Decomposition, nutrient cycling and climate change in Australian tropical rainforests

Thesis submitted by

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STATEMENT OF CONTRIBUTION OF OTHERS

Chapter 5 of this thesis has been published in collaboration with Prof. Steve Williams and Dr Luke Shoo. Prof. Williams and I developed the methodological design for this chapter and Dr Shoo aided in statistical analysis and editing. Chapters 2, 3 and 4 were submitted and in review with journals prior to submission of this thesis. The first round of reviews for chapters 2 and 4 were received prior to thesis submission, and these chapters herein are relative to the reviewed and resubmitted versions. These works are coauthored with my supervisors, along with Dr Luke Shoo (Chapter 4), Collin Storlie (Chapter 3), and Vanessa Valdez-Ramirez (Chapter 3). Dr Shoo provided statistical advice and editorial assistance. Collin Storlie provided extensive field assistance and editorial assistance. Vanessa Valdez-Ramirez provided litterfall samples and data from her own PhD project, which are included in Chapters 3 and 6 with her permission. While undertaking this research, I was responsible for the project design, obtaining research funding and permits, collecting field and laboratory data, statistical analysis and interpretation, and synthesis and preparation of manuscripts for submission to peer reviewed journals. I obtained direct financial support from James Cook University School of Marine and Tropical Biology, the JCU Centre for Tropical Biodiversity and Climate Change and the Skyrail Rainforest Institute.

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The Australian Wet Tropics is a magnificent location of exceptional rarity and complexity. The field trip mornings with the Cowchillas and nights with the Sooty owls were unforgettable.

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Words from some who have inspired me:

"Life is out there in expected abundance. The jungle teems..."

Edward O. Wilson, from the book *The Diversity of Life*, 1992

"We're not scare-mongering
This is really happening"
Radiohead, from the song *Idioteque*, 2000

"it's just a ride, and we can change it any time we like"

William (Bill) Melvin Hicks, from the live show *Revelations*, 1993

THESIS ABSTRACT

Knowledge of the mechanisms that dictate the composition and dynamics of ecosystems is essential for understanding the natural world. It is important to consolidate our understanding of ecosystem processes due to the need to understand and adapt to global anthropogenic climate change. The processes of decomposition and nutrient cycling that occur on the soil surface in forested environments both sustain ecosystems and have a substantial influence on the biosphere at many scales. This encapsulates the processes of plant litterfall, litter decomposition and nutrient release. Litter decomposition and nutrient cycling, although controlled by climate, vegetation and soil communities, are highly spatially and temporally variable. Our lack of understanding of these processes limits our ability to understand and adapt to climate change. The Australian Wet Tropics bioregion of north Queensland is an interesting natural environment in which to investigate the drivers and controls on litter decomposition and nutrient cycling. The region contains a range of tropical rainforest types on a variety of soils and is subject to varied climatic conditions. The risks of adverse effects from climate change are also high for this region, potentially leading to substantial losses of biodiversity and rare plant communities.

Decomposition and nutrient cycling were studied in this region at 21 locations (from near sea level to around 1300 m elevation), covering most of the climate range and soil conditions of the region. The aim was to understand the patterns and controls on these processes and how these controls may deviate from their current states under climate change scenarios. The approach determined spatial and temporal patterns in: leaf litter decomposition rates and nutrient dynamics in leaf litter using the litterbag technique for ~ 420 days; litterfall nutrients and chemical quality (i.e. chemical potential to decompose) of litterfall; litterfall rates and seasonality (in-conjunction with another PhD student); the amount of litter on the soil surface (litter standing crop, LSC) and the seasonality and turnover/duration of litter on the soil surface. Models explaining litter dynamics were then applied to climate change predictions specific to the region to determine the sensitivity of litter processes to climate.

Plant litter chemical quality is a highly significant driver of decomposition and nutrient cycling processes; however, standard methods for determining litter quality indices are often arduous and limited in their ability to explain ecological phenomena. Near infrared spectrometry (NIRS) has the potential to extend standard methods for chemical quantification. NIRS was used here to quantify the concentrations of nutrients, carbon fractions (total carbon and lignocellulose portions) and plant secondary compounds in litterfall, and leaf litter that underwent decomposition. NIRS also accurately predicted litter decomposition rates based on their initial NIR spectral composition (i.e. organic chemical composition) to determine litter decomposability, and was successfully used to model chemical changes in the material during decomposition.

The first exponential decomposition rate constants of *in situ* leaf litter (litter characteristic of each site) ranged from 0.33 y^{-1} (upland microphyll fern forest on granite) to 2.15 (complex mesophyll vine forest on basalt). Decomposition rates were explained well by climate, soil and litter quality, for litter collected *in situ*: average leaf wetness in the dry season (LWDS, moisture condensation) and the initial P content of the leaves ($r^2 = 0.78$, $p < 0.001$, $n = 17$), or LWDS and initial C ($r^2 = 0.75$, $p < 0.001$, $n = 17$); control treatment (a standard leaf litter, no litter quality effect): rainfall seasonality (% dry season days with 0 mm rainfall), soil P, and mean annual temperature ($r^2 = 0.78$, $p < 0.001$, $n = 12$). Nutrients were not mineralised for periods of more than 12 months. Increased temperatures and moisture (especially in the dry season) improved lignocellulose and C mineralisation.

Litterfall leaf litter quality (24 months worth of sampling from 40 study plots at 20 sites) was driven by the combination of soil fertility (nutrient contents), climate (phenolics and C) and species/disturbance (lignocellulose components). Trends in litter quality indicated a negative feedback on soil and nutrient cycling processes in more stressed environments characterised by higher rainfall seasonality and lower soil fertility. Also, short term climate changes were determinants of litter chemical quality, with NIRS predicted decomposability lower, and total phenolic contents higher, in the dry season.

Two year average litterfall rates ranged from 4.89 to 11.29 t ha^{-1} y^{-1} ($n = 40$ plots). No environmental variable could explain litterfall rates but calculations were hindered by the secondary status of the vegetation, particularly resulting from

damage caused by Cyclone Larry at many sites in March 2006. Seasonality of litterfall (vector algebra index) was linearly related to mean annual temperature and soil nitrogen. The temperature effect was partially explained by dry season moisture, however the trend was for higher seasonality in the wetter/cooler uplands (n = 29). LSC was determined in the field by a volumetric method developed especially for this study. LSC values ranged from 3.70 t ha^{-1} to 10.94 t ha^{-1} (n = 36 plots), and were explained by litter quality (NIRS decomposability) and the composition of litterfall, along with soil Na, mean annual temperature and leaf litter C content. LSC turnover quotients ranged from 0.57 to 2.81, and were controlled by similar variables to mean annual LSC. Seasonality in LSC was linearly related to soil Na. Local variability was high for mean annual LSC, with around 35% of the full regional variation contained within single 1 km transects.

Climate change scenarios suggest temperature increases and decreases in dry season rainfall, with associated uncertainty, and dependent on emission scenario (mean for the full range of SRES, WRE450 and WRE550). The predicted changes in climate related to increases in the climate decomposition index (potential for climate driven decomposition, determined from min/max temperatures and monthly rainfall totals/seasonality) of +5.2 to +20.5% from current conditions (average from 40 study plots). Predicted changes in leaf decomposition rate and leaf lignin mineralisation rate (from control litterbag study), and full litter layer turnover rate were determined at 10 year time steps until 2080. For 2080 relative to present day, leaf decay rate showed large uncertainty: -7.46 to +8.15%; lignin mineralisation increased: -0.32 to +3.39%; and litter turnover increased: +5.9 to +24.2. The uncertainty in the leaf decay models were driven by uncertainty in the changes in dry season rainfall. The data suggests increasing decomposition rates from current conditions for poorer (chemical) quality material, such as whole litter standing crop and leaf lignin, compared to less recalcitrant material such as leaf litter. The magnitude of change is predicted to be greater at upland sites than lowland sites due to the non-linear relationship between temperature and the climate decomposition index, and on poorer nutrient soils due to the increasing effect of temperature on the decomposition of low chemical quality litter.

The extent and direction of change in these forests will depend not only on the direct effects of temperature and dry season rainfall and subsequent alterations in

soil level litter processes, but also changes in primary productivity, including the timing and seasonality of litter inputs, and climate-driven succession of vegetation and plant traits such as litter chemical quality. These changes in the landscape feed back to global biogeochemical cycles in complex ways. Increases in litter decay, as mostly predicted to occur from this work, may act to further accelerate global warming. However, the direction of climate change driven changes in primary productivity, vegetation communities and plant litter quality, are essential in determining outcomes.

Chapter 1. Thesis Rationale

1.1. Ecological context

Understanding of the processes that sustain ecosystems is central to ecology and scientific understanding of the natural world (Tansley 1935; Christensen *et al.* 1996; Loreau *et al.* 2001). Ecosystem ecology aims to explain how ecosystems work, by relating quantifiable processes to biotic and abiotic components, such as chemical, geological, climatic and plant and animal communities (Hagen 1992; Chapin *et al.* 2002). Knowledge of the flow of energy and materials through living organisms and the physical environment is a foundation for comprehending the diversity of form and functioning of the planet's physical and biological processes (Chapin *et al.* 2002). These may include the dynamic cycles of water and gases, minerals and nutrients, solar energy and community dynamics (e.g. succession), which are the bases of all ecosystem processes (Hagen 1992). The structure and function of ecosystems are controlled broadly by time, climate, parent material and soils, topography and the potential biota (i.e. the organisms within the particular region) (Dokuchaev 1879; Jenny 1941; Chapin *et al.* 1996). This combination of factors gives rise to ecosystems and the dynamic cycles they contain. Detailed understanding of these ecosystem processes is inherent in any attempts to understand terrestrial ecosystems and predict responses to change (Grime 2002).

Forest litter decomposition determines the breakdown of material on the

forest floor, releases nutrients for continued plant productivity and soil function, and represents a major flux of elements between plants, soils and the atmosphere (Swift *et al.* 1979; Cadisch and Giller 1997). Decomposition processes are controlled broadly by climate, soil fertility and the soil community and the characteristics of the plant communities/material being broken down (Aerts 1997). To obtain a broad understanding of litter decomposition and nutrient cycling processes, local to regional and whole ecosystem scale approaches are required (Townsend *et al.* 2008). Climate, the species composition, successional status and soil fertility determine forest nutrient cycles (Vitousek and Sanford 1986). Litterfall represents the major pathway for transfer of nutrients between plants and soils and material for decomposition (Vitousek and Sanford 1986)**.** At most scales the chemical makeup of the material is the strongest determinant of spatial variation in decomposition rates (Cornwell *et al.* 2008; Zhang *et al.* 2008), and, in this context, is generally termed "litter chemical quality" (Cadisch and Giller 1997). Litter chemical quality is therefore, a particularly important controlling factor in forest nutrient cycles and ecosystem processes in general, and may be highly variable, spatially and temporally, at both local and regional scales (Cornwell *et al.* 2008), especially in tropical rainforests (Townsend *et al.* 2008). Low quality litter is recalcitrant to decay, while high quality litter breaks down fast, quickly releasing nutrients. Climate also directly influences litter quality**,** although clear models of temperature, rainfall and seasonality effects on litter quality at regional scales are rare (Couteaux *et al.* 1995; Aerts 1997).

There is unequivocal scientific evidence that anthropogenic climate change is occurring (Dyurgerov and Meier 2000; Walther *et al.* 2002; Parmesan and Yohe 2003; IPCC 2007). The impact that changes in climate will have on forested

ecosystems and biodiversity as a whole are complex, but relate broadly to interactions between, climate, ecosystem processes and succession and adaption of the biotic communities (Weltzin *et al.* 2003; Marshall *et al.* 2008; Williams *et al.* 2008). Limitations in our ability to predict climate change impacts exist due to our lack of understanding of ecological systems and processes in general (Falkowski *et al.* 2000; Nemani *et al.* 2003). As litter decomposition and nutrient cycling are of intrinsic importance in governing ecosystem functions and biodiversity, knowledge of the patterns and drivers of litter processes on the soil surface, and their sensitivity to climate, are useful to answer questions related to general ecology, and to predict the impacts of climate change from local (e.g. community succession) to global scales (e.g. global cycles).

Wet tropical rainforests in Australia mainly occur in a narrow band on the north-east Queensland coast, between 19^{o} 15' and 15^{o} 30' (near Townsville to just south of Cooktown). These forests have high biodiversity and species endemism and are protected under World Heritage Listing (Myers 1988; McDonald and Lane 2000). The rainforests in this region exists as remnants within mosaics of fire-prone open forests and woodlands, and land cleared for agriculture (Webb 1990; Bowman 2000). The potential in this region for climate-driven changes in forest distribution (Hilbert *et al.* 2001), and substantial losses of biodiversity (Williams *et al.* 2003) into the 21st century are well documented. Despite this knowledge, baseline data explaining the processes in this region that both maintain biodiversity and forest structure, and ecosystem function are lacking.

1.2. Aims of this study

This thesis asks what determines the patterns and drivers of decomposition and nutrient cycling in the north Queensland tropical rainforests and how these may be altered by climate change. What effects changes may have on rainforest ecosystems in general is considered. A conceptual framework developed for this thesis, to assess decomposition and nutrient cycling dynamics in the context of climate change, is shown in Figure 1.1. Climate change driven changes in ecosystem function (Cramer *et al.* 2001), species composition and habitat (Hilbert *et al.* 2001; Williams *et al.* 2003), may occur through alterations in the vegetation and soil communities and their dynamics (Melillo *et al.* 1993; Swift *et al.* 1998; Woodward and Lomas 2004), and the direct effects of climate on primary production, litter composition and decomposition (Aerts 1997; Clark *et al.* 2001b) (Figure 1.1). To understand decomposition and nutrient cycling in this context, information on climate, the vegetation community, soil fertility and soil composition, primary production (esp. litterfall) and the litterfall composition (especially litter chemical quality) and litterfall timing (especially seasonality) are required (Figure 1.1). The main focus of this work is to determine the patterns and drivers of plant litter decomposition and nutrient cycling, in the current climate and relate these to the vegetation communities (i.e. forest type, successional status) and environmental conditions of the sites (i.e. soil composition, elevation/temperature, rainfall and rainfall seasonality, topography). From this information predictions regarding the potential pathways of the effects that projected future climates may have on these processes and the ecosystems in general were made. Data collection focused on the processes of decomposition, litter and nutrient dynamics, and the direct and indirect controls on

these; namely, climate, litter chemical quality and litterfall composition and timing, soil fertility and the vegetation communities (Figure 1.1). Both local (within 1 km) to full regional variability in the processes were considered. The knowledge gained from determining these patterns and controls was then used to explore the sensitivity of plant litter processes in relation to predictions from meteorological climate circulation models for the region. How climate-driven alterations in decomposition and nutrient cycling processes may feed back to promote or diminish rainforest stability and community succession in novel climate space is discussed. An elevational sampling scheme is used to determine climate influences, at sites in tropical rainforest, located throughout the climate space of the Australian Wet tropics. The work is part of a broader biodiversity study in the Centre for Tropical Biodiversity and James Cook University. The focus in this thesis is on nutrients cycled through plant litter, and although other nutrient pathways are acknowledged to be significant, these are outside the scope of this work. Net primary productivity (NPP) is a critical control on litter processes; however, NPP is not covered directly in this thesis and is the topic of another PhD student working at the same sites (Vanessa Valdez-Ramirez, thesis tropic: "Net primary productivity and climate change in Australian tropical rainforests"). Data and samples obtained from the NPP study have been used throughout the current thesis and acknowledged accordingly. Additionally, the direct effects of rising CO_2 through climate change importantly influences the processes studied here. The effects of CO_2 on litter chemical quality and litter processes have been the focus of many studies (Hirschel *et al.* 1997; Cotrufo *et al.* 1998; Norby *et al.* 2001), and are outside the scope of this work. Where relevant, discussion of this important driver is included.

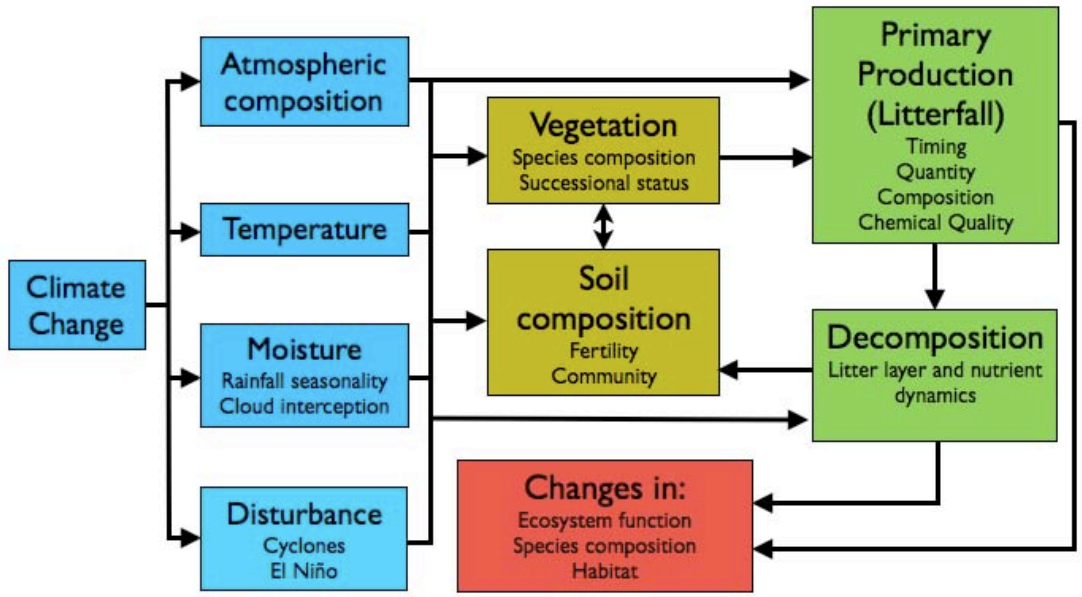

Figure 1.1. Framework for studying tropical rainforest decomposition and nutrient cycling in the context of climate change. Climate based drivers (blue) are all predicted to change in the 21st century, altering vegetation and soil composition (yellow), and plant litter processes (green), leading to changes in ecosystem function and composition (red).

1.3. Study Sites

The AWT bioregion comprises approximately 1.8 million ha of mixed tropical forest (Figure 1.2). Despite previous intense land clearing and selective logging practices, the region is dominated by rainforest now protected under World Heritage listing, covering slightly less than 1 million ha. Rainforests exist within a relatively high range of annual rainfall (around 1.5 m to over 9 m pa). Seasonality in rainfall is particularly important in determining both the distribution of rainforests and the floristic attributes of sites (Kershaw 1994). The importance of fire in shaping these changes, and thus vegetation succession, is also well known (Bowman 2000). The region contains strong gradients in soil attributes, from Cainozoic mesotrophic basalt deposits on the Atherton Tablelands, to more widespread dystrophic Carboniferous - Permian granite and rhyolite deposits, along with other minor mostly oligotrophic

soil types (Isbell *et al.* 1968). The region has a distinct dry season (April - October). Often more than 80% of the rainfall occurs in the wet season/summer months; however, the extent of this seasonality varies substantially between elevations and from north to south (Webb 1978). In this study, the dry season is defined as the period 1st April to 31st October. Climate data used in this study is shown in Appendix 1, and is a combination of real time (data logger) and long term averages. See the relevant chapters for descriptions of variables and collection methods.

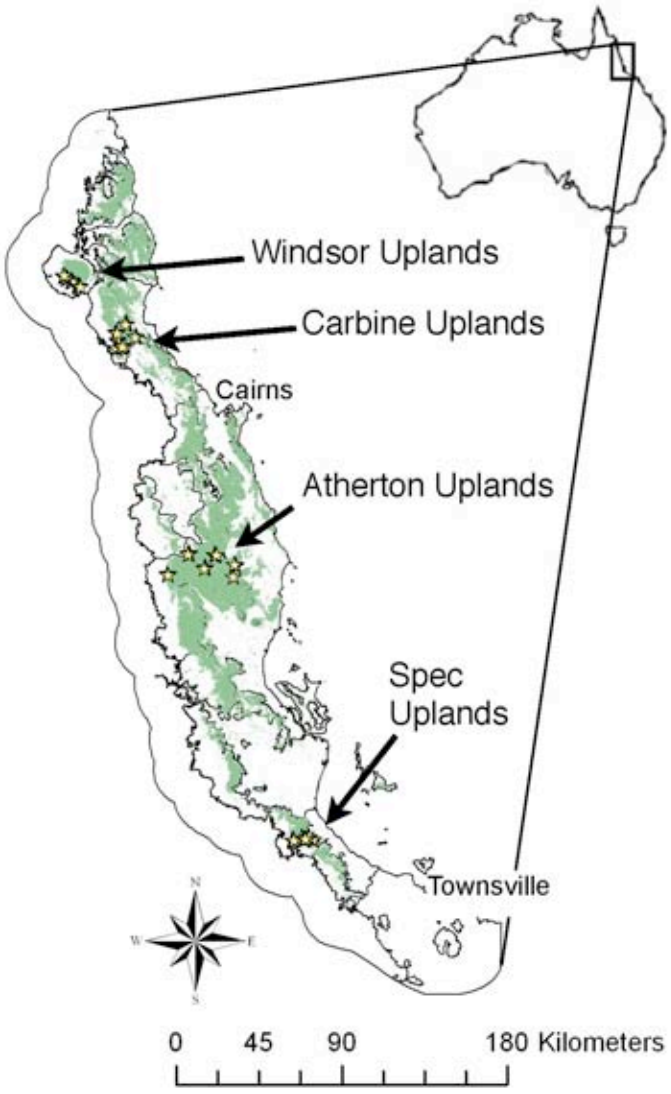

Figure 1.2. Map of the location of study sites in the Australian wet tropics. The four subregions that are the focus of this work are shown: Windsor Uplands, Carbine Uplands, Atherton Uplands and Spec Uplands.

Sites were selected to cover the range of climates of the wet tropics, and are outline below. Sites on the highest peaks (Mt Bellenden Ker, > 1400 m), were not accessible during this study. Elevational transects were studied in four sub-regions: AU, Atherton Uplands (100 m to 900 m a.s.l.); CU, Carbine Uplands (100 m to 1200 m a.s.l.); SU, Spec Uplands (around 300m to 1000 m a.s.l.); WU, Windsor Uplands (around 900 to 1300 m a.s.l.). In this text the sites are referred to by the sub-region, followed by elevation rounded to nearest 100 m, e.g., AU1 = the Atherton Uplands sites at 80 a.s.l. The broad characteristics of the 21 sites are outlined below. All sites contained 1 km transects with 6 plots (200 m apart). Experimental plots were approximately 30 m^2. Two of these plots were the locations of detailed monitoring in this thesis (litterfall and litter standing crop). The remaining plots were used for other aspects of the study as explained in the text. The vegetation types follow Webb (1978) and Specht (1970). Further detail is given in Appendix 2 and the relevant chapters.

Atherton Uplands

AU1: 80 m a.s.l., Cyclone damaged Complex Mesophyll Vine Forest on alluvium/ mudstone.

AU2: 180 m a.s.l., Cyclone damaged Complex Mesophyll Vine Forest on basalt.

AU4: 428 m a.s.l., Cyclone damaged Complex Mesophyll Vine Forest on basalt.

AU6: 630 m a.s.l., Cyclone damaged Notophyll Vine Forest on basalt with areas of exposed granite.

AU8: 840 m a.s.l., Cyclone damaged Notophyll Vine Forest on basalt

AU9: 930 m a.s.l., Notophyll Vine Forest on basalt

Carbine Uplands

CU1: 162 m a.s.l., Mesophyll Vine Forest on granite

CU2: 234 m a.s.l., Mesophyll Vine Forest on granite

CU4: 440 m a.s.l., Mesophyll Vine Forest on granite and mudstone

CU6: 656 m a.s.l., Notophyll Vine Forest on granite

CU8: 820 m a.s.l., Notophyll Vine Forest on granite

CU10: 1016 m a.s.l., Notophyll Vine Forest on granite

CU12: 1210 m a.s.l., Microphyll Fern Forest on granite

Spec Uplands

SU3: 334 m a.s.l., Notophyll Vine Forest on rhyolite

SU6: 671 m a.s.l., Medium Open Forest with regenerating rainforest understory on rhyolite

SU8: 834 m a.s.l., Notophyll Vine Forest on rhyolite

SU9: 899 m a.s.l., Notophyll Vine Forest on granite

SU10: 963 m a.s.l., *Acacia* sp. Closed Forest on rhyolite

Windsor Uplands

WU9: 940 m a.s.l., Notophyll Vine Forest with *Agathis* sp. emergents on granite

WU11: 1071 m a.s.l., Notophyll Vine Forest on granite

WU13: 1280 m a.s.l., Microphyll Fern Forest on granite

The AU2, 4, 6, 8 and 9 plots were generally on Cainozoic basaltic lava flows, with generally deep red, mesotrophic, Ferrosols (Isbell 2002). AU1 plots were Rudosols on alluvium underlain by Devonian mudstone. All CU sub-region plots occurred on Permian granite complexes with dystrophic Kandosols. The SU plots were mostly on Carboniferous acid volcanic Rhyolite rock types, with dystrophic Dermosols, and the WU on late Carboniferous - Permian granite, producing dystrophic Kandosols (Isbell 2002).

Vegetation structure at most sites had been altered to varying extents by anthropogenic activities. This was mostly due to selective logging activities prior to World Heritage listing in 1988, so all had remained relatively undisturbed for at least 20 years. AU1, AU2, AU4, AU6 and AU8 were affected by severe tropical cyclone Larry (category 5) in March 2006 (Turton 2008). The extent of the damage varied between plots, but severe defoliation, although patchy, occurred and much of the canopy was either lost or greatly damaged. By May 2007 all of these plots had regained foliage cover at least in the lower canopy layers, and by 2009 all except AU8A5 had significant canopy coverage (> 90%, based on hemispherical canopy photographs). The vegetation composition of each location is explored in the relevant chapters.

1.4. Thesis structure

This thesis contains six main chapters in addition to this introduction and a general discussion. The main text begins with a description of the method used to determine the plant litter chemical composition, used in the following chapters, with Near Infrared Spectrometry (NIRS) analysis (Chapter 2, Rainforest litter quality and

chemical controls on leaf decomposition: insights with near infrared spectrometry). This thesis uses a large number of sites and there was a need for rapid assessment of both litter chemistry and the litter layer (litter standing crop, LSC). Two methods for rapid assessment are the focus of Chapters 2 and 5. Chapter 5 (Volume measurements for quicker determination of forest litter standing crop) presents a method developed to measure LSC in the field. Chapter 3 (The drivers of plant litter quality and nutrients in Australian tropical rainforests) focuses on the drivers of nutrients and litter chemical quality in litterfall, using material collected in the NPP study. Chapter 4 (Regional patterns and controls of leaf decomposition and nutrient dynamics in Australian tropical rainforests) presents the findings of experimental work that determines the patterns and controls on the physical and chemical dynamics of leaf material decomposing on the soil surface. Chapter 6 (Local and regional scale patterns and controls on litter processes in Australian tropical rainforests) focuses on the patterns and controls on litterfall and whole litter layer dynamics throughout the region. Chapter 7 (Sensitivity of Australian tropical rainforest litter processes to climate change) takes some of the information gained from the preceding chapters to explore the sensitivity of litter dynamics in the north Queensland rainforests to climate change, using predictions from climatic general circulation models (GCMs) specific to the region. The general discussion (Chapter 8) ties the information obtained from the preceding chapters together to make broader conclusions on the patterns and controls of nutrient cycling in the Australian wet tropics region and similar forest types. Chapter 8 also discusses the potential pathways of processes and biogeochemical cycles under climate change, and presents recommendations for future research.

Chapter 2. Rainforest litter quality and chemical controls on leaf decomposition: insights with near infrared spectrometry

(Submitted for publication [*Plant and Soil*], manuscript number: PLSO7234)

2.1. Introduction

Plant litter decomposition and nutrient dynamics in forested ecosystems are determined by complex cycles and feed-backs between the species/chemical composition of the vegetation, the soil biota and the environmental conditions of the site (Tenny and Waksman 1929; Meentemeyer 1978; Swift *et al.* 1979; Aerts 1997). Leaf litter often makes up the most significant portion of material cycled in forests (Swift *et al.* 1979; Vitousek and Sanford 1986) and plant traits, as a function of litter chemical composition, have been shown to drive terrestrial ecosystem process (Berendse 1994; Aerts 1997; Wardle *et al.* 2002; Cornwell *et al.* 2008; Kazakou *et al.* 2009; Ordonez *et al.* 2009). Litter decomposition and feed-backs to plant and soil function is the most significant of these, and litter chemical quality, more so than climate, has recently been shown to be the most significant control on decomposition rates globally (Cornwell *et al.* 2008; Zhang *et al.* 2008). A range chemical variables can explain decomposition rates and a range of indices related to resource/litter quality, climate and soil generally require quantification within a particular study to properly interpret the complexity of the process (Palm and Rowland 1997). These may include measures of litter quality, like nitrogen and phosphorus content, lignin and lignin:N or lignin:P ratios (Aerts 1997; Gohlz *et al.* 2000; Parsons and Congdon 2008). Despite these consistencies, litter decomposition is a complex process, and litter quality effects on decomposition often require simplification (Cadisch and

Giller 1997; Prescott 2005). The use of litter quality variables alone in predicting drivers of decomposition, such as acid detergent lignin, N etc., has pitfalls in that it requires assumptions about what is important in driving decay. It is simple to say for instance, that lignin/recalcitrance and nutrients may control breakdown; however, more holistic approaches that include a more complete picture of the organic chemistry of litter may allow for better appreciation of the effects of different variables and drivers of litter dynamics (Cadisch and Giller 1997; Prescott 2005).

Near infrared reflectance spectroscopy (NIRS) offers rapid, non-invasive and cost-effective analyses of ecological materials (Foley *et al.* 1998). See Shenk *et al.* (1992) for background information on NIRS. NIRS provides comparable precision to standard techniques in quantitative work for standard nutritional components in fresh, litterfall and decomposed leaves; for instance, concentrations of total nitrogen, phosphorus and carbon fractions (e.g. total carbon, acid and neutral detergent lignin and fibre) (Wessman *et al.* 1988; McLellan *et al.* 1991a; McLellan *et al.* 1991b; Gillon *et al.* 1999; Ono *et al.* 2003; Petisco *et al.* 2006) and polyphenolics (Couteaux *et al.* 2005). While most applications use calibrations with actual chemical components, the spectra essentially reflects the whole organic makeup of the material, and thus a more holistic understanding of ecological phenomena has been shown to be possible with NIRS (Foley *et al.* 1998; Gillon *et al.* 1999; Gillon and David 2001; McIlwee *et al.* 2001). This may be especially useful where, like in litter decomposition, interactions among combinations of variables interact to promote or inhibit processes. For example, studies attempting to better understand animal feeding preferences have shown that NIRS models of food choice may provide better predictions of preferences than more standard variables such as fibre content (Lawler *et al.* 2000; McIlwee *et al.* 2001). This broad quantification of phenomena with

NIRS is an improvement on many common approaches for a number of reasons, including time and cost. Also the lack of clarity in what actually constitutes variables such as fibre or lignocellulose portions, both in terms of animal intake and decomposition (due to difficulties in quantification, e.g. proximate acid and neutral detergent fibre) means that the more holistic NIRS methodology may allow more broadly encompassing understandings of ecological sources of variability. The stage of decay of leaf litter (Gillon *et al.* 1993), mineralisation patterns (Bruun *et al.* 2005; Borgen *et al.* 2010) and litter decomposability (Gillon *et al.* 1994; Gillon *et al.* 1999) among others (Ibrahima *et al.* 2007; Vavrova *et al.* 2008), have all been modelled successfully with NIRS. Considering the importance of plant leaf chemical traits in underpinning forest processes, the NIR spectra can provide direct insights into forest function while still allowing application of assumptions based on chemical controls (e.g. lignin or N), or they can also be avoided altogether with more holistic, and potentially more ecologically relevant information.

The goal of this work was to use NIRS: 1) to rapidly quantify the chemical composition of the diverse set of Australian tropical rainforest (ATRF) leaf litter used throughout this thesis, both in freshly senesced (litterfall) and decomposed (litterbag) leaves; 2) to model and predict the stage of decay, and potential *in situ* decomposition, of ATRF leaf litterfall; 3) to compare the ability of NIRS to predict decomposition rates against common explanatory variables, such as litter quality indices, soil and climate; and 4) define the chemical components in litterfall that contribute to NIRS derived litter decomposability. The work presents the NIRS method and benefits for the broader understanding of litter chemical quality. Detailed consideration of the data obtained with this method are presented in Chapters 3, 4 and 6 of this thesis.

2.2. Materials and Methods

2.2.1. *Study Sites*

This chapter includes data from samples collected at all of the 21 study sites in the Australian wet tropics included in this thesis (Appendix 1 and Appendix 2). Leaf litterfall was collected over two years as part of a larger litterfall study (V. Valdez-Ramirez unpublished data), from 40 plots (5 litter traps per plots). Detailed description of the litterfall collection methods are presented in Chapters 3 and 6. Methods for the litterbag study are those of Chapter 4, and are the same as described in Parsons and Congdon (2008). Two litterbag treatments were undertaken: one used leaves collected in the litter traps (one month worth of litterfall collection, October 2007) and exposed at their respective sites (*in situ* study), and the other used leaf litter from the deciduous tree *Archidendron vaillantii* (F.Muell.) F.Muell. (control). The litterbag study spanned approximately 350 days (NIR spectral collection) and around 420 days, 6 collections in total (decay rate calculations).

2.2.2. *Spectra collection*

Leaf samples were oven dried at 40^{o}C to constant weight, and ground using a cyclone mill (Foss Cyclotec 1093 sample mill, North Ryde NSW Australia) until they passed through a 1 mm mesh. Spectra were obtained with a Fourier Transform Near Infrared Spectrophotometer Multipurpose Analyser (MPA) (Bruker Optics Inc., Clayton, Australia), using a 30-position sample wheel, on two sampling occasions in March 2008 and April 2009 (1st and 2nd year collections respectively). Each sample was separated into two 2 cm diameter vials, with spectral reflectance data obtained between 780 - 2780 nm. All samples were packed into the vials with an equal

pressure to minimise errors due to inconsistent light scattering. Spectra were converted to absorbance by the logarithm of the reciprocal of reflectance (log 1/R).

After collection of the spectra, analysis of the chemical composition of the leaf litter was accomplished in four general steps: calibration set selection, wet chemical analysis of the calibration set, model development and prediction of unknowns.

2.2.3. *Calibration set selection*

Principal component analysis (PCA) was used to define the variability in the NIR spectra of the samples and select samples to cover the full range for calibrations. PCA was conducted on two occasions after each spectral sampling time. These analyses treated the litterfall samples (n = 2860) and combined litterbag (*in situ* and control litterbag) samples (n = 865) separately (i.e. litterfall PCA, litterbag PCA and combined PCA). WINISI II software (Foss, North Ryde NSW) was used to select samples for wet chemistry after the first and second spectral collection times. The CENTER and SELECT procedures were used to select two respective representative calibration sets, litterfall and litterbags, using the respective PCA's (Shenk and Westerhaus 1991a; Gillon *et al.* 1999). Samples with global Mahalanobis distances (H) values greater than 3 were considered outliers and deleted (Shenk and Westerhaus 1991b).

Spectral errors were reduced by preprocessing the NIR spectra with standard mathematical algorithms (Shenk *et al.* 1992; Shenk and Westerhaus 1993). For the purpose of calibration set selection in WINISI 1st derivatives were used with standard normal variate transformation combined with detrending (SNV-D) (Helland *et al.* 1995) and the standard WINISI smoothing settings (i.e. 1,4,4,1). 65 samples were initially selected as the litterfall calibration set, representing the 1st year's

collection. Wet chemistry and model development were undertaken on these samples. Another litterfall PCA was then conducted in the second year (2009) to define samples from the second collection that sat as outliers to the first year samples. Samples outside the spectral range of the first year PCA, this time using PCA in the Unscrambler software v9.8 (CAMO software, Norway) and outlier detection statistics (see following), were then added to the calibration set and the models recalculated (see model development). The final litterfall calibration set consisted of 74 samples. The same procedure was used to select the litterbag calibration set, which totalled 73 samples. As the first year spectral collection only contained the first two litterbag collections, wet chemistry was not undertaken on the litterbag calibration set until the second year.

2.2.4. *Wet chemistry of calibration sets*

Total nitrogen and carbon were determined with an Elementar Vario Max CNS Analyser (Elementar, Hanau Germany). Phosphorus was determined following the single digest method (Anderson and Ingram 1989) and colourmetric procedure of Murphy and Riley (1962). Calcium, magnesium and potassium contents were determine via Inductively Coupled Atomic Emission Spectrometry ICP-AES (Varian Liberty Series II, Melbourne Australia) following microwave digestion (Milestone 1200 Mega, Buck Scientific Italy) for the litterfall samples, and atomic absorbance spectrometry (AAS) for the litterbag samples. A selection of samples covering the range of ICP-AES values were used to calibrate between these two methods, and results are presented for the relative ICP-AES values. Acid detergent fibre (lignocellulose), acid detergent lignin (lignin) and α-cellulose were determined using the method of Van Soest (1963) using a FiberCap system (Foss Analytical, Hoganas

Sweden). Total phenolics were determined via a modified Folin-Ciocalteau method (AOAC 1995). All constituents were analysed at least in replicate for all samples. Standard errors of the laboratory measurements (SEL) were calculated. Replicates with the fibre cap method were not determined for every sample due the costs of analysis. Here, internal standards were used to determine a correction factor for each run, with SEL calculated from this variability.

2.2.5. *Model development*

Modified partial least squares regression (PLS1) was used in the Unscrambler software v9.8 (CAMO, Norway) to conduct regressions with the calibration sets and the wet chemical data. Models were constructed with randomised k-fold "leave-10-out" cross validation (Baumann 2003; Forina *et al.* 2004). The software uses the first local minimum number of factors to avoid over-fitting (Faber and Rajkó 2007). Martens uncertainty test was then used to remove non significant spectral variables and further improve models (Esbensen *et al.* 2002). Models were created for the litterfall and decomposition samples, both alone and combined. To pretreat the spectra for model development in the Unscrambler, first and second derivative calculations (Savitsky-Golay), along with SNV-D and multiplicative scatter correction (MSC), and the spectral regions 800 - 2500 nm and 1100 - 2500 nm, were tested to choose the best correlations. Standard error of cross validation (SECV) and the coefficient of determination in cross validation ($r^2_{val.}$) were used to assess the performance of models, along with the RPD statistic (Residual Prediction Deviation: ratio of the standard deviation of the population to the SECV). Other important calibration statistics determined were the standard error of calibration (SEC) and the coefficient of determination of calibration ($r^2_{cal.}$). See Burns and Ciurczak (2007) for

a detailed explanations of these variables. Models with RPD values 2.5 - 3 or higher are generally considered acceptable for analytical purposes; 1.5 - 2.0 may allow differences between high and low values to be determined and < 1.5 are unacceptable for prediction (Williams and Sobering 1992; Saeys *et al.* 2005; Ozaki *et al.* 2006).

2.2.6. *Prediction of unknowns*

The chemical compositions of the unknown samples of each population were predicted using the Unscrambler's PREDICT function (Hoy *et al.* 1998). The performance of the predictions was shown by the Unscrambler's deviation calculation for each sample. The deviation expresses how similar the calibration samples are to the predicted sample, similar to a 95% confidence interval around the predicted value. Inlier and Hotelling T2 statistics were used to determine samples that were not predicted well. These samples were removed from analysis in the proceeding chapters of this thesis. The number of samples from each population outside the range of values in the calibration set was counted, to further test the application of the models.

2.2.7. *Predicting mass loss and potential decomposition rates*

The % dry mass remaining in the litterbag samples was modelled against the NIR spectra of that sample, to assess the ability of the NIR spectra to differentiate between the stages of decay, for both the *in situ* and control leaves. The *in situ* litterbag decomposition rate constants (*k*) were determined from the single exponential decay equation $y = Ae^{-kt}$ where y is the mass remaining at time t. These fit *in situ* mass loss with mean r^2 (for all experiments) of 0.87 (Chapter 4 of this

thesis). The initial NIR spectra of the leaves (the sub-sample not exposed in the litterbags, n = 5 litterbags x 17 sites) was then modelled against the decomposition rate values with PLS. This model of *in situ* leaf decomposability was then used to predict the "potential *in situ"* decomposition rates or decomposability of the litterfall spectra sample set. The ability of the NIRS model to predict *k* was compared to best sub-set regression including environmental variables: soil nutrients, climatic, litter quality (see Chapters 3 and 4) of this thesis for detail on this data). Also for the litterfall samples, the predicted *in situ k* values (for all predictable/statistically valid litterfall samples) were modeled with best sub-set multiple linear regression to determine the actual chemical components or individual chemical drivers of decomposability. The best model was selected from the lowest standard error and bayesian information criterion (R-Software, Package: leaps).

2.3. Results

2.3.1. *PCA on the spectra*

The number of outlier samples removed from the respective litterfall and litterbag populations (H > 3) was low (3 litterfall and 4 litterbags), suggesting the spectral variability of both populations could be contained within a respective calibration for the two litter states. PCA on the combined populations revealed 15 samples with H > 3. The samples selected for wet chemistry sufficiently covered the spectral variability of the samp sets (Figure 2.1).

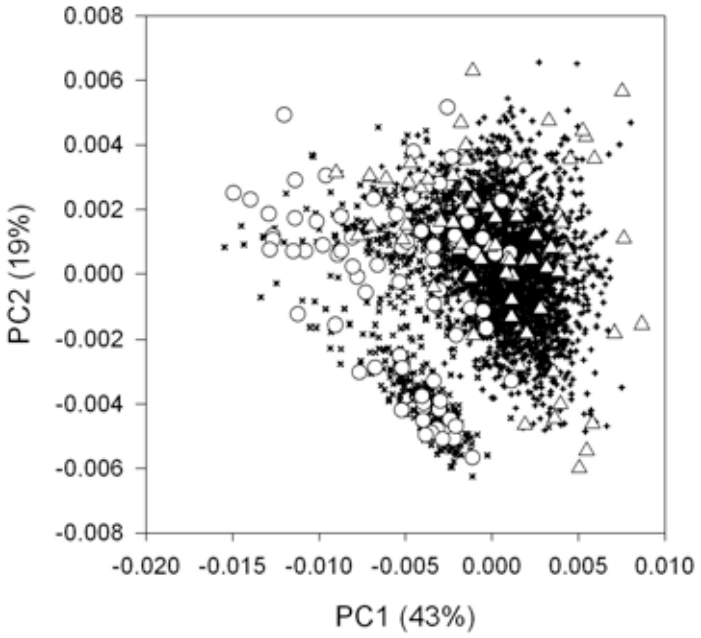

Figure 2.1. First two principal components explaining the variability in the near infrared spectra of leaf litter samples from sites from 80 - 1300 m a.s.l. in Australian tropical rainforests. Included are litterfall (n = 2860) and litterbag decomposed samples up to 1 year exposure (n = 865). Shown are the calibration sets (△ litterfall; ◯ litterbag) and unknown samples (+ litterfall; x litterbag). Shown is a combined PCA for both the litterfall and litterbags.

2.3.2. *Calibrations*

The agreement between the values obtained by chemical analysis and those estimated from NIRS was generally high for all constituents, and all calibrated better in the region 1100 - 2500 nm (Table 2.1). Strong to reasonable correlations were found between the NIR spectra and wet chemical data for all constituents except K, where almost no relationship was found. In cases where RPD was less than 2.5, the models may be limited in their application. This was the case for Mg in the litterbag and combined models. Differences between 1st and 2nd derivative models were minimal, with 1st derivatives in all cases except C (litterfall) and lignocellulose (litterbags and combined) producing better correlations. In all cases the strength of models, based on the SECV and RPD values, went in the order litterfall > litterbags > combined, for the respective constituents (Table 2.1). Thus, models were generally not improved by combining both the LB and LF sets.

Table 2.1. Results from NIRS calibrations of leaf litter constituents from Australian tropical rainforest. Included are the regression statistics, the number of factors in the PLS model, s.d from predictions of litterfall (LF) and litterbags (LB), number of samples predicted by the model higher (+) or lower (-) than the range of values in the calibration set, and the standard error of the laboratory technique (SEL). Total n for litterbag and litterfall populations were 865 and 2860 respectively. Fact = Number of factors used in the model, der =derivative of best first (first or second).

		n	**Mean**	**s.d**	**Range**	r^2_{cal}	**SEC**	r^2_{val}	**SECV**	**RPD**	**Fact.**	**Der**	**SEL**
N	LF	73	1.40	0.45	2.95 - 0.54	0.99	0.05	0.98	0.07	6.43	7	1st	0.02
	LB	68	1.47	0.46	2.18 - 0.70	0.97	0.08	0.95	0.10	4.62	6	1st	
	COM	142	1.43	0.45	2.95 - 0.54	0.96	0.09	0.95	0.10	4.32	9	1st	
P	LF	71	0.04	0.03	0.11 - 0.001	0.98	0.005	0.97	0.005	5.66	5	1st	0.002
	LB	68	0.04	0.021	0.09 - 0.001	0.96	0.004	0.95	0.005	4.29	6	1st	
	COM	133	0.05	0.03	0.13 - 0.001	0.92	0.007	0.88	0.009	2.89	7	1st	
C	LF	73	47.55	3.56	54.84 - 35.54	0.96	0.70	0.94	0.90	3.96	6	2nd	0.45
	LB	69	45.42	3.94	50.94 - 33.89	0.95	0.90	0.93	1.10	3.58	5	1st	
	COM	140	46.48	3.84	53.01 - 33.89	0.90	1.19	0.88	1.33	2.89	5	1st	
lignin	LF	72	33.82	7.16	49.23 - 17.89	0.97	1.23	0.96	1.57	4.65	7	1st	0.61
	LB	72	40.13	4.47	54.22 - 29.63	0.96	0.89	0.94	1.08	4.14	6	1st	
	COM	144	36.97	6.74	54.22 - 17.89	0.93	1.82	0.90	2.09	3.22	8	1st	
α-cell*	LF	71	20.52	3.29	30.14 - 15.21	0.97	0.57	0.95	0.78	4.22	7	1st	0.31
	LB	72	19.54	5.07	31.18 - 11.10	0.96	1.05	0.94	1.27	3.99	4	1st	
	COM	137	19.96	4.34	31.18 -11.10	0.93	1.19	0.90	1.39	3.12	8	1st	
lignocellulose	LF	73	55.85	8.32	71.55 - 38.00	0.97	1.46	0.95	1.84	4.52	7	1st	0.39
	LB	70	62.03	6.34	76.99 - 47.37	0.94	1.56	0.91	1.89	3.35	5	2nd	
	COM	141	59.23	7.78	76.99 - 38.00	0.94	1.86	0.91	2.40	3.24	8	2nd	
Mg	LF	72	0.24	0.07	0.42 - 0.05	0.92	0.02	0.84	0.03	2.54	10	1st	0.01
	LB	72	0.10	0.07	0.26 - 0.001	0.88	0.02	0.83	0.03	2.44	6	1st	
	COM	139	0.17	0.09	0.42 - 0.001	0.87	0.03	0.82	0.04	2.33	8	1st	
Ca	LF	71	1.24	0.89	4.93 - 0.08	0.96	0.18	0.93	0.26	3.56	7	1st	0.03
	LB	71	1.85	1.06	4.44 - 0.32	0.95	0.23	0.94	0.30	3.53	5	1st	
	COM	139	1.48	0.95	4.93 - 0.08	0.90	0.30	0.87	0.36	2.63	7	1st	
K	LF	56	0.30	0.15	0.69 - 0.08	0.56	0.10	0.33	0.12	1.22	4	1st	0.01
Phenol	LF	72	0.49	0.37	1.44 - 0.03	0.91	0.12	0.86	0.14	2.72	5	1st	0.02

*α-cellulose

2.3.3. *Mass loss predictions and in situ decomposability*

NIRS predicted mass loss (% dry mass remaining) with validated r^2 values of 0.72 and 0.74 respectively for the *in situ* and control litterbag samples (Figure 2.2 and Table 2.2). The PLS model for treated 1st derivative NIR spectra (sub-sampled initial spectra prior to decomposition) versus *in situ* leaf decomposition rate had a validated r^2 of 0.78 (s.e. validation = 0.23) (Table 2.3 and Figure 2.3). This is better than the relationships with all the best fitting litter quality indices: initial N (r^2 = 0.55), P (r^2 = 0.64), lignin (r^2 = 0.14), total C (r^2 = 0.49), lignin:N (r^2 = 0.38), lignin:P (r^2 = 0.39), C:P (r^2 = 0.50) and total phenolics (r^2 = 0.41) (Table 2.4 and Chapter 4). The best sub-set model explaining decay rate for the 17 experiments (i.e. irrespective of NIRS), against initial litter quality, climate and soil composition had an r^2 of 0.86 (residual s.e. = 0.18), explained by dry season moisture and leaf litter P and C (Table 2.3).

The NIR decomposability model, when applied to the full litterfall population, reliably predicted *k* in 86.4% of the entire litterfall sample population (n = 2860) based on outlier statistics. The chemical components explaining predicted leaf decomposability in the litterfall samples best were P, total phenolics and total C in best sub-set regression (r^2 = 0.80) (Table 2.5 and Figure 2.4).

Table 2.2. NIRS predictions of mass loss (% original dry mass remaining) in litterbags from 17 sites in Australian tropical rainforest. Show is data for in situ (representative of site) and control leaf litter (Archidendron vaillantii)

	r^2_{cal}	SEC	r^2_{val}	SECV	RPD
In situ	0.75	9.44	0.72	9.89	1.92
Control	0.76	6.34	0.74	6.56	1.99

Table 2.3. Comparison of leaf decomposability indices, of the decomposition constant *k* (y^{-1}) (from exponential regression model mass = Ae^{-kt}), derived from NIRS regressions and best subset linear regression for environment (soil nutrients and climate) and initial litter chemical contents. NIRS predictions were undertaken on 24 months of litterfall samples from the respective sites. Shown is the % of the 2860 samples predictable with the model and the average standard deviation of the predictions. For the best sub-set regressions, the variables entered into the model, coefficient of prediction (adjusted r^2) and residual standard error of the estimate are shown. n = 85 litter samples from 17 sites.

NIRS								NIRS predictions		Standard regression		
In situ decay	Mean	Range	r^2_{cal}	SEC	r^2_{val}	SECV	RPD	% samples incl.	$s.d_{pred}$	lf Variables entered	r^2	SE
k	1.02	2.15 - 0.34	0.81	0.21	0.78	0.23	2.15	86.4	0.34	Dry season moisture, P, C *	0.86	0.19

*Best subset: mean leaf wetness (moisture condensation) in the dry season, initial phosphorus, initial carbon.

Table 2.4. Comparison of predictive abilities (linear regression) of leaf litter chemical properties and in situ decay rates in Australian tropical rainforests from litterbag studies (n = 17 sites).

	r^2	s.e.	p
N	0.55	0.35	< 0.001
P	0.64	0.32	0.001
Ca	0.42	0.40	0.005
C	0.49	0.37	<0.0001
Lignin	0.14	0.49	0.15
Lignin:N	0.38	0.41	0.008
Lignin:P	0.39	0.41	0.007
C:P	0.50	0.37	<0 .001
Total Phenolics	0.41	0.40	0.006

Table 2.5. Best sub-set linear regression results explaining NIR predicted decay rate (k_{nirs}) with chemical components (n = 2471).

Predicted variable	Variable	T value	P (varibles)	Model r^2	Model p	s.e.	BIC
k_{nirs}	(Intercept)	40.27	< 0.0001	0.80	< 0.0001	0.0007	-3678.6
	P	46.44	< 0.0001				
	Total Phenolics	-19.62	< 0.0001				
	C	-35.73	< 0.0001				

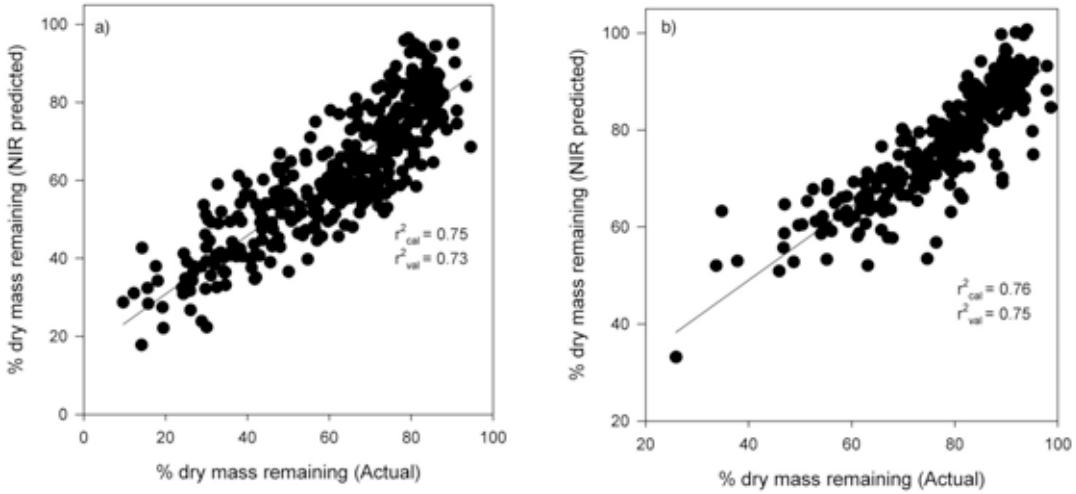

Figure 2.2. Relationship between % dry mass remaining and NIR spectral prediction of % dry mass remaining in litterbags in Australian tropical rainforests. Shown are data from a) *in situ* and b) control litterbags.

