent material are the most fertile, while granite-derived soils are considered to be relatively infertile (Congdon & Herbohn 1993, Spain 1990).

Previous studies in north Queensland have shown that litterfall rates are lower on phosphorus-poor granite-derived soils, than on phosphorus-rich basaltic soils (Brasell *et al.* 1980, Herbohn & Congdon 1993, Spain 1984). However, in a review of nutrient cycling in tropical rain forests, Vitousek and Sanford (1986) found that total above-ground biomass did not vary greatly among sites of different fertility, with the exception of forests occurring on extremely infertile white-sand soils. Differences in soil fertility were more likely to be reflected in nutrient concentrations in individual tissues and fine root biomass (Vitousek & Sanford 1986).

Roots are the primary means of nutrient acquisition by plants and hence have an important role in determining the productivity of forests. The development of an extensive surface root mat is one of the major mechanisms that enhances nutrient conservation in tropical rain forests, particularly those growing on nutrient-poor, heavily leached soils (Cuevas & Medina 1988, Jordan 1985). In these root mats, it is the fine unsuberised roots that are primarily responsible for the uptake of nutrients (Berish & Ewel 1988, Edwards & Grubb 1982, Gower 1987). Uptake is either by direct absorption, or by mycorrhizal association (Berish & Ewel 1988, Went & Stark 1968).

The level of development of fine root mats in tropical rain forests is highly variable, with the biomass of roots less than 5 mm diameter in the top 40 cm of soil ranging from 1.1 t ha^{-1} to 123.4 t ha^{-1} (Gower 1987, Sanford 1985). According to the source-sink theory of resource allocation, based on theorem three of Bloom *et al.* (1985), trees growing on infertile sites should allocate a greater proportion of their resources into fine root production, than those growing on fertile sites, as this "investment" in nutrient acquisition should increase growth and/or reproduction. Vitousek and Sanford (1986) found that the available data suggested that the biomass of functionally active roots is substantially greater on infertile sites. Soil nitrogen has been suggested as the major factor governing below-ground carbon allocation in temperate forest ecosystems (Aber *et al.* 1985, Grier *et al.* 1981, Nadelhoffer *et al.* 1985). However, there is conflicting evidence for the role that nitrogen plays in influencing fine root biomass in tropical rain forests. A nutrient amendment study in a tropical montane forest in Hawaii found that nitrogen addition resulted in a significant reduction in fine root biomass (Gower & Vitousek 1989). In contrast, the availability of nitrogen was not a significant factor influencing fine root biomass at two sites in Panama (Gower 1987). At these sites, the availability of phosphorus and calcium were shown to be the major factors influencing fine root biomass (Gower 1987).

Contrary to the theorem of Bloom *et al.* (1985), others have suggested that the lower below-ground biomass occurring on more fertile sites may be explained by greater rates of fine root turnover (Chapin 1980, Grime 1977). This is supported by work in temperate forests, which has found greater rates of fine root production and turnover on fertile sites than on infertile sites, despite higher fine root biomass on the poorer sites (Nadelhoffer *et al.* 1985).

Most studies of root systems in tropical rain forests have, to date, concentrated on root biomass (Edwards & Grubb 1982, Greenland & Kowal 1960, Klinge 1973a, 1973b, 1975, Klinge & Rodrigues 1974), with only recent studies starting to examine fine root productivity (Cavelier 1989, Cuevas & Medina 1988, Green 1992, Pendry 1994, Sanford 1985). Worldwide, little is known about production and turnover of fine roots (Santantonio & Grace 1987). This is in part due to root systems being notoriously difficult to sample, and that there are no methods to assess production without causing disturbance to the system (Hendricks *et al.* 1993, Sanford 1989).

This study examines fine root dynamics and resource allocation in north Queensland wet tropical rain forests. The aims of this Chapter are to:

1. investigate the relationship between fine root biomass and soil nitrogen and available phosphorus concentrations at a number of sites in north Queensland;
2. examine fine root dynamics at three sites on soils of different origins, and relate fine root dynamics to variations in soil fertility and nutrient stocks within the soils; and
3. estimate above-ground biomass at these three sites, utilising the biomass regressions determined in the preceding Chapter, to examine allocation of biomass between the shoot and fine root systems of these forests.

3.2 Site description

An initial survey to examine the relationship between fine root biomass and soil nitrogen and available phosphorus concentrations was conducted at six sites in north Queensland (Figure 3.1). The scope of the survey was restricted to 6 sites because of the time required to process the (120) samples. To ensure a range of soil fertilities, sites with soil from three different origins, alluvium, basalt and granite, were sampled. Two sampling sites were selected on each soil origin (Table 3.1). All sites were selected to fall within similar rainfall isohyets (1500 - 2500 mm y^{-1}) to minimise variations in fine root biomass due to differences in rainfall (Tracey 1982). Hence the wetter forests between Tully and Mossman were excluded from the survey.

Table 3.1 Location, altitude, rain forest structural type and soil origin for the study sites. Rain forest structural types are from Webb (1978).

Site	Location	Altitude (m)	Rain forest structural type	Soil origin
Broadwater	18° 25′ S 145° 57′ E	50	MFPVF	Alluvial
Mc Ivor River	15° 05′ S 145° 04′ E	90	CMVF (Type 1c)	Alluvial
Mt Fox	18° 51′ S 145° 30′ E	813	CNVF	Basalt
Mt Webb	15° 04′ S 145° 08′ E	120	CNVF (Type 5b)	Basic Volcanic
Kirrama	18° 11′ S 145° 44′ E	600	SNVF + *Agathis* emergents	Granite
Mt Spec	19° 00′ S 146° 10′ E	880	SNVF	Granite

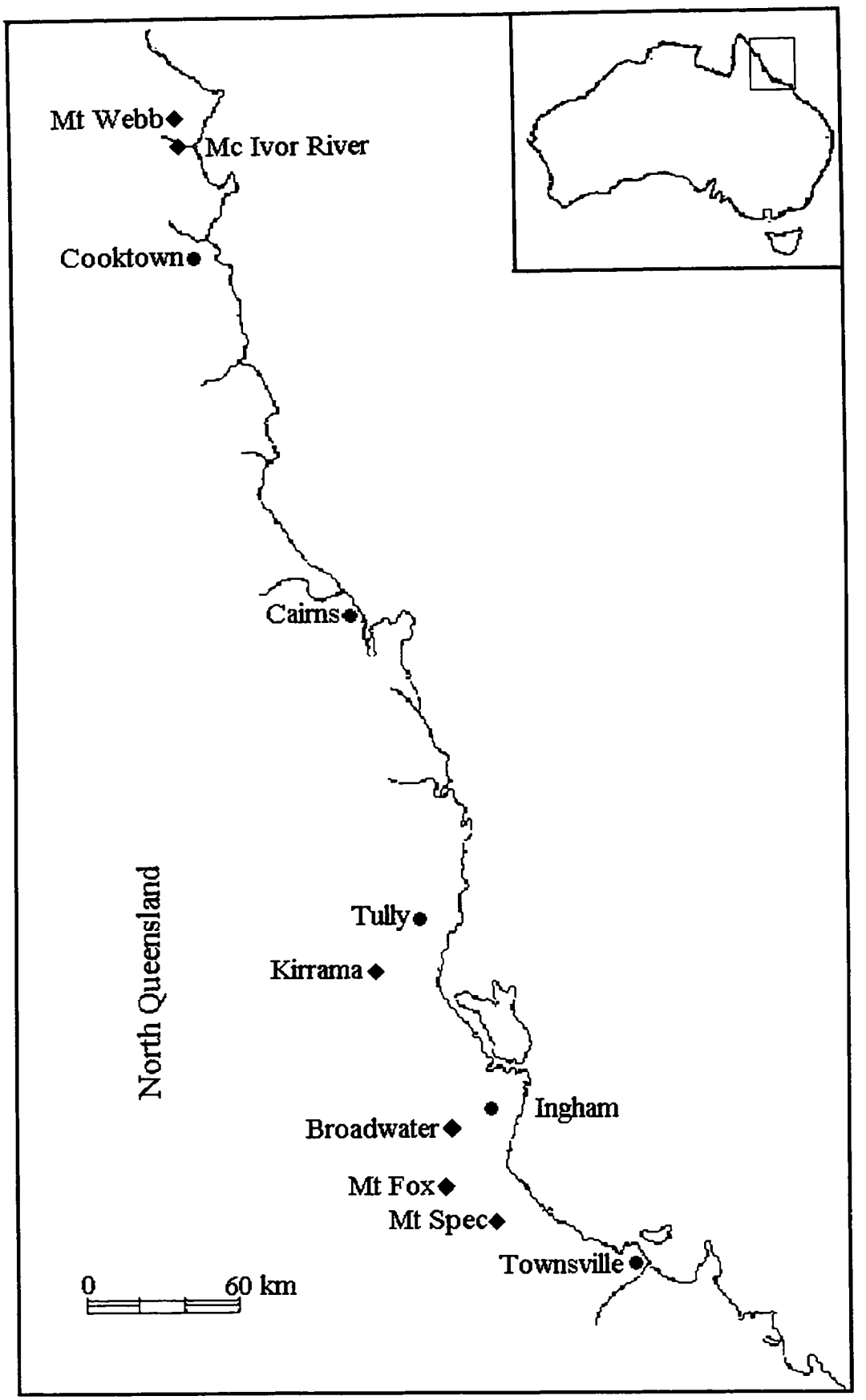


Figure 3.1 Location of study sites, north Queensland, Australia.

Following the initial survey, three of these sites, Broadwater, Mt Fox and Mt Spec, were used to conduct a detailed examination of fine root dynamics and soil fertilities. The selection of these sites was based on a number of criteria: they had to be on soils derived from different origin; they had to be close to one another and the University, to allow regular sampling and to minimise climatic variation; and, they had to be easily accessible.

3.2.1 Alluvial soil site - Broadwater

Located in the Broadwater State Forest, approximately 25 km west of Ingham (Figure 3.1), the forest is a lowland mesophyll vine forest dominated by the feather palm *Archontophoenix alexandrae* (F. Muell.) H. Wendl. & Drude. Other common species include *Elaeocarpus angustifolius* Hyland & Coode, *Ficus virens* Aiton ex. Dryander, *Neolitsea dealbata* (R. Br.) Merr., *Melicope erthyrococca* Benth. and *Myristica insipida* R. Br. The canopy height was approximately 25 m. This site was very prone to flooding, which frequently resulted in the movement of large masses of forest litter throughout the area. Mean annual rainfall for this site is 1830 mm, based on records from the Long-Pocket meteorological substation. The soils at Broadwater are alluvial in origin, with the dominant parent material in the upper catchment being granites and schists. The soil is a gradational brown earth.

3.2.2 Alluvial soil site - Mc Ivor River

The Mc Ivor River site is a complex mesophyll vine forest (CMVF), Type 1C, located on the Mc Ivor River, near Cooktown (Figure 3.1). This forest type occurs in moist to dry lowland areas as gallery forest, and is subjected to periods of low moisture availability. Type 1C CMVF can be distinguished from other types of CMVF by the presence of greater numbers of deciduous trees and fewer trunk epiphytes (Tracey 1982). The canopy height was approximately 30 m. Common species included *Castanospermum australe* (Cunn.) Fraser & Cook, *Myristica muelleri* Warb., and *Barringtonia*

calyptrata R. Br. Mean annual rainfall for the site is approximately 1780 mm (Tracey 1982). The soil was an alluvial-derived red clayey duplex soil.

3.2.3 Basaltic soil site - Mt Fox

This site is located approximately 5 km west of the Mt Fox Township (Figure 3.1). The forest is a complex notophyll vine forest, which is restricted to a creek basin and surrounded by open woodlands dominated by *Eucalyptus tereticornis* F. Muell., and various *Acacia* species. The canopy height was approximately 25 m. Species common to this site include *Acacia aulacocarpa* Cunn. ex Benth., *Archontophoenix alexandrae*, *Cryptocarya leucophylla* B. Hyland, *Elaeocarpus angustifolius*, and *Neolitsea dealbata*. The mean annual rainfall at the site is 1520 mm, based on data from the Upper Stone meteorological substation. The soil at Mt Fox is derived from an olivine basalt and is classified as a basaltic krasnozem (Isbell *et al.* 1968). Krasnozems are strongly-structured red clay soils. The clay content of these soils increases with depth and they are weakly differentiated below the A_1 horizon (Stace *et al.* 1968).

3.2.4 Basaltic soil site - Mt Webb

Mt Webb is an isolated pocket of complex notophyll vine forest, Type 5b of Tracey (1982), situated in the Mt Webb National Park, north of Cooktown (Figure 3.1). This forest is subjected to periods of moisture stress and is characterised by the presence of semi-evergreen and deciduous trees (Tracey 1982). The height of the canopy was approximately 25 m, with emergents to 35 m. Species common to this site were *Streblus pendulinus* (Endl.) F. Muell., *Cordia dichotoma* Forster, and *Terminalia sericocarpa* F. Muell. Mean annual rainfall was approximately 1780 mm. The soils, derived from basic volcanic parent material, are a basaltic krasnozem.

3.2.5 Granite soil site - Mt Spec

This site is located in the simple notophyll vine forest of the Mt Spec State Forest, approximately 5 km from the township of Paluma, and corresponds to plot 3 of Congdon and Herbohn (1993). The canopy height was approximately 20 m. Species common to this site include *Brackenridgea nitida* A. Gray, *Cardwellia sublimis* F. Muell., *Chionanthus axillaris* R. Br., *Darlingia darlingiana* (F. Muell.) L. A. S. Johnson, and *Macaranga subdentata* Benth. Mean annual rainfall for this site is 2630 mm, based on rainfall data from the Paluma meteorological substation. The rainfall pattern is similar to that of the other sites. Monthly mean minimum and maximum temperatures range between 9.6 °C (July) and 26.6°C (March) (Congdon & Herbohn 1993). The soil is a shallow red earth underlain by granite (Isbell *et al.* 1968). It is a red, friable, strongly-structured clay soil with moderate horizon differentiation and a gradational texture profile. It is strongly acidic and relatively infertile (Congdon & Herbohn 1993).

3.2.6 Granitic soil site - Kirrama

This site is located in the Kirrama State Forest, near Cardwell (Figure 3.1). The forest is a simple notophyll vine forest with *Agathis* emergents. Canopy height was approximately 20 m with emergents to 35 m. Species common to this site included *Agathis robusta* Bailey, *Brackenridgea nitida*, *Cardwellia sublimis*, *Macaranga subdentata*, *Acacia aulacocarpa*, and *Corymbia torrelliana* F. Muell. Mean annual rainfall is between 1142 and 2130 mm, based on records from the Kirrama and Cardwell meteorological substations. The soil is a gradational red friable earth of granite origin.

3.3 Methods

3.3.1 Relationships between fine root biomass, soil nitrogen and available phosphorus

One of the problems associated with studies on fine roots is the definition of what constitutes a fine root. This has varied between studies and ranges from all roots less than 2 mm diameter (Cavelier 1992), to all roots less than 5 mm diameter (Klinge & Herrera 1978). The lower of these limits often excludes a large number of unsuberised roots, while the upper limit will often include some woody roots (Pendry 1994). Due to the presence of many unsuberised roots in the 2 to 5 mm size class, all roots less than 5 mm diameter were considered fine roots in this study.

At each site, the fine roots were sampled using a 9 cm diameter soil corer. Five soil cores, to a depth of 40 cm, were taken from randomly selected locations along a 30 m transect. The cores were separated into 10 cm depth increments in the field and placed in plastic bags. Samples were stored at 4°C until sorted. Cores were not frozen due to possible loss of material during the freeze-thaw process (Price & Heitschmidt 1989). The cores were sorted across a series of sieves of decreasing mesh size (5, 2, 1, 0.71, 0.56 and 0.18 mm mesh) and the roots removed. The roots were then separated according to physiological status (alive or dead) and root diameter classes (<1, 1-2 and 2-5 mm). Live roots were distinguished by colour and texture criteria (Gower 1987). All dead roots and those greater than 5 mm diameter were excluded from this study. The roots were then dried at 70°C to a constant mass, and each site's total live root biomass determined from the mean of the five samples for the four depth increments.

The soil that passed through the 0.56 mm sieve was subsampled and total nitrogen and bicarbonate-extractable phosphorus concentrations determined

for each core sample. Total nitrogen analysis involved a Kjeldahl digestion and subsequent colorimetric determination as outlined in Anderson and Ingram (1989). Bicarbonate-extractable phosphorus was extracted following the procedure also outlined in Anderson and Ingram (1989), and determined using the single solution method (Murphy & Riley 1962).

A one-way analyses of variance (ANOVA) was used to examine overall differences in fine root biomass between the sites (Zar 1984). Differences between the means were examined using a Bonferroni comparison of means, with a rejection limit of $P = 0.05$. A Pearson correlation was used to examine the relationship between fine root biomass, and soil nitrogen and available phosphorus concentrations. The analyses were conducted using SYSSTAT 5.05 for Windows (SPSS Incorporated).

3.3.2 Fine root dynamics and soil fertility

Fine root dynamics were examined in detail at Mt Fox, Broadwater and Mt Spec. The study was undertaken over a hundred week period, from February 1992 to February 1994.

3.3.2a Soil Sampling

Five soil cores were taken from random locations within a 25 m by 10 m plot laid out at each site. The cores were collected to a depth of 150 cm using an AMS extendible soil corer (Forestry Suppliers Inc.). Each core was separated in the field into eight depth increments, 0-10, 10-20, 20-30, 30-40, 40-60, 60-90, 90-120 and 120-150 cm, and then the samples were transported to the laboratory. The soil samples were air dried for approximately 2 weeks, and sieved to 2 mm prior to analysis (Rayment & Higginson 1992).

3.3.2b Soil physical and chemical analyses

Dry weight bulk density was determined on a subsample of known volume, after drying to constant weight at 105°C. Organic matter content was determined using a wet oxidation method (Heanes 1984). Total nitrogen, phosphorus and potassium were determined using a sulphuric acid-hydrogen peroxide digestion with a selenium catalyst according to the method outlined in Anderson and Ingram (1989). Nitrogen and phosphorus concentrations in the digests were determined by the colorimetric procedures presented in Anderson and Ingram (1989), while potassium was determined by flame photometry. "Plant-available" phosphorus was extracted using a modification of the Olsen method (Rayment & Higginson 1992), with orthophosphate concentrations in the extracts being determined colorimetrically using the single solution method of Murphy and Riley (1962). This extraction procedure was selected because it gives a good correlation with plant productivity in tropical soils where plant-available phosphorus is often at low levels (Rayment & Higginson 1992), and to some extent mimics the chemical means by which roots bring inorganic phosphate into solution (Tiessen 1989). Cation exchange capacity was determined by the silver-thiourea method as outlined in Rayment and Higginson (1992). Differences in soil nutrient concentrations between the sites were examined using an hierarchical ANOVA (Zar 1984).

Total soil nutrient stocks were determined by multiplying mean nutrient concentrations by mean soil bulk density at each depth. These were then summed to give a total estimate for the profile.

3.3.2c Forest structure and above-ground biomass

The position, diameter at breast height (dbh) and height were determined for all trees taller than 1.5 m within the 25 m by 10 m plot. Diameters at breast height were determined at 1.35 m using a diameter tape, while tree heights were estimated using a clinometer (Claussen & Maycock 1995). Voucher

specimens were collected for all trees. Identification of the species within each plot was accomplished using the keys of Hyland and Whiffin (1993) and Jackes (1990).

Estimates of above-ground biomass were determined from the dbh and height data using the simple allometric biomass regressions determined in Chapter 2. For comparison, the biomass regressions of Brown *et al.* (1989) were also applied to the data.

3.3.2d Fine root biomass

The fine root biomass was initially sampled in April 1992 using a 5.5 cm diameter root corer. Ten cores, to a depth of 50 cm, were taken at randomly selected locations along a 50 m transect at each site. The cores were separated into 0-5, 5-10, 10-20, 20-30, 30-40 and 40-50 cm depth increments. The samples were then sorted following the procedure outlined in Section 3.3.1. All roots less than 5 mm diameter were retained. Differences in fine root biomass between the sites were examined using an hierarchical ANOVA.

Fine root biomass and depth distribution were re-examined to a greater depth in February 1994. Using an extendible soil corer of 5 cm diameter, five cores were taken to a depth of between 120 and 150 cm. The depth of each core was determined by the presence of underlying rock. The cores were separated into 10 cm depth increments and transported back to the laboratory. Roots were separated as described in Section 3.3.1.

3.3.2e Fine root dynamics

Fine root productivity was examined using root ingrowth bags over a 96 week period. The bags were constructed from plastic coated fibreglass screen of 4 mm^2 mesh (Cuevas & Medina 1988). The cylindrical bags were 6 cm in diameter, 10 cm in height and open at the top. Root-free soil was used to fill

the bags. The soil was collected from the site and sieved free of roots immediately prior to placement of the bags in the field.

A total of 70 bags were deployed at random locations within a 50 m x 30 m plot at each site in February 1992. Placement of the bags was within the top 10 cm of the root mat using a 6 cm diameter soil corer. Bags were collected at 12-week intervals for the first 48 weeks, with a final collection at 96 weeks. Ten randomly selected bags were retrieved on each sampling occasion. Retrieval of the bags was achieved by slicing the soil with a knife at a distance of approximately 2 cm from the bag, and the bags plus attached soil were removed from the ground. The soil and roots on the outside of the bags were then carefully removed. Ingrowth bags were sorted in the laboratory, and the roots were separated as described in Section 3.3.1. Differences in root ingrowth at each sampling time were tested using ANOVA. Annual fine root turnover was determined from the fine root production data, based on the data for the 48-week incubated root ingrowth bags, and are expressed as a percentage of the live fine root biomass.

A further twenty root ingrowth bags were used to examine seasonal differences in fine root productivity. The construction, placement and retrieval of the bags followed the procedure outlined above. The bags were incubated in the field for 8 weeks. On each sampling occasion, replacement bags were placed in new randomly selected locations. An hierarchial ANOVA was used to test for differences between sites and sampling times.

Decomposition rates of fine roots at each site were determined by the enclosure method (Santantonio & Grace 1987). This method measures the disappearance of fine roots in small enclosures from which new fine roots are excluded. Fifty enclosures were deployed at random locations within the 50 m x 30 m plot at each site in February 1992. The enclosures, PVC piping of 55

mm internal diameter and 20 cm length, were driven through the superficial root mat into the mineral soil.

The enclosures were collected at twelve week intervals, with ten enclosures being collected at each sampling date. The samples within the enclosures were removed and placed in polyethylene bags. Samples were transported back to the laboratory and stored at 4°C until sorted. The roots were sorted as described before. An exponential decay function was fitted to the data using TableCurve Windows 1.0 (Jandel Scientific) and an estimated annual rate of decomposition was determined from this equation.

3.4 Results

3.4.1 Fine root biomass, soil nitrogen and available phosphorus

Fine root biomass varied significantly between the sites ($P \leq 0.05$) (Table 3.2). The sites with granite-derived soils, Kirrama and Mt Spec, had the highest root biomass (15.0 and 16.4 t ha^{-1} respectively). The biomass at the other sites ranged from 3.7 to 5.4 t ha^{-1}, with no significant difference between the two soil types ($P > 0.05$).

The percentage that roots less than 1 mm and roots less than 2 mm contributed to total live-fine root biomass varied between sites (Table 3.2). The greatest proportion of roots less than 2 mm and 1mm was found at Mt Fox where the soils contain more available phosphorus. Conversely, the lowest proportion contributed by these roots was found at Mt Spec.

No significant correlations were found between available phosphorus concentration and fine root biomass to a depth of 40 cm (Figure 3.2a-c). While a lower fine root biomass was found on the "phosphorus-rich" basaltic

soils and a greater fine root biomass was found on the "phosphorus-poor" granite-derived soils, the alluvial soils of Broadwater and Mc Ivor River possessed low available phosphorus concentrations coupled with low root biomass (Figure 3.2a-c). In contrast, soil nitrogen concentrations were significantly negatively correlated with the biomass of roots less than 1 mm and roots less than 2 mm (Figure 3.2e&f).

Table 3.2 Live-fine root biomass (t ha^{-1}) to a depth of 40 cm. Data are the means of five samples ± the standard error. Values in brackets are the percentage of the total live-fine root biomass that the various root size classes contribute.

