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Environmental controls on wood density in tropical forests

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Environmental controls on wood density in tropical forests

Mireia Torello Raventos

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Abstract

Tropical forests store a larger amount of carbon (C) than boreal and temperate forests. However, the determination of above ground biomass and C stocks in tropical ecosystems usually relies on a combination of remote sensing data together with ground data to develop models that predict forest biomass. One of the major determinants of above ground C stocks that cannot be determined in the field is wood density (ϱ) and tropical ecosystems usually contain a high diversity of tree species, with a wide range of wood densities in comparison with temperate forests.

Summary of the data chapters

This thesis aimed to understand the importance of accounting for the intra and interspecific variation of the ϱ with changing environmental conditions on the calculation of the above ground C on tropical forests. Not including this variation of ϱ could misestimate the C reservoirs on these ecosystems. In total, this thesis includes four data chapters. The first data chapter that is Chapter 2 comprises a novel method to study the ϱ within and between tree species at different study sites in Australia, Papua New Guinea and Vanuatu across different forest types. Chapter 3 and 4 studied the variation of ϱ with elevation (within and between tree species) from a low to mid montane tropical forests in Papua New Guinea and in range from lowland to montane tropical forest in Australia on respectively. Additionally, Chapter 4 also examined the variation of above ground biomass with increasing elevation. Chapter 5 investigated the importance of including ϱ on the estimations of the coarse woody debris residence times. The study was conducted along an altitudinal gradient in a tropical forest in Australia to observe the variation of the decomposition of the wood with the decreasing of mean annual temperature. The aim of using altitudinal gradients as sampling design was to understand the potential effects of climate change on the forest dynamics.

Description of the data chapters

Traditional methods for both field core extraction and laboratory processing for determining the ϱ of trees are generally time consuming and costly. Some trees are very hard to core and the field and the laboratory equipment required to obtain accurate numbers are expensive. There is also the risk of sample damaging during the process of collecting and

transporting the core samples. Because of all of the listed inconveniences, a fast, cheap, non-destructive and efficient field method to determine wood density would help the researchers to facilitate biomass census on tropical forests and with special emphasis those located in remote areas. Chapter 2 develops a field-based method to determine ϱ that relies on a non-destructive ultrasonic technique. We tested the technique on living trees, from different ecosystem types and under a range of climate conditions. The results suggest a positive relationship between ϱ and ultrasonic velocity with a coefficient of variation of 0.66 for intraspecific variation of ϱ and 0.81 for interspecific variation of ϱ. Due to interferences with the ultrasonic pulse velocity, measurements should be conducted in dry weather when temperatures are less than 30 °C. Potential improvements of this technique would include reducing the size of the transducers of the instrument and the development of conversion factors for measurements carried out above 30°C.

Few studies have described ϱ values for trees located on remote forests of Papua New Guinea. Besides, studies of the quantification of the intraspecific and interspecific variation of ϱ in relation to environmental variables are scarce for tropical forests and inexistent for Papua New Guinea. Thus, in this thesis study site elevation was chosen as an environmental gradient for the study of the climatic effects on the variation of ϱ. Therefore, chapter 3 reports the ϱ values from the most common sun-exposed and shaded tree species in the YUS Conservation Area, Papua New Guinea over an elevation range from 1800 m to 3050 m above sea level. Besides, one key focus of this chapter is the study of intra-specific variation of ϱ with elevation (temperature). The results indicate ϱ was negatively related to elevation for sun-exposed trees but with a positive ϱ /elevation relationship for shaded species. Both within and across species, tree size was found to be a significant covariate in models attempting to explain individual tree variations on ϱ: a positive relationship between ϱ with $1/DBH$ provided the best model fit. The results of this study have important implication for future studies on ground-based tropical forest biomass estimates for tropical montane forests.

Australian forests are located in a World Heritage Area and little is known about their role of carbon reservoirs and how they will respond to the effects of climate change. Chapter 4 presents a study along an elevational gradient from 50 m to 1500 m in North Queensland on the a) plot above ground biomass, basal area and tree diameter variation, b) the intra and interspecific variation of wood density for common species along the elevation range and c) the tree growth rates variation according to tree diameter and species. This study also included the effects of soil fertility as potential cause of ϱ variability. The results indicated that tree forest strata, diameter

and growth rates were related. Sun-exposed trees that had bigger average diameters presented bigger growth rates than smaller trees. In addition, results suggested a relationship between forest strata and *ϱ*. For sun-exposed trees, wood density decreased with elevation and the inverse case was for shaded trees. A multi-level statistical analysis of the dataset explained that soil fertility in addition to site elevation were significant drivers of tree wood density variation.

The coarse woody debris (CWD) pool of a forest in composed mainly by death trees, large branches and death leaves. The nutrients that are confined on the death material return to the ecosystems to be reused by living organisms. Throughout this cycle, CWD provides food and habitat to living organisms and increases forest biodiversity. The pace that CWD might degrade can be related to environmental variables (i.e. soil fertility, forest mature stage). However, due to the imminent consequences of climate change on actual and future forest dynamics, this study has focused on the effects of mean annual temperature of the CWD residence times. Thus, Chapter 5 examines coarse woody debris residence time (τ), for different tree species (and therefore with different wood traits) - ranging from low to hard woods – along an elevation gradient from 102 m above sea level (MAT = 23.7 °C) to 1500 m above sea level (MAT = 16.7 °C) in a tropical forests in Australia. The aim was to understand the effects of elevation (temperature) on the chemical and physical decay of CWD. Results suggested that wood density together with Carbon:Nitrogen ratio enable prediction of the variation in τ within decay classes and tree species along an elevation gradient. In addition, τ decreased with increasing decay status of the wood, with temperature also playing an important role, as τ increased with increasing site elevation. The study also suggested the importance of further studies of the effects of seasonal variations in climate in short term field studies, as a single wet season reduced the observed τ of the CWD faster than two wet season and a dry season.

Key words: Wood density, ultrasound technique, above ground biomass, carbon stocks, tropical ecosystems, tropical montane forest, tree diameter, altitudinal gradient, coarse woody debris, residence rime, carbon, nitrogen, plant traits.

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Chapter 1

General introduction

Top of Mount Bellenden Ker, Innisfail, Queensland, Australia

1.1 The significance of tropical forests

It is currently known that the atmospheric carbon (C) pool is increasing due to C releases from fossil fuel consumption, deforestation, land use change and cement production Houghton et al. (2009). Between 1750 and 2011 approximately 555±85 PgC have been released to the atmosphere (IPCC 2013) - about 32 % of this is from land-use change and 67 % from fossil fuel and cement production. Of this amount, 28 % has been absorbed by the oceans and 29 % by terrestrial ecosystems with the remainder having accumulated in the atmosphere, which has grown from 280PgC to 519PgC from 1750 to 2011.

Tropical forests are the terrestrial ecosystem that stores more carbon than any other (Phillips et al. 1998, Malhi and Grace 2000, Phillips et al. (2008)). Moreover, vegetation in terrestrial ecosystems is the largest terrestrial pool of C after soils and stores approximately about one third of the total terrestrial C, and soils are, after the oceans, the major C sink (Eswaran et al. 1993). Tropical forests, on average store approximately 157 MgC ha^{-1} of biomass, a total higher than both temperate forest (96 MgC ha^{-1}) and boreal forests (53 MgC ha^{-1}) (Fig. 1.1). However, the annual C uptake by these reservoirs are not compensating for the actual gross emissions (IPCC 2013), caused mainly by land use degradation. Nevertheless, recent studies from 2000 to 2007 are suggesting that tropical forests are roughly neutral net emissions ecosystems due to the fact that C emissions from deforestation are offset by significant C uptake by forest regrowth; regrowth from tropical forests are thought to sequester more carbon (1.64 PgC year^{-1}) than pristine forests (1.19 PgC year^{-1}) (Pan et al. 2011). Modeled global estimates of the amount of biomass that pristine forests annually accumulate are quantified to 0.49 MgC ha^{-1} year^{-1} (Grace et al. 2014). These ecosystems represent a sink of C for the planet. Estimations of C emissions on the atmosphere when fire occurs on tropical ecosystems have been quantified around 0.007 PgC year^{-1} (Grace et al. 2014). These estimates demonstrate the importance of preserving primary tropical forest, which at present are sequestering C and contributing to mitigation of impacts of anthropogenic climate change.

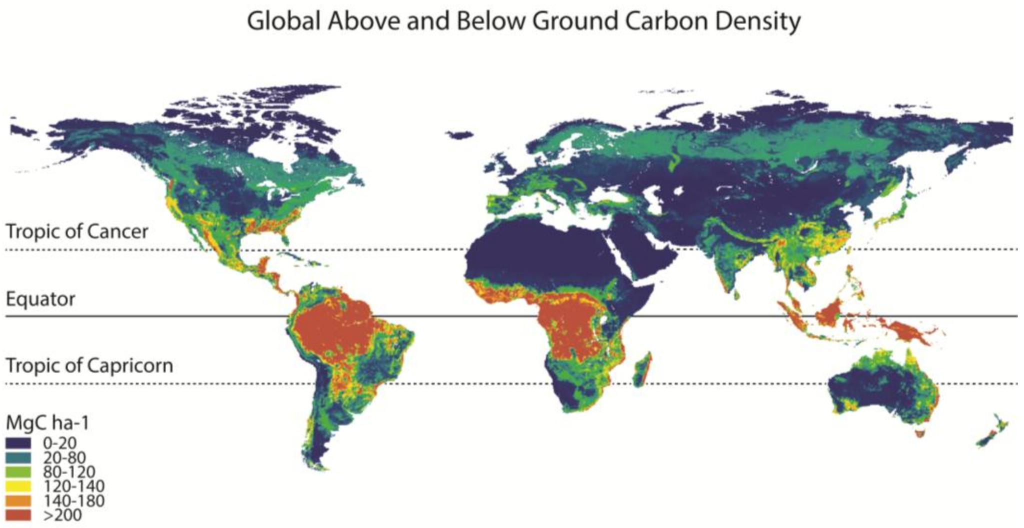


Fig. 1.1: Map showing the distribution of C globally. Data source from *http://cdiac.ornl.gov* (Aaron and Gibbs, 2008). Colors indicate the tons of C per ha. Tropical forests are the ecosystems that store the most C on a unit area basis >200 MgC ha^{-1}. Temperate forests are light green colored and are a reservoir around between 80-120 MgC ha^{-1} and Boreal forests are cyan and store approximately between 20-80 MgC ha^{-1}. Tropical forests are located approximately within 28 degrees from the Equator towards both the Tropic of Cancer and Capricorn, temperate forests are located approximately between 25 degrees and 50 degrees latitude in both hemispheres and forests located more towards the poles are classified as Boreal.

Tropical forests occupy a larger area than temperate or boreal forests (17.5 x 10^6 km^2, 10.4 x 10^6 km^2 and 13.7 x 10^6 km^2 respectively) (Chapin III et al. 2011) and tropical forests have a higher C assimilation rates than boreal forests (0.8± PgC year^{-1} and 0.5±0.1 PgC year^{-1} respectively). Recent studies have demonstrated that at global level forests are experiencing stress responses to climate change. Temperate forests are registering higher tree mortality rates (IPCC 2013) and boreal forest areas may potentially release C release to the atmosphere from the stored carbon in melting permafrost (IPCC 2013).

There remain significant uncertainties about the amount of carbon that is emitted to the atmosphere as a consequence of an increasing rate of land use change in tropical regions (Baccini et al. 2012). The implementation of successful climate change mitigation strategies depends partially on improving the accuracy of models capable of calculating the real carbon stocks of tropical forests and the potential C that could be released to the atmosphere in case of habitat loss (Saatchi et al. 2011), or sequestered by restoration activities. Despite recent improvements in models based on the combination of remote sensing techniques and field data collection, results still present uncertainty (Saatchi et al. 2011). The complexity of ecosystem functioning in tropical forests is such that while global models can assist in elucidating general trends and shifts in C dynamics as consequence of climate change, local studies provide a more nuanced understanding of the major factors affecting these dynamics.

Despite the recent improvements in remote sensing techniques for acquiring terrestrial information on vegetation and C storage, gaining accurate information on biomass is still a technological challenge. Validation of remote sensing data includes the process of sampling tree species to obtain the wood density (ϱ) values. The high diversity of tree species in tropical forests implies a wide range of ϱ. Wood density is after tree diameter, the principal parameter used to convert the volume of the trees in a mass of C (Chave et al. 2005). Baker et al. (2004) highlights the importance of including an accurate value for ϱ through field sampling or field tree species identification and literature research.

Results from previous studies have demonstrated the importance of using accurate ϱ values in allometric equations to calculate C stocks: similar allometric equations with the same input variables for tree diameter and height but with different mean ϱ values (0.58 g cm^{-3} and 0.67 g cm^{-3}) have produced significant different values for mean aboveground biomass estimates for the same study area (Baker et al. 2004). In that study average aboveground biomass ranged from 221 Mg dry mass ha^{-1} to 277 Mg dry mass ha^{-1} respectively when ϱ was included and from 227 Mg dry mass ha^{-1} to 326 Mg dry mass ha^{-1} respectively when excluded. Thus, erroneous ϱ estimates can generate imprecise C stocks calculations and accurate ϱ values from tropical forests trees can only be only obtained with species knowledge or with a destructive sampling through field census data collection.

1.2 The importance of above ground carbon dynamics in tropical forest carbon budgets

Studies of tropical forest C dynamics are important in terms of understanding the flux of C through these ecosystems and the interrelations between the component reservoirs of biomass and soil (IPCC 2013). Trees are mainly composed of C and water. Photosynthesis is the process that plants use for C fixation and trees, after soils, are the main store of C in tropical forests. The rate at which energy, in the form of reduced organic carbon is taken up by an ecosystem is defined as the Gross Primary Production (GPP). In the case of tropical forest, most of this C is stored in the trunks and branches of trees (Malhi and Grace 2000, Malhi et al. 2006, Chave et al. 2008). Net Primary Production (NPP) is defined as GPP minus the energy released, to support the maintenance of tissues through respiration. Fig. 1.2 is a synthesis of the diagrams from Malhi and Grace (2000) and Cornwell et al. (2009) representing the C cycle of the above and below ground components in tropical forest in relation to the factors controlling NPP.

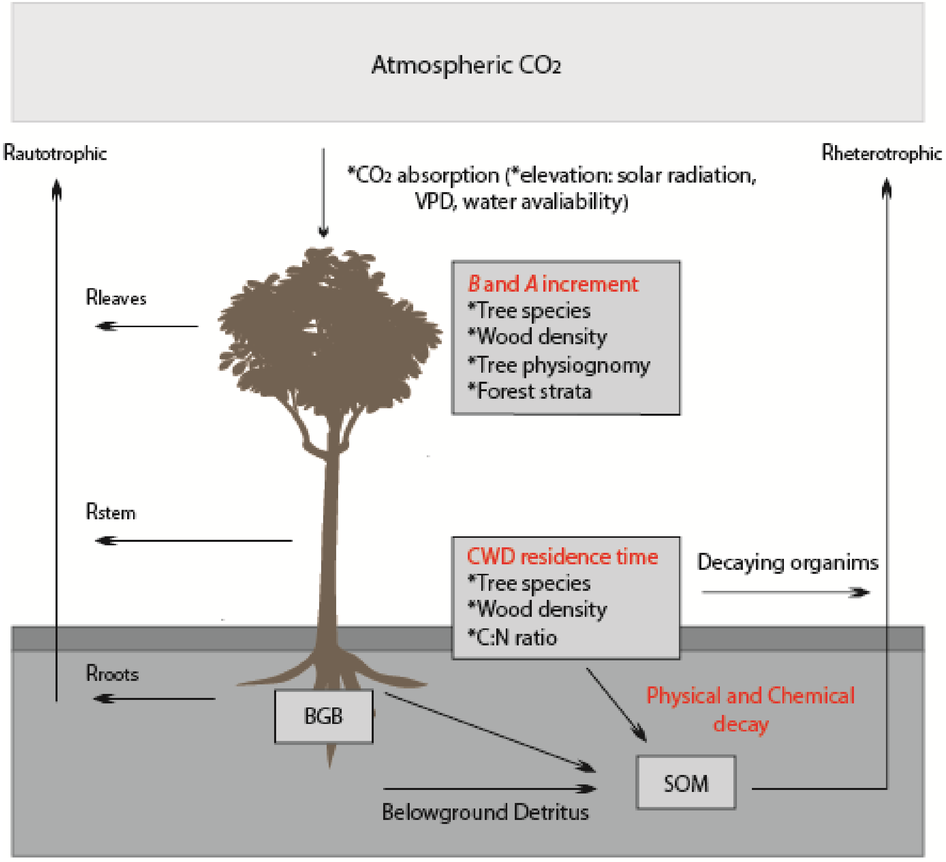


Fig.1.2. Schematic illustrating the above and below C dynamics in tropical forest. *B* is the above ground biomass, *A* is the basal area, BGB is the below ground biomass, CWD is the coarse woody debris, SOM is the soil organic matter and R is respiration. Red font color indicates parameters examined in this thesis. Studied variables in this thesis are indicated with the symbol *. Tree C uptake in this study was measured at different elevations to study the effects of variation of environmental variables with elevation (i.e. solar radiation, VPD, water availability). Control variables for *B* and *A* were tree species, wood density, tree physiognomy and forest strata. Control variables to study the CWD residence times were tree species, wood density and the C:N ratio.

Thus, in order to study how aboveground C budgets might vary over time is very important to holistically examine carbon dynamics. Tropical forests are resilient ecosystems but since 1750 they have been exposed to anthropogenic disturbances through habitat fragmentation and climate change. Consequences of anthropogenic climate change are still uncertain since tropical forests were created hundreds of years ago but the anthropogenic activities currently affecting their dynamics are very recent in earth’s time scale.

Scientists are trying to understand the consequences of anthropogenic activities for tropical forests in order to anticipate possible irreversible consequences and to quantify the past, actual and future terrestrial C storage potential of these ecosystems and the potential amount of C that could be released to the atmosphere as a consequence of land use change.

Publications from the last two decades have shown that there is an effect of climate change on tropical forest productivity but the future consequences of climate change remain uncertain (Phillips et al. 1998, Clark 2004, Fearnside 2004, Lewis et al. 2004, Malhi and Wright 2004, Lewis 2006, Gloor et al. 2009, Lewis et al. 2009a, IPCC 2013). There is however an observed increase of the length of the dry season in short-term experiments on Neotropical forests (Fu et al., 2013). For example, in southern Amazonia the dry season length has increased significantly since 1979 suggesting that drought might be more common in the 21st century (Lewis et al. 2011, Fu et al. 2013). Besides, studies of severe drought in Amazonia have reported an increase in fire frequency and tree mortality as a result (Saatchi et al. 2013). There are no similar long term studies studying changes in seasonality over time in tropical forests in Australia or Papua New Guinea but seems that cyclone frequency is increasing in Australia and might affect forest dynamics (Nott et al. 2007).

In addition, recent results from atmospheric measurements above the Amazon forests (quantifying carbon dioxide and carbon monoxide) have suggested a new finding of the effects of changing seasonal length on tropical forests due to climate change: trees suppressed photosynthesis during the drought season but not during the wet season (Gatti et al. 2014). Carbon estimations from this study suggested that the vegetation was a neutral C pool during the dry periods, but the same region was a sink of C of about 0.25±0.14 PgC year^{-1} during the wet season. Thus, these forests were a net sink for carbon over a full seasonal cycle. This last example highlights a remaining gap in knowledge of tropical forest function and the importance of acquiring accurate data using new technologies or joining existing datasets to increase the understanding of these ecosystems. Australian and Papua New Guinea tropical forests are lacking integrated studies using flux towers. Recently flux towers have been installed via the Terrestrial Ecosystem Research Network (TERN, http://www.tern.org.au/AusPlots-Forests-pg28321.html) in Australia or similar projects. Thus, more long term datasets will become avaliable over time necessary in Australia to study the evolution of these forests and C dynamics over time. Quantification of C dynamics is a necessary prerequisite to efforts to mitigate the effects of climate change, land use change and loss of biodiversity on earth.

Another disturbance that has been suggested to affect above ground C storage in Neotropical tropical forests is an increase in liana biomass due to an increase in the number of canopy gaps in disturbed forests (Phillips et al. 2002, Schnitzer and Bongers 2002, Wright et al. 2004). Lianas can accelerate tree death through stem breakage and also the turnover rate of liana biomass can be between 5-8 % faster than trees (Phillips et al. 2005). Lianas also has been proved that they can be a significant contributor to the total forest biomass in Neotropical forests (*viz.* up to 20 % of abundance from the total woody vegetation (Gentry 1991, Schnitzer and Bongers 2002). Thus, consequences of climate change on future scenarios if liana presence is increasing might be an increase in the size of the CWD C pool. Frequent cyclones in Australian forests promote vine growth (Turton 1992) but yet more studies are necessary to understand how this might affect tree mortality rate and the CWD pool. For example, during the data collection period of this thesis cyclone Yasi impact very seriously on a few study sites. Some of the sites were totally destroyed and others had a high number of tree deaths.

1.3 Previous studies of tropical forest productivity

Tropical forest productivity has been studied for the past four decades. Prior to this period, the difficulty in accessing these often meant there was a paucity of data (Jordan 1971, Lieth 1975). Nowadays it remains challenging to acquire data from remote tropical forests where logistics are complex and operational costs might be extremely high. This is for example the case of Australia and remote areas in Papua New Guinea were access is only possible by charters.