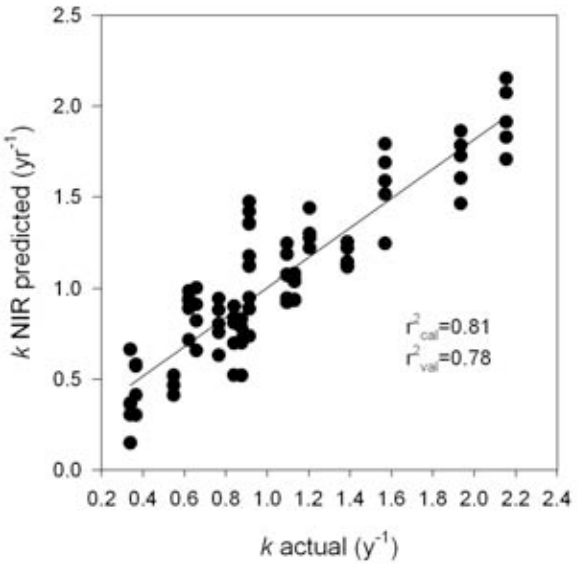

Figure 2.3. Near infrared spectrometry partial least squares regression model of litterbag decomposition rate (*k*) versus the initial NIR spectra of the leaves, from sites in Australian tropical rainforest. n = 85 initial samples from 17 sites/litterbag experiments.

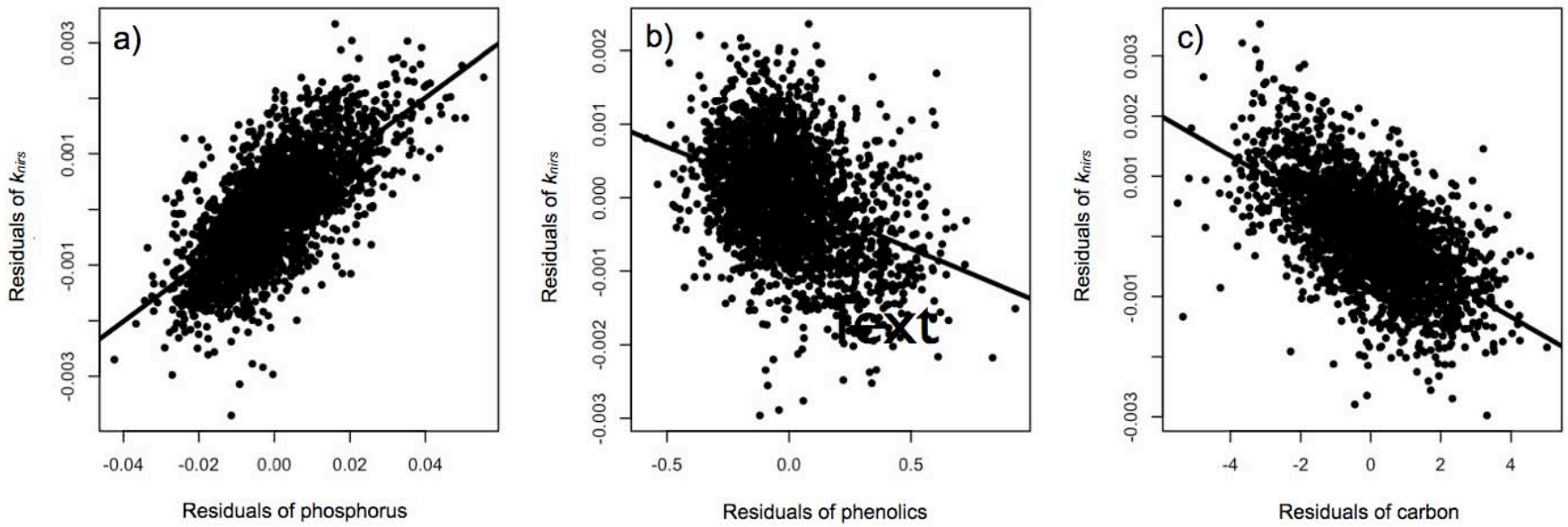

Figure 2.4. Partial linear regression plots explaining NIRS predicted leaf decay rate (k_{nirs}) in litterfall samples from 40 plots in Australian tropical rainforest. a) initial leaf phosphorus; b) total phenolics; c) total carbon. model $r^2 = 0.80$ (Table 2.5).

2.4. Discussion

The chemical information contained in forest litter is directly related to the ecosystem in question, and the litter processes occurring there (Aerts 1997; Cornwell *et al.* 2008). Here, the NIRS technique allowed accurate and insightful quantification nutritional and chemical compositions of leaf litter, and decomposition dynamics. The technique also allowed great savings of money, time, waste and effort to quantify leaf chemical quality variables. The accuracy of the NIR models for chemical components was comparable to other work, and generally of an analytical precision (Gillon *et al.* 1999; Couteaux *et al.* 2005; Petisco *et al.* 2006). In all applications some effort is required in NIRS work to develop calibrations, and great care must be taken to remove outliers (correct PCA application) for sample selection, and then in PLS model development (Shenk and Westerhaus 1991b; Shenk and Westerhaus 1994). Broad based equations (e.g. "combined" in this study) are considered to be potentially as accurate as fine scale calibrations in prediction (Abrams *et al.* 1987; Shenk and Westerhaus 1993; Gillon *et al.* 1999). In many applications the effort required to produce a single broad based global calibration may be less than to produce more than one local model, making it more appealing (Gillon *et al.* 1999).

2.4.1. *Insights into litter decomposition and decomposability*

Forest litter decomposition is a relatively well understood ecosystem process, with global consistencies in the controls on leaf breakdown well documented (Gohlz *et al.* 2000; Parton *et al.* 2007; Cornwell *et al.* 2008; Wieder *et al.* 2009). Here, in modelling the chemical drivers of *in situ* decomposition, the NIR technique, applied

to the initial spectra was almost as accurate as the best sub-set regression that included climate (Table 2.3), and significantly more accurate than any of the litter chemical variables alone (Table 2.4). The NIR technique therefore, performed better than standard explanations with litter quality alone, e.g. inclusive of the more holistic litter quality information in the NIRS model. As the best sub-set regression included variables outside of the information in the NIR technique, i.e. climate, as opposed to just chemical information (in the NIR model), this not only re-emphasises the importance of litter quality in driving decomposition rates, but again presents evidence of the strong plant trait controls on breakdown. The three principle drivers of litter decomposition are litter chemical quality, soil (e.g fertility and biota) and climate (Aerts 1997; Cornwell *et al.* 2008) (see Chapter 4 for further discussion of the controls of leaf decomposition). The spectral information of plant material, as a reflection of the chemistry of the sample, in many ways encapsulates the environmental conditions that produced it. This is so because climate and soil both directly and indirectly influence the chemical composition of litter produced at any single location (Aerts 1997; Close and McArthur 2002; Kitayama *et al.* 2004), including the sites studied here (see Chapter 3 of this thesis). The importance of plant chemical traits in determining decomposition is therefore, often higher than for other contributors (Wardle *et al.* 2002; Chapin 2003; Wright *et al.* 2004; Cornwell *et al.* 2008).

The information making up the litterbag models was only representative of one month worth of litterfall for any given site. Therefore, regressions simply using decomposition rates for each experiment (e.g. n = 17 sites here), are not overly detailed. The predictions of leaf *in situ* decomposability on the other hand, present decay rates over the full range of litterfall samples available, i.e. 24 months of

litterfall for all sites where predictions were statistically valid (~84% of samples). Total P, C and total phenolics were the best predictors of decomposability (Table 2.5). This is in line with other work in tropical forests (Palm and Sanchez 1990; Loranger *et al.* 2002), particularly for P (strongest predictor in the model), which is in very low concentrations in litter and soils and limits ecosystem processes in the Australian wet tropics (see Chapter 3, 4 and 6 of this thesis). Regardless of errors (e.g. regression fit), these predictions are estimates of the potential *in situ* decomposition rate based on initial litter quality, and are reliable within the spectral ranges of the predictable samples (Gillon *et al.* 1994; Gillon *et al.* 1999). They also contain more information than simply P, C and phenolics (e.g. all possible combinations of interest within the NIR range). A scaling up of the results of the litterbag study was thus, provided by the model to include more locations; and therefore, more potential trends could be considered. These may include seasonality in litter decomposability, spatial variability, and relationships between decomposability and other ecosystem processes (see Chapters 3 and 6 of this thesis). The term "litter chemical quality" does not only refer to N, P lignin etc. or even simple ratios of two components, but all the components that combine in plant material to promote or inhibit and decomposition. Recent research has suggested tropical rainforests exist in a "non-Liebig" world of multiple nutrient limitations (Kaspari *et al.* 2008). Use of the detailed organic chemical information in the NIR spectra may enable more holistic insights into chemical limitations on ecosystem processes, beyond just focusing on individual chemical components.

Chapter 3. The drivers of plant litter quality and nutrients in Australian tropical rainforests

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3.1. Introduction

Plants are leading components of terrestrial ecosystem-atmosphere global cycles, using and cycling atmospherically (e.g. C, H, O and N) and geologically (e.g. P, Ca, K) derived elements (Vitousek 1984; Jobbagy and Jackson 2004). The chemical quality of plant litter generally refers to the potential for rapid decomposition and nutrient release, related to nutritional value to decomposers and overall recalcitrance (Couteaux *et al.* 1995; Cadisch and Giller 1997). Litter quality and leaf economics relate directly to many terrestrial ecosystem processes (Berendse 1994; Diaz *et al.* 2004; Cornwell *et al.* 2008; Kazakou *et al.* 2009), and multiple leaf chemical characteristics correspond to plant physiological and metabolic functions (Reich *et al.* 1997; Wright *et al.* 2004; Wright *et al.* 2005), and decomposition (Meentemeyer 1978; Aerts 1997).

Leaf litter nutrients, especially N and P, strongly reflect soil nutrient availability (Vitousek and Farrington 1997; Aerts and Chapin 2000). In nutrient-rich environments, plants turnover large amounts of nutrient-rich litter, and quickly release large amounts of nutrients allowing sustained high soil fertility. Contrastingly, plants in nutrient-poor environments turn over litter slowly, conserving nutrients in their biomass and long lived recalcitrant tissues, reinforcing the infertile conditions (Melillo *et al.* 1982; Hobbie 1992). Foliar and litter C:N:P

ratios relate to soil microbial and whole ecosystem function and are central to plant-climate-soil feedbacks (Enriquez *et al.* 1993; McGroddy *et al.* 2004a). An understanding of the patterns and controls on the spatial and seasonal variability of nutritional constraints within ecosystems, and the basis of C:N:P compositions, is critical to the understanding of ecosystem processes and plant responses to global change (Hungate *et al.* 2003; Elser *et al.* 2010).

Tropical forests are generally more P than N limited due to geological/ substrate age and high rates of leaching associated with high rainfall (Vitousek 1984; Reich and Oleksyn 2004; Elser *et al.* 2007). High N:P ratios reflect P limitation in general, which may be particularly heightened in the leaf litter of rainforests, due to tight nutrient cycles, low P availability relative to N, and high P translocation prior to leaf senescence (Vitousek 1984; Vitousek and Sanford 1986; Hättenschwiler *et al.* 2008). Despite this, foliar N:P varies greatly in tropical rainforest leaves (Townsend *et al.* 2007), and on younger soils N:P can be more similar to other ecosystems where P is generally more abundant (e.g. temperate and boreal forests) (Townsend *et al.* 2008).

Variations in leaf chemical traits can be soil-derived, and due to genetic and physiological constraints regardless of soil type. At levels higher than the individual, physiological responses of plants relate directly to within-community variation (e.g. extent of stoichiometric homeostasis) in leaf traits, and may be at least partially climatically/site driven (Elser *et al.* 2010). Despite some clear latitudinal and geologically derived patterns (McGroody et al. 2004; Townsend et al. 2007), leaf litter chemistry can vary substantially within a region, even at small spatial scales. This implies different nutrient use strategies of plants and may relate to spatially varying nutrient cycling and decomposition dynamics (Wardle *et al.* 2006;

Hättenschwiler *et al.* 2008). Trends regarding nutrients may be particularly difficult to define in tropical rainforests due to high spatial heterogeneity in localised disturbance and edaphic factors, and high species diversity and canopy heterogeneity (e.g. localised variability) (Burghouts and Straalen 1998; Townsend *et al.* 2008). The potential for natural and anthropogenic disturbance in rainforests and localised discrepancies in community structure, within a region with a relatively homogenous climate and soil type, can have marked effects on nutrient cycles and the quality of plant litter produced (Herbohn and Congdon 1993; Herbohn and Congdon 1998; Gleason *et al.* 2008; Parsons and Congdon 2008). Any understanding of nutrient cycles in tropical rainforests must take into account the diversity and broad range of nutrient requirements of plants both at local and regional scales (Townsend *et al.* 2007).

Like N:P, carbon and C fraction concentrations (e.g., lignin) in leaves may be phenotypically, age, disturbance, and nutritionally driven (Coley 1986; Chapin 1991; Mediavilla *et al.* 2008), and may be highly variable within single communities. Despite substantial amounts of research into the impacts of litter quality on ecosystem processes such as decomposition, clear models of the actual drivers of spatial and temporal (e.g., seasonal) variability of litter quality and nutrients are less comprehensive, especially for the tropics (Townsend *et al.* 2008).

In this chapter the environmental drivers of litterfall chemical quality are determined in the wet tropical rainforest region of north Queensland, Australia. Sites distributed throughout the environmental space of the bioregion are used to understand the effects of climate, soil, vegetation community structure and disturbance on litter quality. Near infrared spectroscopy (NIRS) offers an holistic view of the organic chemical makeup of ecological material, and is valuable for

looking for broad trends in plant material and relationships between environmental factors and leaf chemical traits (Foley *et al.* 1998; McIlwee *et al.* 2001). NIRS is used here to explore the relationships between environmental factors and the chemical quality of plant litter.

3.2. Methods

3.2.1. *Study sites*

The two detailed monitoring plots per site were the focus of this chapter. 40 of these plots were used here for litterfall chemical quality composition (Appendix 2). SU9 sites were not included as they did not have a litter traps set up. Most of the sampling for litter chemistry spanned August 2006 - August 2008 (Vanessa Valdez-Ramirez, unpublished data).

Soil profiles were analysed at all plots. Samples were taken for chemical analysis and descriptions were made using the classifications of Isbell (Isbell 2002). Soil chemistry was determined from the mean of three auger cores taken at each plot, based on the fine earth fraction (< 2 mm). The mean of 0 - 10 cm and 20 - 30 cm depth samples were used. Sampling took place in January 2007 (wet season). Nutrients were determined using the single digest method and sodium salicylate (total N) and molybdate (total P) colorimetric methods (Anderson and Ingram 1989; Baethgen and Alley 1989), and atomic absorbance spectrometry (AAS) (Ca, Mg and Na). Soil particle analysis (sand, silt, clay) followed the method of Rhoades (Rhoades 1982).Total organic carbon was measured using the Walkley and Black (Walkley and Black 1934) method.

Plant species richness and composition was determined along 20 x 2 m belt

transects at each plot and coincided with the location of the litter collection traps (see following). All trees and shrubs greater than 1.6 m tall were identified, abundances recorded and heights estimated. Vines, scramblers and lianas were not sampled due to difficulties in collection, so complete plant species richness was not determined. However, the survey produced a standardised measure of number of species for comparisons between the plots, especially relating to the material impacting on the litter processes being studied. The abundance of obligate pioneer/gap colonising species was determined by the natural history notes within Hyland *et al.* (2002). Species "favoured by disturbance" and "characteristic component(s) of rainforest regrowth", were considered to be general pioneers/gap colonisers or very early secondary species indicating signs of disturbance (Denslow 1987). Richness of all individuals counted, trees ≥ 5 m, and the proportion of gap individuals were used in analyses.

3.2.2. *Litterfall nutrients and chemical quality*

Fine litterfall was collected over two years (excluding wood components > 2 cm diameter) (Clark *et al.* 2001a). Traps were made from a 0.25m^2 circular steel hoop with a fibre glass (1 mm fly screen) mesh basket, fixed in place approximately 1 m from the ground (Newbould 1967), arranged in a star formation at least 5 m apart (Vanessa Valdez-Ramirez, unpublished methods). Each plot contained five traps that were emptied at approximate monthly intervals. Collections were oven dried at 40^oC to constant weight. Samples were sorted into leaf, woody, reproductive and unclassified (that which fell through a 2 mm sieve) components.

Leaf litter chemical compositions were determined with near infrared

spectrometry (NIRS), using the method of Chapter 2 of this thesis. Monthly collections were analysed for the first year collection, and bi-monthly collections for the second year. Seasonality in the concentrations of the chemical components was compared between the wet and dry seasons. Models were built with direct estimates of composition from standard wet chemical methods (see below) from a sub-set of samples covering the range of spectra in the dataset. Models were then used to predict the chemical concentrations of the full sample set, producing spatial and temporal data for leaf litter total nitrogen, total phosphorus, total carbon, calcium, magnesium, total phenolics, acid detergent fibre (lignocellulose), acid detergent lignin (lignin) and α-cellulose (Chapter 2). The NIRS models had prediction r^2s of: N 0.99; P 0.98; Mg 0.92; Ca 0.96; C 0.96; lignin 0.97; lignocellulose 0.97; α-cellulose 0.97 and total phenolics 0.91 (Chapter 2 of this thesis). The following wet chemical methods were used: C and N with an auto analyser (Elementar Vario Max CNS Analyser, Elementar, Hanau Germany); P with the molybdate/ascorbic acid method as for soils; Ca and Mg with Inductively Coupled Atomic Emission Spectrometry ICP-AES (Varian Liberty Series II, Melbourne Australia) following microwave digestion (Milestone 1200 Mega, Buck Scientific Italy); lignocellulose, lignin and α-cellulose with the Van Soest (Van Soest 1963) method using a FiberCap system (Foss Analytical, Hoganas Sweden) and total phenolics via a modified Folin-Ciocalteau method (AOAC 1995). The total number of leaf litter samples analysed was 2860.

Unclassified (< 2 mm) and reproductive portions of litterfall collected in January and March 2007 were analysed for N and P using the same method as used for soils. These dates lie between the peak fruiting events for rainforests in the region (Brasell and Sinclair 1983; Spain 1984; Herbohn and Congdon 1993). Five litter trap

samples per plot were analysed for both collections (n = 10 total per plot). Total annual elemental accessions to the forest floor (kg ha^{-1} y^{-1}) were determined for the leaf, unclassified and reproductive portions using the determined values (C, N, P, Mg and Ca for leaves, N and P for reproductive and unclassified material).

3.2.3. *Statistical analysis*

ANOVA, with Tukey post-hoc multiple comparisons, was used to test for differences in litter chemistry between plots. ANOVA was applied with a nested design to control for differences between replicate plots at the same elevation/sub-region: elevational site (e.g., AU1, AU2 etc.) as the fixed factor, and plots within elevation sites as random factors (2 per elevational site (e.g., AU1 nested with 2 plots AU1A1 and AU1A3). Wet and dry season mean chemical compositions were compared with repeated measures ANOVA. Local variance (between plots in the same elevation/ sub-region) was estimated with restricted maximum likelihood models (RML). All models were run in SPSS v17.0.

The relationships between leaf litter chemistry and environment in the region were explored and visually represented with the NIR spectra. Multivariate partial least squares regression (PLS2) (Haaland and Thomas 1988; Helland 1988; Esbensen *et al.* 2002) was applied to the mean NIR spectra (X) of all litterfall samples collected per plot (1100 - 2500 nm, 1st derivative with scatter correction as per Chapter 2 of this thesis), against the mean litter chemical value, and environmental variables (climate and soil) (Y), in the Unscrambler software (v8.0 CAMO, Norway). This analysis defined the variability in the region in terms of leaf litter chemistry and chemical relationships with environment. The Y variables that went into the model

were as follows: litter quality: N, P, Ca, Mg, C, lignocellulose, lignin, α-cellulose and phenolics; soil: P, N, Mg, Ca, K; climate: mean annual temperature (MAT), mean annual precipitation (MAP), mean annual radiation (MAR), MAR of the wettest quarter (MAR-WS) and driest quarter (MAR-DS), proportion of dry season days with 0 mm rainfall (DS0MM) and vegetation composition: the count of individuals on transects, % gap species, and total tree/shrub species richness. Martens uncertainty test was used to remove non-significant spectral regions from the models (Esbensen *et al.* 2002). Acceptable limits for significant correlating variables (with the spectra) were set at ratio of standard error of prediction to sample standard deviation (RPD) values above 1.3. RPD statistics are important in NIR work because stable calibrations can only be obtained when there is reasonable range of values and if the error in estimation is not large compared to the range of values in the calibration. Although the selected value of 1.3 falls just below some recommendations for predictions (e.g., > 1.5) (Williams and Sobering 1992; Saeys *et al.* 2005; Ozaki *et al.* 2006), this limit was considered acceptable in this application as the model was only for exploration of the chemical attributes in relation to environment. Results were interpreted with a combination of the scores (location of samples along each model component) and loadings (amount of variance taken into account by the model for each Y variable) plots of the PLS2 analysis, standard linear and best-subset regression and bivariate (Spearman Rank) correlations.

In the data-set there were cross-correlations between the cyclone damaged plots, MAP and soil fertility. In cases where this, or the severity of the damage alone, confounded analyses, these plots were either omitted or the analysis was run both including and excluding these plots.

3.3. Results

3.3.1. *Study sites*

Mean annual precipitation for the sites ranges from 3436 mm p.a. (AU1) to less than 1500 mm p.a. (SU3 and CU6) (Appendix 1). Higher than average real time rainfall totals were recorded during the study period (Appendix 1). The AU9 plots had much lower annual rainfall than the other AU sites (1846 mm p.a. compared to > 2500 mm p.a.). Rainfall seasonality was lowest in the AU sub-region, more pronounced in WU followed by CU, and highest in the SU (particularly SU3 and SU6). Mean annual temperature ranged from 24 ºC (CU1) to 17 ºC (WU13) (Appendix 1). There was a regional correlation between rainfall/moisture and soil fertility, such that the AU2, AU4, AU6, AU8 sites had both the highest rainfall and the most fertile soils. Contrastingly, the SU sub-region, and to a lesser extent the WU and CU, were generally the driest with the poorest soils. Within each sub-region there were however, exceptions to this trend. For example, the AU9 plots had among the most fertile soils and relatively low rainfall and high rainfall seasonality, and the AU1 plots were on poorer alluvial soils with the highest MAP. The highest abundances of gap/pioneer species were found in the cyclone damaged plots, however other locations also had signs of previous disturbance (Appendix 2).

Soil P, Mg and Ca were magnitudes higher on basalt (AU2, 4, 6, 8 and 9) than on granite, alluvium and rhyolite (all other sites) (Appendix 2). Soil N was more variable than P, but also mostly higher on basalt (see Appendix 2 for all soil data). MAP had a positive linear relationship with soil P, primarily due to the very wet AU sites on basalt ($r^2 = 0.15$, $p = 0.015$).

3.3.2. *Litter chemical concentrations*

There were significant differences between plots for all chemical components ($p < 0.001$, df = 39 and 2859). Leaf litter total N and P were mostly higher on soils derived from basalt (AU2, AU4, AU6, AU8, AU9) (Table 3.1). SU6 plots had the lowest average N and P contents and exceptionally high N:P (199 and 454 respectively). Excluding these plots, mean leaf litter N:P values ranged from 26 (AU2A2) to 73 (WU13A2). Regional mean (± SEM) leaf litter chemical concentrations were as follows: N = 1.30 ± 0.24 mg g^{-1}; P = 0.031 ± 0.02 mg g^{-1}; Ca = 1.01 ± 0.43 mg g^{-1}; Mg = 0.25 ± 0.03 mg g^{-1}; C = 48.5 ± 1.5 mg g^{-1}; lignocellulose = 57.36 ± 2.61 mg g^{-1}; lignin = 35.32 ± 2.2 mg g^{-1}; α-cellulose = 20.26 ± 1.39 mg g^{-1}; phenolics = 0.50 ± 0.16 mg g^{-1}. Ca, lignocellulose, lignin and α-cellulose showed the greatest variation, both regionally and locally, as a percentage of the regional mean (regional variation: Ca 17.8%, lignocellulose 11.9%, lignin 14.0% and α-cellulose 9.5%; local variation: Ca 3.27%, lignocellulose 5.55%, lignin 5.99% and α-cellulose 3.37%), compared to N, P, Mg, C and phenolics (regional variation: N 4.62%, P 0.65%, Mg 0.36%, C 4.60 % and phenolics 4.00%; local variation: N 0.54%, P 0.09 %, Mg 0.06%, C 0.74%, phenolics 0.88%). Nested ANOVA showed significant plots to site (elevation within sub-region) factor effects for all leaf litter chemical variables (F values: N = 19.08; P = 14.99; Ca = 20.47; Mg = 12.01; C = 13.75; lignocellulose = 9.56; lignin = 8.05; phenolics = 11.52, df = 20 and 2859, $p < 0.001$). This suggests the chemical variables varied by plot even within the same levels of control for elevation within sub-region.

Mean N values for reproductive material collected in the wet season 2007 ranged from 0.59 (AU8A5) to 2.25% (AU2A5), and P 0.03 (AU8A5) to 0.18% (AU2A5). For the unclassified portion, concentrations ranged from, N: 0.76

Table 3.1. Mean and s.d. of leaf litter chemical values for total nitrogen, phosphorus, carbon, calcium, magnesium, acid detergent fibre (ADF, lignocellulose portion), acid detergent lignin (lignin), α-cellulose and total phenolics. # = number of litter trap leaf samples used to determine the mean. Data came from near infrared spectrometry analysis of Chapter 2. Means followed by the same letter are not significantly different ($p > 0.05$).

Site/sub-region	N	P	C	Ca	Mg	Lignocellulose	Lignin	α-Cellulose	Phenolics	#
Atherton Uplands										
1A1	1.32±0.19^{hijk}	0.04±0.01^{kl}	47.08±1.54^{cd}	1.27±0.32^{mno}	0.26±0.05^{hijk}	57.38±3.50^{efghijk}	34.62±2.91^{defgh}	20.87±1.43^{ijklm}	0.47±0.15^{defg}	75
1A3	1.35±0.23^{ijk}	0.03±0.02^{ijk}	48.17±1.59^{efghi}	0.92±0.37^{fghijk}	0.26±0.04^{ghijk}	58.18±5.02^{ghijklm}	35.84±4.06^{fghijkl}	20.34±1.87^{ghijk}	0.58±0.19^{fghijk}	75
2A2	1.68±0.21^{lmn}	0.07±0.01^{o}	44.30±3.00^{a}	2.17±0.62^{t}	0.30±0.04^{lm}	56.64±5.06^{defghi}	33.02±4.56^{bcde}	21.70±1.63^{mno}	0.22±0.11^{a}	75
2A5	1.76±0.28^{no}	0.07±0.01^{o}	45.65±1.63^{b}	1.84±0.37^{s}	0.30±0.05^{lm}	57.63±4.06^{fghijkl}	35.41±4.01^{efghijk}	20.61±1.90^{hijklm}	0.31±0.16^{abc}	75
4A2	1.70±0.23^{lmno}	0.06±0.02^{no}	47.27±1.43^{cde}	1.43±0.45^{nop}	0.27±0.04^{hijkl}	58.47±3.87^{hijklmn}	36.93±3.64^{ijklmn}	20.05±1.90^{efghi}	0.33±0.19^{abc}	75
4A5	1.89±0.20^{p}	0.07±0.01^{o}	47.02±1.45^{cd}	1.65±0.44^{qrs}	0.28±0.05^{kl}	55.74±4.83^{bcdefgh}	34.48±4.28^{defgh}	20.28±1.27^{ghij}	0.31±0.12^{abc}	75
6A2	1.39±0.16^{k}	0.03±0.02^{ghijk}	47.56±1.28^{def}	1.44±0.48^{opq}	0.27±0.06^{hijkl}	58.36±3.80^{ghijklm}	34.24±3.36^{cdefg}	22.98±2.50^{p}	0.32±0.14^{abc}	70
6A5	1.60±0.18^{lm}	0.05±0.01^{mn}	46.96±1.35^{cd}	1.78±0.51^{s}	0.31±0.06^{m}	55.67±4.28^{abcdefg}	33.73±3.23^{cdef}	20.40±1.41^{ghijk}	0.36±0.16^{bcd}	70
8A2	1.73±0.17^{mno}	0.05±0.01^{lm}	48.37±1.20^{fghij}	0.99±0.29^{ijkl}	0.25±0.04^{ghijk}	56.34±4.45^{cdefghi}	35.22±3.02^{efghijk}	20.83±1.56^{ijklm}	0.43±0.19^{cde}	75
8A5	1.82±0.18^{op}	0.05±0.01^{mn}	49.20±1.32^{jkl}	1.04±0.30^{jklm}	0.24±0.05^{defg}	57.96±3.88^{ghijklm}	35.67±3.22^{fghijk}	22.35±1.52^{op}	0.29±0.13^{ab}	75
9A2	1.55±0.25^{l}	0.04±0.01^{lm}	49.16±1.33^{ijkl}	1.15±0.37^{lmn}	0.27±0.04^{hijkl}	58.14±3.87^{ghijklm}	35.64±3.03^{fghijk}	21.99±1.28^{nop}	0.35±0.15^{bc}	75
9A5	1.19±0.14^{efg}	0.02±0.01^{defgh}	50.67±1.28^{nop}	0.59±0.32^{abcd}	0.27±0.04^{ijkl}	57.39±4.66^{fghijk}	35.31±3.51^{efghijk}	20.27±1.87^{ghij}	0.59±0.17^{ghijk}	75
Carbine Uplands										
1A1	1.25±0.14^{hij}	0.03±0.01^{jk}	46.61±1.13^{bc}	1.69±0.26^{rs}	0.27±0.04^{ijkl}	53.64±3.89^{abcd}	32.22±3.12^{bcd}	20.33±1.99^{ghij}	0.46±0.19^{def}	70
1A5	1.23±0.21^{ghi}	0.03±0.01^{fghij}	47.59±1.71^{def}	1.56±0.39^{pqr}	0.28±0.05^{jkl}	52.70±6.29^{a}	29.69±5.73^{a}	20.76±2.14^{ijklm}	0.64±0.31^{ijklm}	70
2A2	1.16±0.16^{defg}	0.03±0.01^{efghij}	48.92±1.38^{hijk}	0.84±0.35^{efghij}	0.25±0.04^{defghi}	61.31±6.97^{mn}	38.69±5.56^{mn}	19.47±1.94^{defgh}	0.66±0.23^{jklm}	65
2A5	1.09±0.14^{abcde}	0.02±0.01^{defghi}	49.15±1.06^{jkl}	0.79±0.29^{defghi}	0.25±0.04^{defghi}	55.43±6.38^{abcdefg}	34.75±4.89^{defgh}	18.53±1.56^{cd}	0.70±0.20^{lmn}	65
4A2	1.02±0.12^{a}	0.02±0.01^{bc}	49.24±1.22^{jkl}	0.50±0.30^{abc}	0.21±0.05^{abc}	61.07±6.74^{lmn}	38.84±5.68^{lmn}	20.25±2.02^{ghijk}	0.55±0.19^{fghij}	70
4A5	1.07±0.14^{abcde}	0.02±0.01^{bcd}	47.73±1.57^{def}	0.88±0.36^{ghijk}	0.23±0.05^{bcdef}	59.72±4.78^{ijklmn}	37.10±4.04^{ghijklm}	19.92±1.58^{fghi}	0.68±0.19^{klm}	70
6A2	1.28±0.19^{hijk}	0.03±0.01^{hijk}	49.20±1.71^{jkl}	0.79±0.32^{defghi}	0.28±0.05^{kl}	60.35±5.25^{jklmn}	37.66±4.65^{jklmn}	20.48±1.94^{ghijkl}	0.47±0.13^{defg}	70
6A5	1.14±0.16^{bcdefg}	0.02±0.01^{bcd}	49.00±1.41^{hijk}	0.76±0.38^{defgh}	0.23±0.05^{bcdefg}	59.05±4.76^{hijklmn}	37.02±4.51^{hijklm}	19.76±2.00^{defghi}	0.59±0.21^{fghijk}	70
8A2	1.16±0.13^{efg}	0.02±0.01^{defghi}	49.08±1.48^{hijkl}	0.67±0.30^{bcde}	0.22±0.04^{abcde}	58.72±3.95^{hijklmn}	36.91±3.34^{hijklm}	19.48±1.26^{defg}	0.60±0.14^{hijkl}	70
8A5	1.14±0.12^{bcdefg}	0.02±0.01^{cdefg}	48.55±1.60^{fghij}	0.69±0.27^{bcdef}	0.24±0.05^{cdefg}	61.59±5.53^{n}	39.37±4.41^{n}	19.98±1.95^{efghi}	0.62±0.18^{hijklm}	70
10A2	1.21±0.17^{gh}	0.02±0.01^{defgh}	48.38±1.16^{fghij}	0.93±0.33^{fghijk}	0.27±0.04^{hijk}	56.86±3.84^{efghij}	35.35±2.72^{fghijk}	18.84±2.25^{cde}	0.56±0.18^{fghijk}	65

Table 3.1. cont.

Site/sub-region	N	P	C	Ca	Mg	Lignocellulose	Lignin	α-Cellulose	Phenolics	#
Carbine Uplands										
10A5	1.14±0.22^{cdefg}	0.03±0.01^{ijk}	47.63±1.45^{def}	1.38±0.29^{nop}	0.31±0.05^{m}	54.14±3.89^{abcde}	31.97±3.27^{abc}	22.14±1.86^{op}	0.43±0.18^{cde}	65
12A2	1.21±0.13^{gh}	0.03±0.01^{ghij}	47.93±2.08^{defg}	0.85±0.36^{efghij}	0.27±0.04^{hijkl}	57.29±4.68^{efghij}	35.13±3.77^{efghij}	21.81±1.64^{mno}	0.48±0.14^{defg}	65
12A5	1.10±0.14^{abcdef}	0.03±0.01^{efghij}	49.15±1.32^{jkl}	0.52±0.27^{ab}	0.26±0.05^{hijk}	60.29±4.26^{klmn}	37.54±3.29^{klmn}	21.57±1.49^{klmno}	0.53±0.16^{efghi}	65
Spec Uplands										
3A1	1.15±0.12^{cdefg}	0.02±0.01^{bc}	48.84±1.19^{hijk}	1.02±0.27^{ijkl}	0.23±0.03^{cdefg}	53.82±3.91^{abcd}	31.79±2.70^{ab}	19.05±2.49^{cdef}	0.87±0.33^{n}	75
3A2	1.19±0.14^{efg}	0.02±0.01^{cdef}	48.51±1.19^{fghij}	1.08±0.27^{jklm}	0.23±0.04^{cdefg}	53.11±5.28^{ab}	31.21±4.18^{ab}	19.14±2.14^{cdef}	0.82±0.24^{n}	75
6A2	1.03±0.13^{a}	0.01±0.01^{a}	51.10±1.18^{op}	0.39±0.25^{a}	0.21±0.03^{ab}	60.08± 4.24^{jklmn}	36.96±2.90^{hijklm}	20.86±1.88^{ijklmn}	0.74±0.17^{mn}	75
6A3	1.03±0.12^{a}	0.01±0.01^{a}	51.36±1.00^{p}	0.37±0.23^{a}	0.20±0.02^{a}	60.76±3.18^{lmn}	37.09±2.29^{hijklm}	21.31±1.74^{jklmno}	0.74±0.14^{mn}	75
8A2	1.06±0.19^{abc}	0.02±0.01^{cde}	48.10±1.36^{efgh}	1.00±0.32^{hijkl}	0.22±0.05^{bcdefg}	53.28±6.30^{a}	32.06±4.24^{ab}	20.36±1.91^{ghij}	0.65±0.25^{ijklm}	75
8A3	1.15±0.17^{cdefg}	0.02±0.01^{bcd}	48.70±1.06^{ghijk}	0.94±0.40^{ghijk}	0.23±0.06^{cdefg}	56.88±5.19^{cdefghi}	34.48±4.30^{cdefg}	20.85±1.76^{ijklm}	0.63±0.24^{ijklm}	75
10A1	1.38±0.21^{k}	0.03±0.01^{hijk}	50.38±1.44^{mno}	0.80±0.24^{efghi}	0.20±0.04^{ab}	54.06± 5.08^{abcd}	32.59±3.74^{bcd}	18.88±2.13^{cd}	0.63±0.21^{ijklm}	75
10A2	1.34±0.18^{jk}	0.03±0.01^{hijk}	50.49±1.11^{nop}	0.79±0.24^{defghi}	0.21±0.04^{abc}	54.80±5.50^{abcdef}	33.16±4.04^{bcde}	19.09±1.86^{cdef}	0.64±0.21^{ijklm}	75
Windsor Uplands										
9A2	1.23±0.16^{ghi}	0.03±0.01^{fghij}	50.02±1.19^{lmn}	0.77±0.26^{defgh}	0.24±0.03^{defgh}	53.22±5.32^{abc}	33.57±3.91^{cdef}	16.16±1.14^{a}	0.81±0.20^{n}	70
9A5	1.22±0.18^{gh}	0.03±0.01^{ijk}	49.31±2.46^{jkl}	0.85±0.35^{efghij}	0.24±0.04^{defgh}	54.37±4.62^{abcdef}	34.03±3.22^{cdefg}	17.25±1.45^{ab}	0.73±0.20^{mn}	70
11A2	1.34±0.27^{jk}	0.03±0.01^{ijk}	48.33±1.07^{fghij}	1.07±0.34^{klm}	0.25±0.04^{fghijk}	58.03±5.04^{ghijkl}	36.10±3.32^{fghijkl}	21.52±2.39^{lmno}	0.41±0.17^{bcde}	70
11A5	1.20±0.16^{fgh}	0.03±0.01^{fghij}	48.96±1.12^{hijk}	0.73±0.32^{cdefg}	0.25±0.04^{efghij}	60.36±5.14^{lmn}	38.69±4.32^{mn}	20.28±1.48^{ghijk}	0.49±0.16^{efgh}	70
13A2	1.04±0.23^{ab}	0.01±0.01^{b}	50.78±0.90^{nop}	0.66±0.26^{bcde}	0.22±0.04^{abcd}	55.50±5.32^{abcdefg}	34.75±3.91^{efghi}	18.09±1.53^{bc}	0.72±0.18^{lmn}	70
13A5	1.05±0.16^{abcd}	0.02±0.01^{bc}	49.53±1.25^{klm}	0.76±0.26^{defgh}	0.21±0.03^{abc}	56.13±4.83^{cdefghi}	34.79±3.19^{efghi}	18.94±1.65^{cdef}	0.73±0.19^{mn}	70

(CU8A2) to 1.93% (AU2A5) and P: 0.04 (WU13A2) to 0.16% (AU2A5) (Appendix 7).

3.3.3. *Litter quality relationships with environment*

There were significant relationships for the nine litter chemical variables, along with MAP, MAT, DS0MM, MAR, MAR_WS and soil P with the NIR spectra (Table 3.2). For the environmental variables this suggests that chemical information contained in the NIR spectra relates also to these variables. The scores and Y loadings plots show these relationships (Figure 3.1). The SU6 (open forest) plots were more spectrally/chemically different compared to the other plots. Average leaf litter N, P, Ca and Mg were all negatively correlated with C and phenolic contents (all $p < 0.004$) (C versus N, P, Mg, Ca linear $r^2 = 0.26$, 0.33, 0.46 and 0.62 respectively), visible along component axis 1 in the loadings plot (Figure 3.1.c and d). Without the very wet fertile sites of AU2, 4, 6, 8, this association was still significant for the region for all nutrients except N ($p < 0.05$). Negative correlations between nutrients and lignocellulose and lignin were also present, but only significant for Ca ($p < 0.005$) (Figure 3.2, linear $r^2 = 0.23$, $p = 0.002$). C was positively correlated with leaf litter α-cellulose, phenolics, and all ratios of lignin, lignocellulose and C to N and P ($p < 0.05$). This pattern also occurred when contrasting the distribution of nutrients to ratios of lignocellulose:N, lignin:N, lignocellulose:N and lignocellulose:P and N:P ($p < 0.02$ for all). Leaf litter C and N:P (Figure 3.2.b, $r^2 = 0.33$, $p = 0.002$), N and phenolics, and N:P and phenolics were all linearly distributed ($r^2 = 0.55$, $p = 0.001$) (without SU6, which had exceptionally high N:P values) (Figure 3.2.c). The relationship between N:P and leaf C was better explained by an inverse model (Figure 3.2.b, $r^2 = 0.47$, $p < 0.001$).

Table 3.2. Multivariate partial least squares regression (PLS2) statistics on near infrared spectra of rainforest leaf litter and chemical, climatic and soil nutrient variables. Shown are the correlation coefficients and standard errors, of calibration (r2cal and SEC), and after cross validation (r^2_{val} and SECV), and the ratio of standard error of prediciton to sample standard deviation (RPD). Variables with sufficient correlations with the NIR spectra for use in analysis are shown with an *. Chemistry regression statistics came from regressions used to predict values used in PLS2 with climate and soil. n = 40 (means of litterfall trap leaf samples).

	Variable	r^2_{cal}	SEC	r^2_{val}	SECV	RPD	
Chemistry	N	0.99	0.05	0.98	0.07	6.43	*
	P	0.98	0.005	0.97	0.005	5.66	*
	C	0.96	0.7	0.94	0.9	3.96	*
	Lignin	0.97	1.23	0.96	1.57	4.65	*
	α-cell	0.97	0.57	0.95	0.78	4.22	*
	Lignocellulose	0.97	1.46	0.95	1.84	4.52	*
	Mg	0.92	0.02	0.84	0.03	2.54	*
	Ca	0.96	0.18	0.93	0.26	3.56	*
	Phenolics	0.91	0.12	0.86	0.14	2.72	*
Climate	MAP	0.71	328.3	0.62	383.8	1.61	*
	MAT	0.54	1.45	0.46	1.61	1.35	*
	DS0MM	0.65	5.36	0.55	6.18	1.48	*
	MAR	0.54	0.32	0.53	0.34	1.44	*
	MAR_WS	0.72	0.15	0.69	0.16	1.81	*
	MAR_DS	0.35	0.46	0.19	0.53	1.11	
Soil	Soil N	0.21	0.16	0.08	0.18	0.97	
	Soil P	0.48	0.03	0.37	0.04	1.32	*
	Soil Ca	0.26	0.08	0.19	0.089	1.10	
	Soil Mg	0.26	0.003	0.17	0.003	1.06	
Disturbance	%Gap species	0.14	12.89	0.00	16.31	0.86	
	Individuals	0.26	13.28	0.14	14.67	1.06	
	Species richness	0.23	6.11	0.17	6.83	1.09	

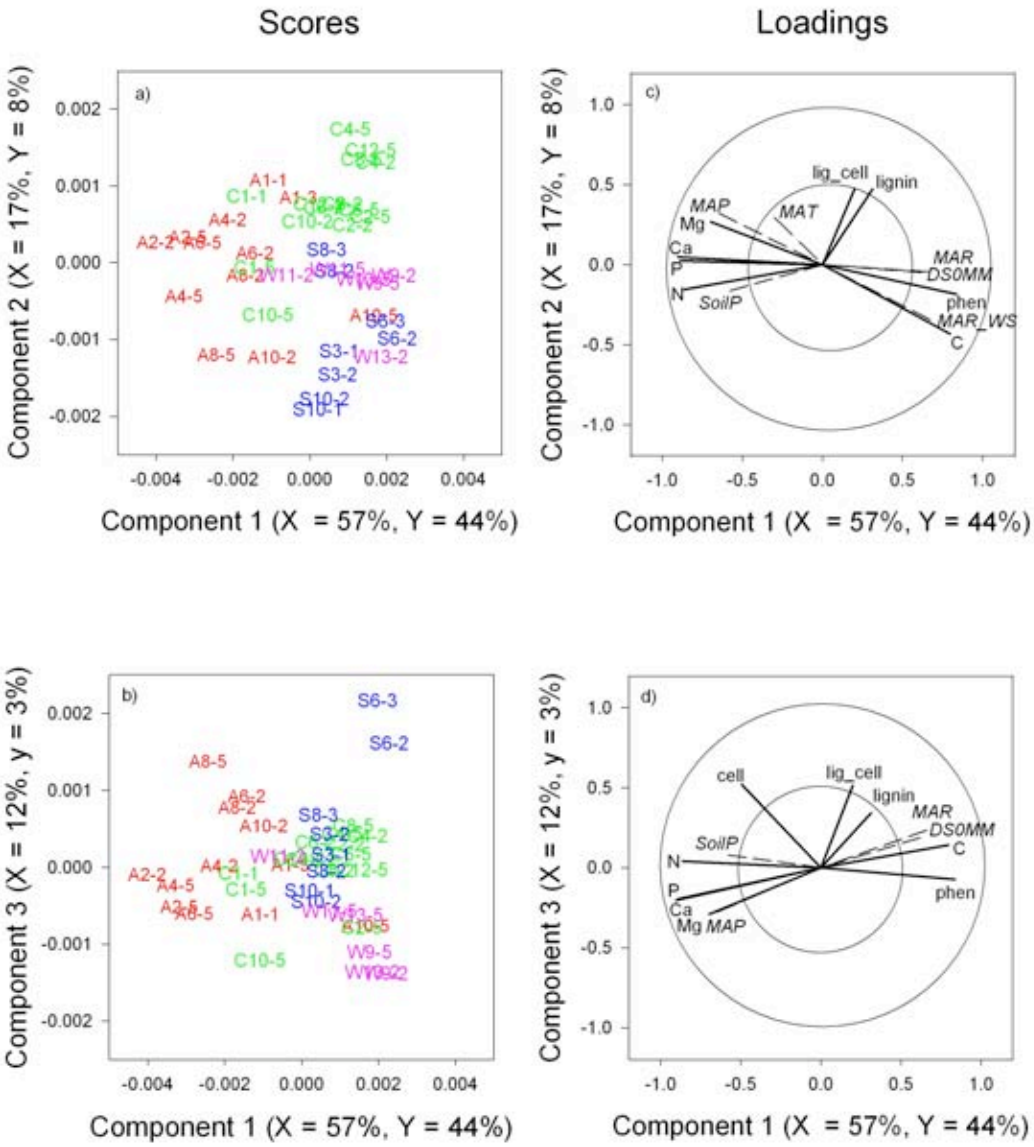

Figure 3.1. Distribution of mean leaf litterfall chemistry, from near infrared spectrometric analysis, of sites in Australian tropical rainforests. Shown is the score plot (a and b) representing the relative spectral variability in mean leaf litterfall, from two years of collections, (n varies through out, generally 65-100 per plots). Multivariate partial least squares (PLS2) correlations, (one model containing leaf chemistry and environmental variables) with the spectra are shown in the loadings plots (c and d), for leaf chemistry (solid lines) and environment (dashed lines). The first three components are shown. Circles represent 50% and 100% explained variance. Colours in the scores plot represent different sub regions, red = Atherton Uplands; green = Carbon Uplands; blue = Spec Uplands; magenta = Windsor Uplands. Site codes represent the sub-region, followed by the approximate elevation and (-) the plot number. See text for variable descriptions and regression statistics.

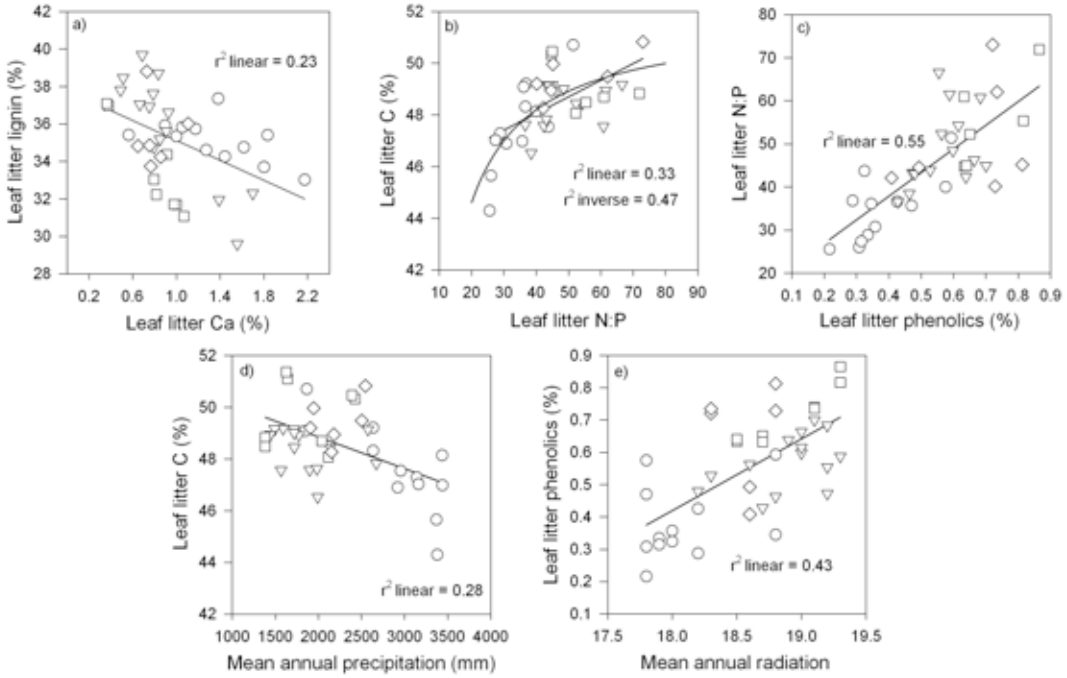

Figure 3.2. Relationships between nutrient cycling variables in Australian tropical rainforests: a) leaf litter Ca versus lignin; b) leaf litter C versus N:P ratio; c) N:P versus phenolics; d) C versus MAP; e) Mean annual radiation versus leaf litter phenolics. Lines of best fit are shown from regression analysis. Symbols represent different sub-regions: AU ○; CU ▽; SU □; WU ◇. n = 38 for a) and b); n = 40 for c), d) and e); a) and b) exclude marginal rainforest plots of the Spec Uplands (600 m a.s.l.) with extremely high N:P values.

Most of the environmental variables correlated along component axis 1 in the loadings plot (Figure 3.1.a and b). In particular, soil P correlated in the direction of nutrients, and DS0MM and MAR annual and wettest quarter means correlated in the direction of phenolics and C (Figure 3.1). The negative correlation between leaf litter nutrients and MAP in the region existed both with and without the AU (2-8) very wet fertile sites: N and MAP (linear $r^2 = 0.42$ $p < 0.001$ all plots, linear $r^2 = 0.17$, $p = 0.021$ ex. AU2-8); P versus MAP (linear $r^2 = 0.51$, $p < 0.001$ all plots, linear $r^2 = 0.24$, $p = 0.008$ ex. AU2-8); P versus DS0MM (linear $r^2 = 0.52$, $p < 0.001$ all plots, linear $r^2 = 0.17$, $p = 0.024$ ex. AU2-8). Total phenolics had a strong positive linear relationship with MAR (Figure 3.2.e, linear $r^2 = 0.43$, $p < 0.001$).

Leaf litter C was negatively linearly related to rainfall (MAP, $r^2 = 0.28$, p

< 0.001, Figure 3.2.d), and significantly correlated with soil P (p = 0.003), but not soil N (p = 0.06). N:P was also linearly related to MAP (r^2 = 0.38 p < 0.001), and MAPCV (r^2 = 0.31 p < 0.001). Further analysis showed leaf litter C contents were driven by a combination of soil nutrients and moisture (best sub-set regressions, Table 3.3). For all plots combined, MAP, MAT and soil Mg were the best explanatory variables of leaf litter C (model r^2 = 0.53). Without the AU2-8 very wet fertile sites, MAPCV and soil P contributed to the model (model r^2 = 0.45).