Site	Origin of soil	Live fine root biomass (t ha^{-1})		
		≤ 1 mm	≤ 2 mm	≤ 5 mm
Broadwater	Alluvial	1.7 ± 0.4 (33)	2.6 ± 0.5 (52)	5.2 ± 1.2
Mc Ivor River	Alluvial	1.6 ± 0.4 (43)	2.1 ± 0.5 (57)	3.7 ± 1.3
Mt Fox	Basalt	1.9 ± 0.5 (45)	2.8 ± 0.4 (67)	4.2 ± 0.8
Mt Webb	Basalt	1.8 ± 0.4 (33)	2.7 ± 0.6 (50)	5.4 ± 1.7
Kirrama	Granite	6.4 ± 1.3 (43)	9.1 ± 1.7 (61)	15.0 ± 3.5
Mt Spec	Granite	3.9 ± 0.75 (24)	7.1 ± 1.1 (43)	16.4 ± 2.9

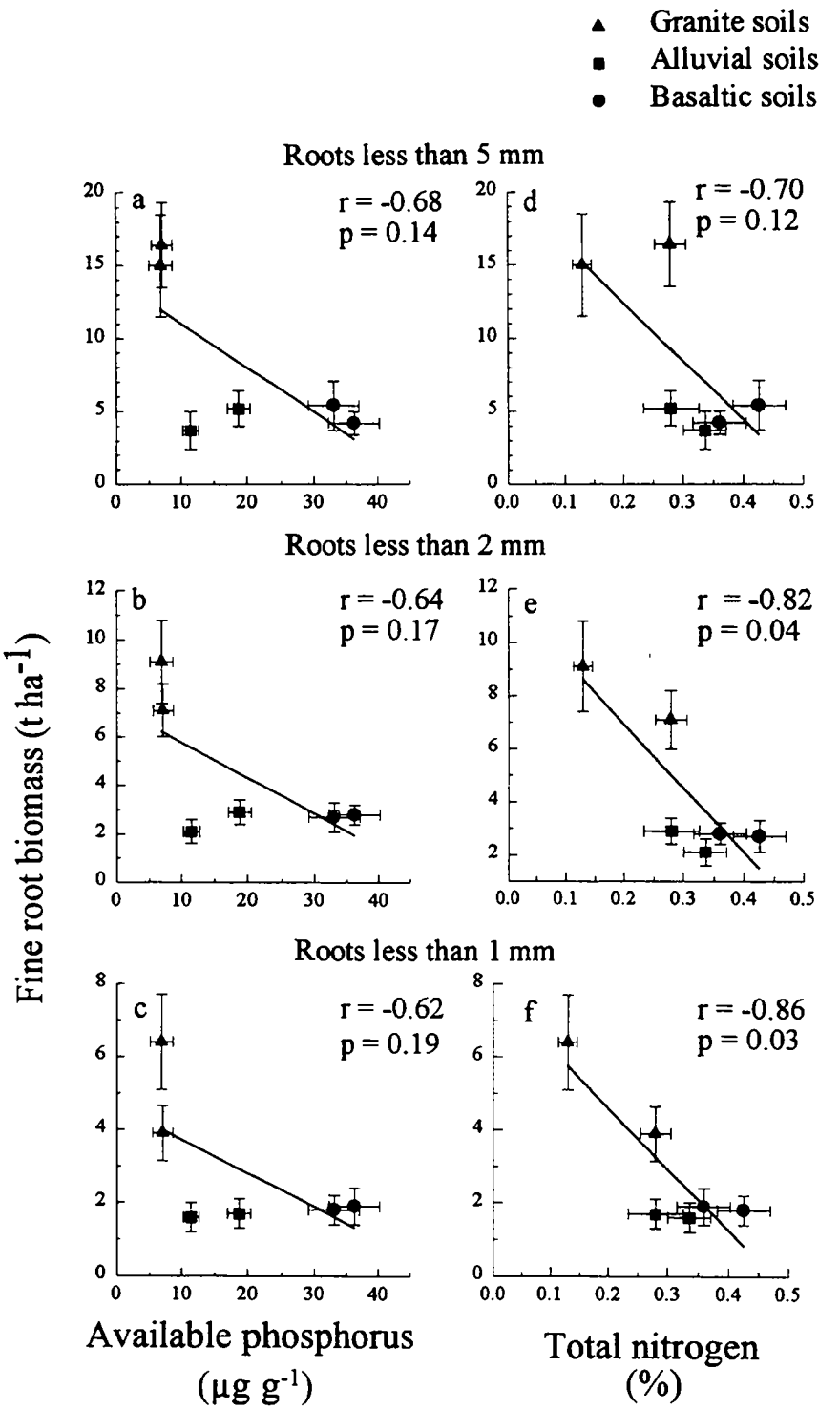


Figure 3.2 Relationship of biomass of fine roots (t ha^{-1}) to soil nitrogen (%) and available phosphorus ($\mu g\ g^{-1}$) for different root size classes. Fine root biomass is the mean of five cores to a depth of 40 cm. Soil nitrogen and available phosphorus are the mean values of five cores taken to 40 cm depth. Bars represent standard errors of the mean.

3.4.2 Fine root dynamics and soil fertility

3.4.2a Soil bulk density, nutrient concentrations and nutrient stocks

Soil bulk densities varied between sites (Figure 3.3). Surface-layer soil bulk densities ranged from 0.4 g cm^{-3} at Broadwater to 0.85 g cm^{-3} at Mt Spec. Broadwater consistently had the lowest bulk densities at all depths, and showed little change with depth. Soil bulk density was low in the top 10 cm at Mt Fox, increased substantially between 10 and 25 cm, and then remained relatively constant below 25 cm. Soil bulk density was greatest at Mt Spec; it increased with depth up to 75 cm and then changed little after this depth.

The concentrations of the soil nutrients were significantly different between sites and depths (Table 3.3). Mean nutrient concentrations decreased down the profile at Broadwater (Table 3.4). Kjeldahl nitrogen and organic carbon concentrations were highest in the top 10 cm of soil and decreased rapidly with depth. Carbon to nitrogen ratios were also greatest in the top 10 cm of soil, but showed only a gradual decrease with depth. Concentrations of available phosphorus were very high throughout the top 30 cm of soil, but decreased rapidly with depth. Potassium concentrations increased with depth down to 30 cm, but decreased gradually further down the profile (Table 3.4). The concentrations of potassium in the top 10 cm of soil were over three times greater at Broadwater than at any other site. The proportion of total phosphorus comprised of available phosphorus was relatively constant in the top 30 cm, and then decreased with depth.

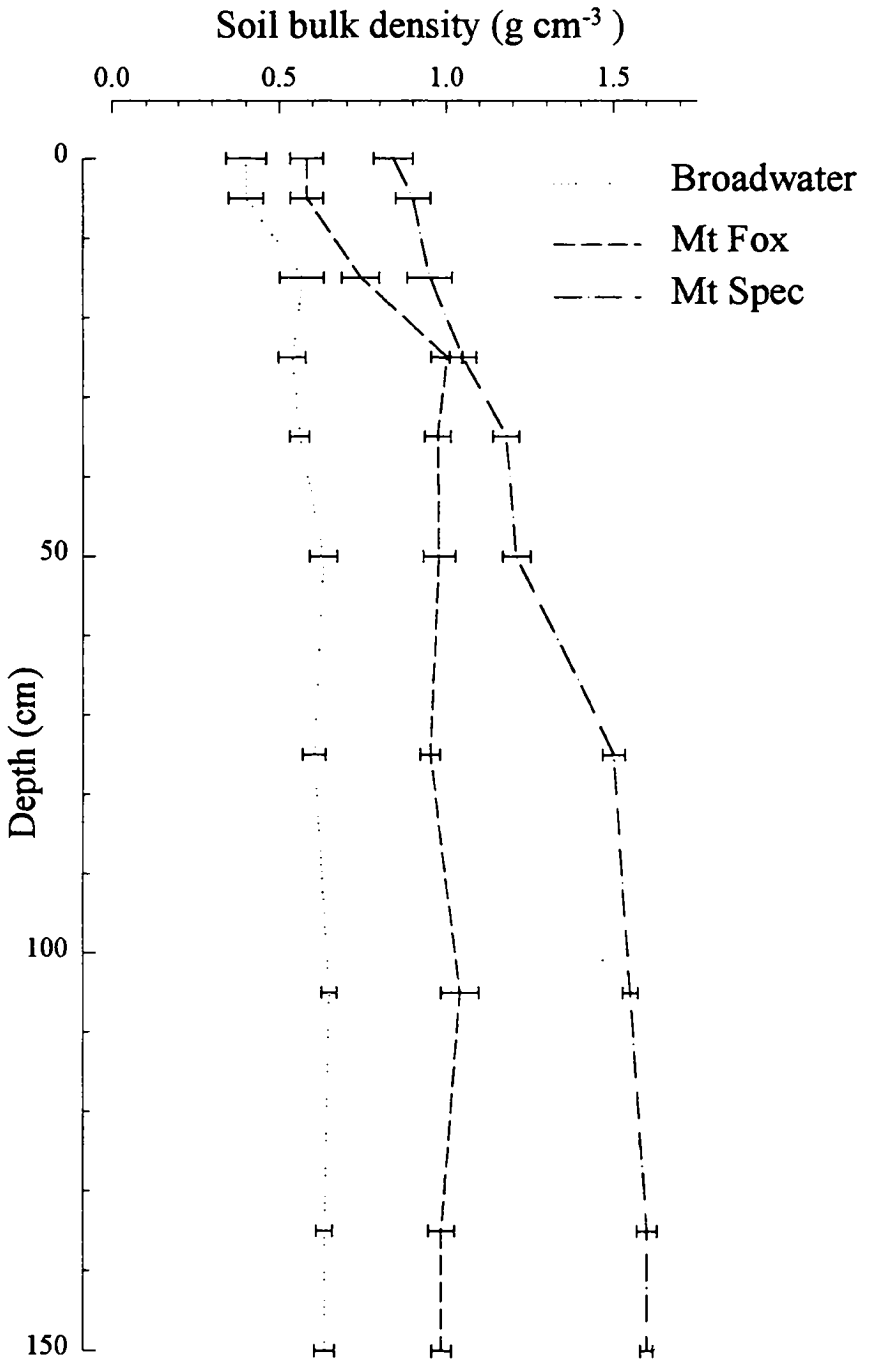


Figure 3.3 Variations in soil bulk densities (g cm^{-3}) down the profile at Broadwater, Mt Fox and Mt Spec. Bars represent SEM.

Table 3.3 Probabilities (P) for an hierarchial ANOVA for soil nutrient concentrations at Broadwater, Mt Fox and Mt Spec. $P < 0.05$ represents a significant difference in soil nutrient concentrations.

	Probabilities				
Source of variance	Total phosphorus	Kjeldahl nitrogen	Potassium	Organic carbon	Available phosphorus
Sites	0.00	0.00	0.00	0.00	0.00
Depths	0.00	0.00	0.00	0.00	0.00
Replicates	0.26	0.13	0.42	0.32	0.28
Sites*Depths	0.00	0.00	0.00	0.00	0.00
Sites*Replicates	0.05	0.12	0.27	0.69	0.56
Depths*Replicates	0.29	0.17	0.90	0.69	0.53

In comparison to Broadwater, total phosphorus concentrations in the top 10 cm of soil were considerably higher in the basaltic soil of Mt Fox (Table 3.5). However, Kjeldahl nitrogen, organic carbon and available phosphorus concentrations were only slightly higher in the surface layer. Kjeldahl nitrogen and organic carbon concentrations exhibited a similar trend at Mt Fox, being greatest in the top 10 cm of soil and decreasing rapidly further down the profile (Table 3.5). Carbon to nitrogen ratios remained relatively constant throughout the profile. Total and available phosphorus also showed a decrease in concentration down the profile, although it was not as substantial as that observed for nitrogen and carbon. The concentrations of both total and available phosphorus were still relatively high in the lower portions of the soil profile. The ratio of available phosphorus to total phosphorus decreased with depth (Table 3.5).

The lowest nutrient concentrations were found in the granitic soils at Mt Spec (Table 3.6). This soil had very low levels of available and total phosphorus, and moderate levels of nitrogen and potassium. The concentrations of all

nutrients decreased with depth, with the exception of potassium which remained relatively constant throughout the profile. The available phosphorus to total phosphorus ratio followed a similar pattern to the other sites and decreased with depth. Carbon to nitrogen ratios were variable throughout the profile.

Cation exchange capacity (CEC) was highest in the top 10 cm of soil at all sites, with the highest CEC being found in the alluvial soil at Broadwater (Table 3.7). The CEC at Broadwater decreased rapidly with depth, from 23 cmol (+) kg^{-1} in the top 10 cm of soil, down to 4 cmol (+) kg^{-1} at 150 cm. The CEC at Mt Fox did not change as markedly with depth, ranging from 20 cmol (+) kg^{-1} in the top cm down to 7.5 cmol (+) kg^{-1} at 150 cm. The granite-derived soils at Mt Spec were found to have the lowest CEC. The exchangeable plant-essential cations (potassium, calcium and magnesium) all decreased with depth (Table 3.7), while exchangeable sodium was either relatively constant with depth, or increased. The greatest concentrations of exchangeable magnesium and potassium were found in the basaltic soils of Mt Fox. Broadwater had the greatest concentration of exchangeable calcium.

Table 3.4 Mean nutrient concentrations in the soil at Broadwater. Values are the means, with associated standard error, for 5 random samples to a depth of 150 cm.

Depth (cm)	Total phosphorus ($\mu g\ g^{-1}$)	Kjeldahl nitrogen ($\mu g\ g^{-1}$)	Potassium ($\mu g\ g^{-1}$)	Organic carbon ($mg\ g^{-1}$)	Bicarbonate extractable phosphorus ($\mu g\ g^{-1}$)	C : N ratios	Available phosphorus to total phosphorus (%)
0-10	300 ± 5	4320 ± 380	1610 ± 100	68 ± 9	25.2 ± 3.5	15.7	8.4
10-20	240 ± 5	2910 ± 350	1660 ± 60	43 ± 6	18.2 ± 1.7	14.8	7.5
20-30	240 ± 15	2440 ± 370	1860 ± 70	32 ± 6	20.4 ± 3.4	13.1	8.5
30-40	180 ± 30	1600 ± 290	1680 ± 180	19 ± 3	11.5 ± 2.6	11.9	6.4
40-60	150 ± 45	1120 ± 450	1480 ± 190	13 ± 6	9.9 ± 0.5	11.7	6.6
60-90	100 ± 5	640 ± 70	1170 ± 70	7 ± 1	4.4 ± 0.2	10.9	4.4
90-120	100 ± 5	760 ± 120	1260 ± 10	5 ± 0.5	3.4 ± 1.0	6.6	3.4
120-150	90 ± 5	650 ± 80	1090 ± 50	7 ± 0.5	2.1 ± 0.3	10.8	2.3

Table 3.5 Mean nutrient concentrations in the soil at Mt Fox. Values are the means, with associated standard error, for 5 random samples to a depth of 150 cm.

Depth (cm)	Total phosphorus ($\mu g\ g^{-1}$)	Kjeldahl nitrogen ($\mu g\ g^{-1}$)	Potassium ($\mu g\ g^{-1}$)	Organic carbon ($mg\ g^{-1}$)	Bicarbonate extractable phosphorus ($\mu g\ g^{-1}$)	C : N ratios	Available phosphorus to total phosphorus (%)
0-10	830 ± 10	5790 ± 300	540 ± 40	74 ± 2.5	30.5 ± 1	12.8	3.7
10-20	800 ± 10	3830 ± 210	440 ± 30	49 ± 1	30.3 ± 1.8	12.8	3.8
20-30	750 ± 20	2570 ± 70	470 ± 40	34 ± 1	26.4 ± 0.8	13.2	3.5
30-40	690 ± 30	2140 ± 70	510 ± 50	26 ± 0.5	20.5 ± 1.2	12.1	2.9
40-60	650 ± 20	1510 ± 90	560 ± 50	18 ± 2	19.8 ± 2.3	11.9	3
60-90	600 ± 20	1070 ± 30	490 ± 50	11± 0.5	16.0 ± 4.7	10.3	2.7
90-120	550 ± 30	950 ± 30	420 ± 30	13 ± 2	13.8 ± 2.8	13.7	2.5
120-150	590 ± 10	950 ± 10	410 ± 10	10 ± 0.5	13.0 ± 1.5	10.5	2.2

Table 3.6 Mean nutrient concentrations in the soil at Mt Spec. Values are the means, with associated standard error, for 5 random samples to a depth of 150 cm.

Depth (cm)	Total phosphorus ($\mu g\ g^{-1}$)	Kjeldahl nitrogen ($\mu g\ g^{-1}$)	Potassium ($\mu g\ g^{-1}$)	Organic carbon ($mg\ g^{-1}$)	Bicarbonate extractable phosphorus ($\mu g\ g^{-1}$)	C : N ratios	Available phosphorus to total phosphorus (%)
0-10	140 ± 5	3990 ± 40	330 ± 10	36 ± 2	8.3 ± 0.9	9	5.9
10-20	120 ± 5	3000 ± 30	320 ± 10	26 ± 0.5	8.9 ± 1.2	8.7	7.4
20-30	120 ± 5	3030 ± 110	320 ± 40	21 ± 0.5	7.0 ± 2.0	6.9	5.8
30-40	75 ± 4	2200 ± 200	400 ± 60	20 ± 1	4.3 ± 1.3	9.1	5.7
40-60	85 ± 3	1300 ± ± 120	270 ± 30	10 ± 0.5	3.9 ± 0.8	7.7	4.6
60-90	65 ± 3	630 ± 60	370 ± 25	8 ± 0.2	1.9 ± 0.4	12.7	2.9
90-120	50 ± 2	440 ± 40	320 ± 40	3 ± 0.3	0.7 ± 0.2	6.8	1.4
120-150	45 ± 4	390 ± 70	310 ± 30	3.1 ± 0.3	0.7 ± 0.1	7.9	1.5

Table 3.7 Cation exchange capacity and exchangeable cations (cmol (+) kg^{-1}) with depth, at three sites in north Queensland.

Site	Depth	Cation exchange capacity and exchangeable cations (cmol (+) kg^{-1})				
		CEC	Sodium	Potassium	Calcium	Magnesium
Broadwater	0-10	23.0	0.16	0.23	18.0	3.20
	10-20	16.0	0.11	0.16	14.0	2.40
	20-30	15.0	0.10	0.08	9.4	1.70
	30-40	8.7	0.10	0.09	5.6	1.20
	40-60	7.0	0.08	0.07	4.9	0.98
	60-90	4.2	0.03	0.04	2.6	0.47
	90-120	4.1	0.07	0.06	3.8	0.68
	120-150	4.0	0.07	0.07	2.8	0.51
Mt Fox	0-10	20.0	0.15	0.70	6.70	7.50
	10-20	14.0	0.14	0.32	1.60	4.90
	20-30	11.0	0.15	0.23	0.57	4.10
	30-40	10.0	0.20	0.12	0.51	3.20
	40-60	15.0	0.28	0.11	0.23	2.30
	60-90	8.8	0.35	0.06	0.27	2.00
	90-120	7.9	0.23	0.07	0.29	1.30
	120-150	7.5	0.42	0.08	0.30	1.20
Mt Spec	0-10	8.0	0.10	0.39	3.50	1.20
	10-20	3.5	0.10	0.10	0.85	0.33
	20-30	2.7	0.09	0.08	0.26	0.19
	30-40	2.0	0.10	0.08	0.23	0.18
	40-60	1.7	0.06	0.07	0.22	0.21
	60-90	2.6	0.08	0.05	0.22	0.19
	90-120	4.3	0.14	0.08	0.34	0.58

Whilst the highest concentrations of nitrogen, phosphorus and carbon were found at Mt Fox, the total nutrient stocks at this site were not necessarily the greatest (Table 3.8). The greatest quantity of carbon occurred at Broadwater, with 203.4 t ha^{-1} occurring in the top 150 cm of soil (Table 3.8). Mt Spec contained the greatest quantities of nitrogen and potassium, with 20,050 and 19,030 kg ha^{-1} respectively, occurring in the top 150 cm of soil. The greatest quantities of total phosphorus and available phosphorus in the top 150 cm of soil occurred at Mt Fox. However, the quantity of available phosphorus in the top 10 and 30 cm of soil was highest at Broadwater.

All sites showed a concentration of carbon, nitrogen, total phosphorus and available phosphorus in the top 10 cm of soil. The percentage contained varied between nutrients, with between 16.2 and 19.5% of the total carbon, 14.8 and 16.7% of the total nitrogen, 5.8 and 9.4% of the total phosphorus, and 7.6 and 13.4% of the total available phosphorus occurring in the top 10 cm of soil. In contrast, little of the total potassium found at the sites was contained in the top 10 cm of soil.

3.4.2b Forest structure and above-ground biomass

Mt Spec had the greatest number of species, tree density and basal area of all sites (Table 3.9). This site had a large number of small trees, giving it the lowest mean diameter at breast height (dbh). Maximum tree height did not vary greatly between sites, but was greatest at Broadwater.

Table 3.8 Total nutrient stocks to different depths in the soils at Broadwater, Mt Fox and Mt Spec. Figures in parentheses represent the percentage of nutrient stock to 150 cm found at each depth.

Site	Depth (cm)	Organic carbon (t ha^{-1})	Total nitrogen (kg ha^{-1})	Total phosphorus (kg ha^{-1})	Total potassium (kg ha^{-1})	Available phosphorus (kg ha^{-1})
Broadwater	0-10	39.6 (19.5)	2510 (14.8)	180 (9.4)	280 (4.3)	14.6 (13.4)
	0-30	103.2 (50.7)	7120 (41.8)	600 (31.2)	910 (14.1)	48.5 (44.7)
	0-150	203.4	17000	1920	6450	108.6
Mt Fox	0-10	29.5 (16.7)	2320 (16.0)	330 (5.8)	220 (5.3)	12.2 (7.6)
	0-30	75.7 (42.9)	5870 (40.5)	1180 (20.8)	720 (17.2)	43.6 (27.1)
	0-150	176.5	14500	5680	4180	160.6
Mt Spec	0-10	30.0 (16.2)	3350 (16.7)	120 (8.6)	930 (4.9)	6.9 (13.2)
	0-30	75.4 (40.1)	8250 (41.1)	360 (25.7)	4020 (21.1)	22.3 (42.7)
	0-150	185.2	20050	1400	19030	52.2

Table 3.9 Structural measures of the vegetation at Broadwater, Mt Fox and Mt Spec, based on a plot 10 m by 25 m.

	Broadwater	Mt Fox	Mt Spec
Tree density (ha^{-1})			
>10 cm dbh	880	680	1240
> 2 m height	2720	6120	13440
Basal area (m^2 ha^{-1})			
>10 cm dbh	42.18	55.51	63.37
> 2 m height	43.79	61.29	72.42
Mean dbh (cm)	8.88	5.16	3.98
Maximum tree height (m)	31.3	29	27.6
No. species	22	37	41

Estimates of above-ground biomass varied considerably depending on which regression was used (Table 3.10). The estimates of above-ground biomass at Mt Fox varied from 167 to 600 t ha^{-1}. Mt Spec and Broadwater also showed considerable variation in above-ground biomass estimates, ranging from 210 to 667 t ha^{-1} and 218 to 482 t ha^{-1}, respectively. Biomass regression equation 1a determined on only those trees greater than 5 cm diameter, yielded estimates of above-ground biomass at Broadwater of 252 t ha^{-1}, Mt Fox 256 t ha^{-1} and Mt Spec 285 t ha^{-1}.

Table 3.10 Estimates of above-ground biomass for the three sites. Estimates were determined using the equations which correspond to the regressions outlined in Table 2.14.

Equations	Estimated above-ground biomass (t ha^{-1})		
	Broadwater	Mt Fox	Mt Spec
Equation 1a	226	205	236
Equation 1c	218	167	210
Brown *et al.* (1989) # 1	482	600	667
Brown *et al.* (1989) # 3	342	395	446
Equation 1a (trees > 5 cm)	252	256	285

3.4.2c Fine root biomass and distribution with depth

All of the sites showed the greatest concentration of fine roots in the top 10 cm of soil (Figure 3.4), with between 45 and 52% of the fine roots being found in the top 10 cm. There was a rapid decrease in fine root biomass with depth, with very few fine roots being found below 50 cm.

Fine root biomass was significantly different between the sites, with Mt Spec having a significantly higher fine root biomass than Mt Fox or Broadwater (Table 3.11). Fine root biomass also differed significantly between sampling depths and between root size classes.

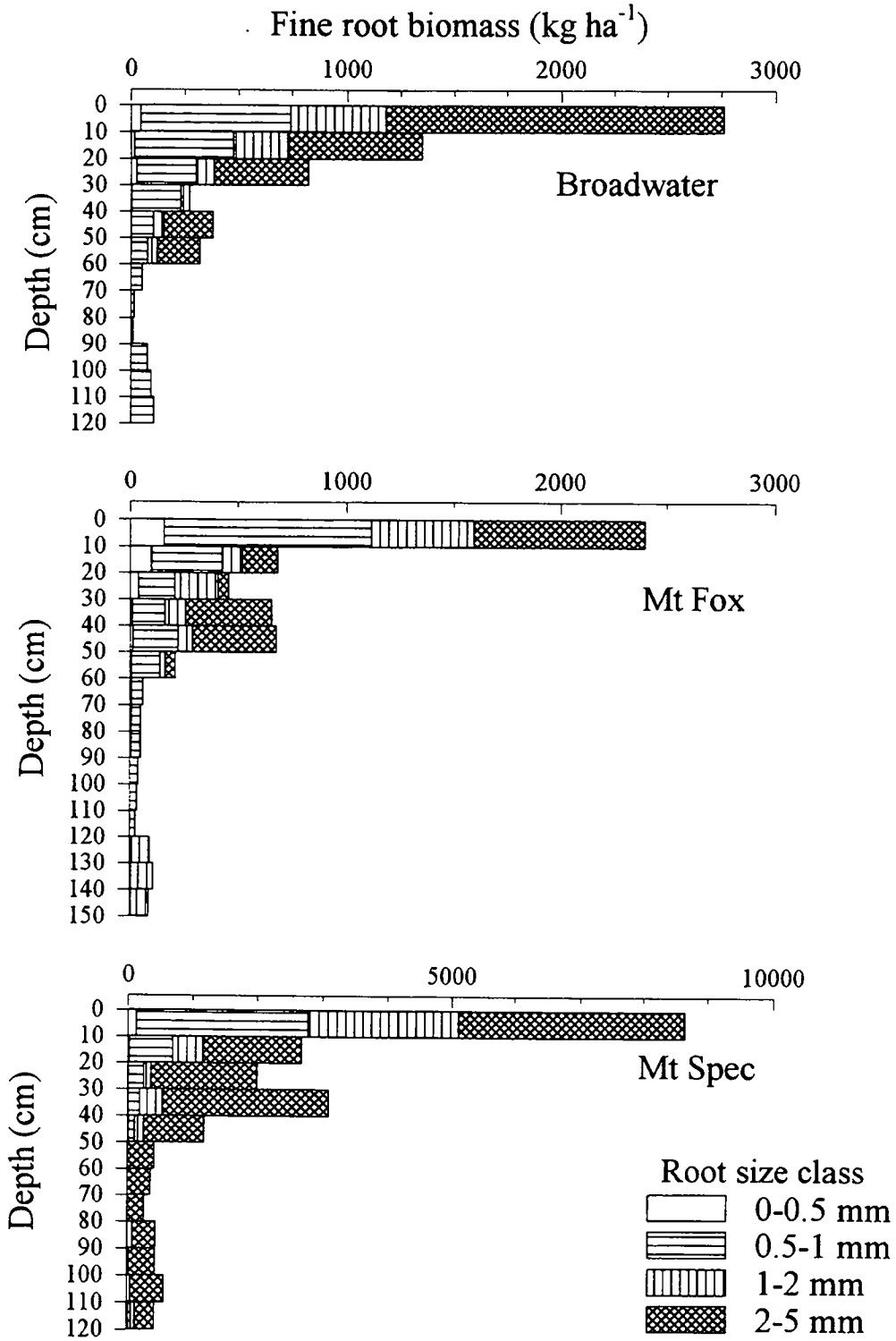


Figure 3.4 **Fine root distribution with depth down the soil profile at Broadwater, Mt Fox and Mt Spec.**

Table 3.11 Probabilities for an hierarchial ANOVA for fine root biomass in the top 50 cm of soil at Broadwater, Mt Fox and Mt Spec. $P < 0.05$ represents a significant difference in fine root biomass.