Pioneer studies of tropical forest productivity focused mainly on the study of leaf and litter fall production and the effects on different soil types on productivity (Jordan 1971). Results suggested higher productivity for forest undergoing succession (Jordan 1971). Later studies also incorporated the effects of nutrients cycles on forest productivity (Jordan and Herrera 1981, Vitousek 1984, Tanner et al. 1998, Herbert and Fownes 1999) and climatic variables such as mean annual temperature and precipitation (Brown and Lugo 1982).

Technological progress has facilitated the access to remote areas for monitoring purposes and also has facilitated the creation of long-term datasets. Contemporary studies using these datasets have contributed to delineating the long-term effects of anthropogenic climate change on tropical forest productivity. For example, Neotropical studies have suggested a trend of increasing NPP over the last two decades (Baker et al. 2004, Lewis et al. 2009b), perhaps explained by an increase of global temperatures or as a recovery effect from site disturbances (*viz.* canopy gaps) (Chave et al. 2008). Recent long-term studies based on datasets spanning the past 30 years - and perhaps more robust than the previous mentioned studies - have suggested a decrease in NPP, in particular in Amazonia and Borneo possibly due to an increase in tree mortality (Phillips et al. 2010). The same pattern has also been observed in latitudinal gradient studies across the globe (Allen et al. 2010). These increases in tree mortality may be related directly to an increase in the occurrence of extreme drought in the past two decades in tropical forests (Allen et al. 2010) and indirectly to an observed trend to increased tree growth rates as a result of CO_2 fertilization (Huntingford et al. 2013). Examples are a recent study in Africa that suggested an increase in tree growth rates unrelated to past forest disturbance (Lewis et al. 2009b) but perhaps to a change on the length of the dry season resulting more severe drought events.

However, other causes like regional climate variation have also been associated with a decrease in observed growth rates in a study in Panama (Feeley et al. 2007). Possible explanations of these divergent responses to environmental changes may lie in inter-continental differences in the evolutionary plant pathways of tropical forest floras and external environmental variables between continents (Morley 2000). However, there are not enough studies at the moment to draw a robust conclusion. A study that compared the capacity for adaptation and response to drought between Australian, West and Central Africa and Amazonia (McJannet et al. 2007a) found that Australian forest were better adapted to short durantion droughts than an Amazonian forests (Saatchi et al. 2013).

Coarse woody debris (CWD) is an important host of ecological biodiversity and an indicator of 'old-status' as well as providing essential habitat for bacteria, fungi, lichens, mossy, birds and animals (Woldendorp and Keenan 2005, Tobin et al. 2007). CWD can account for up to 13 % of C forest stocks (Tobin et al. 2007) yet there have been few studies of CWD dynamics in Australian tropical forests (Woldendorp and Keenan 2005).

1.4 The importance of CWD

The observed trend to increasing tree mortality in tropical forests - as an effect of either increasing tree growth rates as a consequence of a CO_2 fertilization effect and/or due to die-back because during severe drought events – will necessarily impact the CWD pool. Higher tree mortality might increase the accumulation of dead material, but perhaps the CWD residence times might remain unchanged leading to a buildup of CWD stocks (Tobin et al. 2007, Cornwell et al. 2009). The CWD decomposition process returns C to the atmosphere through respiration. To understand the effects of climate change on the rates of tree mortality and the effects that can have over C stocks in the CWD pool, it is essential to understand the factors controlling the decomposition rate of CWD. CWD residence times are dependent on several parameters including temperature, soil fertility, biomass, ϱ, basal area, pool of degrader organisms. Thus, denser woods might take longer to decay because of higher structural complexity and possibly due to higher proportions of secondary chemicals that provide some defense against decay (Cornwell et al. 2009). This is why decay studies of CWD using woods with a range from low to high density woods along an elevation gradient are useful, as they are an opportunity for anticipating to future scenarios under the effects of climate change.

Recent results from the IPCC (2013) are suggesting an increase in the N deposition rates caused by anthropogenic activities. This increase might also potentially alter tropical forest carbon dynamics. As an example, records of N deposition rates in a closed forest in Panama from 1968 to 2007 found similar rates to those in a nearby tree plantation fertilized for a decade (Hietz et al. 2011). Therefore, there is evidence that anthropogenic activities can increase the N deposition on tropical ecosystems, and indirectly affecting the terrestrial CO_2 sink. For example, global studies on deposition rates of fixed N (N ready to be used by living organisms) have shown differences between temperate and tropical regions (Reay et al. 2008). In broad outline, in 2000 was estimated that Europe has a deposition between 750 mgN m^{-2} $year^{-1}$ -3000 mgN m^{-2} $year^{-1}$ and tropical forest in Australia around 100 mgN m^{-2} $year^{-1}$ (Reay et al. 2008).

In this thesis C and N concentrations in CWD were monitored over time to study how the ratio C:N over time for different *ϱs*. Previous studies detected an increase of N availability with decreasing C concentrations during CWD decay, but no previous studies have conducted along elevational gradients to simultaneously investigate the effect of temperature, nor have previous studies used woods of different *ϱ* (Laiho and Prescott 1999, Guo et al. 2006, Olajuyigbe et al. 2011).

1.5 The importance of wood density in tropical forest carbon budgets

Wood density is the second most significant component that defines above ground tropical forest biomass (*B*), after tree diameter and before tree height. Thus, the determination of *ϱ* when C stocks are being calculated is crucial. Accurate measurements require either the identification of the species allowing use of a *ϱ* derived from the existing literature or else sample extraction from the trees for direct laboratory determination of density. Generalization of *ϱ* from the use of data compilations increases the bias error in the dataset and results. Therefore, studies of remote areas using remote sensing techniques benefit from the validation of data though field surveys and tree sampling of *ϱ*. This is how the most successful REDD+ programs have been established (Gibbs et al. 2007, Holly et al. 2007, Mitchard et al. 2014).

The annual variations of tree growth, after tree species wood traits characteristics, define the *ϱ* of an individual tree in seasonal forests. Wood density has a major genetic component but environmental variables may have a significant influence on the intra-annual growth and thereby on *ϱ*. Temperate and tropical seasonal trees present rings that are related to annual seasonal growth and ring widths can vary according to environmental conditions. For example, in temperate or seasonal tropical forests, a dry wet season might create a narrower annual tree ring when compared to an extremely wet season. In contrast, tropical forest trees growing where there is a short or absence of dry season, tree rings related to annual growth are commonly absent. The presence of tree rings might be related to leaf caducity which can happen at different times for different tree species or wood tints neither of which are related to environmental parameters. This is why is very important to understand how ϱ varies along with tree growth from wet to moist and dry tropical forests.

Previous studies of wet montane forests have suggested a decrease of ϱ from the pith towards the bark (Nogueira et al. 2008, Henry et al. 2010) that might be explained as a mechanism of tree support in ecosystems where water is not limiting and growth is dependant only on light availability and soil nutrients. Wood density varies widely from 300 kg m^{-3} to 1500 kg m^{-3} (Ilic 2000, Zanne et al. 2009) and can vary by up to 74 % at the genus level (Chave et al. 2006) and up to 40 % within individuals of the same species (Ilic 2000) collected at different study sites. For example, in a sampling area of 1 ha with 800 trees, a diameter at breast height of 30 cm and an average tree height of 20 m, according to the allometric equation for wet forests of Chave et al. (2005) the average B will be 558.72 Mg ha^{-1} with a variability between 335.23 Mg ha^{-1} and 782.21 Mg ha^{-1} for an intra-specific variation of 40 % and between 413.45 Mg ha^{-1} and 703.99 Mg ha^{-1} for an intra-specific variation of 26 %. Wood density also varies along the bole, decreasing with increasing tree height (Ikonen et al. 2008, Nogueira et al. 2008, Kord 2011). Nogueira et al. (2008) concluded after studying 73 tropical trees that for 87 % of the trees ϱ decreased with tree height with the more extreme case being up to 57 % and on average was 8 %.

More detailed studies within individuals have demonstrated that ϱ varies across tree girth (Nogueira et al. 2008) either increasing or decreasing from the pith towards the bark. Most of the previous studies have been performed in seasonal forests where there is a clear seasonal delimitation of the xylem cells. Inter-annual growth related to seasonality is visible under the microscope. However, wet forests or forests that have a short dry season might not have a differentiated period of xylem formation related to seasonal growth. For this reason it is extremely important to better understand the processes that influence the formation of xylem cells in tropical forests.

Regional studies of ϱ variability have suggested that intra-specific variation can be related to precipitation (Wiemann and Williamson 2002) and soil fertility (Baker et al. 2004, Patiño et al. 2009). Studies of ϱ across large regions and continents have also demonstrated that ϱ is to some degree a phylogenetically conserved trait (Chave et al. 2006, Swenson and Enquist 2007).

However, the complexity of tree wood structures makes it very inaccurate to simply assign ϱ values to unidentified tree species when literature is unavailable.

Moreover, our understanding of the evolution of tropical flora suggests that tree survival is related to the capacity of the tree to adapt to the local environmental conditions. And relatively recent studies have associated ϱ to the likelihood of survival during a drought event (Phillips et al. 2010). Suggestions are that shorter trees with lower ϱ are more likely to survive drought because of their investment in a more efficient hydraulic conductance structures in comparison with trees of higher ϱ (Poorter et al. 2010). Other traits that ϱ has been inversely related to include tree growth rate (Poorter et al. 2010), wood moisture content (ω) (Nogueira et al. 2008) forest strata occupancy (Poorter et al. 2010) and water usage demands (Chave et al. 2006, Malhi et al. 2006, Swenson and Enquist 2007).

1.6 The importance of altitudinal gradients as natural laboratories

Altitudinal gradients represent natural laboratories along which to conduct studies of the impact of a range of climate variables on ecosystem function and carbon cycling (Malhi et al. 2010) (*viz.* temperature, precipitation and soil fertility vary with elevation). Previous studies of tree species diversity along altitudinal gradients have demonstrated a decrease in species diversity with increasing elevation (Stevens 1992, Lieberman et al. 1996) that might be explained by a decrease in the suitability of conditions for tree growth (i.e. solar radiation, water availability, soil fertility, wind exposure) (Moser et al. 2008). This decrease has usually been demarcated by 'critical zones' where one group of species displaces another over a short altitudinal range (Culmsee et al. 2010, Kitayama et al. 2011). The composition of tree species (and thus ϱ) and stature of the vegetation are important factors determining the aboveground biomass along an elevation gradient. For instance, a pioneer meta-analysis on the effects of temperature on tropical moist forest across the Neotropics, Paleotropics, Indomalayan region and Polynesia suggested that the change of the vegetation with elevation was the main cause of significant differences in total carbon stocks (Raich et al. 2006).

Elevation gradients have been used to study the variations of C stocks in relation to temperature. Such studies can be used in assessing the impact of climate change on future tropical forests. A general decrease of the stature of the vegetation with increasing elevation has been related to a decrease in water vapour deficit, temperature, solar radiation, wind exposure and soil fertility with elevation (McJannet et al. 2007a, Feldpausch et al. 2010). For example, studies on altitudinal gradient have reported an increase in soil organic C with increasing elevation (Raich et al. 2006, Zimmermann et al. 2009) because of a decrease in soil microbial activity. Moreover, it has been observed an increase of the tree root mass with elevation that might represent a compensation for the decrease in tree stature at higher elevations, where water availability or soil fertility are low (Moser et al. 2008).

Many studies have reported a decrease in above ground biomass (*B*) with increasing elevation around the globe (Clark and Clark 2000, Schuur and Matson 2001, Kitayama and Aiba 2002, Leuschner et al. 2007, Moser et al. 2008, Asner et al. 2009, Culmsee et al. 2010, Girardin et al. 2010, Slik et al. 2010). However, it has been also observed that the trend of decreasing stature of the vegetation with elevation can be sometimes reversed once the montane cloud base is reached, leading to an increase in *B* above that zone (Alves et al. 2010). Some authors have suggested that the trend of decreasing *B* might be explained by a decrease in soil fertility at higher altitudes (de Castilho et al. 2006, Malhi et al. 2006) or annual rainfall (Schuur and Matson 2001, Malhi et al. 2006, Slik et al. 2010). Table 1.1 is a summary of previous studies along altitudinal gradients in tropical forests. A study along an altitudinal gradient in tropical forests in Borneo across two different soils types, derived from sedimentary and ultrabasic rocks, suggested a decrease in *B* with increasing altitude (decreasing temperature and air pressure), from 700 m to 3100 m asl, decreasing from 432 Mg ha^{-1} to 210 Mg ha^{-1} and from 548 Mg ha^{-1} to 35 Mg ha^{-1} respectively (Kitayama and Aiba 2002). The same study also found a decrease in above ground net primary productivity in related to decreasing temperature.

Table 1.1. Summary of the studies performed along altitudinal gradients in tropical forests.

Author	Location	Lower elev. (m)	Higher elev. (m)	***B*** **(Mg ha^{-1}) lower elev.**	***B*** **(Mg ha^{-1}) higher elev.**
Kitayama and Aiba (2002)	Borneo	700	3100	432	210
				548	35
Girardin et al. (2013)	Peruvian Andes	194	3020	124	47
Culmsee et al. (2010)	Indonesia		2400		323
Moser et al. (2011)	Ecuadorian Andes		3060		112

Another study in the Peruvian Andes found that *B* decreased from 124 Mg ha^{-1} at 194 m elevation to 47 Mg ha^{-1} at 3020 m (Girardin et al. 2010). In Indonesia, values at 2400 m elevation were, however, much higher than the Peruvian study (Girardin et al. 2013) with above ground biomass of 323 Mg ha^{-1} (Culmsee et al. 2010). A study in the South Ecuadorian Andes found *B* much closer to the study from (Girardin et al. 2013) with *B* of 112 Mg ha^{-1} at 3060 m (Moser et al. 2011). In this way, another benefit of studies on altitudinal gradients are the contribution they make to a better understanding tropical montane forests, a very fragile ecosystem that is particularly threatened by climate change (Wallace and McJannet 2012). Previous studies have suggested that these endangered ecosystems are threatened by fog dissipation that could reduce the amount of cloud intercepted water (Williams et al. 2003, Ledo et al. 2009, Ledo et al. 2012, Chu et al. 2014) and expose these ecosystems to increased drought stress.

Wood density traits are phylogenetically conservative and they are very important because they can provide inferences as to ecophysiological functionality in terms of hydraulic structure and mechanical support (Chave et al. 2009). A few studies in seasonal forests have inferred an intra-specific variation of ϱ that is related to mean annual precipitation (Wiemann and Williamson 2002, Baker et al. 2004, Chave et al. 2006, Swenson and Enquist 2007, Baker et al. 2009, Henry et al. 2010); for example results in lowland seasonal tree plantations in the Peruvian Amazon demonstrated that ϱ is negatively correlated with mean annual precipitation (Weber and Sotelo Montes 2008). Also, Hernandez and Restrepo (1995) showed that the intra-specific variation of ϱ was explained by geomorphological variation in eleven regions in Colombia and Venezuela.

1.7 Australia and Papua New Guinea

Australian rainforests represent a World Heritage Area covering about 9000 km^2, located in North Queensland (Russell-Smith 1991). There is general agreement that Australian forests occur in comparatively high rainfall areas or in lower rainfall areas where there is a measure of fire protection (Bowman 2000) as Australian tropical forests are present only in a small area of their total potential distribution, possibly explained by long history of aboriginal fire management. In addition, primarily selective logging was active from mid-late 19th century until 1988 (Vanclay 1994). These forests are also prone to significant natural disturbances such as those due to tropical cyclones (Webb 1958), and predictions of consequences of global warming include an increase in the frequency of these events (Nott et al. 2007).

Previous studies in Australia along elevational gradients through montane forests have demonstrated the importance of cloud interception in determining water availability during the dry season, estimated to be between the 5 % and 30 % of the total annual water available with this figure rising to as much as 40-70 % during the dry season. Thus, the prospect of cloud reduction as consequence of climate change could lead to serious ecological impacts, especially at higher elevations where interception is greatest (Williams et al. 2003, McJannet et al. 2007a, McJannet et al. 2007b). Understanding the relationship between ϱ and elevation – given the hypothesised relationship between ϱ and hydraulic conductance – can help to define the buffering capacity of the trees to resist increased drought stress because of global warming. Also

McJannet et al. (2007a) suggested that Australian forest characteristics (with flora derived from dry forest ancestors; Morley, 2000) may allow trees to survive severe drought. Besides, the low number of canopy emergent trees due to frequent cyclone exposure resulting in fewer trees occupying to water-demanding, sun-exposed emergent niches - resulted in lower transpiration rates than Brazilian and French Guyana forests (McJannet et al. 2007a).

Tropical forests in Papua New Guinea have decreased in area in the last four decades by about 30 % and currently cover about 33 million ha (Shearman et al. 2008). Of the total forest area lost approximately 12.7 % and 12.8 % were lower and upper montane forest respectively (Shearman et al. 2008). Papua New Guinea was, in 2007, the second larger exporter in the world of tropical woods (www.aciar.gov.au). Consequences of forest loss are very critical in Papua New Guinea as the forests contain 5 – 6 % of total global diversity (Shearman et al. 2008). About 98 % of the land is owned by local indigenes that are responsible for forest management and contracts between local landowners and foreign companies for logging concessions have resulted in considerable forest destruction (Putz et al. 2012). Initiatives from foreign conservation organizations are helping communities to develop and manage conservation areas in a diverse country characterized by fertile lands, and a high diversity in language and culture. This is the case of for example of the YUS conservation area (http://www.conservation.org).

Conservation of the land through sustainable management with the oversight of conservation organizations is benefiting the communities by allowing them to gain education and to access to medical assistance. Also, established conservation areas are providing access for researchers to remote areas. Studies quantifying biodiversity and biomass in these remote areas can help to promote conservation initiatives and provide sustainable local livelihoods.

Remote sensing research in Papua New Guinea has demonstrated a significant reduction in montane forest area caused by burning during the drought periods (Shearman et al. 2008). Montane forests in Papua New Guinea represent up to 37 % of the total forest area and are highly biodiverse with a high degree of endemism (Shearman et al. 2008). Broad surveys of aboveground biomass have suggested that, on average, lowland primary forests to contain 111.4 Mg C ha^{-1}, with the lower-montane forests 148.2 Mg C ha^{-1} (Fox et al. 2010). Comparison of Papua New Guinea *B* with other studies from across the tropics suggest that Papua New Guinean forests have a slighter higher capacity for *B* accumulation (Bryan et al. 2010), possibly explained by its comparatively fertile soils. There are only a few studies in Papua New Guinea that have estimated *B* from pristine forests (Bryan et al. 2010). This is highly concerning as the rate of deforestation is extremely high and precise estimates of aboveground biomass loss are difficult to achieve.

1.8 Research objectives and questions

The main objective of this research is to evaluate the importance of ϱ – defined as dry mass of wood per unit of fresh or green volume – for aboveground C dynamics for tropical forests under different environmental controls. Research was conducted in tropical forests in Australia, Papua New Guinea and in a tree plantation in Vanuatu. The main aims of the thesis are to:

- To develop and test a novel non-destructive field method to determine ϱ on living trees across different tree species and forests types.
- To determine the intra-specific variation of ϱ along an elevation gradient in a tropical montane forest in Papua New Guinea.
- To define the determinants of B, productivity and ϱ under different environmental and soil fertility parameters along an elevational gradient in north Queensland, Australia.
- To determine the significance of wood density and climate as controls CWD residence times using an altitudinal gradient in Australia.

1.9 Thesis outline

This dissertation is laid out in 6 chapters, first an introduction chapter (above), followed by four chapters that relate to four individual studies addressing the aims above and a final synthesis chapter. Fieldwork in support of the four main studies was conducted at study sites in Vanuatu, and along altitudinal gradients in northern Australia and Papua New Guinea. Each data chapter is presented in a self-contained paper structure, hence is some duplication of material in the introduction section of each chapter.

Chapter 2 reports the development and validation of a non-destructive ultrasound method to measure ϱ in living trees from tropical forests located in Vanuatu, Papua New Guinea and Australia. The aim was to assess the accuracy and reproducibility of an ultrasound technique by comparing measurements on living trees with a wide range of ϱ (300 kg m^{-3} to 1100 kg m^{-3}). The study determined the applicability and accuracy of the method a) along the bole within tree individuals, b) within species and c) across different species.

Chapter 3 synthesizes the determinants of ϱ variation in relation to tree physiognomic characteristics and site elevation along an altitudinal gradient in a tropical montane forest in Papua New Guinea. Samples were collected from four study sites that were all classified as non-seasonal or everwet forests. A model was created to study the variation of ϱ according to a) niche occupancy – sun-exposed and shaded –, b) tree physiognomy – tree height versus tree diameter – and c) elevation – differences on annual mean temperature, water vapor deficit, annual precipitation, solar radiation.

Chapter 4 investigates the determinants of structural attributes of the vegetation – stature, productivity, growth rates, ϱ and niche occupancy (sun-exposed or shaded) for species at 18 study sites on an elevational transect in tropical forests of Northern Australia. The study sites varied from dry forests (7 month dry season length) to moist to wet forests (1 months dry season length). A model was created to determine the main determinants of the variation of ϱ according to individual and species physiognomic characteristics and also under different environmental conditions.