Table 3.3. Best sub-set regression results explaining leaf litter C content (n = mean value from 40 plots).

	Variable	p	Std. Reg coeff.	Model r^2	Model p
All sites	MAP	0.002	-0.399	0.53	0.001
	Soil Mg	0.000	-0.495		
Exc. AU2-8*	MAT	0.004	-0.499	0.45	0.001
	MAPCV	0.038	0.364		
	Soil P	0.017	-0.387		

*excluding Atherton Upland very wet basaltic soil sites.

There was a significant effect of season (wet/dry) on leaf litter chemical concentrations for N, lignin, lignocellulose (higher in the wet, p < 0.010), and phenolics (higher in the dry, p < 0.001) (repeated measures ANOVA, Table 3.4). No significant season effect existed for the other chemical variables (p > 0.05). The effect of plot on seasonality was significant for all components except lignocellulose (p = 0.06) (Table 3.4).

Standardised overall tree/shrub species richness (both all individuals and trees ≥ 5 m) had a positive linear relationship with leaf litter lignin (all plants: Figure 3.3.a, r^2 = 0.18, p = 0.009; trees ≥ 5 m: Figure 3.3.b, r^2 = 0.21, p = 0.014) (see

Appendix 2 for richness data). The percentage of gap coloniser species was positively linearly related to α-cellulose (Figure 3.3.c, p = 0.012).

Table 3.4. Results of repeated measures ANOVA for seasonal concentrations, wet (Oct 31st - April 1st) and dry season, of leaf litter chemical components from plots in Australian tropical rainforests (n = 40).

Variable	Effect	df	F	Dry mean	Wet mean	p
N	Season	1	4.903	1.28	1.30	0.019
	Season*site	39	2.242			0.000
P	Season	1	1.477	0.03	0.03	0.225
	Season*site	39	2.001			0.000
Mg	Season	1	0.068	0.25	0.25	0.794
	Season*site	39	2.673			0.000
Ca	Season	1	0.930	0.99	1.03	0.355
	Season*site	39	2.064			0.000
C	Season	1	0.009	48.61	48.62	0.927
	Season*site	39	2.302			0.000
lignin	Season	1	135.50	34.27	36.00	0.000
	Season*site	39	1.824			0.002
lignocellulose	Season	1	190.62	55.91	58.52	0.000
	Season*site	39	1.385			0.059
α-cellulose	Season	1	25.35	20.05	20.39	0.000
	Season*site	39	4.765			0.000
Phenolics	Season	1	306.34	0.58	0.44	0.000
	Season*site	39	2.410			0.000

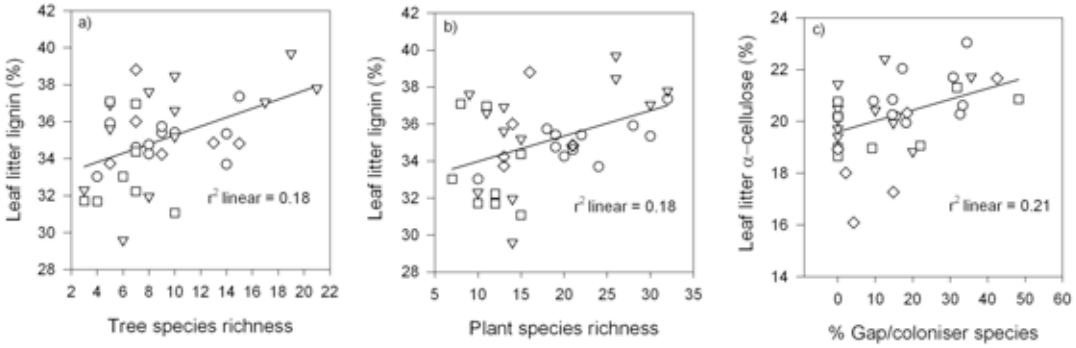

Figure 3.3. Relationships between plant species community and leaf chemical attributes, a) Species richness of trees ≥ 5 m contributing to litter traps and leaf litter lignin; b) Overall relative plant (tree and shrub) species richness (> 1.6 m) versus lignin; c) proportion of general gap coloniser species versus α-cellulose. Symbols represent sub-regions and are the same as in Figure 3.2.

3.3.4. *Nutrient accessions*

The range of total leaf nutrient accessions were: 30.3 (AU6A2) - 128.8 (CU6A2) kg N ha^{-1} y^{-1}; 0.09 (SU6A3) - 3.4 (AU2A2) kg P ha^{-1} y^{-1}; 5.14 (AU8A5) - 27.6 (CU6A2) kg Mg ha^{-1} y^{-1} and 14.99 (SU6A3) - 114.21 (AU2A2) kg Ca ha^{-1} y^{-1} (Appendix 8). Carbon accessions were 4899.1 (CU6A2) - 1024.8 (AU8A5) kg C ha^{-1} y^{-1} and were linearly related to MAP, both including and excluding the cyclone damaged plots (all plots: r^2 = 0.36, p = 0.001; no cyclone: r^2 = 0.21, p = 0.01, Figure 3.4.a), excluding one extreme outlier (CU6A2, very high litterfall). Ca leaf accessions were linearly related to lignin concentrations both with and without the cyclone damaged plots (r^2 = 0.24 p = 0.002 and r^2 = 0.26 p = 0.005 respectively), not including an extreme outlier (AU2A2, with very high Ca contents).

Ranges of N and P accessions from reproductive material were: 0.84 (AU8A5) - 10.52 kg N ha^{-1} y^{-1} (CU2A2); 0.04 (AU8A5) - 0.70 kg P ha^{-1} y^{-1} (CU6A2) (Appendix 8). N and P accessions from the unclassified component of litterfall ranged from 1.88 (CU8A2) - 9.63 kg N ha^{-1} y^{-1} (AU2A2) and 0.10 (WU13A2) - 0.72 kg P ha^{-1} y^{-1} (AU2A5). Both N and P unclassified accessions were linearly related to MAT (r^2 = 0.22, p = 0.002 and r^2 = 0.16 p = 0.01 respectively) (Figure 3.5.a and Figure 3.5.b).

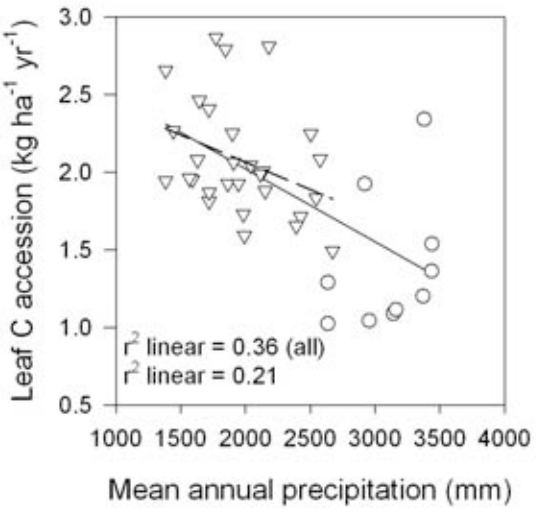

Figure 3.4. Leaf litter chemical accession (kg ha^{-1} y^{-1}) relationships: C versus Mean annual precipitation. Regression line is significant ($p < 0.05$) both including all plots (solid line), and without the cyclone damaged sites (dotted line).

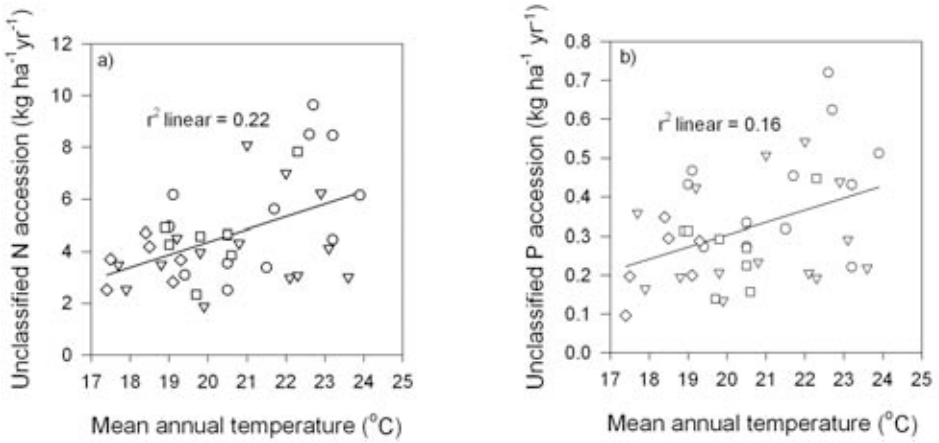

Figure 3.5. Nutrient accession (kg ha^{-1} y^{-1}) from unclassified (< 2 mm) portion of litterfall relationships with mean annual temperature (MAT), for a) nitrogen and b) phosphorus. Symbols represent the four sub-regions, see preceding figures for legend.

3.4. Discussion

The environmental controls on litter quality included both edaphic, climatic and species composition/disturbance effects. The Australian wet tropics bio-region contains substantial diversity in the chemical compositions of plant litter cycled. Leaf nutrient accessions found were in the order C > N > Ca > Mg > P, and are similar to other tropical forests (Vitousek and Sanford 1986).

Comparing the chemical composition of the leaf litter throughout the region, there was a broad negative correlation between chemical and environmental factors that promote, and inhibit, nutrient cycling and decomposition processes. Inhibiting chemical constituents like total phenolics and, potentially total C, corresponded with generally drier conditions, and low litter nutrients (Figure 3.2.a and b). The antithesis of this existed in the wettest areas (esp. Atherton midlands), where richer soils produced more nutrient-rich litter. However, in some cases the pattern appears to be an artifact of wet sites occurring on more fertile soils, and most of the drier sites on older oligotrophic soils. Thus, the trend of increasing leaf litter P with MAP and to some extent N and MAP (see following), may be explained by these correlations. However, there were also clear trends between recalcitrant chemical components and climate and soil fertility that were likely caused by actual soil and climate effects alone. High contents of limiting chemical components slows nitrification and other nutrient turnover, decomposition and general nutrient cycling (Meentemeyer 1978; Aber and Melillo 1982; Melillo *et al.* 1982; Horner *et al.* 1988; Fox *et al.* 1990), both in decaying material in the litter, and in the soil/litter layer due to the build up of polyphenols from leachates (Hättenschwiler and Vitousek 2000). This trend was seen here for phenolic compounds, lignin and carbon. The impacts of this polarity on ecosystem processes are notably high. While phenolic compounds are traditionally

considered as plant deterrents to herbivory (Coley 1986), they are also antioxidants and concentrations increase where there are risks of photodamage, such as in higher light environments, in addition to on low nutrient soils (Newberry and de Foresta 1985; Close *et al.* 2001; Close and McArthur 2002). The correlation between phenolics and solar radiation (Figure 3.2.e) and nutrient limitation in AWT rainforests (e.g., especially P (N:P ratio), Figure 3.2.c), is evidence of this. The trend for higher concentrations of phenolic compounds in leaf litter during the dry season in these forests may also be a response to environmental stresses brought on by prolonged reductions in moisture availability and light stress during this time (Hättenschwiler and Vitousek 2000; Close and McArthur 2002). This is also a sign of plant sensitivity, over the short term, to changes in the environment with radiation, moisture and/or nutrient stress resulting in short term changes in phenolic compound production (Close and McArthur 2002).

Elemental nutrient concentrations in leaf litterfall were regionally variable. Leaf litter nitrogen contents on basalt were within the lower range of other values on moderately fertile soils (e.g. Alfisols), and upper range of infertile Oxisols and Ultisols (Vitousek and Sanford 1986). Litterfall nutrient concentrations in other plots on lower fertility soils were similar to sites in tropical forests on Spodosols and Oxisols (Vitousek 1984; Vitousek and Sanford 1986). Leaf litter P contents here were mostly low compared to rainforests, even on basalt (mid-low range for tropical forests). The regional mean was similar to that found on infertile Spodosols and Oxisols (Vitousek and Sanford 1986; Yuan and Chen 2009). Very low P in leaf litter generally relates to low available P in soils and/or significant P resorption prior to litterfall (Ares and Gleason 2007). Nutrient resorption prior to litterfall is an essential aspect of efficient nutrient cycles (Vitousek 1982), and is known to be significant in

Australian tropical rainforests (Herbohn 1993). In rainforests P may be withdrawn from leaves in greater proportions than other elements (Vitousek and Sanford 1986; Hättenschwiler *et al.* 2008), stressing the importance of this element to continued growth, and the general limitation of P in the majority of rainforest soils (Vitousek 2004).

Leaf litter carbon contents here were related to other litter nutrients, soil fertility and precipitation (Table 3.3). In particular, low C contents occurred together with higher nutrient soils (Mg and P) and litter (especially low N:P ratio), and higher, less seasonal rainfall. The moisture effect can be explained by C-rich leachates washing from the material while still attached to the plant (e.g. during senescence) (Wieder *et al.* 2009). This variability is of interest to studies quantifying the C cycle in similar forests, especially when applying the commonly used value of 50% C (Clark *et al.* 2001b). For instance, mean leaf litter C at one very wet, relatively nutrient-rich plot (i.e. AU2) was 44.3%, relating to a mean C accession to soils from leaves of 2.31 t C ha^{-1} y^{-1}. With the assumed 50% C, this equates to 2.61 t C ha^{-1} y^{-1}, and a significant difference from the true mean (t test, T = -6.05, p = 0.002 df = 4). Thus, the use of 50% C in leaf litter is a likely an over-simplification. The composition and fate of C leachates is an important and under quantified component of rainforest nutrient cycles (Wieder *et al.* 2009).

In nutrient-poor environments, litter recalcitrance causes slower litter turnover, and nutrients are concentrated in vegetation biomass and long-lived recalcitrant tissues, substantiating nutrient-poor conditions (Melillo *et al.* 1982; Hobbie 1992). The negative correlation between leaf litter lignin and Ca in AWT is further testament to this characteristic of forests in general. High lignin contents relate to different leaf production strategies and longer lived tissues (Kikuzawa

1995). Cellular lignification in plants can be a phenotypic response to nutrient stress and decreasing soil fertility (Chapin 1991). The suggestion of Kitayama et al. (Kitayama *et al.* 2004), that lower lignin contents are adaptive to recycle minerals without limiting decomposition in less productive environments, is not supported by this work. The highest lignin contents were found in nutritionally poorer areas, which are unlikely to be comparatively more productive (e.g. CU4 compared to AU4). Generally this data suggests high lignin contents relate to cation (Ca) limited conditions and disturbance (Figure 3.2.a and Figure 3.3). Other work has suggested longer lived photosynthetic organs may have higher lignin contents (Mediavilla *et al.* 2008). The positive trend of lignin and species richness seen here could be caused by plots with more longer lived individuals and slower leaf turnover rates, producing on average higher lignin leaf tissues. Many of the sites containing high species richness here were candidates for intermediate disturbance type effects on vegetation structure and richness (Ward and Stanford 1983; Collins *et al.* 1995), mostly from selective logging more than 20 year ago (e.g. old snig roads and clearings; S. Parsons personal observation). This lead to a high proliferation of shade tolerant individuals (mostly sapling to understory aged/sized individuals at the time of study), and raised species richness. Such disturbance effects also explain the high local variability in lignocellulose and Ca leaf litter contents, along with small scale spatial variability in soil nutrient availability. Chemical variability per unit richness in live leaves is higher in the lowlands than in the uplands in AWT rainforests (Asner *et al.* 2009), but this trend was not visible in leaf litter here through the method applied.

Fast growing gap colonising species may have different nutrient cycling and decomposition properties compared to slow growing shade tolerant individuals (Coley 1988; Denslow *et al.* 1998; Poorter *et al.* 2004; Parsons and Congdon 2008).

In areas with a higher proliferation of pioneer/early secondary species, there were higher cellulose contents and lower lignocellulose:cellulose ratios (higher portion of cellulose in acid detergent fibre portion, Figure 3.3.c). These locations contained high abundances of individuals with a 'live fast die young' life history strategy (Wright *et al.* 2004). The trend of low quality litter in gaps in the Spec uplands noted by Parsons and Congdon (2008) was not found to be a general trend throughout the Australian wet tropics. The species responsible for this pattern, *Alphitonia petriei*, while present along road sides (e.g. large gaps) throughout the regional study area, was less common within the plots examined in the present study.

The reason for the seasonal difference in N noted here is unclear, but could have been due to greater resorption of N from abscising leaves in the dry season, or higher concentrations of green (N rich) leaves falling in the wet. Schuur and Maston (2001) noted decreased N contents with MAP in tropical forests. Contrastingly, trends of increasing N and lignin contents, and overall recalcitrance, with higher annual precipitation were noted in the species *Metrosideros polymorpha* in the Hawaiian island study of Austin and Vitousek (2000). For lignocellulose, the cause behind the seasonal trend is also somewhat unclear. Such changes in leaf litter may be due to seasonal moisture-driven carbon - nutrient balances, increased allocation of defence compounds due to increased herbivore pressures in the wet season (although not for phenolics), or higher proportions of more older/senesced lignocellulose-rich leaves being cycled in the wet season (Austin and Vitousek 2000). Despite these uncertainties, as the majority of litter in AWT falls in the wet season (Brasell *et al.* 1980; Herbohn and Congdon 1993), the seasonal chemical dynamic relates directly to climate-driven alterations in litter quality, with impacts on soil/litter processes. Especially, seasonality in nutrient pulses from litterfall and rainfall (throughfall and

stemflow) are generally high in these forests (Herbohn and Congdon 1993; McJannet *et al.* 2007). In tropical forests, especially on poor soils, these environmental fluctuations and resulting nutrient pulses are essential to maintain adequate rates of nutrient mineralisation, plant uptake and forest productivity (Lodge *et al.* 1994).

Ultra-fine (unclassified) litterfall provides significant inputs of particulate material and nutrients to the forest floor. This material can include atmospheric dust, pollen and other flower parts, insect frass and droppings, fragmented leaves, fine plant bark and woody material, and as seen here may be relatively nutrient rich (Veneklaas 1991; Herbohn and Congdon 1993). Inputs from this component to soils in AWT were especially high for P (regional unclassified mean = 51% of leaf P inputs), showing the importance of this vector for plant and soil processes. Some climatic sensitivity of this input is also implied by the correlation between ultra-fine litterfall and temperature, with inputs being generally lower in upland forests (Figure 3.5). The causes of this are unclear, however may be influenced by higher invertebrate biomass in the lowlands (Olson 1994).

This chapter has shown that litter chemical quality is determined by a combination of soil type, the vegetation community (including disturbance and successional status), climate and changes due to season. Litterfall trends in these forests are further explored in Chapter 6 of this thesis.

Chapter 4. Regional patterns and controls of leaf decomposition and nutrient dynamics in Australian tropical rainforests

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4.1. Introduction

Plant litter decomposition is an essential ecosystem process and crucial in driving forest carbon (C) and other nutrient cycles. Even small increases in global decomposition rates could accelerate global warming (Chapin *et al.* 2002). It is well documented that climate, litter quality and the composition of the soil and soil biota most often control litter decomposition rates and nutrient dynamics in forested ecosystems (Meentemeyer 1978; Swift *et al.* 1979; Melillo *et al.* 1982; Aerts 1997; Adair *et al.* 2008). Across biomes temperature, moisture availability, litter quality (such as N and P and ratios of lignin to nutrients), are valuable in predicting decomposition rates and nutrient release patterns (Vitousek *et al.* 1994; Aerts 1997; Gohlz *et al.* 2000; Parton *et al.* 2007; Cornwell *et al.* 2008).

Decomposition generally occurs rapidly in the wet tropics, with high rainfall and temperatures promoting fast breakdown (Lloyd and Taylor 1994; Gohlz *et al.* 2000; Adair *et al.* 2008). Throughout the tropics, precipitation is the most significant determinant in variability in litter decay (Powers *et al.* 2009), however, when climatic conditions do not limit breakdown (e.g. abundant moisture and high temperatures), litter quality controls on decomposition rates may be enhanced (Aerts

1997). Importantly though, other unique controls may also exist on litter decomposition in tropical rainforests when compared to other biomes (Adair *et al.* 2008). For instance, overly high moisture in soils in very wet conditions may inhibit microbial activity due to soil anoxia (Schuur 2001), although not always (Wieder *et al.* 2009), and due to seasonal drought where rainfall seasonality is high (Austin and Vitousek 2000). This often coincides with highly weathered nutrient-poor soils, especially for phosphorus (P), causing the production of poor quality, recalcitrant litters (Vitousek 1984; Vitousek and Sanford 1986). Unlike nitrogen, which is often relatively high in rainforest leaf litter (Yuan and Chen 2009), P contents are usually very low due to low P in soils and tight cycling and re-absorption strategies of plants prior to litterfall (Townsend *et al.* 2007). Phosphorus limitation of microbes is widely considered to be a strong determinant of limitations in ecosystem processes in wet tropical rainforests (Cleveland *et al.* 2002; Cleveland *et al.* 2006; Wieder *et al.* 2009), although diverse suites of nutrients may combine to control plant and litter processes (Kaspari *et al.* 2008). In such environments, the processes allowing nutrient release to plant roots are tightened when elements are in high demand by microbes, due to immobilisation dynamics in the litter layer and soils. This occurs when demand from microbes outpaces availability (Vitousek and Howarth 1991) and, for N and P at least, is common in tropical rainforests at least in the early stages of decomposition (Vitousek and Sanford 1986; Tanner *et al.* 1998; Hobbie and Vitousek 2000; Parsons and Congdon 2008). This bottleneck of nutrient availability presents conditions for the slowing of ecosystem processes particularly at the soil level (Chapman *et al.* 2006). Seasonal pulses of nutrients released from litter back to plants, either through leaching or movement out of the microbial sub-systems, are of great importance to rainforest function as a whole (Cornejo *et al.* 1994; Lodge *et al.*

1997). Importantly though, other unique controls may also exist on litter decomposition in tropical rainforests when compared to other biomes (Adair *et al.* 2008). For instance, overly high moisture in soils in very wet conditions may inhibit microbial activity due to soil anoxia (Schuur 2001), although not always (Wieder *et al.* 2009), and due to seasonal drought where rainfall seasonality is high (Austin and Vitousek 2000). This often coincides with highly weathered nutrient-poor soils, especially for phosphorus (P), causing the production of poor quality, recalcitrant litters (Vitousek 1984; Vitousek and Sanford 1986). Unlike nitrogen, which is often relatively high in rainforest leaf litter (Yuan and Chen 2009), P contents are usually very low due to low P in soils and tight cycling and re-absorption strategies of plants prior to litterfall (Townsend *et al.* 2007). Phosphorus limitation of microbes is widely considered to be a strong determinant of limitations in ecosystem processes in wet tropical rainforests (Cleveland *et al.* 2002; Cleveland *et al.* 2006; Wieder *et al.* 2009), although diverse suites of nutrients may combine to control plant and litter processes (Kaspari *et al.* 2008). In such environments, the processes allowing nutrient release to plant roots are more tightly coupled when elements are in high demand by microbes, due to immobilisation dynamics in the litter layer and soils. This occurs when demand from microbes outpaces availability (Vitousek and Howarth 1991) and, for N and P at least, is common in tropical rainforests at least in the early stages of decomposition (Vitousek and Sanford 1986; Tanner *et al.* 1998; Hobbie and Vitousek 2000; Parsons and Congdon 2008). This bottleneck of nutrient availability presents conditions for the slowing of ecosystem processes particularly at the soil level (Chapman *et al.* 2006). Seasonal pulses of nutrients released from litter back to plants, either through leaching or movement out of the microbial sub-systems, are of great importance to rainforest function as a whole (Cornejo *et al.*

1994; Lodge *et al.* 1994).

Initial litter quality (at litterfall) is known to strongly control patterns of C and nutrient release at many scales (Palm and Sanchez 1990; Aerts 1997). Soil fertility and species composition generally control litter quality. Moderation of leaf traits (including substrate quality) by climate is generally only minor, and up to 40% of global litter quality variation can be found at individual sites (Cornwell *et al.* 2008). In tropical rainforest, potential for localised variations in decomposition rates and soil processes is high, due to exceptionally high species diversity, and thus heterogeneity in canopy chemistry (Townsend *et al.* 2007; Townsend *et al.* 2008). Understanding of variability in soil surface processes hinders understanding of ecosystem processes in general, and decomposition and nutrient cycling in particular (Wieder *et al.* 2009).

The Australian Wet Tropics (AWT) bioregion is a good natural experiment to interrogate many of these questions in tropical rainforest. Similarly, data from Australian tropical rainforests is lacking from both global data sets and recent pan-tropical studies of litter decay (Gohlz *et al.* 2000; Liski *et al.* 2003; Adair *et al.* 2008; Powers *et al.* 2009). The wet tropical region of Australia consists of a range of tropical climates, with high regional range in rainfall (total and seasonality), temperature (elevational gradients), and soil fertility (old oligotrophic and newer more fertile basaltic formations) (Tracey 1982; Spain 1990). Higher mean annual precipitation generally relates to lower rainfall seasonality in the region, with seasonality driving much of the variability in rainforest distributions (Hopkins *et al.* 1993). Furthermore, the area contains numerous rainforest formations and significant biodiversity and local endemism. The risk of negative climate change impacts is very high here, with future scenarios suggesting shifts from rainforest to drier, e.g.

sclerophyll forests, changes in ecologically significant upland rainforest types (Hilbert *et al.* 2001), and substantial losses in biodiversity and endemic species (Williams *et al.* 2003).

A total of 18 locations throughout the AWT from near sea level to ~1300 m a.s.l are used to model litter decay for the region. Litterbags were used to study decomposition of leaves representative to each locality, as well as a common substrate to control for the effects of litter quality. Near infrared spectroscopy (NIRS) is valuable for looking for broad trends related to the organic chemical content of plant material and relationships between environmental factors and leaf chemical traits (Gillon *et al.* 1993; Foley *et al.* 1998; Gillon *et al.* 1999; McIlwee *et al.* 2001; Chapter 2 of this thesis). NIRS is used here to determine nutrient and litter quality components, and view chemical changes occurring in the material during decomposition.

Considering the potential for spatially varying conditions for decomposition in this region and limitations due to substrate quality may be high in these forests, leaf litter decomposition rates are modelled here with climate, soil and litter chemical quality data. The following questions are also asked: what is the regional variability in decomposition rates of leaf litter in the AWT rainforest; how much of the regional variability in decomposition is due to substrate quality; how important is rainfall seasonality in driving this variability; are very high rainfall sites (e.g. > 3000 mm y^{-1}) limited in decomposition rates compared to mid range rainfall sites; and what governs changes in litter recalcitrance and nutrient immobilisation and release in these forests, particularly in regards to N and P, on older oligotrophic soils and younger more fertile ones? Strong regional controls on leaf decay are expected to come from variability in litter chemical quality, driven primarily by parent material.

However, considering the varied climate throughout the region, both in terms of temperature (elevation) and rainfall (esp. seasonality), climate, and most likely rainfall, should significantly contribute to the regional variations in litter decay rates here, similar to other tropical rainforests (Powers *et al.* 2009). Other work in the region has noted long term immobilisation patterns of nutrients at two oligotrophic upland sites in the AWT (Parsons and Congdon 2008). Mineralisation of nutrients is expected to be slow, even for tropical rainforest here, but also spatially varied due to variations in soil fertility.

4.2. Methods

4.2.1. *Study sites*

Leaf decomposition was studied in four sub-regions in the AWT. Sites were distributed along elevational transects**:** Atherton Uplands (AU 80 m a.s.l.; 428 m; 630 m; 840 m and 930 m); Carbine Uplands (CU: 115 m; 234 m; 440 m; 656 m; 820 m; 1016 m and 1210 m); Spec Uplands (SU: 334 m; 834 m; 899 m and 963 m) and Windsor Uplands (WU: 940 m; 1100 m and 1294 m) (Appendix 9).

Both long term averages and real time climate data were used. Long term averages came from BIOCLIM, for mean annual precipition (MAP), mean annual temperature (MAT) and rainfall seasonality (MAPCV). Real time data came from the Australian Water Availability Project (AWAP) for rainfall (Raupach *et al.* 2008), and on site data loggers (HOBO type, Onset computer corporation USA and and Hygro-Button loggers Progs Plus France): leaf wetness (moisture condensation under cover, related to humidity, cloud interception), air temperature (AirT), soil temperature (soilT) and humidity (means for study period).

4.2.2. *Litterbags*

Leaf decomposition was studied with the litterbag method (Bocock and Gilbert 1957). Two naturally abscised/senesced leaf substrates were used: "*in situ"* litterfall leaves (collected on site) and a common control treatment from the semi deciduous rainforest tree *Archidendron vaillantii* (F.Muell.) F.Muell (Mimosaceae) ("control"). Care was made to select leaves in a relatively homogenous condition, that is, with little microbial attack and no signs of severe leaching. The goal of the control experiment was to determine decomposition dynamics independent of the litter quality differences present in the *in situ* samples. *A.vaillantii* was chosen as it produced a large amount of naturally abscised leaves to permit a detailed litterbag study, and the species is native and relatively common to all sub-regions used here (Hyland *et al.* 2002). The control leaves were collected from locations on Mt Spec (SU) and Mt Windsor (WU) during *A. vaillantii's* leaf drop from July to September 2007. Collections from the different locations were pooled and mixed well. The *in situ* leaf litter was collected in litterfall traps in September - November 2007. The traps were made from a 0.25 m^2 circular metal ring with a glass (1 mm fly screen) mesh basket, fixed in place approximately 1 m from the ground (Newbould 1967). Traps were placed in a star formation at least 5 m apart. The material represents the first main fall of litter leaves of the beginning of the wet season, and is close to the peak litter fall time for these sites. The goal of using this material was to follow the decomposition of this peak litterfall for > 12 months, beyond the next major litter fall. The use of bulk litter such as this can have some impact on decomposition rates (Gartner and Cardon 2004). However, the use of mixed litter in the *in situ* samples was undertaken here for the purpose of characterising the litter decomposition

dynamics of the specific sites; thus, decomposition rates were relative to the species composition (including mixing effects) of the communities in question.

Samples were dried and the leaf component separated. They were then combined from 10 litter traps and mixed well. Noticeably damaged or heavily fragmented leaves were excluded from both treatments. The litterbags were the same design as those used by Parsons and Congdon (2008) (15 x 15 cm, 2 mm mesh stapled shut with 3 cm gaps along the edges to allow faunal movement). Approximately 5 g of dried leaves was placed inside each bag.

The *in situ* experiment was run at 17 plots, and the control experiment at 12 plots, within the sites mentioned above. The control experiment was not run at all sites due to limitations in the amount of leaf material available. Placements of the control litterbags were selected to cover the climate and soil fertility space of the *in situ* sites. Litterbags were placed on the soil surface in January 2008, and subsequent removals (6 x removals, 5 litterbags per plot per removal) took place in February (~20 days), March (~50 days), May (~ 110 days), September (~230 days), December (~ 350 days) and April 2009 (~ 430 days). Due to distances between sites not all samples were collected on the same day, however care was taken to make exposure times as similar as possible, and they generally only differed by 2-3 days at most. Determination of the initial chemical characteristics (substrate quality) was undertaken with a subset of five 5 g samples kept aside from those deployed in the field.

Retrieved litterbag samples were dried at 40 ^{o}C until constant weight. They were then cleaned of all soil and weighed. Samples were ground through a 1 mm mesh with a cyclone mill (Foss Cyclotec 1093 sample mill, North Ryde NSW Australia), and then scanned with a near infrared spectrometer. NIRS models were

built to quantify chemical components in the material using the methods of Chapter 2 of this thesis, using standard NIRS methods for ecological materials (Shenk *et al.* 1992; Burns and Ciurczak 2007). The NIRS method is of comparable accuracy to standard methods for analysing chemical components in plant matter, and allows substantial savings in chemical waste, time and effort (Foley *et al.* 1998; Gillon *et al.* 1999). More holistic appreciations of chemical relationships with ecological phenomena are also possible with NIRS (Gillon *et al.* 1993; Foley *et al.* 1998; Gillon *et al.* 1999) Models were developed from a sub-set of samples, which were analysed using standard chemical techniques. The samples from the final collection (~440 days) samples were not included in the NIRS scans as many sample portions were too small for adequate spectral analyses with the method used. The chemical components determined with NIRS for the initial substrates and after decomposition were: total N, P, Ca, C, acid detergent lignin (lignin); acid detergent fibre (lignocellulose); α-cellulose (Van Soest 1963), and total phenolics (Folin and Ciocalteu 1927; AOAC 1995). Models for Mg while accurate for the initial contents were considered inaccurate for subsequent comparisons after application on the soil surface due to errors in the NIR models (Chapter 2). The total number of samples was 90 for the initial contents (17 *in situ* sites x 5 samples; 5 control), and 720 after decomposition (17 x *in situ* + 12 x control x 5 litterbags x 5 collections, minus 1 site/ time not collected - WU13 ~20 days).

4.2.3. *NIRS representation of chemical changes during decomposition*

Changes in the chemical composition of the material in the litterbags during decomposition were visualsed from variability in the NIR spectra, while also being analysed statistically with more standard methods (see statistics section).

Considering the NIR spectrum contains most of the significant chemical information in the samples (Foley *et al.* 1998), the variability in the spectra provides a map of changes during decomposition. While principal component analysis (PCA) on the spectra provides all of this information, there may also be extraneous information in a PCA not related to the components of interest, and valuable information may be obscured (Krzanowski *et al.* 1995). PCA, followed by canonical correlation analysis of the principal components (CAP), was used on the decomposition spectral data to better show features related to changes occurring in the decomposing leaves. This method of component reduction and selection allows the most prominent patterns and ecologically important information to be considered, without including extraneous random variation (Anderson and Willis 2003). CAP analysis works by finding axes in the PCA that maximise variability between groups (Anderson and Willis 2003), and has been shown to be a valuable method of discriminant analysis of spectral samples (Evans *et al.* 1993; Hourant *et al.* 2000; Middleton *et al.* 2009). The raw data matrix (Y) consisted of the mean NIR spectra (following 1st derivative with pretreatments) of the litter bag samples per litterbag collection time and the initial spectra before decomposition (generally totalling 6 spectral samples per site). Separate analyses were undertaken for the *in situ* and control treatments. The PCA yielded axis from which a representative number of axes (m) were selected. The selection of m was based on the number of axes resulting in minimal residual sum of squares for the X variables (Anderson and Willis 2003). Constrained canonical discriminate correlation analysis (CCorA) was used on these to re-plot the PCA data based on correlations with site and time exposed as predictor groups (X), and based on Bray - Curtis dissimilarity (Anderson and Willis 2003; Middleton *et al.* 2009). Time was standardised for each site due to the slight differences in exposure periods

(i.e. collections were rounded to 20 days; 50 days, 110 days, 230 days and 350 days for all samples). Significant effects were evaluated in terms of *p* values derived from permutation with leave one out cross validation (9999 iterations). The CAP software of Anderson (2002) was used for this representation.

4.2.4. *Statistical analysis*

Regression analysis was used to determine leaf decay constants. Long term litter decomposition studies generally show a two phase pattern of mass loss, thus double (two-pool) exponential decay models often represent mass loss well (Olson 1963; Wieder and Lang 1982). Data was modelled with both the single ($y = Ae^{-kt}$) and double/two-pool ($y = Be^{-ct} + De^{-ft}$) exponential decay models (where y is the % original dry mass remaining at time t, *k* is the single exponential decay constant ($year^{-1}$), and A, B, c, D and f are constants). In a similar fashion to the pan-tropical study of Powers *et al.* (2009), the two-pool model did not improve the fit of the models in 99% of cases (data not shown), thus only the *k* values from the one-pool model were used in further analyses.

Factorial ANOVA was used initially to test for differences in mass loss on the data set with mass versus time and site as factors; however, strong heterogeneity of variances, even following transformations, did not permit this analysis. Mass loss values for the final collection (converted to % loss per year) were compared statistically using ANOVA following ln transformations, with Tukey poc-hoc multiple comparisons (SPSS v17). Litter exponential *k* values were modelled with best sub-set regressions to determine the environmental (climate and soil) and chemical (litter quality) controls on decomposition. The climate variables used were

as follows: MAP, MAT, MAPCV, real time rain (total over the course of the experiment, rain), % dry season days with 0 mm rainfall (DS0MM), SoilT, AirT and average leaf wetness in the dry season (LWDS). Soil data used were: total N, P, Mg, Ca, Na, TOC, sand, silt, clay (means for 0 - 10 cm and 20 - 30 cm depths). The climate decomposition index (CDI) (Lloyd and Taylor 1994; Adair *et al.* 2008) and the arc-tangent form of the CDI (CDI_{arc}) (Del Grosso *et al.* 2005) are also used. The CDI variables use the combination of temperature and moisture stress to predictive the climatic potential for decomposition, and have been shown to be useful in modelling global decomposition rates (Adair *et al.* 2008). See Appendix 3 for equations used to calculate CDI. Tree species richness were included in models of *in situ* decay.

To explain decomposition rates, best sub-set regressions (R project software, library: leaps) were performed with all environmental variables and separately using groups of variables: "soil", "climate" and "initial leaf chemistry". Pathways of effects were then determined from standardised linear regression coefficients for the best model variables, against *in situ* and control *k*, to show relative effects of the controls on decomposition. Decomposition rate was considered to be directly determined by climate, soil and initial leaf chemistry. Care was taken to not allow significantly cross correlated variables in the models that may have confounded relationships with decay rates (Petraitis *et al.* 1996). Model variables were chosen from the full suite potential explanatory variables; however, only one variable representing the same phenomenon (e.g. long term MAT vs real time MAT, the rainfall seasonality measurements etc.) was used. These were the best correlating variable with decay rate determined through bivariate correlation analysis and the outputs from the regression runs. In cases where further cross-correlation were noted following this,

Table 4.1. Initial chemical characteristics of litterbag contents ± 1 s.d. Control = *Archidedendron vaillantii* litter, others represent the values for in situ litter respective of each site. Shown is total nitrogen, phosphorus, carbon, calcium, magnesium, acid detergent fibre, acid detergent lignin, cellulose and total phenolics. Means followed by the same letter are not significantly different ($p > 0.05$) based on ANOVA with Tukey post hoc multiple comparisons (ANOVA, $p < 0.0001$ $F = 16.19$, $df = 40$).

SITE	N	P	C	Ca	Mg	Lignocellulose	Lignin	α-cellulose	Phenolics
Control	1.89±0.13^{f}	0.017±0.01^{a}	49.8±0.5^{bcd}	0.25±0.13^{a}	0.08±0.02^{a}	67.5±2.2^{f}	41.8± 2.2^{de}	29.0±0.9^{f}	0.81±0.14^{fg}
AU1	1.32±0.16^{cd}	0.061±0.01^{de}	48.7±1.7^{abc}	1.19±0.56^{bcd}	0.26±0.05^{cde}	58.6±2.5^{abcd}	34.7±1.5^{abcd}	21.3±2.2^{cde}	0.48±0.09^{abcef}
AU4	1.65±0.22^{e}	0.083±0.01^{f}	47.0±1.3^{a}	2.12±0.46^{e}	0.29±0.02^{e}	53.8±3.7^{ab}	30.5±4.5^{a}	21.5±1.2^{cde}	0.33±0.10^{ab}
AU6	1.46±0.30^{de}	0.062±0.01^{cde}	47.8±1.5^{ab}	1.43±0.62^{cd}	0.26±0.04^{cde}	57.2±2.1^{abcd}	34.1±2.1^{abcd}	22.2±1.3^{de}	0.44±0.03^{abc}
AU8	1.70±0.23^{e}	0.072±0.01^{e}	49.2±0.5^{abcd}	0.90±0.19^{abcd}	0.23±0.03^{cde}	54.3±3.2^{ab}	33.3±3.0^{abcd}	21.4±1.0^{cde}	0.50±0.07^{abcd}
AU9	1.25±0.09^{cd}	0.050±0.02^{bce}	50.2±1.3^{cd}	0.86±0.12^{abc}	0.27±0.02^{de}	56.1±3.8^{bcd}	33.7±3.1^{abcd}	21.8±1.4^{cde}	0.50±0.09^{abcd}
CU1	1.13±0.02^{abc}	0.043±0.001^{bcde}	47.8±0.8^{ab}	1.55±0.14^{d}	0.25±0.02^{cde}	54.5±2.0^{ab}	31.0±1.5^{ab}	21.8±1.2^{c}	0.61±0.04^{cdef}
CU4	0.85±0.07^{a}	0.024±0.001^{a}	50.1±0.6^{cd}	0.25±0.21^{a}	0.23±0.02^{bcde}	66.1±3.8^{e}	44.0±3.6^{e}	17.8±1.3^{ab}	0.80±0.08^{ef}
CU6	1.05±0.08^{abc}	0.038±0.01^{ab}	49.8±0.3^{bcd}	0.75±0.23^{ab}	0.27±0.03^{de}	61.7±2.2^{cde}	38.3±2.7^{d}	20.5±1.6^{bcde}	0.62±0.09^{cdef}
CU8	1.08±0.08^{abc}	0.039±0.001^{abc}	50.1±0.7^{cd}	0.72±0.17^{ab}	0.23±0.04^{bcde}	57.5±2.3^{bcd}	35.0±2.1^{abcd}	20.5±1.2^{bcde}	0.68±0.04^{def}
CU10	0.94±0.10^{ab}	0.032±0.01^{abc}	47.7±1.1^{ab}	1.21±0.16^{bcd}	0.29±0.01^{e}	53.3±2.7^{ab}	32.2±2.1^{abc}	18.9±1.4^{abcde}	0.73±0.09^{ef}
CU12	1.02±0.03^{abc}	0.039±0.001^{abc}	49.2±0.5^{bcd}	0.85±0.12^{abc}	0.26±0.01^{cde}	57.8±1.5^{bcd}	34.5±0.8^{abcd}	23.0±1.3^{e}	0.51±0.07^{bcd}
SU3	1.20±0.11^{bcd}	0.044±0.01^{abc}	48.9±0.5^{abcd}	1.25±0.29^{bcd}	0.20±0.02^{abc}	57.2±0.50^{abcd}	33.4±1.6^{abcd}	20.2±1.7^{bcde}	0.66±0.09^{d}
SU8	1.05±0.12^{abc}	0.043±0.01^{abcd}	48.8±1.0^{abcd}	1.29±0.34^{bcd}	0.14±0.06^{a}	61.9±1.4^{de}	36.2±1.1^{bcd}	22.2±0.8^{de}	0.29±0.11^{abcdef}
SU10	1.10±0.06^{abc}	0.040±0.01^{ab}	50.9±1.0^{d}	0.70±0.21^{ab}	0.17±0.02^{ab}	59.1±2.1^{bcd}	35.2±1.8^{abcd}	20.7±0.6^{bcde}	0.60±0.05^{cde}
WU9	1.16±0.15^{bcd}	0.041±0.001^{bcde}	50.7±1.1^{cd}	0.76±0.25^{ab}	0.23±0.02^{bcde}	51.4±2.5^{a}	31.4±2.0^{ab}	17.0±1.5^{a}	1.01±0.12^{g}
WU11	1.08±0.04^{abc}	0.038±0.001^{abcd}	49.2±0.6^{bcd}	0.63±0.20^{ab}	0.23±0.03^{bcde}	57.5±4.1^{bcd}	37.2±3.0^{cd}	19.7±1.0^{abcd}	0.64±0.06^{cdef}
WU13	0.93±0.06^{ab}	0.027±0.01^{ab}	50.2±0.4^{cd}	0.79±0.11^{abc}	0.21±0.01^{bc}	55.7±2.0^{abc}	33.9±1.4^{abcd}	19.1±0.7^{abce}	0.82±0.05^{fg}

models were then re-run with the cross correlated variables split into separate models.

The visual representation of the CAP analysis, simple linear regressions and bivariate correlations were used to explain the influence of environment on patterns and changes in nutrient and carbon fractions throughout the region occurring during decomposition.

4.3. Results

Mean annual precipitation (MAP) for the sites ranged from 3436 mm y^{-1} (AU1) to < 1500 mm y^{-1} (SU3 and CU6). However, total rainfall was well above the annual average for the time of this study, and significant rainfall events also occurred late in the study (i.e. after > 12 months, ~February - March 2009). Rainfall seasonality was generally lowest in the AU sub-region, and highest in the SU sub-region particularly SU3. Mean annual temperature (MAT) at these sites ranges from 24 ^{o}C (CU1) to 17 ^{o}C (WU13) (Appendix 1 and see Appendix 9 for climate data specific to the litterbag study period).

4.3.1. *Initial litterbag chemistry*

In the *in situ* samples, mean initial chemical components ranged from: N 0.85 (CU4) to 1.70% (AU8); P to 0.24 (CU4) to 0.72% (AU8); Ca 0.25 (CU4) to 2.12% (AU4); Mg 0.14 (SU8) to 0.29% (AU4); C 47.02 (AU4) to 50.89% (SU10); lignocellulose 51.41% (WU9) to 66.09% (CU4); lignin 30.48 (AU4) to 44.0% (CU4); α-cellulose 17.04% (WU9) to 23.04**%** (CU12) and total phenolics 0.33% (AU4) to 1.01% (WU9) (Table 4.1). N, P, Mg and Ca contents were generally higher on the AU

basalt sites, particularly AU4 and AU8. The control leaves had the highest initial N, among the lowest other nutrients (P, Ca and Mg) and highest carbon fractions (C, lignocellulose and lignin) and phenolics compared to all of the *in situ* leaves.

4.3.2. *Litterbag mass loss*

Mass loss was fastest overall for the *in situ* litter at AU4 (k = 2.15, 79.3% loss per year based on the final collection value), and slowest at WU13 (k = 0.62, 37.1% loss per year) (Table 4.2 and Figure 4.1.a). Generally the AU sites, particularly AU1, 4 and 6 along with CU10 decomposed the fastest, and the WU sites the slowest *in situ* (Table 4.2). For the control leaves (Table 4.3 and Figure 4.1.b), between site variability in mass loss was generally lower than in the *in situ* samples, as were decay rates. AU1 and AU9 had the fastest control mass loss rates: k = 1.13 and 0.91; 71.5% and 68.2% lost per year. The SU3, 9, 10 and WU13 and CU10 and CU12 control showed the least mass loss (Table 4.3). Mass loss generally followed exponential decay, however a pulse of more rapid mass loss between ~350 days and the end of the experiment (2nd wet season) was seen in some treatments, especially CU controls (Figure 4.1.b).

Coefficients of variations for one-pool exponential decay were 65 - 96% for all regressions (Table 4.2 and Table 4.3). *In situ* and control k values related to the % mass loss per day at the 6th collection (linear $r^2 > 0.90$, $p < 0.001$), suggesting the k values were representative of the datasets. Cross correlation was common between variables used in the best sub-set regressions (Appendix 4 for correlation tables).

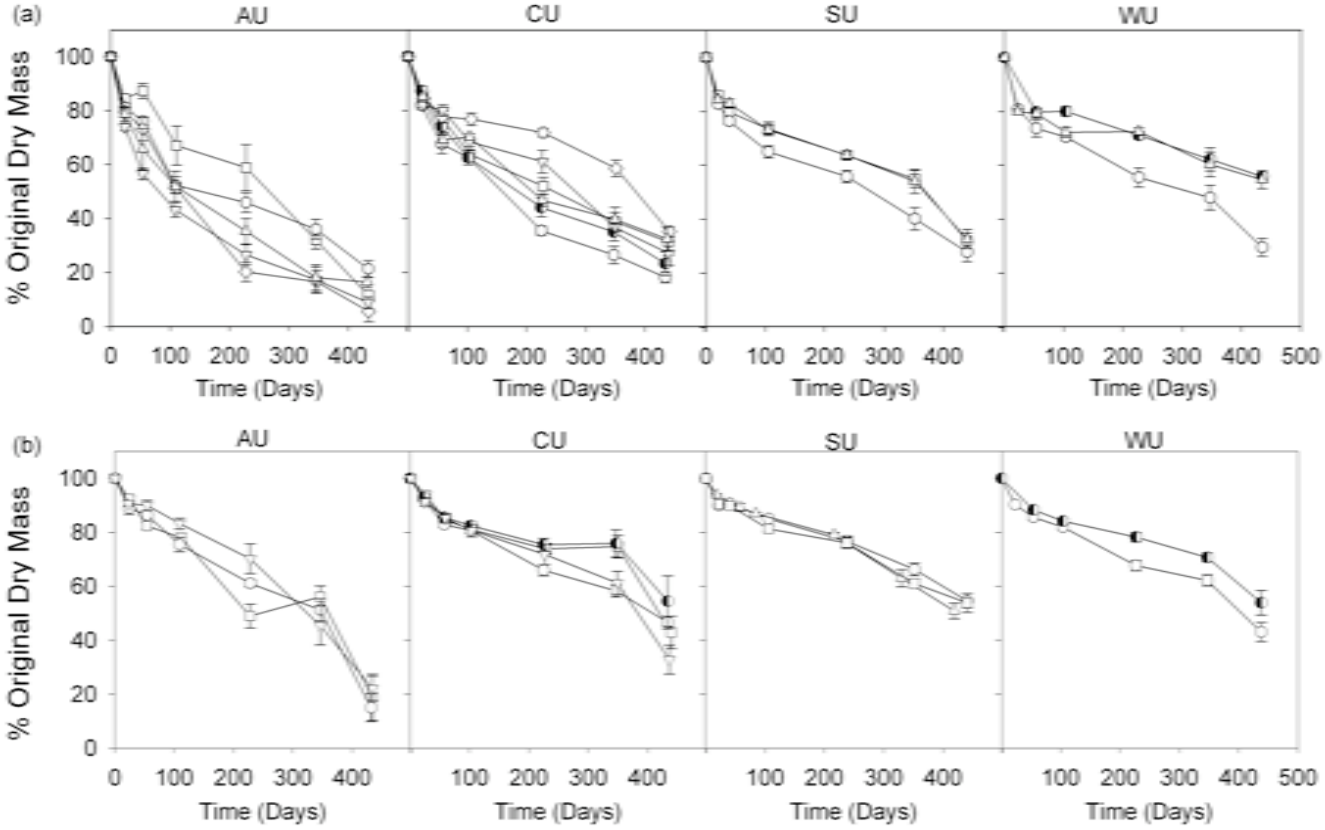

Figure 4.1. Mass loss as mean % original dry mass ± 1 s.e. (n = 5) remaining over time of (a) *in situ* (representative of litterfall at the site) and (b) control *Archidendron vaillantii* leaves in litterbags decomposed in Australian tropical rainforest. Sites came from four sub-regions: AU: Atherton Uplands; CU: Carbine Uplands; SU: Spec Uplands; WU: Windsor Uplands. Sites are from different (approximate) elevations within each sub-region: □ - 100 m a.s.l. (CU and AU) and 300 m a.s.l. (SU); ◇ - 400 m a.s.l. (AU and CU); ▽ - 600 m a.s.l (AU and CU); △ - 800 m a.s.l. (AU and CU) and 900 m a.s.l. (WU); ○ - 900 m a.s.l. (AU), 1000 m a.s.l. (CU and SU) and 1100 m a.s.l. (WU); ◐ - 1200 m a.s.l. (CU) and 1300 m a.s.l. (WU).

Table 4.2. Decomposition data from *in situ* litterbag study at sites in Australian tropical rainforest. Shown are the sites; number of days of exposure on the soil surface; r^2 from first exponential decay regression analysis; decomposition rate (*k*) from first exponential decay function; actual % dry mass remaining ± 1 s.d. at the end of experiment; standardised (time) % loss per year (based on value at ~440 days). Means followed by the same letter are not significantly different based on ANOVA ($p > 0.05$) with Tukey post hoc multiple comparisons. ANOVA 440d: df = 16 and 67, $p < 0.001$, $F = 17.78$.