Source of variance	Probability	Degrees of freedom
Sites	0.00	2
Depths	0.00	4
Size classes	0.00	3
Replicates	0.37	9
Sites*Depths	0.00	8
Sites* Size classes	0.00	6
Sites*Replicates	0.47	18
Depths*Size Classes	0.00	12
Depths*Replicates	0.12	36
Size Classes*Replicates	0.72	27
Sites*Depths*Size classes	0.00	24
Sites*Depths*Replicates	0.04	72
Sites*Size classes*Replicates	0.86	54

Broadwater had the lowest biomass of fine roots (7.7 t ha^{-1}) (Table 3.12). The majority of live-roots at this site were between 2 and 5 mm diameter, although this size class only comprised about 18% of the dead-fine root biomass. The distribution of live fine roots with depth at Broadwater was correlated with all soil variables examined, except total potassium concentrations (Table 3.13).

The total fine root biomass at Mt Fox was approximately 9 t ha^{-1} (Table 3.14). The majority of live roots in the top 30 cm were less than 2 mm diameter. Roots greater than 2 mm contributed only about 24% of the site's fine root biomass, and about 8% of the dead fine roots. The distribution of roots less than 1 mm and those less than 2 mm was correlated with soil nitrogen concentrations over depth (Table 3.15).

Table 3.12 Live, dead and total fine root biomass (kg ha^{-1}) for four size classes, and their distribution with depth at Broadwater. Values are means ± SEM of 10 replicate cores.

Status	Soil depth (cm)	Root size class (mm)					
		0-0.5	0.5-1	1-2	2-5	Total (0-2)	Total
Live	0-5	26 ± 6	260 ± 40	190 ± 50	950 ± 200	476 ± 90	1426 ± 250
	5-10	17 ± 6	440 ± 80	250 ± 80	630 ± 220	707 ± 120	1337 ± 290
	10-20	15 ± 1	460 ± 80	260 ± 90	610 ± 330	735 ± 140	1345 ± 420
	20-30	25 ± 10	280 ± 110	80 ± 40	440 ± 230	385 ± 100	825 ± 250
	30-40	1 ± 0.5	230 ± 140	40 ± 30	0	271 ± 170	271 ± 170
	40-50	0	100 ± 30	50 ± 35	230 ± 140	150 ± 50	380 ± 150
	Total	84 ± 18	1770 ± 360	870 ± 240	2860 ± 840	2724 ± 500	5584 ± 1150
Dead	0-5	39 ± 9	450 ± 90	30 ± 10	0	519 ± 90	519 ± 90
	5-10	15 ± 3	280 ± 20	50 ± 10	20 ± 20	345 ± 20	365 ± 40
	10-20	16 ± 4	310 ± 80	80 ± 30	20 ± 20	406 ± 100	426 ± 120
	20-30	4 ± 2	280 ± 100	30 ± 10	320 ± 180	314 ± 100	634 ± 260
	30-40	0	50 ± 30	20 ± 10	30 ± 30	70 ± 30	100 ± 50
	40-50	0	30 ± 20	10 ± 10	0	40 ± 30	40 ± 30
	Total	74 ± 14	1400 ± 260	220 ± 60	390 ± 190	1694 ± 280	2084 ± 440
Total	0-5	65 ± 12	710 ± 130	220 ± 50	950 ± 250	995 ± 170	1945 ± 330
	5-10	32 ± 8	720 ± 100	300 ± 80	650 ± 210	1052 ± 140	1702 ± 300
	10-20	31 ± 5	770 ± 130	340 ± 100	630 ± 350	1141 ± 220	1771 ± 540
	20-30	29 ± 17	560 ± 190	110 ± 50	760 ± 370	699 ± 200	1459 ± 500
	30-40	1 ± 0.5	280 ± 180	60 ± 40	30 ± 30	341 ± 180	371 ± 210
	40-50	0	130 ± 40	60 ± 40	230 ± 140	190 ± 60	420 ± 160
	Total	158 ± 32	3170 ± 560	1090 ± 270	3250 ± 1010	4418 ± 730	7668 ± 1530

Table 3.13 Correlation matrix for fine root biomass and soil fertility, with depth, at Broadwater. Variables include: roots less than 1 mm diameter (< 1 mm); roots less than 2 mm diameter (< 2 mm); roots less than 5 mm diameter (< 5 mm); available phosphorus (Ava P); total phosphorus (P); Kjeldahl nitrogen (N); total potassium (K); and carbon to nitrogen ratio (C:N). Correlation coefficients higher than 0.87 are significant at the 5% level and are indicated with an asterisk.

	< 1 mm	< 2 mm	< 5 mm	Ava P	P	N	K	C:N
< 1 mm	1.00							
< 2 mm	0.99*	1.00						
< 5 mm	0.97*	0.98*	1.00					
Ava P	0.90*	0.87	0.88*	1.00				
P	0.95*	0.92*	0.91*	0.99*	1.00			
N	0.98*	0.99*	0.86	0.79	0.86	1.00		
K	0.10	0.01	-0.05	0.41	0.37	-0.10	1.00	
C:N	0.97*	0.97*	0.94*	0.89*	0.93*	0.94*	-0.11	1.00

Table 3.14 Live, dead and total fine root biomass (kg ha^{-1}) for four size classes, and their distribution with depth at Mt Fox. Values are means ± SEM of 10 replicate cores.

Status	Soil depth (cm)	Root size class (mm)					
		0-0.5	0.5-1	1-2	2-5	Total (0-2)	Total
Live	0-5	50 ± 34	610 ± 140	190 ± 70	500 ± 200	850 ± 120	1350 ± 220
	5-10	106 ± 79	350 ± 100	290 ± 100	300 ± 190	746 ± 150	1046 ± 250
	10-20	97 ± 66	330 ± 50	90 ± 50	170 ± 90	517 ± 50	687 ± 70
	20-30	37 ± 23	170 ± 40	200 ± 50	50 ± 50	407 ± 70	457 ± 100
	30-40	10 ± 4	150 ± 50	100 ± 40	400 ± 200	260 ± 60	660 ± 200
	40-50	12 ± 5	210 ± 50	70 ± 40	390 ± 160	292 ± 70	682 ± 180
	Total	312 ± 160	1820 ± 320	940 ± 260	1810 ± 670	3072 ± 390	4882 ± 770
Dead	0-5	69 ± 34	1240 ± 240	120 ± 60	40 ± 30	1429 ± 230	1469 ± 250
	5-10	53 ± 25	640 ± 80	100 ± 50	210 ± 110	793 ± 120	1003 ± 200
	10-20	86 ± 67	530 ± 80	50 ± 30	0	666 ± 90	666 ± 90
	20-30	43 ± 19	380 ± 120	30 ± 10	0	453 ± 120	453 ± 120
	30-40	27 ± 14	200 ± 50	20 ± 10	0	247 ± 50	247 ± 50
	40-50	27 ± 11	170 ± 30	5 ± 2	50 ± 40	202 ± 20	252 ± 30
	Total	305 ± 128	3160 ± 450	325 ± 120	300 ± 140	3790 ± 470	4090 ± 560
Total	0-5	119 ± 67	1850 ± 280	310 ± 80	540 ± 180	2279 ± 200	2819 ± 290
	5-10	159 ± 104	990 ± 180	390 ± 120	510 ± 220	1539 ± 200	2049 ± 310
	10-20	183 ± 133	860 ± 110	140 ± 60	170 ± 90	1183 ± 120	1353 ± 150
	20-30	80 ± 41	550 ± 150	230 ± 60	50 ± 50	860 ± 140	910 ± 170
	30-40	37 ± 17	350 ± 70	120 ± 40	400 ± 200	507 ± 100	907 ± 250
	40-50	39 ± 16	380 ± 40	75 ± 40	450 ± 150	494 ± 70	944 ± 190
	Total	617 ± 284	4980 ± 620	1265 ± 300	2120 ± 670	6862 ± 620	8982 ± 1020

Table 3.15 Correlation matrix for fine root biomass and soil fertility, with depth, at Mt Fox. Variables include: roots less than 1 mm diameter (< 1 mm); roots less than 2 mm diameter (< 2 mm); roots less than 5 mm diameter (< 5 mm); available phosphorus (Ava P); total phosphorus (P); Kjeldahl nitrogen (N); total potassium (K); and carbon to nitrogen ratio (C:N). Correlation coefficients higher than 0.87 are significant at the 5% level and are indicated with an asterisk.

	< 1 mm	< 2 mm	< 5 mm	Ava P	P	N	K	C:N
< 1 mm	1.00							
< 2 mm	0.99*	1.00						
< 5 mm	0.97*	0.97*	1.00					
Ava P	0.70	0.68	0.52	1.00				
P	0.77	0.76	0.62	0.98*	1.00			
N	0.94*	0.93*	0.86	0.87	0.93*	1.00		
K	0.24	0.26	0.44	-0.50	-0.43	-0.08	1.00	
C:N	0.33	0.38	0.16	0.81	0.77	0.93*	-0.43	1.00

The total fine root biomass to a depth of 50 cm at Mt Spec was approximately 27 t ha^{-1}, of which live fine roots comprised 17.6 t ha^{-1} (Table 3.16). The majority of the roots in the top 5 cm were less than 2 mm diameter. This size class comprised a decreasing proportion of the total fine roots with increasing depth, with the 40-50 depth increment being comprised mainly of roots greater than 2 mm. The roots at the lower depth tended to be woodier. Roots greater than 2 mm diameter contributed approximately 40% of the total fine root biomass, but only about 6% of the dead fine roots. The distribution of live-fine roots with depth was not correlated with any of the soil variables examined (Table 3.17).

3.4.2d Fine root dynamics

The biomass of fine roots accumulated in the root ingrowth bags at Broadwater, Mt Fox and Mt Spec were significantly different for all durations of incubation, with the exception of the 24-week incubation (Table 3.18). The greatest rate of root production for Broadwater was found after eight weeks incubation. The biomass of fine roots accumulated in the ingrowth bags at Broadwater showed only a slight increase after the eight week samples (Figure 3.5). After the first four weeks in the field at Mt Fox, the root ingrowth bags showed a relatively constant rate of fine root accumulation up to 48 weeks. After this there was a decrease in the rate of fine root accumulation in the ingrowth bags (Table 3.18). The accumulation of fine roots at Mt Spec was initially slow, but increased rapidly after the third month (Figure 3.6). The rate of root production were still found to be increasing after the first 48 weeks of sampling.

Estimated rates of annual fine root production, based on the 48-week incubation period, were 2340 kg ha^{-1} y^{-1} at Broadwater, 3280 kg ha^{-1} y^{-1} at Mt Fox and 2820 kg ha^{-1} y^{-1} at Mt Spec.

Table 3.16 Live, dead and total fine root biomass (kg ha^{-1}) for four size classes, and their distribution with depth at Mt Spec. Values are means ± SEM of 10 replicate cores.

Status	Soil depth (cm)	Root size class (mm)					
		0-0.5	0.5-1	1-2	2-5	Total (0-2)	Total
Live	0-5	73 ± 25	1710 ± 355	1380 ± 270	1410 ± 360	3163 ± 460	4573 ± 710
	5-10	46 ± 15	960 ± 260	940 ± 300	2120 ± 640	1946 ± 500	4066 ± 1050
	10-20	23 ± 7	670 ± 140	470 ± 150	1520 ± 450	1163 ± 250	2683 ± 630
	20-30	4 ± 3	230 ± 130	110 ± 60	1650 ± 1030	344 ± 180	1994 ± 1220
	30-40	5 ± 1	170 ± 30	350 ± 180	2570 ± 260	525 ± 30	3095 ± 60
	40-50	13 ± 9	90 ± 50	130 ± 50	940 ± 340	233 ± 60	1173 ± 230
	Total	164 ± 44	3830 ± 720	3380 ± 760	10210 ± 2310	7374 ± 1110	17584 ± 2930
Dead	0-5	96 ± 34	2040 ± 280	740 ± 300	40 ± 20	2876 ± 370	2916 ± 380
	5-10	75 ± 32	1580 ± 280	800 ± 290	80 ± 40	2455 ± 490	2535 ± 520
	10-20	31 ± 9	1200 ± 210	440 ± 90	70 ± 40	1671 ± 230	1741 ± 260
	20-30	5 ± 1	650 ± 170	190 ± 30	0	845 ± 140	845 ± 140
	30-40	27 ± 4	430 ± 130	170 ± 20	270 ± 190	627 ± 20	897 ± 40
	40-50	9 ± 2	330 ± 140	110 ± 10	50 ± 40	449 ± 160	499 ± 200
	Total	243 ± 62	6230 ± 910	2450 ± 560	510 ± 250	8923 ± 1060	9433 ± 1160
Total	0-5	169 ± 46	3750 ± 600	2120 ± 440	1450 ± 370	6039 ± 710	7489 ± 950
	5-10	121 ± 46	2540 ± 430	1740 ± 490	2200 ± 650	4401 ± 870	6601 ± 1450
	10-20	54 ± 15	1870 ± 300	910 ± 130	1590 ± 450	2834 ± 350	4424 ± 700
	20-30	9 ± 4	880 ± 300	300 ± 30	1650 ± 1030	1189 ± 330	2839 ± 1350
	30-40	32 ± 5	600 ± 160	520 ± 200	2840 ± 450	1152 ± 40	3992 ± 90
	40-50	22 ± 11	420 ± 190	240 ± 60	990 ± 300	682 ± 20	1672 ± 40
	Total	407 ± 89	10060 ± 1490	5830 ± 1010	10720 ± 2440	16287 ± 1740	27017 ± 3430

Table 3.17 Correlation matrix for fine root biomass and soil fertility, with depth, at Mt Spec. Variables include: roots less than 1 mm diameter (< 1 mm); roots less than 2 mm diameter (< 2 mm); roots less than 5 mm diameter (< 5 mm); available phosphorus (Ava P); total phosphorus (P); Kjeldahl nitrogen (N); total potassium (K); and carbon to nitrogen ratio (C:N). Correlation coefficients higher than 0.87 are significant at the 5% level and are indicated with an asterisk.

	< 1 mm	< 2 mm	< 5 mm	Ava P	P	N	K	C:N
< 1 mm	1.00							
< 2 mm	1.00*	1.00						
< 5 mm	0.97*	0.98*	1.00					
Ava P	0.60	0.56	0.50	1.00				
P	0.75	0.71	0.64	0.91*	1.00			
N	0.87	0.85	0.80	0.91*	0.93*	1.00		
K	0.02	0.06	0.25	-0.06	-0.23	0.01	1.00	
C:N	0.48	0.51	0.58	0.15	-0.02	0.35	0.58	1.00

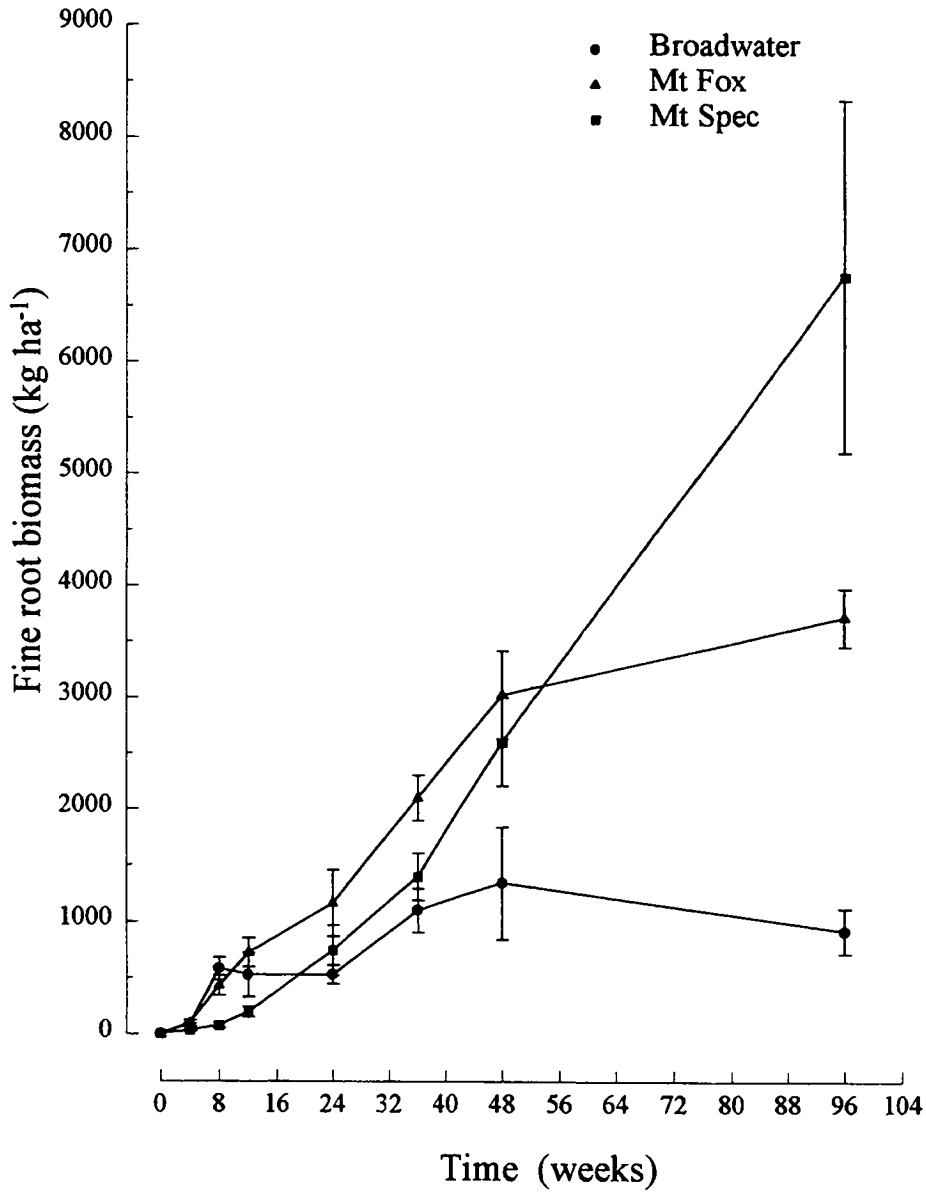


Figure 3.5 Fine root accumulation in root ingrowth bags at Broadwater, Mt Fox and Mt Spec. Bars represent standard errors based on 10 samples.

Table 3.18 Weekly fine root production (± SEM) at Broadwater, Mt Fox and Mt Spec. Fine root production was determined from the mean accumulated fine root biomass in 10 root ingrowth bags at each sampling date divided by the length of incubation period. Probability represents a comparison of fine root production between sites for each sampling date using ANOVAs.

Incubation time (weeks)	Fine root production (kg ha^{-1} $week^{-1}$)			Probability
	Broadwater	Mt Fox	Mt Spec	
4	19 ± 3	23 ± 7	7 ± 1	0.04
8	72 ± 12	53 ± 11	9 ± 3	0.00
12	43 ± 16	60 ± 11	16 ± 4	0.01
24	22 ± 4	48 ± 12	31 ± 9	0.11
36	30 ± 5	58 ± 5	39 ± 5	0.04
48	45 ± 10	63 ± 8	54 ± 8	0.04
96	10 ± 1	39 ± 3	70 ± 16	0.00

The biomass of fine roots accumulated in ingrowth bags incubated for 8 week periods varied significantly over the course of the year (Table 3.19). Fine root production was greatest at all sites during the wet seasons (Figures 3.6). The maximum rate of root production varied between site and sampling time. Estimated annual rates of fine root production based on the combined data of the 7 incubations of the 8-week incubated ingrowth bags were substantially lower than those determined from the single incubation of ingrowth bags for 48 weeks. Broadwater had the highest rate of root production (1620 kg ha^{-1} y^{-1}), while Mt Spec had the lowest (520 kg ha^{-1} y^{-1}). The annual rate of root production at Mt Fox based on the 8-week bags was 1530 kg ha^{-1} y^{-1}.

Table 3.19 Probabilities (P) for an hierarchial ANOVA of fine root biomass accumulated in root ingrowth bags after 8-week periods of incubation in the field. $P < 0.05$ represents a significant difference in fine root biomass.

Source	Probabilities	Degrees of freedom
Site	0.00	2
Time	0.00	6
Size	0.00	2
Replicate	0.02	19
Site*Time	0.00	12
Site*Size	0.00	4
Site*Replicate	0.00	38
Time*Size	0.00	12
Time*Replicate	0.00	114
Size*Replicate	0.17	38
Site*Time*Size	0.00	24
Site*Time*Replicate	0.00	228
Site*Size*Replicate	0.17	76
Time*Size*Replicate	0.20	228

The biomass of fine roots within the root enclosures decreased over time (Figure 3.7). Estimated annual rates of fine root decomposition varied between sites (Table 3.20), with Mt Spec having the highest rate of fine root decomposition. The estimated time taken for the disappearance of 50% of the fine roots varied from 130 to 839 days.

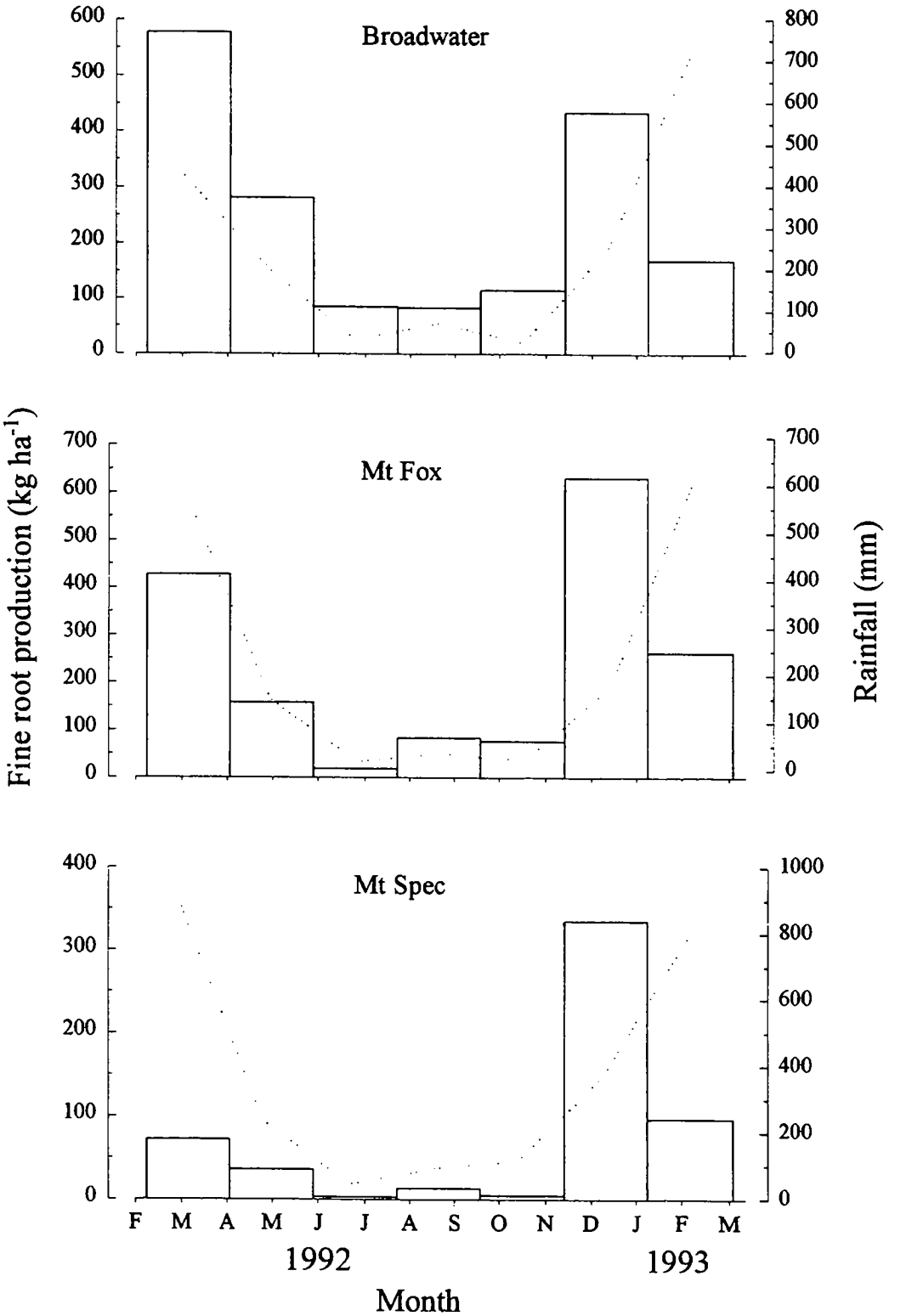


Figure 3.6 Accumulated biomass of fine roots, in root ingrowth bags, after 8-week periods in the field at Broadwater, Mt Fox and Mt Spec. The dotted line represents rainfall totals for the 8-week incubation periods.