Chapter 5 describes an experiment designed to measure the impact of temperature on coarse woody debris residence times for six tree species in tropical forests in Australia with a range of wood densities between 300 kg m^{-3} and 1000 kg m^{-3}. Wood samples were collected from three different decay classes: fresh, mid-decayed and decayed. In order to determine the impact of mean annual temperature on debris residence times, wood samples were placed at three sites along an elevational gradient from 50 m to 1500 m asl. After six and fifteen months samples were retrieved to determine mass loss over time and variation on C and N abundances. A multi-level analysis was developed to identify the significant variables that defined the wood residence times along the elevation gradient.

Finally, chapter 6 summarizes the main results of the different chapters and provides a general synthesis. Implications of the effects climate change on tropical forests are also discussed.

Chapter 2

Non-destructive, in-field determination of wood density in tropical forests

Elaeocarpus grandis tree at Daintree Rainforest Observatory, Cape Tribulation, Queensland, Australia

2.1 Introduction

Tropical forests are a significant store of terrestrial carbon (C) (Phillips et al. 1998, Malhi and Grace 2000, Phillips et al. 2008). Initiatives such as the Forest Carbon Index (www.forestcarbonindex.org) promote tropical forests as a low-cost opportunity for conservation and re-growth to mitigate climate change, since the price of carbon credits decrease towards the tropics. For example, prices in the United States and Russia have an average value between $40 and $50 per tonne of C dioxide equivalent of greenhouse gas emissions, but this can decrease to less than $10 for tropical forests in Brazil or equatorial Africa. The limited access to remote areas and the high cost of the logistics associated with access make it very difficult to estimate tropical forest C stocks in many parts of the world (Houghton et al. 2009, Meyer et al. 2013). Broad estimations from the IPCC (2011) suggest that tropical forests contain up to 157 MgC ha^{-1} of carbon, higher than that temperate forests (96 MgC ha^{-1}) or boreal forests (53 MgC ha^{-1}). Tropical ecosystems are highly diverse, and the impacts of environmental variables such as climate, soil characteristics, slope of the terrain (Ferry et al. 2010), and disturbances (Gleason et al. 2010) can affect species distribution and the woody structure of the vegetation. This makes the process of obtaining accurate estimations of C stocks difficult (Baker et al. 2004, Chave et al. 2005, Malhi et al. 2006).

Tropical forests are suffering from both the impact of deforestation and the effects of the anthropogenic climate change. Initiatives to reduce global C emissions such as REDD+ (Reducing Emissions from Deforestation and Forest Degradation) are combining the use of remote sensing data with field measurements (Gibbs et al. 2007) to obtain estimates of above ground biomass (B). In order of importance, global allometric equations to estimate B include tree diameter at breast height (DBH), ϱ, and H (Baker et al. 2004, Chave et al. 2005, Feldpausch et al. 2010). Baker et al. (2004) and Chave et al. (2005) confirmed that ϱ is the key factor required to convert tree volume into a stock of C. Modern remote sensing data acquisition using Lidar technologies can measure H, DBH, and canopy density, but not ϱ. Therefore, field measurements are still necessary to generate the relationship between ground-based and Lidar datasets. The high biodiversity of tropical forests results in a potentially wide range of ϱ for trees with $DBH >$ 10 cm, meaning trees that are usually included in C stock assessments. In addition, large trees with $DBH >$ 70 cm can contribute up to one third of the total biomass at a site (Chave et al. 2003). Hence, total C stocks calculated are highly dependent on the ϱ assumed for large trees.

Measurements of ϱ using traditional techniques are carried out destructively using an increment borer, or from a disc if the tree is felled. Field sampling can be very time consuming and physically demanding, with cores liable to break during extraction or transport. Sample processing is a costly, laborious, and intensive exercise with the amount of effort increasing in proportion to the number of species that may be present at a site assessed for C stocks. In addition, sample processing can follow different protocols, creating additional uncertainty in the merging of disparate datasets. These uncertainties affect the estimation of C stocks (Nogueira et al. 2008). For example, core volume can be measured by measuring the total length and diameter with a calliper (Parolin and Worbes 2000), or by submerging the sample in water (Ilic 2000). ϱ is reported as the oven dry mass divided by fresh or green volume, excluding the tree bark (Williamson and Wiemann 2010).

Variation in ϱ at the species level only accounts for 26 % of the total variance among species (Chave et al. 2003). Thus, the application of genus data when species values are unknown is likely unreliable (Baker et al. 2004, Chave et al. 2005). Large ϱ datasets such as The Global Wood Density (GWD) (Zanne et al. 2009) can be used to substitute for missing values at the local/regional level. This enables estimation with higher reliability due to the larger sample set that is available in comparison to local/regional datasets (Flores and Coomes 2011). However, the GWD database contains fewer values for tropical trees, which exhibit a broad range of ϱ. Therefore, additional local measurements of ϱ might be necessary to provide an accurate estimate of C stocks. For example, intra-specific wood trait variations suggest a variation of ϱ for tropical forest trees between 646 kg m^{-3} and 1076 kg m^{-3} for samples from Australia and Papua New Guinea (Zanne et al. 2009).

Available research suggests that ϱ decreases up the tree stem (Ikonen et al. 2008, Nogueira et al. 2008, Kord 2011). This could possibly result in an overestimation of C stocks. Additionally, wood density can also vary radially. Radial variation of ϱ is caused by the intra-annual variation of wood density. Intra-annual variation is mainly driven by seasonality rather than variation in the cell walls density along the tree radius (Meinzer et al. 2003). Dendrochonological techniques have demonstrated that in seasonal tropical forests, extreme weather events can cause a significant decrease or increase of tree growth rate (i.e. drought events) (Bouriaud et al. 2005) and thereby in ϱ.

In order to facilitate the measurement of wood density in tropical forests, this study aimed to test a non-destructive and rapid field method based on ultrasonic techniques. Ultrasonic techniques measure the time it takes an acoustic pulse with a frequency above approximately 20,000 Hz to travel between two points. Acoustic sound propagation through wood is determined by the elastic constants of the material and by its anatomical structure (Price

1929, Gonçalez et al. 2001, Gelder et al. 2006, Auty and Achim 2008). Some relevant studies are summarized in Table 2.1. Velocity is higher in perpendicular measurements in comparison with longitudinal measurements where the sound travels across the cell wall fibres along the compressed longitudinal cells (Price 1929, Bucur 1983, Bucur and Feeney 1992, Ross and Hunt 2000, Wang and Chuang 2000, Ross et al. 2004, Bucur 2006, Mahon et al. 2009, Dikrallah et al. 2010). Therefore, measurements perpendicular to the grain orientation are the most accurate for the study of intra-annual cell growth of trees and the anisotropic characteristics of the wood. Additionally, angiosperms have more complex wood cell structures than gymnosperms. Gymnosperms have a cell diameter size of approximately of 0.051 mm, while that of angiosperms is between 0.0127 mm and 0.254 mm (Hoadley 1990). Additionally, medullary rays are numerous in conifers and can vary in length between 0.020 mm and 0.080 mm (Price 1929). In angiosperms, these rays can vary from 0.010 mm for a single cell up to 3 mm for cell associations, and they can form aggregates through the xylem (Hoadley 1990).

Table 2.1. Summary of previous ultrasound studies to study wood density. CoD is coefficient of determination.

Author	Instrument and kHz	Type of meas. (intra- or inter-specific) and directional meas. along the wood grains*	CoD btwn wood density and pulse velocity	Wood moisture content (ω) (%)	Temp. (°C)	Relative humidity (%)
de Oliveira and Sales (2006)	Sylvatest ultrasonic apparatus (22)	Intra-specific. Radial Inter-specific. Radial	0.80-0.88 0.31	12	28	65
Acuña et al. (2006)	Sylvatest ultrasonic apparatus (30)	Intra-specific. Angular fibres Inter-specific. Angular fibres	0.91-0.99 0.922	12	n/a	n/a
Gonçalez et al. (2001)	PANAMETRICS, UA5052 (80)	Intra-specific. Radial	0.72-0.87	10-12	n/a	n/a
Bucur (1983)	Hewlett Packard 214A, Tektronic 7603 7B5A 7A18 (1000)	Intra-specific. Radial	0.99	Living trees (>30)	n/a	n/a
Bucur (2006)	(1000)	Inter-specific. Radial	0.68	12	n/a	n/a
(Polge 1984)	(80)	Intra-specific. Along	0.99	Saturated	n/a	100
Solórzano-Naranjo (2012)	Sylvatest ultrasonic apparatus (22)	Inter-specific. Radial	0.19	Living trees (>30)	n/a	n/a

*Radial is along the tree radius and along means along the tree bole.

Previous studies using ultrasonic techniques have demonstrated the applicability of this technique for dead trees. For example, Bucur (1995) conducted a comparative study of wood anisotropy in relation to acoustic pulse velocity between broadleaf and conifer species. They demonstrated that higher pulse velocities were associated with higher ϱ, with density explaining up to 68 % of the observed correlation. Recent studies exploring the correlation between ϱ and acoustic velocity have confirmed the potential of this technique to provide an indirect measure of ϱ. Grabianowski et al. (2006) reported a relationship of about 0.96 between acoustic velocity and ϱ in standing *Pinus radiata* trees of different age. In addition, Oliveira and Sales (2006) demonstrated that ultrasonic velocity increased with ϱ across a number of tropical tree species with a coefficient of determination of 0.80 to 0.88 within species, but with a much lower value of only 0.31 between species.

Based on previous applications of ultrasonic techniques on wood, measuring ϱ through the application of acoustic techniques might offer scope for the rapid and non-destructive investigation of ϱ in standing trees. The results from previous studies suggest that air temperature and wood moisture might influence the velocity of an ultrasonic soundwave through wood. Wood moisture can affect the velocity of an ultrasonic pulse, particularly in relation to the fibre saturation point (FSP). FSP is defined as either the point at which no free water is present within the cells in the wood but where some saturated bound water is still present in the cell walls (Siau 1984), or the minimum moisture content required in equilibrium with a saturated atmosphere (Barkas 1935). Many studies have found a negative relationship between wood moisture and ϱ when measured above the FSP (Sakai et al. 1990, Oliveira et al. 2005), with the latter having a coefficient of determination of 0.97 for longitudinal measurements and 0.78 for transverse measurements. In contrast, Ross and Hunt (2000) found that acoustic velocity was not affected by ω above the FSP. Wang and Chuang (2000), Ilic (2001), Wang et al. (2004), Brashaw et al. (2004), Han et al. (2005) and Dickrallah et al. (2010) have also reported an increase of acoustic velocity with decreasing wood moisture content (ω). Mora et al. (2009) found that acoustic velocity was 32 % slower through the wood of living trees compared with dried logs (12 % moisture).

Even though previous experiments conducted in laboratories suggest that this technique can provide a measure of wood density, there are potential complications associated with developing a field methodology. Unlike laboratory conditions, measurements might be subject to fluctuations in environmental conditions such as variable air temperature and daily precipitation.

New field methodologies using ultrasonic techniques to study wood density in living trees need to be tested against potential environmental disturbances to account for such variation.

The aim of this study is to develop a rapid and non-destructive field method to accurately determine ϱ in living trees. In this way, generating data to complement existing global ϱ datasets would be easier and probably less costly and time consuming. A reliable acoustic-based method could be used to help determine the environmental effects on ϱ across regions. Such a method could remove the need for identifying species and collecting core samples, as well as reduce laboratory time and costs.

2.2 Material and methods

2.2.1 Ultrasonic measurements

Ultrasound measurements were performed using a TICO Ultrasonic Testing Instrument, which is usually used to assess concrete (European Standard EN12504-4:2004, former BS 1881 Part 203, ASTM C 59). The operating frequency of the exponential transducers was 54 kHz. During the process of developing the field methodology for this new method, several issues were contemplated. Firstly, according to the operating instructions, measurements outside the range of 10 ºC to 30 ºC must be corrected through the application of a correction factor due to the sensitivity of pulse velocity to temperature in concrete (Jones and Facaoaru 1969; The European Standard EN12504-4:2004 Bucur 1995). The same may be true for wood. Thus, it was decided to test the equipment outside the range of 10 °C to 30 °C to evaluate the accuracy of the measurements. In addition, because the tropical forests at the study sites mainly had two seasons (wet and dry), measurements were performed in both seasons to determine any possible effects of seasonality on the accuracy (temperature, surface wetness, sunny versus rainy days).

Secondly, in order to avoid inaccurate measurements, we excluded trees with $DBH < 10$ cm in selecting trees for measurement, as well as damaged, infested trees, those that had a visible hole along the bole, and those that were buttressed or leaning > 10 degrees at breast height (1.3 m height, $H_{1.3}$). Radial ultrasound measurements were performed on trees to determine the relationship between ϱ and pulse velocity. Prior to measurement, the tree bark was removed from a 5 cm diameter area using 40 grit sandpaper. Following surface preparation, ultrasonic measurements were carried out after applying coupling gel to the ultrasonic transducers and placing them facing each other on opposite sides of the tree (Fig. 2.1) along cardinal points of measurement (North-South and East-West). All measurements were made in triplicate. Temperature (T_a) and relative humidity (RH) at the time of each measurement were recorded. The distance between the measuring points was determined using a Häglof 80 cm calliper. One person (M.T-R) carried out all measurements, since the ability of the measurer can influence the results (Bucur 1983; 1995).

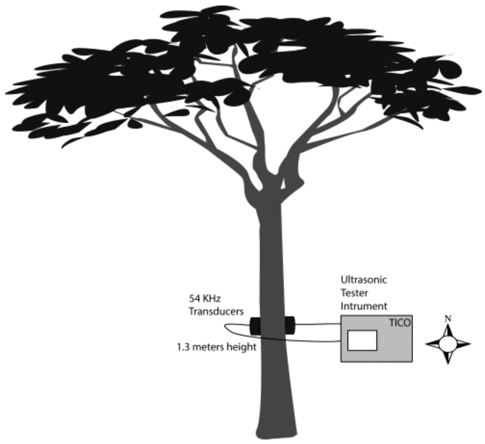


Fig. 2.1: Illustration of how the ultrasonic tester instrument was placed on trees to measure the total time that pulse velocity travelled from one transducer to another. Distance between the two points was measured using a calliper.

Thirdly, during field data collection and in the laboratory, we measured non-living trees that were decaying to observe the reliability of the ultrasound testing equipment. In cases with holes inside the tree, either the ultrasonic measurement was not possible because the equipment was not able to send the signal from the receiver to the transducer, or the resulting travelling time was much faster than expected for its diameter. Fourthly, in order to check for consistency between two readings in living trees, measurements were done at $H_{1.3}$ and at 40 cm above or below, depending on the shape of the tree.

Ultrasonic velocity was calculated according to:

$$V = \frac{d\ (cm)}{t\ (microseconds)} \qquad \text{(Eqn.1)}$$

where V is the pulse velocity, d is the distance between the transducers in cm and at the time t in microseconds of the pulse travelling time.

2.2.2 Study sites

This study was conducted at a site in Vanuatu and one in Papua New Guinea, as well as four sites in Australia (Fig. 2.2). Measurements were conducted to study the variation of ϱ within individual trees along the bole, the intra-specific variation of ϱ, and the inter-specific variation of ϱ. A range of species from low- to high-density woods were examined. The aim was to develop a robust and non-destructive method to study ϱ by the use of ultrasound techniques. Each study site was selected to study either the seasonal effects that climate could have on the ultrasonic equipment or to study the accuracy of measuring the intra-specific and inter-specific variation of

ϱ from ultrasonic measurements. We aimed to test the equipment at temperatures above 30 °C and below 10 °C. We also tested the effects of wetness on the surface contact area of the measurements. Trees with a wide range of ϱs including gymnosperms and angiosperms were examined. However, we first needed to test the precision of the equipment to measure the intra-specific variation of ϱ in a tree plantation, where variability of the ϱ is likely the lowest.

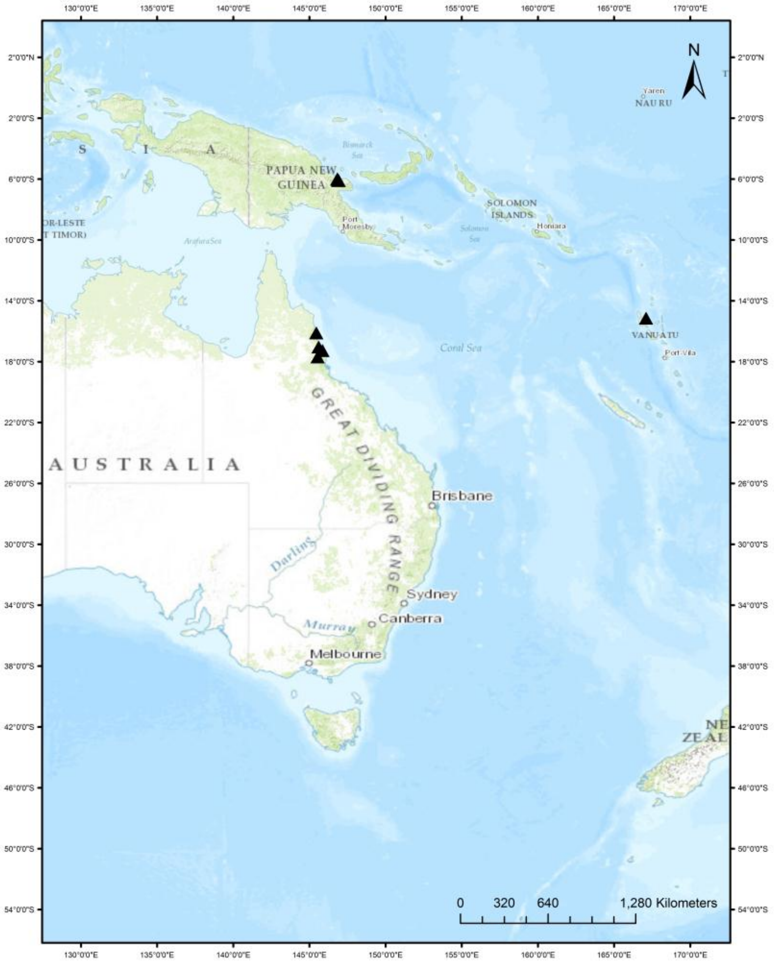


Fig. 2.2. Location of the study sites in Australia, Vanuatu, and Papua New Guinea.

The first series of measurements was carried out in a tree plantation of *Endospermum meullosum* on Espiritu Santo Island, Vanuatu (Kole). The planted trees were expected to have lower variability in ϱ than randomly selected trees in tropical forests. The first set of measurements was carried out on a tree plantation to study the intra-specific variation of ϱ and the effects of T_a > 30 °C on the ultrasonic measurements. The study sites were located at an elevation of 100 m above sea level (asl). The region receives an annual precipitation (MAP) of 2128 mm, with an annual mean temperature (MAT) of 24.5 °C and a dry season length (DSL, when evapotranspiration exceeds precipitation) of three months (www.meteo.gov.vu) (Table 2.1).

Measurements were carried out in December 2010. The trees were 11 years old and had a mean stem *DBH* of approximately 30 cm at the time of measurement. In total, eight trees in each of 10 different families originally sourced from two different locations within Vanuatu (Settle et al. 2012) were measured at a height of 1.3 m ($H_{1.3}$) over the course of 10 days. Temperatures during the day regularly exceeded 30 ˚C, except in the early morning and late afternoon. The first 6 days were sunny with daytime temperatures between 28 °C and 36 °C. During the last days, four days of irregular precipitation occurred. To avoid excessive temperature measurements, measurements were taken between 8 pm and 5 am. In addition, five buffer trees of the same species planted around experimental site areas were destructively harvested to obtain wood samples and to measure the accuracy of the ultrasonic equipment. Wood discs (10 cm thick) were cut from each of the five trees at $H_{1.3}$, at half tree height ($H_{1/2}$), and at three-quarter tree height ($H_{3/4}$). Ultrasound measurements were carried out on the wood discs during the evening of the collection day when $T_a < 30$ °C. The discs were stored under wet conditions before and after being transported to Australia for laboratory ϱ determination.

Table 2.2. Site coordinates, mean annual precipitation and temperature, altitude and seasonally index of all the samples sites.

Country	Site	Latitude	Longitude	MAP (mm)	MAT (ºC)	Elev. (m)	DSL
Vanuatu, Espirito Santo Island							
	Kole	-15.135	167.095	1035	24.5	100	0
Australia, Queensland							
	Daintree Rainforest Observatory (DRO)	-16.103	145.447	2087	25.2	50	7
	Bellenden Ker (BKT-01)	-17.264	145.854	8188	16.7	1590	0
	Davies Creek National Park (DCR-01)	-17.026	145.597	2050	21.2	683	5
	Misty Mountains National Park (KBL-03)	-17.685	145.535	1398	19.1	1050	7
Papua New Guinea (PNG), Huon Peninsula							
	YUS transect	-6.096	145.924	2824	11.7	3052	0

The second set of measurements was performed at the Daintree Rainforest Observatory (DRO) which as a canopy crane that was used to measure the variation of ϱ along the bole. In addition, measurements were carried out during the wet and dry seasons in order to study any effects of seasonality on the equipment. The initial idea of the project was to develop a methodology that could be used during both dry and wet seasons. During the wet season, environmental conditions might be less favourable for obtaining reliable measurements. For example, tree bark might be wet because of daily precipitation or water running along the stem via cloud interception, and T_a might easily exceed 30 °C. In addition, the amount of water stored in the stem during the wet season is larger than during the dry season (personal observation using tree dendrometer bands). In order to study the ϱ variation of the trees along the stem and the degree to which seasonal climate variations might affect the ultrasonic V, multiple measurements on the same trees were performed DRO during both the dry and the wet seasons.