Site	Days	1exp r^2	1exp *k*	% remaining end ± s.d	% loss y^{-1} ± s.d (~440d)
Atherton					
AU1	434	0.82	1.20	11.6±2.5	$74.4±2.1^{efg}$
AU4	435	0.94	2.15	5.49±7.5	$79.3±6.3^{g}$
AU6	434	0.92	1.93	8.82±4.9	$76.7±4.2^{fg}$
AU8	432	0.86	1.57	16.4±4.4	$70.6±3.7^{defg}$
AU9	434	0.88	1.10	21.3±7.0	$66.2±5.9^{bcdefg}$
Carbine					
CU1	439	0.90	0.91	31.3±11.3	$57.1±9.4^{bcd}$
CU4	435	0.81	0.55	35.2±4.1	$53.7±3.4^{b}$
CU6	434	0.90	0.91	27.0±9.9	$60.6±8.2^{bcde}$
CU8	432	0.89	0.88	32.4±10.3	$56.5±8.6^{bc}$
CU10	434	0.95	1.39	18.2±4.6	$68.8±3.9^{cdefg}$
CU12	434	0.92	1.13	23.3±9.8	$64.5±8.3^{bcdef}$
Windsor					
WU9	435	0.70	0.33	54.6±7.5	$38.1±6.3^{a}$
WU11	435	0.85	0.77	29.6±7.4	$59.1±6.2^{bcd}$
WU13	435	0.79	0.37	22.8±3.2	$37.1±2.7^{a}$
Spec					
SU3	440	0.87	0.62	32.0±6.4	$56.4±5.3^{bc}$
SU8	440	0.86	0.66	32.7±7.8	$55.9±6.5^{bc}$
SU10	440	0.90	0.84	27.9±8.2	$59.9±6.8^{bcd}$

Table 4.3. Decomposition data from control (*Archidendron vaillantii*) leaf litterbag study in Australian tropical rainforest. Included sites are the same as in Table 2 except Spec 900 site. See Table 1 for variable definitions. Means followed by the same letter are not significantly different ($p > 0.05$) based on ANOVA with Tuckey post hoc multiple comparisons. 440d df = 11 and 51, $F = 9.190$ $p < 0.001$.

Site	Days	1exp r^2	1exp k	% end ± s.d	% loss y^{-1} ± s.d
Atherton					
AU1	434	0.79	1.13	18.88±19.1	68.23±16.05^{c}
AU6	434	0.81	0.95	22.15±8.9	65.47±7.51^{bc}
AU9	434	0.84	0.91	14.99±10.4	71.50±8.71^{c}
Carbine					
CU1	439	0.68	0.47	42.95±13.4	47.43±11.11^{ab}
CU4	434	0.79	0.66	32.82±12.1	55.73±10.00^{abc}
CU10	434	0.94	0.29	46.60±5.2	44.91±4.39^{a}
CU12	434	0.65	0.33	54.46±16.2	41.48±10.63^{a}
Windsor					
WU11	435	0.91	0.55	43.03±7.8	47.80±6.57^{ab}
WU13	435	0.78	0.40	53.89±10.2	37.55±9.16^{a}
Spec					
SU3	440	0.90	0.44	53.84±7.8	38.29±6.44^{a}
SU9	419	0.91	0.51	50.87±6.5	42.80±5.63^{a}
SU10	440	0.91	0.40	54.62 ± 6.0	37.64±4.95^{a}

The control *k* values were explained best by dry season rainfall (DS0MM), MAT and soil P (model $r^2 = 0.71$, res. s.e. = 0.15, n = 12, Figure 4.2.a and Appendix 5 for regression statistics). The same variables were included in the models with climate and soil treated separately (climate model $r^2 = 0.63$ and residual s.e. = 0.17; soil model $r^2 = 0.52$ and residual s.e. = 0.20, respectively). None of the three variables were significantly cross-correlated (Appendix 4, $p > 0.24$). Alone, MAT was not a significant predictor of *k* ($p = 0.21$). Standardised regression coefficients for decomposition rate independent of litter quality were in order of effect size, DS0MM (-0.560) > Soil P (+0.355) > MAT (+0.280). DS0MM was correlated

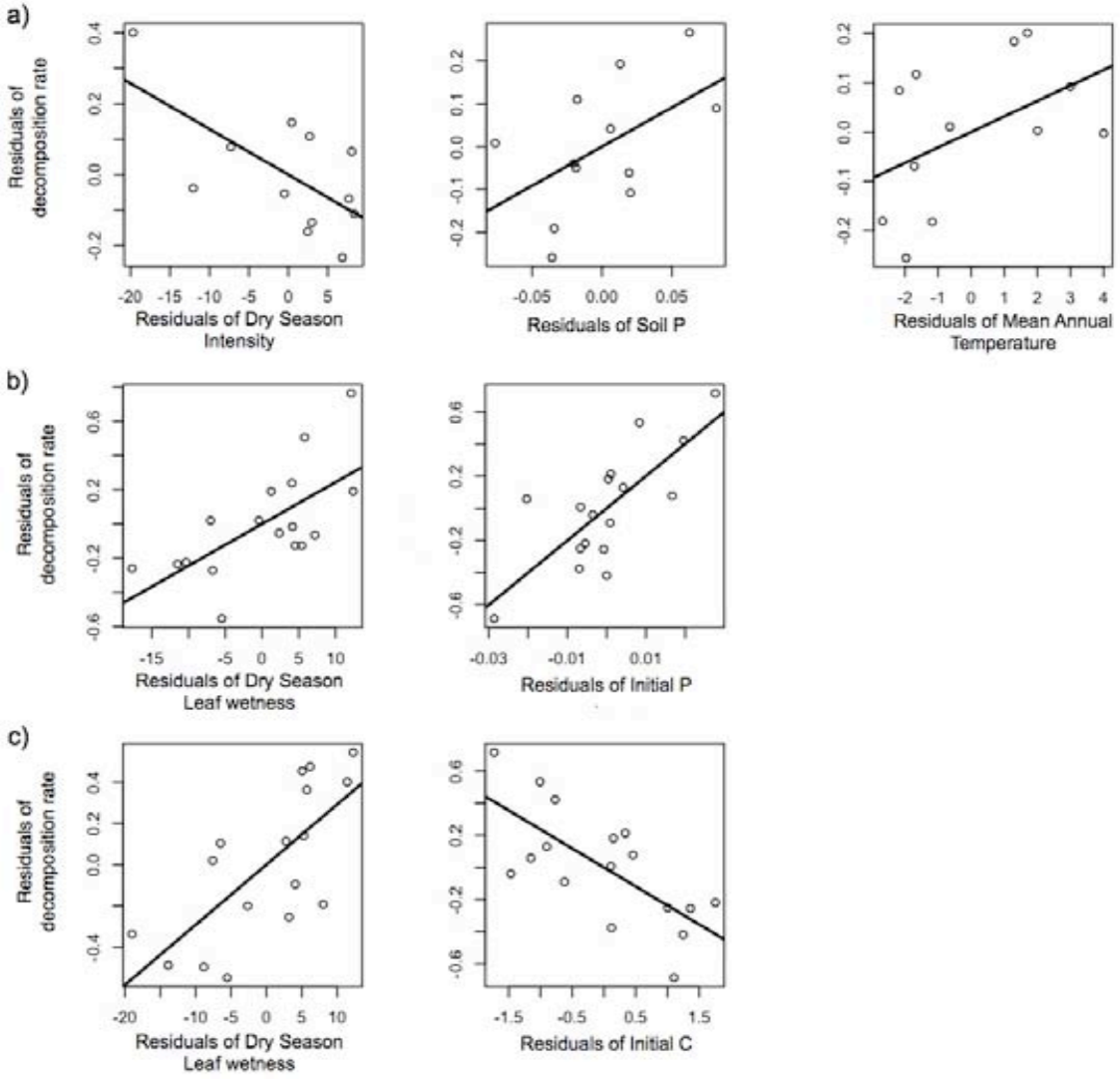

Figure 4.2. Partial plots from best sub-set multiple linear regression analysis of leaf decomposition rates, a) control leaf litter decay rate ~ mean annual temperature + % dry season days with 0 mm rainfall + soil P, model $r^2 = 0.71$, $p < 0.001$; b) *in situ* leaf litter decay rate ~ average dry season leaf wetness + leaf litter initial phosphorus, $r^2 = 0.78$ $p < 0.001$ (model 1); c) in situ leaf litter decay rate ~ average dry season leaf wetness + leaf litter initial carbon, $r^2 = 0.75$, $p < 0.001$ (model 2).

significantly with MAP ($r < 0.001$). CDI and CDI_{arc} were not significant predictors of control or *in situ* litter decay ($p > 0.05$).

With variables split into class groups the *in situ* models contained: Initial chemistry: Mg, P and C (model $r^2 = 0.78$, res. s.e. = 0.24, $p < 0.001$); climate: MAP and LWDS (model $r^2 = 0.72$, res. s.e. = 0.27, $p < 0.000$) and soil: soil P and soil Na (model $r^2 = 0.54$, res. s.e. = 0.34, $p < 0.001$) (Appendix 4). Post-hoc analysis showed initial P and C were significantly cross correlated despite this having no effect in the best sub-set regression ($p = 0.03$). LWDS was not correlated with either of the included leaf chemical variables, ($p > 0.05$). Thus, two models with P and C treated separately against LWDS were calculated, with the effect of P greater than LWDS (+0.595 and +0.434 respectively, $r^2 = 0.78$ $p < 0.001$, Figure 4.2.b and c), and the effect of LWDS greater than C (+0.540 and -0.526 respectively, $r^2 = 0.75$, $p < 0.001$). Thus effects on *in situ k* were in the order, initial P > dry season moisture > initial C. The initial C:P ratio combined with LWDS, had an $r^2 = 0.72$, $p < 0.001$.

Initial P correlated significantly with leaf N and Ca (positive), lignin, α-cellulose, phenolics, C:N, C:P, lignin:N, lignin:P, lignocellulose:N and lignocellulose:P (negative) ($p < 0.05$) (Appendix 4), but was a better predictor of *k* than any of these variables. Soil TOC was significantly correlated with control *k* ($p < 0.001$). Tree species richness was not significantly correlated with *in situ* decay rate ($p = 0.60$), and did not significantly contribute to the models.

4.3.3. *Leaf chemical dynamics*

Canonical analysis of the NIR spectra for both litterbag treatments provided dimension reductions of the principal component axes representing chemical changes

during decomposition. This produced a map of the NIR spectral (chemical) changes in leaf litter. For the control, five principle components explained 99% of the variability, which was reduced to two CAP axes (Figure 4.3.a, $p = 0.0001$, $\delta^2 = 0.86$ and 0.20 respectively) from m = 4 PCA components. The *in situ* PCA had seven principal components explaining 99% of the spectral variability, and was reduced to two CAP axes (Figure 4.3.b, $p = 0.0001$, $\delta^2 = 0.82$ and 0.36 respectively) from m = 4 PCA components. As mass loss progressed, samples were forced from left to right in the ordinations, representing physical and chemical changes in the leaves. The NIR spectral variability increased with decomposition rate (samples forced to top right of both Figure 4.3 CAP plots). Actual plots of changes in chemical components over time are shown in Appendix 6.

N, P and Ca immobilisation (increases) were evident with loss of mass (Figure 4.3.a and b, left to right progression of samples with mass loss) (Appendix 6), with increases in concentrations (cf. absolute amounts) of these elements generally occurring. This is confirmed by linear regression correlations for mass against % element remaining at that time, r^2's: N = 0.28, P = 0.79 and Ca = 0.59, all $p < 0.001$ for control litter; %N = 0.19, %P = 0.26, $p < 0.001$ for the *in situ* litter. N increases were generally less pronounced at the sites that had faster decomposition rates (Figure 4.3). Only one site (AU6, control) showed evidence of mineralisation of N towards the end of the experiment (between ~225 and ~350 days). An early leaching phase was evident in the control and the *in situ* litters at some sites for N, P and Ca (Appendix 6). P increases in the control were strongly correlated with decomposition rate, i.e. *k* versus % original P after 350 days, $r^2 = 0.85$, $p < 0.001$.

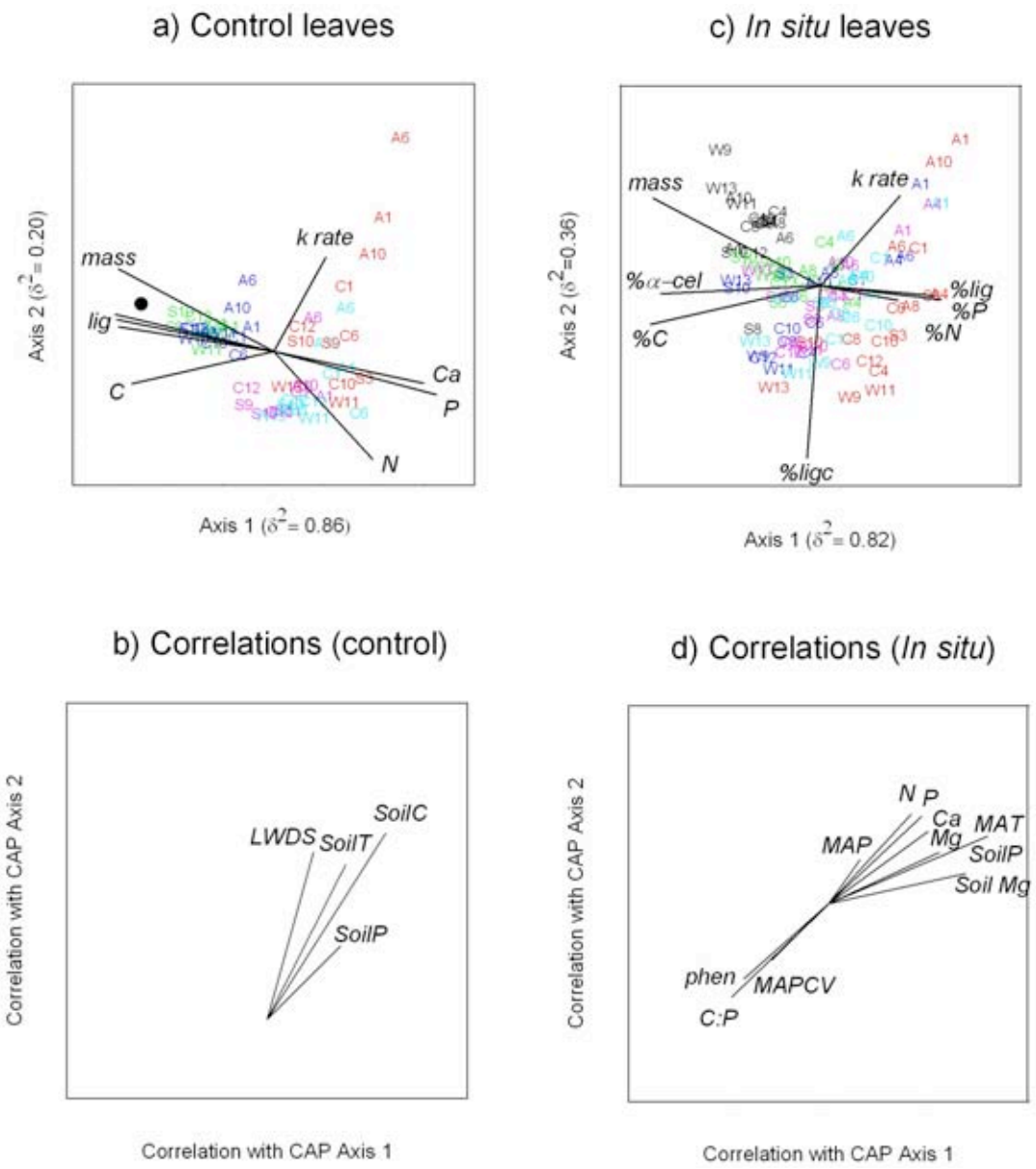

Figure 4.3. Chemical changes and influence of litter quality and environment on leaf litter during decomposition in Australian tropical rainforest from near infrared spectral analysis, (a) and (b) control leaf litter (independent of litter quality); (c) and (d) *in situ* leaf litter. Plots a) and c) represent canonical correlations of principle component analysis run on the spectra (1st derivative with scatter correction), reducing the number of PC factors to those correlating significantly with groups related to site and time exposed (total 350 days). Sites shown are represented by two letters: first is the sub-region (A = Atherton Uplands; C = Carbine Uplands; S = Spec Uplands; W = Windsor Uplands), second is the elevation (e.g. 1 = ~ 100 m a.s.l, 12 = ~1200 m a.s.l.). Colors represent time exposed (black = initial composition; green = ~ 20 days; blue = ~50 days; pink = ~110 days; cyan = ~ 225 days; red = ~350 days). Correlations of the axes with mass loss (mass), decomposition rate (*k*), C, N, P, Ca and lignin (lig), lignocellulose (ligc) and α-cellulose (α-cel) (lig represents all three lignocellulose components in a), as actual concentrations (a) and % original contents (b), along with correlation with environmental variables (c) and with initial chemical composition and environment (d) are shown. See text for full variable definitions.

With higher temperature, more pronounced decreases in leaf C (as % original content) occurred (best correlations: control SoilT linear correlation with C $r^2 = 0.15$, $p = 0.003$, Figure 4.3.b; *in situ* MAT $r^2 = 0.21$ $p = 0.003$ Figure 4.3.c). *In situ* % original lignocellulose also decreased more in areas with higher MAT ($p = 0.011$, Figure 4.3.c). Control C and lignin losses were linearly related to DS0MM (C $r^2 = 0.66$, $p = 0.001$; lignin $r^2 = 0.54$, $p = 0.007$).

Carbon fractions (lignocellulose, lignin and α-cellulose) and C generally decreased with mass (control C verses mass: linear r^2's of lignocellulose = 0.73, lignin = 0.72, α-cellulose = 0.79 and C = 0.52, all $p < 0.001$). The only exception was lignin in the *in situ* litter, which generally increased relative to *k*. *In situ* % original P was linearly positively correlated with % original lignin ($r^2 = 0.35$, $p < 0.001$), and % original N ($r^2 = 0.14$, $p < 0.001$). Lignocellulose in the *in situ* leaves increased in the early stages of decomposition, particularly when mass loss was high (e.g. AU), and then decreased towards the end of the experiment, more so with faster *k* rates (Figure 4.3.c and Appendix 6).

Carbon fractions were significantly negatively correlated with nutrient content (decreased with greater immobilisation) during decomposition e.g. control: N, $r^2 = 0.15$ with lignocellulose; 0.14 with lignin and 0.33 with α-cellulose; P, $r^2 = 0.96$ with lignocellulose, 0.87 with lignin and 0.96 with α-cellulose; and Ca, $r^2 = 0.86$ with lignocellulose, 0.75 with lignin and 0.74 with α-cellulose (Figure 4.3.b) and in the *in situ*: N, $r^2 = 0.29$ with α-cellulose, $r^2 = 0.10$ with C; $r^2 = 0.57$; $r^2 = 0.25$ with C (Figure 4.3.c).

In situ overall % original C also decreased more with high soil Mg ($p < 0.001$), and α-cellulose with high soil P ($p < 0.001$). N contents of the control litter were negatively correlated with soil organic carbon ($p = 0.028$), but soil N, P, Mg or

Ca were not correlated significantly with changes in any of the chemical components in the control bags ($p > 0.05$).

Lower initial total phenolics and higher initial P were correlated with greater C ($r^2 = 0.10$ and 0.11 respectively), and α-cellulose ($r^2 = 0.20$ and 0.17 respectively) losses ($p < 0.001$). Similar relationships with C loss also existed for initial N, Mg and Ca, however correlations were lower or not statistically significant ($p < 0.05$). Initial C:P ratio was also a predictor of carbon loss ($r^2 = 0.14$, $p = 0.012$).

MAP and dry season moisture (DS0MM, MAPCV and LWDS) were not significantly correlated with changes in any of the nutrients (N, P or Ca) in either treatments ($p > 0.05$). In the *in situ* litter samples, higher MAP related to greater α-cellulose decreases (linear $r^2 = 0.15$, $p < 0.001$).

4.4. Discussion

This work notably adds to global litter decomposition data sets for the tropics, as Australian tropical forest litter decomposition is conspicuously absent from both tropical and global analyses (Gohlz *et al.* 2000; Liski *et al.* 2003; Adair *et al.* 2008; Powers *et al.* 2009). The most significant controls on leaf decomposition dynamics in the Australian wet tropical (AWT) rainforests were a combination of initial litter quality (especially phosphorus), dry season rainfall and moisture inputs (including cloud interception), soil fertility (especially phosphorus), and temperature. These trends are in line with global decomposition dynamics shown at many scales (Aerts 1997; Cornwell *et al.* 2008; Adair *et al.* 2008; Zhang *et al.* 2008; Powers *et al.* 2009). The consequences of changes in these controls for litter dynamics and forest function in a changing climate are notable. Future climate scenarios suggest higher

temperatures, raised cloud bases (Pounds *et al.* 1999; Foster 2001) and increasing dry season intensities for the region studied (Suppiah *et al.* 2007; Suppiah *et al.* 2009) and other seasonally wet tropical forests (Borchert 1998). These scenarios relate to changes in vegetation community structure (Hilbert *et al.* 2001) and reductions in rainforest biodiversity (Williams *et al.* 2003). Below, the broader questions posed in this work are answered.

Leaf litter decay rates in AWT rainforests show a range of values similar to those found over a wide variety of biomes at a global scale. However, the decay rates obseved in this work were generally slower than the average for tropical forests (pan-tropical study average decay rate = 3.08 y^{-1}, compared to 1.02 y^{-1} for the *in situ* leaves in this study) (Powers *et al.* 2009). These discrepancies are likely to be due to a combination of very poor soils, highly seasonal rainfall and possibly the higher latitude of the AWT than many of the pan-tropical study sites. In comparison to the global data set for evergreen naturally senesced leaves, (Long Term Intersite Decomposition - LIDET dataset, Gohlz et al. (2000), the most rapid mass loss in AWT occurred at rates similar to those of some tropical forests (e.g. Atherton lowlands and lowland Central America); however, the slowest observed here (e.g. Windsor uplands) were closer to those occurring in temperate conifer forest, or much drier tropical forest (e.g ~700 mm rainfall y^{-1}) (Gohlz *et al.* 2000). The rainforest decay rates of this present study were mostly faster than those occurring in tall open *Eucalyptus grandis* forest (wet sclerophyll) (Parsons and Congdon 2008), except in the case of the upland Mt Windsor sites, and the nutrient-poor Carbine 400 m elevation site.

Simple climate and litter quality based models describe litter decomposition well at many spatial scales (Trofymow *et al.* 2002; Liski *et al.* 2003; Adair *et al.*

2008; Harmon *et al.* 2009). The models here confirm the importance of litter quality and moisture (esp. seasonality), like in global data sets, and for this regional scale study models are of comparable predictive power (Liski *et al.* 2003; Adair *et al.* 2008; Zhang *et al.* 2008). While the combination of temperature and moisture seasonality effects on decay expressed by the climate decomposition index (CDI) (Taylor *et al.* 1989; Del Grosso *et al.* 2005; Adair *et al.* 2008) predicts decomposition well for widely varying biomes (Adair *et al.* 2008), as seen here, like Powers et al. (2009), CDI was not a predictor of leaf litter decomposition rates in tropical forests. This may be due to lower temperature ranges in the tropics (Powers *et al.* 2009). However, the temperature effect for the control leaf litter suggests the range of MAT in the elevational distribution of these sites was large enough to significantly influence decomposition rates.

Temperature effects on leaf litter decomposition were most significant for C dynamics and to a lesser extent lignocellulose. This promotion of C and lignocellulose mineralisation by temperature may be explained by heightened microbial activity in warmer conditions (Donnelly *et al.* 1990), and also potentially greater litter invertebrate abundance (i.e. in lowlands) (Olson 1994). Differences between sites due to other factors not quantified here, such as water soluble C fractions could also have played a role (Swift *et al.* 1979; Wieder *et al.* 2009). Soluble C fractions are an under studied component in decomposition studies, and have been shown to predict mass loss in other wet tropical forests (Wieder *et al.* 2009). Nevertheless, the combination of high temperatures and seasonal moisture inputs leads to faster carbon and lignocellulose losses from decomposing litters in these forests, potentially driven largely by increased microbial activity in more favourable climatic conditions (Donnelly *et al.* 1990).

The general substrate control hypothesis on decomposition, support for which has been found by many authors at varying spatial scales (Meentemeyer 1978; Melillo *et al.* 1982; Taylor *et al.* 1989; e.g.Vitousek *et al.* 1994; Aerts 1997; Cornwell *et al.* 2008), generally held true within the AWT region, especially in regards to phosphorus (this chapter) along with total phenolics and carbon (Chapter 2). However, climate and in particular moisture seasonality and general moisture inputs (e.g. leaf wetness variable) were significant influences on mass loss (Figure 4.2). For instance, independent of litter quality, moisture and moisture seasonality were the strongest predictors of decomposition rate, only slightly more so than soil P. Moisture seasonality controls decomposition rates in other tropical rainforests (Wieder and Wright 1995), and generally higher and more consistent annual moisture leads to greater microbial biomass and activity in decomposing litters (Donnelly *et al.* 1990). Powers et al. (2009) showed that litter decomposition over the tropics varies linearly with mean annual precipitation. The results from tropical Australia confirm this trend to an extent, because rainfall seasonality is strongly correlated with total annual precipitation throughout the region. However, as occurred the years of this study, dry season rainfall can be low, while annual rainfall exceptionally high, due to substantial falls in the wet (e.g. the SU3 site total rainfall over the 420 days of the study was > 4000 mm but nearly half of this total fell in two months of the 2008-2009 wet season). When litter quality was taken into account, the P content of the litter provided the strongest regional promotion of mass loss. The combination of constantly wet conditions and high litter P, and also soil P, provides very favourable conditions for decomposition in these forests.

Generally if the demand for nutrients from microbes occurs quicker than mineralisation, then nutrient limitation is likely to constrain decomposition (Vitousek

and Howarth 1991). Thus, the > 12 month nutrient immobilisation that occurs throughout the Australian wet tropics is a sign of limitations by nutrients on decomposition processes. This was seen at all sites, including the relatively nutrient-rich sites on basalt (AU). N contents of litterfall were generally high in AWT, while P contents were very low (also see Chapter 3 of this thesis), even for tropical rainforests (Vitousek and Sanford 1986). Litterfall throughout the region is characterised by high leaf litter N:P ratios, especially those on highly weathered soils, (e.g. CU, SU and WU) (Herbohn and Congdon 1998; Chapter 3 of this thesis). High N:P both in fresh leaves and litter suggests P limitations, and is a general trait of tropical rainforests globally (Vitousek 1984; Vitousek and Farrington 1997; Reich and Oleksyn 2004). Considering this, and the strong explanatory power of P in litter and soil found in this study for most aspects of decomposition, the case for P limitation is very strong, adding to evidence of general P limitation in tropical rainforests (Vitousek 1984; Vitousek and Sanford 1986; Herbert and Fownes 1995; Saker *et al.* 1999; Hobbie and Vitousek 2000). Trends regarding P promotion of decomposition rates are a common feature in tropical rainforests (Vitousek 1998; Hobbie and Vitousek 2000; McGroddy *et al.* 2004b; Parsons and Congdon 2008). Here, this occurred firstly due to higher P concentrations in litter produced on soils with high available P and faster decomposition rates, and secondly, as seen through strong soil P effects on the breakdown of the control litter, through generally more fertile soil conditions. Correlations between soil fertility and microbial activity have been found elsewhere, with generally higher growth rates of bacteria in more fertile soils (Torsvik and Øvreås 2002). Element deficiencies at any stage of decomposition, both in the soil and on the litter substrate, limit microbial activity and litter breakdown (Swift *et al.* 1979; Lavelle *et al.* 1993). Also, less consistent moisture

throughout the year exacerbates these effects at least in terms of mass loss. In the AWT initial P is an indicator of a whole suite of potential litter quality inhibitors and promoters of decomposition (e.g. N, lignin, Ca, Mg, phenolics, C:N, C:P, lignin:N, lignin:P, lignocellulose:N, lignocellulose:P); however, initial P alone gave a greater correlation with leaf decomposition rate than any of these variables. Despite these broad trends, the findings of Kaspari *et al.* (2008) show that the existence of a primary limiting nutrient underlying ecosystem processes may not apply to tropical forests, and interactions among suites nutrients are responsible for directly controlling litter decay. The occurrence of strong Ca immobilsation at all sites is the present study is some testament to this. Similarly, the results of Chapter 2 of this thesis show that the whole organic chemical make up of litter is highly correlated with decomposition rates. Notwithstanding, P is certainly in the lowest relative abundance in litter and soils in these forests, and tight P cycling strategies such as reabsorption prior to litterfall is significant in tropical rainforsts (Herbohn 1993; Gleason *et al.* 2009).

Soil nutrients other than P, e.g. soil N and cations (e.g. Mg), also promoted decomposition particularly through losses seen in lignocellulose (soil N) and total C (soil Mg). Both of these nutrients, like litter quality, were also positively correlated with soil and leaf litter P. Sodium on the other hand was not significantly related to soil P, but is an essential nutrient to detritivores, and has been shown to directly limit litter decay in other tropical forests (Kaspari *et al.* 2009). While not a significant determinant of leaf litter decay in the AWT, soil Na content is correlated with whole litter layer turnover rate and overage annual litter standing crop in Australian tropical rainforests (S. Parsons, unpublished data; Chapter 6 of this thesis). The same trend applies to leaf litter initial C as a strong predictor of decomposition rates, and also for

overall litter layer (litter standing crop) dynamics (S. Parsons, unpublished data; Chapter 6).

Seasonal drought has a strong presence in many Australian tropical rainforests, as with many other tropical areas. Here, the effects of rainfall seasonality are also periodically elevated by El Niño and southern oscillation effects (Chiew *et al.* 1998). In AWT, the timing of peak litterfall at the start of the wet season is poised to take advantage of moisture conditions that favour decomposition. Leaf wetness, particularly in the dry season, along with rainfall in the dry season, are useful predictors of rainforest decomposition rates. Leaf wetness for instance, emulates the surface of a leaf (under cover from rainfall), while measuring the presence of surface moisture and the duration of moisture on the surface. Low readings relate to conditions of high evaporative water loss, thus low dry season values may relate to more drying out of the litter layer. Also, high readings may relate to periods of intense cloud interception/striping water inputs, which are particularly significant in these forests (McJannet *et al.* 2007). More consistent moisture throughout the year contributes greatly to faster decomposition rates in seasonal tropical rainforest such as in the AWT (Cornejo *et al.* 1994; Lodge *et al.* 1994). Seasonality is also the principle driver of rainforest distributions and rainforest types in AWT, along with other locations globally (Borchert 1998).

Many of the sites in this study fall at the wet end of the spectrum of tropical climates (> 2000 and > 2500 mm p.a. for 10 and 6 of the 17 *in situ* sites respectively), especially in the year of this study where some very high rainfall totals occurred. These wetter locations also include the majority of the faster mass losses quantified here. This work, and a recent study in similar environs (Wieder *et al.* 2009), back up the premise, that in very wet tropical rainforests at least in the range

seen here (up ~ 4000 mm p.a.), the effect of soil anoxia and decreased microbial activity in slowing decomposition, as suggested by Schuur (2001), may be somewhat uncommon, at least in forests with relatively well drained soils such as most of the very wet AU sites (Wieder *et al.* 2009). Sites with rainfall so high that it may limit decomposition in such a way however, may be found in AWT on the highest peaks that were not included here, which can receive MAP in excess of 9 m y^{-1}.

The concentrations of the recalcitrant lignocellulose portions generally decreased as decomposition continued, and nutrients were taken up and immobilised by microbes. N, P and Ca increases correlated negatively with decreases in this recalcitrance (i.e. lignin and lignocellulose), as did higher temperatures and more consistent rainfall. Promotion of lignin degradation by N fertilisation has been shown in another tropical site (Hobbie 2000). Importantly here, the greater correlation of P with changes in this recalcitrance suggests potentially stronger P promotion of lignocellulose decomposition in these forests, e.g. than N. The initial lignocellulose (lignocellulose and lignin) inhibited decomposition, especially seen through decreasing immobilisation trends in N and P. The inhibitory properties of high lignocellulose contents on decomposition, and their effect on lowering microbial immobilisation rates and microbial productivity, and overall substrate mineralisation rates, are well documented (Melillo *et al.* 1982; Salamanca *et al.* 2003; Parsons and Congdon 2008). The increases in *in situ* lignin could have been due to humified soil substances interfering with the measurements (see below), and or actual lignin not decomposing as rapidly as the remainder of the dry matter. The latter of these occurred in the *in situ* leaves, coinciding with greater P immobilisation (e.g. positive correlation between % original P and % original lignin). Any differences in the control/*in situ* dynamics could be attributed to the lower nutrients and very high

recalcitrant fractions in the controls, or the effects of using homogenous litter types on decomposition dynamics in litterbags (Gartner and Cardon 2004), although evidence for the latter is lacking in this data set, and potentially insignificant (Hector *et al.* 2000; Wardle *et al.* 2006). There may have also been ligninolytic fungal associations with the *A. vaillantii* leaves that were not present in high (effective) abundance in the mixed *in situ* leaves (Osono 2007). Fragmentation of the samples, and therefore some losses from the litterbags became evident especially between the final two collections (2nd wet season). While this may represent inaccuracies in the litterbag method, it also suggests the movement of a pulse of heavily decomposed fine (< 2 mm) organic matter to further down into the litter layer in the second wet season, and important soil C formation. Regarding the lignocellulose, lignin and α-cellulose changes during decomposition, it should be noted that these measures potentially include compounds with similar properties that build up during decomposition (mainly humic substances produced by soil organisms) that differ from true lignocellulose. This is due to the proximate nature of their quantification (McClaugherty and Berg 1987; Salamanca *et al.* 1998). It has been suggested however, that non-lignocellulose like substances only make a minor contribution in masking lignin decay, so the acid detergent values probably reflect actual lignocellulose (Fioretto *et al.* 2005).

4.5. Conclusion

The rainforests of the Australian Wet Tropics contain a wide range of conditions for mineral cycling and decomposition dynamics. The data here suggest nutrient limitation and litter quality controls on nutrient cycling over the entire region.

Despite this, moisture seasonality drives much of the variability in decomposition dynamics in these forests. Dry season intensity controls many aspects of ecosystem function here, and also rainforest distributions in AWT (Hopkins *et al.* 1993), and in other tropical rainforests globally (Borchert 1998). Decreased moisture inputs in the dry season alone under future climates may cause a slowing of decomposition rates in these forests; however, increased temperatures could have an opposite effect, causing decreases in litter duration times on the soil surface. Modelling of the sensitivity of litter processes to climate change predictions may help disentangle the effect of both increasing temperatures and decreasing dry season rainfall on litter duration on the soil surface. This is the focus of Chapter 7 of this thesis.

Chapter 5. Volume measurements for quicker determination of forest litter standing crop

(Accepted for publication [*2009, Journal of Tropical Ecology, 25, 665-669, Short Communication*])

Litter standing crop (LSC) is the quantity of plant detritus on the floor in forested environments. Knowledge of LSC is important in understanding many ecological phenomena. These include studies of litterfall, decomposition/litter turnover rates and nutrient cycling (Anderson and Swift 1983; Dent *et al.* 2006), general plant performance (Benitez-Malvido and Kossmann-Ferraz), other ecosystem processes such as the effects of fire (Odiwe and Muoghalu 2003) and fauna (Levings and Windsor 1985; Frith and Frith 1990; Giaretta *et al.* 1999). The determination of accurate annual average LSC data, may require monitoring over long periods due to seasonality and sometimes sporadic nature of litterfall and decomposition rates (Clark *et al.* 2001b). Furthermore, the effects of topography and water movement create the need for both representative site selection and sufficient spatial coverage.

Standard methods for LSC quantification typically involve removing quadrats from the site and determining dry weight (Anderson and Swift 1983; Spain 1984; Goma-Tchimbakala and Bernhard-Reversat 2006). Less common approaches include measuring litter depth, or weighing LSC on site and removing subsamples that are dried in the laboratory and the moisture component subtracted (Day Jr 1979; Nascimento and Laurance 2002). Generally 0.25 – 1 m^2 quadrats (Edwards 1977; Proctor *et al.* 1983; Spain 1984; Scott *et al.* 1992; Songwe *et al.* 1995; Nascimento and Laurance 2002), or sometimes larger (Tanner 1981) are sampled, with intensities

varying widely from two to four times per year to monthly collections. Replication is dependant on logistics and the goals of the study, but adequacy of sampling is usually unknown. The approach of taking samples from the site to determine dry weights has drawbacks in regard to the time and effort required for accurate analyses, particularly when numerous sites are being studied. Removing litter from the site also creates disturbance with possible carry-on affects to other processes that may be of interest. Significant effort can be necessary for drying and weighing following the fieldwork. The method of subsampling to determine moisture content can also be problematic, as many samples may be needed to accurately cover the range of moisture within the litter layer temporally and spatially. Most importantly, logistical demands inherent in these commonly used methods limit the capacity of researchers to sample spatial and temporal variability in the litter layer, which can be particularly high at most scales of interest and change seasonally (Proctor *et al.* 1983).

A new method for the determination of LSC has been developed here, using measurements of volume, calibrated with dry-weight data. The method is logistically less demanding thereby permitting greater replication and spatial coverage of LSC in the field. An added bonus is that removal of LSC from the site is not required. This method is designed for applications where total LSC is required only and a detailed breakdown of the various components of litter (e.g. leaves, stems, flowers, fruit) is not of interest. The method and benefits are outlined below through comparison with the dry-weight approach. Data comes from primarily studies using this method. For full consideration of LSC dynamics in Australian tropical rainforest using this method see Chapter 6 of this thesis.

The basis of the volumetric method works in much the same way as the commonly used LSC measurement techniques for fine litter (Gong and Ong 1983;

Proctor *et al.* 1983). Randomly chosen sampling points are used to collect fine litter (excluding heavily fragmented portions considered as part of the mineral soil portion and woody material > 2 cm diameter) from within 0.25 - m^2 quadrats. The material is placed into a specially designed measuring cylinder (Figure 5.1.a) ('compression cylinder'). Any included woody material is broken into portions small enough to fit horizontal in the apparatus to reduce obstructions. The material is then compressed flat using a compression stick and the volume recorded directly from a scale bar. The compression cylinder consists of 400 mm of 150-mm-diameter PVC tubing. Two vertical guide holes are cut into the tubing for viewing the volume of litter during measurements, on one side from just below the top to approximately half way down the tubing, and, on the opposite side, from the bottom to approximately half way up the tubing (Figure 5.1.a). This enables the volume (up to ~ 3.5 L at once) to be read while still maintaining the structural integrity of the compression cylinder during litter compaction. An additional square piece of PVC (~ 5 mm thickness) is plastic welded to the bottom of the tubing to provide a stable base Figure 5.1.a). Volumetric scales, in litres, for this diameter of tubing are laminated to the sides adjacent to the vertical guide holes. The compression stick consists of 900 mm of wood dowel with a 140-mm-diameter flat PVC disc attached via steel brackets (Figure 5.1.b). The collected litter is compressed into the cylinder with at least three firm downward thrusts. The operator then leans down on the litter with the compression stick, and with a firm compressive force (their own body weight) on the litter, records the volume. For most adult operators this level of force is enough to consistently compress litter. The material can then be emptied out in the original location on the forest floor, either spread out or left in a pile in order to recognise areas that have already been sampled.

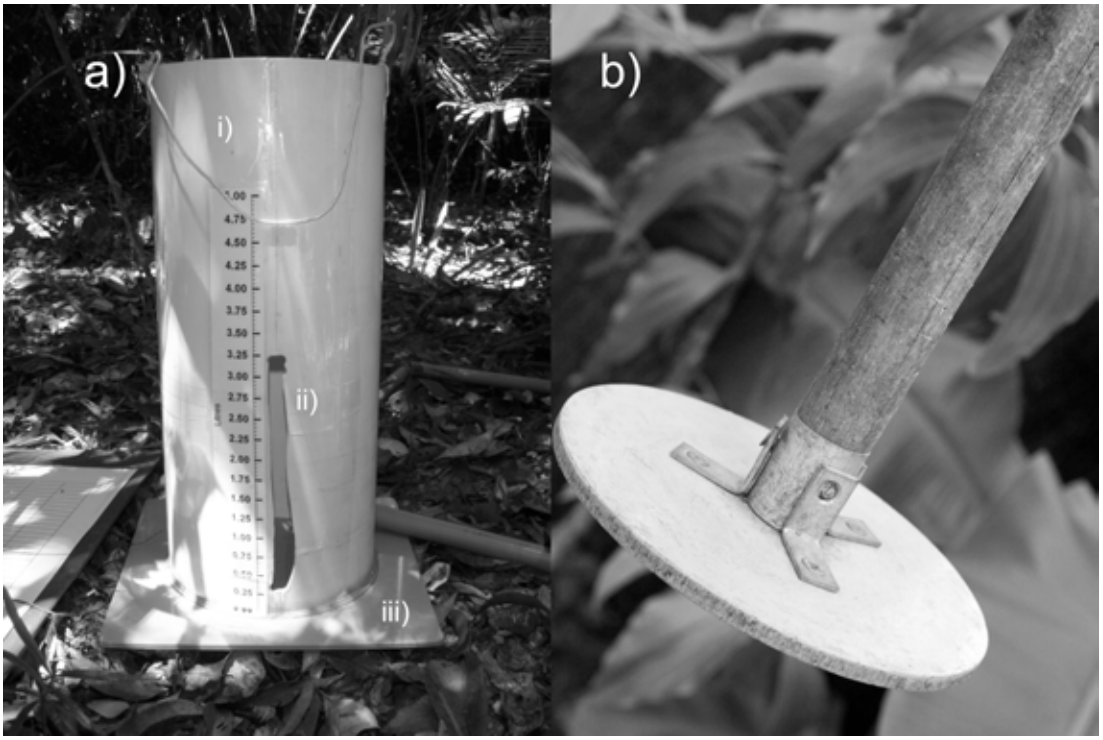

Figure 5.1. Volumetric device used to measure volume of fine-litter standing crop consisting of: compression cylinder (a) and compression stick (b). Cylinder consists of 150-mm PVC tubing (i), plastic-welded base (iii); guide hole to view volume in litres (ii).

The compression cylinder was designed to be used with 0.25 m^2 quadrats, based on the range of litter collected in the north Queensland study area from dry weighed LSCs between March 2007 - January 2008. A portion of these collections of dry weights were also used to develop calibrations between dry weight and volume (Figure 5.2, n = 190). This enables comparisons of LSC between other studies, and the determination of other factors where dry weight is of interest, such as litter turnover rates (annual litterfall / sum of the annual LSC). Calibration equations of volume versus mass were calculated using both linear and non-linear regressions. Spatial and temporal subsets of the data set were used to test the generality of the LSC calibrations. Spatial subsets were sub-regions (Windsor Uplands (WU) and Spec Uplands (SU): seasonally dry rain forest and wet sclerophyll rain forest;

Carbine Uplands (CU): complex rain forest, and Atherton Uplands (AU): complex rain forest with many sites influenced by a recent severe cyclone) and temporal subsets/seasons (wet: collected February; dry: September 2008).

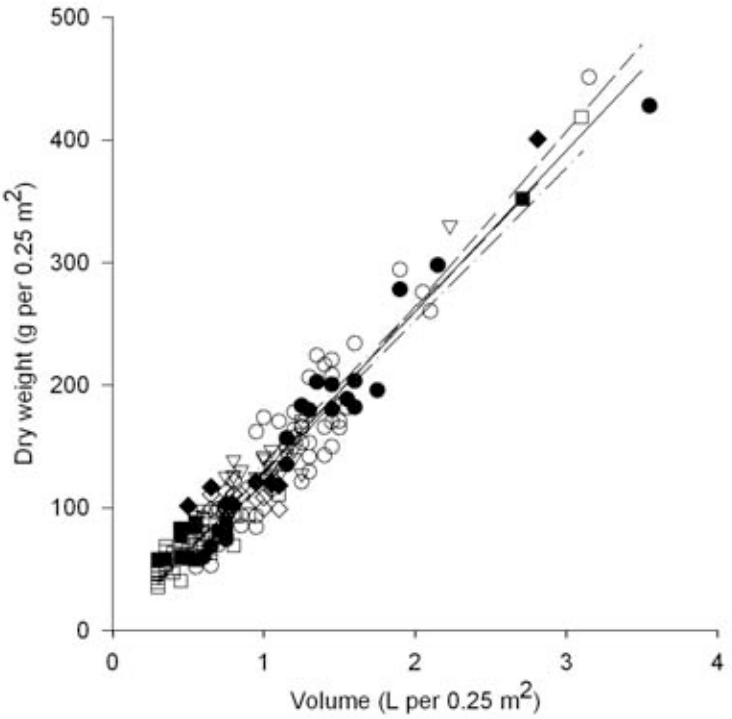

Figure 5.2. Litter standing crop data showing calibration from linear regressions between litter standing crop volume and dry weight (n = 190) taken from sites in Australian tropical rain forest. Included are samples from different sub-regions and collection seasons: Atherton uplands ─ - - (r^2 = 0.90), ○ (Wet, n = 50), ● (Dry, n = 17); Carbine uplands · ─ · (r^2 = 0.94), □ (Wet, n = 51), ■ (Dry, n = 20); Windsor uplands ·· ─ ·· (r^2 = 0.81), ▽ (Wet, n = 20); Spec Uplands ─ ─ ─ (r^2 = 0.87), ◇ (Wet, n = 22), ♦ (Dry, n= 10); Seasonal lines not shown: wet r^2 = 0.91, dry r^2 = 0.94; combined regression ── (r^2 = 0.92).

There was a strong linear relationship between litter volume and dry weight for the combined data (Dry Weight = -1.87 + (131 × Volume), r^2 = 0.92) (Figure 5.2). The relationship was not improved by the application of more complex non-linear functions (i.e. quadratic function: r^2 = 0.92). There was no evidence to suggest that either the slope or intercept for calibrations differed temporally, (ANCOVA, $F_{1,187}$ =

0.74, p = 0.85), or spatially (ANCOVA, $F_{3, 185} = 2.08$, p = 0.11), across the range of litter volumes encountered in rain forest within the region between June 2007 and May 2009 (mean = 1.17 L; median = 1.05 L; range = 0.10 - 5 L; n = 4950). This was the case even allowing for the fact that a number of AU plots were affected by cyclone damage. The AU plot may have had comparably higher proportions of woody material, but the affect on the calibrations was minor. Considering this the linear functions were acceptable, and combined linear regression is applicable to all of the sites within this common range of values. The lower r^2 for SU and WU were likely to have been influenced by their comparably small sample sizes.

The amount of effort required to adequately measure LSC can be considerable and can limit the coverage of estimates and representativeness of sampling designs. In the case of this study, removing samples to determine dry weight back in the laboratory required travelling large distances, which is likely to be the case in many ecological research settings. For example, on one occasion where 15 of the sites were sampled, removing just ten 0.25 m^2 quadrats of wet litter (n = 150) meant that > 20 kg dry weight (~ 150 L) of material needed to be transported. Both the dry weight and volume method require the same amount of time to collect a single sample, ~ 30 s. However, the dry weight method adds additional effort of ~20 s per sample for drying (not including actual drying time) and requires a great deal of space to complete the processing. An additional ~30 s per sample was then necessary for weighing. The volume method, once calibrated, equates to a significant saving in time and effort per unit area measured, e.g. from the data a minimum of ~5.3 min m^{-2} using dry weight was reduced to ~2.0 min m^{-2} (38 %) by adopting the volume method. Thus, with the volumetric method sample sizes can easily be increased to improve spatial coverage without significantly increasing effort.

In designing this study it is important to understand the number of samples necessary to get statistical power from the data. The requirement in this thesis was for comparisons of LSC between sites distributed along elevational transects within the four sub-regions (see following chapter). Each site contains six points distributed 200 m apart. An acceptable maximum sampling scheme in regards to time spent at each site was considered to be 10 LSC volumes per point (n = 60 per site). Post hoc power analyses is used to demonstrate the analytical benefit of increased litter sampling facilitated by the volume method (S + for Windows, EnvironmentalsStats module, TIBCO Software Inc. California). The goal of the power analysis is to determine the range of minimum detectable differences (MDD) (effect size) for comparisons with ANOVA ($\alpha = 0.05$, for 80% power), between sites (e.g. regional/ site differences). Table 5.1 shows the mean LSC estimates for entire transects (mean of six points) used in this analysis, sampled on one occasion per site in 2007/2008. Only data sets with homogenic variances were used in the analysis. The generally high variability is a characteristic of LSC, particularly at sites situated on steep slopes in upland situations. The range of MDD for comparisons between entire transects (n = 60) was 0.07 - 0.13 kg m^{-2} (Figure 5.3), with significant escalation of MDD with < 30 samples. This range appears generally acceptable for statistical comparisons considering the range of means, 0.47 - 0.98kg m^{-2}. Sites with low MDD generally came from areas with more moderate slopes. For instance, WU11 is relatively flat compared to CU12 which has a highly variable but generally steep topography within the six sampling points.

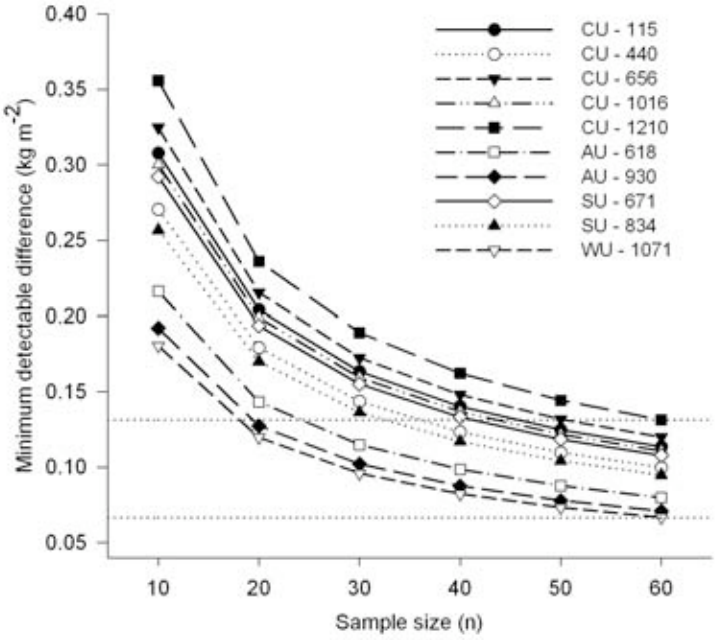

Figure 5.3. Minimum detectable difference (effect size) calculated via power analysis (α = 5% for 80% power) of mean litter standing crop sampled along transects (six points per transect, 10 samples per point) in Australian tropical rain forest. Horizontal dotted lines represent the range of effect size for these sets of samples.

Table 5.1. Litter standing crop data (mean ± SD) used in power analysis for minimum detectable difference sampled in Australian tropical rainforests using the litter volume method and calibration. Elevational transects come from three regions: CU – Carbine Uplands; AU – Atherton Uplands; SU - Spec Uplands; WU – Windsor Uplands. CU and AU sampled in October 2007; SU June 2008; WU March 2008. N = 60 per transect, sampled along six points (10 samples per point).

Transect – altitude (m asl)	Litter standing crop (kg m^{-2})
CU1 – 115	0.77 ± 0.31
CU4 – 440	0.68 ± 0.27
CU6 – 656	0.69 ± 0.33
CU10 – 1016	0.74 ± 0.30
CU12 – 1210	0.89 ± 0.36
AU6 – 618	0.69 ± 0.22
AU9 – 930	0.55 ± 0.19
SU6 – 671	0.98 ± 0.29
SU8 – 834	0.47 ± 0.26
WU11 – 1071	0.57 ± 0.18

Sampling LSC depends greatly on the site or area being covered, and the goals of the study. In this regional-scale study, dry weight measurements were not deemed feasible due to large sample numbers. The volumetric approach fulfils the needs for a quick and easily replicable method to cover a large area with total fine LSC. In this study it is possible with the volumetric approach, using the same time/effort, to increase sample sizes from ~ 37 dry weights to ~ 60 volumes at the site level. On average, with the data shown above, this allows for improvements in MDD of 23%. This method is recommended mostly where total fine-litter data is required over many sampling periods (e.g. to view seasonal changes in LSC), and where numerous sites and long-term monitoring may be important (e.g. >12 mo). The lack of litter removal from the site also lessens the impacts of research activities on the ecosystem and importantly on the processes being studied. Detecting changes in ecosystem processes, such as those related to LSC, is of significant importance in monitoring forest processes, particular in light of current climate change.