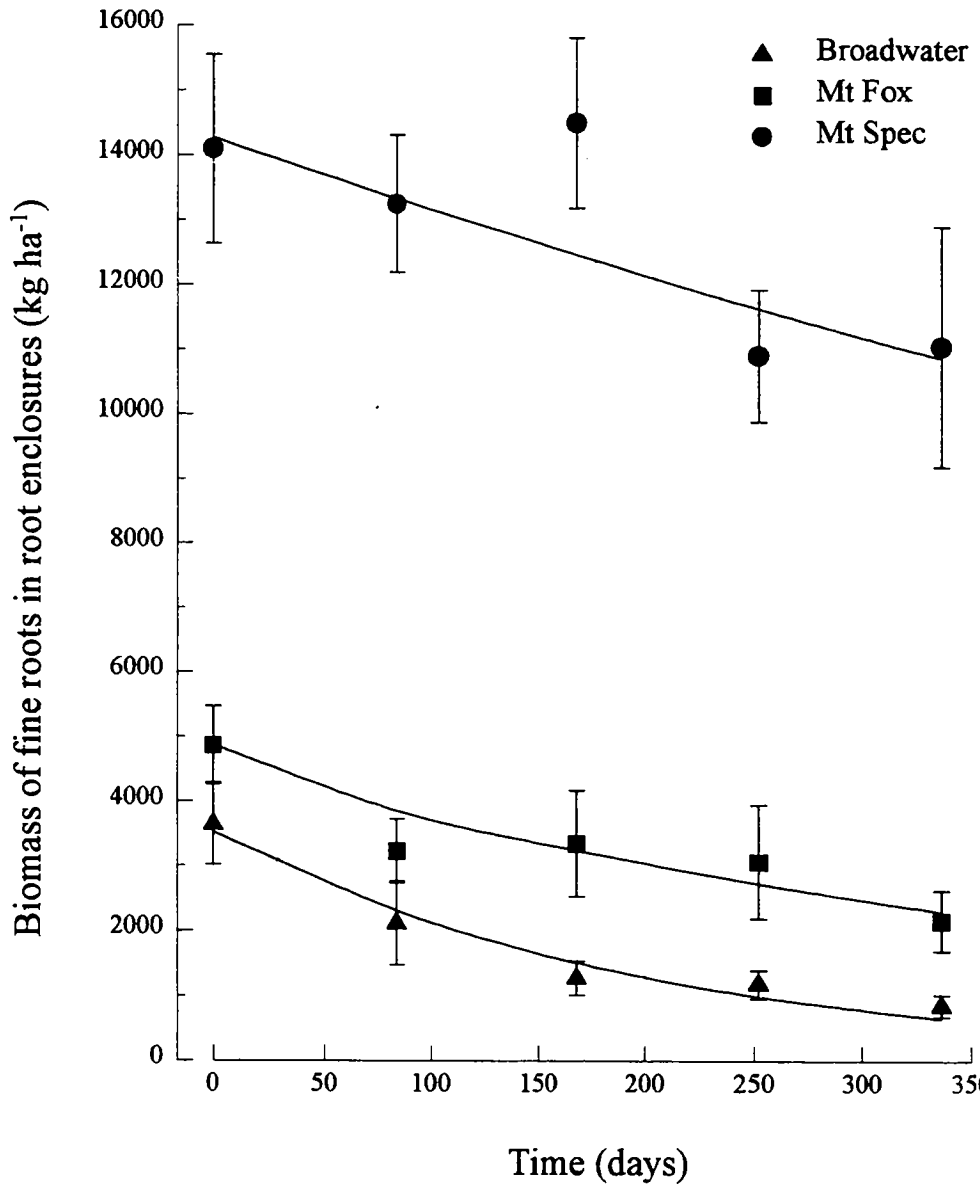


Figure 3.7 Decomposition of fine roots at Broadwater, Mt Fox and Mt Spec. Data shows the biomass of fine roots in root enclosures at each sampling interval.

Table 3.20 Estimated annual rates of fine root decomposition and time taken for the loss of 50% and 95% of fine roots from the root enclosures for Broadwater, Mt Fox and Mt Spec.

Site	Decomposition rates (kg ha^{-1} y^{-1})	t_{50} (days)	t_{95} (days)
Broadwater	2970	130	584
Mt Fox	2410	306	1428
Mt Spec	3650	839	3635

3.5 Discussion

3.5.1 Comparison of soil fertilities at Broadwater, Mt Fox and Mt Spec

All three sites had significantly different concentrations of total phosphorus (Table 3.3), reflecting differences in soil origin. Basalts are known to have a higher phosphorus content than granites (Tate 1985, Tiessen *et al.* 1984, Wild 1988). Basaltic rocks in north Queensland have been found to contain between 0.39 and 0.59% phosphate complexes (Isbell *et al.* 1976), while granites contain between 0.03 and 0.12% (Richards 1980). Alluvial soils tend to be more variable in total phosphorus concentrations, and these are determined, in part, by the types of parent materials that occur within the catchment (Murtha 1986).

The total phosphorus concentrations reported in this study were all lower than mean concentrations reported in the literature (Table 3.22). Mt Fox and Mt Spec are the lowest values reported for their respective soil parent material. These lower than average concentrations of total phosphorus could be due to variations in phosphate content of the parent material, differences in pedological processes at the sites, or differences in the analytical techniques used to determine total phosphorus levels.

Table 3.21 Range of chemical concentrations (% dry weight) in basaltic and granitic rocks from north Queensland. The data for the basalt was determined by Isbell *et al.* (1976) for a range of basalts occurring in the wet tropics. The data for granite was obtained from Richards (1980).

Chemical	Basalt	Granite
SiO_2	48.7 - 52.2	67.4-77.0
TiO_2	2 - 2.5	0.1-0.6
Fe_2O_3	2 - 7.3	0.2-1.1
FeO	4.1 - 8.4	1.1-2.9
Al_2O_3	13.7 - 17.8	12.2-15.2
MnO	0.14 - 0.21	0.02-0.08
MgO	5.1 - 9.9	0.1-1.3
CaO	8.5 - 10.1	0.7-3.7
K_2O	1.15 - 1.8	3.3-4.8
P_2O_5	0.39 - 0.59	0.03-0.12

Different sources of soil parent materials are known to have different levels of phosphorus. The soils at Mt Fox are derived from an olivine basalt which is known to have lower phosphorus levels than other types of basalt (Stace *et al.* 1968). The lithology of granites in north Queensland is variable and includes quartz gabbro, acid biotite and granodiorite (Laffan 1988). These minerals have a range of weatherability and chemical compositions, and the relative proportion of these minerals within the granite will affect the fertility of the soil (Laffan 1988, Mohr *et al.* 1972).

The formation of soil is a complex process which is influenced by climate, topography, time and biological influences. The spatial variability of these factors, and their interactions, result in the formation of a high diversity of soils from a single soil origin (Spain 1991). Within the wet tropics of north

Queensland, the spatial variability of soil-forming factors has resulted in the formation of over a hundred different soil series from the soil origins examined in this study (Cannon *et al.* 1992, Laffan 1988, Murtha 1986, 1989, Thompson & Cannon 1988).

There are a variety of techniques which have been used to determine total phosphorus concentrations in soil (Anderson & Ingram 1989, Rayment & Higginson 1992). The sulphuric-acid digestion utilised in this study may not have been completely effective in releasing phosphorus from some of the calcium and aluminum-phosphate complexes, which may have led to an underestimation of the total phosphorus concentrations.

The high concentrations of total phosphorus in the soils of Mt Fox were associated with high concentrations of available phosphorus. A greater percentage of the total phosphorus, however, was available to plants in the alluvial soils at Broadwater. The concentrations of available phosphorus were not significantly different between these two sites and, while lower than the mean values determined for these soil groups, they were within the ranges reported for north Queensland soils (Table 3.22). The granite-derived soils had extremely low concentrations of available phosphorus. The concentrations of available phosphorus in the top 10 cm were substantially lower than those reported in Table 3.22, and by Congdon and Herbohn (1993) for a nearby plot.

All sites showed a decrease in both total and available phosphorus with depth (Tables 3.4, 3.5 & 3.6). The higher levels of total and available phosphorus in the surface soil probably result from the mineralisation and release of nutrients from organic matter accumulated from litterfall (Gillman 1976, Spain 1984).

Table 3.22 Mean concentrations and ranges of selected soil nutrients in the top 10 cm of soils derived from alluvium, basalt and granite in north Queensland. Data compiled from Cannon *et al.* (1992), Laffan (1988), Murtha (1986, 1989), Murtha *et al.* (1994) and Spain *et al.* (1989).

Mean Range	Soil origin		
	Alluvial	Basalt	Granite
Total - C (mg g^{-1})	37 13 - 64	48 5 - 74	30 28 - 60
Total - N ($\mu g\ g^{-1}$)	2700 1100 - 3900	4000 300 - 5300	2800 1800 - 3400
Total - K ($\mu g\ g^{-1}$)	18500 1700 - 34800	2800 300 - 11200	5900 600 - 15900
Total - P ($\mu g\ g^{-1}$)	490 30 - 950	3300 950 - 5380	330 200 - 700
Available - P ($\mu g\ g^{-1}$)	32.5 5 - 80	40 8 - 130	13 14 - 20
CEC (cmol (+) kg^{-1})	23.5 4 - 19	23 9 - 50	16 2 - 36
Exchangeable K (cmol (+) kg^{-1})	0.6 0.1 - 1.5	0.7 0.3 - 2.2	0.2 0.1 - 0.3
Exchangeable Ca (cmol (+) kg^{-1})	2.2 0.2 - 7.4	8.2 0.7 - 27.9	1.3 0.1 - 3.4
Exchangeable Mg (cmol (+) kg^{-1})	1.6 0.7 - 3.0	2.6 0.8 - 6.7	0.9 0.1 - 1.3
Exchangeable Na (cmol (+) kg^{-1})	0.04 0.02 - 0.12	0.13 0.04 - 0.34	0.10 0.02 - 0.23

All sites had higher Kjeldahl nitrogen concentrations than the ranges reported in Table 3.22. Soil organic carbon concentrations were also high at each site. There are a variety of factors that could cause these high nitrogen and carbon values. Differences in altitude and climatic conditions between the sites of this study and those listed in Table 3.22 may be important. Spain (1990) found an inverse relationship between carbon and nitrogen concentrations and altitude or temperature. Differences in the methods used to determine soil

organic carbon may also be important. The studies listed in Table 3.22 used the Walkley-Black method, which does not heat the acidified dichromate solution. This lack of heating can result in an incomplete oxidation of organic matter and, as a consequence, underestimate the values for organic carbon (Rayment & Higginson 1992). Carbon to nitrogen ratios are a useful indicator of site quality as they are related to the speed of mineralisation and immobilisation of organic matter (Rayment & Higginson 1992). The surface soils of Broadwater and Mt Fox had C to N ratios that indicated that the humus is well broken down (Rayment & Higginson 1992, Yamakura & Sahunalu 1990).

The cation exchange capacities (CEC) were within the range recorded for north Queensland soils (Table 3.22). Soils derived from alluvium and basalt tend to have greater cation exchange capacities and exchangeable cations than soils from granite (Teitzel & Bruce 1971b, 1972a). Soils derived from granite are dominated by minerals with low CEC. The greatest CEC occurred in the top 10 cm of soil at all sites, and decreased with soil depth. Organic matter is the main source of CEC in tropical soils (Gillman 1976).

Exchangeable cation levels varied between sites. All sites had the greatest levels in the top 10 cm of soil, and levels decreased with increasing soil depth. Exchangeable potassium content was low at Broadwater and Mt Spec, and apart from the top 10 cm at both sites, was below 0.2 cmol (+) kg^{-1}, a level widely considered to be critical for plant growth in Queensland (Teitzel & Bruce 1971b). While no critical exchangeable magnesium values have been documented for the soils of tropical Australia (Hailes *et al.* 1997), the concentrations determined in this study were below levels that are considered to represent magnesium deficiencies in New South Wales soils (Cumming & Elliot 1991).

The total nitrogen levels at these three sites were substantially lower than those reported by Edwards and Grubb (1982) for an extremely fertile alluvium of predominantly volcanic origin (Table 3.23). Total phosphorus stocks of the sites examined in this study were also substantially lower than those reported by Edwards and Grubb (1982), however, the quantity of available phosphorus in the soils at Mt Fox and Broadwater were substantially greater (Table 3.23). However, it is unclear whether these differences result from different methodologies, or are due to differences in availability of phosphorus between the sites.

3.5.2 Comparison of the above-ground vegetation at Broadwater, Mt Fox and Mt Spec

Despite the significant differences in levels of soil fertility between the three sites, there were few differences in the structural measures and biomass of the above-ground vegetation, however, the small plot size used in this study may affect these estimates (Congdon & Herbohn 1993).

The maximum tree heights were similar for all sites (Table 3.9). The nutrient-poor soil of Mt Spec had the greatest basal area. The basal areas determined in this study are within the range reported for previous studies on the rain forests of north Queensland (Table 3.24). The number of stems per hectare varied substantially between sites, with Mt Spec having the greatest number of stems per hectare. Stem density at Mt Spec was at the upper end of the range reported for rain forests growing on granite-derived soils (Table 3.24). Stem density at Mt Fox was at the lower end of the range reported for rain forests on basalt-derived soils (Table 3.24).

Table 3.23 Nutrient concentrations recorded in a range of tropical rain forest soils.

Location	Depth (cm)	Organic C (t ha^{-1})	Soil nutrients (kg ha^{-1})				Source
			Total N	Total P	Total K	Available P	
Australia							This study
- Broadwater	0-30	103.2	7120	600	910	48.5	
- Mt Fox	0-30	75.7	5870	1180	720	43.6	
- Mt Spec	0-30	75.4	8250	360	4020	22.3	
Brazil							Edmistem (1970)
- El Verde	0-30	-	4260	71	58	-	
Brunei							Pendry (1994)
- Belalong (200 m)	0-20	124	2450	436	-	0.4	
- Belalong (500 m)	0-20	149	2800	424	-	0.4	
- Belalong (850 m)	0-20	157	3050	435	-	0.4	
Jamaica							Tanner (1977)
- Mor ridge	0-45	250	9000	-	-	-	
- Mull ridge	0-40	90	7000	-	-	-	
- Wet slope	0-30	30	3000	-	-	-	
- Gap	0-40	80	9000	-	-	-	
New Guinea							Edwards & Grubb (1982)
- Ridge (I)	0-30	200	19300	2220	-	13.3	
- Ridge (II)	0-30	-	18800	3040	-	13.8	
- Valley	0-30	-	21200	2940	-	16.4	
- Slope	0-30	-	17600	2030	-	20.5	

Table 3.23 *continued.*

Location	Depth (cm)	Organic C (t ha^{-1})	Soil nutrients (kg ha^{-1})				Source
			Total N	Total P	Total K	Available P	
Malaysia (Sabah)							Green (1992)
- Danum	0-30	-	1450	650	-	0.7	
Malaysia (Sarawak)							Proctor *et al.* (1983)
- Alluvial	0-30	120	7800	420	95	-	
- Dipterocarp	0-30	99	6000	360	96	-	
- Heath	0-30	160	7800	190	50	-	
- Limestone	0-30	82	5000	120	46	-	

Table 3.24 Basal area and stem density of north Queensland rain forests for trees greater than 10 cm diameter.

Soil origin	Stem density (tree ha^{-1})	Basal area (m^2 ha^{-1})	Sources
Alluvium			
- Broadwater	880	42.2	This study
- Arsenic Creek	-	43.8	Stocker & Unwin (1989)
- Gosschalk	-	48.0	
- West Claudie	-	43.0	
Basalt			
- Mt Fox	680	55.5	This study
- Plot 594	1324	79.8	Nicholson *et al.* (1988)
- Pin Gin Hill	724	35.6	Spain (1984)
- Gadarra	844	63.0	
- Danbulla	740	33.7	
- Clarke Ra.	-	60.2	Stocker & Unwin (1989)
- Curtain Fig	-	63.0	
Granite			
- Mt Spec	1240	63.4	This study
- Mt Spec (plot 1)	1133	83.7	Congdon & Herbohn (1993)
- Mt Spec (plot 3)	1500	121.3	
- Plot 591	957	69.6	Nicholson *et al.* (1988)
- Plot 625/2	934	61.4	
- Plot 408	827	56.0	
- Plot 207	870	69.0	
- Agapetes	-	58.8	Stocker & Unwin (1989)
- Burgoo	-	40.6	
- Downfall	-	28.2	
- Emerald	-	63.4	
- Little Pine	-	36.0	
- North Mary	-	60.8	
- Robson	-	37.8	

Above-ground biomass estimates obtained in this study varied widely depending on which biomass regression was used (Table 3.10). As mentioned in the preceding Chapter it is extremely difficult to test and calibrate a biomass regression generated at one site for application at another. There is only one published biomass estimate for a north Queensland tropical rain forest with which to compare the data of this study. Holt and Spain (1986) estimated the above-ground biomass at one rain forest site in north Queensland using regression equations developed by Cannell (1984) which

relate above-ground woody biomass to basal area and mean stand height. Their estimate for a complex notophyll vine forest on basaltic soils was 548 t ha^{-1}. However, the suitability of the model used and the accuracy of their estimate were never examined. The biomass estimates for Broadwater, Mt Fox and Mt Spec, determined from regression 1a for all trees greater than 5 cm diameter, were within the ranges reported in Table 3.25.

Previous studies have found little evidence to suggest that forest stature or above-ground biomass are related to soil fertility levels (Ashton & Hall 1992, Proctor *et al.* 1983, Vitousek & Sanford 1986). In a study of the mixed dipterocarp forest of northern Borneo, Ashton and Hall (1992) found no correlation between forest stature and extractable soil nutrient concentrations. Similarly, Vitousek and Sanford (1986) found little difference in above-ground biomass at sites with different soil fertilities, with the exception of sites occurring on the most-infertile white-sand soils.

3.5.3 Fine root biomass

There are few data with which to compare the present study. Comparisons with other studies are complicated by the lack of standard sampling and sorting techniques, depths and root sizes. The biomass of roots less than 5 mm determined in this study are within the range, 1.1 to 123.4 t ha^{-1}, reported in previous published studies on tropical rain forests (Table 3.26). A number of the studies listed in Table 3.26 do not differentiate between live and dead roots.

Table 3.25 Above-ground biomass estimates for tropical rain forests. The estimates for the Australian sites were determined using biomass regressions, while all others sites were determined by harvesting the vegetation.

Soil fertility class	Biomass ($t\ ha^{-1}$)	Source
Moderately fertile		
Australia		
- Broadwater	252	This study
- Mt Fox	256	
- Gadgarra	584	Holt & Spain (1986)
Ghana	233	Greenland & Kowal (1960)
New Guinea	310	Grubb & Edwards (1982)
Panama	316	Golley *et al.* (1975)
Venezuela	402	Hase & Fölster (1982)
Mean	320	
Infertile		
Australia - Mt Spec	285	This study
Brazil	406	Klinge (1975)
Colombia	182	Fölster *et al.* (1976)
India		
- Agumbe	420	Rai & Proctor (1986)
- Bannadapare	454	
- Kagneri	460	
- South Bhadra	649	
Ivory Coast		
- Banco	510	Bernhard-Reversat (1977)
- Yapo	470	
Venezuela	335	Jordan & Uhl (1978)
Mean	430	

This study found no significant correlation between available phosphorus concentration and fine root biomass (Figure 3.2a-c). In contrast to Gower's (1987) study, soil nitrogen concentrations were negatively correlated with the biomass of roots less than 1 mm and 2 mm (Figure 3.2e&f). When data from

other published studies (Cavelier 1992, Green 1992, Kellman 1990, Pendry 1994, Sanford 1985) are included in the analysis, only available phosphorus concentration was significantly negatively correlated with fine root biomass (Figure 3.8), with no significant correlation being found for soil nitrogen concentration.

Table 3.26 Fine root biomass recorded in tropical rain forests.

Location		Depth	Fine root biomass (t ha^{-1})				Source
			Root diameter class (mm)				
		(cm)	<1	<2	<5	<6	
Australia	Broadwater	30	1.5	2.3	5.0	-	This study
	Kirrama	30	5.5	7.5	12.0	-	
	Mc Ivor River	30	1.4	1.8	2.9	-	
	Mt Fox	30	1.7	2.5	3.8	-	
	Mt Spec	30	3.7	6.6	13.2	-	
	Mt Webb	30	1.4	2.2	4.4	-	
	Banksia	30	-	3.0	-	-	Sam (1995)
	Ecotone	30	-	0.9	-	-	
	Kauri	30	-	1.1	-	-	
	Maple	30	-	1.1	-	-	
	Ridge	30	-	2.2	-	-	
	Upland	30	-	2.4	-	-	
Brazil	Latosol	27	3.1	5.3	-	9.3	Klinge (1973)
	Podzol	29	3.4	4.9	-	9.2	
Costa Rica	Terrace	30	0.2	0.5	1.1	-	Gower (1987)
	Upland	30	0.5	1.1	1.6	-	
	Premontane	30	-	2.4	-	-	Raich (1980)
Ghana	Upper slope	30	-	3.8	5.6	-	Lawson *et al.* (1970)
	Middle slope	30	-	10.2	12.4	-	
	Bottom slope	30	-	3.4	4.8	-	
Ivory Coast	Banco P.	30	-	12.6	15.9	-	Huttel (1975)
	Banco T.	30	-	11.0	16.8	-	
	Yapo	30	-	12.4	18.4	-	
Mexico	Recent sand	40	-	3.5	-	-	Kellman (1990)
	Weathered sand	40	-	4.8	-	-	

Table 3.26 continued.

Location		Depth	Fine root biomass (t ha^{-1})				Source
			Root diameter class (mm)				
		(cm)	<1	<2	<5	<6	
New Guinea	Montane	25	-	-	-	4	Edwards & Grubb (1982)
Panama	Semideciduous	30	1.4	2.8	4.7	-	Cavelier (1992)
	Montane	30	2.0	4.0	6.6	-	
Tanzania	Montane	30	-	-	8.5	-	Lundgren (1978)
Venezuela	Caatinga Ya-I	40	-	-	44.4	-	Klinge & Herrera (1978)
	Caatinga Ya-II	40	-	-	58.6	-	
	Caatinga Cu-III	40	-	-	25.3	-	
	Caatinga Cu-IV	40	-	-	67.9	-	
	Caatinga Cu-VII	40	-	-	123.4	-	
	Caatinga Cu-X	40	-	-	53.0	-	
	Bana	30	11.4	14.7	22.9	-	Sanford (1985)
	Caatinga/Bana	30	11.0	15.7	23.7	-	
	Caatinga	30	12.8	17.9	27.1	-	
	Tierra Firme	30	10.3	13.8	20.4	-	
	TF/Caatinga	30	35.4	39.5	46.2	-	
	Oxisols	34	-	-	28.3	-	Stark & Spratt (1977)

At all sites examined in this study, the greatest concentration of fine roots was within the top 10 cm of soil, and this decreased rapidly with increasing depth (Figure 3.4). This is similar to the findings of other published studies (Cavelier 1992, Kellman 1990, Pendry 1994, Sam 1995). The proliferation of fine roots in the top few centimetres of soils is important for the conservation of nutrients within tropical rain forests (Jenik 1978, Klinge 1973). These roots are involved in the uptake of nutrients, either by direct absorption or via mycorrhizal associations. These surface roots have access to the highest concentrations of nutrients in the soil at the top of the profile, and to the nutrients returned to the soil in litterfall and throughfall.

The concentration of roots in the top few centimetres of soils has given rise to the misconception that tropical rain forest trees are shallow rooted, and the role of deeper roots is often underestimated (Bruenig 1996). Nepstad *et al.*

(1994) reported maximum rooting depths of 18 m for an Amazonian rain forest. The occurrence of these fine roots further down the soil profile is important for plant-water relationships, particularly in rain forests with distinct dry seasons. During the wet season, plants extract water from the shallow surface layers where the root density is greatest (Nepstad *et al.* 1994). As these layers dry out during the dry season, there is a progressive shift towards using water from deeper down the soil profile (Canadell *et al.* 1996, Nepstad *et al.* 1994). The importance of these deep occurring roots for plant-water balance in tropical rain forests may further be enhanced through the process of hydraulic lift (Canadell *et al.* 1996). Hydraulic lift is a mechanism utilised by plants to pump water from deep soil layers into the uppermost parts of the soil profile. The water taken up by plants from the deep soil layers during the night is released from the fine roots in the upper soil layer (Caldwell *et al.* 1991). This is then utilised the following day by the same plants or others within the immediate vicinity. While there is some evidence of hydraulic lift for a tropical heath forest in Brunei (Becker *pers. comm.*), the importance of this in the wet tropical rain forests of north Queensland has not been determined.

Hydraulic lift is also thought to play a significant role in mitigating fine root mortality during the dry season (Caldwell *et al.* 1991). Fine roots are susceptible to moderate decreases in soil water availability, with Dean (1979) reporting a significant increase in fine root mortality when soil water potential dropped below -10 kPa. The daily efflux of water from the fine roots associated with hydraulic lift is important in maintaining soil water potential above critical levels (Caldwell *et al.* 1991), and may also play an important role in maintaining mycorrhizal associations and soil nutrient availability during the dry season (Caldwell *et al.* 1991, Nye & Tinker 1977).