DRO is at an elevation of 50 m asl, and the region receives an annual precipitation of 2087 mm, with a MAT of 25.2 °C and DSL of 7 months. Measurements were performed during the dry and wet seasons of 2012 using the canopy crane at a height of 10 m (H_{10}). Measurements were also made during the dry season of 2013 from the ground at only 1.3 m ($H_{1.3}$). Ground measurements were only performed during the dry season because previous data analysis from data collected in 2012 showed that measurements performed during the wet season were not accurate (see below). A total of eighteen trees (canopy trees) were measured, representing five species (*Cardwellia sublimis*, *Castanospermum Castenospermum australe*, *Cryptocarya mackinnoniana*, *Elaeocarpus grandis,* and *Litsea leefeana*). All five measured species were canopy trees. During the wet season, measurements were restricted to very early in the morning and late at night to avoid extreme T_a. For this site, it was not possible to obtain a destructive sample of the trees for further laboratory determination of ϱ, so ϱ values for each species were obtained from the literature (Zanne et al. 2009, Illic et al. 2010).

In a tropical montane forest, precipitation is present all year around, and tree wood structure might therefore be different from that in seasonal forests. The ultrasonic equipment was tested in such a region with MAP of 8188 mm, MAT of 16.7 °C, and no month when potential evapotranspiration exceeds precipitation. The equipment stopped working after measuring a few trees. Ten trees were measured at $H_{1.3}$ on the summit of Mt. Bellenden Ker (BKT-01) south of Cairns (Queensland, Australia) at an elevation of 1590 m asl in December 2010. The selected tree species were four undetermined tree species and *Flindersia pimenteliana*. Climatic conditions at the time of sampling were dry and cloudy with $18^{\circ}C < T_a < 23^{\circ}C$.

Sampling was done before the daily precipitation started (rain usually started after 11 am during that time of the year: personal observation). Core samples were obtained using a hand-increment borer from outside the bark towards the pith. Samples were then transported to the laboratory inside sealed plastic bags for ϱ determination.

The next study site chosen was a seasonal tropical forest in Australia. This forest site presented a wide range of ϱ. Measurements were performed at the end of the dry season (April 2013). The site was a permanent forest site (KBL-03) located in Misty Mountains National Park (Queensland, Australia) (Torello-Raventos et al. 2013). Twelve trees were measured at $H_{1.3}$ from 5 different tree species: *Balanops australiana*, *Beilchmiedia bancroftii*, *Cardwellia sublimis*, *Drypetes acuminata,* and *Gossia dallachiana*. The site was located at an elevation of 1050 m asl in a region with MAP of 1398 mm, MAT of 19.1 °C, and DSL of 7 months. Climatic conditions were dry and sunny with $20\ °C < T_a < 25\ °C$. Measurements were carried out between 11 am and 5 pm. Core samples were obtained from a tree core from outside the bark of each tree towards the pith. The samples were sealed inside plastic straws and transported to the laboratory for determination of ϱ.

The next study site was selected with the aim of testing the ultrasonic equipment in a tropical montane forest where precipitation is present all year around. The daily temperature was around 10 °C during the month that measurements were taken. The previous study sites were selected with a different purpose: to study the effects of seasonality and daily precipitation on the accuracy of the pulse measurements. This study site offered the opportunity to study the effects of the measurements when $T_a \leq 10\ °C$. Ten forest trees were measured in February 2012 at the YUS Conservation Area on the Huon Peninsula in Papua New Guinea (PNG) (Yus transect). The species sampled were *Sauraia altiterra*, *Quintinia ledermannii*, *Sphenostemon papuanum*, *Dacrycarpus cinctus*, *Libocedrus papuana*, and *Podocarpus crassigemmis*. The site was located at an elevation of 3052 m asl in a region with MAP of 2824 mm, MAT of 11.7 °C, and no month where potential evapotranspiration exceeds precipitation. Climatic conditions during sampling varied from sunny to cloudy with $10\ °C < T_a < 12\ °C$. Acoustic measurements and subsequent wood core sampling were carried out between midday and 4 pm at $H_{1.3}$. A wood core sample was obtained using a hand-increment borer from outside the bark towards the pith and stored in plastic drinking straws. Green volume was measured in the field, and dry weight was measured later in Australia.

With the purpose of contrasting the previous measurements done in tropical forests, we selected one last study site in a savannah. Five *Eucalyptus sp.* trees were measured during the dry season in Davies Creek National Park (DCR-01) (Queensland, Australia) (Torello-Raventos et al.

2013), at an elevation of 683 m in April of 2010 between 10 am and 1 pm at $H_{1.3}$. The region has a MAP of 2050 mm, MAT of 21.2 °C, elevation of 683 m asl, and DSL of 5 months. This study site was selected to obtain ultrasonic measurements from very dense wood. Tropical forests in Australia have only a few species that have highly dense wood, and these are not common. Climatic conditions were dry and sunny with $25\ °C < T_a < 27\ °C$. Wood core samples of 2.5 cm x 2.5 cm x 3 cm were obtained using a hand-increment borer from outside the bark towards the pith and transported to the laboratory sealed inside plastic bags for ϱ determination.

2.2.3 Wood specific gravity

Wood samples were collected from the Mt. Bellenden Ker, Davies Creek National Park, Papua New Guinea, and Misty Mountains National Park sites. The volume of the samples collected in Vanutau was measured according to Heinrichs and Lassen (1970) (Eqn. 2). Wood samples were initially weighed in air and then again after complete submersion in water using a GR series analytical balance (A&D Company) to determine the volume of the sample. The volume of the samples collected at the other sites was measured by using an electronic digital calliper (0.01-mm resolution) of 50 cm length (ISO 9001). Thereafter, the samples were dried at 60 °C to constant weight. Specific ϱ for each sample was calculated according to Eqn. 3.

$$v\ (cm^3) = \frac{W_{air}\ (g)}{W_{air}\ (g) - W_{liquid}\ (g)}\ \rho_{water}(\frac{g}{cm^3}) \qquad \text{(Eqn. 2)}$$

$$\rho_{specific} = \frac{W_{ovendried}}{v\ (cm^3)} \qquad \text{(Eqn. 3)}$$

where $\boldsymbol{v}$ is the green volume of the sample, W_{air} is the air weight of the sample, W_{liquid} is the weight of the water, ϱ_{water} is the density of the water, $\varrho_{\text{specific}}$ is the specific density, and W_{oven} is the dried weight of the sample.

2.2.4 Ash content estimation

One tree species, *Cardwellia sublimis,* had extremely high ultrasonic velocity measurements compared to the rest of the measured tree species. In order to understand this difference, literature on wood properties from this tree species was consulted. It was thought that faster measurements could result from having mineral deposits in the tree species. Previous studies usually reported a very low abundance of aluminium in wood cells of most tree families in Australia (Webb 1953, Kukachka and Miller 1980). However, there are three species in the Australian-New Guinea flora that have been recorded as accumulating large quantities of this metal: *Cardwellia sublimis*, *Orites excelsa*, and *Qualia sp.* (Webb 1953). Also, an extremely rare case was reported for the species *Cardwellia sublimis* in a region close to our study area at the DRO, where a tree contained up to 40.9 % of its total weight as aluminium (Webb 1953). For this reason, we sampled trees of this species at the KBL-03 site to measure the total ash content of the wood. The same species was used for ultrasonic measurements at the DRO study site, but no samples could be obtained due to the impact of tree coring on long-term monitoring activities. In taking these samples, we sought to test the hypothesis that aluminium-rich ash deposits may affect V.

Wood ash content was calculated for a range of tree diameters at breast height (*DBH*) between 20 cm and 50 cm from KBL-03 (*Cardwellia sublimis* at KBL-03; 39 cm < *DBH* < 65 cm). The samples were analysed following the protocol D 1762-81-Standard Test Method for Chemical Analysis of Wood Charcoal: 1 g of the sample was placed in the furnace at 750 °C for 6 hours consecutively and then for 1 hour until weight loss was less than 0.0001 g.

2.2.5 Statistical analysis

All analyses were done using the R statistical platform (R Development Core Team 2012). Regression analyses were carried out using the graphics and *stats* packages. The standard error of the mean of the V was calculated using the *gplots* package. Comparisons of the means were performed using the *stats* package.

2.3 Results

First, we studied the accuracy of the ultrasonic equipment by determining the variability of the measurements in a tree plantation where trees were planted all together in the same year with growth under the same climate and soil conditions. We expected the intraspecific variation of wood density for these trees to be lower than for natural trees occurring at different forest sites. The ultrasonic technique was then tested across different types of forests (with seasonality ranging from wet to moist and dry forests according to Chave et al. (2005)). This was done to study how different climatic conditions might affect the measurements on the intra- and inter-specific variation of wood density. Last, we selected a savannah in order to test consistency on the inter-specific variation of ϱ across very different ecosystems, but still within the tropics.

2.3.1 Intra-specific variation of wood density for *Endospermum medullosum* in Vanuatu

Trees in the plantation

The ϱ for the tree species *Endospermum medullosum* in the tree plantation ranged between 260 kg m^{-3} and 350 kg m^{-3}. Temperature (T_a) and wetness of the surface contact area had a significant effect on pulse velocity (V). High V was found for all measurements where (a) T_a was >30 °C (0.17 cm µs^{-1} < V < 0.32 cm µs^{-1}) and (b) the surface of the bark was wet due to rain

(0.17 cm $\mu s^{-1} < V < 0.36$ cm μs^{-1}) (Table 2.3). Compared with such conditions, the mean V for measurements carried out at $T_a < 30$ °C and in dry conditions was significantly slower ($p < 0.05$), with a range of 0.12 cm $\mu s^{-1} < V < 0.14$ cm μs^{-1}.

Table 2.3. Summary of the plantation tree species *E. medullosum* of the number of trees, the number of measurements, maximum, and minimum for all the sampled trees in Vanuatu.

Species and range ϱ	**No.**	**No.**	**External variables**	**ϱ (kg m^{-3}) ^{b}**			**V (cm µs $^{-1}$) ^{b}**		
from literature ^{c}	**trees**	**meas.**	**Temp. (˚C)**	**Avg.**	**Min.**	**Max.**	**Avg.**	**Min.**	**Max.**
E. medullosum *(261-354)*	22	132	Plantation Wet bark $T_a < 30$	310	260	360	0.24	0.17	0.36
E. medullosum *(261-354)*	50	300	Plantation $T_a > 30$	310	260	360	0.23	0.17	0.32
E. medullosum *(261-354)*	15	45	Plantation $T_a < 30$	310	260	360	0.13	0.12	0.14
E. medullosum *(261-354)*	1	6	Buffer $T_a < 30$	400	380	410	0.14	0.14	0.14
E. medullosum *(261-354)*	1	6	Buffer $T_a < 30$	380	340	420	0.13	0.13	0.13
E. medullosum *(261-354)*	1	6	Buffer $T_a < 30$	450	420	490	0.14	0.14	0.14
E. medullosum *(261-354)*	1	6	Buffer $T_a < 30$	400	370	440	0.14	0.14	0.14
E. medullosum *(261-354)*	1	6	Buffer $T_a < 30$	490	480	500	0.15	0.15	0.15

^{a} Values are means of a number of measurements. ^{b} Literature values available for the species *E. medullosum* are from (Settle et al. 2012).

Buffer trees

Measurements from the buffer trees at $T_a < 30$ °C on dry days present ranges of 0.13 cm $\mu s^{-1} < V < 0.15$ cm μs^{-1} and 340 kg m$^{-3} < \varrho < 500$ kg m^{-3}. These results indicate that the buffer trees had a higher ϱ than the trees within the experimental sites.

Radial measurements of both V and ϱ were carried out at different tree heights of $H_{1.3}$, $H_{1/2}$, and $H_{3/4}$ for the buffer trees in the tree plantation (Table 2.4). A decrease in V at each higher point along the stem corresponded with a decrease in measured ϱ. Measurements at $H_{1.3}$ and $H_{1/2}$ had a range of 0.13 cm $\mu s^{-1} < V < 0.15$ cm μs^{-1}. The range of densities was 340 kg m^{-3} $< \varrho < 500$ kg m^{-3}. At $H_{1/2}$, the range of densities was 300 kg m$^{-3} < \varrho < 350$ kg m^{-3}. At $H_{3/4}$, the range of V was 0.10 cm $\mu s^{-1} < V < 0.14$ cm μs^{-1}, and the range of densities was 310 kg m$^{-3} < \varrho <$

330 kg m^{-3}. The means of V along the stem between $H_{1.3}$ and $H_{1/2}$ and between $H_{1.3}$ and $H_{3/4}$ were significantly different ($p < 0.1$), although no statistical differences were found between $H_{1/2}$ and $H_{3/4}$.

Table 2.4. Summary of the buffer tree species *E. medullosum* for the number of trees sampled, the number of measurements done, and the average, and coefficient of variation for velocity (C.V.$_V$) for all the sampled trees in Vanuatu.

Tree ID	No. meas.	V (cm µs^{-1}) $H_{1.3}$	ϱ (kg m^{-3}) $H_{1.3}$	V (cm µs^{-1}) $H_{0.5}$	ϱ (kg m^{-3}) $H_{0.5}$	V (cm µs^{-1}) $H_{0.7}$	ϱ (kg m^{-3}) $H_{0.7}$	C.V.$_V$ (%) $H_{1.3}$ - $H_{0.5}$	C.V.$_V$ (%) $H_{1.3}$ - $H_{0.7}$
1	6	0.14	450	0.12	330	0.12	330	0.12	0.14
2	6	0.14	390	0.12	320	0.11	320	0.11	0.16
3	6	0.14	380	0.12	320	0.11	320	0.09	0.19
4	6	0.13	380	0.13	330	0.12	320	0.03	0.09

[a] Values are means of a number of measurements.

2.3.2 Seasonal effects on the ultrasonic velocity

Seasonal variation of V

Measurements at Daintree Rainforest Observatory (DRO) were carried out on the same trees during both wet and dry seasons. The results are presented in Table 2.5. Repeated measurements were performed at the same location on the bole on each occasion. The range of ultrasound velocities was greater when measurements were performed during the wet season at $T_a > 30$ °C (0.08 cm µs^{-1} < V < 1.06 cm µs^{-1}) than for measurements taken at $T_a < 30$ °C (0.13 cm µs^{-1} < V < 0.24 cm µs^{-1}) or during the dry season (0.12 cm µs^{-1} < V < 0.20 cm µs^{-1}). Mean measurements of V at $T_a < 30$ °C were significantly faster ($p < 0.05$) in the wet season than in the dry season across all species.

Based on the height V measurements for the tree species *Cardwellia sublimis* at DRO, tree core samples were obtained from another nearby study site to measure the total ash content of the wood. Wood density for the trees sampled at DRO was extracted from available literature, since DRO is a permanent study area, and wood cores could not be acquired. The tree core samples of the tree species *Cardwellia sublimis* were collected at KBL-03, a seasonal forest site in Australia. Specimens for ultrasonic measurements had a similar *DBH* at both the DRO and KBL-03 study sites. ϱ from the wood cores collected at KBL-03 ranged from 480 kg m^{-3} to 540 kg m^{-3}.

Table 2.5. Species, number of trees sampled, point of measurement (POM), number of measurements done, maximum, and minimum for all the sampled trees at the Daintree Rainforest Observatory.

Tree species and range	**No.**	**No.**	**Season, T_a (ºC) and point**	***V*** **(cm µs $^{-1}$)** [a]		
of ϱ (kg m^{-3})	**trees**	**meas.**	**of measurement (m)**	**Avg.**	**Min.**	**Max.**
Cardwellia sublimis (480-540)[d]						
	4	96	Dry 10	0.18	0.17	0.19
		32	Dry 1.3	0.18	0.17	0.19
		48	Wet- $T_a > 30$	0.25	0.13	1.06
		48	Wet- $T_a < 30$	0.21	0.17	0.24
Castanospermum austral (596-650) [b]						
	4	96	Dry 10	0.16	0.15	0.18
		32	Dry 1.3	0.17	0.16	0.19
		48	Wet- $T_a > 30$	0.25	0.09	0.87
		48	Wet- $T_a < 30$	0.17	0.17	0.18
Cryptocarya mackinnoniana (742-758) [b]						
	4	96	Dry 10	0.17	0.17	0.18
		32	Dry 1.3	0.19	0.17	0.20
		48	Wet- $T_a > 30$	0.25	0.09	0.73
		48	Wet- $T_a < 30$	0.21	0.18	0.24
Elaeocarpus grandis (495) [c]						
	5	120	Dry 10	0.14	0.13	0.15
		40	Dry 1.3	0.15	0.14	0.16
		60	Wet- $T_a > 30$	0.23	0.12	0.51
		60	Wet- $T_a < 30$	0.21	0.19	0.23
Litsea leefeana (411.439) [b]						
	3	72	Dry 10	0.13	0.13	0.14
		24	Dry 1.3	0.13	0.12	0.15
		36	Wet- $T_a > 30$	0.19	0.08	0.64
		36	Wet- $T_a < 30$	0.15	0.13	0.20

[a] Values are means of a number of measurements. [b] ϱ obtained from (Zanne et al. 2009). [c] ϱ from (Erskine et al. 2005). [d] Values obtained from samples collected at KBL-03.

2.3.3 Intra-specific variation along the tree stem

Throughout the dry season at the DRO, similar pulse velocities were obtained in measurements for the same trees performed at $H_{1.3}$ and H_{10} for the species *Cardwellia sublimis* and *Litsea leefeana*. In contrast, higher velocities at $H_{1.3}$ were observed for the species *Castenospermum australe* (0.16 cm µs^{-1} < V < to 0.17 cm µs^{-1}), *Cryptocarya mackinnoniana* (0.17 cm µs^{-1} < V < 0.19 cm µs^{-1}), and *Elaeocarpus grandis* (0.14 cm µs^{-1} < V < 0.15 cm µs^{-1}) than at H_{10}. Measurements at $H_{1.3}$ and H_{10} were also significantly different ($p < 0.05$). The higher V at $H_{1.3}$ compared with H_{10}

measured during the dry season reflects the higher ϱ measured at $H_{1.3}$ compared with H_{10} in all species except *Cardwellia sublimis* (Table 2.5).

2.3.4 Inter-specific variation of wood density across the Mt. Bellenden Ker, Davies Creek, KBL-03, and Papua New Guinea study sites

The range of average values of V and ϱ for all the species measured at these study sites were 0.12 cm $\mu s^{-1} < V <$ 0.23 cm μs^{-1} and 360 kg $m^{-3} < \varrho <$ 1010 kg m^{-3}. The highest ranges of V were acquired from Davies Creek National Park: 0.18 cm $\mu s^{-1} < V <$ 0.23 cm μs^{-1} and 770 kg $m^{-3} < \varrho <$ 1010 kg m^{-3}. The lowest V was obtained from study sites both classified as tropical montane forests: Mt. Bellenden Ker located in Australia and the site located in Papua New Guinea (PNG). PNG V varied from 0.14 cm μs^{-1} to 0.21 cm μs^{-1}, and the range of ϱ was 360 kg $m^{-3} < \varrho <$ 650 kg m^{-3}. The ranges of Mt. Bellenden Ker V and ϱ were 0.12 cm $\mu s^{-1} < V <$ 0.17 cm μs^{-1} and 420 kg $m^{-3} < \varrho <$ 650 kg m^{-3}.

Table 2.6. Species, number of trees sampled, number of measurements, maximum, and minimum for all the sampled trees at BKT-01, DCR-01, PNG, and KBL-03.

Species and range of ϱ (kg m^{-3})	No. trees	No. meas.	ϱ (kg m^{-3}) [a]			V (cm μs^{-1}) [a]		
			Avg.	Min.	Max.	Avg.	Min.	Max.
BKT-01								
Angiosperms								
Flindersia pimenteliana (480-594) [b]	6	72	470	430	500	0.13	0.12	0.14
Indet 1	1	12	590	590	590	0.17	0.17	0.17
Indet 2	1	12	500	500	500	0.14	0.14	0.14
Indet 3	1	12	650	650	650	0.16	0.15	0.16
Indet 4	1	12	420	420	420	0.12	0.12	0.12
DCR-01								
Angiosperms								
Corymbia citriodora (765) [b]	3	18	810	n/a	n/a	0.20	0.18	0.21
Eucalyptus portuensis	1	6	770	n/a	n/a	0.18	0.18	0.19
Eucalyptus drepanophylla (900) [c]	1	6	1010	n/a	n/a	0.22	0.22	0.23
Papua New Guinea								
Angiosperms								
Sauraia altiterra (302) [b]	2	12	360	360	360	0.15	0.14	0.15
Quintinia ledermannii (440) [b]	2	12	500	490	520	0.16	0.15	0.17
Sphenostemon papuanum	2	12	620	580	650	0.19	0.17	0.21
Gymnosperms								
Dacrycarpus cinctus (460) [b]	1	6	470	n/a	n/a	0.14	0.14	0.14
Libocedrus papuana (390) [b]	2	12	430	370	500	0.15	0.14	0.15

Podocarpus crassigemmis	1	6	490	n/a	n/a	0.15	0.15	0.16
KBL-03								
Angiosperms								
Balanops Australiana (705-755) [b]	1	6	620	n/a	n/a	0.16	0.16	0.16
Beilchmiedia bancroftii (496-646) [b]	1	6	570	n/a	n/a	0.16	0.15	0.16
Cardwellia sublimis (446-500) [b]	5	30	480	450	540	0.18	0.16	0.20
Drypetes acuminate (910 at 12% humidity) [d]	3	18	660	660	670	0.18	0.18	0.19
Gossia dallachiana (814) [b]	2	12	860	n/a	n/a	0.20	0.18	0.20

[a] Values are means of number of measurements. [b] ϱ values obtained from Zanne et al. (2009). [c] ϱ were obtained from Ilic et al. (2010). [d] ϱ at 12 % of moisture content from Cause et al. (1989).