Chapter 6. Local and regional scale patterns and controls on litter processes in Australian tropical rainforests

6.1. Introduction

The pathways that litterfall and litter on the soil surface follow in forested ecosystems relate to complex interactions between plant communities, climate and soils (Vitousek and Sanford 1986; Facelli and Pickett 1991). These include litterfall production, the accumulation of litter on the mineral soil surface, subsequent decomposition, mineralisation and formation of soil organic matter, and fluxes to the atmosphere (Swift *et al.* 1979; Vitousek and Sanford 1986). Tropical rainforest soil processes occur within a nutrient-poor setting of high species-driven chemical heterogeneity, and complex interactions with litter quality, microbes and other decomposers (Swift *et al.* 1979; Vitousek and Sanford 1986; Tanner *et al.* 1998; Townsend *et al.* 2008). In tropical rainforests with seasonal rainfall trends both litterfall and decomposition dynamics show distinct seasonality (Wieder and Lang 1982; Chave *et al.* 2009). These intra-annual variations have a large bearing on soil processes, plant nutrient uptake, and continued productivity. Litterfall in wet tropical forest with distinct dry spells generally peaks in the late dry season and into the early wet season, with seasonal moisture stress potentially inhibiting decomposition and nutrient release due to moisture stress, and resulting in the accumulation of litter on the ground (Swift *et al.* 1979; Wieder and Wright 1995). Temporal variations in litter and nutrient inputs are controlled by environmental factors such as rainfall seasonality (Chave *et al.* 2009) and solar radiation (Myneni *et al.* 2007), and

decomposition and nutrient release/availability often controlling the magnitude of these inputs (Wood *et al.* 2009). Flushes of litterfall with rainfall may result in short term ephemeral enhancement of soil nutrient availability with significance to the maintenance of forest function (Swift *et al.* 1979; Swift *et al.* 1981; Lodge *et al.* 1994; Wieder and Wright 1995; Wood *et al.* 2009). Forest floor litter standing crops (LSC) generally peak with litterfall (Spain 1984; Morellato 1992). The extent by which LSC varies within a year is based on litterfall and decomposition rates, with both driven by climatic and edaphic factors, and other characteristics of the vegetation community (Swift *et al.* 1979). Decomposition rates and nutrient mineralisation are slower in the dry season than the wet season, so the timing of litterfall is important for sustained soil fertility (Wieder and Lang 1982).

Plant litter quality and nutritional characteristics of soils may be particularly important in explaining both litterfall rates (Chave *et al.* 2009), and decomposition/ litter layer dynamics (Anderson *et al.* 1983; Cornejo *et al.* 1994; Vitousek *et al.* 1994; Parsons and Congdon 2008; Chapters 2 and 4 of this thesis) in this biome. However, litter quality and thus, litter decomposability, is generally highly variable in tropical rainforests, even at local scales (Townsend *et al.* 2007; Townsend *et al.* 2008; Chapter 3 of this thesis). Changes in the amount of litter on the ground can have a significant negative impact on biodiversity, for instance, amphibians and reptiles, in the currently changing climate (Whitfield *et al.* 2007).

In addition to a propensity for high rates of intra-annual rainfall seasonality, seasonally wet tropical forests are prone to inter-annual variations in rainfall caused by El Niño Southern Oscillation (ENSO) events, and are expected to be highly sensitive to climate change particularly through increased temperatures and changes in dry season moisture inputs (Hulme and Viner 1998; Borchert 1998; Suppiah *et al.*

2007). Considering the essential timing and seasonality of these inputs on processes in tropical rainforests, this chapter asks how climatic and nutritional (litter quality and soil) factors influence litterfall rates and litterfall seasonality, the amount and annual variability in litter (standing crop) on the soil surface and litter turnover in Australian tropical rainforests?

6.2. Methods

6.2.1. *Study sites*

Two of the six plots (detailed monitoring plots) per site throughout the Australian wet tropics were used for detailed monitoring (detailed monitoring plots) of litterfall and LSC: the remaining four were sampled on fewer occasions to determine spatial variance in LSC (see following). For the sites AU1, AU2, AU4 and SU3 only the two detailed monitoring plots were used.

6.2.2. *Litterfall*

See Chapter 3 for litterfall collection techniques. Litterfall data collected from May 2007 to July 2009 was used for litter turnover and seasonality calculations as this period coincides with the LSC collections (see following).

6.2.3. *Litter standing crop and litter turnover*

Fine litter standing crop (LSC) (not including woody material > 2 cm diameter) was measured over 24 months at 36 of the 40 detailed monitoring plots. The volumetric method of Parsons *et al.* (2009) (Chapter 5 of this thesis) was used. The benefits of the volumetric method in sampling numerous sites are discussed in Chapter 5 of this thesis. Sampling intensity varied between sites for the detailed monitoring plots,

however means were determined from 10 to 20 0.25 m^2 quadrats every two to three months, over 24 months. This level of sampling provided enough statistical power to explain the variability in LSC at these sites (Chapter 5 of this thesis). Litter was replaced on the soil surface after each measurement, and sampling locations were in close proximity to the litter traps. Dry weight samples, used to create calibrations between volume and dry weight, were also included in the analysis (see Chapter 5).

LSC data were also collected from the remaining 4 of the 6 sampling plots at each site on 4 - 5 occasions separated by at least 3 months to determine annual LSC means. This data was used together with the LSC means from the detailed monitoring plots to determine the spatial variability in LSC (see statistics sections). The total number of plots sampled for LSC was 93, including 36 detailed monitoring plots.

LSC and litterfall rates were used to determine litter turnover quotients k_{tot} (y^{-1}) for the detailed monitoring plots, with the equation:

$$k_{tot} = \frac{\sum L_{ann}}{LSC_{ave}}$$

Where L_{ann} is the annual litterfall (t ha^{-1} y^{-1}), and LSC_{ave} is the average annual LSC (t ha^{-1}).

Leaf litter chemistry (N, P, Ca, Mg, C, lignin, lignocellulose, α-cellulose and total phenolics), was determined using the NIRS methods of Chapter 2 of this thesis. Mean chemical values for each plot were used in analyses (see Chapter 3, Table 3.1).

6.2.4. *Litter seasonality*

An index of seasonality in litterfall (total SLLF, and leaf LSLLF) and in LSC (SLLSC) was calculated using vector algebra (Wright and Calderon 1995;

Zimmerman *et al.* 2007; Chave *et al.* 2009). This method was employed because linear or Julian time scales fail in seasonality measurements when the process being studied occurs year round. For example, if peaks or troughs in litterfall or LSC occur primarily between December and January, the linear mean would incorrectly fall in June (Wright and Calderon 1995; Zimmerman *et al.* 2007). The average value from the collection month was used, and the month of sampling was converted to a number between 0 (1 January) to 330 (1 December). This allows the data to be presented in a polar plot (month/days = degrees). The length of the vectors for each month is the mean litterfall (total or leaf) or LSC value for that month (i), L_{mon} (t ha^{-1} y^{-1}) or LSC_{mon} (t ha^{-1}). For litterfall, the month used was the mid point (date) between that collection and the preceding collection. The mean vector (m) from the monthly collection L_{mon} and LSC_{mon} vectors were derived from the following equation, using litterfall as an example:

$$m_x = \frac{1}{12}\sum L_{mon}\cos(30\times i), \quad m_y = \frac{1}{12}\sum L_{mon}\sin(30\times i) \qquad \text{(eq. 1)}$$

The angle of the mean vector (Φ, eq. 2) is a measure of the mean litterfall date, and the length m, (eq. 3), is the extent of the temporal concentration (Jammalamadaka and Sengupta 2001; Zimmerman *et al.* 2007; Chave *et al.* 2009).

$$\phi = \arctan\frac{m_y}{m_x} \quad if\ x > 0, \qquad \phi = 180 + \arctan\frac{m_y}{m_x} \quad if\ x < 0 \qquad \text{(eq. 2)}$$

$$m = (m_x^{\,2} + m_y^{\,2})^{\frac{1}{2}} \qquad \text{(eq. 3)}$$

Finally the seasonality index is defined:

$$SL = \frac{\|m\|}{L} \qquad \text{(eq. 4).}$$

Where L is the annual litterfall rate, or LSC mean. SL measures the extent to which litterfall or LSC is distributed evenly throughout the year (e.g SL ≈ 1 indicates that litter fell mostly in 1 month, SL ≈ 0 indicates an even distribution over 12 months).

6.2.5. *Leaf litter decomposability and climate decomposition index*

Leaf litterfall decomposability (k_{nirs}) was predicted with the NIRS model presented in Chapter 2, calculated from the litterbag work of Chapter 4, for the litterfall samples from Chapter 3. This was achieved using partial least squares regression analysis on the mean initial NIR spectra (1st derivative with scatter correction 1100 - 2500 nm) of leaf sub-samples, prior to decomposition (Chapter 2 of this thesis), (5 per site) versus the subsequent *k* decomposition constant of the material *in situ* (1st exponential decay rate, see following). This value is holistic chemical representation of the potential *in situ* decomposability/decay rate of leaf material produced at a site (Chapter 2 of this thesis). The model was used to predict the potential *in situ* k_{nirs} of 24 months of litterfall samples for all 40 plots in the region. The full sample set consisted of 2860 litterfall samples (spectra), spanning 24 months of litterfall collections. Climate decomposition index (CDI) was calculated for each location using the equations in Adair *et al.* (2008). Both the standard CDI of Lloyd and Taylor (1994) (CDI) and the arc-tangent form (CDI_{arc}) (Del Grosso *et al.* 2005; Adair *et al.* 2008) were used in models. CDI is a strong predictor of decomposition dynamics related to the climate-driven soil decomposition capacity of the environment (Lloyd and Taylor 1994; Del Grosso *et al.* 2005; Parton *et al.* 2007; Adair *et al.* 2008). See Appendix 3 for the equations used to calculate CDI.

6.2.6. *Statistical analysis*

Differences between plots for litterfall and LSC were tested with ANOVA. Spatial and temporal differences in litterfall and LSC were analysed with factorial ANOVA, with site and time (month) as factors. Transformations were used on the data to improve homogeneity of variance. To test for differences in LSC between plots at the same site (local differences versus regional differences), nested ANOVA was used, with elevational site (e.g. AU1, AU2 etc.) as the fixed factor, and plots within elevation sites as random factors (2 per elevational site, e.g. AU1 nested with 2 plots AU1A1 and AU1A3. Only the detailed monitoring plots were used for this. Variance components between these hierarchies were also estimated with restricted maximum likelihood models (RML, SPSS v17.0).

Mean annual litterfall, LSC, and total litter turnover (k_{tot}), SLLF (total and leaf), and SLLSC were modelled with best sub-set linear regressions to determine the environmental (climate and soil) and chemical (litter quality) controls on the litter layer and litter layer dynamics. To explain turnover and seasonality in LSC, the mean k_{nirs} values were also included as variables. The environmental variables were as follows: MAP, MAT, coefficient of variation in monthly rainfall totals/rainfall seasonality (MAPCV) (BIOCLIM); real time rain (over the course of the experiment), % dry season days with 0 mm rainfall (DS0MM) from the Australian Water Availability Project (Raupach *et al.* 2008); real time annual average soil temperature (SoilT), average leaf wetness (moisture condensation) in the dry season (LWDS) and average humidity in the dry season (HUMDS) from on-site data loggers, in addition to CDI and CDI_{arc} (see Appendix 1 for raw data). Soil data used were: total N, P, C, clay, sand, silt, Mg, Ca and Na (see Appendix 2 for raw data). To

explore the effects of plant species richness and disturbance on litter processes, the species richness of all plants and those 5 m or taller, and the % Gap coloniser species (based on descriptions in (Hyland *et al.* 2002)), were included in regressions. See Appendix 2 for raw data and Chapter 3 for the method used to determine species richness.

6.3. Results

6.3.1. *Litterfall and litterfall seasonality*

Average annual litterfall ranged from 4.89 t ha^{-1} y^{-1} (cyclone damaged Atherton 600 m elevation plot 2) to 11.29 t ha^{1} y^{-1} (Carbine uplands 600 m elevation plot 2) (Table 6.1). Based on the within plot spatial variability there were significant effects of site (df = 39 F = 10.37), time/month, (df = 11 F = 164.85) and site by time (df = 369 F = 2.68) for total litterfall ($p < 0.001$ for all).

For total and leaf litterfall, the mean variance between all plots (n = 40) was 3.15 and 1.84 t ha^{-1} y^{-1} respectively, and between replicate plots at the same site, 3.04 and 1.37 t ha^{-1} y^{-1} (n = 20 x 2 of 5 litter traps). Mean annual litterfall was not significantly explained by any of the environmental variables for all plots, or with the cyclone damaged AU plots excluded ($p < 0.05$).

The mean angle of total SLLF related to months between September and February (end of the dry to end of the wet season), with most peaking between October and December (Table 6.1, Figure 6.1.a and Appendix 10). The mean litterfall date for the whole region was at the beginning of January (361.4º, Figure 6.1.a). The cyclone damaged AU sites generally had later peaks in litterfall than the other sites, particularly in the lowlands (Table 6.1). MAP and leaf litter P were both

Table 6.1. Litter data used in this study, mean annual litter standing crop (LSC) (t ha^{-1}), litterfall (t ha^{-1} yr^{-1}), LSC turnover (k_{tot}), seasonality in LSC (SLSC, from vector algebra analysis), the mean angle of LSC where January is 0 and 360 degrees with 30° monthly intervals and leaf litter decomposability index (k_{nirs}, NIRS chemical decomposability exponential decay rates) from litterbag studies and near infrared spectral analysis. LSC and litterfall data are two year averages (2008 and 2009), errors represent standard deviations between collection times (LSC), and spatial variability (litterfall). ND = no data.

		Mean LSC (2 yr)	Mean Litterfall (2 yr)	SLLF (total)	SLLF (leaf)	Mean angle (LF total)	LSC (k_{tot})	SLLSC	Mean angle (LSC)	k_{nirs}
Atherton Uplands	AU1A1	4.50 ± 1.59^{bcd}	7.79 ± 4.65^{ab}	0.26	0.11	11.74	1.73	0.27	40.64	1.68
	AU1A3	5.73 ± 1.89^{fghijk}	5.52 ± 1.20^{ab}	0.29	0.06	356.36	0.96	0.14	272.81	1.54
	AU2A2	4.83 ± 1.45^{defg}	10.85 ± 5.09^{b}	0.22	0.10	5.80	2.25	0.15	9.57	2.25
	AU2A5	N/D	5.09 ± 5.01^{ab}	0.25	0.14	351.20	ND	ND	ND	2.25
	AU4A2	3.52 ± 0.71^{ab}	9.90 ± 9.80^{ab}	0.31	0.35	351.20	2.81	0.19	332.62	1.94
	AU4A5	4.54 ± 2.43^{bcde}	7.39 ± 2.34^{ab}	0.21	0.31	275.65	1.63	0.33	12.91	2.21
	AU6A2	4.79 ± 1.49^{cdefg}	4.89 ± 2.69^{a}	0.34	0.28	355.31	1.02	0.16	4.91	1.52
	AU6A5	3.99 ± 1.34^{bc}	5.97 ± 0.84^{ab}	0.30	0.36	337.57	1.50	0.13	344.70	2.08
	AU8A2	4.01 ± 2.44^{a}	5.44 ± 1.21^{ab}	0.36	0.38	357.22	1.36	0.34	327.36	1.78
	AU8A5	ND	6.94 ± 3.75^{ab}	0.34	0.47	41.49	ND	ND	ND	1.68
	AU9A2	6.36 ± 1.64^{ghijkl}	9.19 ± 3.78^{ab}	0.26	0.34	351.20	1.45	0.20	301.47	1.50
	AU9A5	5.65 ± 1.32^{ghijkl}	5.58 ± 0.85^{ab}	0.35	0.46	341.10	0.99	0.07	294.32	0.97
Carbine Uplands	CU1A1	3.70 ± 1.59^{ab}	5.47 ± 0.95^{ab}	0.18	0.22	323.79	1.48	0.21	43.98	1.77
	CU1A5	5.31 ± 2.05^{defghi}	6.69 ± 1.02^{ab}	0.18	0.33	369.30	1.26	0.14	342.52	1.70
	CU2A2	ND	9.43 ± 3.67^{ab}	0.12	0.30	286.41	ND	ND	ND	1.05
	CU2A5	ND	7.29 ± 2.03^{ab}	0.18	0.33	358.00	ND	ND	ND	0.99
	CU4A2	4.71 ± 0.97^{cdef}	7.80 ± 2.01^{ab}	0.19	0.40	335.41	1.65	0.04	64.34	0.83
	CU4A5	3.81 ± 1.10^{ab}	6.75 ± 2.25^{ab}	0.30	0.37	349.18	1.77	0.17	65.56	1.17
	CU6A2	6.45 ± 1.38^{ijklmn}	11.29 ± 3.32^{b}	0.23	0.30	322.18	1.75	0.21	334.51	1.26
	CU6A5	5.94 ± 1.32^{ghijkl}	7.58 ± 0.96^{ab}	0.38	0.53	354.58	1.28	0.21	74.20	0.91
	CU8A2	5.45 ± 1.64^{defg}	5.45 ± 0.90^{ab}	0.30	0.38	329.04	1.00	0.22	76.56	1.15
	CU8A5	5.97 ± 1.63^{fghijk}	6.84 ± 1.97^{ab}	0.35	0.40	306.85	1.14	0.24	353.93	0.99

Table 6.1. cont.

		Mean LSC (2 yr)	Mean Litterfall (2 yr)	SLLF (total)	SLLF (leaf)	Mean angle (LF total)	LSC (k_{tot})	SLLSC	Mean angle (LSC)	k_{nirs}
Carbine Uplands	CU10A2	5.85±0.97^{ghijkl}	7.66±1.24^{ab}	0.23	0.34	324.48	1.31	0.16	49.29	1.32
	CU10A5	4.94±1.15^{defgh}	10.12±5.61^{ab}	0.35	0.36	339.35	2.05	0.15	32.75	1.54
	CU12A2	7.05±2.11^{ijklmn}	6.00±2.18^{ab}	0.31	0.30	295.41	0.85	0.18	52.42	1.29
	CU12A5	7.14±1.50^{klmn}	7.58±2.20^{ab}	0.35	0.39	324.79	1.06	0.14	5.97	0.84
Spec Uplands	SU3A1	6.43±2.05^{jklmn}	10.70±1.60^{b}	0.11	0.14	327.26	0.97	0.19	18.79	0.84
	SU3A2	7.18±1.34^{lmn}	6.99±3.60^{ab}	0.19	0.27	286.94	1.66	0.12	74.08	0.92
	SU6A2	10.94±1.96^{q}	10.40±0.86^{b}	0.24	0.24	330.78	0.95	0.14	295.98	0.35
	SU6A3	9.29±1.61^{opq}	8.16±3.21^{ab}	0.26	0.29	347.28	0.88	0.14	62.52	0.31
	SU8A2	6.59±1.48^{ijklmn}	7.61±1.01^{ab}	0.32	0.32	333.85	1.15	0.14	63.76	1.07
	SU8A3	6.26±0.66^{hijklm}	8.33±1.51^{ab}	0.34	0.30	331.41	1.33	0.16	5.84	1.07
	SU10A1	6.21±1.09^{ghijkl}	6.83±1.14^{ab}	0.42	0.46	321.82	1.10	0.16	41.84	1.08
	SU10A2	6.92±1.08^{lmn}	6.86±1.76^{ab}	0.41	0.44	325.89	0.99	0.18	30.51	1.07
Windsor Uplands	WU9A2	9.99±2.41^{pq}	5.79±1.83^{ab}	0.15	0.24	326.31	0.58	0.04	384.01	0.92
	WU9A5	10.53±2.74^{q}	7.82±2.39^{ab}	0.07	0.25	274.90	0.74	0.07	290.84	0.93
	WU11A2	5.14±1.07^{efghij}	6.11±1.70^{ab}	0.18	0.37	274.58	1.19	0.07	79.82	1.37
	WU11A5	7.32±1.39^{mno}	8.79±3.42^{ab}	0.27	0.30	314.98	1.20	0.04	304.90	1.16
	WU13A2	7.90±1.45^{mno}	5.93±2.57^{ab}	0.42	0.32	348.84	0.75	0.05	312.96	0.75
	WU13A5	8.76±1.67^{nop}	7.16±2.43^{ab}	0.12	0.31	340.78	0.82	0.10	23.78	0.90

linearly related to the litterfall mean angle/date. This relationship was due to cross correlation between rainfall and litterfall nutrients for the cyclone damaged plots. There were no relationships for mean angle and climate or fertility in the rest of the region when the damaged plots were excluded ($p > 0.05$).

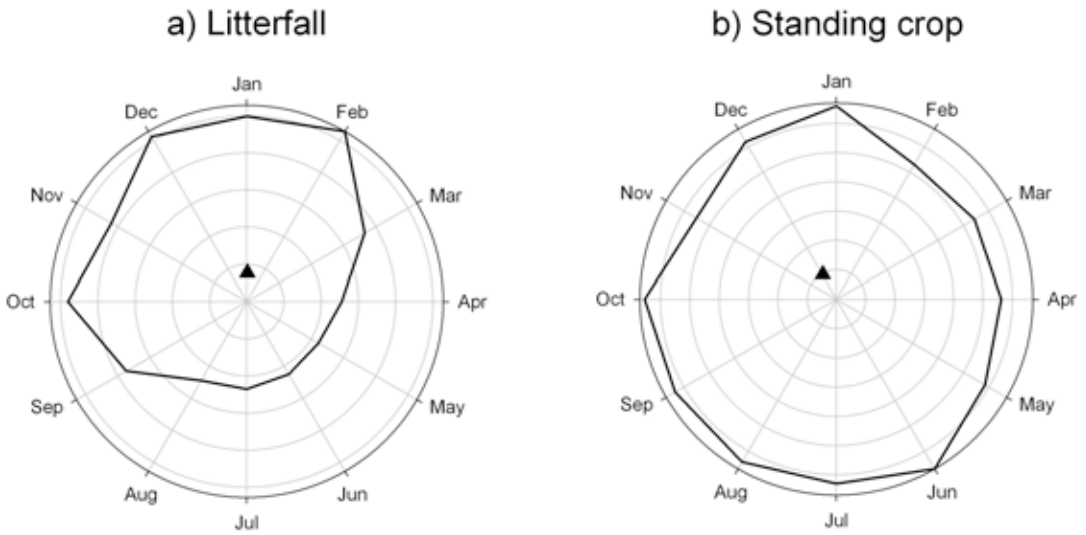

Figure 6.1. Polar plot representation of monthly (a) litterfall and (b) litter standing crop (LSC) in Australian tropical rainforests. Data are the region monthly means from 40 plots. Radial axes are in t $ha^{-1}y^{-1}$ (litterfall), and t ha^{-1} (standing crop). ▲ represent the mean litterfall and LSC date and the extent of the temporal seasonality (calculated using the equations explained in the methods.

The range in total and leaf litterfall seasonality across the region was 0.07 - 0.42 (mean = 0.27) and 0.06 - 0.53 (mean = 0.31) respectively (Table 6.1). The multiple regression model for litterfall seasonality contained real time under canopy temperature (AirT, partial $r^2 = 0.31$, Figure 6.2.a) and soil N (partial $r^2 = 0.21$, Figure 6.2.b), (model $r^2 = 0.41$, $p = 0.03$, Appendix 11.a and b). The cyclone damaged Atherton plots showed markedly different seasonality patterns than the other plots, so were removed from further analysis. With the exclusion of the cyclone sites, mean annual temperature was significantly negatively correlated with rainfall seasonality

(DS0MM with MAT, p = 0.005). Litterfall seasonality was not significantly correlated with rainfall or moisture seasonality alone (p = 0.99 for DS0MM, p = 0.60 for LWDS and p = 0.53 for MAP), but explained the residual variation in the relationship with elevation/temperature: total litterfall seasonality versus elevation (partial r^2 = 0.33, positive relationship) and DS0MM (partial r^2 = 0.21, positive relationship).

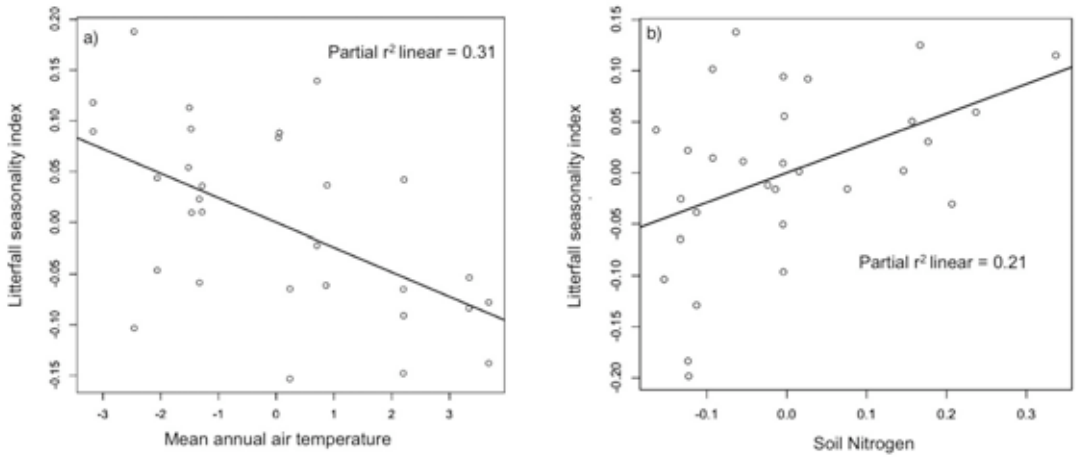

Figure 6.2. Partial plots from regression analysis showing relationships between litterfall seasonality and a) mean annual temperature; b) soil nitrogen. Cyclone damaged plots are excluded, n = 29. The relationship between temperature and litterfall seasonality may be partially driven by correlations with rainfall seasonality (see text for description).

6.3.2. *Leaf decomposability*

The NIRS model predicted *in situ k* in 86% of the full litterfall sample population (predicted n = 2471), including collections spanning all months of the year from all 40 plots. Other samples could not be predicted as they were outside the spectral range of the calibrated data (Chapter 2). Mean k_{nirs} (24 months of litterfall) was highest for the Atherton sub-region (1.78 y^{-1}), compared to Carbine (1.20 y^{-1}), Spec (1.08 y^{-1}) and Windsor (1.01 y^{-1}) (Table 6.1). The highest predicted k_{nirs} was at both

of the AU2 plots (2.25 y^{-1}). The lowest k_{nirs} was at both of the Spec uplands 600m plots (0.31 and 0.35 y^{-1})**.** For the whole region, mean k_{nirs} was higher in the wet season (mean = 1.30 y^{-1}) than in the dry season (mean = 1.19 y^{-1}) (p = 0.001, Table 6.2).

Table 6.2. Repeated measures ANOVA results comparing wet and dry season mean litterfall decomposability (exponential decay rates from litterbag studies and near infrared spectra analysis).

	p	df	F	Wet mean (y^{-1})	Dry mean (y^{-1})
Season	0.001	1	33.684	1.30±0.57	1.19±0.56
Season*Plot	0.001	39	2.010		

The mean within-plot spatial variance in k_{nirs} ranged from 0.03 to 0.20 y^{-1}, mean = 0.08 y^{-1}. Between plot (local) variation in k_{nirs} (same elevation/sub-region) from RML was 0.03, compared to a regional variance of 0.23 y^{-1}. Differences between plots were particularly high where there were local differences in soil fertility, e.g. AU9; and vegetation structure, e.g. CU12.

6.3.3. *Litter standing crop*

For the detailed monitoring sites, two year average LSC ranged from 3.70 t ha^{-1} (AU8A2) to 10.94 t ha^{-1} (SU6A2) (regional mean 6.21 ± 1.55 t ha^{-1}) (Table 6.1). LSC generally peaked in the early wet season and then declined over these months, and then accumulated slightly over the dry season (Figure 6.1.b, Appendix 12 for all plots). Some locations also had minor peaks around June - July (Appendix 12). Differences in LSC due to time (month) and plot and the combination of plot and

time were significant (month df = 11, F = 20.59 $p < 0.001$), plot (df = 35, F = 34.42, $p < 0.001$), and time by plot (df = 257, F = 3.289, $p < 0.001$). Generally the WU, SU and CU sub-regions had higher annual LSC than the AU sub-region (Table 6.1).

ANOVA showed significant nested factor(plots) / main factor (elevation within sub-region) effects for LSC (df = 17 F = 8.42, $p < 0.001$) suggesting LSC varied by plot even within the same level of control for elevation within sub-region. Regional variance in LSC (RML) for the detailed monitoring plots was 3.46 t ha^{-1}. Mean within site/along transect variance (along 1 km transects) was 1.20 t ha^{-1} (n = 93 plots, 19 sites/transects).

Detailed monitoring plot LSC means were best explained by the proportion of wood in the litterfall (negative relationship), MAPCV (negative), soil Na (negative), k_{nirs} (negative) and slope (positive) and the annual litterfall (positive) (model r^2 = 0.75, Appendix 11.c). While this combination explained LSC well, the best single environmental variable to correlate with LSC was LWDS (r^2 = 0.31, $p < 0.001$, Figure 6.3.a). Leaf C alone explained LSC best of all the leaf litter chemical components (positive relationship) (r^2 = 0.46, Figure 6.3.b and Appendix 11.d). The combined litter quality information in the k_{nirs} indices explained LSC with an r^2 = 0.54 (Figure 6.3.c, $p < 0.001$). LSC was also linearly related to MAT (r^2 = 0.14, p = 0.022), and CDI_{arc} (r^2 = 0.16, p = 0.015). There was no correlation between any of the dry season intensity variables and MAT with all of the plots included ($p > 0.05$).

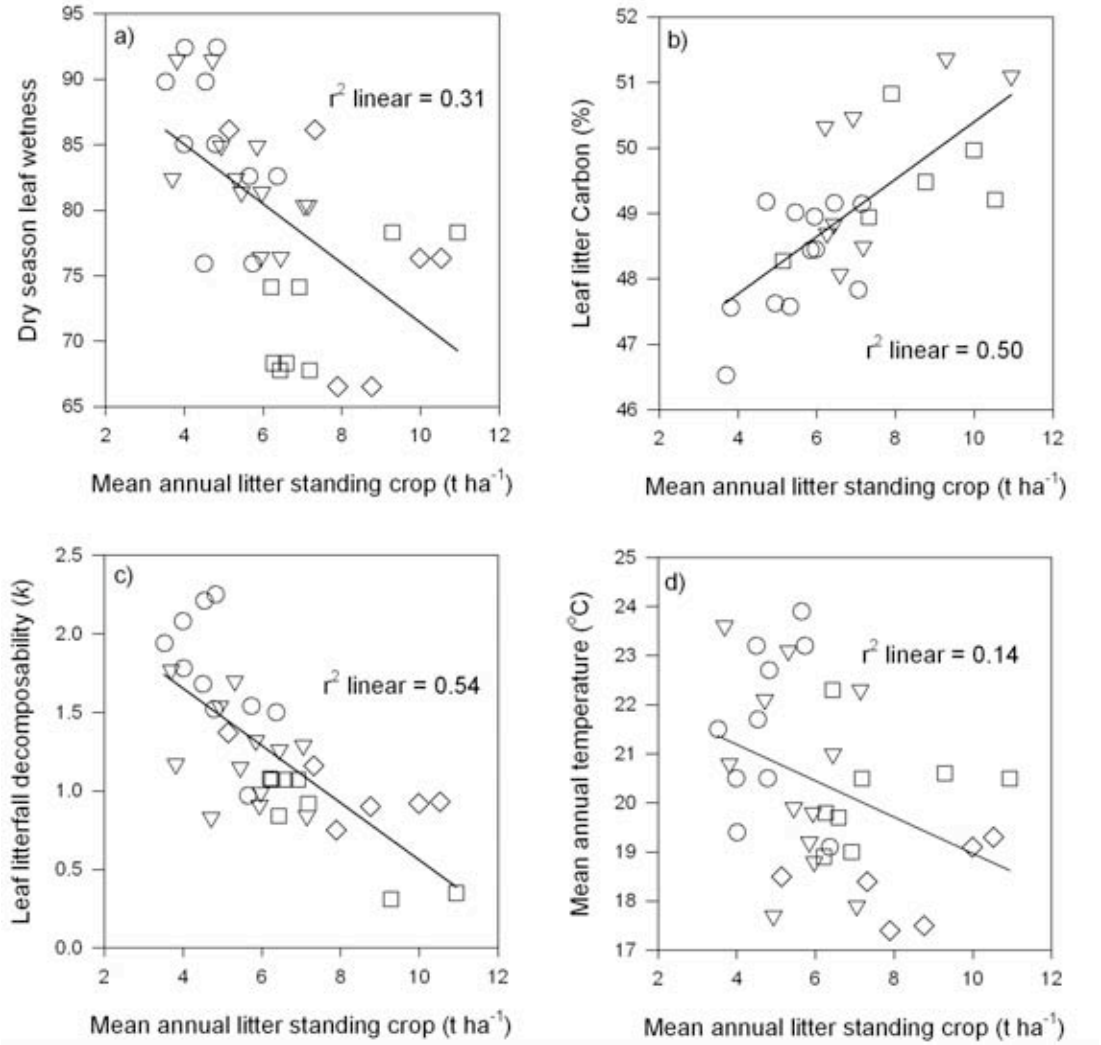

Figure 6.3. Relationship between litter standing crop with a) leaf wetness during the dry season (LWDS); b) leaf litter carbon; c) *in situ* leaf decomposability (exponential decay rate, from near infrared spectra analysis); d) mean annual temperature. Symbols represent different sub-regions: AU ○; CU ▽; SU □; WU ◇. n = 36 for all.

6.3.4. *Litter standing crop turnover and seasonality*

LSC annual turnover k_{tot} values ranged from 0.57 (WU9A5) to 2.81 (AU4A2) (Table 6.1). Overall regional variance in turnover was 0.21, compared to 0.03 between plots at the same elevation in the same sub-region. Turnover, k_{tot},was greater at sites with less wood in the litterfall, lower MAPCV, higher soil Na, more decomposable leaf

litter (k_{nirs}) and on less steep slopes (model $r^2 = 0.62$, Appendix 11.e). A simpler model explained k_{tot} with CDI_{arc} and leaf litterfall total phenolics (model $r^2 = 0.49$ $p < 0.001$, Figure 6.4, Appendix 11.f for regression statistics). Of all of the environmental variables, LWDS correlated best with k_{tot} ($r^2 = 0.26$, $p < 0.001$, Figure 6.5.a), followed by CDI_{arc} ($r^2 = 0.19$, $p = 0.001$, Figure 6.5.d) and AirT ($r^2 = 0.19$, $p = 0.01$). The four outlier plots visible in Figure 6.5.a were the WU9, SU8 and SU3 plots, which had very low LWDS values. Of the leaf chemical components, C explained k_{tot} the best ($r^2 = 0.44$, Figure 6.5.b, Appendix 11.g), slightly better than total phenolics (linear $r^2 = 0.35$, $p < 0.001$). Leaf decomposability explained k_{tot} with an $r^2 = 0.38$, $p < 0.001$ (Figure 6.5.c).

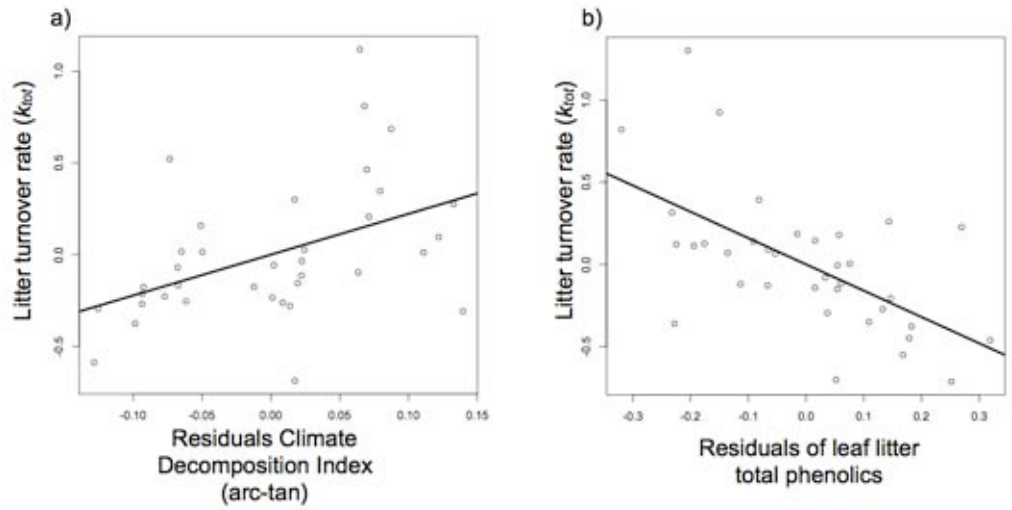

Figure 6.4. Partial linear regression plots of simple model explaining litter turnover rate (k_{tot}) in Australian tropical rainforest, for a) climate decomposition index arc tangent form (CDI_{arc}); b) leaf litter total phenolics. Model $r^2 = 0.49$, $p < 0.001$, $n = 36$.

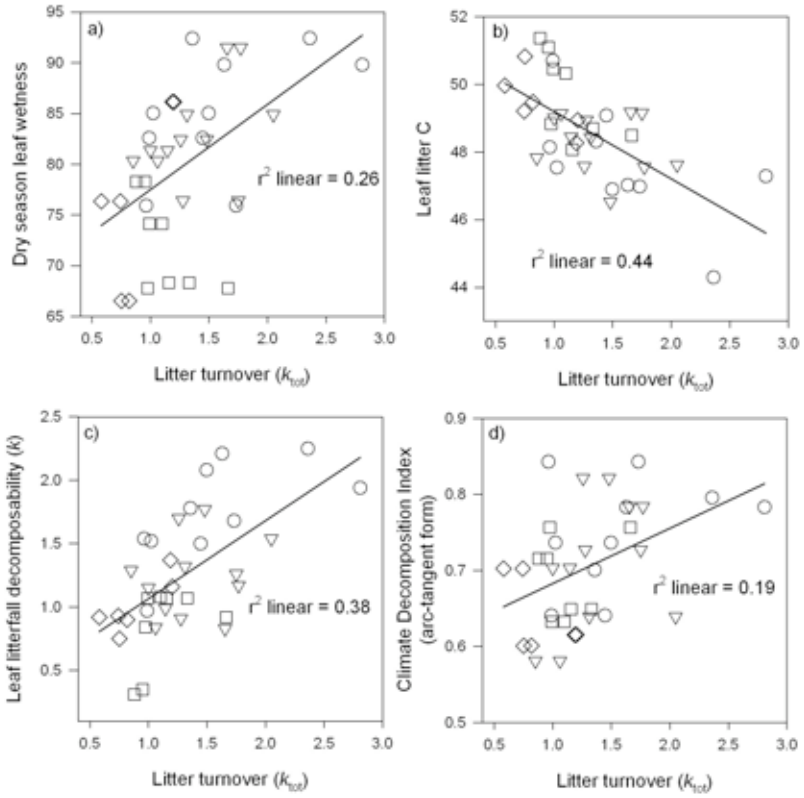

Figure 6.5. Relationship between litter layer turnover rate (k_{tot}) with a) leaf wetness during the dry season (LWDS); b) leaf litter total carbon; c) leaf litter phenolics; d) climate decomposition index (arc-tangent form). n = 36.

Seasonality in LSC was less variable throughout the region than seasonality in litterfall (SLLSC variance = 0.005; SLLF = 0.008). Peak LSC occurred for all sites in September - March (Table 6.1, mean angles). Examples of relatively high seasonality and low seasonality existed in the data set (Appendix 12), however most sites annually showed fairly even LSC distributions throughout the year (regional mean = 0.16, Figure 6.1.b). For the whole region mean LSC date was November (330.9^{o}, Figure 6.1.b). Some peaks in LSC also occurred as single monthly instances (e.g. LSC spiking one month but not equally high the next). This situation explains some of the high SLLSC values (esp. AU4, AU8). Considering this, these two sites were removed from further analysis.

The best sub-set regression of environmental variables explaining SLLSC included soil Na (model $r^2 = 0.42$, $p < 0.001$, Figure 6.6.a, Appendix 11.h), excluding the CU4A2 plot (outlier high soil Na content). No climate variables correlated significantly with SLLSC ($p < 0.05$). Leaf litter C:N ratio was the best explanatory leaf litter chemical variable for SLLSC, but the relationship was not significant (model $r^2 = 0.12$, $p = 0.045$). Annual mean LSC was also negatively linearly related to SLLSC ($r^2 = 0.16$, $p = 0.02$, Figure 6.6.b).

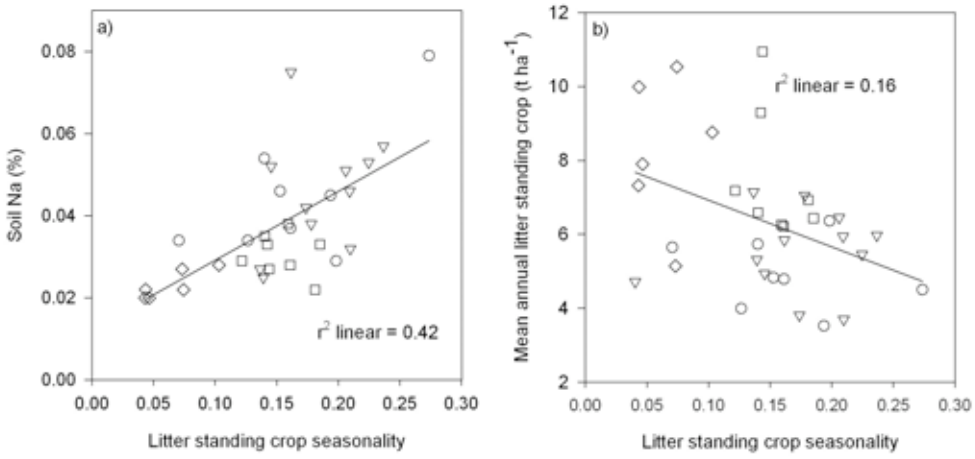

Figure 6.6. Relationship between litter layer seasonality (SLLSC) with a) soil Na; b) mean annual litter standing crop. Legend is the same as in Figure 4. n =36.

6.4. Discussion

Although no drivers were found here for annual litterfall totals, a broad combination of factors were shown to control the amount of litter on the soil surface, the variability and duration/turnover of this material on the soil surface and the constancy of inputs. Chave *et al.* (2009) compared litterfall dynamics throughout South American tropical forests, and determined that the amount of litterfall did not vary consistently with annual precipitation or temperature, but with soil/litter

nutrients, e.g. leaf litter N:P (i.e. phosphorus limitation) (Chave *et al.* 2009). Attempts to determine such trends in the current study were hindered by the cyclone damage of the majority of sites on fertile soils. Notwithstanding, the regional average litterfall rate in the AWT was 7.45 t ha^{-1} y^{-1} (7.61 excluding the cyclone damaged plots). These values are slightly lower than the mean of 8.61 t ha^{-1} y^{-1} for South American rainforests (Chave *et al.* 2009). However, the potential for higher litterfall rates than those quantified existed in the range of sites, particularly the Atherton plots. For instance, one of the Atherton 200 m plots (rich soil by a river bed) had the highest litterfall rate in 2008-2009 (> 12 t ha^{-1} y^{-1}), despite almost complete canopy loss in 2006. On similar soils on the Atherton Tablelands, Spain (1984) recorded high litterfall rates in excess of 10 t ha^{-1} y^{-1}. Similarly, previous work in AWT (Brasell *et al.* 1980; Spain 1984; Herbohn and Congdon 1993) noted a general trend of higher (up to two fold) litterfall rates in the wetter and more fertile Atherton region, compared to sites on more oligotrophic granitic soils (Herbohn and Congdon 1993; Stocker *et al.* 1995). Based on the leaf litter C contents of Chapter 3 of this thesis, and applying these to total litterfall values, C inputs here equated to 3.69 t C ha^{-1} y^{-1}, which is slightly lower than the mean for old growth forests in South America (4.0 t C ha^{-1} y^{-1} old growth forests) (Chave *et al.* 2009).

The seasonal trends in litterfall in the current study agreed with those found for other locations in Australian tropical rainforests (Brasell *et al.* 1980; Spain 1984; Herbohn and Congdon 1993), with the largest falls of the year occurring late in the dry (e.g. October) to the beginning of the wet (e.g. transition months, November - December), and continuing into the wet season (mean date in January, Figure 6.1.a). The higher quality/decomposability of material falling in the wetter months in these forests suggests that the chemical composition of material promotes rapid

decomposition and mineralisation, compared to that falling in drier times, i.e. April - October. The chemical components potentially explaining this discrepancy are the polyphenols, which have higher concentrations in dry season litterfall in these forests (Chapter 3 of this thesis), possibly as a response to light stress (Close and McArthur 2002). Around the time of the first large falls of litterfall, the amount of litter on the soil surface peaks, (i.e. November) in these forests, and then declines through decomposition, while at the same time being replaced by litterfall over the wet season (Figure 6.1.b). This replenishment of the litter layer works to balance out the amount of litter on the soil surface, which remains relatively consistent throughout the year (Figure 6.1.b, Appendix 12 and see following). The accumulation of litter with the onset of the rains creates a pulse of nutrients in the early wet season, particularly from leachates (Lodge *et al.* 1994). However, the following nutrient immobilisation, which is a ubiquitous phenomenon at the sites studied here (see Chapter 4 of this thesis) and most other tropical rainforests (Vitousek 1984; Vitousek and Sanford 1986), delays the return of most nutrients held in the new litterfall to plants (i.e. from the same litter falling that year), to plants. Immobilisation patterns in these forests generally last for more than 12 months (Palm and Sanchez 1990; Tian *et al.* 1992; Lodge *et al.* 1994; Parsons and Congdon 2008; Chapter 4 of this thesis); however, following this the heavily fragmented material (e.g. > 1 year on soil), is then incorporated into soil organic matter where significant mineralisation for plant uptake occurs (Brown and Lugo 1982).

Litterfall in Australian tropical rainforests is slightly more seasonal than in South America (mean = 0.21 compared to 0.17 in South America), based on the total litterfall seasonality (index) means of this study, and those of Chave *et al.* (2009). The timing of litterfall in both cases may be driven by water stress, especially when

peaks occur in the dry season, although experimental evidence for this is lacking (Wieder and Wright 1995). Moreover, remote sensing over the Amazon Basin has shown that seasonal swings in leaf area, and therefore litterfall, in tropical forests are related to seasonality in solar radiation (Myneni *et al.* 2007). These authors propose that this tend may be an opportunistic means of utilising high light during the dry season for net new leaf growth, with net abscission occurring in the cloudy wet season (Myneni *et al.* 2007). This would explain the timing of litterfall found here and in other seasonal tropical rainforests.

Here seasonality in litterfall was related to mean annual temperature, and to a lesser extent to soil N. For soil N, seasonality was greater at plots with of higher soil N, which may be a sign of a forest response to higher available nutrients, and a decreased need for more consistent litter inputs/replenishment for soil nutrients. Unlike the Chave *et al.* (2009) data set, seasonality in litterfall in Australian tropical rainforests was higher at more seasonally wet (upland) sites (i.e. higher in the lowlands). The cause of this discrepancy is unclear, however the highly seasonal rainfall of the Australian wet tropics may be a factor.

The range of turnover rates found in this study are similar to those of other tropical rainforests, and the fastest estimates globally (Anderson and Swift 1983) (e.g. Atherton 400 m elevation); however, like leaf decomposition in AWT forests (Chapter 4 of this thesis), the lowest turnover rates were more similar to those of temperate forests (Anderson and Swift 1983). Slower turnover leads to greater accumulation and duration of litter (high litter standing crop) on the soil surface, which correlates with slow decomposition and longer periods of immobilisation. This causes bottlenecks in nutrient return to plants (e.g. lower leaf decomposability = slower mineralisation, which correlates with higher annual LSC) (Lodge *et al.* 1994).

Decomposition and seasonal fluctuations of the litter layer in Australian tropical rainforests are driven by litter quality (especially P, C, phenolics and Ca), and moisture seasonality (Chapter 2 and 4 of this thesis), the proportion of wood in the litterfall and quantity of litterfall, and soil sodium (this study). Temperature effects are also significant with annual LSCs generally higher, and duration on the soil surface lower, in the uplands. The combined temperature and rainfall seasonality information in the climate decomposition index is valuable in explaining decomposition in a variety of forests, including tropical rainforests (Parton *et al.* 2007; Adair *et al.* 2008). The effect here for LSC and litter turnover was stronger than for leaves (Chapter 4). As the CDI relates more to temperature than to moisture (Taylor *et al.* 1989; Del Grosso *et al.* 2005), this trend seen here (and trends with of LSC with temperature alone) suggests greater sensitivity of whole LSC, than leaf material, to temperature. This is in line with research showing greater temperature sensitivity of decomposition to temperature in poor chemical quality material (Fierer *et al.* 2005; Davidson and Janssens 2006).

Spatial variation in litter dynamics may be greater in tropical forests than other biomes even at small local scales, due to high species diversity and high heterogeneity in canopy and soil compositions, and high rates of localised disturbance (Townsend *et al.* 2008). Spatial variability in LSC was locally high in the present study area, with around 35% of the mean regional variance contained within 1 km long tracts of forest. This is probably driven largely by spatially varying litterfall rates and compositions (litter quality and wood proportions), micro-climates and soil compositions (e.g. Na), and the movement and accumulation of material especially on slopes. Sodium is both a limiting and essential nutrient to detritivores, and low abundances of Na have been shown to limit carbon cycling in tropical

rainforest (Kaspari *et al.* 2009). The main variable explaining mean LSC and turnover in these sites was the quality/decomposability of the litter (i.e. litter quality). Litter quality and leaf chemical traits are particularly important in explaining decomposition processes (Melillo *et al.* 1982; Cornwell *et al.* 2008), and are related in these forests to soil nutrients, climate and disturbance/succession (Chapter 3 of this thesis). Litter decomposability may vary substantially within a small area, mostly due to environmental heterogeneity, differences in traits between neighbouring species and also leaves at different stages of decay falling to the ground (e.g. after being caught in the canopy) (Herbohn and Congdon 1993; Townsend *et al.* 2007; Townsend *et al.* 2008; Wieder *et al.* 2009; Asner *et al.* 2009). For the AWT region, within plot spatial variability in leaf litter decomposability, relative to the site mean, was approximately 35% of the whole regional variation. This is curiously similar to the local variance of total LSC. Local variation in leaf litter chemistry also follows this trend. For example, Chapter 3 of this thesis showed the local variance in litter chemical variables to be 43% of the regional variance for lignin, 22% for phenolics, 12% for N, and 13% for P. Understanding this fine scale variation is essential for predictions of how nutrient cycling and decomposition may respond in tropical forests undergoing rapid disturbance and change (Wieder *et al.* 2009).

Chapter 7. Sensitivity of Australian tropical rainforest litter processes to climate change

7.1. Introduction

Terrestrial ecosystems and climate are inherently connected. The effects of climate on forest ecosystem processes needs to be fully understood in order to determine how forest function will be affected by climate change (Thomas *et al.* 2004; Clark 2007). This is especially true for tropical rainforests, which contain a disproportionately large amount of the World's carbon pool (Dixon *et al.* 1994) and account for between one third and half of the World's terrestrial net primary productivity (Melillo *et al.* 1993; Clark *et al.* 2001b). Models of global ecosystem processes mostly predict declining productivity for tropical forests (White *et al.* 2000; Cramer *et al.* 2001; Fung *et al.* 2005), in addition to large scale tropical forest die-offs this century (Jones *et al.* 2003; Cowling *et al.* 2004). Nevertheless, large uncertainty exists in regards to key forest processes (Clark 2007). Litter decomposition is central to atmospheric and plant/soil responses to change as it determines the flux of carbon and nutrients between soils and the atmosphere (Couteaux *et al.* 1995; Cao and Woodward 1998b). Predictions of how decomposition processes respond to climate will aid in the understanding of the likely pathways of change in forest processes and biodiversity as a whole (Loreau *et al.* 2001; Williams *et al.* 2008).

Increasing temperatures and changed rainfall patterns in tropical regions are already occurring globally (Clark 2007). Current conditions see rainfall totals, in particular dry season rainfall, decreasing in many tropical forests, including north

tropical Africa, India, tropical south east Asia and north eastern Australia (Malhi and Wright 2004; Suppiah *et al.* 2007). Consensus from climate general circulation models (GCM) are that these trends in the tropics will continue throughout this century and the next (IPCC 2007), leading to general losses of biodiversity (Williams *et al.* 2003; Thomas *et al.* 2004), altered rainforest distribution (Hulme and Viner 1998; Hilbert *et al.* 2001) and ecosystem function (Melillo *et al.* 1993; Scholes and van Breemen 1997; Cao and Woodward 1998a; Petchey *et al.* 1999).

The sensitivity of tropical forest litter decomposition to both temperature (i.e. latitudinal and elevational) (Aerts 1997; Holland *et al.* 2000; Liski *et al.* 2003) and rainfall seasonality/annual drought (Cornejo *et al.* 1994; Liski *et al.* 2003; Xuluc-Tolosa *et al.* 2003; Parsons and Congdon 2008; Chapters 4 and 6 of this thesis) are well documented. Climate driven changes in decomposition rates relate to alterations in ephemeral nutrient release, productivity and whole community function. Litter quality remains the strongest determinant of mass loss from litter at most scales (Cornwell *et al.* 2008; Zhang *et al.* 2008), and is also at least partially climate driven (Aerts 1997; Chapter 3 of this thesis). Temperature effects plant litter decomposition processes in complex ways, through direct effects like increasing metabolic rates of decomposing organisms, and indirect effects such as altering decomposer community structure and litter quality (Aerts 1997; Liski *et al.* 2003). Similarly, increased seasonality of rainfall lowers microbial biomass and function for decomposition (Wardle 1998; Yavitt *et al.* 2004), and indirectly influences the quality of litter cycled and soil organic structure (Brown and Lugo 1982; Couteaux *et al.* 1995). Temperature effects on decomposition are also heavily influenced by litter chemical quality, with low quality (e.g. high fibre, low nutrients, low available energy), responding more to increased temperatures than high quality (e.g. low fibre, high

nutrients, high available energy) litters (Fierer *et al.* 2005; Conant *et al.* 2008).