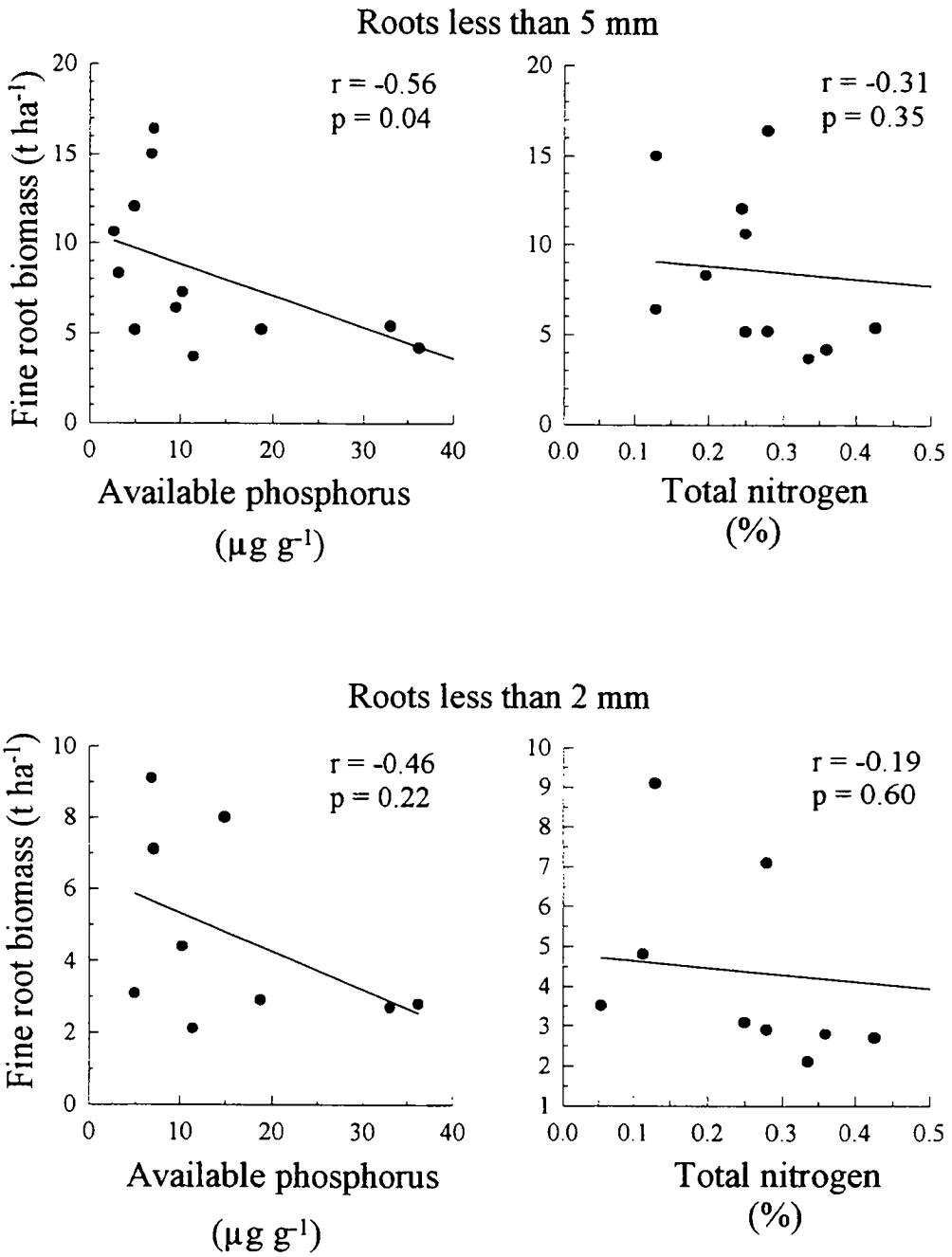


Figure 3.8 **Relationship between the biomass of fine roots (t ha^{-1}) and concentrations of soil nitrogen (%) and available phosphorus ($\mu g\ g^{-1}$) for tropical rain forests. Data are from this study, Cavelier (1992), Green (1992), Kellman (1990), Pendry (1994) and Sanford (1985).**

3.5.4 Fine root dynamics

There were significant differences in the annual rates of fine root production between the sites (Table 3.18). The estimates of fine root production determined in this study are relatively high with in excess of 3.2 t ha^{-1} y^{-1} of fine roots being produced in the top 10 cm of top soil at Mt Fox. Rates of fine root production for tropical forests have been found to vary between studies using root ingrowth bags, ranging from 0.5 t ha^{-1} y^{-1} for a lower montane rain forest in Brunei to 11.2 t ha^{-1} y^{-1} for a Terra Firme forest in Venezuela (Table 3.27). There are problems, however, in comparing the results found in this study and those listed in Table 3.27. Different rooting substrates, soil depths and incubation times were used in these studies.

The effects of different rooting substrate on fine root production in root ingrowth bags is unclear. Green (1992) found no significant difference between rates of root growth in perlite and soil for a lowland mixed dipterocarp forest in Sabah. Proctor (unpublished in Pendry 1994), however, found a significant difference in root growth within these two substrates.

Most root production studies utilising root ingrowth bags use a single incubation period of between five and eight months (Cavelier 1989, Green 1992, Pendry 1994). Estimated rates of fine root production obtained in this study varied between different durations of incubation (Table 3.18). Estimates using a series of 8-week incubated bags over a 56 week sampling period substantially underestimated the rates of production compared to bags incubated for 48 weeks. Incubation time has been found to have a significant influence on fine root production in temperate perennial grasslands, with long-term incubations (2-12 months) yielding higher estimates than short-term incubations (1 month) (Steen 1985). This is probably due to the disturbance effect associated with the insertion of the ingrowth bags into the soil (Neill 1992).

Table 3.27 Fine root production in tropical rain forests measured by the root ingrowth method.

Location	Root size class (mm)	Substrate	Depth (cm)	Fine root production ($t\ ha^{-1}\ y^{-1}$)	Source
Australia					
- Broadwater	< 5	Soil	10	2.34	This study
- Mt Fox	< 5	Soil	10	3.28	
- Mt Spec	< 5	Soil	10	2.82	
Brunei					
- Belalong (250 m)	< 5	Perlite	20	0.92	Pendry (1994)
- Belalong (500 m)	< 5	Perlite	20	2.16	
- Belalong (850 m)	< 5	Perlite	20	0.48	
Indonesia					
- Barito Ulu	< 5	Perlite	20	0.96	Proctor unpublished in Pendry
- Barito Ulu	< 5	Soil	20	5.02	(1994)
- Barito Ulu	< 5	Perlite	20	0.90	
- Barito Ulu	< 5	Soil	20	1.82	
- Barito Ulu	< 5	Perlite	20	0.87	
- Barito Ulu	< 5	Soil	20	2.28	
Malaysia					
- Danum	< 5	Perlite	30	2.63	Green (1992)
- Danum	< 5	Soil	30	2.12	
Panama					
- Gigante Peninsula	< 2	Soil	25	3.70	Cavelier (1989)
- Cordillera Central	< 2	Soil	25	1.14	
Venezuela					
- San Carlos	< 2	Soil	10	2.47	Sanford (1985)
- San Carlos		Vermiculite	10	11.17	Cuevas & Medina (1988)
- San Carlos		Vermiculite	10	1.20	
- San Carlos		Vermiculite	10	2.35	

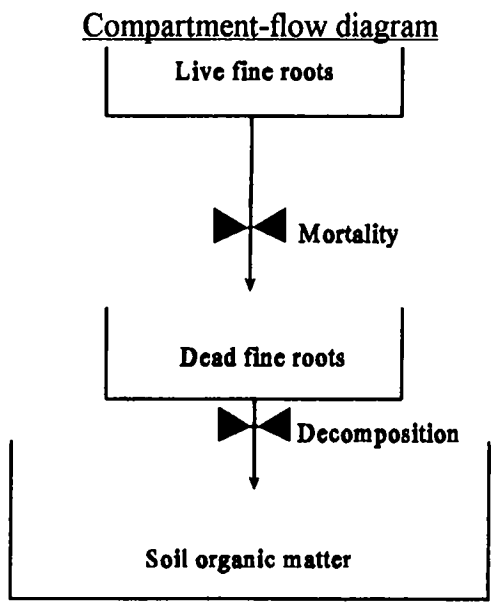
Different sites showed different responses to the period of incubation (Table 3.18). After the first 8 weeks, there was a relatively constant rate of fine root accumulation at Broadwater and Mt Fox. Both of these sites appeared to reach saturation after 48 weeks, and the rate of root accumulation decreased. The rate of fine root accumulation showed more variation at Mt Spec, and was found to increase with increasing incubation time. The increasing rate of accumulation in the poorer soils of Mt Spec may, in part, be due to selective exploitation of the soil in the root ingrowth bags (St. John *et al.* 1983). Fine roots have been found to concentrate in localised sites of high nutrient availability in the soil (St. John *et al.* 1983). While root ingrowth bags may not alter nutrient availability, they create micro sites within the rhizosphere where there is reduced resistance to penetration and reduced root competition which may result in enhanced root ingrowth (Neill 1992).

Very little is known about the decomposition of fine roots in any ecosystem (Vogt *et al.* 1991), and this is particularly true of rain forest ecosystems. Long-term decomposition studies have found that the rate of decomposition is rapid in the first year, with between 20% and 40% of root material being lost from root-litter bags, although this decreases with time (Lõhmus & Ivask 1995). The rate of decomposition of fine roots is influenced by the availability of water, soil temperature and the chemical quality of the roots (Berg 1984, Santantonio & Grace 1987, van Praag 1991, Vogt *et al.* 1991). Fine root decomposition in this study seemed to be related to water availability, with Mt Spec having the greatest annual rainfall and the greatest rate of fine root decomposition.

Comparisons between studies is difficult due to differences in methods used to assess fine root decomposition. The most commonly used methods are root litterbags and enclosure methods (Vogt *et al.* 1991). These different methods

are known to yield significantly different rates of fine root decomposition at the same site (Gholz *et al.* 1986), and both techniques are known to have both advantages and disadvantages. The enclosure method is known to overestimate rates of decay if the enclosures are not sufficiently large (Vogt *et al.* 1991). This overestimation results from higher soil moisture and nutrient levels being retained in the enclosures due to lack of uptake by living roots .

The dynamics of fine roots at the three sites in this study were found to be substantially different (Figure 3.9). The nutrient-rich soil of Mt Fox had the faster rates of root turnover, with an estimated turnover of 137% of the fine roots annually. Conversely, the nutrient-poor soil of Mt Spec had a substantially lower rate of fine root turnover, with approximately 33% of the fine roots being turned over annually. While there was a significant difference in fine root production between the sites, it was less than the difference in the rate of turnover. This tends to suggest that there are differences in root longevities between the sites, with Mt Spec maintaining its high fine root biomass with slower rates of fine root turnover and greater fine root longevity. Little information is available regarding the longevity of fine roots for tropical rain forests. Fine roots in temperate ecosystems have been found to live from a few weeks to as long as 12 years (Kolesnikov 1971, Vogt & Bloomfield 1992). Fine root longevity is known to be affected by a number of abiotic factors, particularly soil moisture, nutrient availability and temperature (Vogt & Bloomfield 1992). The role that soil nutrient status plays in determining fine root longevity is unclear (Vogt & Bloomfield 1992). Persson (1983) reported greater rates of fine root turnover and shorter root longevity for *Pinus sylvestris* on nutrient-rich sites compared to nutrient-impoverished sites. Conversely, Alexander and Fairley (1983) reported increased fine root longevity of *Picea sitchensis* with increased nitrogen fertilisation.



	Broadwater	Mt Fox	Mt Spec
Production ($kg\ ha^{-1}\ y^{-1}$)	2340	3280	2820
Turnover (%)	(85)	(137)	(33)
Live fine roots ($kg\ ha^{-1}$)	2760	2400	8640
Mortality	?	?	?
Dead fine roots ($kg\ ha^{-1}$)	880	2470	5450
Decomposition ($kg\ ha^{-1}\ y^{-1}$)	2970	2410	3650
Soil organic matter ($kg\ ha^{-1}$)	39590	29480	29950

Figure 3.9 Fine root dynamics at Broadwater, Mt Fox and Mt Spect represented by the compartment-flow diagram of Santantonio and Grace (1987).

The lower rate of fine root production in the nutrient-poor soil at Mt Spec may be a consequence of greater carbon allocation to mycorrhizal associations. Mycorrhizal associations have been found to yield a greater benefit to plants growing on nutrient-poor soils (Jordan 1989). The mycorrhizal hyphae extend into the soil and serve as an extension of the root system, which is physiologically and geometrically more efficient for nutrient uptake than the root system of the plant (Mukerji *et al.* 1991). Mycorrhizae may also provide a direct pathway for the transfer of nutrients from the decomposing litter to the fine roots (Went & Stark 1968). The cost in terms of photosynthates of supporting mycorrhizal associations is hard to estimate, and is dependent on the type of association formed (Fogel 1990, Gianinazzi-Pearson & Gianinazzi 1983). The cost of maintaining ectomycorrhizae is greater than for vesicular-arbuscular mycorrhizae (Fogel 1990).

3.5.5 Resource allocation in rain forests

The source-sink theorem of resource allocation predicts that forests growing on infertile soils should allocate a greater proportion of resources to fine roots than those growing on fertile soils, as this "investment" in nutrient acquisition should increase growth and/or reproduction (Bloom *et al.* 1985).

The standing crop of live fine roots to estimated total above-ground biomass ratios obtained in this study ranged from 1.9 to 6.2%, with the greatest fine root to above-ground biomass ratio occurring at the nutrient-poor site of Mt Spec (Table 3.28). In previously published studies, these ratios have ranged from 0.8 to 7.1%. While differences in sampling depth and root size classes hamper the comparison of these studies, in general, the greatest ratios were found in forests on low fertility soils, supporting the theorem of Bloom *et al.* (1985).

Table 3.28 Biomass allocation (t ha^{-1}) in tropical rain forests, with the ratio of fine roots to above-ground biomass expressed as a percentage given in parentheses. Above-ground biomass estimates were obtained by harvesting the vegetation, with the exception of the data from this study which were determined using biomass regressions. Fine root biomass is for roots less than 5 mm diameter, with the exception of Greenland and Kowal (1960) and Klinge (1975) where estimates include all roots less than 6 mm.

Soil fertility	Biomass		Sampling depth (cm)	Source
	Above-ground (t ha^{-1})	Fine roots (t ha^{-1})		
Moderately fertile				
- Broadwater	252	5.6 (2.2)	50	This study
- Mt Fox	256	4.9 (1.9)	50	This study
- Ghana	238	4.9 (2.1)	120	Greenland & Kowal (1960)
- New Guinea	310	2.8 (0.8)	25	Edwards & Grubb (1982)
Infertile				
- Mt Spec	285	17.6 (6.2)	50	This study
- Brazil	406	15.3 (3.8)	107	Klinge (1975, 1976)
- Venezuela	348	24.6 (7.1)	-	Grimm & Fassbender (1981)

There are, however, a number of possible sources of error associated with the estimates obtained in this study. Firstly, above-ground biomass estimates were determined from biomass regressions, and estimates varied substantially depending on which regression was utilised (Table 3.10). Without further testing of the regressions on the sites of interest, it is not possible to examine the accuracy of the estimates. The incomplete recovery of fine roots from the soil and the incorrect classification into live and dead fractions are other possible sources of error in fine root biomass estimates. The dry sieving technique used to separate fine roots from the soil in this study is thought to be adequate for the separation of roots between 2 to 5 mm in diameter, but can result in the loss of up to 40% of roots less than 2 mm diameter (Fogel 1983). It is extremely difficult to distinguish between live and dead fine roots, and the possibility for error is great (Böhm 1979). Classification of fine roots

into live and dead fractions is based either on morphological criteria or on the reaction to vital stains (Fogel 1983). Classification based on morphological criteria are thought to be subjective and susceptible to variation in root morphology between species, while vital staining is time consuming and different species react differently to the stains (Fogel 1983).

A comparison of fine root and shoot productivity between the three sites is difficult due to a lack of leaf production data. While the leaf litterfall data of Herbohn & Congdon (1993) for two sites in the Mt Spec State Forest can be used as an indication of leaf production at the Mt Spec site examined in this study, there are no leaf litterfall data for Mt Fox or Broadwater. The only available leaf litterfall data for rain forests on basaltic soils in north Queensland are those of Brasell *et al.* (1980) and Spain (1984). Because the sites examined in these studies had substantially greater annual rainfall than Mt Fox, it is not known how comparable these data are to Mt Fox.

Based on the available data, the annual rate of fine root production was approximately 72% of the annual leaf litterfall rate at Mt Spec (Table 3.29), while fine root production at Mt Fox was approximately 60% of the annual leaf litterfall rate reported for rain forests on basalt-derived soils in north Queensland. The ratio of fine root to shoot production determined from previously published studies is highly variable, ranging from 8 to 266% of leaf production, with no clear trends between sites on soils of differing fertility (Table 3.29).

This lack of a clear trend between soil fertility and fine root to shoot productivity is in contrast to the theory of Bloom *et al.* (1985), who predict that trees growing on infertile sites should allocate a greater proportion of their resources into fine root production than those growing on fertile sites. The lack of a clear relationship between soil fertility and resource allocation

may be due to a number of factors. Firstly, all of the studies listed in Table 3.29 examined fine roots only. No data are available on carbon allocation to mycorrhizal associations. These associations might utilise a greater proportion of the carbon allocated below-ground at sites with low fine root to shoot production ratios. Secondly, the different methods used to determine fine root production may have a substantial effect on the results obtained. The studies reported in Sanford and Cuevas (1996) and Vitousek and Sanford (1986) used sequential coring to estimate fine root production, while those of this study and Pendry (1994) used root ingrowth bags. It is unknown how production estimates compare between the two methods. Neill (1992) reported that estimates based on long-term ingrowth bags are comparable to those determined by soil coring, however, others have reported significant differences in estimates obtained by the two methods (Green 1992, Sanford 1985). Furthermore, the studies using root ingrowth bags to estimate fine root production used different rooting substrates. Pendry (1994) utilised perlite as his rooting substrate, while root-free soil was used in this study. The effect of different rooting substrate on estimates of fine root production remain unknown (Green 1992, Pendry 1994).

In general, fine root biomass of tropical rain forests is greatest on nutrient-poor sites and lowest on more fertile sites. However, it is unknown whether this variation is due to differences in available phosphorus, soil nitrogen or some other, as yet, undetermined factor. In contrast, above-ground biomass does not vary substantially over a range of soil fertilities. The greater fine root biomass on nutrient-poor sites results in rain forests growing on these soils supporting a greater fine root biomass relative to their above-ground biomass, as compared to rain forests growing on nutrient-rich soils. There is, however, no clear trend in the relationship between soil fertility and the ratio of fine root to shoot production.

Table 3.29 Leaf litterfall and fine root production (t ha^{-1} y^{-1}) in tropical rain forests. The ratio of fine root to leaf production expressed as a percentage is given in parentheses. Fine root production data is for the top10 cm of soil, except for Pendry (1994) where data is for the top 20 cm.

Soil fertility	Production		Source
	Leaf litterfall (t ha^{-1} y^{-1})	Fine roots (t ha^{-1} y^{-1})	
Moderately fertile			
- Mt Fox	5.5	3.3 (60)	Brasell *at al.* (1980), Spain (1984)/This study
- Costa Rica	7.2	4.1 (57)	Sanford & Cuevas (1996)
Infertile			
- Mt Spec	3.9	2.8 (72)	Herbohn & Congdon (1993)/ This study
- Brunei (250 m)	7.9	0.9 (11)	Pendry & Proctor (1996)/Pendry (1994)
- Brunei (500 m)	7.9	2.2 (28)	Pendry & Proctor (1996)/Pendry (1994)
- Brunei (850 m)	6.0	0.5 (8)	Pendry & Proctor (1996)/Pendry (1994)
- Costa Rica	7.6	14.8 (195)	Sanford & Cuevas (1996)
- Venezuela	5.8	15.4 (266)	Vitousek & Sanford (1986)

Whether plants on nutrient-poor sites allocate greater resources to fine roots as predicted by Bloom *et al.* (1985), or whether differences in fine root biomass are due to slower rates of fine root turnover and greater root longevities at nutrient-poor sites, is unclear. The nutrient-rich sites of Mt Fox and Broadwater had small standing crops of fine roots and fast rates of fine root turnover, and the rain forest on the nutrient-poor soil at Mt Spec had a large standing crop with a slow turnover of fine roots. However, it is possible that differences in the allocation of resources to mycorrhizal associations may exist between rain forests growing on nutrient-rich and nutrient-poor soils. Such differences could be due to greater mycorrhizal costs at nutrient-poor sites. However, at present there are no data regarding the allocation of resources to mycorrhizal associations to confirm or reject this possibility.

In conclusion, fine root dynamics in tropical rain forests remain one of the least known components of these ecosystems. This is due, in part, to root systems being difficult and extremely laborious to sample. Most of the methods employed to examine fine root dynamics cause disturbance to the system being examined (Hendrick *et al.* 1993), and all have several significant possible sources of error.

CHAPTER 4
Nutrient dynamics in fine roots

4.1 Introduction

Soil nutrient status is seen as a major factor influencing nutrient cycling patterns in tropical rain forests (Vitousek & Sanford 1986). Two distinct systems of nutrient cycling based upon the nutrient status of the soil have been recognised (Jordan & Herrera 1981). On nutrient-deficient soils, the majority of the nutrients are retained within the biomass and are tightly cycled. This system, referred to as an oligotrophic system, has highly developed nutrient conserving mechanisms and is characterised by low rates of nutrient accession in litterfall (Herbohn & Congdon 1998). This is in contrast to the eutrophic system found in forests on relatively nutrient rich soils, which is a more open system of nutrient cycling. There is less development of nutrient conserving mechanisms and more nutrients are returned to the soil by litterfall within these forests (Brasell *et al.* 1980). However, the lack of information on the role of fine roots as a pathway of nutrient return to the soil, impedes our understanding of nutrient cycling in tropical rain forests.

The importance of fine roots as a nutrient conserving mechanism within tropical rain forests is well documented (Jordan 1989). Their role as a nutrient store and as a pathway for the return of nutrients from the vegetation to the soil has largely been ignored, with most studies concentrating on the above-ground portion of the vegetation. The few studies that have examined nutrient stocks in the above- and below-ground parts of the vegetation have shown that, while fine roots account for approximately 10% of the total biomass, they account for approximately 20% of the total nitrogen and 16% of the total phosphorus contained within the vegetation (Vitousek & Sanford 1986). Furthermore, while the concentrations of

nutrients within fine roots are generally lower than those found within the foliage, the rate of turnover of fine roots can be considerably higher than that of the foliage (Nambiar 1987, Vitousek & Sanford 1986). Sanford and Cuevas (1996) estimated that 190 kg ha^{-1} y^{-1} of nitrogen and 9 kg ha^{-1} y^{-1} of phosphorus were returned to the soil-nutrient pool by fine roots in the top 10 cm of soil for a Venezuelan tierra firme forest. Litterfall at this site was found to contribute only 121 and 2 kg ha^{-1} y^{-1} of nitrogen and phosphorus (Cuevas & Medina 1986).

This study examined the nutrient dynamics within fine roots at the three main sites investigated in Chapter 3. The aims of the work described in this Chapter were to:

1. estimate the total nutrient standing stocks within the fine roots and the rate of turnover of nutrients at these three sites;
2. examine variations in fine root nutrient concentrations within different root size classes; and
3. investigate whether nutrients are retranslocated from fine roots prior to senescence.

4.2 Methods

4.2.1 Nutrient dynamics in fine roots

Root samples collected for the study described in the preceding chapter were used in this study. Total nutrient stock estimates were determined for the samples taken to examine fine root biomass at each site. The number of samples analysed varied between root size class and sampling depth and was determined by the quantity of material available (Table 4.1).

Table 4.1 Number of root samples analysed per root size class and sampling depth at each site.

Depth (cm)	Root size class (mm)			
	0-0.5	0.5-1	1-2	2-5
0-10	4	10	10	6
10-20	Bulked to yield 2 samples	5	3	Bulked to yield 2 samples
20-30		5	3	
30-40		3	3	
40-50		3	3	

The samples were digested using a modified Kjeldahl digestion as outlined in Chapter 2. Nitrogen and phosphorus concentrations were determined by the colorimetric procedures presented in Anderson and Ingram (1989). Calcium and magnesium concentrations were determined by atomic absorption spectrophotometry, while potassium concentrations were determined by flame photometry.

The unequal number of replicates within each root size class and within each depth limited statistical analysis of the data. A series of one-way analyses of variance (ANOVA) were used to examine differences in fine root nutrient concentrations between sites and within different root size classes. Firstly, differences in fine root nutrient concentrations between sites for all root size classes were examined. Then, separate ANOVAs were performed for each root size class to examine differences between the three sites. Finally, differences between root size classes within a site were examined.

Nutrient stocks contained in the fine roots were determined by multiplying mean nutrient concentration by the estimated fine root biomass for each root size class and each sampling depth. These were then summed to give total nutrient stocks contained within the fine roots in the top 50 cm of soil.

Estimates of annual nutrient allocation to fine roots in the top 10 cm of soil were determined from the 48-week root ingrowth samples. The number of samples analysed varied between sites and root size class, and was determined by the quantity of material available. Ten replicates were analysed per site for roots that were 0.5-1 mm diameter. Three replicates were analysed for the other three size classes, with the exception of the Mt Spec 0-0.5 mm size class where only two replicates were possible. All samples were analysed as described above. Annual nutrient allocation was determined by multiplying mean nutrient concentration by mean annual rate of root production as determined in Chapter 3. Rates of nutrient turnover were then determined by dividing annual allocation by total nutrient stocks in the live fine roots.

4.2.2 Nutrient retranslocation from fine roots

The retranslocation of nutrients from fine roots was examined using the method of Nambiar (1987). This method measures the difference in calcium concentration relative to concentrations of nitrogen, phosphorus, potassium and magnesium in live and dead roots. Material obtained from the 96-week root ingrowth bag experiment (Chapter 3) was used for this analysis. Only the 0.5-1 mm diameter size class of roots provided enough material for analysis. Ten replicates of live and dead fine roots were analysed for each site. Variations in nutrient concentrations and nutrient ratios between live and dead roots were examined using a series of Students t-tests.

4.3 Results

4.3.1 Nutrient concentrations within fine roots

The mean concentrations of nutrients within the fine roots differed significantly between sites (Table 4.2). Calcium concentrations in fine roots differed significantly between sites across the whole range of root size classes.

Table 4.2 Probabilities for a series of one-way ANOVAs examining differences in fine root nutrient concentrations between sites for all root size classes, within the different sizes classes and between the size classes within each site.

	Nitrogen	Phosphorus	Potassium	Magnesium	Calcium
Overall	0.00	0.00	0.00	0.00	0.00
Variations in nutrient concentrations within each root size class between the sites					
0-0.5 mm	0.71	0.08	0.30	0.02	0.00
0.5-1 mm	0.00	0.00	0.24	0.00	0.00
1-2 mm	0.02	0.00	0.00	0.00	0.00
2-5 mm	0.50	0.00	0.03	0.32	0.00
Variations in nutrient concentrations between root size classes at each site					
Broadwater	0.00	0.00	0.01	0.37	0.09
Mt Fox	0.00	0.00	0.00	0.00	0.02
Mt Spec	0.00	0.06	0.00	0.00	0.03

There were significant differences in fine root nutrient concentrations within the different root size classes, with a few exceptions (Table 4.2). Nitrogen and phosphorus concentrations decreased with increasing root size (Figure 4.1). Potassium, magnesium and calcium concentrations varied between root size classes.

Mt Fox had the greatest concentration of phosphorus within the fine roots across the whole range of fine root size classes (Figure 4.1). Calcium concentrations in fine roots were greatest at Broadwater.

4.3.2 Nutrient dynamics within fine roots

Total nutrient stocks within the fine roots varied between sites and were in part determined by the quantity of fine roots at each site (Table 4.3). Mt Spec which had the highest fine root biomass, generally had the highest nutrient stocks within the fine roots.