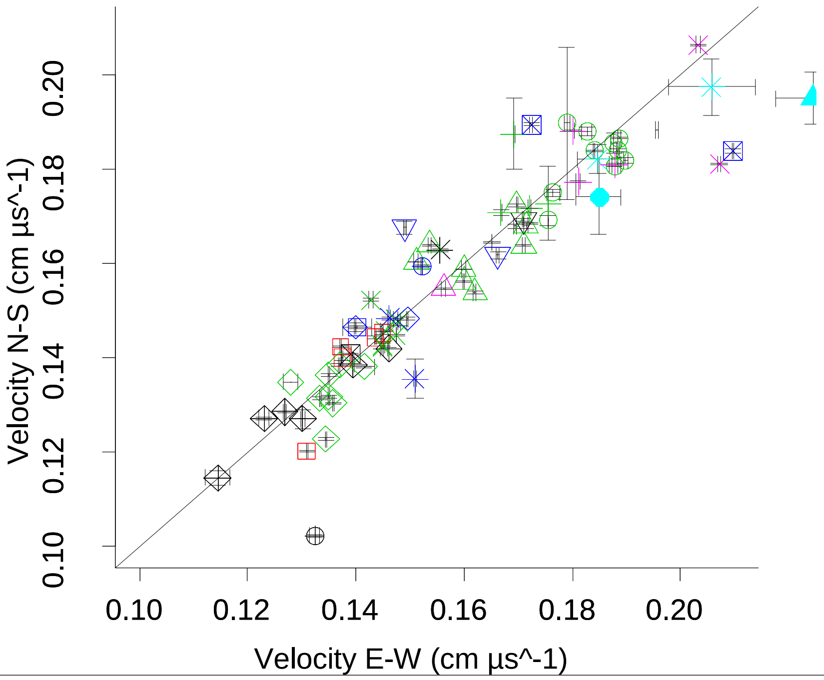
2.3.4 Total ash content of *Cardwellia sublimis*

The total amount of ash content for the *Cardwellia sublimis* specimens collected at KBL-03 was 0.42 % for a specimen with a *DBH* of 20 cm and between 2.5 % and 4 % for a specimen with a *DBH* of 50 cm.

2.4 Discussion

2.4.1 Reproducibility of pulse velocity measurements

We tested an instrument originally designed to detect cracks in cement for evaluating ϱ in living trees. It was first very important to verify the reproducibility of the V measurements on individual trees. To examine the consistency between each triplicate measurement of each tree for each cardinal measurement (North-South and East-West), we plotted the average of the triplicate measurements against a 1:1 line for all trees for all study sites (Fig. 2.3). We also plotted the standard error of the mean for each triplicate measurement. Values ranged from 0 % to 0.8 % with an average of 0.066 % for the N-S measurements and from 0 % to 1.6 % with an average of 1.1 % for the E-W measurements. The results clearly indicate that the error measurement of V on an individual tree is consistently small, regardless of species or ϱ. This indicates that the instrument performs consistently when measuring trees across a wide range of wood densities. The analysis of variance indicates that there is no significant difference between the measurements carried out on the same tree at the different cardinal points of measurement ($p < 0.1$).

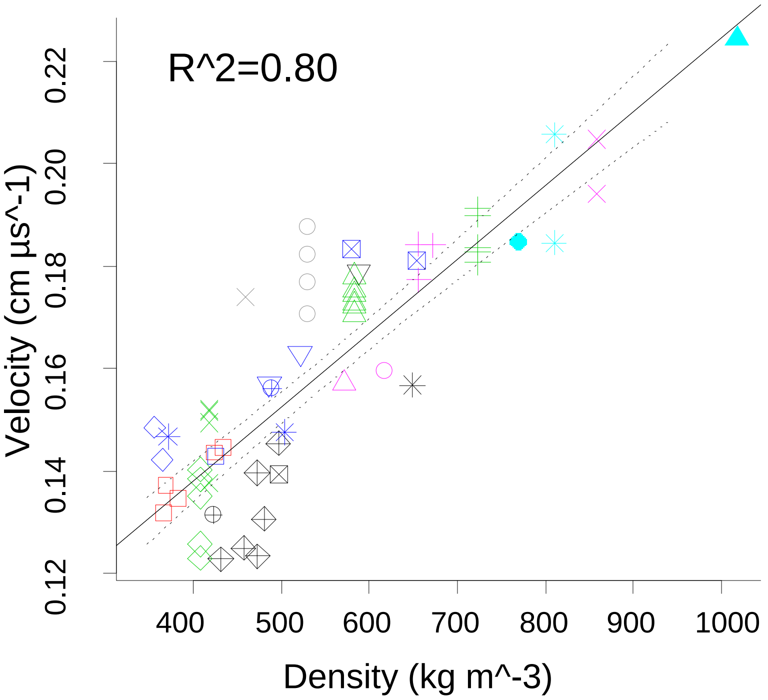


BKT-01: Flindersia pimenteliena (⟐), Elaeocarpus ferruginiflorus (⊕), Indet I (∇), Indet 2 (⊠) and Indet 3 (✳). DRO *Litsea leefeana* (◊), *Cardwellia sublimis* (o), *Elaeocarpus grandis* (x), *Castanospermum australe* (Δ) and *Cryptocarya mackinnoniana* (+). DCR-01: *Corymbia citriodora* (✳), *Eucalyptus portuensis* (•) and *Eucalyptus drepanophylla* (▲). KBL-03: *Beilchmedia bancroftii* (△), *Drypetes acuminate* (+) and *Gossia dallachiana* (✕). PNG: *Dacrycarpus cinctus* (□), *Sauraia altiterra* (◇), *Quintinia ledermnnii* (▽), *Sphenoutemon papuanum* (⊠), *Libocedrus papuana* (✳) and *Podocarpus crassigemmis* (⊕). Vanuatu: *Endospermum meullosum* (□).

Fig. 2.3. Plot of the perpendicular measurements of V at the North-South and East-West cardinal points at all the sites. The error bars in the graph represent standard errors of the mean.

2.4.2 Inter-specific variation of wood density

The aim of this study was to develop a non-destructive method to measure a wide range of ϱ in tropical trees in the field. The relationship between ϱ and V for all species at all the study sites is shown in Fig. 2.4. Each dot in the figure represents the average value for all the measurements performed at each tree. In this figure, measurements at $T_a > 30$ °C and when the outer surface was wet were excluded. The results show that there is a clear positive relationship between ϱ and V, except for the species *Cardwellia sublimis* located at DRO. The adjusted coefficient of determination improves to a value of 0.80 when the tree species *Cardwellia sublimis* is excluded, and it decreases to 0.72 when the tree species is included (Fig. 2.4).



BKT-01: Flindersia pimenteliena (⟐), Elaeocarpus ferruginiflorus (⊕), Indet I (▽), Indet 2 (⊠) and Indet 3 (✳). DRO: *Litsea leefeana* (◇), *Cardwellia sublimis* (○), *Elaeocarpus grandis* (x), *Castanospermum australe* (△) and *Cryptocarya mackinnoniana* (+). DCR-01: *Corymbia citriodora* (✳), *Eucalyptus portuensis* (●) and *Eucalyptus drepanophylla* (▲). KBL-03: *Beilchmedia bancroftii* (△), *Drypetes acuminate* (+), *Ballanops australiana* (○),*Cardwellia sublimis* (×) and *Gossia dallachiana* (×). PNG: *Dacrycarpus cinctus* (□), *Sauraia altiterra* (◇), *Quintinia ledermnnii* (▽), *Sphenoutemon papuanum* (⊠) , *Libocedrus papuana* (✳) and *Podocarpus crassigemmis* (⊕). Vanuatu: *Endospermum meullosum* (□).

Fig. 2.4. Relationship between V and ρ for all the sites. Adjusted coefficient of determination is 0.80, and the fitted curve is y = 0.1462x + 0.0793, excluding the species *Cardwellia sublimis* at both sites. Confidence intervals are calculated at 95 %.

The results indicated that the ultrasound equipment used in this study was effective for both gymnosperms and angiosperms. The similar relationship between ρ and ultrasonic V suggests that the technique is broadly applicable for both types of wood. Measurements performed at the PNG site for gymnosperms trees presented similar values for angiosperm trees at similar ρ. The literature shows that gymnosperms have a primitive wood structure in comparison to angiosperms (Hoadley 1990), which contain a more diverse range of cell types, cell sizes, and other more complex features. The lower level of anisotropy of softwoods was reflected with lower V for gymnosperms than for angisoperms. Our results are comparable to those of Bucur (1995), who found a positive relationship between ρ and V for both gymnosperms and angiosperms with a coefficient of determination of 0.68.

The results at the Mt. Bellenden Ker site for the species *Flindersia pimentaliana* presented slower velocities than expected for the values of ϱ acquired from the sampled wood cores. This might be explained by the fact that this study site has a MAP that is considerably higher than in the other study sites (8188 mm), which might contribute to low values of both ϱ and V. The sampling strategy has allowed for measurements from a wide range of ϱ, from both gymnosperms and angiosperms in different ecosystems at different times of the year under different climatic conditions. From the results of this sampling design, it is believed that the range of V within species or between species with similar ϱ might be explained by the natural diversity of cell arrangement in living trees by factors such as tree age or environmental conditions, including climate, soil fertility, canopy disturbance, and light availability (Patiño et al. 2009). Thus, according to the results of this study, the calculation of the inter-specific variation of wood density using ultrasonic techniques is possible.

2.4.3 Effect of accumulated mineral deposits in wood

The species *Cardwellia sublimis* was present at two study sites: DRO and KBL-03. Ultrasonic measurements of V from this species at both sites (Tables 2.5 and 2.6) presented higher V than the rest of the measured tree species with similar ϱ (Fig. 2.4). Velocities presented a range of $0.17 \text{ cm } \mu\text{s}^{-1} < V < 0.19 \text{ cm } \mu\text{s}^{-1}$ for a ϱ range of $480 \text{ kg m}^{-3} < \varrho < 540 \text{ kg m}^{-3}$. These results contrast with those for other tree species with similar ϱ, which presented much lower V values. For example, *Castenospermum australe* with $\varrho = 580 \text{ kg m}^{-3}$ has a lower average V of 0.17 cm μs^{-1}. Likewise, for *Cryptocarya mackinnonianna,* $\varrho = 720 \text{ kg m}^{-3}$, with a lower average V of 0.19 cm μs^{-1}. Thus, calculations of ϱ in *Cardwellia sublimis* based on V measurements would over-estimate the actual value by a factor of approximately 1.3. The difference in expected versus obtained velocities at both sites (DRO at $H_{1.3}$ (Table 2.3) and KBL-03 (Table 2.5)) were statistically significant ($p < 0.01$). The results from the total ash contents for the tree species *Cardwellia sublimis* for the samples collected at the KBL-03 study site presented higher ash contents (average value 3.2%). These results, along with other documented examples of this species containing anomalously high Al contents, may explain the faster observed velocities for *Cardwellia sublimis* (and hence anomalously high-calculated ϱ) than other species that have a similar ϱ. The reason might be the presence of Al which might increase the transmission velocity of the pulse velocity or the presence of less empty spaces in the wood cells.

2.4.4 Intra-specific variations of wood density

The aim of developing a non-destructive technique for studying ϱ was to create a method that could be applied to living trees in the field. This in turn requires an assessment of the sensitivity of the technique to environmental conditions. The study sites selected for this purpose were the Daintree Rainforest Observatory in Australia and the tree plantation in Vanuatu.

Vanuatu: measurements at $H_{1.3}$

Measurements of ϱ in *E. medullosum* varied by ~30 % with a range of 310 kg m^{-3} < ϱ < 510 kg m^{-3}. The results showed a positive relationship ($R^2 = 0.66$) between *V* and ϱ for both the buffer trees and the experimental trees in the tree plantation (Fig. 2.5). Figure 2.5 shows that the tree species *E. medullosum* in Vanuatu presented a wide range of *V* when measurements were taken at $T_a > 30$ °C (♦), or when the outer part of the tree was wet due to precipitation (□). Under such conditions, the relationship between *V* and ϱ was not significant ($p > 0.001$). In contrast, a moderate positive relationship ($R^2 = 0.66$) between ϱ and *V* was evident when measurements were taken on dry bark at T_a <30 °C.

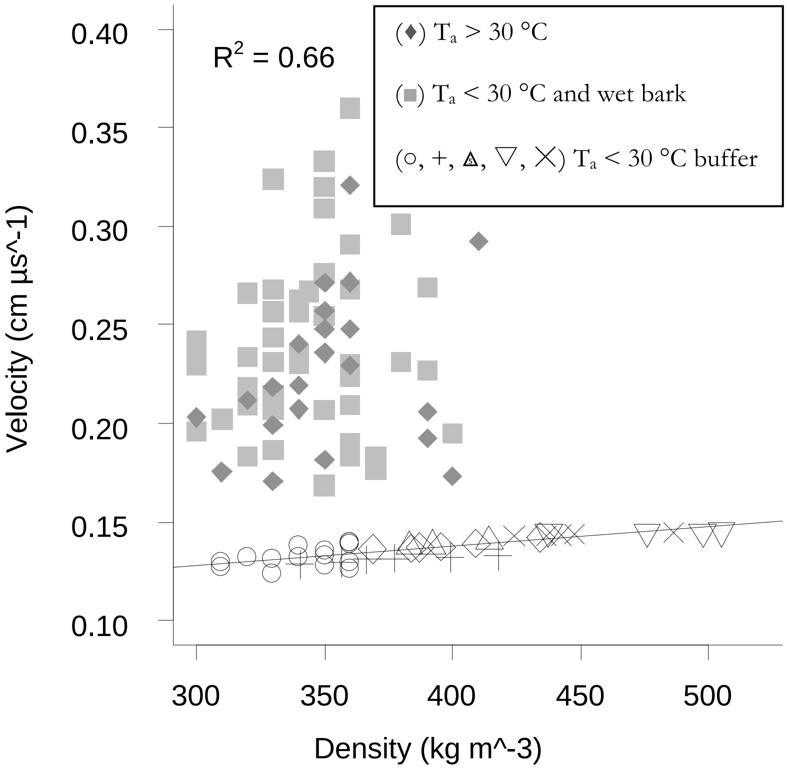


Fig. 2.5: Intra-specific variation of ϱ and *V* to explain the influence of T_a and bark moisture on *V* of *E. medullosum* in Vanuatu. Coefficient of determination is 0.66, and fitted equation is y=0.09865x + 0.09798.

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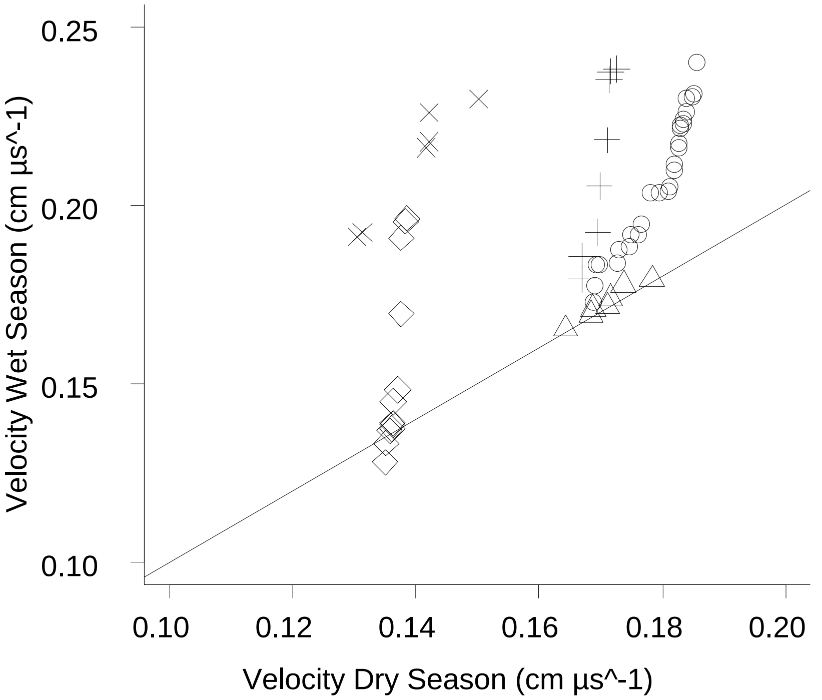
The effect of temperature on *V* for all species measured at the DRO is illustrated in Fig. 2.6 for measurements at H_{10}. The measured *V* at H_{10} during the dry season is plotted against the measurements during the wet season at T_a < 30 °C. The 1:1 line in Fig. 2.5 shows that measurements during the wet season are much faster than those during the dry season. If seasonality had no effect on *V*, all the measurements taken for the same trees should follow the 1:1 line. Therefore, according to these results, *V* measured during the wet season was higher in most cases than in the dry season, and measurements at $H_{1.3}$ during the wet season at T_a > 30 °C were unreliable, so they were excluded in further analysis. These results might be explained by the sensitivity of the transducers at high humidity or when T_a is around 30 °C, which appears to compromise the reliability of ultrasonic measurements. Therefore, the outcomes suggest that the dry season is the preferred time of the year for reliable measurement of *V* in wood in tropical forests.



Litsea leefeana (◇), *Cardwellia sublimis* (○), *Elaeocarpus grandis* (✕), *Castanospermum australe* (△) and *Cryptocarya mackinnoniana* (+).

Fig. 2.6. *V* during the dry season versus the wet season at H_{10} for all species at the DRO. All measurements included in these graphs were recorded at T_a < 30 °C.

Similarly, an increase in *V* was found when measurements were carried out at T_a > 30 °C by Jones and Fąc̨aoaru (1969) and the European Standard EN12504-4: 2004 for concrete, and for wood by Bucur (1995). The standards developed for this instrument (EN12504-4:200) include a *V* conversion factor for measurements at T_a > 30 °C. However, the conversion was developed for concrete and not applicable for wood. In this study, it was not possible to develop a similar conversion factor to apply to living trees due to the large range of species and *ϱ* tested.

Bucur (1995) also tested the effect of surface wetness and concluded that wet surfaces result in higher *V* through wood.

Anomalous readings of *V* can result from conducting ultrasonic measurements during the wet season, when rainfall or canopy interception can wet the tree surface and T_a is usually > 30 °C. Thus, measurements should be conducted during the dry season under dry conditions while avoiding the middle of the day when T_a is highest. Thus, the diurnal courses from the roots of water towards the canopy for consumption might interfere with the ultrasonic pulse, preventing transmission from the sender to the receiver transducers.

2.4.5 Measurements along the bole

Vanuatu

Measurements for *E. medullosum* of *V* versus *ϱ* were also found to decrease with increasing *H* up the tree stem (Fig. 2.7). This suggests intra-specific variation of *ϱ* along the bole. *V* decreased by approximately 0.02 cm μs^{-1}, and *ϱ* decreased by approximately of 8 kg m^{-3}.

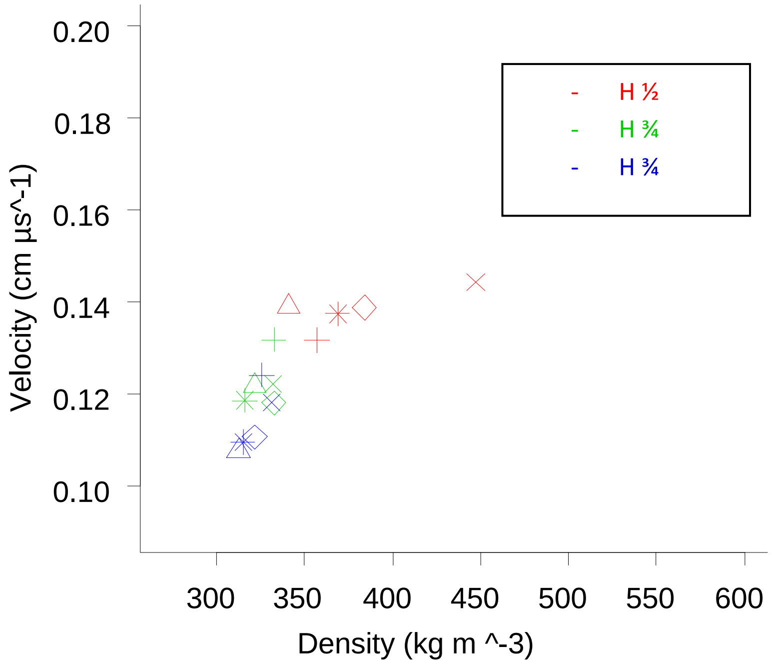


Fig. 2.7. Wood density versus *V* for the measurements along the stem for 5 different individual trees of *E. medullosum* in Vanuatu.