Little is known about the sensitivity of decomposition dynamics at local and regional scales in the context of currently predicted GCM scenarios. Understanding the effects of these scenarios on decomposition is essential, particularly in regards to how increased temperatures (potentially having a positive effect on litter breakdown), and increased dry season intensity (negative effect on litter breakdown), may combine to alter litter decomposition processes. Here models of litter decomposition dynamics are used, from studies undertaken throughout the north Queensland wet tropics, to predict future litter dynamics. GCM projections specific to the rainforest region from Suppiah *et al.* (2007) and Suppiah *et al.* (2009) are combined with the models to assess the sensitivity of the processes in the context of these scenarios, from present, until 2080. The climate decomposition index (CDI) is determined for these GCM's to also predict future responses of this variable. CDI is a strong predictor of litter dynamics at different scales (Lloyd and Taylor 1994; Parton *et al.* 2007; Adair *et al.* 2008; Chapter 6 of this thesis).

The sensitivity of litter processes to change are hypothesised to be largely dependant on the composition of the material, particularly due to the increasing sensitivity of decomposition to temperature with decreasing litter chemical quality (Fierer *et al.* 2005). For example, generally poorer chemical quality material, such as standing crops with high concentrations of lignified material, should more sensitive to temperature change than higher chemical quality material, such as leaf litter.

7.2. Methods

7.2.1. *Study location*

The raw data and explanatory models for this work comes from litter decomposition and nutrient cycling studies undertaken in the north Queensland rainforest region in Chapters 3, 4 and 6 of this thesis. Detailed descriptions of the study plots and region can be found in these Chapters and Appendix 1 and Appendix 2. Study plots covered an elevational range from 80 - 1300 m a.s.l., and were situated on a range of soil types. A total of 40 study plots were used to determine future anomalies from present day conditions, with sub-sets of these plots used to develop the predictive models. These forests are seasonally wet tropical rainforests, of differing degrees of complexity, with a marked dry season occurring in the winter months. Mean annual temperature in the region has already risen by 0.8^{o}C since 1950, and dry season rainfall has fallen in large areas (Suppiah *et al.* 2007; Suppiah *et al.* 2009).

7.2.2. *Litter decomposition models*

The dynamics of litter on the soil surface in these forests is strongly related to both temperature and dry season intensity (Chapters 4 and 6 of this thesis). The variables which were modelled were: leaf litter decomposition rate (k_{leaf}), (one-pool exponential decay constant, y^{-1}), lignin mineralisation rate (lignin % y^{-1}), and whole litter layer turnover rate (k_{tot}) (Table 7.1). Temperature here refers to the real time under the canopy mean annual temperature (AitT), in ^{o}C, determined from on-site data loggers over the study period (2007-2009). The leaf litter models came from litterbag experiments (~440 days total exposure, 12 experiments/plots in total) using

freshly senesced leaves of the Australian tropical rainforest plant *Archidendron vaillantii* (Chapter 4 of this thesis). This litter contains common chemical characteristics of tropical rainforest leaf litter, i.e. very low P and relatively high lignin contents (Meentemeyer 1978; Aerts 1997; Townsend *et al.* 2007). Litter turnover was determined from the mass balance between fine litterfall (in t ha^{-1} y^{-1}) and fine litter standing crop (LSC), (in t ha^{-1}) (excluding wood < 2 cm diameter) collected over 24 months (36 plots in total) (Chapters 5 and 6 of this thesis). Models were produced with best sub-set linear regressions using bayesian information coefficients to determine the best model. All of the predictive models cover the full range in elevations, AitT (16.0 - 23.5 ^{o}C), and soil conditions. Dry season intensity in the k_{leaf} and lignin mineralisation models came from the proportion of dry season days with 0 mm rainfall (DS0MM) (Appendix 1). Future rainfall projections were based on changes in dry half year (June- November, DRF) totals, thus linear regression was used to calculate future DS0MM values (r^2 = 0.68) (Table 7.1). This approach was necessary to allow the best sub-set regression model to be used, while including temperature and dry season intensity as predictors, and removing errors due to collinearity. DS0MM and DRF values came from real time data, over the course of the litterbag studies, from the Australian Water Availability Project (Raupach *et al.* 2008). Litter quality and soil nutrients were included as explanatory variables in k_{leaf} (soil P) and k_{tot} (average leaf litter total phenolic content, PHENOL), as determined in Chapters 2 and 3 of this thesis (Table 7.1). An assumption of the predictive approach was that these variables remain constant within the future climates.

The CDI incorporates seasonality in moisture and temperature to explain how they interact to drive soil respiration and decomposition (Lloyd and Taylor 1994;

Adair *et al.* 2008). The equations used here for calculating CDI can be found in Adair *et al.* (2008), and used monthly mean maximum and minimum temperatures and monthly rainfall totals. The arc-tangent form of CDI (CDI_{arc}) (Del Grosso *et al.* 2005; Adair *et al.* 2008) provided better predictive power for k_{tot} than CDI (Chapter 6 of this thesis). Predictive models were significant for all decomposition variables: k_{leaf} ($r^2 = 0.77$, $p < 0.001$); lignin % y^{-1} ($r^2 = 0.69$, $p = 0.009$) and k_{tot} ($r^2 = 0.49$, $p < 0.001$). The relative influence of each explanatory variable in the models, based on standardised linear regression coefficients, were: k_{leaf} (DS0MM 47.4%; soil P 33.2%; AitT 19.4%); Lignin % y^{-1} (DS0MM 60.2%; AitT 39.8%); k_{tot} (CDI_{arc} 40.0%, PHENOL 60.0%).

Table 7.1. Models describing litter decomposition dynamics in Australian tropical rainforests used in climate change sensitivity analysis: standard leaf litter first exponential decay rate (k_{leaf}, y^{-1}); lignin mineralisation as % original lignin lost per year and total litter layer annual turnover rate (sum annual litterfall/mean annual litter standing crop, k_{tot}).

Variable	Model	r^2	n	BIC	p
k_{leaf}	0.622 - 0.013*DS0MM + 0.029* AitT + 1.63*SoilP	0.77	12	-7.84	< 0.001
Lignin % y^{-1}	27.54 - 0.22*DS0MM + 0.61*AitT	0.69	12	-5.16	0.009
k_{tot}	0.631+2.20*CDI_{arc} -1.57*PHENOL	0.49	36	-12.85	<0.001
DS0MM	69.18 - 0.052*DRF	0.68	40	NA	< 0.001

AitT, under canopy mean annual temperature (°C); DS0MM, % dry season days with 0 mm rainfall; SoilP, mean soil phosphorus 0-20 cm; CDI_{arc}, Climate Decomposition Index (arctangent model), see Del Grosso *et al.* (2005) and Adair *et al.* (2008); DRF, dry half year rainfall (June - November). BIC = Bayesian Information Coefficient.

7.2.3. *Climate scenarios and sensitivity models*

Projected future scenarios for AirT, DRF and CDI_{arc}, for 10 year time steps from 2020 to 2080, were calculated using the GCM predictions of Suppiah *et al.* (2007) and Suppiah *et al.* (2009). By altering AitT, DRF and or CDI_{arc} values in the litter decomposition models in Table 7.1 and Table 7.2, predicted future anomalies in litter

processes, from the 2007-2009 recorded values, were determined. Input values came from climate and soil and litter nutrient data for 40 plots in the region (i.e. with available input data based on 2007-2009 climate/soil/litterfall), including those where the decomposition data was collected(see Appendix 2 for plot descriptions). Future CDI_{arc} values were calculated by altering the inputs in the equations in Adair *et al.* (2008) based on the predictions in Table 7.2. Climate data from three future emission scenarios were used, namely the mean of the full range SRES emission scenarios (SRES), and atmospheric CO_2 stabilisation at 450 ppm (WRE450) and 550 ppm (WRE550) (IPCC 2000; IPCC 2007; Suppiah *et al.* 2007). Modelled changes in litter dynamics were determined using the range of values for warm/dry (upper) and wet/cool (lower) bounds in the projected climatic changes.

Table 7.2. Future climate scenarios for years 2020-2080 for the tropical rainforest region of north Queensland Australia after Suppiah *et al.* (2007, 2009). Shown is the lower (-) and upper (+) bounds of predictions for change in mean annual temperature (AitT, in ^{o}C), dry half year rainfall June - November (DRF, %), and the climate decomposition index (CDI_{arc}, arc-tangent value, %). CDI_{arc} as calculated with the equations in Adair *et al.* (2008) using the climate scenarios below (values are means for 40 study plots, see text). Scenarios represent the mean of the full range of SRES and atmospheric CO_2 stabilisation at 450 ppm (WRE450) and 550 ppm (WRE550). Changes are relative to 1990 values except CDI_{arc} (relative to 2007 - 2009).

		2020		2030		2040		2050		2060		2070		2080	
		-	+	-	+	-	+	-	+	-	+	-	+	-	+
SRES	Temp	0.3	0.9	0.5	1.4	0.6	1.9	0.7	2.5	0.9	3.3	1.0	4.2	1.1	5.0
	DRF	1	-12	2	-17	3	-23	4	-31	5	-41	6	-50	7	-60
	CDI_{arc}	1.4	4.3	2.5	6.8	3.0	9.1	3.5	11.7	4.4	15.0	5.0	18.2	5.5.	20.5
WRE450	Temp	0.3	0.7	0.4	1.0	0.6	1.3	0.7	1.6	0.8	1.9	0.9	2.2	1.0	2.4
	DRF	1	-9	1	-12	2	-16	2	-20	3	-23	3	-25	3	-30
	CDI_{arc}	1.6	3.5	2.1	5.0	3.1	6.4	3.6	7.9	4.2	9.2	4.7	10.6	5.2	11.4
WRE550	Temp	0.3	0.7	0.5	1.1	0.7	1.5	0.8	1.8	1.0	2.2	1.2	2.6	1.3	2.9
	DRF	1	-9	2	-13	2	-18	3	-23	3	-30	4	-35	4	-35
	CDI_{arc}	1.6	3.5	2.5	5.5	3.6	7.4	4.2	8.8	5.2	10.5	6.2	12.2	6.7	13.6

The means of GCM predicted temperature increases for the Australian tropical rainforest region by 2080 are: SRES +3.1 ^{o}C; WRE450 +1.7 ^{o}C; WRE550 + 2.1 ^{o}C (Table 7.2). Dry half year rainfall projections for 2020 to 2080 contain large uncertainty; however, the mean projections for all three scenarios denote increased seasonal drying/dry season intensity. Projected means for 2080 are: SRES -26.5%; WRE450 -13.5% and WRE550 -15.5% (Table 7.2). Predicted changes in CDI_{arc} for 2080, as means for all 40 study plots, were: SRES +15.8%; WRE450 +8.5% and WRE550 +10.1%. Regarding conditions for the promotion of rainforest stability, the scenarios can be: worst case (much warmer and much drier, i.e. upper extremes of predictions); best case (slightly warmer and slightly wetter, i.e. lower extremes of predictions); most realistic case (warmer and slighty drier, i.e. mean of predictions). The three emission scenarios are ordered from best case to worst: WRE450; WRE550; SRES.

7.3. Results

7.3.1. *Sensitivity of leaf litter decomposition rate to climate change scenarios*

Models of future leaf decomposition rates showed large uncertainty (increases and decreases) (Figure 7.1.a). A very small increase in the mean leaf litter decay rate around 2030 was evident, with rates plateauing following this, for all three emission scenarios. For SRES, the range of predicted k_{leaf} rates was: 2050 -4.22 to +4.97% (average +0.37%) from observed 2007-2009 values; 2080 -7.46 to +8.15% (average +0.34) change in k_{leaf}. WRE450 changes in k_{leaf} were: 2050 -2.78 to +4.00% (average +0.61%); 2080 -4.16 to 5.78% (average +0.81%). For WRE550 this was: 2050 -3.37 to +4.91% (average +0.77%); 2080 -4.43 to +7.56% (average +1.57%) (Figure 7.1.a). Between 2060 and 2080 the WRE predictions showed variability in the lower

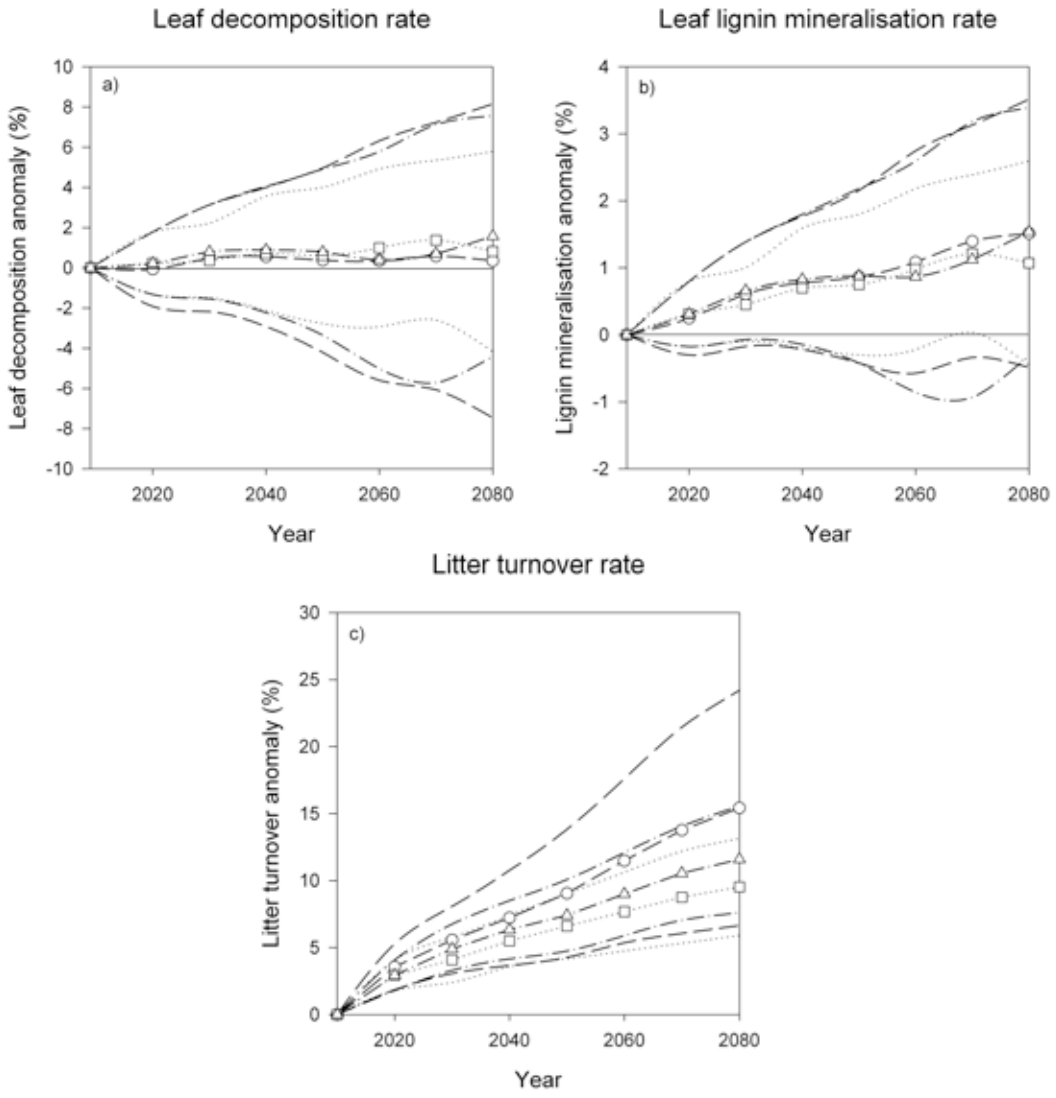

Figure 7.1. Projected future changes in Australian tropical rainforest litter processes, as % anomalies from 2007-2009 observed values, based on models presented above and the climate change scenarios of Suppiah *et al.* (2007) in Table 2, for: (a) leaf litter exponential decay rate; (b) leaf litter lignin mineralisation rate; (c) annual total litter turnover rate. Lines and symbols represent three different emission scenarios: ---- and ○ average of full range of SRES; ···· and □ 450 ppm CO_2 stabilisation; -·- △ 550 ppm CO_2 stabilisation. Symbols and thick lines are the mean of range of values (most realistic case) predicted by the models for upper (worst case) and lower (best case) boundaries of the climate scenarios.

estimates, comparing each emission scenario. This was due to differences in rainfall seasonality and the stabilisation of temperature (Table 7.2 and Figure 7.1.a).

7.3.2. *Sensitivity of leaf litter lignin mineralisation to climate change scenarios*

The mean predicted lignin mineralisation rates showed steady increases, for all three emission scenarios, but with broad uncertainty ranges (Figure 7.1.b). Changes from 2007-2009 for SRES with associated uncertainty were: 2050 -0.42 to +2.16% (average +0.87%); 2080 -0.49 to + 3.52 (average +1.51%). For the WRE450 scenario: 2050 -0.30 to +1.80% (average +0.75%); 2080 -0.45 to +2.59% (average +1.07%). For WRE550 stabilisation, changes were: 2050 -0.43 to 2.18% (average +0.88%); 2080 -0.32 to 3.39% (average +1.53%) (Figure 7.1.b).

7.3.3. *Sensitivity of litter layer turnover rates to climate change scenarios*

Predicted increases in future litter turnover rates dominated the models, however the extent of these increases depended on the emission scenario (Figure 7.1.c). For the SRES mean k_{tot} changes ranged from: 2050 +4.3 to +13.8% (average + 9.0%); 2080 +6.6 to +24.2% (average 15.4%). For WRE450 k_{tot} increases were: 2050 +4.2 to +0.2% (average +6.6%); 2080 +13.1 to +5.9% (average +9.5%). For WRE550 changes were: 2050 +4.7 to +10.1% (average +7.4%); 2080 +7.6 to +15.6% (average +11.6%). Predicted future anomalies in k_{tot} increased disproportionately between plots. Upland/cooler k_{tot} was predicted to increase at faster rates (as % anomaly compared to present) than lowland/warmer locations (Figure 7.2). Outliers in the data in Figure 7.2 (high k_{tot} anomaly relative to elevation) were plots with relatively high rainfall seasonality.

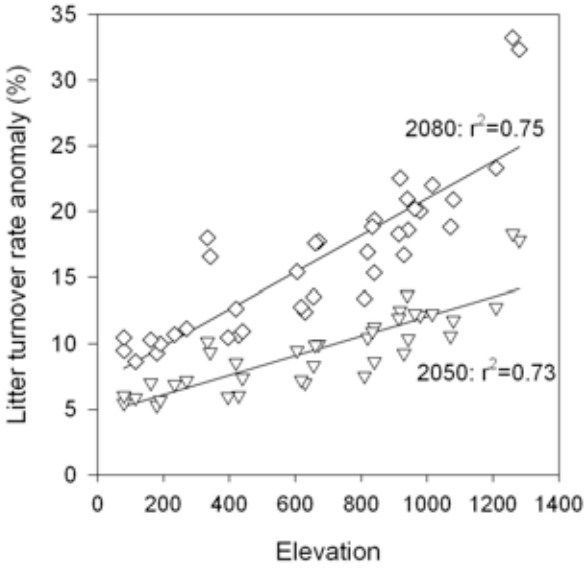

Figure 7.2. Relationships between predicted future anomaly in litter turnover rate and elevation, shown for 40 plots in Australian tropical rainforest. Data is for the mean of the full range of SRES future emission scenarios, with predictive values shown for years 2050 and 2080.

7.4. Discussion

7.4.1. *Predicted sensitivity of decomposition to future climates*

Models showed varied projected changes in litter decomposition dynamics under climate change scenarios. Large uncertainty was prevalent, especially where dry season rainfall had a strong influence in the model (i.e. k_{leaf} and to a lesser extent lignin mineralisation). For the worst case climate scenarios the mean predictions of the models suggested slight increases in decay rate, compared to present day values, but much uncertainty (Figure 7.1.a). The generally consistent leaf decay rates up to 2080, compared to current conditions, and irrespective of emission scenario, relates to a balancing of the accelerating effects of higher temperatures by the slowing effects of less moisture (Couteaux *et al.* 1995). On the other hand, for lignin

mineralisation and whole litter turnover, increases from today's conditions were more clearly suggested by the models (Figure 7.1.b and c). This discrepancy was driven by temperature having a more significant influence than, for instance, in the k_{leaf} model. Lignin mineralisation also strongly correlates with overall C mineralisation here (Chapter 4 of this thesis). The trend of increasing rates under future climates for poorer chemical quality components, compared to the large uncertainty for leaf decay (Figure 7.1.a), may be explained by the increasing sensitivity of decomposition to temperature in less easily decomposable material (i.e. poor chemical quality material decay more sensitive to temperature than high quality material) (Fierer *et al.* 2005; Conant *et al.* 2008). While carbon loss from decaying leaves may be driven by a combination of leaching and microbial mineralisation/ respiration, lignin decomposition is conducted by highly specialised organisms (Lewis and Yamamoto 1990; Hammel 1997), which are sensitive to moisture and temperature (Donnelly *et al.* 1990). Despite the complexities in defining wood decomposition (e.g. scaling up to whole litter standing crop turnover) compared to leaf litter (Swift *et al.* 1979), there should be an increasing importance of temperature on decomposition in such less easily decomposed (poor quality) material (Fierer *et al.* 2005), but dependent also on wood chemical quality (Weedon *et al.* 2009). Mean annual LSC and turnover are more closely related to temperature than dry season intensity in Australian tropical rainforests (Chapter 6 of this thesis). Less amendable material can remain on the soil surface for extended periods as more easily decomposed material rapidly disappears, thus poor quality material generally makes up large portions of litter standing crop (Spain 1984).

The CDI is a strong predictor of decomposition, including nutrient mineralisation, at numerous scales (Parton *et al.* 2007; Adair *et al.* 2008). The

climatic potential for decomposition, as predicted by the CDI, increases in these future predictions, despite co-occurring increasing rainfall seasonality occurring with increasing temperature. CDI is a better predictor of k_{tot} for whole litter layer turnover, as temperature explains more of the variability than moisture indices (Chapter 6 of this thesis). Significant increases in decay rates from the current conditions are therefore suggested within both the worst and best case boundaries for layer turnover (i.e. rainfall seasonality does not balance the accelerating effects of temperature in any scenario) (Figure 7.1.c). Also differences between the three emission scenarios are more evident for k_{tot}, because of the influence of temperature, i.e. the mean of the full range of SRES showing greater increased rates than the two CO_2 stabilisation scenarios (Figure 7.1.c). Due to the inverse relationship between the CDI and temperature (e.g. effective activation energy for decomposition) (Del Grosso *et al.* 2005; Adair *et al.* 2008), spatially varied degrees of change in future litter layer turnover rates are suggested by the models (Figure 7.2). The proportion of change in k_{tot} from current conditions under future climate scenarios is therefore suggested to be greater in the uplands (low annual temperature) than the lowlands (high annual temperature).

7.4.2. *Implications of climate change scenarios on litter processes*

If we take, on its own, the mean, "most realistic" climate scenario modelled effects on litter decomposition for Australian tropical rainforests, we should expect this ecosystem to see an increasing trend in mineralisation of litter material on the soil surface over the next 70 years (i.e. slightly warmer, slightly drier scenario). Increasing decay rates may be especially prominent for more recalcitrant C components and in relation to whole litter standing crops (see Figure 7.1.b and c),

and in upland rainforests more so compared to lowland rainforests (Figure 7.2). With the importance of litter quality in regulating temperature effects of decay, poor quality litters (e.g. on low nutrient soils), should also respond more so than high quality litters (e.g. high nutrient soils). In particular, whole litter layer turnover rates may increase but would be similarly dependent on wood chemical quality and temperature interactions (Fierer *et al.* 2005; Weedon *et al.* 2009). However, these suggested increases in decay rates may only be slight, especially if falls in dry season rainfall remain near the mean of the predicted values. Any higher rates of seasonal drying (e.g. than that of the means) would see shifts towards slower decomposition relative to present, at least for high quality material (especially leaf litter) (Figure 7.1.a). Similarly, here changes in dry season rainfall were used, which show more consistency in the GCMs predictions, than mean annual precipitation (Suppiah *et al.* 2007; Suppiah *et al.* 2009). Future annual rainfall changes (e.g. including wet season) can not be predicted accurately with the GCMs; however, if overall annual rainfall totals fall in the future climate, then a change in decomposition processes towards a longer litter duration on the soil surface, compared to present day conditions, would occur. This may be especially true in the Australian wet tropics if El Niño events (i.e. low rainfall years) become more common, as some models predict (Hulme and Viner 1998; Suppiah *et al.* 2009).

Of potentially greater importance may be changes in vegetation types in the altered climate space (Anderson 1991). These may override many of the climate effects in terms of future ecosystem processes (Prescott 2010), particularly due to the effect of community succession on litter quality (Cornwell *et al.* 2008), and thus, the inherent impact that changes in litter quality have on decay. There is growing evidence that climate-driven changes in litter decomposition, and associated

feedbacks to primary productivity, and soil fertility, are likely to be less significant than the direct effects of shifts in plant species composition, and especially associated changes in litter quality (Hobbie 1996; Wardle *et al.* 2009). In the Australian wet tropics, this broadly relates to decreases in the total rainforest area, greater coverage of lowland (mesophyll) type rainforest of lowered complexity, and overall increases in areas of open forests and woodland communities close to ecotones, rainforest boundaries and rain shadows (Hilbert *et al.* 2001). The conditions for shorter litter duration on the soil surface in rainforest, as shown here, occurs within a climate space that does not have an analogue in the current wet tropical bioregion of Australia. These environmental characteristics as a whole are generally less suitable for rainforest and co-occurring biodiversity (Hilbert *et al.* 2001; Williams *et al.* 2003).

The effects of changes in vegetation and subsequent changes in litter quality in the new climate space can potentially be inferred from knowledge of the litter characterstics of species that currently occur in warmer, more seasonally dry, tropical forests. For instance, the *Allocasuarina* sp. ecotonal forests in Australia produce poor quality litter with very high fibre and phenolic contents, while also containing $N_{2=}$fixing dominance like the similar niche occurrences of *Acacia* spp. on rainforest margins (Sanginga *et al.* 1989; Barnet and Catt 1991; Chapter 3 of this thesis). this could led to either both positive and negative effects on average litter quality over the region. To make such predictions however, we must also take into account direct climate change effects on litter quality. The potential for decreased litter quality with climate change exists; for example, heightened dry season intensity, CO_2, and temperature, may increase plant secondary compound production, due to increased light stress, and increase fibre and reduced nitrogen/nutrients (Coley 1998; Close and

McArthur 2002) and Chapter 3 of this thesis. Total phenolics are strong predictors of litter turnover and annual LSC (Chapter 6 of this thesis), and general decomposition (Palm and Rowland 1997). Any climate induced increases in litter recalcitrance (e.g. phenols) co-occurring with the changes in litter turnover shown in Figure 7.1.c would work against the increasing trend in decomposition rates. Additional reductions in canopy cover and increased deciduousness, potentially associated with seasonal rainfall reductions (Webb 1959; Webb 1978), may act to further increase evaporation rates under the canopy, lowering potential decomposition in the novel climate space.

Moisture influences on decomposition under future climates may have been underemphasised in this work to some extent. This is so because changes in cloud interception/stripping may have a large bearing on changes in decay rates not necessarily taken into direct account in the rainfall variables used by these models. Chapter 4 showed this moisture input in the dry season to be highly correlated with *in situ* decay rates and more so than dry season rainfall. The predicted decrease in cloud interception (raising cloud bases) in rainforest, in the new climate space (Pounds *et al.* 1999; Foster 2001; Pounds and Puschendorf 2004), may therefore, act to reduce increase litter duration on the soil surface, more than what the models in Figure 7.1 suggest.

Irrespective of the potential for changes in decomposition shown here, it is not possible to predict changes in the C-cycle or C-balance for forests based on changes in decomposition (as described here) alone. This is due to the complexities in soil carbon composition and turnover, photosynthesis and NPP (e.g. litter inputs), and feedbacks to the atmosphere, and year to year variations in decay dynamics (Melillo *et al.* 1993; Davidson and Janssens 2006; Sayer *et al.* 2007). Other factors

such as the influence of increased N deposition in the future are also significant (Matson *et al.* 1999). NPP is predicted to decrease in tropical forests, potentially leading to decreased litter inputs (Fung *et al.* 2005). This together with increased litter turnover directly relates to less litter on the ground annually (lower LSC). Similarly, with increased variability in rainfall inputs, the seasonality of litterfall is likely to increase, leading to ephemeral shortages in nutrient returns to plants (Chave *et al.* 2009; Chapter 6 of this thesis). This reduction of litter material on the soil surface may also have adverse effects on biodiversity, for instance litter dwelling amphibians and reptiles, as has been shown in another tropical forest (Whitfield *et al.* 2007). This scenario, coinciding with the already well documented predictions of adverse effects of future climates on rainforest biota (Hughes 2000; Williams *et al.* 2003), adds to knowledge of the risks to biodiversity in general.

For plants, slower decomposition slows nutrient release (Swift *et al.* 1979), so in the scenarios suggesting faster decomposition, seasonal nutrient enhancement is highlighted, but changes in the timing of litter inputs will govern any changes (see above). As predicted increases in decay are largely driven by higher temperature, moisture stress may also shift this in the opposite direction. Moreover, changes are likely to be driven by biotic controls on decomposition, so shifts in decomposer foodwebs are likely to dominate nutrient release pathways (Swift *et al.* 1998), along with co-occurring plant functional types (Cornwell *et al.* 2008; Ayres *et al.* 2009). Soil organism impacts on decomposition are largely climate dependent (Wall *et al.* 2008). For instance, higher temperatures raise litter invertebrate abundances (Olson 1994), and microbial communities are detrimentally affected by less moisture (Wardle 1992). The communities of soil organisms that directly or indirectly affect decomposition remain poorly understood, particularly due to difficulties in studying

the soil micro-biota. The lack of understanding of the pathways for litter community succession make predictions of future decomposition challenging (Prescott 2010). There remains much uncertainty in how litter processes will respond to climate changes, particularly due to the uncertainty in the extent of future changes in rainfall.

Chapter 8. General Discussion

A key goal of ecology is to identify patterns across ecosystems and distinguish the mechanisms determining these patterns. This thesis asked what mechanisms determine the patterns and drivers of decomposition and nutrient cycling in the rainforest communities of the Australian wet tropics bioregion. A comprehensive data set was obtained on the processes of litter decomposition and nutrients on the soil surface, filling many information gaps outlined in Figure 1.1. The results clearly demonstrate the complexity of rainforest litter processes and the importance of both biotic and abiotic controls on decomposition and nutrient cycling. The rainforests of the Australian Wet Tropics contain varied conditions for these ecosystem processes. A combination of climate and litter chemical quality was, broadly speaking, the most important determinant of decomposition and nutrient cycling processes. This chapter presents the major findings of this thesis in regards to the regional patterns and environmental drivers of decomposition and nutrient cycling in these forests, and the potential climate change impacts on processes and the forest communities.

8.1. Summary of major findings

8.1.1. *Litter chemical quality and nutrients*

The near infrared spectrometry (NIRS) method was highly effective in accurately determining litter chemical components. The method also offered a unique way of viewing relationships in regards to the whole organic chemical makeup of the

material (e.g. Figure 3.1 and Figure 4.3 and see following).

The distribution of plant litter quality in the wet tropics bioregion was largely driven by soil fertility; however, climatic and species (disturbance/succession) effects were related to the chemical composition of litterfall. Moreover, high leaf litter recalcitrance occurred in more nutrient-poor areas (i.e. soil effects of litter nutrients and nutrient effects on phenolics, Figure 3.1 and Figure 3.2) and climatically stressed environments (i.e. solar radiation/dry season intensity effects on phenolics, Figure 3.2). This provides a further limitation on nutrient cycling in more stressed conditions. There were also seasonal effects on litter chemical quality, with higher leaf litter recalcitrance occurring in the dry season, probably due to phenolics (Chapters 3 and 6). The relates to short-term changes in litter quality caused by ephemeral short-term climatic changes (Hättenschwiler and Vitousek 2000; Close and McArthur 2002). Increased dry season intensities in the current changing climate in the Australian wet tropics (Suppiah *et al.* 2007; Suppiah *et al.* 2009), and other seasonally wet tropical regions (Borchert 1998), may have direct impacts on litter quality in general.

As Townsend et al. (2007) stressed, the high local variability in litter quality in tropical rainforests needs to be properly quantified to improve understanding and models of large scale rainforest nutrient and carbon cycles. This may be especially true for cations (e.g. Ca) and lignocellulose portions, shown in this thesis to be highly spatially variable (Chapter 3). Accounting for this variation and the drivers of this variability in rainforests is essential to enable accurate understanding of future responses of rainforest nutrient cycles in a changing climate. The results of this work indicate this relates particularly to the influence of soil fertility and disturbance-driven impacts on plant communities, at both local and larger scales, and on plant life

history strategies and their effects on litter quality. This heterogeneity leads to localised variability in litter layer coverage and depth, and nutrient cycles as w whole (Chapters 3 and 6).

8.1.2. *Litter decomposition and nutrient dynamics*

The results suggest that there are nutrient limitations and strong litter quality and climate controls on decomposition and nutrient dynamics on the soil surface. This was especially true for phosphorus. Of all elements, P was in comparatively the lowest concentration, as in most tropical forests (Vitousek *et al.* 2010), however, concentrations were at the oligotrophic extreme, even for this biome (Vitousek and Sanford 1986). As found in other studies in tropical forests, nutrients are immobilised on the soil surface for long periods i.e. > 12 months until any nutrient mineralisation was seen) (Chapter 4). However, the results also generally support the premise that tropical forests exist in a "non-Liebig" world of multiple nutrient limitations (Kaspari *et al.* 2008), shown by the correlative power of all litter nutrients tested and soil sodium with leaf litter decay, and also by the immobilisation of cations (i.e. Ca) during decomposition (Chapters 4 and 6). The strong relationship in the NIRS model between the initial (before decomposition) organic chemical makeup of the leaves and the *in situ* decomposition rates (Chapter 2) is further testament to the broad chemical controls on litter processes, and the strong litter quality controls on decomposition rates for forests in general. Litter dynamics in Australian tropical rainforests generally support global trends, which suggest litter chemical quality to be the strongest control on litter decay (Cornwell *et al.* 2008; Zhang *et al.* 2008). However, irrespective of the strong litter quality controls on

decomposition, moisture seasonality drove a significant amount of the variability in decomposition dynamics in the Australian wet tropical rainforests, including the impacts of atmospheric moisture inputs (e.g. cloud stripping, shown by the leaf wetness variable in Chapters 4 and 6). Dry season intensity controls many aspects of ecosystem function and also rainforest distributions in AWT (Hopkins *et al.* 1993), and in other tropical rainforests globally (Borchert 1998). Based on this, decreased moisture inputs in the dry season alone under future climates (i.e. irrespective of temperature increases) would cause a slowing of decomposition rates in these forests. However, temperature is also a significant driver of decomposition, as was seen in the control litterbag study (Figure 4.2), and for litter standing crop (Figure 6.3.d), litter turnover (Figure 6.5.d), seen through the climate decomposition index, and lignin mineralisation (Appendix 5 and Table 7.1). This supports increased temperatures causing decreased litter duration on the soil surface in Australian tropical rainforests. The potential for these two contrasting climatic effects to combine to alter Australian tropical forest structure and function are discussed in the section below. Varied sensitivity during decomposition to temperature existed between materials, i.e. whole litter standing crop > leaf lignin > leaves (Chapters 4, 6 and 7). This trend confirms that the temperature sensitivity of litter decomposition increases with decreased litter quality (Fierer *et al.* 2005; Davidson and Janssens 2006).

8.1.3. *Litter processes and climate change in Australian tropical rainforests*

The main data chapters of this thesis (Chapters 3, 4 and 6) showed climatic controls on litter dynamics to be prominent in Australian tropical rainforests. Applying future

climate model predictions to these trends (Chapter 7) indicates the following:

- Leaf decomposition rates on average will not change dramatically from current rates up to 2080. However, if dry season rainfall rates fall to near the lower range of predictions, an opposite slowing of decay rates will occur (Figure 7.1.a).
- The leaf litter lignin mineralisation rates in leaves will either increase or remain at around current rates, dependent largely on changes in dry season rainfall (Figure 7.1.b).
- Increases in whole litter layer turnover rates are more probable than for leaf turnover and leaf litter lignin mineralisation rates (Figure 7.1.c).
- Whole litter layer turnover is predicted to increase more in upland forests (low mean annual temperature) than lowland forests (high mean annual temperature) (Figure 7.2).
- Sites on poorer soils (e.g. Spec, Carbine and Windsor uplands) are predicted to be more sensitive to change than those on richer soils (e.g. Atherton uplands), due to the changing sensitivity of decay to temperature with litter quality.

Within the bounds of the future climate predictions, these results point mostly to increased litter turnover rates into the 21st centuary in the Australian wet tropics. For litter dwelling fauna, faster decomposition and shorter litter duration on the ground means potential reductions in habitat and a need to alter life strategies. The extent of this change, however, depends greatly on the extent of changes in dry season rainfall. This factor is significant, as the seasonality of rainfall is essential in sustaining rainforest types in the Australian wet tropics and tropical rainforests globally.

The predictions mentioned above need to taken tentatively, as there are other

factors not considered directly by the climate models in Chapter 7, that may shift processes in different directions. Any change in climate is likely to lead to altered litter and nutrient dynamics and may facilitate changes in vegetation communities. More importantly, significant falls in dry season rainfall would cause succession of vegetation types towards more dry forest types and woodland communities (Hilbert *et al.* 2001), leading to significant loss of biodiversity (Hughes 2000; Williams *et al.* 2003). The effects of this would be particularly heightened if annual rainfall totals drop significantly, a factor which the climate models can not predict (Suppiah *et al.* 2007; Suppiah *et al.* 2009). A change in the vegetation makeup may be facilitated at least partly by altered soil and litter processes. These may include ephemeral nutrient shortages in the longer dry season, or enhancement of soil nutrients through faster decay, along with altered soil temperatures and soil moisture and changed under canopy micro-climate. The direct effects of climate and CO_2 on litter chemical quality, and changes in overall heterogeneity in litter quality (e.g. loss of plant biodiversity/canopy heterogeneity), will have a direct impact on litter decomposition and the dynamics of nutrients. These factors combined suggest litter quality will be lower with longer dry seasons and higher atmospheric CO_2, therefore forcing systems towards slower litter decay (Chapter 3 and Norby *et al.* 2001). An even more complex picture for general ecosystem processes in Australian tropical rainforests, and other tropical forests exists. This is due primarily to the effects of alterations in NPP and litter inputs (including the timing and seasonality of falls, Chapter 6), atmospheric nitrogen deposition, the direct effects of CO_2 on soils and productivity, and the occurrence of disturbances such as cyclones and El Niño events, in addition to transformations of the landscape caused by fire. At a global scale, increased decomposition rates, as predicted here, may lead to an acceleration of global

warming in the short term (Chapin *et al.* 2002); however, changes in rainfall and the outcomes of vegetation succession and subsequent changes in litter quality and primary productivity will have a large bearing on this premise.

8.1.4. *Future research directions*

Considering the scope of this field of ecology it is not possible to list here all of the areas where further research is needed, but some recommendations for future research directions particularly related to the Australian wet tropics are detailed below.

Litter decomposition, as determined by litter decay rates, is relatively well understood, due to large scale meta-analyses, and numerous regional scale studies such as in this thesis. Other aspects of litter decomposition are less well understood, particularly related to controls. There is a lack of understanding of the pathways of litter microbial and faunal community succession (e.g. into a warmer drier climate space) (Prescott 2010). Litter manipulation (including soil organism) and fertilisation experiments, may help determine how nutrients and other drivers such as these combine to limit and control ecosystem processes such as primary productivity and decomposition. Similarly, the lack of understanding of the spatial heterogeneity in litter chemical quality, although determined to an extent here for rainforests in the Australian wet tropics, is not detailed for other tropical forest types. This limits our ability to assess how litter and leaf characteristics may change in the changing climate. A combination of spatial analysis techniques such as remote sensing of canopy chemistry (Townsend *et al.* 2008), and species-based approaches (e.g. to determine phenotypic effects of climate and soils on litter quality), would help

uncover large scale trends. This, combined with further analysis to determine the pathways of vegetation succession in the changed climate, will help determine the areas most vulnerable to losses of significant biodiversity, facilitated through changes in ecosystem processes, and point out locations for management focus.

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Appendix 1. Climate data for sites used in this thesis. Shown is real time data (from on site data loggers) and long term averages (BIOCLIM)**.** See relevant text for variable descriptions.

Site	Elevation (m a.s.l.)	Mean annual temperature (°C)	Mean annual temperature real time (°C)	Mean annual precipitation (mm)	Mean annual radiation	Real time annual rainfall (mm)	% Dry season days 0 mm rainfall	Dry season leaf wetness	Rainfall seasonality	CDI	CDIarc
AU1	80	23.2	23.5	3436	17.8	3419	33.5	75.9	75.0	1.65	0.84
AU2	180	22.7	21.8	3379	17.8	3411	33.3	92.4	77.0	1.50	0.80
AU4	428	21.5	21.6	3142	17.9	3284	30.8	89.8	72.0	1.47	0.78
AU6	630	20.5	19.9	2955	18.0	3054	30.4	85.0	69.0	1.33	0.74
AU8	840	19.4	19.2	2635	18.2	3021	30.7	92.4	70.0	1.24	0.70
AU9	930	19.0	17.8	1846	18.8	1867	39.1	82.6	77.0	1.12	0.64
CU1	162	23.6	22.5	1899	18.8	2778	50.8	82.4	97.0	1.56	0.82
CU2	234	23.1	22.8	1772	19.0	2373	50.9	67.8	97.0	1.60	0.83
CU4	440	22.0	21.3	1591	19.2	2139	52.0	91.5	97.0	1.45	0.78
CU6	656	20.8	19.8	1494	19.2	2040	50.0	76.4	95.0	1.31	0.73
CU8	820	19.8	19.2	1719	19.0	2040	50.0	81.4	90.0	1.24	0.70
CU10	1016	18.8	17.7	2137	18.6	2528	50.9	84.9	84.0	1.11	0.64
CU12	1210	17.7	16.0	2672	18.2	2925	49.1	80.3	78.0	1.00	0.58
SU3	334	22.3	21.3	1384	19.3	1594	55.5	67.8	105.0	1.40	0.76
SU6	671	20.5	20.0	1631	19.1	1594	55.5	78.3	102.0	1.28	0.72
SU8	834	19.7	17.9	2116	18.7	1658	55.0	68.3	99.0	1.13	0.65
SU10	963	19.0	17.6	2393	18.5	1829	54.7	74.1	96.0	1.10	0.63
WU9	940	19.1	19.4	1946	18.8	2151	42.1	76.3	87.0	1.25	0.70
WU11	1071	18.5	17.1	2153	18.6	2825	40.0	86.1	84.0	1.06	0.62
WU13	1280	17.4	16.7	2546	18.3	3067	38.0	66.5	80.0	1.03	0.60

Appendix 2. Characteristics of the detailed monitoring plots used in this thesis. Shown are the vegetation characteristics, geology, soil description and soil chemical composition. See end of table for legend.

Plot	Veg type[$]	Plant species richness[¢]	Tree species richness[¢]	Individuals[¢]	Gap species (%)[¢]	Geology[€]	Soil description[£]	Soil N	Soil P	Soil Ca	Soil Na	Soil Mg	Soil K	Soil TOC
AU1A1	CS/CMVF	21	7	42	14.6	A/M	Rudosol	0.27±0.001^{b}	0.030±0.0001^{a}	0.060±0.003	0.079±0.01^{fg}	0.0082±0.003^{i}	0.87±0.08^{l}	18.91±1.57^{cd}
								bcde		efgh				efghIj
AU1A3	CS/CMVF	28	5	49	32.6	A/M	Rudosol	0.22±0.06^{b}	0.021±0.001^{ab}	0.060±0.012	0.054±0.003	0.0049±0.001^{fg}	0.53±0.09^{jk}	19.27±4.09^{cd}
										defgh	cdef	hi	l	efghIj
AU2A2	CS/CMVF	10	4	15	30.8	A/B	Hydrosol/ Ferrosol	0.11±0.01^{a}	0.029±0.007^{abc}	0.185±0.011^{j}	0.046±0.003	0.0187±0.001^{j}	0.66±0.05^{kl}	12.55±0.03^{ab}
									de	k	bcdef			cd
AU2A5	CS/CMVF	22	9	31	33.3	A	Ferrosol	0.33±0.01^{c}	0.065±0.000^{bcd}	0.254±0.011	0.040±0.010	0.0058±0.001^{fg}	0.39±0.03^{Ij}	17.28±2.20^{bc}
									efg	kl	abcd	hi	kl	defghIj
AU4A2	CS/CMVF	32	15	58	18.2	B	Ferrosol	0.40±0.13^{c}	0.163±0.009^{gh}	0.159±0.007^{i}	0.045±0.005	0.0037±0.001^{cd}	0.05±0.00^{ab}	17.45±1.21^{bc}
										jk	bcdef	efghi	cd	defghI
AU4A5	CS/CMVF	19	8	27	15.4	B	Ferrosol	1.01±0.03^{f}	0.195±0.001^{cde}	0.380±0.002	0.043±0.01^{a}	0.0045±0.001^{de}	0.06±0.00^{ab}	34.08±5.76^{lm}
									fg	m	bcde	fghi	cde	
AU6A2	CS/NVF	20	8	32	34.4	G/B	Ferrosol	0.73±0.22^{e}	0.097±0.010^{def}	0.369±0.037^{l}	0.037±0.01^{a}	0.0027±0.001^{bc}	0.07±0.01^{ab}	20.66±4.47^{gh}
									g	m	bcd	defghi	cdefgh	lj
AU6A5	CS/NVF	24	14	64	14.5	B	Ferrosol	0.46±0.03^{cde}	0.123±0.006^{fgh}	0.24±0.008	0.034±0.01^{a}	0.0039±0.002^{cd}	0.07±0.01^{ab}	18.6±2.77^{bcde}
										k	bcd	efghi	cdefg	fghI
AU8A2	CS/NVF	30	14	42	9.5	B	Ferrosol	0.34±0.03^{c}	0.139±0.004^{gh}	0.038±0.000	0.040±0.01^{a}	0.0034±0.002^{bc}	0.04±0.01^{ab}	19.78±0.11^{cd}
										abcdefgh	bcd	defghi	c	efghIj
AU8A5	CS/NVF	ND	ND	ND	ND	B	Ferrosol	0.35±0.13^{c}	0.101±0.003^{efg}	0.025±0.001	0.032±0.003	0.0038±0.001^{cd}	0.02±0.00^{a}	26.54±5.05^{hI}
										abcdefg	abcd	efghi		jkl
AU9A2	NVF	18	9	31	17.2	B	Ferrosol	0.47±0.14^{cde}	0.216±0.008^{h}	0.056±0.003	0.029±0.008	0.0026±0.001^{bc}	0.03±0.00^{ab}	22.37±2.48^{gh}
										cdefgh	abcd	defghi		lj
AU9A5	NVF	19	10	29	0.0	B	Ferrosol	0.50±0.18^{de}	0.102±0.005^{efg}	0.012±0.001	0.034±0.007	20.0044±0.001	0.02±0.00^{a}	23.27±0.11^{gh}
									h	abc	abcd	7^{cdefghi}		lj
CU1A1	MVF	10	3	26	0.0	G	Kandosol	0.28±0.08^{b}	0.021±0.002^{ab}	0.039±0.003	0.032±0.001	0.0025±0.0002	0.12±0.01^{bc}	17.51±1.10^{bc}
										abcdefgh	abcd	bcdefghi	defghI	defghI
CU1A3	MVF	14	6	26	0.0	G	Kandosol	0.21±0.09^{ab}	0.033±0.002^{abc}	0.100±0.009	0.025±0.008	0.0016±0.0001	0.11±0.01^{bc}	18.84±1.37^{cd}
									de	hij	ab	bcdefg	defghI	efghIj

Appendix 2. continued.

Plot	Veg type[$]	Plant species richness[¢]	Tree species richness[¢]	Individuals[¢]	Gap species (%)[¢]	Geology[€]	Soil description[£]	Soil N	Soil P	Soil Ca	Soil Na	Soil Mg	Soil K	Soil TOC
CU2A1	MVF	ND	ND	ND	ND	G	Kandosol	0.26±0.09^{ab}	0.026±0.01^{abcd}	0.038±0.002^{abcdefgh}	0.028±0.005^{abc}	0.0034±0.002^{bc} ^{defghi}	0.18±0.01^{de} ^{fghIjk}	18.75±3.45^{de} ^{fghIj}
CU2A5	MVF	ND	ND	ND	ND	G	Kandosol	0.26±0.12^{ab}	0.018±0.002^{ab}	0.006±0.003^{a}	0.049±0.009^{bcdef}	0.0031±0.0004^{bcdefghi}	0.12±0.01^{bc} ^{defghI}	16.91±2.92^{cd} ^{efghIj}
CU4A2	MVF	26	10	54	10.0	G	Kandosol	0.34±0.10^{c}	0.013±0.002^{ab}	0.012±0.001^{abc}	0.091±0.018^{g}	0.0081±0.005^{hi}	0.43±0.08^{Ij} ^{kl}	22.37±0.19^{gh} ^{Ij}
CU4A5	MVF	11	10	22	0.0	G	Kandosol	0.26±0.10^{ab}	0.010±0.0001^{a}	0.017±0.005^{abcde}	0.042±0.014^{abcd}	0.0061±0.002^{gh} ^{i}	0.22±0.13^{de} ^{fghIjk}	16.11±2.53^{ab} ^{cdefgh}
CU6A2	NVF	9	8	21	0.0	G	Kandosol	0.24±0.05^{b}	0.026±0.007^{abc} ^{d}	0.014±0.002^{abcde}	0.051±0.020^{bcdef}	0.0047±0.002^{ef} ^{ghi}	0.21±0.20^{cd} ^{efghIj}	8.27±1.81^{bcde} ^{fghI}
CU6A5	NVF	13	5	41	0.0	G	Kandosol	0.20±0.001^{b}	0.018±0.003^{ab}	0.014±0.001^{abcde}	0.046±0.004^{bcdef}	0.0061±0.001^{gh} ^{i}	0.54±0.15^{jk} ^{l}	11.39±0.11^{bc} ^{defghIj}
CU8A2	NVF	30	17	79	0.0	G	Kandosol	0.10±0.001^{a}	0.022±0.001^{abc}	0.013±0.001^{abc}	0.053±0.003^{cdef}	0.0025±0.0003^{bcdefghi}	0.50±0.05^{jk} ^{l}	28.96±0.36^{k}
CU8A5	NVF	26	19	63	14.8	G	Kandosol	0.29±0.03^{b}	0.016±0.000^{ab}	0.010±0.000^{ab}	0.057±0.016^{defg}	0.0053±0.003^{fg} ^{hi}	0.38±0.03^{Ij} ^{kl}	13.74±1.30^{ab} ^{cdefgh}
CU10A2	NVF	13	5	30	20.0	G	Kandosol	0.13±0.08^{a}	0.047±0.003^{abc} ^{def}	0.020±0.001^{abcde}	0.075±0.007^{efg}	0.0057±0.002^{fg} ^{hi}	0.42±0.10^{Ij} ^{kl}	5.42±1.35^{ab}
CU10A5	NVF	14	8	24	12.5	G	Kandosol	0.26±0.10^{ab}	0.039±0.008^{abc} ^{de}	0.019±0.003^{abcde}	0.052±0.006^{cdef}	0.0018±0.001^{bc} ^{defg}	0.32±0.10^{Ij} ^{kl}	7.61±4.57^{ab}
CU12A2	MFF	15	10	45	35.6	G	Kandosol	0.13±0.02^{ab}	0.039±0.005^{abc} ^{de}	0.010±0.004^{ab}	0.038±0.009^{abcd}	0.0023±0.0004^{bcdefgh}	0.31±0.11^{hI} ^{jkl}	7.71±0.22^{abc}
CU12A5	MFF	32	21	68	0.0	G	Kandosol	0.17±0.07^{ab}	0.035±0.004^{abc} ^{de}	0.015±0.01^{ab} ^{cd}	0.027±0.006^{abc}	0.0018±0.001^{bc} ^{defg}	0.28±0.11^{fg} ^{hIjkl}	21.72±4.02^{hI} ^{j}
SU3A1	NVF	12	4	41	9.1	R	Dermosol	0.26±0.10^{ab}	0.018±0.001^{ab}	0.042±0.03^{ab} ^{cdefgh}	0.033±0.014^{abcd}	0.0017±0.001^{bc} ^{de}	0.17±0.02^{de} ^{fghIjk}	10.37±1.96^{ab} ^{cdefg}
SU3A2	NVF	15	10	22	22.0	R	Dermosol	0.25±0.17^{ab}	0.018±0.003^{ab}	0.082±0.02^{gh} ^{i}	0.029±0.007^{abcd}	0.0048±0.01^{bcde} ^{fg}	0.15±0.05^{cd} ^{efghIj}	9.68±2.30^{abcd} ^{e}

Appendix 2. continued.