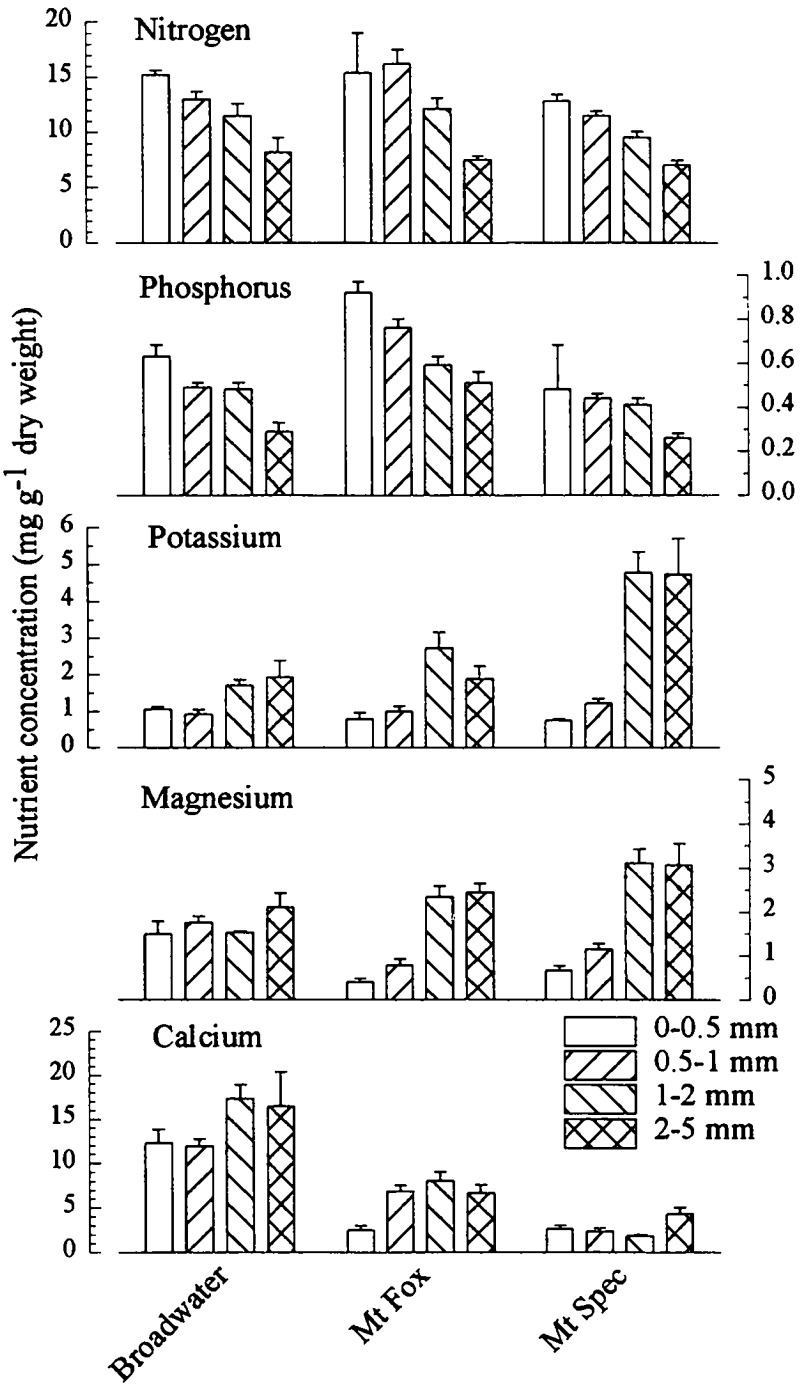


Figure 4.1 Fine root nutrient concentrations (mg g^{-1}) across a range of fine root size classes for Broadwater, Mt Fox and Mt Spec. Data are for roots in the top 10 cm of soil and the number of replicates analysed within each size class is given in Table 4.1. Bars indicate standard errors.

Table 4.3 Total nutrient stocks in the fine roots, to depths of 10 and 50 cm, at Broadwater, Mt Fox and Mt Spec.

Site	Depth (cm)	Status	Fine root biomass (kg ha^{-1})	Fine root nutrient content (kg ha^{-1})				
				Nitrogen	Phosphorus	Potassium	Magnesium	Calcium
Broadwater	0-10	Live	2760 ± 520	27.7 ± 6.1	1.0 ± 0.2	4.5 ± 0.7	5.3 ± 0.8	43.4 ± 7.7
		Dead	880 ± 130	15.4 ± 2.4	0.5 ± 0.1	0.8 ± 0.2	1.0 ± 0.2	10.9 ± 1.9
		Total	3640 ± 630	43.1 ± 8.4	1.5 ± 0.3	5.3 ± 0.8	6.3 ± 0.9	54.3 ± 8.4
	0-50	Live	5580 ± 1150	59.0 ± 18.2	2.1 ± 0.6	10.2 ± 2.6	9.3 ± 2.9	74.8 ± 23.5
		Dead	2090 ± 440	29.0 ± 7.0	0.9 ± 0.3	1.7 ± 0.5	1.9 ± 0.5	21.2 ± 5.7
		Total	7670 ± 1530	88.0 ± 22.9	3.0 ± 0.9	11.9 ± 3.0	11.2 ± 3.3	96.0 ± 25.4
Mt Fox	0-10	Live	2400 ± 400	29.7 ± 5.7	1.6 ± 0.3	3.9 ± 0.7	3.9 ± 0.7	16.0 ± 3.2
		Dead	2470 ± 400	42.5 ± 6.1	2.1 ± 0.3	1.7 ± 0.4	1.7 ± 0.5	15.8 ± 3.0
		Total	4870 ± 600	72.2 ± 10.2	3.7 ± 0.5	5.6 ± 0.8	5.6 ± 0.8	31.8 ± 4.8
	0-50	Live	4880 ± 770	57.0 ± 11.8	3.1 ± 0.7	8.5 ± 1.5	6.8 ± 1.1	27.2 ± 5.7
		Dead	4090 ± 560	68.4 ± 14.1	3.5 ± 0.7	2.7 ± 0.7	2.7 ± 0.9	22.1 ± 4.9
		Total	8970 ± 1020	125.4 ± 20.6	6.6 ± 1.1	11.2 ± 1.7	9.5 ± 1.6	49.3 ± 6.9
Mt Spec	0-10	Live	8640 ± 1710	79.0 ± 14.8	3.1 ± 0.6	31.0 ± 3.0	21.1 ± 2.3	25.8 ± 4.8
		Dead	5450 ± 860	69.2 ± 12.3	2.4 ± 0.4	7.5 ± 1.6	6.9 ± 1.3	13.4 ± 2.0
		Total	14090 ± 2400	148.2 ± 21.9	5.5 ± 0.7	38.5 ± 4.1	28.0 ± 3.1	39.2 ± 5.5
	0-50	Live	17580 ± 2930	147.3 ± 35.3	5.3 ± 1.2	53.7 ± 8.8	36.1 ± 8.6	58.8 ± 16.0
		Dead	9430 ± 1160	115.2 ± 22.8	3.7 ± 0.7	11.1 ± 2.4	10.0 ± 2.2	19.6 ± 4.0
		Total	27010 ± 3430	262.5 ± 55.5	9.0 ± 1.7	64.8 ± 10.3	46.1 ± 9.1	78.4 ± 17.6

The majority of nutrients contained within the fine roots were found in the top 10 cm of soil, reflecting the concentration of fine roots within this zone. The percentage of total nutrient stocks of roots down to 50 cm that were contained in the top 10 cm of soil varied between nutrients and sites, but fell between 44.5% and 64.5%.

The estimated annual nutrient allocation and turnover within fine roots varied between sites (Table 4.4). Allocation of nitrogen and phosphorus to fine roots was greatest at Mt Fox, 51 and 3.0 kg ha^{-1} y^{-1} respectively. Quantities of magnesium and calcium allocated to fine roots were greatest at Broadwater, while allocation of potassium to fine roots was greatest at Mt Spec (Table 4.4).

The percentage of annual nutrient turnover within live fine roots was greatest at Mt Fox for all nutrients. This site was found to turn over between 91 and 192% of its total nutrient stocks annually (Table 4.4). Mt Spec had the lowest rates of nutrient turnover of all the nutrients examined. Phosphorus had the fastest rate of turnover at all sites (Table 4.4).

Table 4.4 Annual nutrient allocation and turnover in fine roots in the top 10 cm of soil for Broadwater, Mt Fox and Mt Spec. Nutrient turnover, expressed as a percentage, is given in parentheses.

	Fine root production (kg ha^{-1} y^{-1})	Annual nutrient allocation (kg ha^{-1} y^{-1})				
		Nitrogen	Phosphorus	Potassium	Magnesium	Calcium
Broadwater	2340	25 ± 5	1.2 ± 0.2	2.6 ± 0.6	4.2 ± 0.9	31 ± 6
	(85)	(92)	(114)	(58)	(80)	(73)
Mt Fox	3280	51 ± 7	3.0 ± 0.4	7.0 ± 1.2	3.5 ± 0.8	20 ± 3
	(137)	(173)	(192)	(181)	(91)	(127)
Mt Spec	2820	31 ± 4	1.2 ± 0.2	7.6 ± 1.4	2.4 ± 0.4	7 ± 1
	(33)	(39)	(39)	(25)	(11)	(27)

4.3.3 Retranslocation of nutrients from fine roots

Based on the nutrient ratios in the fine roots obtained from the 96 week ingrowth bag experiment, there seemed to be little evidence of retranslocation of nutrients from fine roots prior to senescence (Tables 4.5, 4.6 & 4.7). Few significant differences were found in live and dead fine root nutrient concentrations. Magnesium concentrations in fine roots were significantly lower in dead fine roots at Mt Fox (Table 4.6), while nitrogen and phosphorus concentrations in dead fine roots were significantly higher at Broadwater and Mt Spec (Tables 4.5 & 4.7). No significant differences were found in the nutrient to calcium ratios at any of the sites (Tables 4.5, 4.6 & 4.7).

Table 4.5 Mean nutrient concentrations and nutrient to calcium ratios in the 0.5-1 mm diameter roots in the root ingrowth bags at Broadwater.

	Nutrient concentration (mg g^{-1})		P
	Live	Dead	
Nitrogen	13.2 ± 1.0	19.2 ± 0.9	0.00*
Phosphorus	0.47 ± 0.02	0.59 ± 0.04	0.01*
Potassium	0.91 ± 0.18	0.92 ± 0.09	0.96
Magnesium	1.83 ± 0.18	1.51 ± 0.15	0.20
Calcium	12.2 ± 1.0	13.7 ± 1.1	0.35
	Nutrient ratios		
Nitrogen to Calcium	1.16 ± 0.16	1.47 ± 0.15	0.18
Phosphorus to Calcium	0.041 ± 0.005	0.045 ± 0.005	0.56
Potassium to Calcium	0.080 ± 0.018	0.072 ± 0.011	0.72
Magnesium to Calcium	0.16 ± 0.02	0.11 ± 0.01	0.10

Table 4.6 Mean nutrient concentrations and nutrient to calcium ratios in the 0.5-1 mm diameter roots in the root ingrowth bags at Mt Fox.

	Nutrient concentration (mg g^{-1})		P
	Live	Dead	
Nitrogen	16.5 ± 1.8	18.3 ± 1.1	0.38
Phosphorus	0.72 ± 0.04	0.92 ± 0.05	0.06
Potassium	0.82 ± 0.13	0.59 ± 0.07	0.11
Magnesium	0.73 ± 0.20	0.21 ± 0.03	0.04*
Calcium	7.3 ± 1.0	6.6 ± 0.9	0.64
	Nutrient ratios		
Nitrogen to Calcium	2.5 ± 0.4	3.3 ± 0.5	0.23
Phosphorus to Calcium	0.11 ± 0.01	0.17 ± 0.03	0.09
Potassium to Calcium	0.13 ± 0.02	0.10 ± 0.01	0.40
Magnesium to Calcium	0.11 ± 0.03	0.04 ± 0.01	0.06

Table 4.7 Mean nutrient concentrations and nutrient to calcium ratios in the 0.5-1 mm diameter roots in the root ingrowth bags at Mt Spec.

	Nutrient concentration (mg g^{-1})		P
	Live	Dead	
Nitrogen	10.9 ± 0.4	13.4 ± 0.5	0.00*
Phosphorus	0.42 ± 0.03	0.52 ± 0.03	0.02*
Potassium	1.13 ± 0.15	1.24 ± 0.13	0.56
Magnesium	1.16 ± 0.14	1.17 ± 0.13	0.95
Calcium	2.45 ± 0.62	2.34 ± 0.42	0.88
	Nutrient ratios		
Nitrogen to Calcium	6.5 ± 0.7	7.4 ± 0.9	0.42
Phosphorus to Calcium	0.25 ± 0.03	0.29 ± 0.04	0.36
Potassium to Calcium	0.72 ± 0.14	0.70 ± 0.10	0.92
Magnesium to Calcium	0.74 ± 0.14	0.63 ± 0.08	0.51

4.4 Discussion

Few published data exist regarding nutrient concentrations and nutrient stocks within fine roots of tropical rain forests (Edwards & Grubb 1982, Greenland & Kowal 1960, Klinge 1975, 1976, Vitousek & Sanford 1986). In addition, comparisons between studies are hampered by a lack of standardised methods and small sample sizes. The number of replicates analysed in published studies of fine root nutrient dynamics in tropical forests has ranged from a single sample (Greenland & Kowal 1960, Klinge 1975, 1976) to six samples (Edwards & Grubb 1982).

The nutrient concentrations within fine roots, determined in this study, are within the range reported in the literature, with the exception of mean calcium concentrations at Broadwater (Table 4.8). High concentrations of nutrients within the soil were generally reflected by high concentrations within the fine roots. Mt Fox was found to have the highest phosphorus concentrations in fine roots. Similarly, the high levels of exchangeable calcium at Broadwater were reflected by high concentrations within the fine roots. Soil magnesium and potassium concentrations were not reflected in fine root concentrations, with the highest fine root concentrations of these nutrients being found at Mt Spec. Nutrient concentrations in fine roots are controlled by the nutrient demand in different tissues, as well as by the availability and supply of nutrients in the soil (Helmisaari 1991).

The majority of nutrients contained within the fine roots were found in the top 10 cm of soil (Table 4.3). This was a consequence of all study sites having the greatest concentration of fine roots near the surface. The total nutrient stocks at Mt Spec were generally higher than those reported in previous studies due to the large quantity of fine roots found at this site (Table 4.9). Previous studies have

Table 4.8 Mean nutrient concentrations within fine roots

Location	Depth (cm)	Size (mm)	Mean nutrient concentration (mg g^{-1})					Source
			N	P	K	Mg	Ca	
Australia								
- Broadwater	10	<5	12.0	0.48	1.4	1.7	14.5	This study
- Mt Fox	10	<5	12.8	0.70	1.6	1.5	6.0	
- Mt Spec	10	<5	10.2	0.39	2.8	2.0	2.8	
Brazil								
- Latosols	10	<6	10.1	0.14	0.6	0.7	0.5	Klinge (1976)
- Podsols	10	<6	10.3	0.26	0.9	0.9	1.3	Klinge (1975)
Ghana								
- 50 year old forest	120	<6.4	13.7	0.79	5.6	1.0	8.8	Greenland & Kowal (1960)
New Guinea								
- Montane	25	<5	7.4	0.33	4.1	6.1	7.3	Edwards & Grubb (1982)

Table 4.9 Nutrient stocks in fine roots recorded for tropical rain forests.

Location	Depth (cm)	Root diameter (mm)	Biomass (kg ha^{-1})	Nutrient stocks (kg ha^{-1})					Source
				N	P	K	Mg	Ca	
Australia									
- Broadwater	50	<5	7670	88	3.0	11.9	11.1	96.0	This study
- Mt Fox	50	<5	8980	125	6.6	11.2	9.5	49.4	
- Mt Spec	50	<5	27020	262	9.0	64.8	46.1	78.4	
Brazil									
- Latosols	47	<6	13725	114	1.5	7.9	6.7	13.4	Klinge (1976)
- Podsols	53	<6	15910	153	2.8	9.7	11.5	10.6	Klinge (1975)
Ghana									
- 50 year old forest	122	<6.4	5060	70	4.0	28.4	10.3	44.3	Greenland & Kowal (1960)
New Guinea									
- Montane	25	<5	2800	21	0.9	11.0	17.0	20.0	Edwards & Grubb (1982)
Venezuela									
- Montane	-	<5	24600	157	9.0	58.0	25	108.0	Grimm & Fassbender (1981)

found that the percentage of total nutrient stocks contained within fine roots varies between 1.3 and 14.2% of the total nutrient stocks contained within the vegetation (Table 4.10).

The estimates of annual nitrogen and phosphorus turnover at all sites investigated in this study were lower than the 190 kg ha^{-1} y^{-1} of nitrogen and 9 kg ha^{-1} y^{-1} of phosphorus reported by Sanford and Cuevas (1996). They found that fine root production and turnover exceeded litterfall as a source of nutrient input in a Venezuelan tierra firme forest.

Table 4.10 The percentage of the total biomass and nutrients contained within fine roots recorded for various tropical rain forests.

Location	Fine roots (%)						Source
	Biomass	N	P	K	Mg	Ca	
Brazil	3.3	5.2	3.1	2.1	3.3	4.0	Klinge (1975)
Ghana	1.9	3.6	3.3	3.3	1.5	1.7	Greenland & Kowal (1960)
New Guinea	0.8	2.6	2.4	1.4	7.2	1.3	Edwards & Grubb (1982)
Venezuela	6.1	15.2	13.4	3.9	9.8	12.0	Grimm & Fassbender (1981)

There are few measurements of nutrient accessions in litterfall for north Queensland rain forests (Brasell *et al.* 1980, Herbohn 1995). Mt Spec is the only site examined in this study, for which nutrient accession data are available (Table 4.11). Litterfall in this forest contributed 59.5 and 2.1 kg ha^{-1} y^{-1} of nitrogen and phosphorus annually to the soil (Herbohn 1995), compared to 31 and 1.2 kg ha^{-1} y^{-1} of nitrogen and phosphorus by fine roots to 10 cm depth. Indeed, fine roots to 50 cm depth return as much H and P as does litterfall. While no data are available for Broadwater or Mt Fox, there are data available for three sites on basalt-derived soils in north Queensland (Brasell *et al.* 1980). Brasell *et al.* (1980) reported that litterfall contributed 129 and 11.2 kg ha^{-1} y^{-1} of nitrogen and

phosphorus annually to the soil (Table 4.11). This compares with 51 and 3.0 kg ha^{-1} y^{-1} of N and P returned by fine roots to 10 cm depth recorded at Mt Fox.

Table 4. 11 Nutrient input into soils from litterfall and fine roots in the top 10 cm of soil, for north Queensland wet tropical rainforests. The estimated nutrient input from fine roots for the top 50 cm of soil is given in parentheses.

Soil origin	Nutrient turnover (kg ha^{-1} y^{-1})					Source
	Nitrogen	Phosphorus	Potassium	Magnesium	Calcium	
Alluviual						
- fine roots	25 (54)	1.2 (2.4)	2.6 (5.9)	4.2 (7.4)	31 (54)	This study
Basalt						
- litterfall	129	11.2	58	32	192	Brasell *et al.* (1980)
- fine roots	51 (99)	3.0 (6.0)	7 (15)	3.5 (6.2)	20 (35)	This study
Granite						
- litterfall	59.5	2.1	23	15.5	54.5	Herbohn (1995)
- fine roots	31 (57.5)	1.2 (2.1)	7.6 (13.4)	2.4 (4.0)	7 (15.9)	This study

Nitrogen and phosphorus concentrations within fine roots were found to decrease with increasing root diameter. This trend has also been reported in other studies (Fogel & Hunt 1983, McClaugherty *et al.* 1982, Nambiar 1987, Vogt *et al.* 1983), and has been suggested as evidence for nutrient retranslocation from fine roots (Helmisaari 1991). This study found no evidence of retranslocation of nutrients from fine roots prior to senescence. However, this may in part be due to problems in applying Nambiar's (1987) method to tropical forests. This method makes two assumptions which may not have been met in the present study. Firstly, it is assumed that calcium transfer does not occur from plant roots prior to senescence (Nambiar 1987). This will depend on whether the calcium is complexed, or not, in cell walls and in oxalate crystals (Thomas 1970). The second assumption, and the one most likely to be violated in tropical forests, is that any differences in nutrient ratios between individual samples is less than differences between live and dead roots. Previously, Nambiar's (1987)

methodology has been used in monocultures which are only subject to intra-specific variation in root nutrient concentrations/ratios. Within tropical forest, there is likely to be substantial inter-specific variation which may mask any changes in nutrient concentrations/ratios due to retranslocation (Bloomfield *et al.* 1993). The only available data on variation in fine root nutrient concentrations/ratios for individual species within a site suggest that inter-specific variations in fine root nutrient ratios may be significant (Table 4.12).

Table 4.12 Fine root nutrient to calcium ratios for *Dacryodes excelsa* and *Prestoea montana* from a subtropical wet forest in Puerto Rico (Based on the data of Bloomfield *et al.* 1993).

Species	N to Ca	P to Ca	K to Ca	Mg to Ca
Dacryodes excelsa	4.7	0.20	0.4	0.15
Prestoea montana	2.9	0.22	1.5	0.80

The importance of nutrient retranslocation from fine roots is unclear, as it has been examined in few studies, and these have often yielded conflicting results (Aerts *et al.* 1992, Cuevas 1995, Meier *et al.* 1985, Nambiar 1987, Vogt *et al.* 1987). Cuevas (1995) suggested that nutrient withdrawal from senescent roots may be an important nutrient conserving mechanism for seasonally dry tropical forests, based on the consistently lower concentration of nutrients in dead roots compared to live roots observed by Singh (1989). Nutrient transfer from live fine roots prior to senescence is thought to occur in *Abies amabilis* (Meier *et al.* 1985, Vogt *et al.* 1995). Similarly, the possible existence of nitrogen retranslocation from *Acer saccharum* roots with senescence has been suggested by Golfarb *et al.* (1990). In contrast, Aerts *et al.* (1992) found little evidence of nitrogen and phosphorus retranslocation from fine roots for a dry heathland ecosystem. Similarly, no evidence of nutrient retranslocation from fine roots was found for *Pinus radiata* (Nambiar 1987).

Nutrient analyses of fine roots have a number of possible sources of error (Misra 1994). Errors may arise from soil adhering to the roots, the method of separation of the roots from the soils, and storage conditions of the samples (Böhm 1979, Misra 1994). The magnitude of error arising from soil adhering to fine roots is dependant on the type of soil, its nutrient status, and the nutrient status of the roots (Misra 1994). Fine root nutrient concentrations in this study were generally greater than soil nutrient concentrations. Therefore, any soil contaminant should result in an underestimation of nutrient concentrations within the roots. Misra (1994) showed that typical variation in soil contamination was between 5 and 20% of the root sample. The dry separation of roots used in this study eliminates the possiblility of nutrient leaching which is associated with wet sieving techniques, however, it is likely to substantially underestimate fine root biomass (Fogel 1983, Misra 1994). The effect of this will be greater for estimates of biomass and nutrient stocks for dead fine roots. A further possible source of error is changes in nutrient concentrations due to long-term storage. Long-term storage of samples at 1-2°C does not cause significant changes in fine root biomass (Persson 1990). However, Misra (1994) found significantly lower concentrations of nitrogen, phosphorus and potassium in roots that had been stored frozen for 15 days. The effect of long-term storage at 1-2°C on nutrient concentrations remains to be determined. The significance of these sources of error in the estimates determined in this study are unknown. It is likely that these errors, compounded with errors in fine root biomass estimates, have resulted in an underestimation of nutrient standing stock and nutrient turnover within fine roots.

While fine roots only contain a relatively small proportion of the total nutrient stocks within the vegetation at a site, their rapid rate of turnover and moderately high nutrient concentrations suggests that they are at least as important as litterfall in returning nutrients to the soil in tropical forests.

CHAPTER 5

Seasonal changes in fine root productivity and soil nutrient availability

5.1 Introduction

The wet tropics of north Queensland has a distinct seasonal climate with hot wet summers and mild dry winters (Congdon & Herbohn 1993). Several studies examining litterfall in the rain forests of north Queensland have found distinct seasonal patterns, with heaviest falls occuring from late in the dry season to the end of the wet season (Brasell *et al.* 1980, Herbohn & Congdon 1993, Spain 1984).

Litterfall is the major pathway for the return of dead organic matter and nutrients from the above-ground portion of the vegetation to the soil surface (Spain 1984). Through the process of decomposition, the nutrients contained within the dead organic matter are released. Rates of decomposition have been found to be affected by environmental factors, particularly rainfall and temperature (Spain 1984). The marked seasonality in climate in many parts of northeast Queensland results in a highly variable decomposition rate of dead organic matter, and hence a highly variable rate of nutrient release. Distinct seasonal variation in the availability of major plant nutrients has been found to occur in soils at Mt Spec, using ion exchange resin bags (Congdon & Maycock in prep.).

Ion exchange resin bags have recently gained popularity as a means to estimate the availability of soil nutrients in the field (Binkley & Matson 1983, Gibson 1986, Gibson *et al.* 1985, Lajtha 1988, Yavitt & Wright 1996). They are thought to mimic a plant's ability in their uptake of nutrients from the soil solution (Sibbesen 1978).

Fine roots are the primary means by which plants take up nutrients. Nutrient acquisition is either by direct absorption, or by mycorrhizal association (Berish & Ewel 1988, Stark & Jordan 1978, Went & Stark 1968). Previous studies have shown marked seasonal variation in the standing crop of live fine roots, with considerable fine root mortality occurring during the dry season (Kummerow *et al.* 1990, Singh & Singh 1981, Srivastava *et al.* 1986). This mass mortality reduces the nutrient absorption capacity of the forest at a time when large influxes of nutrients may enter the system (Kellman *et al.* 1982). Fine root production can also show distinct seasonal trends, with peak production occurring early in the wet season (Kavanagh & Kellman 1992).

The aims of this study were to:

1. examine whether there are seasonal variations in fine root production at Broadwater, Mt Fox and Mt Spec; and
2. investigate whether increased fine root production coincides with increased soil nutrient availability.