Daintree Rainforest Observatory

Measurements along the stem were conducted at $H_{1.3}$ and H_{10} during the wet season. The results suggested that *ϱ* decreased up the tree bole along with *V* (Fig. 2.8), although in this case, destructive sampling and conventional ϱ determination could not confirm the result. The results also suggested that species with higher ϱ had a higher proportional decrease along the bole, except for the species *Cardwellia sublimis*. The result might again be explained by the presence of aluminium deposits in the wood cells along the tree bole.

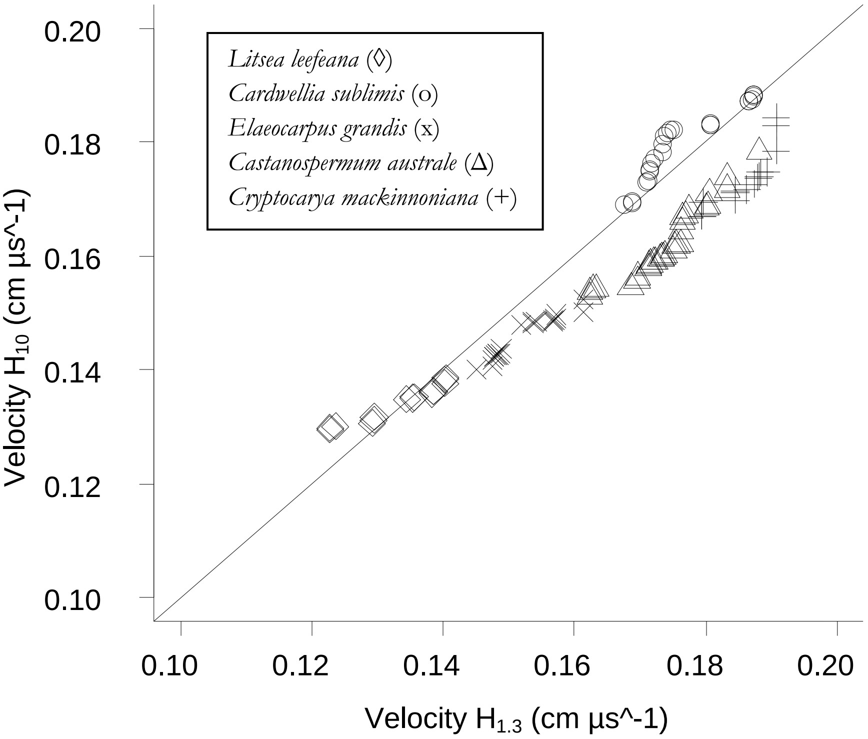


Fig. 2.8. *V* measured during the dry season at $H_{1.3}$ versus H_{10} for all the species measured at DRO.

Previous studies have also reported a decrease in ϱ up the bole (Ikonen et al. 2008, Nogueira et al. 2008, and Kord 2011). These studies confirm that the decrease in *V* along the bole (H_{10}) may be indicative of lower ϱ higher up the tree stem. Estimations of ϱ through the measured *V* along the tree stem for *Castenospermum australe* and *Elaeocarpus grandis* (0.01 cm μs^{-1}), as shown in Fig. 2.8, would suggest a decrease of ϱ from $H_{1.3}$ to H_{10} of approximately of 8 kg m^{-3}.

2.5 Conclusions

This is the first field study that used ultrasonic techniques to investigate ϱ in the context of C stock determination of aboveground biomass. The study has demonstrated that ultrasonic pulse velocity measurements have the potential to provide a low-cost, field-deployable solution to measure ϱ in tropical ecosystems, particularly for species in tropical rainforests. There is a clear positive relationship between *V* and ϱ, both within and between species at ϱ in the range of 350 kg m^{-3} < ϱ < 1000 kg m^{-3}. The results of the study also indicate that T_a > 30 °C and wet tree surfaces influence *V*. Thus, such conditions must be avoided to obtain an accurate result.

Measurements during the wet season were slow and time consuming due to poor coupling between the transducers and the trees, irrespective of whether a reliable measurement was achieved. This suggests that high humidity also affects the reliability of the measurements. We limited our sample set to straight trees without deformities, internal decay, or holes. It is unlikely that ultrasonic pulse velocity would yield a reliable estimate of density where decay or holes are present in a tree, although the technique may be applicable to leaning trees.

Tropical forests generally contain a large number of species, and there are large uncertainties associated with using global ϱ databases, particularly given the often-considerable intra-specific range of ϱ from 0 to 47 % (Zanne et al. 2009). These issues, combined with the promising results obtained in this study, warrant further development of the ultrasonic pulse velocity technique for in-field density determination. The technique may be particularly valuable for directly measuring the ϱ of large trees, which can contain one third of the total proportion of the above ground C biomass in tropical forests (Chave et al. 2003). The ϱ of such trees may vary considerably across their diameter (Nogueira et al. 2005 and Nogueira et al. 2008). Coring large trees to the pith is particularly difficult when measuring average ϱ across the whole stem by traditional techniques.

The instrument used in this study was developed for use on concrete. There are other instruments designed for use on timber (SilvaTest Duo, Fakopp TreeSonic), as indicated in Table 2.2. However, these are optimized to provide information on the structural properties of wood that are of interest to the timber industry. Transducer designs and operating frequencies could be optimized to more reliably determine ϱ than was possible in this study. For example, the transducers used in this study required a flat surface free of bark to ensure good transducer coupling. This issue would be circumvented by using spike transducers. The issues associated with anomalous measurements at T_a > 30 °C and in high humidity or rain might also be addressed through transducer design and calibration.

According to Oliveira et al. (2005) and Bucur and Feeney (1992), the physical properties of wood are strongly dependent on the quantity of water contained within the walls of wood cells. Several studies have demonstrated that measurements performed on green wood are slower than measurements on dry wood (Bucur and Feeney 1992, Oliveira et al. 2005, Bucur 2006). Wood moisture also produces stronger variability in ultrasonic velocity than the structural characteristics of the wood (Bucur and Feeney 1992, Oliveira et al. 2005, de Oliveira and Sales 2006). Thus, the velocity of sound in air at 20 °C is approximately 0.04 cm μs^{-1}, while that in water is approximately 4 times faster (approximately 0.15 cm μs^{-1} at 20 °C). The velocity of sound on wood cell walls is between approximately 0.1 cm μs^{-1} and 0.2 cm μs^{-1} when measured radially (Büyüksarı and As 2013). Therefore, properties such as elastic conductivity, mechanical strength, and elasticity are strongly affected by the water content in wood cells (Oliveira et al. 2005).

Chapter 3

Wood density determinants along an altitudinal gradient in Papua New Guinea

Aerial view en route to Sapmanga, YUS transect, Papua New Guinea

3.1 Introduction

Tropical forests are under the threat of anthropological effects, and deforestation is the primary cause (Hansen et al. 2013). Ecologically, these are a significant fraction of global biodiversity (Gibbs et al. 2007), and in terms of global carbon (C) storage, they represent a significant sink of terrestrial carbon (Phillips et al. 1998, Malhi and Grace 2000, Phillips et al. 2008). In terms of global estimations of C, broad estimates have suggested that tropical forests contain on average, 157 MgC ha^{-1} of living biomass, a figure higher than both temperate forest (96 MgC ha^{-1}) and boreal forests (53 MgC ha^{-1}) (IPCC, 2013). Therefore, global research on tropical forests quantifying the ecological and economic benefits of preservation can help to encourage their protection.

3.1.1 Altitudinal gradients as natural laboratories

Altitudinal gradients represent natural laboratories in which to conduct studies on the impact of a range of climate variables (Malhi et al. 2010). This is because mean annual temperature (MAT) typically decreases with elevation. Precipitation regimes vary in a less systematic manner as a consequence of variations in landscape topography and site location. Overall, altitudinal transect studies suggest a tendency toward decreasing stand-level above ground biomass (*B*) with elevation (Clark and Clark 2000, Schuur and Matson 2001, Kitayama and Aiba 2002, Leuschner et al. 2007, Moser et al. 2008, Asner et al. 2009, Culmsee et al. 2010, Girardin et al. 2010, Slik et al. 2010). Nevertheless, differences in climatic and soil conditions as well as stand-level species distributions may result in stand structure and physiological responses to altitudinal variations beyond those predictable on the basis of climate alone. For example, although a study in the Peruvian Andes found a decrease in *B* from 124 MgC ha^{-1} at 194 m elevation to 47 MgC ha^{-1} at 3020 m (Girardin et al. 2010), another study in Indonesia found that *B* at 2400 m elevation was eight-fold higher than reported by Girardin et al. (2010), at 323 Mg dry mass ha^{-1}(Culmsee et al. 2010). Although a third study in the South Ecuadorian Andes found montane *B* much closer to that found by Girardin et al. (2013), measuring 112 Mg dry mass ha^{-1} at 3060 m (Moser et al. 2011), the overall dissimilarity of *B* at similar altitudes reinforces the importance of accounting for region-specific variability. As a final example, a study investigating moist forests in Brazil found a positive relationship between *B* and elevation, finding 209 Mg dry mass ha^{-1} in lowland forest and an average up to 283 Mg dry mass ha^{-1} in montane forests (Alves et al. 2010).

3.1.2 Allometric estimations of above-ground biomass

Allometric equations are widely used to estimate tropical forest *B* and include, in typical order of importance, diameter at breast height (*DBH*), specific density of wood (*ϱ*), and tree height (*H;* Baker et al. 2004, Chave et al. 2005, Feldpausch et al. 2012). As Feldpausch et al. (2012) and Marshall et al. (2012) demonstrated, it is important to include *H* when optimizing the quantification of *B*. Of interest in altitudinal studies is that *H* typically decreases at a faster rate than *DBH* as elevation increases (Feldpausch et al. 2010). Indeed, under certain conditions, greater stand-level *DBH* is also associated with lower *H* (Alves et al. 2010). One recent study describing the *H*:*DBH* relationships across Africa, South America, and Australia at the regional, continental, and pan-tropical level suggested that elevation-associated changes in *H*:*DBH* allometry may be associated with variations in MAT and not MAP (Feldpausch et al. 2010). It was suggested that this might be because water availability is usually not limiting for lowland and montane tropical forests. Nevertheless, those authors also noted that decreases in vapor water deficit (VPD) and UV light, and increases in wind exposure also typically occur as elevation increases,inevitably causing changes in soil physical and chemical characteristics.

3.1.3 The importance of tropical montane forests

Global warming may pose a threat to tropical montane forests through for example, increases in the duration/frequency of fog-free periods (McJannet et al. 2007a, McJannet et al. 2007b, Ledo et al. 2009, Ledo et al. 2012, Chu et al. 2014). Thus, the attainment of more knowledge is crucial to an understanding of their ecosystem function (Bruijnzeel and Veneklaas 1998, Schwarzkopf et al. 2011) and to quantify both their roles as C sinks/sources at the global scale and their importance as ecological biodiversity habitats (Wallace and McJannet 2012). Unfortunately, limited access to such remote locations and high logistical costs associated with operating in these isolated regions has made the direct estimation of tropical montane forest carbon stocks and fluxes a very difficult task (Houghton et al. 2009, Girardin et al. 2013, Meyer et al. 2013); this is certainly the case in Papua New Guinea. While remote sensing techniques provide tools for estimating *B*, the resultant modelled C assessments would require validation using field-based measurements to account for local variables not detectable using airborne topographic mapping methods. These include variations in allometry related to tree species composition and *ϱ*-dependent climatic variables or soil characteristics (Ferry et al. 2010, Feldpausch et al. 2011, Marshall et al. 2012) and disturbance history (Gleason et al. 2010).

3.1.4 Wood density

The phylogenetically conservative component, ϱ, has been demonstrated to be related to tree functionality in terms of hydraulic structure and mechanical support. For example, studies of co-existing rainforest tree species in Bolivia relating plant performance to wood trait variations (Poorter et al. 2010) found tree growth to be positively related to potential specific hydraulic conductance (K_p) and negatively related to ϱ. This was in a semi-wet forest for which the dry season length (DSL), where evapotranspiration exceeds precipitation, was only one month. That study, together with that of Zach et al. (2010) in a lower montane tropical forest in Indonesia, which had a DSL of 1-2 months, suggests that taller sun-exposed trees are characterized by low wood densities and high stem hydraulic conductivities (Ks) because of higher water demand compared to shaded trees. Both of these studies also found that the diameters of stem vessels were positively related to H. Broad scale analyses of species distributions in the Neotropics have further pointed out that variations in ϱ, presumably relating to the hydraulic architecture of trees, are a key link to tree biomass variations, this presumably relating it to the capacity of the various tree species to adapt to environmental transpiration and daily water usage demands (Chave et al. 2006, Malhi et al. 2006, Swenson and Enquist 2007). Also, Swenson and Enquist (2007) have suggested that the more efficient K of angiosperms might have caused the confinement of gymnosperms to higher latitudes and elevations where the environment generally is less hydraulically stressful.

Tree growth is a complex process and dependent on several variables (e.g., soil fertility, precipitation, and canopy spread), but also strongly related to variations in ϱ (Chave et al. 2009). In accounting for these differences, Henry et al. (2010) attributed 62% of the observed variability in ϱ for Ghanian forest individuals, to tree species, guild status (non-pioneer light-demanding species, pioneer species, and shaded tolerant species), and to pith-to-bark distance and tree size. Variations in ϱ in two lowland tropical forest areas in Central Brazil and the Mato Grosso region of Brazil with DSLs of 3 and 6 months, respectively, were found to be strongly related to the ω of the bole (Nogueira et al. 2008). In dense forests, ϱ was found to decrease nearer the bark, (denser heartwood) in 82% of trees. This result contrasted with results found in open forest dominated by low-ϱ-colonizing tree species, where ϱ increased toward the bark in 63% of species. These variations of radial ϱ are strongly related to the forest dynamics and light availability (i.e., when forest disturbances open canopy gaps).

Wood density has also been inversely related to K and xylem anatomy in Australia. Species adapted to seasonally dry conditions have more efficient hydraulic architectures – wider xylem vessels, lower ϱs, and higher maximum rates of sapwood-specific K – but, as a result, are more vulnerable to embolism (Choat et al. 2005). Another study of the intra- and inter-specific variation of tree vulnerability to embolism on a precipitation gradient from wet to seasonal forest for nine *Cordia sp.* found that trees growing in wetter forests presented higher risks of embolism than species growing in drier forests (Choat et al. 2007). However, the same study found no relationship between wood traits that could be related to hydraulic capacity (e.g., xylem vessel diameter or sapwood-specific *K*).

In this study, we used a dataset throughout an altitudinal gradient in a tropical montane forest between 1800 m and 3000 m asl in Papua New Guinea. We henceforth provide an analysis of the patterns of the intra-specific and inter-specific variation of wood density. The objectives of this study, located on an altitudinal transect, were to determine

- how wood density varies between sun-exposed and shaded tree species along the elevational gradient,
- how wood density within species varies along the radius for sun-exposed and shaded tree species, and
- which site effects influence wood density along the elevational gradient.

3.2 Materials and methods

3.2.1 Study site

This study was conducted in the 76,000 ha Yopno-Uruwa-Som conservation area located on the northern fall of the Saruwaged mountain range on the Huon Peninsula in Morobe Province of Papua New Guinea (Fig. 3.1). During 2010, nine permanent sites were established by Conservation International along an altitudinal transect ranging from the lowlands to 2939 m elevation. Of these sites, we sampled a subset of sites (a14, a13, a11, and a10) encompassing an elevation gradient extending from 1753 m to 2939 m (Table 3.1). Further site information is available (Dieleman et al. 2013).

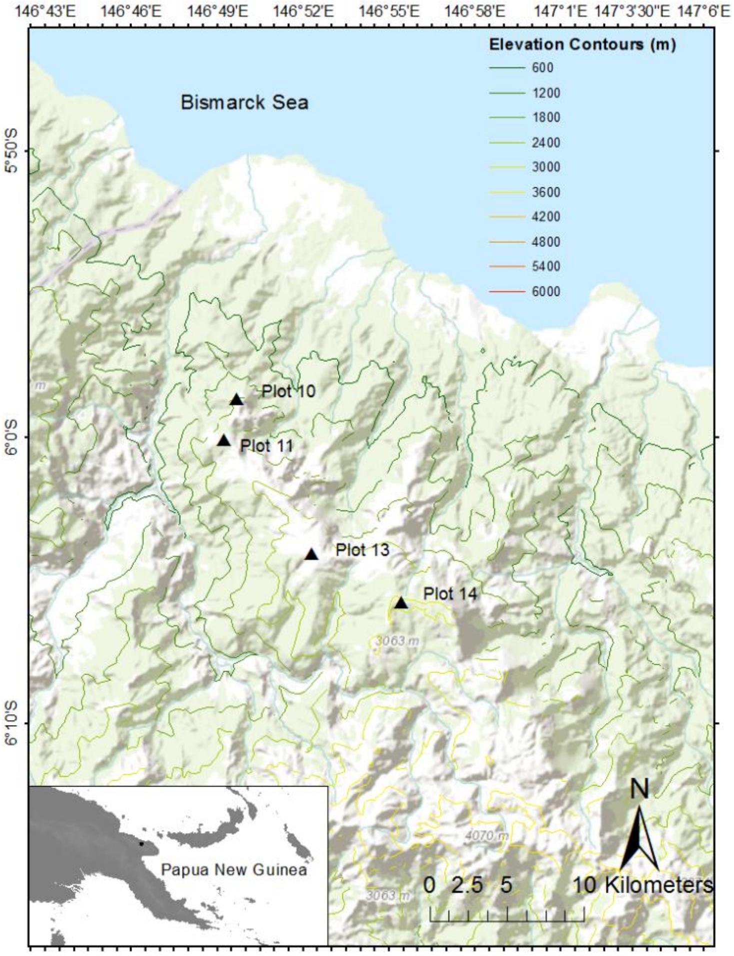


Figure 3.1. Location of the study sites at the Conservation Area at Papua New Guinea.

Table 3.1.:Site characteristics. MAT: mean annual temperature; MAP: mean annual precipitation; *DBH:* diameter at breast height; *H:* height; SD: standard deviation.

Site	**Elev. (m)**	**MAT (°C)**	**MAP (mm)**	***DBH* (m)**		***H* (m)**	
				Range (Mean)	**SD**	**Maximum (Mean)**	**SD**
a14	2939	10	4218	0.1-1.43 (0.28)	19.9	31 (12)	7.6
a13	2800	10.5	4090	0.1-1.74 (0.27)	18.2	35 (12.5)	7.9
a11	2195	14.4	3643	0.1-1.21 (0.35)	26.8	45 (22)	9.6
a10	1753	16.2	3484	0.1-1.34 (0.32)	24.4	38 (22.3)	8.8

Information on species occurrence and vegetation structure is scarce in Papua New Guinea. Previous studies by several authors (Robbins 1961, Johns 1977, Smith 1985) have, nevertheless, classified vegetation formation types according to elevation and defined lowland forests (between 1000 m and 2000 m), montane forests (between 2000 m and 3000 m), sub-alpine forests (between 3000 m and 4000 m), and alpine forests (above 4000 m). Typical vegetation formation of the species sampled are, when available, therefore also included (Tables 3.3 and 4.4).

Species in this study were categorized as sun-exposed or shaded according to various criteria. At the study sites, botanists were asked which tree species were commonly found as canopy trees and shaded trees. Additionally, sampled trees were noted as sun-exposed or shaded at the moment they were sampled in the field.

The fieldwork for this study was completed in February 2012. Before this study, information on species identification and occurrence was incomplete. Thus, based on previous surveys undertaken as part of the site establishment process, and through consultation with local villagers, we targeted what were generally commonly-occurring and well-known species.

Sixty-three trees from eighteen of the most common tree species were sampled next to permanent site 14 (site a14), and *DBH* was measured. This was the rainiest yet coolest of the study sites, and in no month was there a potential for evapotranspiration exceeding precipitation. Vegetation was of upper montane forest, as defined by Johns (1977), and was composed primarily of crooked and stunted angiosperms in a subordinate layer and emergent conifers in an upper layer.

Fifty-one trees from twelve species were sampled next to permanent site 13 (site a13). Average temperature and precipitation were similar to those in site a14 and, likewise, in no month was there a potential for evapotranspiration exceeding precipitation.

Forty-three trees from ten species were sampled next to permanent site 11 (site a11). As with the two more-elevated sites, in no month was there a potential for evapotranspiration exceeding precipitation. Vegetation at sites a11 and a13 was consistent with that defined as mid montane forest, consisting of trees taller than those in upper montane forests. Both angiosperms and emergent conifers (Johns, 1977) were common (Tables 3.3 and 4.3).

Table 3.2. Taxonomic classifications and calculated wood densities and average *DBH* of sun-exposed sampled species. Kendall tau log rank correlation was testing the variation of wood density between elevation (independent variable). ω: wood moisture content; *DBH:* diameter at breast height; n.s.: none sampled; n/a: not applicable.