Plot	Veg type[$]	Plant species richness[¢]	Tree species richness[¢]	Individuals[¢]	Gap species (%)[¢]	Geology[€]	Soil description[£]	Soil N	Soil P	Soil Ca	Soil Na	Soil Mg	Soil K	Soil TOC
SU6A1	MOF	11	7	27	48.2	R	Dermosol	0.41±0.03^{c}	0.009±0.001^{a}	0.049±0.03^{bc} defgh	0.027±0.004 abc	0.0014±0.001^{cd} efghi	0.25±0.12^{ef} ghIjkl	34.23±2.36^{lm}
SU6A2	MOF	8	5	22	31.8	R	Dermosol	0.14±0.10^{ab}	0.008±0.002^{a}	0.228±0.02^{k}	0.033±0.011 abcd	0.0004±0.0001 bcdef	0.35±0.07^{fj} kl	20.23±4.78^{gh} Ij
SU8A1	NVF	10	3	28	0.0	R	Dermosol	0.44±0.04^{cde}	0.013±0.001^{ab}	0.009±0.002 ab	0.035±0.01^{a} bcd	0.0018±0.001^{b}	0.25±0.17^{ef} ghIjkl	3.2±0.39^{a}
SU8A2	NVF	15	7	26	0.0	R	Dermosol	0.42±0.31^{abc}	0.037±0.0001^{a} bcde	0.029±0.004 abcdefg	0.038±0.004 abcd	0.0047±0.0002 bcdefg	0.30±0.03^{hI} jkl	14.31±2.60^{ab} cdefgh
SU10A2	A-CF	12	7	20	0.0	G	Kandosol	0.43±0.30^{abc}	0.011±0.002^{abc}	0.026±0.01^{ab} cdef	0.028±0.005 abcd	0.0006±0.001^{bc} de	0.24±0.04^{ef} ghIjkl	22.1±2.03^{hIj}
SU10A5	A-CF	7	6	16	0.0	G	Kandosol	0.60±0.29^{e}	0.022±0.002^{ab}	0.018±0.005 abcde	0.022±0.001 ab	0.0002±0.0003 b	0.26±0.05^{fg} hIjkl	15.18±1.00^{fg} hIj
WU9A2	NVF-AG	13	5	40	4.2	G	Kandosol	0.11±0.01^{ab}	0.016±0.0001^{a} bc	0.023±0.04^{ab} cdefg	0.022±0.001 abcd	0.0002±0.003^{b}	0.19±0.02^{fj} kl	10.18±2.01^{ab} cdefg
WU9A5	NVF-AG	13	9	24	14.8	G	Kandosol	0.14±0.10^{ab}	0.018±0002^{abc}	0.023±0.04^{ab} cdefg	0.022±0.001 ab	0.0002±0.003^{v}	0.19±0.02^{fj} kl	12.15±1.9^{abcd} efg
WU11A2	NVF	14	7	27	42.5	G	Kandosol	0.15±0.06^{ab}	0.028±0.003^{abc} de	0.097±0.08^{fg} hi	0.027±0.005 abc	0.0008±0.001^{ef} ghi	0.24±0.18^{cd} efghIj	9.88±0.23^{abcd} ef
WU11A5	NVF	16	7	27	18.5	G	Kandosol	0.15±0.04^{ab}	0.024±0.000^{1ab} c	0.018±0.005 abcde	0.020±0.005 a	0.0004±0.0001 bcd	0.13±0.16^{ab} cdefg	18.45±8.25^{cd} efghIj
WU13A2	MFF	21	15	48	2.1	G	Kandosol	0.17±0.07^{ab}	0.014±0.004^{ab}	0.010±0.006 ab	0.020±0.002 a	0.0002±0.001^{bc}	0.08±0.05^{ab} cdef	14.16±2.66^{ab} cdefghI
WU13A5	MFF	21	13	35	0.0	G	Kandosol	0.14±0.02^{ab}	0.019±0.006^{ab}	0.039±0.03^{ab} cdefg	0.028±0.002 abc	0.0001±0.0001 a	0.12±0.02^{bc} defghI	25.06±8.11^{hI} j

[$]CS = cyclone damaged; CMVF complex mesophyll vine forest; MVF = mesophyll vine forest; NVF = notophyll vine forest; MFF = microphyll fern forest; MOF = medium open forest with regenerating rainforest understory; A-CF = Acacia sp. closed forest; NVF-AG = notophyll vine forest with Agathis sp. emergents (after Webb 1978 and Specht 1970). [¢]from belt transect work (20 x 2 m), count of all plant species (trees and shrubs > 1.6 m), trees ≥ 5 m, number of individuals, % gap/pioneer/early secondary species (After Hyland et al. 2002); [€]A= Alluvium, R = rhyolite, B = basalt, M = mudstone; [£]after Isbell 2002.

Appendix 3. Mathematical expressions used to calculate the Climate Decomposition Index variable used in this thesis after Lloyd and Taylor (1989) and Adair et al. (2009).

Annual CDIs are the mean value of monthly CDI_i values, which are calculated as a function of the mean monthly air temperature (T_i), monthly precipitation (PPT_i) and the monthly potential evapotranspiration (PET_i). PET_i is calculated using solar radiation (calculated from latitude and time of the year), monthly maximum air temperature and relative humidity (Adair et al. 2009).

$$CDI = F_T(T_i) \times F_W(PPT_i, PET_i), \quad (1)$$

$$F_W(PPT_i, PET_i) = \frac{1}{1 + 30 \times \exp\left(-8.5 \times \frac{PPT_i}{PET_i}\right)}, \quad (2)$$

$$F_T(T_i) = 0.5766 \times \exp\left[308.56 \times \left(\frac{1}{56.02} - \frac{1}{(273 + T_i) - 227.13}\right)\right], \quad (3)$$

where F_W (PPT_i, PET_i) and F_T(T_i) are the monthly effects of water stress and temperature on decomposition (Lloyd and Taylor 1989).

Appendix 4a. Spearman rank correlations and significance values of initial litter chemistry variables used in best sub-set regression analysis explaining leaf litter decomposition rates in Australian tropical rainforest.

(a)	N	ADF	ADL	Ca	Cellulose	Mg	P	C	Phenolics	C:N	C:P	ADL:N	ADL:P	ADF:N	ADF:P
N	1.000														
	.														
ADF	-0.390	1.000													
	0.122	.													
ADL	-0.493	0.914	1.000												
	0.045	0.000	.												
Ca	0.505	-0.419	-0.659	1.000											
	0.039	0.094	0.004	.											
Cellulose	0.385	0.179	-0.074	0.539	1.000										
	0.127	0.492	0.779	0.026	.										
Mg	0.152	-0.289	-0.294	0.299	0.167	1.000									
	0.560	0.260	0.252	0.244	0.523	.									
P	0.946	-0.301	-0.505	0.681	0.583	0.162	1.000								
	0.000	0.240	0.039	0.003	0.014	0.535	.								
C	-0.287	0.233	0.373	-0.787	-0.316	-0.436	-0.397	1.000							
	0.264	0.368	0.141	0.000	0.216	0.080	0.115	.							
Phenolics	-0.569	-0.199	0.025	-0.574	-0.868	-0.223	-0.723	0.453	1.000						
	0.017	0.445	0.926	0.016	0.000	0.390	0.001	0.068	.						
C:N	-0.993	0.392	0.500	-0.544	-0.407	-0.194	-0.944	0.355	0.591	1.000					
	0.000	0.119	0.041	0.024	0.105	0.456	0.000	0.162	0.013	.					
C:P	-0.931	0.326	0.522	-0.699	-0.630	-0.208	-0.980	0.446	0.750	0.939	1.000				
	0.000	0.202	0.032	0.002	0.007	0.422	0.000	0.073	0.001	0.000	.				
ADL:N	-0.951	0.515	0.637	-0.542	-0.407	-0.248	-0.914	0.297	0.515	0.944	0.914	1.000			
	0.000	0.035	0.006	0.025	0.105	0.338	0.000	0.248	0.035	0.000	0.000	.			
ADL:P	-0.941	0.360	0.556	-0.684	-0.600	-0.216	-0.985	0.412	0.706	0.944	0.995	0.939	1.000		
	0.000	0.155	0.020	0.002	0.011	0.406	0.000	0.101	0.002	0.000	0.000	0.000	.		
ADF:N	-0.953	0.569	0.610	-0.446	-0.279	-0.255	-0.860	0.252	0.402	0.946	0.865	0.961	0.890	1.000	
	0.000	0.017	0.009	0.073	0.277	0.323	0.000	0.328	0.110	0.000	0.000	0.000	0.000	.	
ADF:P	-0.956	0.392	0.551	-0.623	-0.515	-0.179	-0.978	0.343	0.645	0.951	0.968	0.951	0.983	0.917	1.000
	0.000	0.119	0.022	0.008	0.035	0.492	0.000	0.178	0.005	0.000	0.000	0.000	0.000	0.000	.

Appendix 4b. Spearman rank correlations and significance values of soil compositions used in best sub-set regression analysis explaining leaf litter decomposition rates in Australian tropical rainforest.

(b)	Soil N	Soil P	Soil C	Soil pH	Soil cond.	Soil Mg	Sand	Silt	Clay	Soil K	Soil Ca	Soil Na
Soil N	1.000											
	.											
Soil P	0.341	1.000										
	0.181	.										
Soil TOC	0.336	0.309	1.000									
	0.188	0.227	.									
Soil pH	0.444	0.377	-0.029	1.000								
	0.074	0.136	0.911	.								
Soil cond.	0.500	0.193	0.483	0.139	1.000							
	0.041	0.459	0.049	0.596	.							
Soil Mg	-0.056	0.197	0.373	-0.166	-0.114	1.000						
	0.830	0.448	0.141	0.525	0.663	.						
Sand	-0.606	-0.298	-0.604	0.041	-0.470	-0.328	1.000					
	0.010	0.246	0.010	0.877	0.057	0.199	.					
Silt	0.606	0.038	0.563	-0.005	0.247	0.440	-0.758	1.000				
	0.010	0.885	0.019	0.985	0.338	0.077	0.000	.				
Clay	0.333	0.340	0.582	-0.140	0.421	0.223	-0.757	0.265	1.000			
	0.192	0.182	0.014	0.592	0.092	0.389	0.000	0.303	.			
Soil K	-0.586	-0.524	-0.314	-0.372	-0.267	0.341	0.405	-0.092	-0.454	1.000		
	0.013	0.031	0.220	0.142	0.300	0.181	0.107	0.725	0.067	.		
Soil Ca	0.407	0.454	0.230	0.754	0.136	0.056	-0.222	0.320	-0.049	-0.338	1.000	
	0.105	0.067	0.374	0.000	0.602	0.830	0.392	0.210	0.852	0.184	.	
Soil Na	-0.299	0.186	0.279	-0.395	-0.222	0.875	-0.216	0.259	0.234	0.512	-0.157	1.000
	0.244	0.474	0.277	0.117	0.392	0.000	0.405	0.316	0.365	0.036	0.548	.

Appendix 4c. Spearman rank correlations and significance values of climate data used in best sub-set regression analysis explaining leaf litter decomposition rates in Australian tropical rainforest.

(c)	MAT	AirT	SoilT	Rain	MAP	DS0MM	MAPCV	LWDS
MAT	1.000							
	.							
AirT	0.920	1.000						
	0.000	.						
SoilT	0.756	0.757	1.000					
	0.000	0.000	.					
Rain	0.194	0.321	0.139	1.000				
	0.456	0.209	0.596	.				
MAP	-0.152	-0.076	0.074	0.735	1.000			
	0.560	0.772	0.779	0.001	.			
DS0MM	0.039	-0.101	-0.092	-0.521	-0.673	1.000		
	0.881	0.701	0.726	0.032	0.003	.		
MAPCV	0.178	0.063	0.075	-0.504	-0.769	0.922	1.000	
	0.494	0.812	0.775	0.039	0.000	0.000	.	
LWDS	0.081	0.093	-0.078	0.291	0.292	-0.477	-0.611	1.000
	0.757	0.722	0.765	0.258	0.256	0.053	0.009	.

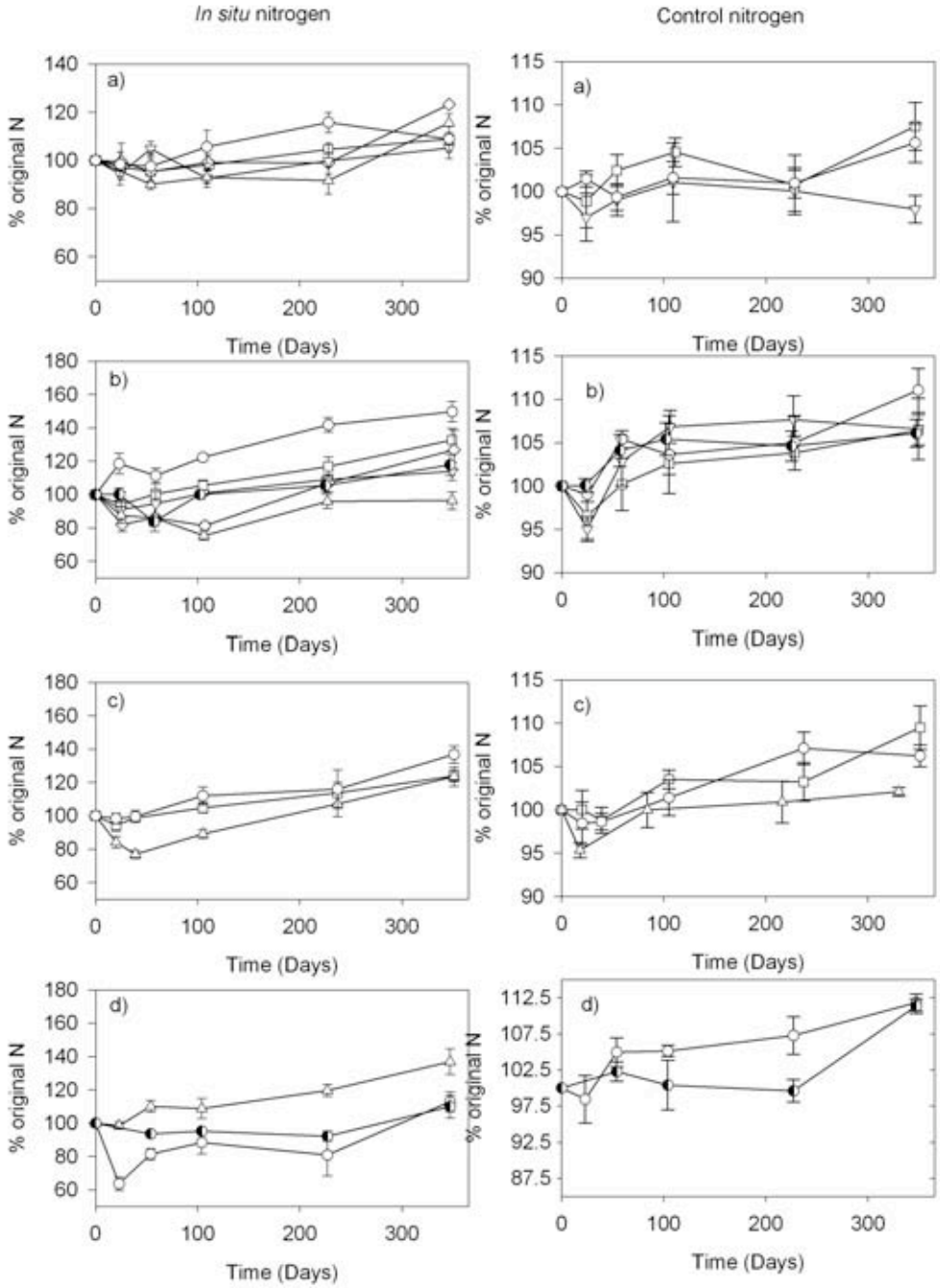
Appendix 5a. Results from best sub-set regression analysis on control *Archidendron vaillantii* leaf litter decomposition rate (*k*) for soil, climate and the best sub-set, and lignin decay (as % lignin loss yr^{-1}) best sub-set.

		Model	Est.	Std. err	t	p	Residuals					BIC
Control k	Soil	(Intercept)	0.42	0.075	5.68	0.00	**Min**	**1st Q**	**Median**	**3rd Q**	**Max**	-4.03
		SoilP	3.26	0.99	3.31	0.01	-0.28	-0.12	-0.05	0.04	0.47	
							Res. SE	**df**	**Adj. R^2**	**F**	**Model p**	
							0.20	10.00	0.52	10.94	0.008	
	Climate	(Intercept)	0.40	0.60	0.67	0.52	**Min**	**1st Q**	**Median**	**3rd Q**	**Max**	-6.96
		MAT	0.06	0.03	2.14	0.06	-0.24	-0.08	0.03	0.08	0.26	
		ds0mm	-0.02	0.00	-3.80	0.00	**Res. SE**	**df**	**Adj. R^2**	**F**	**Model p**	
							0.17	9.00	0.63	10.46	0.00	
	Best ss	(Intercept)	-0.09	0.59	-0.15	0.89	**Min**	**1st Q**	**Median**	**3rd Q**	**Max**	-8.66
		SoilP	1.74	0.95	1.83	0.11	-0.25	-0.07	0.02	0.07	0.17	
		MAT	0.06	0.02	2.73	0.03	**Res. SE**	**df**	**Adj. R^2**	**F**	**Model p**	
		ds0mm	-0.01	0.00	-2.82	0.02	0.15	8.00	0.71	9.90	0.00	
Control lignin (% yr^{-1})	Best ss	(Intercept)	27.54	7.39	3.73	0.004	**Min**	**1st Q**	**Median**	**3rd Q**	**Max**	-5.16
		AirT	0.61	0.30	2.02	0.07	-2.93	-1.78	0.036	1.30	4.18	
		ds0mm	-0.22	0.07	-3.07	0.01	**Res. SE**	**df**	**Adj. R^2**	**F**	**Model p**	
							2.39	9	0.57	8.37	0.009	

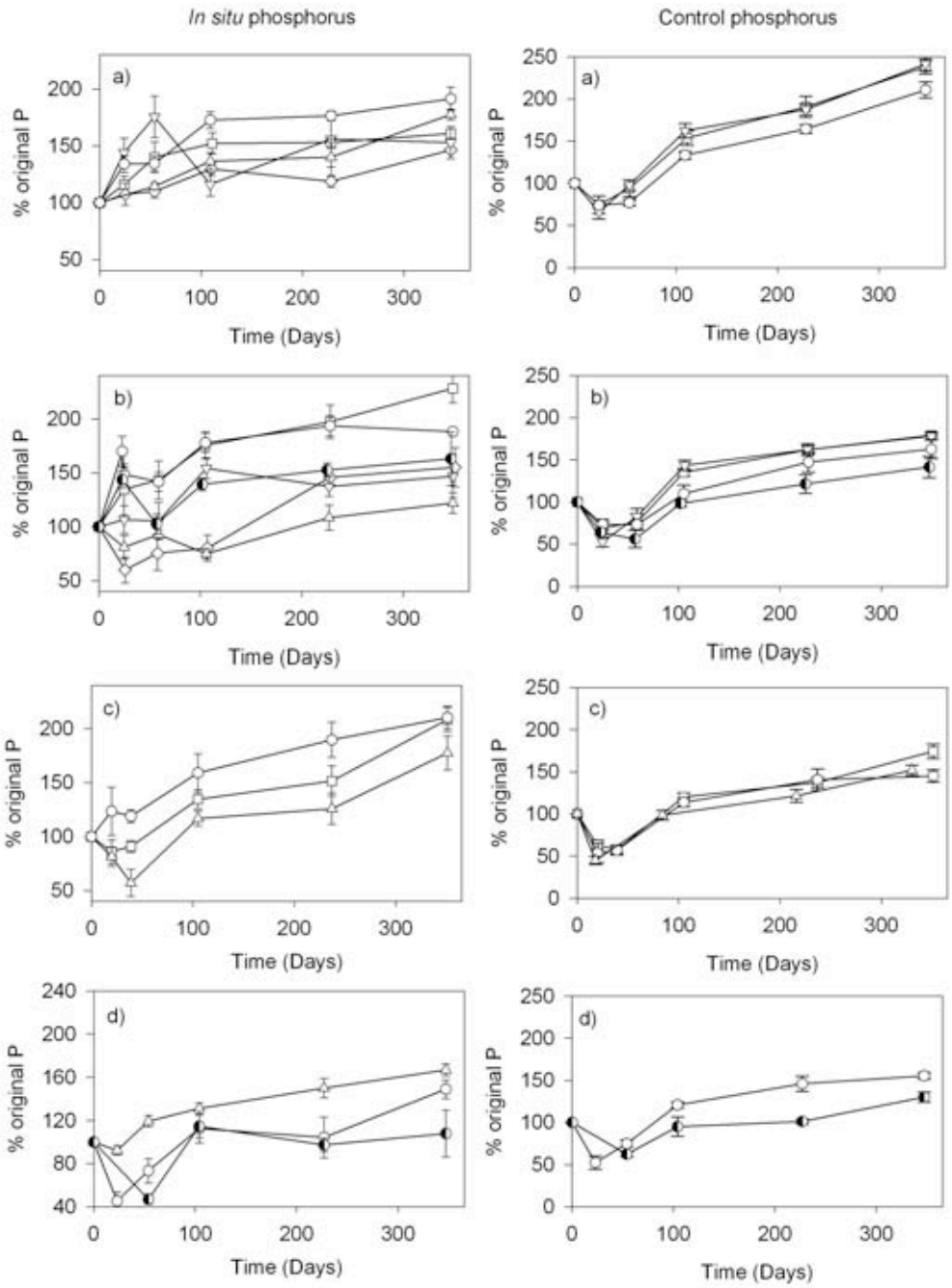
Appendix 5b. Results from best sub-set regression analysis on *in situ* litterbag decomposition rate (*k*). Models are for Initial chemistry, soil composition, climate and the best sub-set combination. LF* = initial leaf P and C.

		Model	Est.	Std. err	t	p	Residuals					BIC
In situ k	Initial Chem	(Intercept)	6.63	3.34178	1.983	0.069	**Min**	**1st Q**	**Median**	**3rd Q**	**Max**	-18.06
		Mg	3.41	1.66158	2.053	0.061	-0.35	-0.14	-0.003	0.12	0.39	
		P	18.65	4.53395	4.113	0.001	**Res. SE**	**df**	**Adj. R^2**	**F**	**Model p**	
		C	-0.147	0.06326	-2.329	0.037	0.24	13	0.78	13	0.000	
	Soil	(Intercept)	0.35	0.22	1.63	0.12	**Min**	**1st Q**	**Median**	**3rd Q**	**Max**	-7.14
		Soil P	6.48	1.49	4.34	0.00	-0.72	-0.12	0.06	0.20	0.50	
		Soil Na	7.69	4.29	1.79	0.10	**Res. SE**	**df**	**Adj. R^2**	**F**	**Model p**	
							0.34	14.00	0.54	10.56	0.000	
	Climate	(Intercept)	-2.82	0.63	-4.52	0.00	**Min**	**1st Q**	**Median**	**3rd Q**	**Max**	-15.25
		MAP	0.00	0.00	3.73	0.00	-0.36	-0.14	-0.05	0.14	0.53	
		LWDS	0.03	0.01	4.70	0.00	**Res. SE**	**df**	**Adj. R^2**	**F**	**Model p**	
							0.27	14.00	0.72	21.31	0.000	
	Best ss	(Intercept)	6.58	2.50	2.63	0.021	**Min**	**1st Q**	**Median**	**3rd Q**	**Max**	-26.21
		LWDS	0.021	0.006	3.85	0.002	-0.25	-0.10	0.001	0.149	0.252	
		LFP	15.09	3.75	4.02	0.0015	**Res. SE**	**df**	**Adj. R^2**	**F**	**Model p**	
		LFC	-0.163	0.047	-3.43	0.0044	0.19	13	0.87	35.1	0.000	

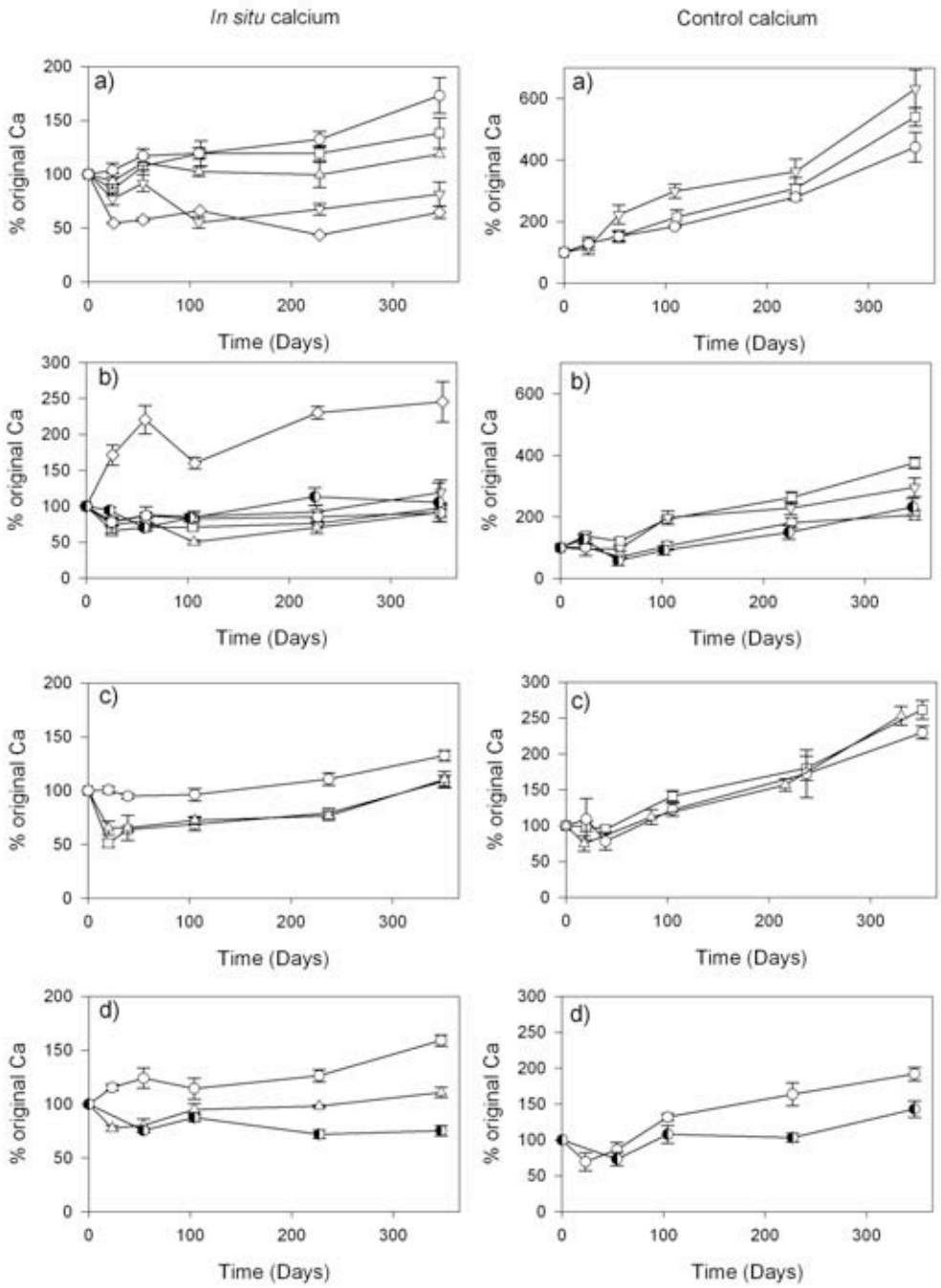
Appendix 6. Plots of % remaining over time of chemical components of *in situ* and control leaf litter during decomposition. Plots are of total N, P, C, Ca, acid detergent fibre, acid detergent lignin and cellulose. Sites came from four sub-regions: (a) AU: Atherton uplands; (b) CU: Carbine uplands; (c) SU: Spec uplands; (d) WU: Windsor uplands. Sites are from different (approximate) elevations within each sub-region: □ - 100 m a.s.l. (CU and AU) and 300 m a.s.l. (SU); ◇ - 400 m a.s.l. (AU and CU); ▽ - 600 m a.s.l (AU and CU); △ - 800 m a.s.l. (AU and CU) and 900 m a.s.l. (WU); ◯ - 900 m a.s.l. (AU), 1000 m a.s.l. (CU and SU) and 1100 m a.s.l. (WU); ◐ - 1200 m a.s.l. (CU) and 1300 m a.s.l. (WU). See Table 1 for actual m a.s.l.



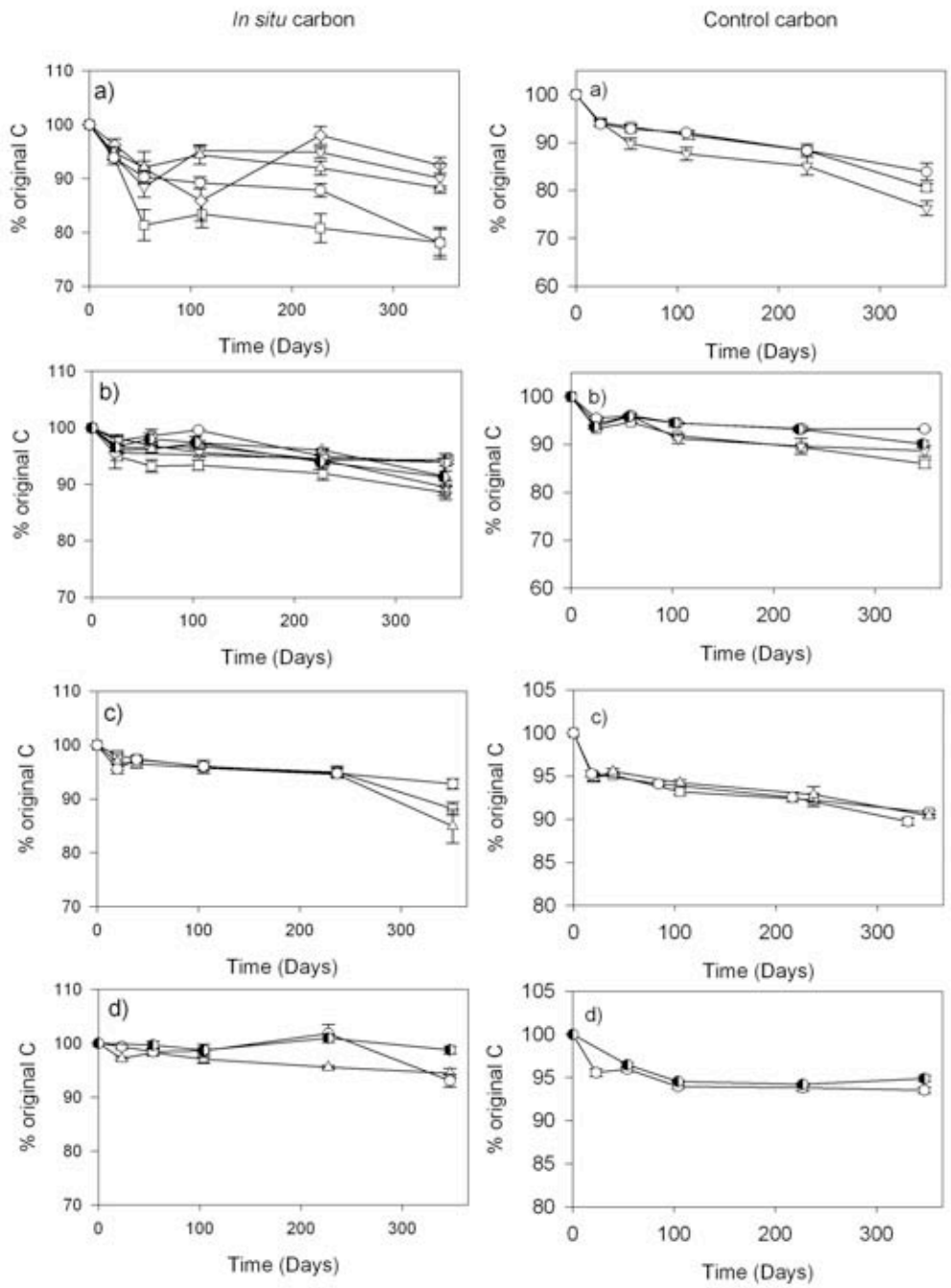
Appendix 6. continued.



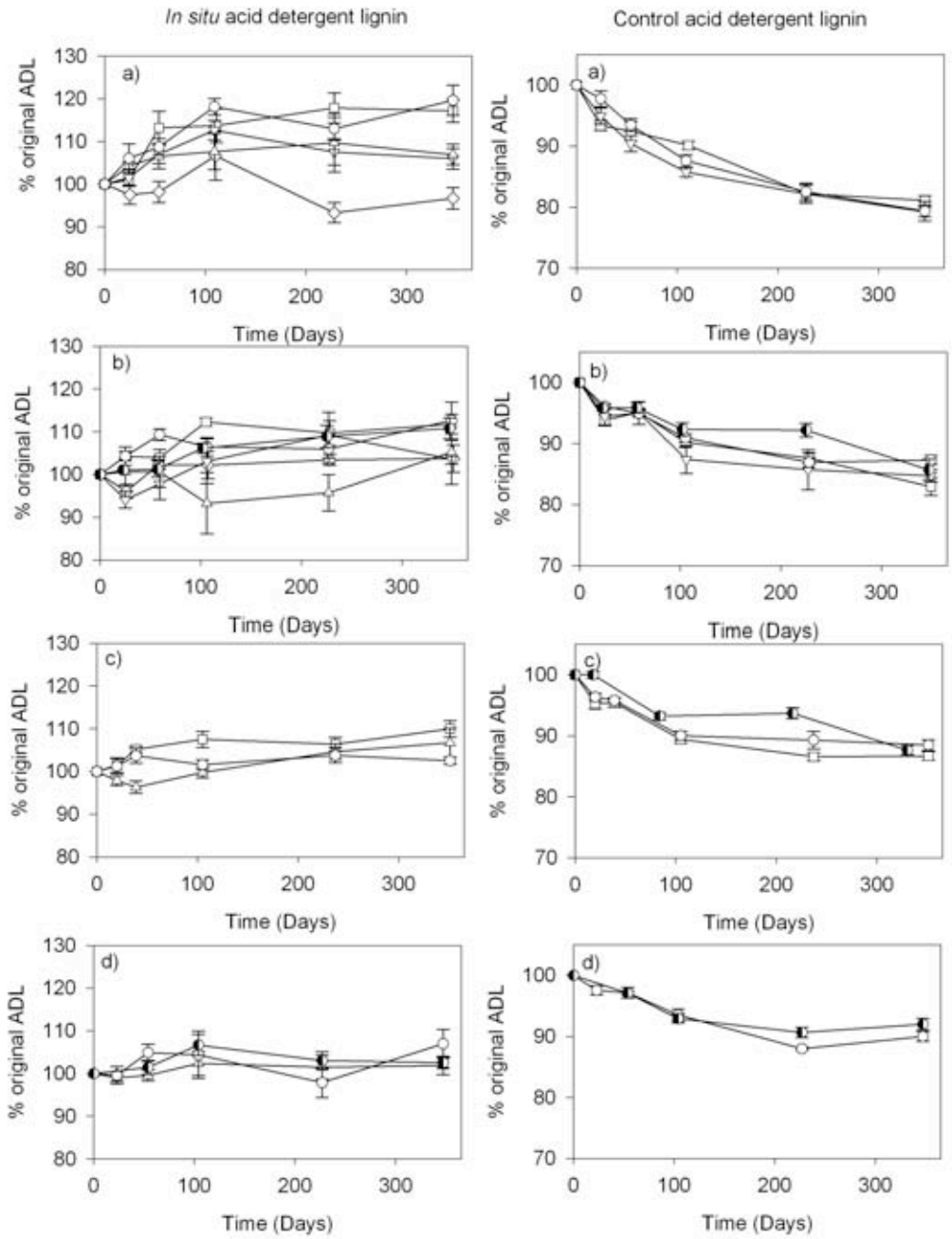
Appendix 6. continued.



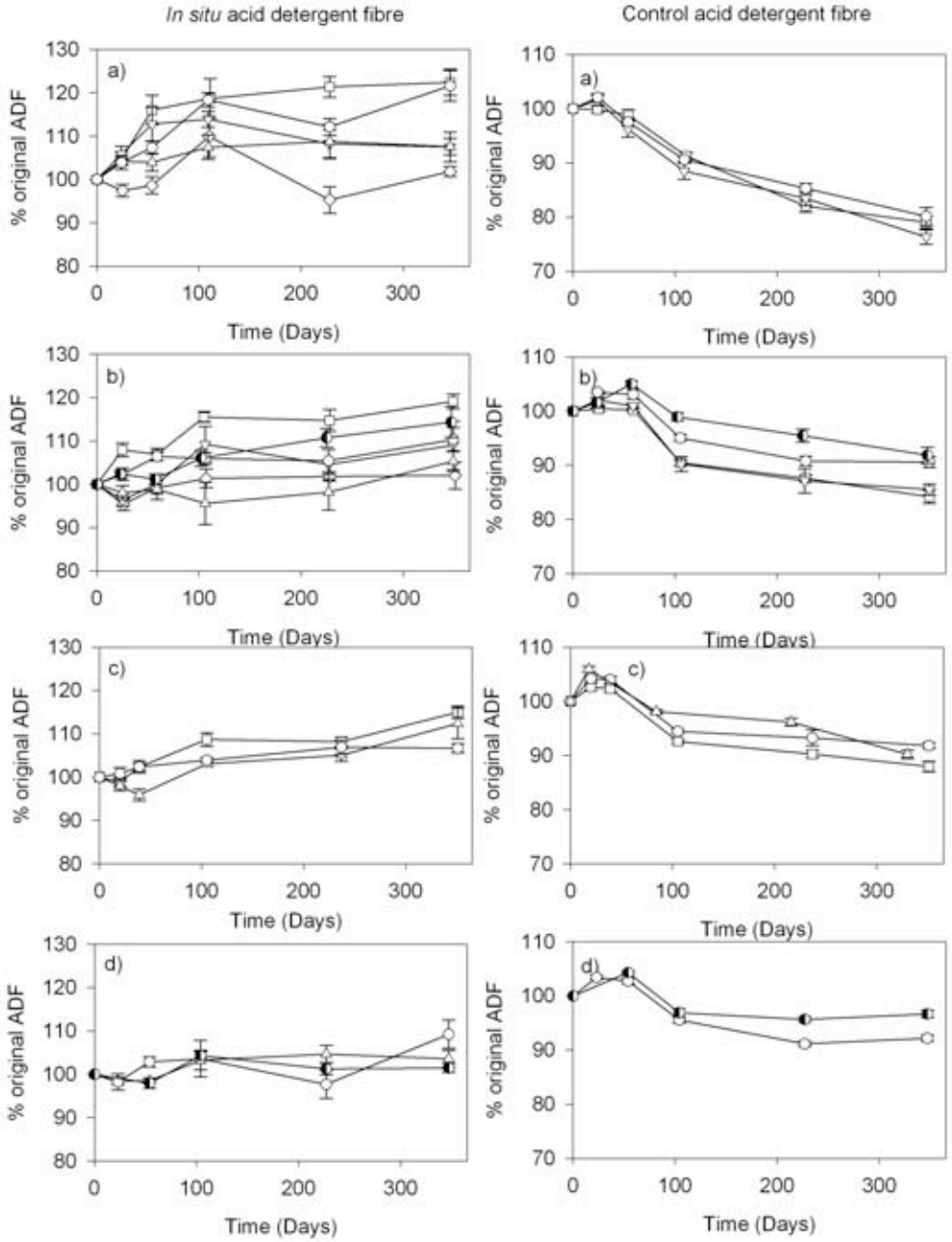
Appendix 6. continued.



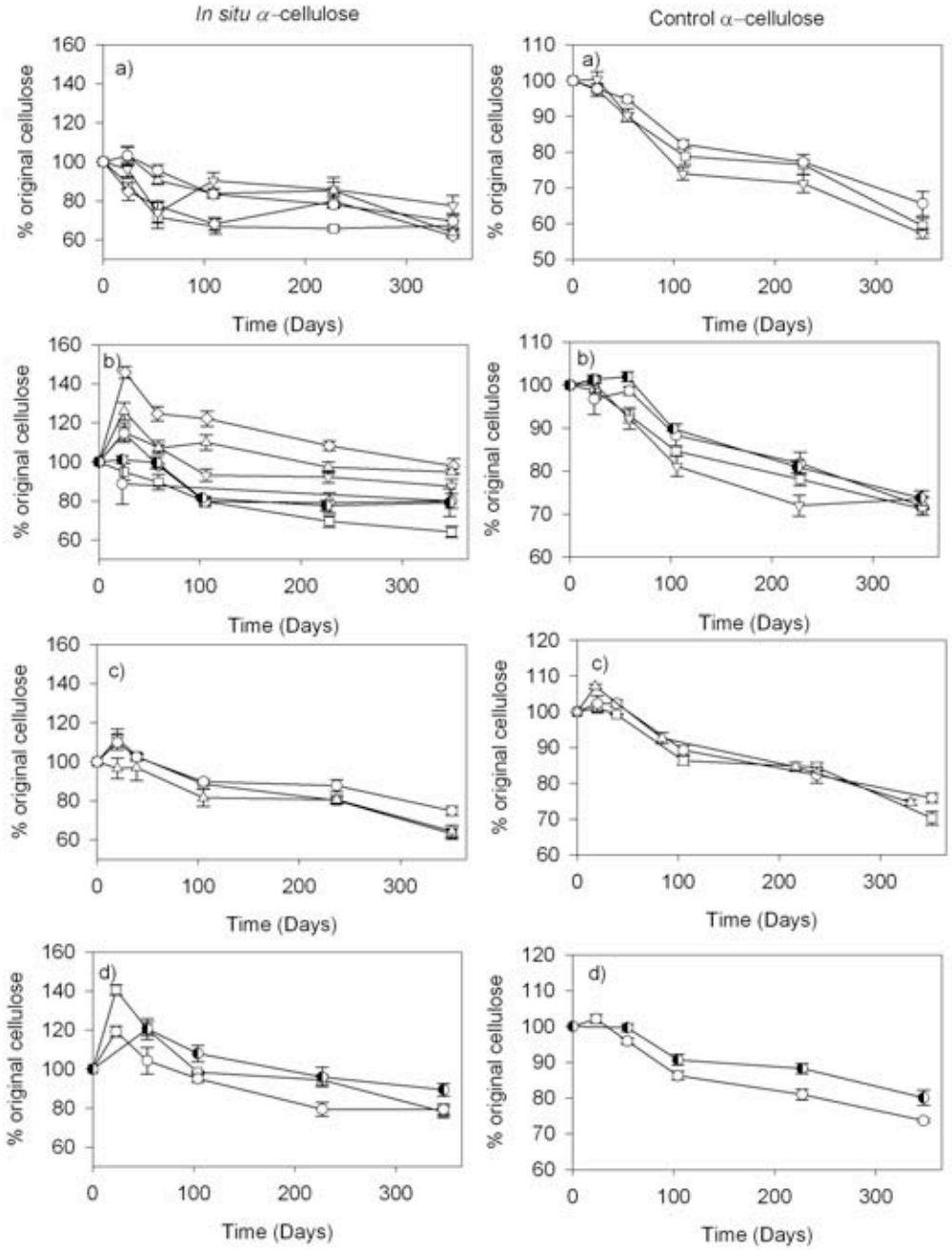
Appendix 6. continued.



Appendix 6. continued.



Appendix 6. continued.



Appendix 7. Nutrient contents of reproductive and unclassified materials (n = 10 per plot).

	Reproductive		Unclassified	
Site	N	P	N	P
Atherton Uplands				
1A1	1.45 ± 0.27	0.07 ± 0.01	1.92 ± 0.31	0.10 ± 0.01
1A3	2.03 ± 0.32	0.09 ± 0.01	1.57 ± 0.27	0.08 ± 0.004
2A2	1.62 ± 0.29	0.11 ± 0.01	1.50 ± 0.24	0.10 ± 0.01
2A5	2.25 ± 0.33	0.18 ± 0.02	1.93 ± 0.32	0.16 ± 0.01
4A2	1.63 ± 0.31	0.16 ± 0.02	1.45 ± 0.23	0.14 ± 0.01
4A5	1.84 ± 0.32	0.15 ± 0.02	1.67 ± 0.31	0.13 ± 0.01
6A2	1.46 ± 0.27	0.10 ± 0.01	1.33 ± 0.21	0.12 ± 0.01
6A5	1.34 ± 0.24	0.10 ± 0.01	1.03 ± 0.13	0.11 ± 0.01
8A2	2.20 ± 0.33	0.12 ± 0.01	1.23 ± 0.19	0.11 ± 0.01
8A5	0.59 ± 0.06	0.03 ± 0.003	1.60 ± 0.27	0.14 ± 0.01
9A2	1.43 ± 0.26	0.10 ± 0.01	1.63 ± 0.28	0.12 ± 0.01
9A5	0.86 ± 0.11	0.08 ± 0.01	1.57 ± 0.24	0.13 ± 0.01
Carbine Uplands				
1A1	1.30 ± 0.23	0.09 ± 0.01	1.09 ± 0.16	0.08 ± 0.005
1A5	0.80 ± 0.08	0.06 ± 0.01	1.09 ± 0.16	0.08 ± 0.004
2A2	0.77 ± 0.08	0.05 ± 0.00	1.04 ± 0.14	0.07 ± 0.004
2A5	0.94 ± 0.13	0.07 ± 0.01	1.40 ± 0.22	0.11 ± 0.01
4A2	1.05 ± 0.20	0.07 ± 0.01	0.88 ± 0.10	0.06 ± 0.004
4A5	1.10 ± 0.21	0.09 ± 0.01	1.19 ± 0.19	0.06 ± 0.004
6A2	0.91 ± 0.12	0.07 ± 0.01	0.90 ± 0.10	0.06 ± 0.003
6A5	1.51 ± 0.28	0.08 ± 0.01	1.15 ± 0.18	0.06 ± 0.003
8A2	1.35 ± 0.24	0.07 ± 0.01	0.76 ± 0.06	0.05 ± 0.003
8A5	1.55 ± 0.28	0.09 ± 0.01	1.08 ± 0.16	0.06 ± 0.003
10A2	0.93 ± 0.13	0.07 ± 0.01	1.10 ± 0.17	0.10 ± 0.01
10A5	1.13 ± 0.22	0.10 ± 0.01	1.43 ± 0.23	0.15 ± 0.01

Appendix 7. continued.

	Reproductive				Unclassified			
Site	N		P		N		P	
12A2	0.95	± 0.14	0.06	± 0.01	1.18	± 0.18	0.08	± 0.004
12A5	0.96	± 0.15	0.07	± 0.01	0.93	± 0.11	0.06	± 0.003
Spec Uplands								
3A1	1.64	± 0.32	0.07	± 0.01	1.63	± 0.27	0.09	± 0.01
3A2	0.74	± 0.07	0.05	± 0.005	1.21	± 0.19	0.06	± 0.003
6A2	0.91	± 0.13	0.05	± 0.005	1.02	± 0.12	0.05	± 0.002
6A3	0.72	± 0.06	0.04	± 0.004	0.88	± 0.08	0.04	± 0.001
8A2	0.95	± 0.14	0.05	± 0.01	1.13	± 0.18	0.07	± 0.004
8A3	1.09	± 0.20	0.08	± 0.01	1.32	± 0.20	0.08	± 0.005
10A1	0.83	± 0.11	0.05	± 0.01	1.76	± 0.31	0.11	± 0.01
10A2	1.15	± 0.22	0.07	± 0.01	1.63	± 0.30	0.12	± 0.01
Windsor Uplands								
9A2	0.99	± 0.16	0.05	± 0.01	1.11	± 0.17	0.08	± 0.005
9A5	1.27	± 0.22	0.07	± 0.01	1.04	± 0.14	0.08	± 0.005
11A2	1.47	± 0.28	0.07	± 0.01	1.28	± 0.20	0.09	± 0.005
11A5	1.01	± 0.18	0.07	± 0.01	0.86	± 0.08	0.06	± 0.004
13A2	1.33	± 0.23	0.04	± 0.004	0.94	± 0.11	0.04	± 0.002
13A2	0.99	± 0.17	0.06	± 0.01	0.94	± 0.12	0.05	± 0.002

Appendix 8. Annual nutrient accessions from litterfall (kg ha^{-1} y^{-1})

	Leaf					Unclassified		Reproductive	
	N	C	Mg	Ca	P	N	P	N	P
AU1A1	42.89±7.7^{abc}	1538.61±276.07^{abcdfghi}	8.57±1.54^{abcdef}	42.09±7.55^{hijklmn}	1.21±0.22^{efhij}	8.46±3.67^{fg}	0.43±0.19^{defg}	1.76±1.08^{abc}	0.08±0.05^{abc}
AU1A3	38±9.15^{ab}	1364.04±328.25^{abcdefg}	7.24±1.74^{abcde}	26.14±6.29^{abcdefh}	0.96±0.23^{cdefhi}	4.46±1.32^{bcdefg}	0.22±0.07^{abcde}	3.83±2.61^{abc}	0.17±0.12^{abcd}
AU2A2	88.94±32.94^{ef}	2343.11±867.76^{ghij}	15.42±5.71^{f}	114.21±42.3^{o}	3.48±1.29^{m}	9.63±3.72^{g}	0.62±0.24^{fg}	4.20±3.14^{abc}	0.27±0.20^{bcd}
AU2A5	46.92±17.79^{abcd}	1201.32±455.59^{abcde}	7.80±2.96^{abcde}	48.00±18.2^{hijklmn}	1.79±0.68^{ijkl}	8.49±2.77^{fg}	0.72±0.23^{g}	4.51±3.33^{abc}	0.35±0.26^{bcd}
AU4A2	38.99±11.81^{ab}	1089.84±330.16^{abc}	6.38±1.93^{abc}	32.97±9.99^{bcdefhij}	1.36±0.41^{efhijk}	3.38±0.83^{abcdef}	0.32±0.08^{bcdefg}	3.27±0.64^{abc}	0.32±0.06^{bcd}
AU4A5	44.82±12.73^{abc}	1115.22±316.84^{abcd}	6.77±1.92^{abcd}	40.18±11.41^{efhijklm}	1.66±0.47^{ijk}	5.61±2.43^{bcdefg}	0.45±0.20^{defg}	2.18±3.49^{ab}	0.18±0.29^{abcd}
AU6A2	30.3±14.61^{a}	1044.03±503.38^{a}	5.92±2.85^{ab}	30.93±14.91^{bcdefhi}	0.69±0.33^{cd}	3.55±2.38^{abcd}	0.33±0.22^{bcdefg}	4.08±2.54^{abc}	0.28±0.17^{bcd}
AU6A5	65.81±8.19^{bcde}	1925.16±239.54^{defghij}	12.58±1.57^{ef}	70.52±8.77^{mno}	2.15±0.27^{jklm}	2.51±0.31^{abcd}	0.27±0.03^{bcdef}	3.98±3.00^{abc}	0.31±0.23^{bcd}
AU8A2	45.7±5.32^{abcde}	1290.7±150.16^{abcdef}	6.71±0.78^{abcd}	26.86±3.12^{abcdefh}	1.26±0.15^{efhij}	3.10±0.47^{abcde}	0.27±0.04^{bcdef}	3.50±2.09^{abc}	0.20±0.12^{abcd}
AU8A5	37.83±10.06^{ab}	1024.83±272.64^{ab}	5.14±1.37^{a}	21.74±5.78^{abcd}	1.03±0.28^{defhi}	4.94±2.44^{bcdefg}	0.43±0.21^{cdefg}	0.85±0.65^{a}	0.04±0.03^{a}
AU9A2	87.32±33.29^{def}	2793.52±1064.87^{ij}	15.32±5.84^{f}	65.52±24.98^{lmno}	2.50±0.95^{klm}	6.16±1.96^{cdefg}	0.47±0.15^{defg}	2.95±1.43^{abc}	0.20±0.10^{abcd}
AU9A5	45.11±4.16^{abcd}	1927.15±177.71^{defghij}	10.42±0.96^{cdef}	22.07±2.03^{abcde}	0.87±0.08^{cdefh}	6.14±1.69^{cdefg}	0.51±0.14^{efg}	4.03±2.49^{abc}	0.39±0.24^{bcd}
CU1A1	43.28±5.32^{abc}	1591.59±195.54^{abcdefhj}	9.23±1.13^{bcdef}	58.08±7.14^{klmn}	1.12±0.14^{efhi}	3.01±0.42^{abcd}	0.22±0.03^{abcde}	2.54±1.78^{abc}	0.17±0.12^{abcd}
CU1A5	58.21±10.25^{bcde}	2250.78±396.35^{fghij}	13.12±2.31^{ef}	73.04±12.86^{no}	1.39±0.24^{fhijk}	4.12±0.88^{bcdefg}	0.29±0.06^{bcdefg}	2.53±1.19^{abc}	0.19±0.09^{abcd}
CU2A2	69.06±7.57^{cde}	2867.79±314.48^{jk}	14.41±1.58^{f}	50.52±5.54^{ijklmn}	1.47±0.16^{hijk}	6.22±3.94^{bcdefg}	0.44±0.28^{cdefg}	10.53±7.70^{c}	0.65±0.48^{cd}
CU2A5	54.48±12.43^{bcde}	2405.92±548.99^{ghij}	12.01±2.74^{def}	41.83±9.54^{fhijklm}	1.19±0.27^{efhij}	6.99±4.00^{defg}	0.54±0.31^{efg}	5.86±4.90^{abc}	0.41±0.34^{bcd}
CU4A2	40.19±9.88^{abc}	1952.71±480.14^{cdefghij}	8.38±2.06^{abcdef}	19.54±4.8^{abc}	0.61±0.15^{cd}	2.98±0.54^{abcd}	0.21±0.04^{abcde}	4.14±4.23^{abc}	0.29±0.29^{abcd}
CU4A5	43.61±8.01^{abc}	1961.86±360.25^{defghij}	9.33±1.71^{bcdef}	35.66±6.55^{defhijkl}	0.73±0.13^{cde}	4.31±1.51^{bcdefg}	0.23±0.08^{abcde}	4.82±4.86^{abc}	0.37±0.37^{bcd}
CU6A2	128.76±15.72^{f}	4899.07±598.01^{k}	27.60±3.37^{g}	76.25±9.31^{no}	2.99±0.37^{lm}	8.08±2.08^{fg}	0.51±0.13^{efg}	9.27±5.04^{c}	0.70±0.38^{d}
CU6A5	52.87±10.17^{bcde}	2266.32±435.98^{fghij}	10.58±2.04^{cdef}	32.68±6.29^{bcdefhjk}	0.86±0.16^{cdefh}	3.96±1.66^{bcdefg}	0.21±0.09^{abcd}	4.42±3.54^{abc}	0.22±0.18^{abcd}
CU8A2	43.42±12.34^{abc}	1813.06±515.1^{bcdefghj}	8.19±2.33^{abcdef}	23.41±6.65^{abcdef}	0.89±0.25^{cdefh}	1.88±1.86^{a}	0.13±0.13^{a}	1.57±0.51^{abc}	0.08±0.03^{abcd}
CU8A5	44.28±7.8^{abc}	1872.14±329.67^{cdefghij}	9.02±1.59^{abcdef}	26.23±4.62^{abcdefh}	0.81±0.14^{cdef}	3.50±1.10^{abcdef}	0.20±0.06^{abcd}	4.69±2.07^{abc}	0.27±0.12^{bcd}

Appendix 8. continued.