5.2 Methods

Root ingrowth bags were used to examine fine root productivity. The construction, placement and retrieval of these bags follows the procedure outlined in Chapter 3. Twenty bags were incubated in the field for 4 week periods over 13 months. On each sampling occasion, replacement bags were placed in new randomly selected locations.

Fine nylon mesh bags (5 cm x 4 cm) were prepared containing 4 g of cation exchange resin (BDH Amberlite IR-120) or anion exchange resin (BDH Amberlite IRA-400). The cation exchange resins were prepared according to the

method of Krause and Ramlal (1987), while the anion exchange resins were converted to bicarbonate form (Sibbesen 1978).

Twenty resin bags of each type were deployed at random locations within the plot at each site in the following manner. The surface soil was lifted and a resin bag was inserted at approximately 7.5 cm depth. The soil was then pressed gently back in place. Bags were incubated for 4 weeks. On each sampling occasion, replacement bags were placed in new randomly selected locations.

After 4 weeks incubation, the resin bags were collected and returned to the laboratory in polyethylene bags. The bags were washed thoroughly with deionised water, and the adsorbed nutrients extracted as described below. The extracts were clear, and consequently they were not filtered to minimise the chance of contamination.

Anion exchange resins were extracted in 100 mL of 0.05 M $NaHCO_3$ for 90 minutes (Sibbesen 1978). The extract was analysed for phosphate using the single solution method of Murphy and Riley (1962).

Cation resin bags were extracted in 50 mL of 0.1 M HCl for 60 minutes (Krause & Ramlal 1987), and the extract was analysed for ammonium, potassium, calcium and magnesium. Ammonium was determined by the indophenol blue method (Keeney & Nelson 1982), while potassium was determined by flame photometry. Calcium and magnesium were determined by atomic absorption spectrophotometry.

Rainfall data for the study period were obtained from the Bureau of Meteorology, Townsville. Data are expressed as nutrients extracted by the resin, rainfall and fine root production per 28 day period. Differences in fine root production and

soil nutrient availability between sampling dates at each site, and differences between sites at each sampling date, was tested for significance using one-way ANOVA (Zar 1984). Correlation analysis were used to test for significant relationships between fine root production, rainfall and nutrient concentrations.

5.3 Results

Rainfall at all three sites was distinctly seasonal, with most rain falling in the summer wet season (Figure 5.1). The quantity of fine roots accumulated in the root ingrowth bags differed significantly between sampling dates (Table 5.1). While fine root production exhibited seasonal variation, with the greatest rates of fine root production at all sites occurring during the wet season (Figure 5.2), fine root production at Broadwater was not correlated to 28-day rainfall (Table 5.2).

Table 5.1 Probabilities for one-way ANOVA examining temporal differences in fine root production and soil nutrient availability between sampling dates (n = 20).

Site	Probabilities					
	Fine root production	Ammonium	Phosphorus	Potassium	Magnesium	Calcium
Broadwater	0.00	0.00	0.00	0.00	0.00	0.00
Mt Fox	0.00	0.00	0.00	0.00	0.00	0.00
Mt Spec	0.00	0.00	0.00	0.00	0.00	0.00

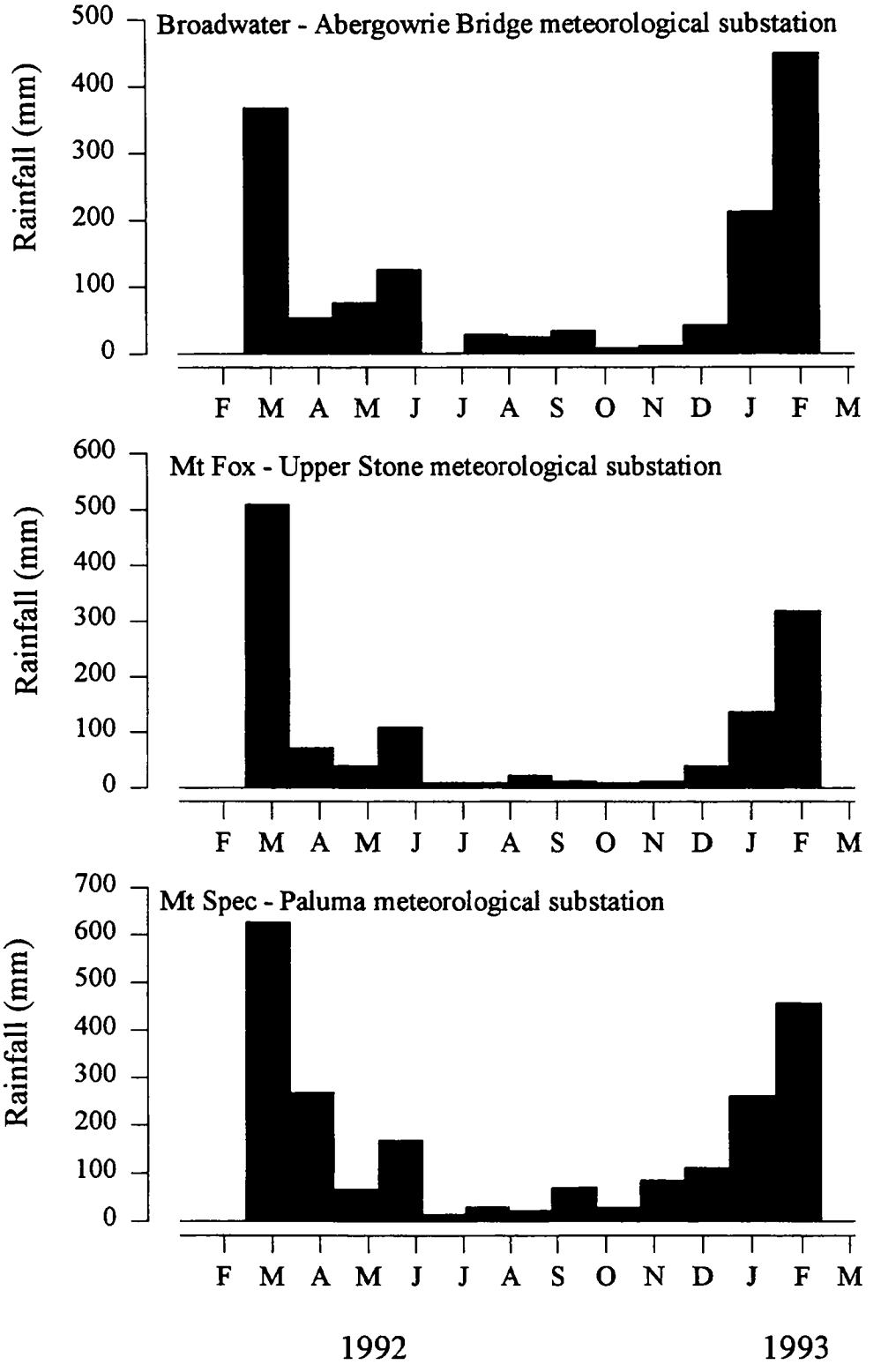


Figure 5.1 Rainfall recorded at the nearest meteorological substation to each study site for each period of resin bag incubation during the study period.

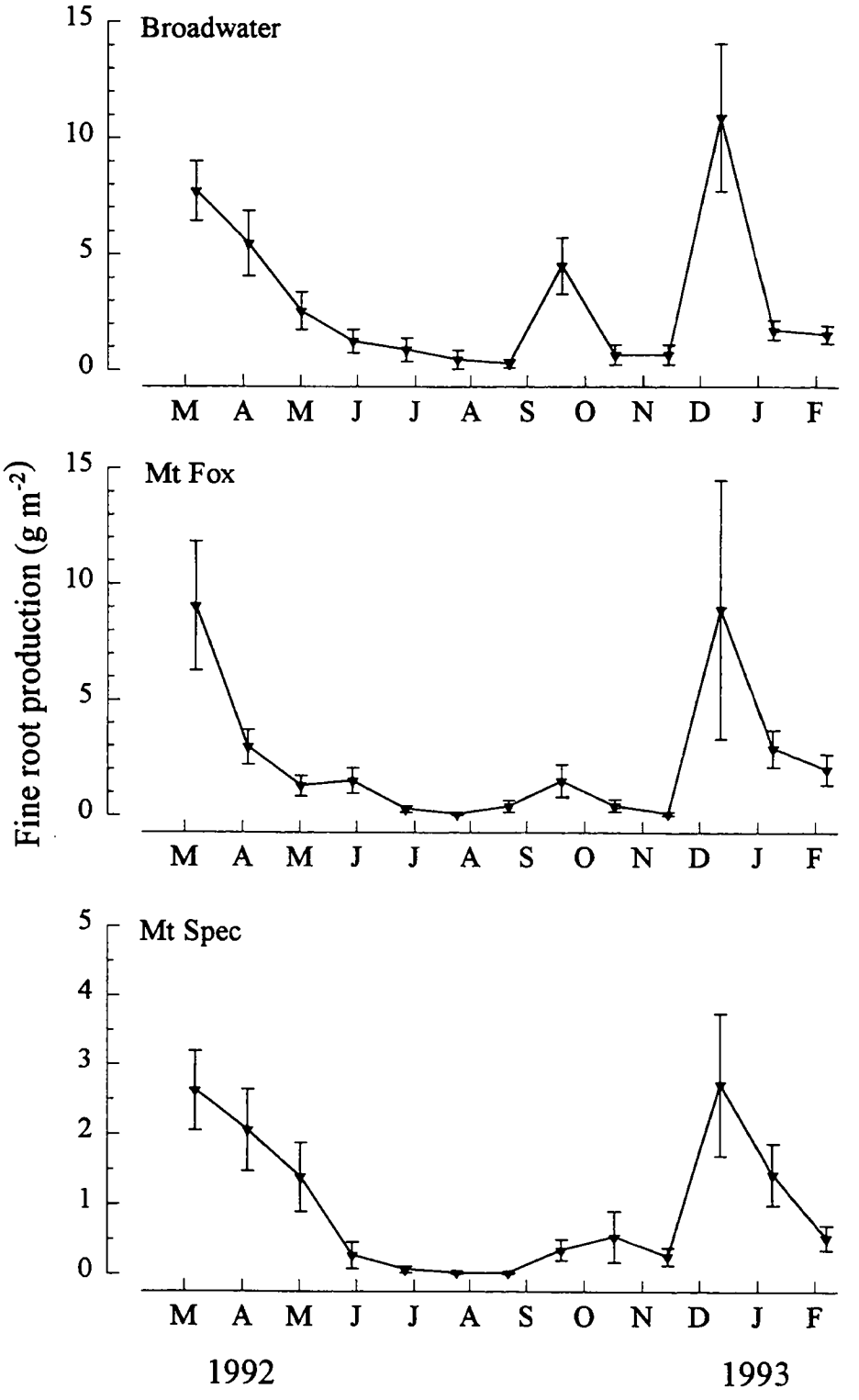


Figure 5.2 Seasonal changes in fine root production measured as root accumulation in 28-day incubated root ingrowth bags for Broadwater, Mt Fox and Mt Spec. Bars indicate the SEM.

Table 5.2 Probabilities for correlation analysis for fine root production against rainfall and soil nutrient availability (n = 13). The asterisk denotes a significant correlation ($P < 0.05$).

Site	Probabilities					
	Rainfall	Ammonium	Phosphorus	Potassium	Magnesium	Calcium
Broadwater	0.74	0.04*	0.16	0.02*	0.62	0.83
Mt Fox	0.04*	0.26	0.02*	0.07	0.91	0.96
Mt Spec	0.04*	0.25	0.04*	0.01*	0.01*	0.89

The quantity of fine roots accumulated within the root ingrowth bags varied between sites (Figure 5.2, Table 5.3). Lower rates of fine root production were recorded at Mt Spec than at Broadwater and Mt Fox, however, few significant differences in quantities of fine roots produced were found between the sites (Table 5.3).

The quantity of nutrients absorbed by the resin bags varied significantly between sampling dates (Figures 5.3, 5.4, 5.5, 5.6 & 5.7, Table 5.1). For most sampling dates, significant differences in soil nutrient availability were found between the sites (Table 5.3). Mt Spec was found to have a significantly greater quantity of ammonium-nitrogen absorbed by the resin bags than the other two sites (Figure 5.3), but ammonium availability was not correlated to 28-day rainfall totals (Table 5.4). Concentrations of phosphorus absorbed by the resin bags varied during the year (Figure 5.4), and were correlated to 28-day rainfall totals at all sites (Table 5.4).

Table 5.3 Probabilities for one-way ANOVAS examining variations in fine root production and soil nutrient availability between the sites for each sampling date (n = 20). The dash indicates no samples.

Sampling date	Probabilities					
	Fine root production	Ammonium	Phosphorus	Potassium	Magnesium	Calcium
March 92	0.04	0.16	0.00	0.00	0.01	0.00
April 92	0.04	0.04	0.01	0.00	0.04	.00
Early May 92	0.29	0.00	0.00	0.00	0.00	0.00
Late May 92	0.11	0.00	0.00	0.00	0.01	0.00
June 93	0.11	0.00	0.00	0.00	0.00	0.00
July 92	0.28	0.00	0.00	0.00	0.82	0.00
August 92	0.36	0.00	0.01	0.00	0.00	0.00
September 92	0.00	0.00	-	0.02	0.01	0.00
October 92	0.90	0.00	0.00	0.00	0.01	0.97
November 92	0.28	0.00	0.10	0.00	0.00	0.00
December 92	0.27	0.00	0.07	0.00	0.25	0.00
January 93	0.32	0.00	0.09	0.09	0.00	0.00
February 93	0.07	0.00	0.00	-	0.09	0.00

With the exception of Mt Spec, potassium and magnesium concentrations were not correlated to 28-day rainfall total (Table 5.4), although higher concentrations were generally recorded at times of high rainfall. Potassium concentrations in extracts were significantly higher at Mt Spec (Figure 5.5). Magnesium concentrations in the resin bag extracts varied between sites and sampling dates, but no sites showed consistently greater concentrations (Figure 5.6). Resin bags from Broadwater had significantly higher calcium concentrations in the extracts (Figure 5.7, Table 5.3).

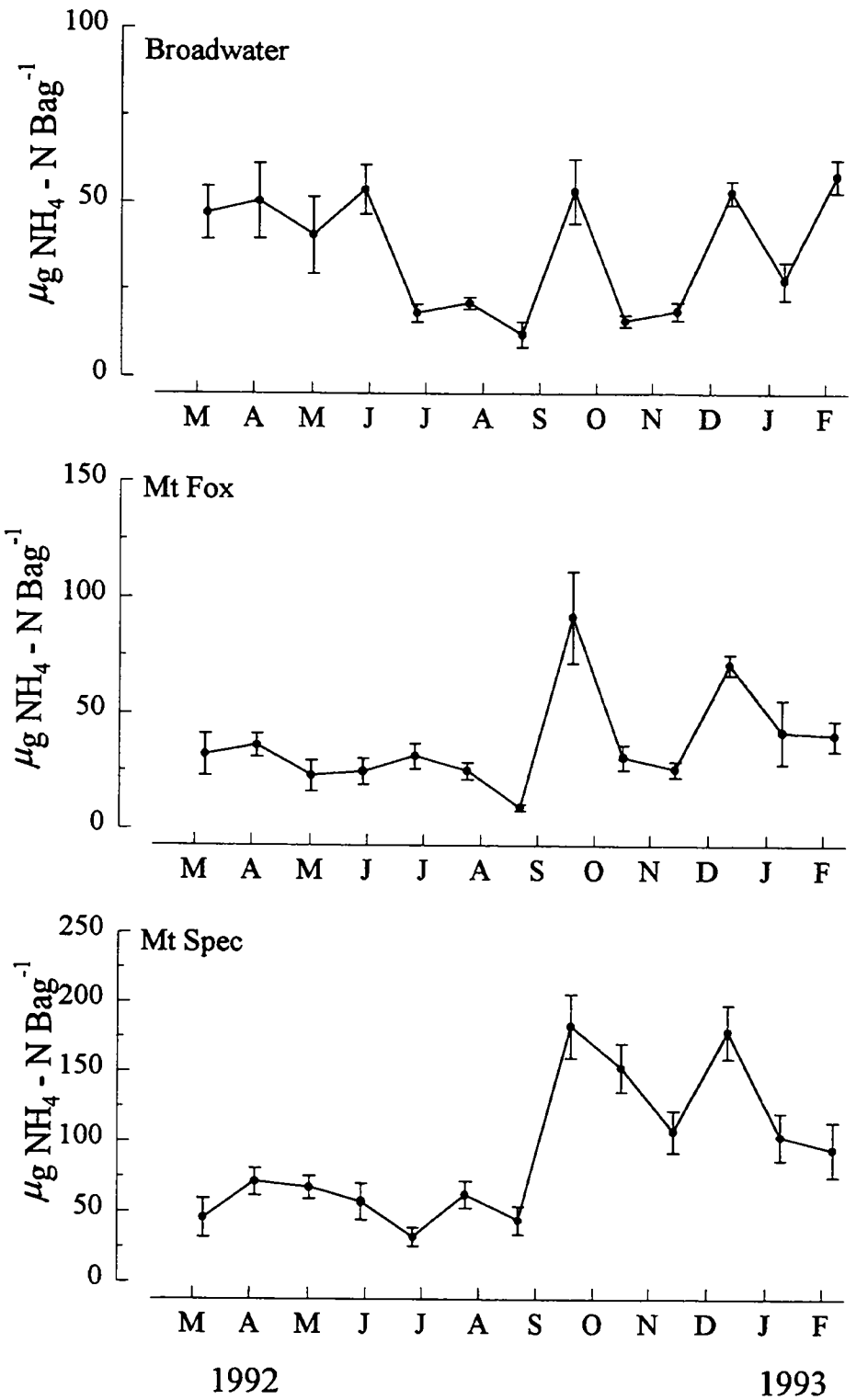


Figure 5.3 Seasonal changes in the availability of ammonium-nitrogen measured as ion sorption by 20 resin bags incubated in the soil at Broadwater, Mt Fox and Mt Spec. Bars indicate the SEM.

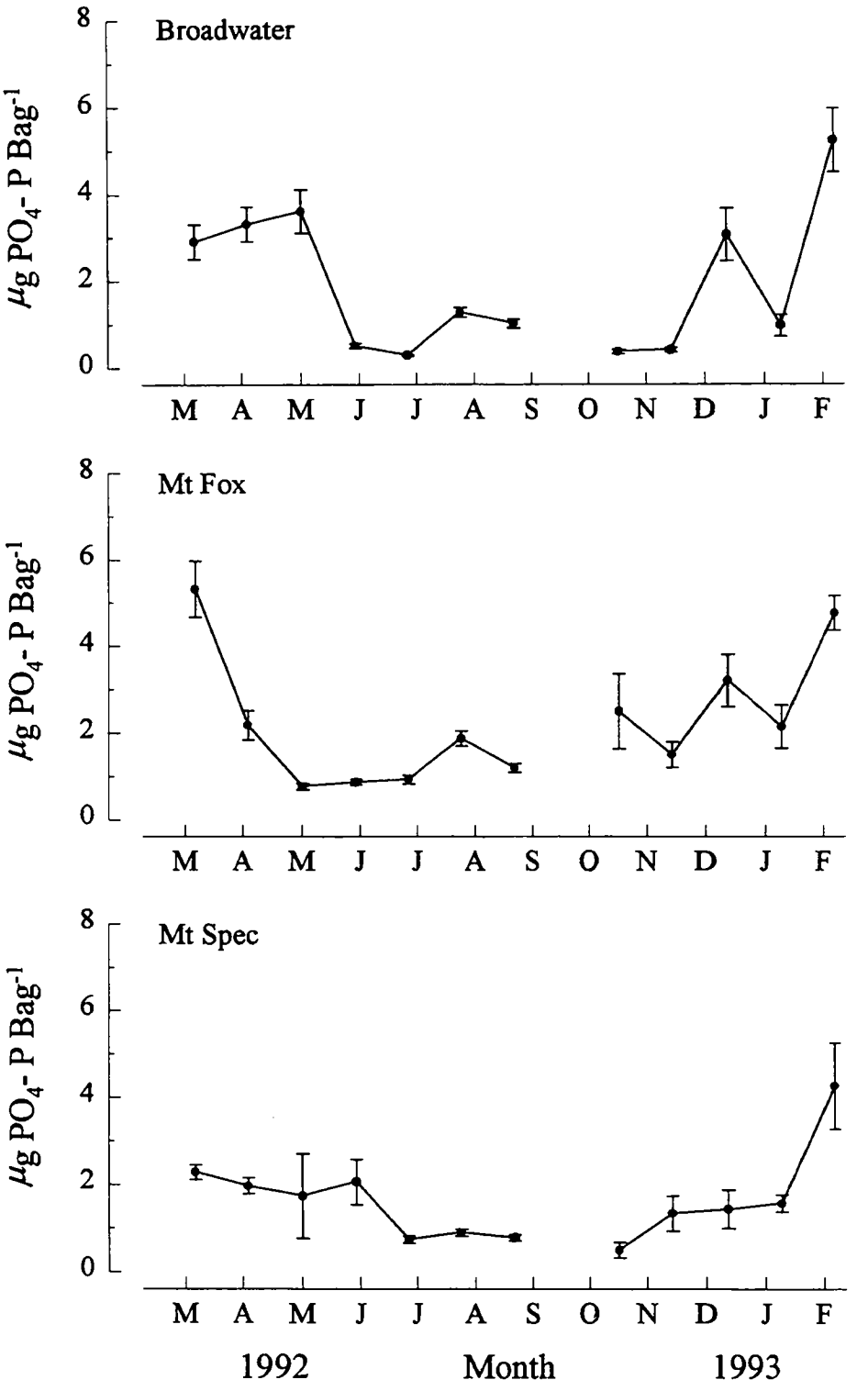


Figure 5.4 Seasonal changes in phosphate availability measured as ion sorption by 20 resin bags incubated in the soil at Broadwater, Mt Fox and Mt Spec. Bars indicate the SEM.

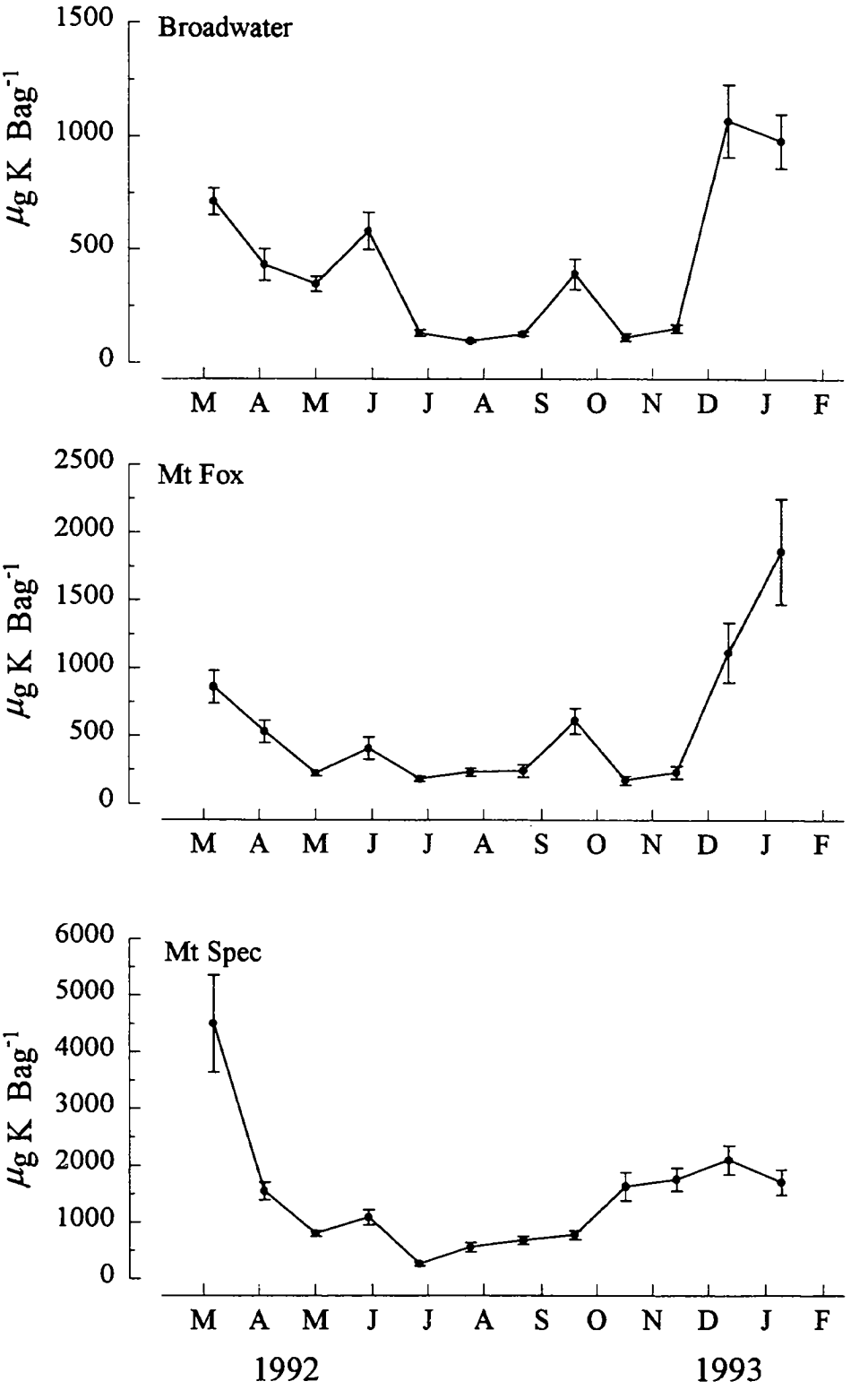


Figure 5.5 Seasonal changes in potassium availability measured as ion sorption by 20 resin bags incubated in the soil at Broadwater, Mt Fox and Mt Spec. Bars indicate the SEM.