Family	**Tree species**	**Montane forest sp. occurrence (literature)**	**n**	**Sampled density range (kg m^{-3})**	**Literature density range (kg m^{-3})**	**Avg. ω (%)**	**Study sites sp. occurrence Avg. *DBH* (m)**				**Kendall tau**
							a14	**a13**	**a11**	**a10**	
				Class: Conifers							
Actinidiaceae	*Saurauia altiterra*	Upper[a]	19	286-369	320-579[d]	93.9	0.23	0.26	0.31	0.16	0.27*
Cupressaceae	*Libocedrus papuanum*	Upper[a]	16	304-473	309	80.96	0.53	0.47	0.31	0.18	0.51***
Podocarpaceae	*Dacrycarpus cinctus*	Mid-Upper[a]	8	349-441	460	68.29	0.33	0.34	n.s.	n.s.	-0.24
	Dacrycarpus imbricatus	Mid-Upper[a]	5	341-502	370-450	n.s.	n.s.	n.s.	0.44	n.s.	n/a
	Phyllocladus hypophyllus	Mid[a]	7	378-476	460-490	59.68	0.50	0.42	n.s.	n.s.	0.13
	Podocarpus crassigemnis	Mid[a]	19	271-574	360-700[d]	74.12	0.29	0.40	0.53	0.56	0.13
				Class: Angiosperms							
Myrtaceae	*Decaspermum torbessii*	Mid[c]/Cloud[b]	2	513-573	701-763[d]	n.s.	0.31	n.s.	n.s.	n.s.	n/a
	Syzydium adelphicum	Lower[a]	8	413-548	474-883[d]	65.32	0.27	0.27	n.s.	n.s.	0.44*
	Syzygium benjamina	Lower[a]	2	539-587	474-883[d]	n.s.	0.65	n.s.	n.s.	n.s.	n/a
Atherospermataceae	*Dryadodaphne crassa*	Mid[a]	8	397-477	469-550[d]	67.02	n.s.	n.s.	0.62	0.62	0.63*
Cunoniaceae	*Indet sp.*	Mid[a]	10	409-563	300-833[e]	66.57	0.87	n.s.	0.33	0.35	-0.29
	Schizomeria serrata	Mid[a]	4	285-413	480-551	n.s.	n.s.	n.s.	n.s.	0.21	n/a
Icacinaceae	*Platea excelsa*	n/a	6	265-319	330-400	91.04	n.s.	n.s.	0.35	0.28	0.09
Rosaceae	*Prunus grisea*	n/a	10	379-536	550	72.65	0.40	0.23	n.s.	n.s.	0.33
Fagaceae	*Lithocarpus schlechteri*	Lower[a]	3	506-651	610	n.s.	n.s.	n.s.	n.s.	0.38	n/a

Paracryphiales	*Quintinia ledermamnii*	Lower[b]/Cloud[b]	9	378-471	440	77.93	0.42	0.28	n.s.	n.s.	0.45*
	Sphenostemon papuanum	Lower[b]	12	411-668	469[d]	70.41	0.18	n.s.	n.s.	0.12	0.64***
Rutaceae	*Zanthoxylum conspersipuctatum*	Lower[b]/Cloud[b]	4	373-385	368-970[d]	n.s.	n.s.	n.s.	n.s.	0.31	n/a

[a]Johns (1977). [b] Robbins (1961). [c]Smith (1985). [d]Wood density range at genus level from Zanne et al. (2009). [e]Wood density range at family level from Zanne et al. (2009).
*$p < 0.1$. ***$p < 0.01$.

Table 3.3. For specific angiosperms, taxonomic classifications and calculated wood densities and average *DBH* of shaded sampled species. Kendall tau log rank correlation was between elevation (independent variable) and wood density. *DBH:* diameter at breast height; n.s.: none sampled; n/a: not applicable.

Family	**Tree species**	**Montane forest sp. occurrence (literature)**	**n**	**Sampled density range (kg m^{-3})**	**Literature density range (kg m^{-3})**	**Study sites sp. occurrence Avg. *DBH* (m)**				**Kendall tau**
						a14	**a13**	**a11**	**a10**	
Rutaceae	*Acronychia murina*	Lower[a]	7	302-590	370-719[b]	0.26	0.16	0.21	0.14	-0.93
Pentaphylacaceae	*Eurya tigans*	Lower[a]/ Cloud[a]	1	448	430-620[b]	0.26	n.s.	n.s.	n.s.	n/a
Euphorbiaceae	*Macaranga trichanthera*	n/a	13	241-404	230-700[b]	0.27	0.29	0.23	0.31	-0.85
Primulaceae	*Myrsine leucantha*	n/a	5	494-677	594-824[b]	n.s.	0.23	n.s.	n.s.	n/a
Ochnaceae	*Schuurmansia elegans*	Cloud[a]	2	611-638	540-982[c]	0.34	n.s.	n.s.	n.s.	n/a
Rubiaceae	*Timonius belensis*	Lower[a]	6	355-551	460-760[b]	0.24	0.15	0.19	n.s.	-0.3
Winteraceae	*Zygogynum argentea*	n/a	3	378-491	460-512[b]	0.16	n.s.	n.s.	n.s.	n/a

[a]Robbins (1961). [b]Wood density range at genus level from Zanne et al. (2009).

Sixty four trees from thirteen species were sampled next to permanent site 10 (site a10). In no month was there a potential for evapotranspiration exceeding precipitation. It was the warmest yet least rainy area in the study.

3.2.2 Wood density, saturated wood moisture content, tree diameter and height.

All tree core sampling was carried out adjacent to the permanent sites to avoid any disturbance within the established sites themselves. Trees with *DBH* < 0.10 m, or which were multi-stemmed, leaning more than 10°, fluted, hollow, rotten, or snapped were excluded from sampling. Some trees were sampled at a second time, 90° from the first in a horizontal plane, to study ϱ consistency within individuals. Samples were collected using a Suunto 400-mm increment borer, and sample length was measured after collection using an electronic digital calliper (0.01-mm resolution) of 50 cm length (ISO 9001). Cores were subsequently stored in drinking straws prior to weighing at night after all the fieldwork was completed for the day. Subsequently, samples were transferred to 70% ethanol for preservation. Samples were transferred propylene glycol solution, a a non-harzadous preservation material before shipment to Australia. The increment borer was cleaned in 70% ethanol after each core was taken.

Tree height was estimated using a LaserAce® hypsometer (Measurement Devices Ltd., Aberdeen, Scotland, U. K.), and *DBH* was determined using a 5m enamelled steel diameter tape (349D; RICHTER Deformationsmesstechnik GmbH, Burkersdorf, Germany). Canopy Light Index was measured using a convex hemispherical densitometer (Model C; Forestry Suppliers, U.S), and measurements were carried out in the cardinal directions north-south or east-west and at a distance from the tree that ensured the tree stem was not reflected in the instrument. Forest overstory density was calculated according to the method described by (Lemmon 1956).

To ensure that correct tree species were sampled at each site, vouchers of all tree species were pressed and preserved in ethanol at each site. These vouchers were later identified at the Forest Research Institute in Lae, which also issued permits to export the samples from Papua New Guinea to Australia.

Wood samples were dried at 40 °C for three weeks to avoid rapid dehydration and to preserve the structure of the wood. Samples were then dried at 105 °C to constant weight. Wood specific density was calculated as $\varrho = m/v$ where m was the dry weight of the sample core and v was the associated green or fresh volume.

3.2.3 Soil chemical and physical characteristics

Soil samples were collected in 2010 by Dieleman et al. (2013) and results for soil C and N presented here are extracted from that publication (Table 3.4). For additional soil chemistry information, pooled samples from the upper 0.3 m from the same sites were analyzed for exchangeable cations and total phosphorus as described in Quesada et al. (2010). These are summarized in Table 3.4.

Table 3.4. Soil characteristics of the study sites along the altitudinal gradient. Pooled samples from the first 0.3 m depth of the same study site were analyzed for exchangeable cations and total phosphorus as described by Quesada et al. (2010).

Site	Ca	Mg	K	Na	SB	P	C	N	pH	Sand fraction
	(mg g^{-1})					(mg g^{-1})	(%)	(mg g^{-1})		
a14	42.4	8.1	1.2	1.6	39.1	1150	224	12.5	4.47	0.4
a13	20.0	4.3	0.6	1.8	26.6	857	204	12	4.54	0.70
a11	49.9	21.5	2.1	1.5	58.4	1637	185	13.7	4.93	0.82
a10	31.3	4.8	1.6	1.3	39.0	1691	166	11	4.91	0.74

3.2.4 Data analysis

Non-linear regression

All analyses were performed using the R statistical platform using the package titled *stats*. Regression analyses were used to estimate the relationships between H and DBH for various tree species across the sites and ϱ. Relationships between H, DBH, and ϱ were considered asymptotic functions because tree height growth tends to terminate in older trees (Kira 1978).

To study the effect of elevation on ϱ, we first performed a Kendall tau rank correlation as a non-parametric test to measure their partial correlations (Legendre and Legendre 2012). We also performed a test for significance to determine if the two variables were independent. Analysis was carried out using the package titled *Kendall.*

Multi-level model

The dataset in this study presented nested sources of variability; wood density varied within and along the study sites. Multi-level analyses were selected as a primary source of analysis because they allow testing the data without assuming homogeneity of regression, unlike analyses of covariates.

We developed a null model to examine the variance component of the model, including tree species as a random effect. The intercept is the general mean. The equation is

$$\rho_{isp} = \gamma_{000} + U_s + R_{isp}, \quad (1)$$

where ϱ_{isp} is the ϱ for the individual measurement i for species s at site p, γ_{000} is an averaged term for all the sampled species, U_s is the random variable that controls the variation between tree species at the group level, and R_{isp} is the residual at the individual level. We included site instead of temperature as a continuous variable because the temperature was not significant. This might be explained because of the small temperature range that the collected data covered. We then developed a multi-level analysis to study ϱ variations by adding a site-dependent deviation or fixed effect:

$$\rho_{isp} = \gamma_{000} + \beta_{001} P + U_s + R_{isp}, \quad (2)$$

where $\beta_{001}P$ is an intercept term that can vary between sites, where P is site. Thereafter, we added a canopy niche effect of the classification of individuals as either sun-exposed or shaded:

$$\rho_{isp} = \gamma_{000} + \beta_{001} P + \beta_2 PN_{0s} + U_s + R_{isp}, \quad (3)$$

where $\beta_2 PN_{0s}$ is the intercept for the canopy niche location for the tree species, being N the canopy niche location – sun-exposed or shaded. Finallly, we added $1/DBH_{isp}$ as a covariate:

$$\rho_{isp} = \gamma_{000} + \beta_{001} P + \beta_2 PN_{0s} + \beta_3/DBH_{isp} + U_s + R_{isp}, \quad (4)$$

where β_3/DBH_{isp} is a fixed effect variable describing the preliminary effect of DBH to better explain the relationship between ϱ and DBH.

All explanatory variables were tested for statistical significance and for unduly high variance inflation factors. The model included a random factor term for the tree species present in this study.

Variance of the residuals and covariance were defined as

$$\mathrm{var}(R_{isp})=\sigma^2 \quad , \quad \mathrm{var}(U_s)=\tau_0^2 \quad , \quad \mathrm{cov}(U_{isp})=\tau_{01}$$

Multilevel models were constructed using the package titled *nlme*. Model selection was determined by analysis of the residuals and the Akaike information criterion (AIC) value because lower values indicated a better fit of the model. The approach followed was according to Snijders and Bosker (1999) who created models by first creating an empty or null model and then improved on it by adding explanatory variables. The next step was to calculate the deviation between the predicted values and those measured in the field. We used $(\varrho_{tp} - \bar{\varrho}_{tp}) / \varrho_{tp}$ where $\bar{\varrho}_{tp}$ is the fitted value.

Centering of DBH

The data for *DBH* varied between 10 cm and 109.3 cm, and to better explain the fixed effect of *DBH,* we centered the variables (Snijders and Bosker 1999) to have a mean of 0. The model intercept that gave an average ϱ at the (harmonic) mean for a given intercept, in this case, was site a14.

Model validation

We tested the heteroscedasticity of the residuals at level two: Residuals were plotted versus 1/*DBH* and predicted wood densities were plotted against measured ϱ values for the models *Site/niche* and *Site/niche + 1/DBH.*

3.3 Results

3.3.1 Wood density variation

Tables 3.2 and 3.3 detail the results for the six gymnosperm and 18 angiosperm species sampled. The tables show observations on a species basis, and include the Kendall tau, a non-parametric measure of partial correlation between *DBH* and elevation (Legendre and Legendre 2012), where elevation is the independent covariate. Although we were able to sample only five species (*Saurauia altiterra, Libocedrus papuanum, Podocarpus crassigemnis, Acronychia murina,* and *Macaranga trichanthera)* at all four sites, of the remaining 19 species, ten were found at two or three of the sites, and only nine were restricted to only one site. Average *DBH* for sun-exposed species along the altitudinal gradient decreased for the tree species *Libocedrus papuanum*, *Phyllocladus hypophyllus*, *Indet sp.*, *Platea excelsa*, *Prunus grisea*, *Quintinia ledermamnii,* and *Sphenostemom papuanum*, but increased for *Podocarpus crassigemnis* andremained similar for *Dacrycarpus cinctus*, *Syzydium adelphicum,* and *Dryadodaphne crassa.* No clear trend was seen for *Saurauia altiterra.* By contrast, ϱ for the shaded species showed the increasing trend with elevation.

There is limited agreement between our data and that previously published on species habitat associations . For example, *Syzydium sp.* was lowland-affiliated according to Johns (1977), but sampled in this study only at higher elevations. There was better agreement between our observed ϱs and those previously presented in the literature: We found significant overlap in all but a few cases. Examination of the Kendall taus for the sun-exposed species (Table 3.3; original data shown in Appendix Ch. 3, Fig. 1) reveals that of the 12 species in this category and sampled at multiple sites, ϱ decreased with increasing elevation in all but two cases, *D. cinctus* and one unidentified species. By contrast, among the sub-canopy species (Table 3.4), ϱ for all three species tended to increase with increasing elevation (original data shown in Appendix Ch. 3, Fig. 2).

Wood density, H and DBH

The results in Appendix Ch. 3, Fig. 3 and summarized in Table 3.5 show that *DBH* was a better predictor for ϱ than it is at predicting *H* for most of the tree species studied because there is a negative relationship between ϱ and *DBH*. However, some exceptions were found. Of note is the sun-exposed species *Dryadodaphne crassa*, in which a slight positive relationship was seen between ϱ and *DBH,* and *Podocarpus crassigemnis* and *Saurauia altiterra,* in which nearly insignificant relationships were found between ϱ and both *H* ($R^2 = 0.002$) and ϱ and *DBH* ($R^2 = 0.006$). Two of three shaded species (*Acronychia murina* and *Macaranga trichanthera*) showed a positive relationship between ϱ and *DBH*. *T. belensis* showed no relationship between ϱ and either *DBH* or *H*. Nevertheless, this species maintained a positive relationship between *H* and *DBH* ($R^2 = 0.45$). Overall, our dataset suggests a positive relationship between *DBH* and *H* with a coefficient of determination between *H* and *DBH* of 0.21 for site a14, of 0.55 for site a13, of 0.37 for site a11, and of 0.47 for site a10. The study sites a13, a11, and a10 together present a coefficient of determinationof 0.42.

Table 3.5. Summary of parameters by species. Coefficients of determination (CoD) greater than 0.25 are in bold.

Tree species	n	***DBH* (m) and *H* (m)**	**Param. a**	**Param.b**	**CoD**	***CoD H* (m) vs. *DBH* (m)**
Sun-exposed species						
Dacrycarpus cinctus	8					0.11
		DBH	1.7533	-0.004	0.11	
		H	16.659	0.003	0.003	
Dryadophne crassa	8					0.11
		DBH	0.2911	0.0017	0.13	
		H	10.831	0.0006	0.001	
Indet sp.	10					**0.73**
		DBH	58.2500	-0.011	**0.69**	
		H	51.628	-0.003	0.21	
Libocedrus papuanum	16					**0.5**
		DBH	22.6880	-0.011	**0.79**	
		H	473.59	-0.009	**0.64**	
Phyllocladus hypophyllus	7					**0.64**
		DBH	3.1936	-0.005	0.07	
		H	25.258	-0.001	0.03	
Platea excelsa	6					0.06
		DBH	15.2320	-0.013	**0.48**	
		H	51.848	-0.005	0.19	
Podocarpus crassigemnis	19					0.002
		DBH	0.4778	-0.0004	0.002	
		H	16.192	0.0002	0.002	
Prunus grisea	10					**0.45**
		DBH	3.0039	-0.005	**0.39**	
		H	25.814	-0.001	0.09	
Quintinia ledermamnii	9					0.22
		DBH	0.007	0.0087	**0.26**	
		H	24.569	0.000004	0.02	
Sauravia altiterra	19					0.06
		DBH	0.1013	0.0023	0.002	
		H	61.668	-0.005	0.06	
Sphenostemon papuanum	12					0.8
		DBH	0.6666	-0.003	**0.81**	
		H	39.684	-0.003	0.5	
Syzydium adelphicum	8					**0.59**
		DBH	0.9773	-0.003	0.16	
		H	61.64	-0.003	**0.33**	
Shaded species						
Acronychia murina	7					**0.6**
		DBH	0.0630	0.0026	**0.76**	
		H	2.5934	0.0031	**0.83**	
Macaranga trichanthera	12					0.23
		DBH	0.1224	0.0023	0.1	
		H	7.1558	0.0015	0.2	
Timonius belensis	6					**0.45**
		DBH	0.3129	-0.001	0.08	
		H	12.113	0.00005	0.0001	

Parameters a and b are from the exponential equation y = a*exp(b*x), where y is wood density.

3.3.2 Wood density and niche occupation

Wood densities ranged from 241 kg m^{-3} to 677 kg m^{-3}, and the mean (± SD) ϱ for the sun-exposed species was 416 ± 85 kg m^{-3} and for shaded species was 446 ±145 kg m^{-3} (Table 3.2

and Table 3.3). This niche occupation effect on ϱ was significant ($p = 0.093$). The variation in ϱ between species was, however, highly significant within each niche grouping ($p > 0.001$). Among the sun-exposed species, the lowest mean was 329 ± 23 kg m^{-3} (*Saurauia altiterra*) and the highest, 574 ± 73 kg m^{-3} (*Lithocarpus schelerii*). Among the shaded species, differences of ϱ were significant ($p > 0.001$), varying from 271 ±21 kg m^{-3} (*Macaranga trichantera*) *to* 625 ±19 kg m^{-3} (*Schuurmansia elegans*).

3.3.3 Additive mixed modelling

Table 3.6 compares the simple *Null* model with that including site effects only. Here we found a *Null* model intercept ϱ of 443 kg m^{-3}, a species-associated variance of 6813, and an unexplained variance (reflecting within-species variability as well as any experimental error) of 2887. Thus, before accounting for any site effects, about 70% of the dataset variation was attributable to species identity. By also using potential site-to-site variation, a modest improvement in the model fit was achieved and, though the three lower-elevation sites gave rise to higher ϱs, this was significant only in the case of the second-highest site, a13. Note that species identity has been implicitly included in the model as part of the random effects term. Our fixed-effect estimates thus give an indication of any site effects on ϱ not mediated through differences in species composition. This, then, means that when all species are considered as potentially responding in the same way to any differences in location, only minor effects on ϱ are discernable.

Table 3.6. Estimates for the *Null* and *Site Effects* models.

Fixed Effect	***Null model***				***Study Sites***			
Parametric terms	**Coefficient**	**S.E.**	***t***	***p***	**Coefficient**	**S.E.**	***t***	***p***
Intercept (a14)	443.1	17.3	25.7	0.0001	432.9	18.7	23.2	0.0001
a13					23.5	11.7	2.01	0.0458
a11					7.0	14.1	0.50	0.6177
a10					15.0	12.9	1.17	0.2441
Random effect	**Variance component**				**Variance component**			
Level 2 variance (species)								
$\tau_0^2 = \mathrm{var}(U_{0S})$	6813				6981			
Level 2 variance								
$\sigma_0^2 = \mathrm{var}(R_{i,S})$	2887				2850			
AIC	2108				2089			

It is also evident from Tables 3.2 and 3.3 that the ϱs of sun-exposed species versus shaded species may have been effected by elevation in opposite directions, and indeed, as is shown in Table 3.7, allowing for this through the light-niche/site interaction term, a significantly improved model fit because AIC values decreased from 2108 to 2089, a clear and significant sign that ϱ declines with elevation for sun-exposed species but inclines for shaded species.

Inclusion of 1/*DBH* as a covariate further served to improve the model ($\chi^2 = 0.80$, $p =$ 0.0001; Table 3.7). The centered variable of ϱ when 1/*DBH* = 1 is 392 kg m^{-3}. Noting that the mean population 1/*DBH* was 0.04 m^{-1} (0.25 m), this means that as *DBH* increased up to 0.25 m, the fitted scaling coefficient decreases to 28 kg m^{-3}. As an example, ϱ at site a13 for a sun-exposed species with *DBH* = 0.1 m is modelled at 488 kg m^{-3}. When *DBH* = 1 m, ϱ is predicted to be substantially less, at 425 kg m^{-3}.

Table 3.7. Estimates for the Site/niche and Site/niche + 1/*DBH* effect models.