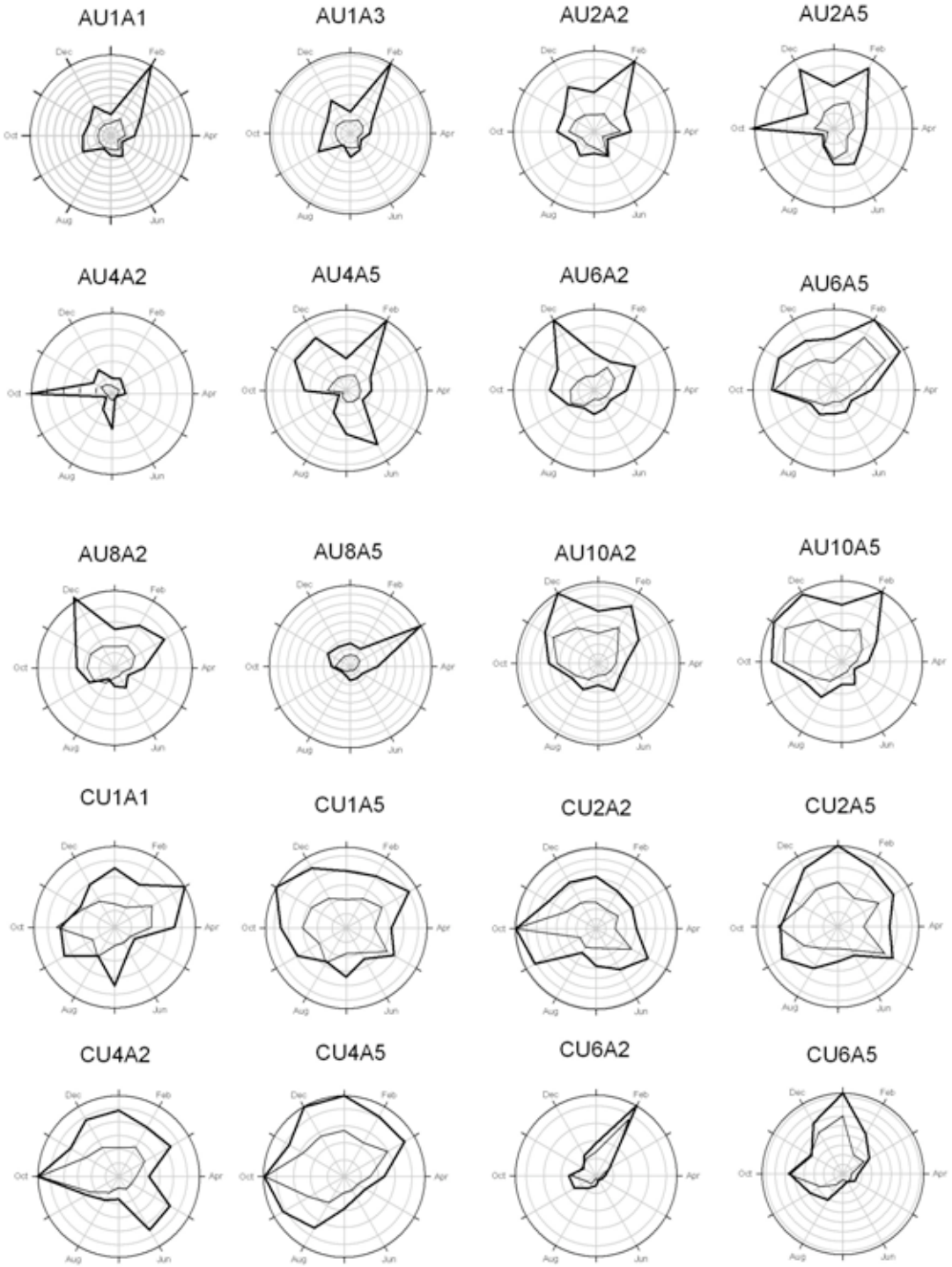
	Leaf					Unclassified		Reproductive	
	N	C	Mg	Ca	P	N	P	N	P
CU8A5	44.28±7.8^{abc}	1872.14±329.67^{cdefghij}	9.02±1.59^{abcdef}	26.23±4.62^{abcdefh}	0.81±0.14^{cdef}	3.50±1.10^{abcdef}	0.20±0.06^{abcd}	4.69±2.07^{abc}	0.27±0.12^{bcd}
CU10A2	51.63±6.06^{bcde}	2006.66±235.55^{efghij}	10.83±1.27^{cdef}	40.02±4.7^{efhijklm}	0.98±0.11^{defhi}	4.51±0.96^{bcdefg}	0.42±0.09^{defg}	5.01±1.00^{bc}	0.37±0.07^{bcd}
CU10A5	43.3±5.19^{abc}	1730.91±207.37^{abcdefhj}	11.2±1.34^{cdef}	51.63±6.19^{jklmn}	1.15±0.14^{efhi}	3.49±0.32^{abcdef}	0.36±0.03^{cdefg}	5.37±6.58^{abc}	0.49±0.59^{bcd}
CU12A2	38.42±14.37^{ab}	1492.49±558.03^{abcdefh}	8.56±3.2^{abcdef}	27.24±10.18^{abcdefh}	0.89±0.33^{cdefh}	2.53±0.95^{abc}	0.17±0.06^{abc}	2.96±3.36^{abc}	0.17±0.20^{abcd}
CU12A5	46.91±11.01^{abcde}	2083.85±489.04^{efghij}	11.41±2.68^{cdef}	20.76±4.87^{abcd}	1.06±0.25^{defhi}	3.07±0.55^{abcde}	0.19±0.03^{abcd}	2.01±1.39^{abc}	0.14±0.10^{abcd}
SU3A1	45.77±13.16^{abcde}	1943.69±567.08^{defghijk}	9.15±3.71^{bcdef}	40.05±8.24^{efhijkm}	0.80±0.24^{cdefg}	7.83±2.41^{efg}	0.45±0.14^{defg}	2.53±0.85^{abc}	0.11±0.04^{abcd}
SU3A2	65.20±17.25^{cde}	2658.06±657.82^{ij}	12.60±4.87^{def}	59.18±10.85^{klmn}	1.09±0.20^{efhi}	6.48±	0.31±	6.85±	0.65±
SU6A2	49.81±4.79^{abcde}	2462.99±236.84^{hij}	9.96±0.96^{cdef}	18.37±1.77^{ab}	0.25±0.02^{b}	4.66±1.02^{bcdefg}	0.22±0.05^{abcde}	5.07±2.47^{abc}	0.25±0.12^{bcd}
SU6A3	41.88±1.91^{abc}	2079.46±94.58^{efghij}	7.94±0.36^{abcdef}	15.00±0.68^{a}	0.09±0.00^{a}	3.86±0.43^{bcdefg}	0.16±0.02^{abc}	3.28±1.68^{abc}	0.17±0.09^{abcd}
SU8A2	43.89±3.05^{abc}	1989.05±138.3^{efghij}	9.21±0.64^{bcdef}	40.55±2.82^{fhijklm}	0.83±0.06^{cdefh}	2.33±0.47^{ab}	0.14±0.03^{ab}	4.15±2.65^{abc}	0.23±0.15^{abcd}
SU8A3	48.4±6.05^{abcde}	2044.54±255.47^{efghij}	9.61±1.2^{bcdef}	39.65±4.95^{efhijkm}	0.79±0.10^{cdef}	4.58±0.84^{bcdefg}	0.29±0.05^{bcdefg}	2.80±0.82^{abc}	0.20±0.06^{abcd}
SU10A1	46.54±9.43^{abcde}	1712.53±346.98^{abcdefhj}	6.91±1.4^{abcd}	27.05±5.48^{abcdefh}	1.06±0.21^{defhi}	4.92±1.45^{bcdefg}	0.31±0.09^{bcdefg}	1.31±1.16^{ab}	0.08±0.07^{ab}
SU10A2	43.96±5.18^{abc}	1654.42±195.09^{abcdefgj}	6.78±0.8^{abcd}	25.8±3.04^{abcdefh}	0.99±0.12^{defhi}	4.26±0.67^{bcdefg}	0.31±0.05^{bcdefg}	5.30±4.01^{abc}	0.31±0.24^{abcd}
WU9A2	47.11±11.83^{abcde}	1927.2±483.94^{cdefghij}	9.40±2.36^{abcdef}	31.27±7.85^{bcdefhij}	1.05±0.26^{defhi}	2.82±1.05^{abcd}	0.20±0.07^{abcd}	4.08±3.21^{abc}	0.21±0.17^{abcd}
WU9A5	51.22±13.04^{abcde}	2063.7±525.33^{efghij}	10.33±2.63^{cdef}	37.64±9.58^{defhijkl}	1.28±0.33^{efhij}	3.67±0.76^{bcdefg}	0.29±0.06^{bcdefg}	3.87±2.70^{abc}	0.21±0.15^{abcd}
WU11A2	51.91±8.14^{bcde}	1878.98±294.57^{cdefghij}	9.96±1.56^{cdef}	39.91±6.26^{efhijkm}	1.26±0.20^{efhij}	4.18±1.97^{bcdefg}	0.29±0.14^{bcdef}	2.85±1.55^{abc}	0.13±0.07^{abcd}
WU11A5	68.06±18.77^{bcde}	2811.72±775.28^{ijk}	14.52±40^{f}	42.13±11.62^{fhijklm}	1.56±0.43^{hijk}	4.71±2.67^{bcdefg}	0.35±0.20^{bcdefg}	5.14±6.50^{abc}	0.35±0.44^{abcd}
WU13A2	38.02±6.29^{abc}	1833.83±303.34^{bcdefghj}	7.94±1.31^{abcdef}	24.66±4.08^{abcdef}	0.52±0.09^{c}	2.52±0.73^{abc}	0.10±0.03^{a}	3.36±1.69^{abc}	0.10±0.05^{abcd}
WU13A5	47.35±10.3^{abcde}	2247.27±489.08^{fghij}	9.54±2.08^{bcdef}	34.88±7.59^{cdefhijl}	0.77±0.17^{cdef}	3.70± 1.32^{abcdef}	0.20±0.07^{abcd}	4.59±1.31^{abc}	0.28±0.08^{bcd}

Appendix 9. Characteristics of sites used for litterbag study in Australian tropical rainforests. Shown are the sub-regions and site codes, total rainfall over study (Rain, ~420 days), rainfall seasonality (DS0MM, proportion of dry season, 1st April - 31st October, days with 0 mm rainfall), mean leaf wetness in the dry season (LWDS, from sensor) and litterbags applied at the site

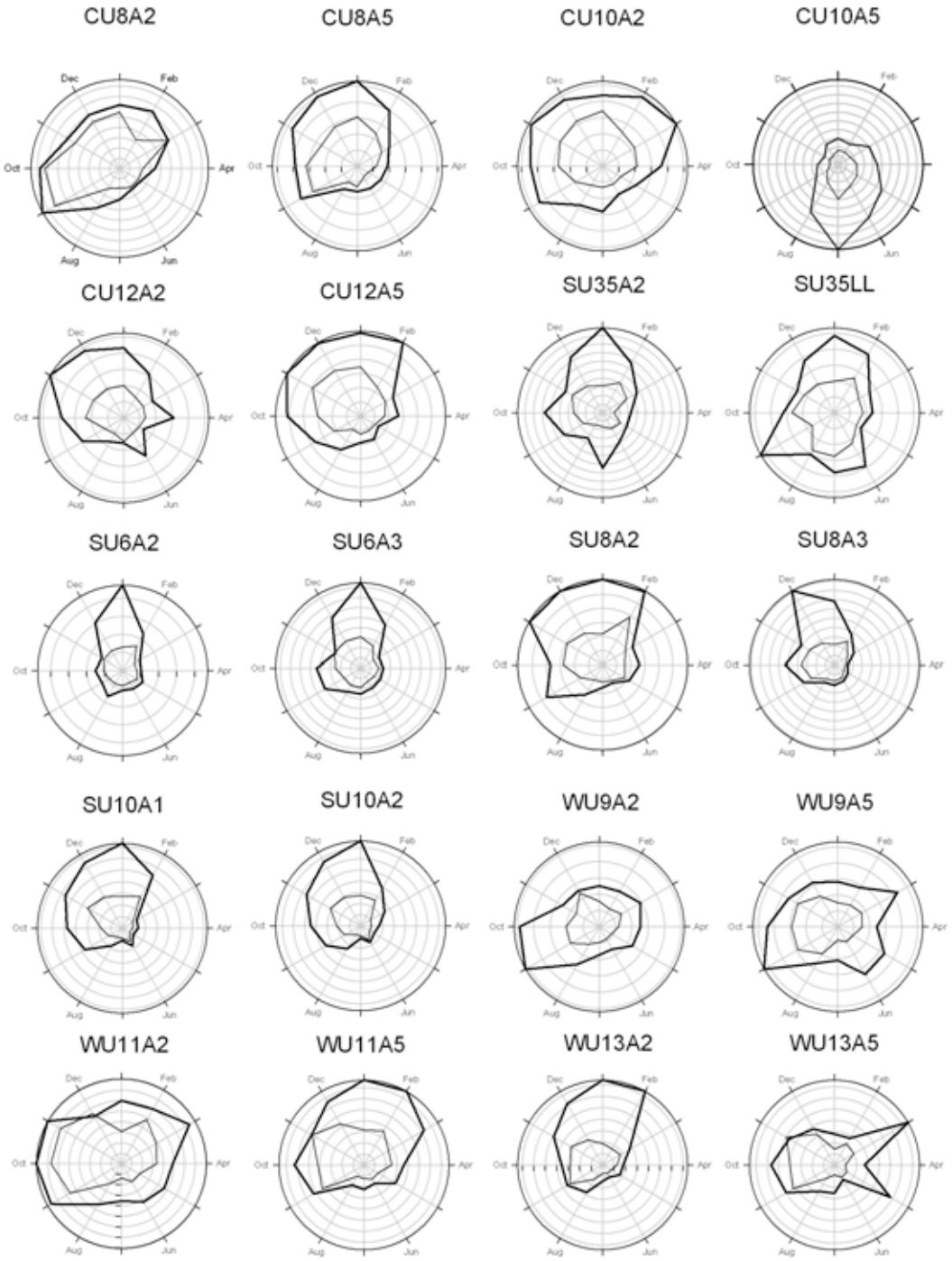
Sub-region	Site	Rain (mm)	DS0MM (%)	LWDS (%)	Litterbags
Atherton	AU1	4990	35.1	77.2	I, C
	AU4	4609	34.1	94.2	I
	AU6	4119	33.2	93.3	I, C
	AU8	3993	31.3	95.6	I
	AU9	2579	43.5	91.9	I, C
Carbine	CU1	3817	55.1	81.6	I, C
	CU4	3103	58.4	88.9	I
	CU6	2934	55.6	75.0	I, C
	CU8	2934	55.6	86.1	I
	CU10	3374	57.9	91.4	I, C
	CU12	3771	54.2	86.1	I, C
Spec	SU3	4191	62.2	75.3	I, C
	SU8	3851	61.2	70.5	I
	SU9	2874	62.2	62.2	C
	SU10	3031	60.8	84.3	I, C
Windsor	WU9	3090	47.7	76.5	I
	WU11	3184	44.9	86.5	I, C
	WU13	3532	41.1	61.6	I, C

[a] I = *In situ* litterbags, C = control litterbags

Appendix 10. Polar plots representing the annual distribution of litterfall in Australian tropical rainforest. Radial axes are in t $ha^{-1}y^{-1}$.



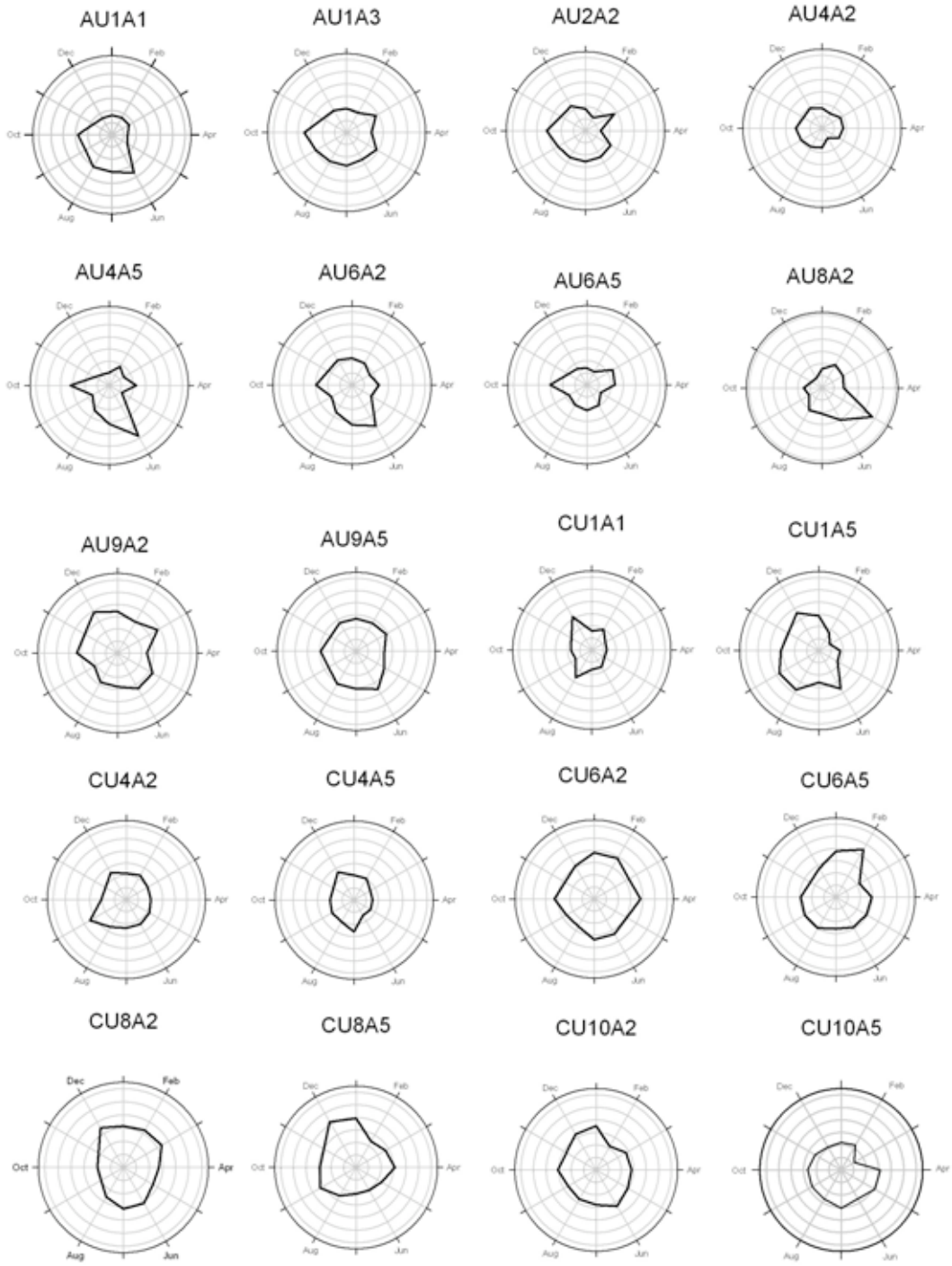
Appendix 10. continued.



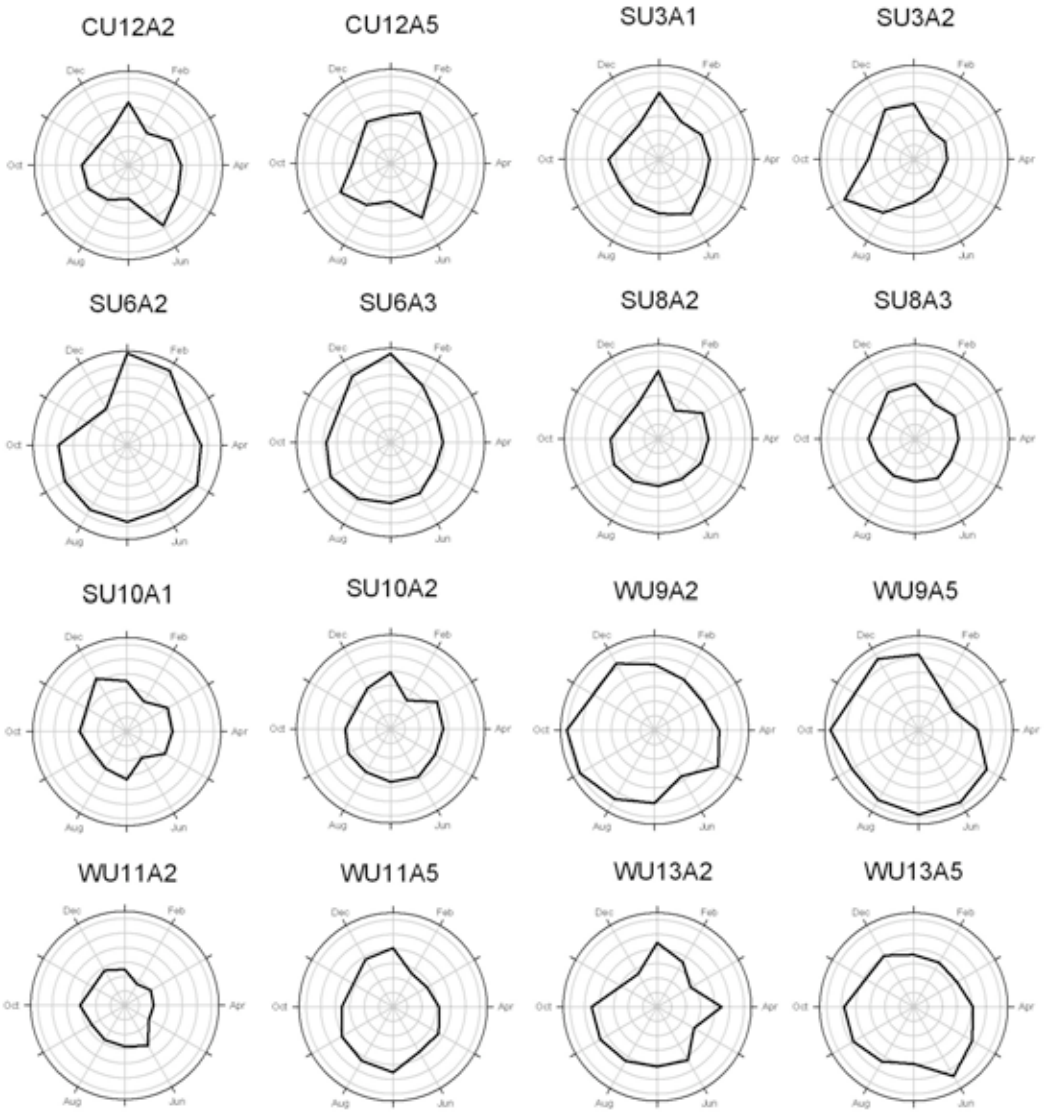
Appendix 11. Results from best sub-set regression analysis on litterfall seasonality, litter standing crop (LSC), LSC turnover and LSC seasonality. Separate analyses were undertaken for environmental and site variables (env) and leaf litterfall chemical characteristics. See text for variables definitions.

		Model	**Est.**	**Std. err**	**t**	**p**	**Residuals**					**BIC**
Total litterfall seasonality (all plots)	a) Env	(Intercept)	0.54	0.149	3.658	0.0008						3.41
		AirT	-0.016	0.007	-2.164	0.037	**Min**	**1st Q**	**Median**	**3rd Q**	**Max**	
		Soil N	0.152	0.074	2.066	0.046	-0.19	-0.05	0.015	0.048	0.13	
							Res. SE	**df**	**Adj. R^2**	**F**	**Model p**	
							0.08	37	0.13	3.90	0.030	
Total litterfall seasonality (no cyclone damaged plots)	b) Env	(Intercept)	0.64	0.14	4.73	0.0001	**Min**	**1st Q**	**Median**	**3rd Q**	**Max**	-1.25
		Soil N	0.29	0.11	2.64	0.014	-0.16	-0.040	-0.004	0.053	0.16	
		AirT	-0.024	0.007	-3.48	0.0017	**Res. SE**	**df**	**Adj. R^2**	**F**	**Model p**	
							0.08	27	0.37	9.49	0.0008	
LSC	c) Env	(Intercept)	12.35	2.43	5.075	0.0001	**Min**	**1st Q**	**Median**	**3rd Q**	**Max**	-30.98
		MAPCV	-0.053	0.020	-2.645	0.013	-2.09	-0.51	-0.099	0.32	2.37	
		Soil Na	-46.31	10.35	-4.474	0.0001	**Res. SE**	**df**	**Adj. R^2**	**F**	**Model p**	
		k (NIRS)	-2.87	0.54	-5.339	0.00001	0.95	29	0.75	18.11	0.0001	
		%wood	0.072	0.031	2.347	0.026						
		SLOPE	0.073	0.034	2.137	0.040						
		LF	0.26	0.096	2.727	0.010						
	d) Leaf Chem	(Intercept)	-37.05	8.029	-4.615	0.0000	**Min**	**1st Q**	**Median**	**3rd Q**	**Max**	-15.07
		C	0.890	0.165	5.391	0.0000	-2.437	-0.721	-0.263	0.665	3.780	
							Res. SE	**df**	**Adj. R^2**	**F**	**Model p**	
							1.405	34	0.46	29.06	0.0001	
LSCK	e) Env(1)	(Intercept)	0.094	0.734	0.128	0.899	**Min**	**1st Q**	**Median**	**3rd Q**	**Max**	-18.64
		MAPCV	0.011	0.0059	1.852	0.074	-0.37	-0.18	-0.044	0.16	0.75	
		Soil Na	9.95	3.13	3.180	0.0034	**Res. SE**	**df**	**Adj. R^2**	**F**	**Model p**	
		k (NIRS)	0.51	0.16	3.544	0.0037	0.29	30	0.62	12.3	0.0001	
		%wood	-0.031	0.009	-3.380	0.0020						
		SLOPE	-0.024	0.010	-2.353	0.0254						
	f) Env(2)	(Intercept)	0.631	0.615	1.027	0.312	**Min**	**1st Q**	**Median**	**3rd Q**	**Max**	-12.85
		CDI_{arc}	2.200	0.772	2.850	0.007	-0.72	-0.18	-0.04	0.13	0.98	
		Phenol	-1.568	0.372	-4.214	0.0001	**Res. SE**	**df**	**Adj. R^2**	**F**	**Model p**	
							0.35	33	0.45	15.29	0.0001	
	g) Leaf Chem	(Intercept)	11.496	2.069	5.558	0.000	**Min**	**1st Q**	**Median**	**3rd Q**	**Max**	-12.26
		C	-0.210	0.043	-4.932	0.000	-0.61	-0.26	-0.011	0.160	1.23	
							Res. SE	**df**	**Adj. R^2**	**F**	**Model p**	
							0.36	34	0.40	24.33	0.000	
SLLSC	h) Env	(Intercept)	0.056	0.021	2.65	0.012	**Min**	**1st Q**	**Median**	**3rd Q**	**Max**	-6.84
		Soil Na	2.50	0.528	4.73	0.001	-0.18	-0.02	0.012	0.04	0.15	
							Res. SE	**df**	**Adj. R^2**	**F**	**Model p**	
							0.044	32	0.40	22.34	0.0001	

Appendix 12. Polar plots representing the distribution of litter standing crop over 12 months in Australian tropical rainforest. Radial axes are in t ha^{-1}.



Appendix 12. continued.



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SHORT COMMUNICATION

Volume measurements for quicker determination of forest litter standing crop

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Litter standing crop (LSC) is the quantity of plant detritus on the floor in forested environments. Knowledge of LSC is important in understanding many ecological phenomena. These include studies of litterfall, decomposition/litter turnover rates and nutrient cycling (Anderson *et al.* 1983, Dent *et al.* 2006), general plant performance (Benítez-Malvido & Kossmann-Ferraz 1999), other ecosystem processes such as the effects of fire (Odiwe & Muoghalu 2003) and fauna (Frith & Frith 1990, Giaretta *et al.* 1999, Levings & Windsor 1985). The determination of accurate annual average LSC data, may require monitoring over long periods due to seasonality and sometimes sporadic nature of litterfall and decomposition rates (Clark *et al.* 2001). Furthermore, the effects of topography and water movement create the need for both representative site selection and sufficient spatial coverage.

Standard methods for LSC quantification typically either involved removing quadrats from the site and determining dry weight (Anderson *et al.* 1983, Goma-Tchimbakala & Bernhard-Reversat 2006, Spain 1984). Less common approaches include measuring litter depth, or weighing LSC on site and removing subsamples that are dried in the laboratory and the moisture component subtracted (Day 1979, Nascimento & Laurance 2002). Generally 0.25–1-m^2 quadrats (Edwards 1977, Nascimento & Laurance 2002, Proctor *et al.* 1983, Scott *et al.* 1992, Songwe *et al.* 1995, Spain 1984), or sometimes larger (Tanner 1981) are sampled, with intensities varying widely from two to four times per year to monthly collections. Replication is dependent on logistics and the goals of the study, but adequacy of sampling is usually unknown. The approach of taking samples from the site to determine dry weights has drawbacks in regard to the time and effort required for accurate analyses, particularly when numerous sites are being studied. Removing litter from the site also creates disturbance with possible carry-on effects to other processes that may be of interest. Significant effort can be necessary for drying and weighing following the fieldwork. The method of subsampling to determine moisture content can also be problematic, as many samples may be needed to accurately cover the range of moisture within the litter layer temporally and spatially. Most importantly, logistical demands inherent in these commonly used methods limit the capacity of researchers to sample spatial and temporal variability in the litter layer, which can be particularly high at most scales of interest and change seasonally (Proctor *et al.* 1983).

We have developed a new method for the determination of LSC using measurements of volume, calibrated with dry-weight data. The method is logistically less demanding thereby permitting greater replication and spatial coverage of LSC in the field. An added bonus is that removal of LSC from the site is not required. This method is designed for applications where total LSC is required only and a detailed breakdown of the various components of litter (e.g. leaves, stems, flowers, fruit) is not of interest. The method is being utilized as part of a multidisciplinary research project examining the determinants of biodiversity patterns and how they may be affected by climate change. These include studies of decomposition and nutrient cycling, plant productivity and many aspects of animal ecology. Our study area covers most of the Australian Wet Tropics World Heritage Area between just north of Townsville, and south of

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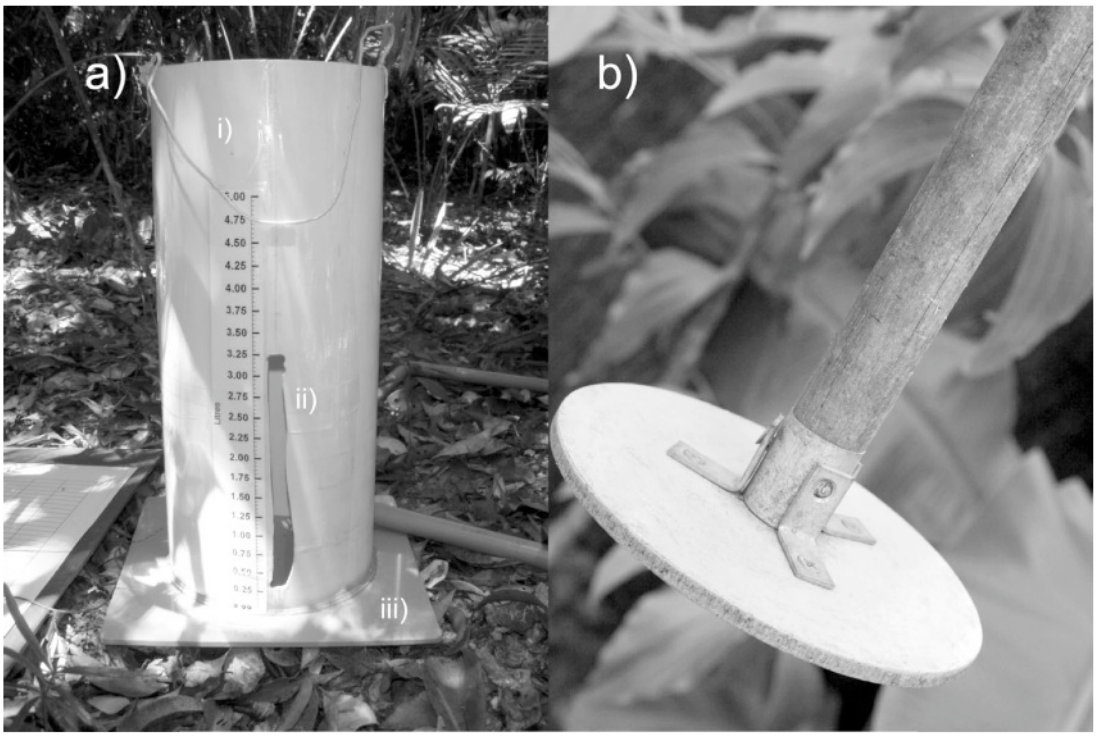


Figure 1. Volumetric device used to measure volume of fine-litter standing crop consisting of: compression cylinder (a) and compression stick (b). Cylinder consists of 150-mm PVC tubing (i), plastic-welded base (iii); guide hole to view volume in litres (ii).

Cooktown, north Queensland, Australia. We have sites from ~100–1600 m asl in closed tropical rain forest of varying complexity. The method and benefits are outlined below through comparison with the dry-weight approach.

The basis of the volumetric method works in much the same way as the commonly used LSC measurement techniques for fine litter (Gong & Ong 1983, Proctor *et al.* 1983). We use randomly chosen sampling points to collect fine litter (excluding heavily fragmented portions considered as part of the mineral soil portion and woody material > 2 cm diameter) from within 0.25-m^2 quadrats. The material is placed into a specially designed measuring cylinder (Figure 1a) ('compression cylinder'). Any included woody material is broken into portions small enough to fit horizontal in the apparatus to reduce obstructions. The material is then compressed flat using a compression stick and the volume recorded directly from a scale bar. The compression cylinder consists of ~400 mm of 150-mm-diameter PVC tubing. Two vertical guide holes are cut into the tubing for viewing the volume of litter during measurements, on one side from just below the top to approximately half way down the tubing, and, on the opposite side, from the bottom to approximately half way up the tubing (Figure 1a). This enables the volume (up to ~ 3.5 L at once) to be read while still maintaining the structural integrity of the compression cylinder during litter compaction. An additional square piece of PVC (~ 5 mm thickness) is plastic welded to the bottom of the tubing to provide a stable base (Figure 1a). Volumetric scales, in litres, for this diameter of tubing are laminated to the sides adjacent to the vertical guide holes. The compression stick consists of 900 mm of wood dowel with a 140-mm-diameter flat PVC disc attached via steel brackets (Figure 1b). The collected litter is compressed into the cylinder with at least three firm downward thrusts. The operator then leans down on the litter with the compression stick, and with a firm compressive force (their own body weight) on the litter, records the volume. For most adult operators this level of force is enough to consistently compress litter. The material can then be emptied out in the original location on the forest floor, either spread out or left in a pile in order to recognize areas that have already been sampled.

Our compression cylinder was designed to be used with 0.25-m^2 quadrats, based on the range of litter collected in our study area from dry weighed LSCs between March 2007–January 2008. A portion of these collections of dry weights were also used to develop calibrations between dry weight and volume (Figure 2, $n = 190$). This enables comparisons of LSC between other studies, and the determination of other factors where dry weight is of interest, such as litter turnover rates (annual litterfall/sum of the annual LSC). Calibration

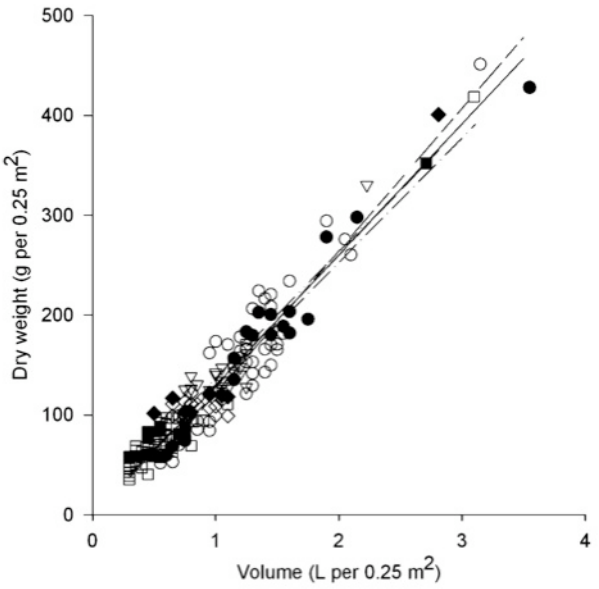


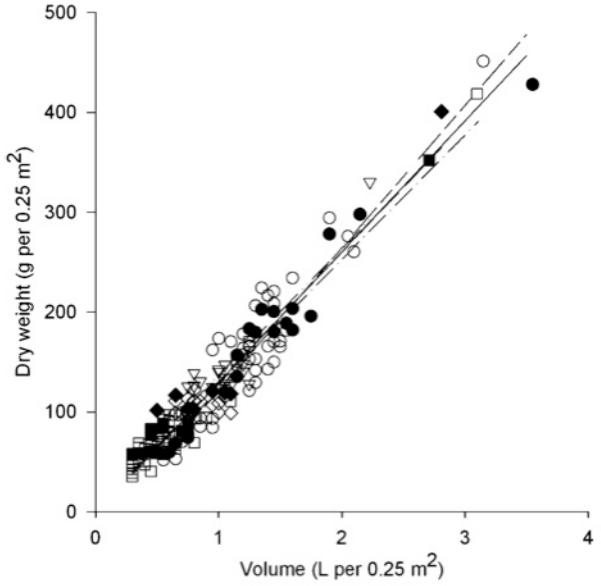
Figure 2. Litter standing crop data showing calibration from linear regressions between litter standing crop volume and dry weight (n = 190) taken from sites in Australian tropical rain forest. Included are samples from different sub-regions and collection seasons: Atherton uplands – - - ($r^2 = 0.90$), ○ (Wet, n = 50), ● (Dry, n = 17); Carbine uplands – ($r^2 = 0.94$), □ (Wet, n = 51), ■ (Dry, n = 20); Windsor uplands ·· – ·· ($r^2 = 0.81$), ▽ (Wet, n = 20); Spec Uplands – – – ($r^2 = 0.87$), ◇ (Wet, n = 22), ♦ (Dry, n = 10); Seasonal lines not shown: wet $r^2 = 0.91$, dry $r^2 = 0.94$; combined regression —- ($r^2 = 0.92$).

equations of volume verses mass were calculated using both linear and non-linear regressions. We examined spatial and temporal subsets of the data set to test the generality of the LSC calibrations. Spatial subsets were sub-regions (Windsor Uplands (WU) and Spec Uplands (SU): seasonally dry rain forest and wet sclerophyll rain forest; Carbine Uplands (CU): complex rain forest, and Atherton Uplands (AU): complex rain forest with many sites influenced by a recent severe cyclone) and temporal subsets/seasons (wet: collected February; dry: September 2008).

There was a strong linear relationship between litter volume and dry weight for the combined data (Dry Weight $= -1.87 + (131 \times \text{Volume})$, $r^2 = 0.92$) (Figure 2). The relationship was not improved by the application of more complex non-linear functions (i.e. quadratic function: $r^2 = 0.92$). There was no evidence to suggest that either the slope or intercept for calibrations differed temporally (ANCOVA, $F_{1,187} = 0.74$, $P = 0.85$), or spatially (ANCOVA, $F_{3,185} = 2.08$, $P = 0.11$), across the range of litter volumes encountered in rain forest within our region between June 2007 and May 2009 (mean = 1.17 L; median = 1.05 L; range = 0.10–5 L; n = 4950). This was the case even allowing for the fact that a number of AU plots were affected by cyclone damage. The AU plot may have had comparably higher proportions of woody material, but the affect on the calibrations was minor. Considering this we accept that the linear functions, and combined linear regression is applicable to all of our sites within this common range of values. The lower r^2 for SU and WU were likely to have been influenced by their comparably small sample sizes.

The amount of effort required to adequately measure LSC can be considerable and can limit the coverage of estimates and representativeness of sampling designs. In the case of our own study, removing samples to determine dry weight back in our laboratory required travelling large distances, which is likely to be the case in many ecological research settings. For example, on one occasion where 15 of our sites were sampled, removing just ten 0.25-m^2 quadrats of wet litter (n = 150) meant that > 20 kg dry weight (~ 150 L) of material needed to be transported. Both the dry weight and volume method require the same amount of time to collect a single sample, ~ 30 s. However, the dry weight method adds additional effort of ~20 s per sample for drying (not including actual drying time) and requires a great deal of space to complete the processing. An additional ~30 s per sample was then necessary for weighing. The volume method, once calibrated, equates to a significant saving in time and effort per unit area measured, e.g. from our data a minimum of ~5.3 min m^{-2} using dry weight was reduced to ~2.0 min m^{-2} (38 %) by adopting the volume method. Thus, with the volumetric method we can easily increase sample sizes to improve spatial coverage without significantly increasing effort.

In designing our study it is important to understand the number of samples necessary to get statistical power from the data. We require comparisons of LSC between sites distributed along elevational transects within the four sub-regions. Each site contains six points distributed 200 m apart. An acceptable maximum sampling scheme in regards to time spent at each site was considered to be 10 LSC volumes per point (n = 60 per site). We use post hoc power analyses to demonstrate the analytical benefit of increased litter sampling facilitated by our volume method (S + for Windows, EnvironmentalsStats module, TIBCO Software Inc. CA). The goal of the power analysis is to determine the range of minimum detectable differences (MDD) (effect size) for comparisons with ANOVA ($\alpha = 0.05$, for 80% power), between sites (e.g. regional/site differences). Table 1 shows the mean LSC estimates for entire transects (mean of six points) used in this analysis, sampled on one occasion per site in 2007/2008. Only data sets with homogenic variances were used in the analysis. The generally high variability is a characteristic of LSC, particularly at sites situated on steep slopes in upland situations. The range of MDD for comparisons between entire transects (n = 60) was 0.07–0.13 kg m^{-2} (Figure 3), with significant escalation of MDD with < 30 samples. This range appears generally acceptable for statistical comparisons considering the range of means,



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There was a strong linear relationship between litter volume and dry weight for the combined data (Dry Weight $= -1.87 + (131 \times \text{Volume})$, $r^2 = 0.92$) (Figure 2). The relationship was not improved by the application of more complex non-linear functions (i.e. quadratic function: $r^2 = 0.92$). There was no evidence to suggest that either the slope or intercept for calibrations differed temporally (ANCOVA, $F_{1,187} = 0.74$, $P = 0.85$), or spatially (ANCOVA, $F_{3,185} = 2.08$, $P = 0.11$), across the range of litter volumes encountered in rain forest within our region between June 2007 and May 2009 (mean = 1.17 L; median = 1.05 L; range = 0.10–5 L; n = 4950). This was the case even allowing for the fact that a number of AU plots were affected by cyclone damage. The AU plot may have had comparably higher proportions of woody material, but the affect on the calibrations was minor. Considering this we accept that the linear functions, and combined linear regression is applicable to all of our sites within this common range of values. The lower r^2 for SU and WU were likely to have been influenced by their comparably small sample sizes.

The amount of effort required to adequately measure LSC can be considerable and can limit the coverage of estimates and representativeness of sampling designs. In the case of our own study, removing samples to determine dry weight back in our laboratory required travelling large distances, which is likely to be the case in many ecological research settings. For example, on one occasion where 15 of our sites were sampled, removing just ten 0.25-m^2 quadrats of wet litter (n = 150) meant that > 20 kg dry weight (~ 150 L) of material needed to be transported. Both the dry weight and volume method require the same amount of time to collect a single sample, ~ 30 s. However, the dry weight method adds additional effort of ~20 s per sample for drying (not including actual drying time) and requires a great deal of space to complete the processing. An additional ~30 s per sample was then necessary for weighing. The volume method, once calibrated, equates to a significant saving in time and effort per unit area measured, e.g. from our data a minimum of ~5.3 min m^{-2} using dry weight was reduced to ~2.0 min m^{-2} (38 %) by adopting the volume method. Thus, with the volumetric method we can easily increase sample sizes to improve spatial coverage without significantly increasing effort.

In designing our study it is important to understand the number of samples necessary to get statistical power from the data. We require comparisons of LSC between sites distributed along elevational transects within the four sub-regions. Each site contains six points distributed 200 m apart. An acceptable maximum sampling scheme in regards to time spent at each site was considered to be 10 LSC volumes per point (n = 60 per site). We use post hoc power analyses to demonstrate the analytical benefit of increased litter sampling facilitated by our volume method (S + for Windows, EnvironmentalsStats module, TIBCO Software Inc. CA). The goal of the power analysis is to determine the range of minimum detectable differences (MDD) (effect size) for comparisons with ANOVA ($\alpha = 0.05$, for 80% power), between sites (e.g. regional/site differences). Table 1 shows the mean LSC estimates for entire transects (mean of six points) used in this analysis, sampled on one occasion per site in 2007/2008. Only data sets with homogenic variances were used in the analysis. The generally high variability is a characteristic of LSC, particularly at sites situated on steep slopes in upland situations. The range of MDD for comparisons between entire transects (n = 60) was 0.07–0.13 kg m^{-2} (Figure 3), with significant escalation of MDD with < 30 samples. This range appears generally acceptable for statistical comparisons considering the range of means,

Table 1. Litter standing crop (mean ± SD) used in power analysis for minimum detectable difference sampled in Australian tropical rain forest using the litter volume method and calibration. Elevational transects come from three regions: CU – Carbine Uplands; AU – Atherton Uplands; SU – Spec Uplands; WU – Windsor Uplands. CU and AU sampled in October 2007; SU June 2008; WU March 2008. N = 60 per transect, sampled along six points (10 samples per point).

Transect – altitude (m asl)	Litter standing crop (kg m^{-2})
CU – 115	0.77 ± 0.31
CU – 440	0.68 ± 0.27
CU – 656	0.69 ± 0.33
CU – 1016	0.74 ± 0.30
CU – 1210	0.89 ± 0.36
AU – 618	0.69 ± 0.22
AU – 930	0.55 ± 0.19
SU – 671	0.98 ± 0.29
SU – 834	0.47 ± 0.26
WU – 1071	0.57 ± 0.18

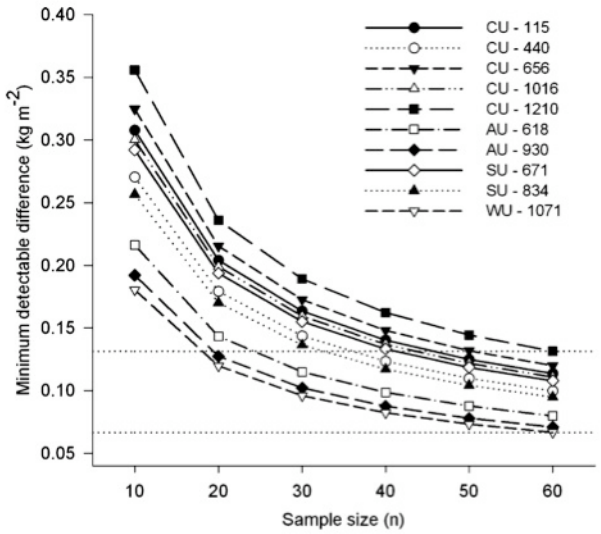

Figure 3. Minimum detectable difference (effect size) calculated via power analysis (α = 5% for 80% power) of mean litter standing crop sampled along transects (six points per transect, 10 samples per point) in Australian tropical rain forest. Horizontal dotted lines represent the range of effect size for these sets of samples.

0.47–0.98 kg m^{-2}. Sites with low MDD generally came from areas with more moderate slopes. For instance, WU – 1071 is relatively flat compared to CU – 1210 which has a highly variable but generally steep topography within the six sampling points.

Sampling LSC depends greatly on the site or area being covered, and the goals of the study. In our regional-scale study, dry weight measurements not deemed feasible due to large sample numbers. The volumetric approach fulfils our needs for a quick and easily replicable method to cover a large area with total fine LSC. In our study it is possible with the volumetric approach, using the same time/effort, to increase sample sizes from ~ 37 dry weights to ~ 60 volumes at the site level. On average, with the data shown above, this allows for improvements in MDD of 23%. We recommend our method mostly where total fine-litter data is required over many sampling periods (e.g. to view seasonal changes in LSC), and where numerous sites and long-term monitoring may be important (e.g. > 12 mo). The lack of litter removal from the site also lessens the impacts of our activities on the ecosystem and importantly on the processes being studied. Detecting changes in ecosystem processes, such as those related to LSC, is of significant importance in monitoring forest processes, particular in light of current climate change.

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