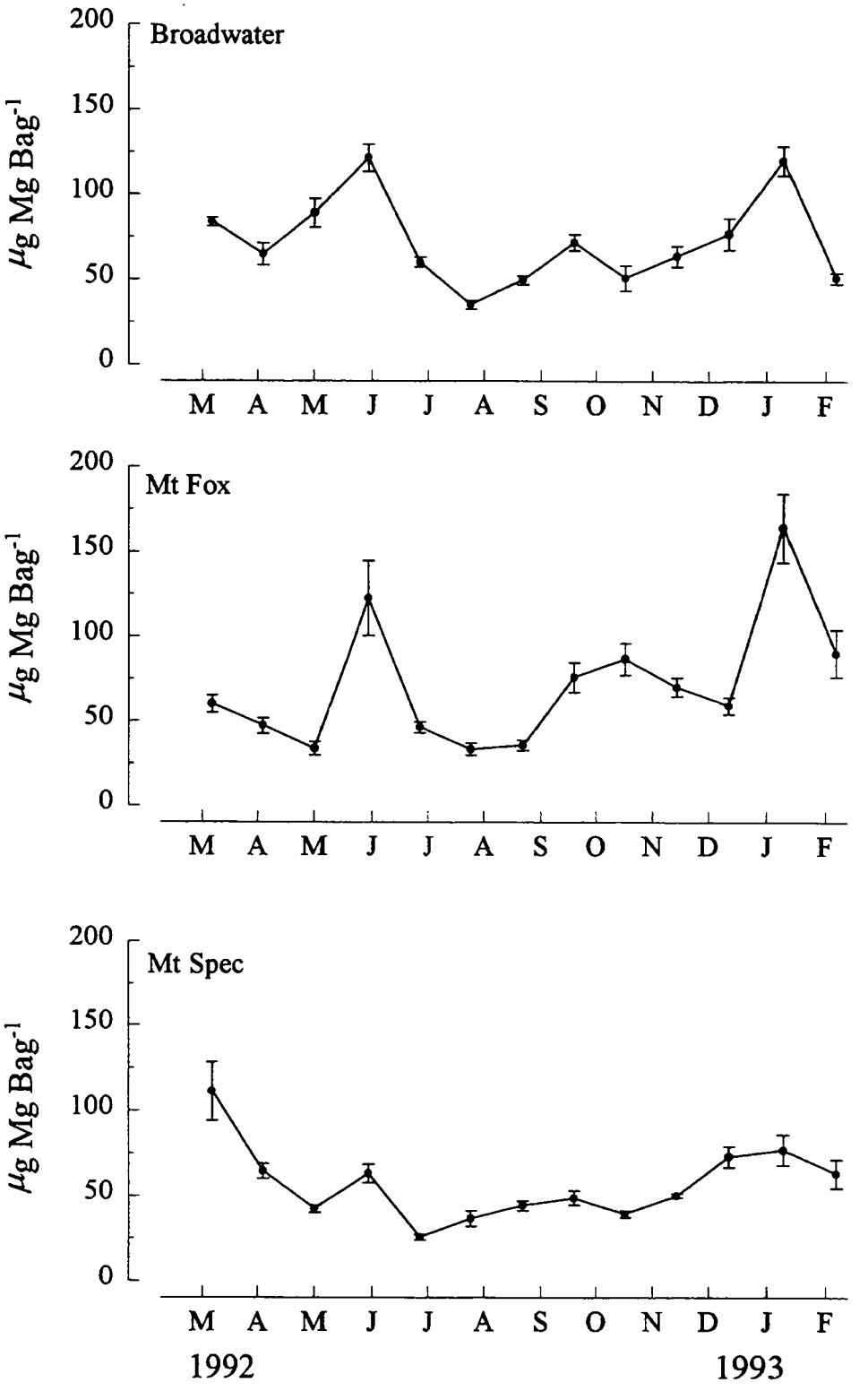


Figure 5.6 Seasonal changes in magnesium availability measured as ion sorption by 20 resin bags incubated in the soil at Broadwater, Mt Fox and Mt Spec. Bars indicate the SEM.

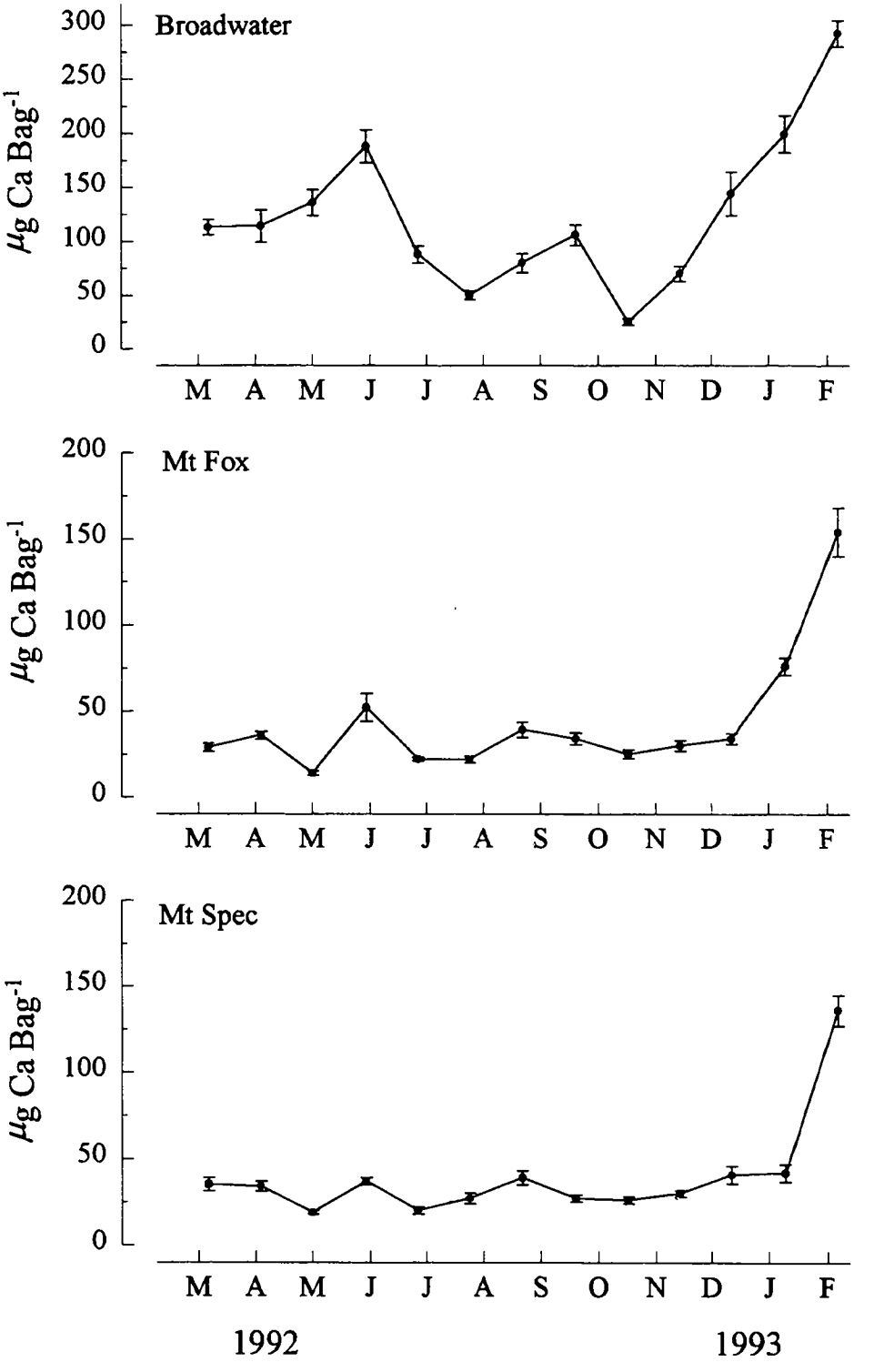


Figure 5.7 Seasonal changes in calcium availability measured as ion sorption by 20 resin bags incubated in the soil at Broadwater, Mt Fox and Mt Spec. Bars indicate the SEM.

Table 5.4 Probabilities for correlation analysis between soil nutrient availability and rainfall for Broadwater, Mt Fox and Mt Spec.

Site	Probabilities				
	Ammonium	Phosphorus	Potassium	Magnesium	Calcium
Broadwater	0.11	0.04*	0.08	0.61	0.01*
Mt Fox	0.81	0.02*	0.27	0.52	0.15
Mt Spec	0.57	0.00*	0.00*	0.00*	0.07

All sites showed some correlation between fine root production and soil nutrient availability (Table 5.2) Fine root production at Broadwater was correlated with the availability of ammonium and potassium, while fine root production at Mt Fox was correlated with available phosphorus. Fine root production at Mt Spec was correlated with phosphorus, potassium and magnesium (Table 5.2).

5.4 Discussion

The ion exchange resin method is thought to be a good indicator of the nutrients available to plants (Binkley & Vitousek 1989). This is because the resins behave in a similar manner to a plant root in their uptake of nutrients from the soil solution (Sibbesen 1978). They adsorb nutrients from water leaching through the soil profile (Crabtree & Kirby 1985), as well as mimicking the exchange properties of plant roots and accumulating nutrients that diffuse through water-filled spaces (Yang *et al.* 1991). Consequently, variations in quantities of nutrients adsorbed by ion exchange resins are believed to reflect changes in nutrient availability to plants (Binkley & Vitousek 1989). However, the simultaneous uptake of water and nutrients by plant roots creates localised gradients in both soil water potential and nutrient concentrations in the soil solution (Jungk 1992). Replenishment occurs by the combined processes of nutrient diffusion and mass flow (Jungk 1992). As these processes occur

simultaneously and are interdependent, it is not possible to calculate exactly what proportion of the total nutrients absorbed by a plant arrives by mass flow or by diffusion (Jungk 1992, Nye & Tinker 1977). Mass flow is thought to be particularly significant in the supply of calcium and magnesium to a plant, while potassium and phosphorus is thought to be supplied predominantly by diffusion (Barber 1984).

The soil solution acts as the immediate source of nutrients for plants (Gillman & Bell 1978, Wild 1989), and their concentrations can vary by an order of magnitude annually (Yavitt & Wright 1996). Previous work in north Queensland utilising resin bags has found a seasonal pattern in soil nutrient availability in the Mt Spec State Forest (Congdon & Maycock in prep.). However, few distinct seasonal patterns were found in this study.

In contrast to Congdon and Maycock (in prep.), no seasonal patterns in the availability of ammonia were found in the present study. The availability of ammonia was low, but relatively constant, from March to August at Mt Fox and Mt Spec (Figure 5.3), while 28-day rainfall totals decreased during this time from in excess of 500 mm to less than 30 mm (Figure 5.1). This relatively constant accumulation of ammonia by the ion exchange resin bags may be the result of the soils staying wet enough during the dry season to permit substantial ion diffusion. Yavitt and Wright (1996) reported substantial diffusion of ammonium during a dry season in a Panamanian lowland rain forest. Ammonium concentrations increased from September onwards, when rainfall began to increase (Fig 5.1).

The availability of phosphorus was correlated to 28-day rainfall total at all sites (Table 5.4). Potassium availability was correlated to 28-day rainfall total only at Mt Spec. However, Mt Fox and Broadwater did exhibit seasonal variations in

potassium availability (Figure 5.5). These seasonal patterns may be due to these nutrients being readily mobilised from leaf litter and other sources (Cornejo *et al.* 1994). There are several possible sources of inorganic nutrients at the beginning of the wet season (Congdon & Maycock in prep.). Nutrients may be released through the decomposition of litter, leached from litter or washed from the forest canopy (Brasell & Sinclair 1983, Cornejo *et al.* 1994, Cuevas & Medina 1986, 1988).

The standing crop and decomposition of litter on the forest floor in tropical forests shows distinct seasonal trends (Brasell & Sinclair 1983, Spain 1984). Litterfall in the wet tropics of north Queensland is strongly seasonal, with most occurring from late in the dry season through the wet season (Brasell *et al.* 1980, Herbohn & Congdon 1993, Spain 1984). Decreased moisture availability and lower temperatures during the dry season reduce the rates of litter decomposition and result in an accumulation of large standing crops of litter (Spain 1984). Increases in moisture availability and temperatures at the start of the wet season result in rapid breakdown of the accumulated litter (Brasell & Sinclair 1983). Several studies have found an initial pulse release of phosphorus and potassium during the early stages of litter decomposition, with significant losses of phosphorus and potassium from litter occurring in the first month of decay (Cornejo *et al.* 1994, Swift *et al.* 1979). Conversely, the release of magnesium and calcium from litter occurs late in the decomposition process, with no changes in magnesium and calcium levels in litter occurring until after four months of decay (Cornejo *et al.* 1994).

Rainfall leaches nutrients from the canopy via throughfall and stemflow (Brasell & Sinclair 1983). Nutrient concentrations can be high during the early rains as accumulated dust and other material is washed down from the leaves, but decrease with further rainfall through dilution and exhaustion of the less readily

mobilised nutrients (Congdon & Maycock in prep.). Throughfall is a major pathway for the cycling of potassium and magnesium in rain forests (Brasell & Sinclair 1983, Gosz *et al.* 1975). The absence of clear correlations between some of the ion exchange resin nutrient concentrations and rainfall may be partly explained by this high early wet season pulse, and decreasing concentrations with dilution and leaching as rainfall peaks.

Fine root production at all sites was found to show distinct seasonal patterns, with peak production occurring during the start of the wet season (Figure 5.1). Similar patterns have been reported for moist and dry tropical rain forests (Kavanagh & Kellman 1992, Kummerow *et al.* 1990, Sanford & Cuevas 1996, Singh & Srivastava 1985, Srivastava *et al.* 1986). Changes in soil moisture conditions are implicated as the cue to root proliferation (Kavanagh & Kellman 1992). The reduction in fine root growth towards the end of the wet season is likely to be a result of the depletion of carbohydrate reserves, rather than changes in soil moisture or nutrient availability (Kavanagh & Kellman 1992, Kellman & Roulet 1990, Singh & Singh 1981).

Fine root proliferation was found to coincide with increased soil nutrient availability, particularly phosphorus (Table 5.2). Phosphorus has been implicated as being potential limiting to productivity in the tropical rain forests of north Queensland (Gillman *et al.* 1985). The proliferation of fine roots during the periods of increased phosphorus availability is possibly an important nutrient conserving mechanism in these forests.

The significantly lower rate of fine root production found in the nutrient-poor soil of Mt Spec is in contrast to the predictions of Bloom *et al.* (1985), who stated that forests on nutrient-poor soils should allocate more resources to below-

ground systems. The slow rate of fine root production and high biomass at this site tends to suggest greater root longevities as discussed in Chapter 3. Further work is required to investigate whether the sites show differences in root longevities, and whether a seasonal decline in live fine root biomass does occur at these sites.

Other possible explanations for the lower fine root production observed at Mt Spec are an increased allocation of carbon to mycorrhizal associations (Jordan 1989), or a greater susceptibility to the disturbance effect associated with the insertion of root ingrowth bags into the soil (Neill 1992).

In conclusion, fine root production measured using root ingrowth bags was found to show distinct seasonal variations, with peak production occurring during the wet season. Fine root proliferation coincided with increased phosphorus availability at all sites. This might be an important nutrient conserving mechanism in these potentially phosphorus-limited soils.

CHAPTER 6
General Discussion

6.1 Aims and overview of the thesis

The aim of this study was to examine aspects of plant-soil nutrient relationships in rain forests of north Queensland. Specifically the thesis examined: the influence of soil fertility on fine root dynamics, the influence of soil fertility on allocation of biomass between the shoot and fine root systems in forests on soils of differing fertilities, nutrient dynamics within the fine roots on soils of differing fertility and seasonal variations in fine root productivity and soil nutrient availability.

Chapter 2 examined above-ground biomass and nutrient distribution within the vegetation recolonising an old log loading ramp in the Mt Spec State Forest. This data was used to derive biomass regressions. Thirteen regressions, based on three allometric models and an exponential model were tested and the most suitable regressions selected. These regressions were then compared to other published biomass regressions for tropical forests.

Chapter 3 involved a study of fine root dynamics and the allocation of biomass between the shoot (total above-ground) and fine root systems of forests on soils of differing fertility. Firstly, the relationship between fine root biomass and soil fertility was examined at six sites in north Queensland, with measurements of total nitrogen and available phosphorus being used as indicators of soil fertility. Following the initial survey, three of these sites on soils derived from different origins were selected to examine the influence of soil fertility on fine root dynamics and biomass allocation. The nutrient status of the soil at the three sites was characterised, and total nutrient stocks within the soil determined. The most

suitable biomass regressions determined in Chapter 2 were applied to vegetation measurements at the three sites to estimate above-ground biomass. The generalised equations of Brown *et al.* (1989) were also used to estimate biomass. Fine root biomass, production and decomposition were examined using root cores, ingrowth bags and enclosures. This data was used to investigate the influence of soil fertility on fine root dynamics and allocation of biomass between the above-ground vegetation and the fine roots at each of the three sites.

The influence of soil fertility on fine root nutrient concentrations and nutrient dynamics within fine roots were examined in Chapter 4. Nutrient concentrations were determined for the fine root samples (Chapter 3). This data was then combined with the fine root biomass and production data (Chapter 3) to estimate total nutrient standing stocks within fine roots, and the rate of turnover of nutrients at the three sites. Nutrient concentrations within live and dead fine roots were also examined to investigate whether nutrients were retranslocated prior to senescence.

Chapter 5 investigated seasonal variations in fine root production and soil nutrient availability. Variations in the biomass of fine roots accumulated in short-term root ingrowth bags were related to changes in rainfall and concentrations of nutrients adsorbed by bags of ion exchange resins.

6.2 Biomass, nutrient standing stocks and biomass regressions

The above-ground biomass and nutrient standing stocks within the vegetation recolonising the loading ramp are amongst the lowest published values for similar aged secondary rain forests. Nutrient content per tonne of biomass was also found to be substantially lower than in other published studies. The removal and

compaction of the soil during ramp construction are the most likely causes for this reduction in biomass and nutrient accumulation in the recolonising vegetation.

Above-ground biomass was found to be closely correlated with diameter at breast height (dbh) and height. This suggests that biomass can be confidently estimated from these measurements at other sites with similar species composition and growth conditions. The equations utilising both dbh and tree height yielded better estimates than the equations using dbh or tree height alone. The accuracy of the regression was improved by incorporating these two variables as separate independent variables, rather than combined as a single variable. Surprisingly, the inclusion of wood density in the regression equations did not significantly improve the estimation of biomass. The inclusion of the variable allometric ratio in the regressions did not improve the accuracy of the total above-ground biomass regressions. Bias induced by logarithmic transformation varied from 11 to 51%, highlighting the importance of determining correction factors for these regressions.

Whether the regressions determined in this study are applicable to a broader range of sites is uncertain. All of the regressions determined in this study substantially underestimate biomass when applied to the data set of Ovington and Olson (1970). However, few published biomass regressions were found to give accurate estimates for their site. The closest estimates obtained from the ramp site regressions were based only on trees greater than 5 cm diameter. Few published biomass regressions were suitable for estimating biomass at the ramp site, as most were found to substantially overestimate biomass.

While the regressions determined in this study may be applied to other sites in north Queensland, the estimates obtained must be viewed with caution as

differences in species composition, tree architecture and stem allometry may result in significant errors in biomass estimates. However, this is a feature common to all biomass regressions, and is not specific to the regressions determined in this study.

6.3 Soil fertility, fine root dynamics and resource allocation

Generally, fine root biomass was greatest on nutrient-poor sites and lowest on more fertile sites. However, it is unknown whether this is due to differences in available phosphorus or some other, as yet, undetermined factor. In contrast to Gower (1987), no significant relationship between available phosphorus concentration and fine root biomass was found at the six sites examined in this study. However, when data from other studies were included in the analysis a significant negative correlation was found between fine root biomass and available phosphorus concentrations.

The three main study sites, with soils from different origin, have significantly different soil nutrient concentrations. The alluvial and basalt-derived soils of Broadwater and Mt Fox were more fertile than the granite-derived soils of Mt Spec. The former soils had high concentrations of available and total phosphorus, and greater quantities of exchangeable cations. Despite these differences in soil fertilities between the three sites, there were few differences in the structural measures and above-ground biomass of the vegetation. However, fine root dynamics were substantially different between sites.

Fine root biomass was significantly different between the sites, with Mt Spec having a significantly greater biomass of fine roots. Fine root production was also significantly different, with Mt Fox having the greatest rate of fine root production. These differences in standing crop and production of fine roots

suggest differences in fine root turnover between the sites. The estimated annual rates of fine root turnover were 85% at Broadwater, 137% at Mt Fox, and 33% at Mt Spec. This suggests that there are differences in root longevities between the sites, with Mt Spec maintaining its high fine root biomass with slower rates of fine root turnover and greater fine root longevity.

Bloom *et al.* (1985) predict that forests growing on nutrient-poor soils should allocate a greater proportion of their resources into fine roots as this "investment'" in nutrient acquisition should yield increased growth and/or reproduction. This and other studies show that rain forests growing on "nutrient-poor" soils support a greater fine root biomass relative to their above-ground biomass than those on nutrient-rich soils. The ratio of standing crop of live fine roots to estimated total above-ground biomass ranged from 1.9 to 6.2% in this study.

Whether plants on nutrient-poor sites allocate greater resources to fine roots as predicted by Bloom *et al.* (1985), or differences are due to slower rates of fine root turnover and greater root longevities, is unclear. The nutrient-rich sites of Mt Fox and Broadwater had small standing crops of fine roots and fast rates of fine root turnover, while the rain forest on the nutrient-poor soils at Mt Spec had a large standing crop with slow turnover of fine roots. There is no data available on resource allocation to mycorrhizal associations, so differences in allocation could be due to greater mycorrhizal cost at the nutrient poor-site.

6.4 Nutrient dynamics in fine roots

Fine roots are as important as litterfall in returning nutrients to the soil in tropical forests. Fine roots contain only a relatively small proportion of the total nutrient stocks within the vegetation (1.3 and 14.2% in previously published studies). However, the rapid rate of turnover and moderately high nutrient concentrations

within fine roots results in large quantities of nutrients being cycled through fine roots. Annual litterfall at Mt Spec contributes 59.5 and 2.1 kg ha^{-1} y^{-1} of nitrogen and phosphorus respectively to the soil (Herbohn 1995). Fine roots in the top 10 cm of soil contributed 31 kg N and 1.2 kg P ha^{-1} y^{-1}, while fine roots to 50 cm depth contribute as much as litterfall. While no data are available for Broadwater or Mt Fox, there are data available for three sites on basalt-derived soils in north Queensland (Brasell *et al.* 1980). Brasell *et al.* (1980) reported that litterfall contributed 129 and 11.2 kg ha^{-1} y^{-1} of nitrogen and phosphorus annually to the soil. This compares with 51 and 3.0 kg ha^{-1} y^{-1} of N and P from fine roots in the top 10 cm recorded at Mt Fox.

This study found no evidence of retranslocation of nutrients from fine roots prior to senescence. However, this may in part be due to problems in applying Nambiar's (1987) method to tropical forests. This method makes two assumptions which may not have been met in the present study. The importance of nutrient retranslocation from fine roots is unclear, as it has been examined in few studies, and these have often yielded conflicting results (Aerts *et al.* 1992, Cuevas 1995, Meier *et al.* 1985, Nambiar 1987, Vogt *et al.* 1987).

6.5 Seasonal variation in fine root production and soil nutrient availability

Measurements of fine root production using root ingrowth bags showed distinct seasonal variations, with peak production occurring during the wet season. Fine root proliferation coincided with increased phosphorus availability at all sites. This might be an important nutrient conserving mechanism in these potentially phosphorus-limited soils.

The significantly lower rate of fine root production found in the nutrient-poor soil of Mt Spec is in contrast to the predictions of Bloom *et al.* (1985). Other

possible explanations for the lower fine root production observed at Mt Spec are an increased allocation of carbon to mycorrhizal associations (Jordan 1989), or a greater susceptibility to the disturbance effect associated with the insertion of root ingrowth bags into the soil (Neill 1992).

6.6 Significance of this study

Root systems remain one of the least known aspects of tropical rain forests. This lack of knowledge represents a gap in our understanding of rain forest ecosystem dynamics. Similarly, we have little information on the allocation of resources between the above-ground and below-ground portions of tropical forests. The results of this study contribute towards our understanding in a number of ways.

Firstly, this study provides the first quantitative data on the influence of soil fertility on fine root dynamics and resource allocation in Australian tropical rain forests. This data indicates that rain forests on nutrient-poor sites maintain a greater fine root biomass, and ratio between fine root to above-ground biomass, compared to nutrient-rich sites. This appears to be due to greater root life-spans at the nutrient-poor sites, rather than greater rates of fine root production.

Secondly, while a number of previous studies have investigated above-ground fluxes within the rain forests of north Queensland (Brasell & Sinclair 1983, Brasell *et al.* 1980, Congdon & Herbohn 1993, Herbohn 1995, Herbohn & Congdon 1993, Spain 1984), this study provides the first data on nutrient dynamics within fine roots. This data greatly adds to our understanding of nutrient cycling within these forests, and provides information on the role of soil fertility on nutrient dynamics within fine roots.

Finally, the results of this study are an integral component of a long-term study of nutrient cycling in logged and unlogged forest plots in the Birthday Creek catchment of the Mt Spec State Forest. After completion of related studies, it will be possible to develop a comprehensive nutrient budget for this catchment. To date, there have been few comprehensive catchment studies in tropical forests (Bruijnzeel 1991). This study provide direct estimates of biomass and nutrient stocks within the vegetation at a disturbed site, and a means to estimate these measures at other sites within this catchment. The data on fine root turnover and nutrient dynamics within fine roots provide data on the below-ground processes within this forest.

A large number of questions regarding root systems and plant allocation of resources within tropical forests, and the influence of soil fertility on these processes remain to be answered. Very little is know about allocation to mycorrhizal associations and how this is affected by soil fertility. Similarly, more information is required on the importance of the deeper roots in nutrient cycling and ecosystem dynamics of tropical forests. Finally, further data is required on the relationship between fine root productivity and soil fertility.

In conclusion, the current study has contributed towards our understanding of the effects of soil fertility on fine root dynamics and resource allocation in tropical forests. It has shown that there are intrinsic differences in fine root dynamics and resource allocation on soils of differing fertility, despite a similarity in above-ground biomass, with rain forests on nutrient-poor soils having a greater standing crop of fine roots and a slower rate of fine root turnover than rain forests on richer soils. This study has also shown that there are distinct seasonal variations in fine root production, with peak production coinciding with increased soil nutrient availability, and that fine roots are an important means of return of nutrients from the vegetation to the soils.

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