Fixed Effect	**Site/niche**				**Site/niche + 1/DBH**			
Parametric terms	**Coefficient**	**S.E.**	***t***	***p***	**Coefficient**	**S.E.**	***t***	***p***
Intercept (a14)	385.87	20.56	18.765	0.0001	392.06	20.95	18.718	0.0001
a13	26.37	10.90	2.419	0.0167	26.05	10.58	2.462	0.0149
a11	47.04	14.29	3.291	0.0012	45.16	13.91	3.247	0.0014
a10	54.33	12.37	4.393	0.0001	43.64	12.54	3.479	0.0007
a14*shaded	149.89	28.61	5.240	0.0001	145.71	28.21	5.165	0.0001
a13*shaded	-16.48	29.14	-0.566	0.5724	-24.58	28.44	-0.864	0.3887
a11*shaded	-136.51	28.22	-4.837	0.0001	-141.15	27.46	-5.140	0.0001
a10*shaded	-229.94	42.37	-5.427	0.0001	-241.76	41.29	-5.855	0.0001
1/DBH					701.58	223.1	3.145	0.0020
Random effect	**Variance component**		**Fraction of total**		**Variance component**		**Fraction of total**	
Level 2 variance (species)								
$\tau_0^2 = \mathrm{var}(U_{0S})$	7632				8032			
Level 2 variance								
$\sigma_0^2 = \mathrm{var}(R_{i,S})$	2127				2001			
AIC	2013				1194			

Interestingly, as the model fit was improved, both the absolute and proportional amounts of the random effect variance attributable to species increased at the expense of the residual variance. It was also found that the model *site/niche* + *1/DBH* explained variation in ϱ much better than when H or $1/H$ was substituted for the reciprocal DBH term. Interestingly the term *site/niche* * *1/DBH* was not significant for the shaded species. Thus, $1/DBH$ was added only as a simple covariate. Soils were non-significant in the model. Therefore, according to the results from the models, soil had no significant effect on the variation of ϱ.

Validation for *Site/niche* and *Site/niche + 1/DBH* models indicate a good fit. Both models (Fig. 3.2) presented heterogeneous residuals when the standards of residuals were plotted against $1/DBH$ for the model *Site/niche* and *Site/niche + 1/DBH* models. The graphical results of the fitted ϱ versus the measured ϱ gave a well-fitted line for the models *Site/niche* and *Site/niche + 1/DBH*. Fig. 3.2 represents the modelled ϱ versus the measured ϱ from the collected wood samples for the models *Site/niche* and *Site/niche + 1/DBH*.

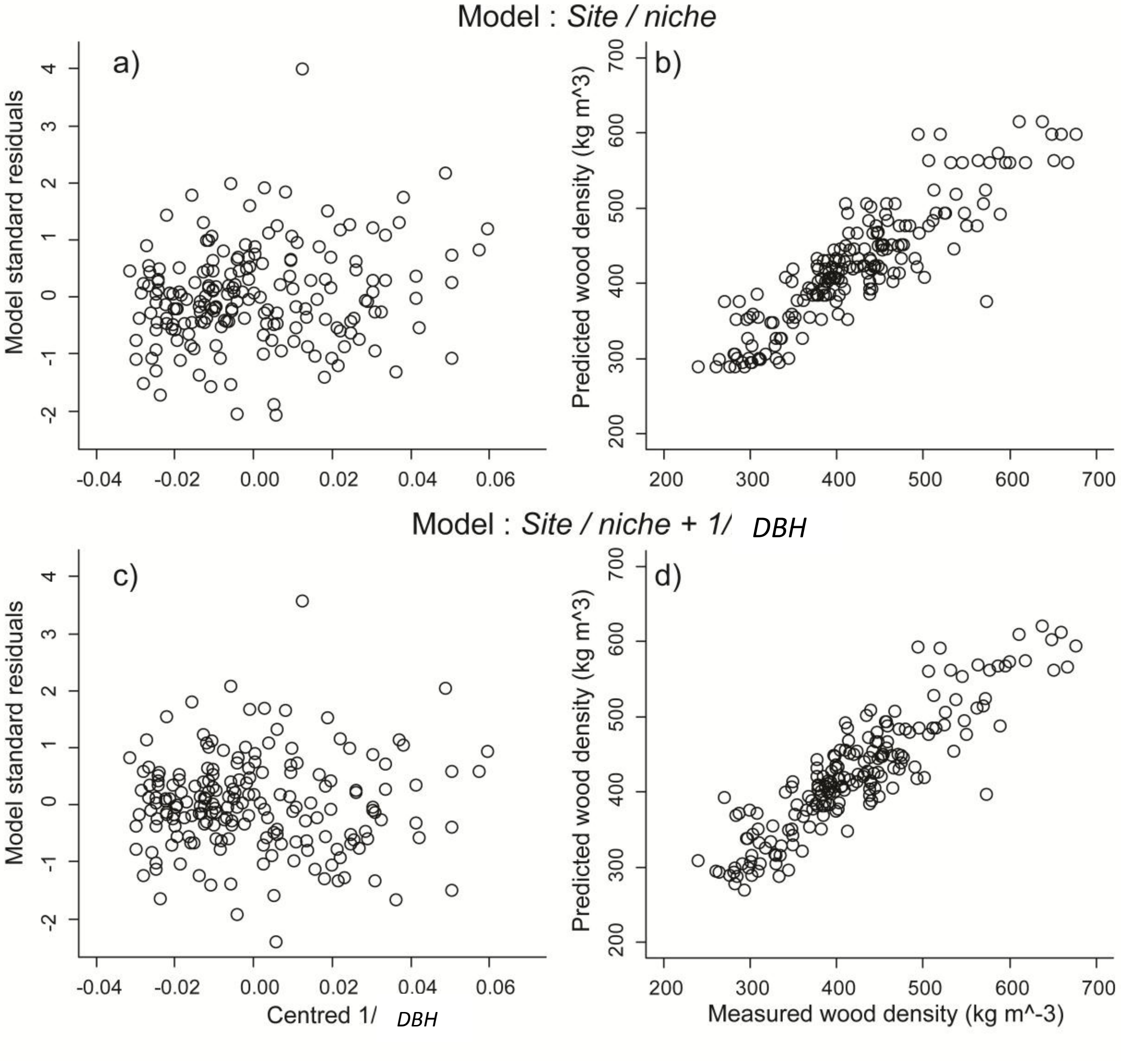


Fig. 3.2. Residuals versus $1/DBH$ (m) and versus wood density (kg m^{-3}) for the model *Site/niche* (a and b, respectively) and for the model *Site/niche + 1/DBH* (c and d, respectively).

3.3.4 Standard error of the mean

Selected trees were cored twice to study ϱ consistency within individuals. The standard error of the mean was calculated (Fig.3.3). Table 3.5 is a summary by species and site. The ranges of the standard errors of the means were between 0.49 for one *Podocarpus crassigemnis* individual anhd 49.5 for one *Libocedrus papuanum* individual.

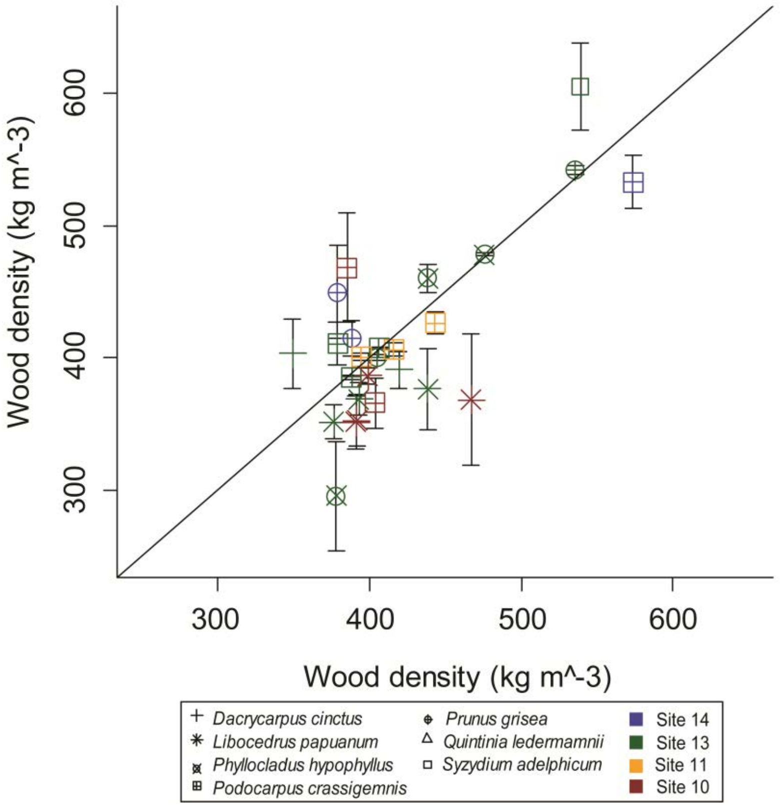


Fig.3.3. Standard errors of the means for wood density (kg m^{-3}) in sun-exposed individuals that were sampled twice.

3.4 Discussion

Previous studies of regional intra-specific variation of tropical forest trees have found that ϱ has a tendency to decline as MAP increases (Wiemann and Williamson 2002, Baker et al. 2004, Chave et al. 2006, Swenson and Enquist 2007, Baker et al. 2009, Henry et al. 2010). Soil fertility has also been implicated as a significant variable (Baker et al. 2004, Patiño et al. 2009), although no systematic differences with climate or soils have been reported (Nogueira et al. 2008). A general trend of decreasing ϱ with elevation has also been described recently in a lower montane evergreen forest (Hernández et al. 2012) and across the Neotropics (Chave et al. 2006). In addition, Wiemann and Williamson (2002) demonstrated that precipitation was a better predictor of variation in ϱ than MAT. These studies suggest that there is an inter-specific relationship between ϱ and environmental variables. The work here is the first to investigate these phenomena in Papua New Guinean forests, focusing on intra-specific variations of ϱ relative to edaphic and environmental variables.

3.4.1 Wood density

The overall average ϱ in this study was 422 kg m^{-3}. This study was conducted in a tropical montane forest where trees had a limited exposure to drought (Zach et al., 2010), and growth conditions were generally more favourable. Thus, lower ϱs were expected, compared to tropical seasonal forests. Lower ϱs of sun-exposed species was commensurate with their higher hydraulic efficiency in comparison with shaded species (Zach et al., 2010).

Previous studies in montane forests in the Peruvian Andes reported average values for ϱ between 560 kg m^{-3} and 580 kg m^{-3} at elevations between 3200 m and 3500 m and precipitation of 1560 mm (Giradin et al., 2013). Generalist studies of tropical forests reported average values in seasonal forests in Africa of 590 kg m^{-3} (Henry et al. 2010), in Brazil, 640 kg m^{-3} (Nogueira et al., 2008), and in Peru, between 540 kg m^{-3} and 670 kg m^{-3} (Gonzalez et al. 2014). Of note is that ϱ for trees assimilated in current databases have generally been derived from commercial forestry studies with an emphasis on large size classes. Thus, using these values without accounting for the *DBH* effect on ϱ, as demonstrated here, may result in an underestimation of stand level *B* and C stocks.

3.4.2 Conifer and angiosperms distribution

Our study shows that *DBH* in conifers decreases most markedly with elevation (Table 3.3). This might be explained by gymnosperms having a relatively primitive structure (Hoadley 1990) as compared to angiosperms, the latter containing a more diverse range of cell types, cell sizes, and other more complex features. Thus, angiosperms should have a higher capacity to adapt to lower elevation conditions, thereby displacing conifers (Swenson and Enquist 2007).

3.4.3 Niche status: ϱ variation with elevation depends on light environment

Previous studies have suggested that ϱ explains the capacity of a tree to survive or adapt to changing environmental conditions (Malhi et al. 2006, Poorter et al. 2010). Only a few studies in seasonal forests have suggested an intra-specific variation of ϱ with P; for example, results in lowland seasonal tree plantations of the species *Guazuma crinita* in the Peruvian Amazon demonstrated that ϱ is negatively correlated with precipitation (Weber and Sotelo Montes 2008). Also, Hernandez and Restrepo (1995) showed that geographical variation explained differences in the intra-specific variation of ϱ in *Alnus acuminata*. Moreover, it has been demonstrated that MAT and atmospheric pressure decrease while UV light increases with elevation, leading to progressive modifications in tree growing conditions and stature of the vegetation (Feldpausch et al., 2010; Wallace and McJannet, 2012). In this study, UV light availability was not measured.

Previous studies have explained a relationship between sun exposure of the tree (niche) and hydraulic demands (Poorter et al. 2010, Zach et al. 2010). The results of this study suggest that the hydraulic traits of sun-exposed species exhibit a stronger association with tree size than is found in shaded species because low wood densities facilitate a higher K in the taller sun-exposed trees. In contrast, the increase in ϱ with site elevation among shaded species might be explained based on a dissimilar investment on structural and morphological physiognomies. Shaded species generally produce structures that maximize leaf light exposure in lower light regimes under the canopy strata (Poorter 1999, Poorter et al. 2010).

3.4.4 Intra-specific variation of wood density related to tree diameter and location

The model that best predicted ϱ variation within tree species with site elevation included the niche and $1/DBH$ as significant variables. Henry et al. (2010) similarly reported that niche occupation and the size of the trees influenced ϱ in a seasonal forest in Ghana. The results of our models also suggested that DBH is significantly negatively related to ϱ, and not H. The same results were obtained by (Henry et al. (2010)).

Our results suggest that tree allometry for ϱ is better conserved radially with DBH rather than with H, and here we note that H can decline with elevation in a way that is typically more pronounced than for DBH (Grubb 1977, Feldpausch et al. 2010). In this study, no measured soil property (Table 3.2) showed any consistent relationship with site dependent variations in ϱ (Table 3.7), with the possible exception of soil sand content. Thus, where the climate is the main source of variation, the effects of soil physics and chemistry are minor. This need not always be the case, of course. For example, the variation in stand-level wood densities across the Amazon Basin depended on both soils and climate (Quesada et al. 2012).

3.5 Conclusion

This study presents wood densities for 25 tree species in the Yopno-Uruwa-Som transect in Papua New Guinea. Our results emphasize the importance of accounting for variations in ϱ with tree size, and we found that DBH was a better predictor than H for intra-specific variation of ϱ in the tropical montane forests studied. This finding should enable more accurate estimations of B in the future by incorporating the variability of ϱ with DBH. Important elevation effects were also noted as part of this study. This elevation response is, however, complicated. Although sun-exposed species have generally lower ϱs than shaded species, elevation-dependent changes in wood density go in different directions.

Chapter 4

Above ground biomass determinants in relation to altitude in a tropical forest in Australia

View from the top of the canopy crane at the Daintree Rainforest Observatory, Cape Tribulation, Queensland, Australia

4.1 Introduction

There is a strong need to preserve present forests for both their high value of biodiversity and their crucial role in global carbon (C) cycling (Gibbs et al. 2007, IPCC 2013). Tropical forests store a substantial amount of terrestrial C, mainly in the soils (IPCC 2013) and in above ground biomass (Phillips et al. 1998, Malhi and Grace 2000, Phillips et al. 2008). These ecosystems store 60% of the total mass of C that plants assimilate through photosynthesis (Grace et al. 2014). General estimates from the IPCC (2011) quantified that tropical forests store more C in woody biomass (157 MgC ha^{-1}) than both temperate (96 MgC ha^{-1}) and boreal (53 MgC ha^{-1}) forests. Currently, tropical forests are suffering from both the pressure of high deforestation rates, which causes land fragmentation, and from the effects of climate change (Achard et al. 2002, Hansen et al. 2013, IPCC 2013). Both anthropogenic impacts produce uncertainty regarding the future responses of these ecosystems and their C reservoirs.

Initiatives to quantify the past, present, and future C stocks are being established across the tropics for these ecosystems, as are the ecological and economic value of land preservation as C sinks and biodiversity. Studies to estimate how climate change can affect tropical forest C stocks should consider gradual spatial changes in temperature and precipitation, as both are being modified by human activities. Altitudinal gradients are a desirable methodology to use in scientific experiments that focus on understanding the effects of climate change on tropical forests (Malhi et al. 2010). The elevational gradient provides a natural decrease of temperature with increasing elevation. In addition, landscapes and topography vary across the landscape, perhaps causing different precipitation or other climatic variables.

North Queensland Australian rainforests represent a World Heritage Area and cover about 9000 km^2. Australian tropical forests have suffered from anthropogenic impacts, primarily selective logging from the mid-late, 20th century until, 1988 (Vanclay 1994), and also from significant natural disturbances such as tropical cyclones (Webb 1958). The effects of cyclones on Australian tropical forests are comparable to those reported in previous studies from Africa, Malaya, and the West Indies (Webb 1958). Wind damage results in dense vine understories with more open canopies than regions not exposed to cyclone disturbance. Moreover, it has been observed that climate change is potentially increasing the frequency of these events (Nott et al. 2007). Canopy gaps increase fire risk and create favourable conditions for the middle strata layer to grow and for flowering species to reproduce (Webb 1958, Turton 1992, Metcalfe et al. 2008).

Previous ecophysiological studies have suggested that Australian forests might have lower transpiration rates than Brazilian and French Guyana forests, a phenomenon that might be related either to their evolutionary history (Morley 2000) or in Far North Queensalnd it could be because of the different structure of these forests, as the number of canopy emergent trees is usually low due to frequent cyclone exposure (McJannet et al. (2007a). Similar studies have also stressed the significance of mean annual rainfall and the length of the dry season in determining Australian high-elevation rainforest distribution, together with soil, water table depth, and local microclimate effects (McJannet et al. 2007a, McJannet et al. 2007b, Wallace and McJannet 2012). Additionally, elevational studies on daily plant transpiration in tropical forests in Australia have suggested a positive relationship with water vapour deficit (VPD) and solar radiation. The results of these Australian studies suggest that a decrease of mean annual rainfall or a decrease of water interception by montane forests could represent a more immediate and significant future threat to Australian tropical forests than changes in temperature (McJannet et al. 2007b, Wallace and McJannet 2012).

Daily plant transpiration is strongly related to the gross primary productivity (GPP), which is a function of the net primary productivity (NPP) (Jasechko et al. 2013). NPP is composed of the Gross Primary Productivity (GPP), which is the carbon dioxide that vegetation takes up during photosynthesis (Malhi and Grace 2000, Malhi et al. 2006, Chave et al. 2008), minus the C lost via respiration. Understanding the mechanism that enhances CO_2 fixation by trees via photosynthesis is fundamental to predicting how climate change will impact C reservoirs. For example, a recent study on Amazonian forests highlighted the importance of understanding the mechanisms controlling NPP. The results suggested that during the wet season, trees were increasing C storage through photosynthesis, but during the dry season, this process was inhibited due to a decrease of atmospheric moisture and soil water availability (Gatti et al. 2014). Thus, predicted changes in the length of the dry season as a consequence of climate change might have a significant impact on the C reservoirs. Also, GPP might also be affected by the predicted consequences of climate change in the tropical forests – a CO_2 fertilization effect on the vegetation (Huntingford et al. 2013) might enhance tree death by increasing tree growth rates and saturating tree productivity or by dieback of the rainforests through drought (Cox et al. 2004).

Elevational gradients have been demonstrated to be an excellent tool for studying the possible effects of anthropogenic climate change on C reservoirs by estimating how above ground biomass (*B*) varies with elevation. *B* is generally estimated using allometric equations that include, in order of importance, the diameter at breast height (*DBH)*, specific wood density (ϱ), and tree height (*H*) (Chave et al. 2005, Feldpausch et al. 2010). Both Baker et al. (2004) and

Chave et al. (2005) confirmed that ϱ is a key factor in converting tree volume into stocks of carbon, always after *DBH*. Many studies have confirmed that ϱ values to be used in the allometric equations need to be gained from field measurements from the area of study or from available literature (Chave et al. 2005, Nogueira et al. 2008, Henry et al. 2010). Moreover, comparison between *B* estimations from different sources might result in poor overall evaluations if variations in ϱ are ignored (Baker et al. 2004, Chave et al. 2005). Feldpausch et al. (2012) and Marshall et al. (2012) also demonstrated the importance of measuring and including *H* in general allometric equations to arrive at better estimates of *B* in tropical forests.

Several studies have found a trend of *B* decreasing with increasing elevation (Clark and Clark 2000, Schuur and Matson 2001, Kitayama and Aiba 2002, Leuschner et al. 2007, Moser et al. 2008, Asner et al. 2009, Culmsee et al. 2010, Girardin et al. 2010, Slik et al. 2010). For example, a decrease in biomass at increasing altitude has been found in previous studies on the Peruvian Andes, where *B* decreased from 124 MgC ha^{-1} at 194 m to 47 MgC ha^{-1} at 3020 m (Girardin et al. 2010). However, the value of 323 MgC ha^{-1} in Indonesia at a similar elevation of 2400 m (Culmsee et al. 2010) was considerably higher than that reported by Girardin et al. (2013). In addition, in a study on a tropical montane forest in Ecuador, *B* also decreased from 208 Mg dry mass ha^{-1} to 74 Mg dry mass ha^{-1} within an elevation range of 1050 m to 3060 m (Leuschner et al. 2007). However, exceptions of the general trend of decreasing *B* with altitude in tropical forests reinforces the importance of considering the geographic variability in controls on *B*. Alves et al. (2010), for example, reported an increase in *B* with increasing elevation with values of 209 Mg dry mass ha^{-1} for lowland forest and up to 283 Mg dry mass ha^{-1} for montane forest. Also, altitudinal gradients through tropical montane forest have demonstrated a gradual decline of the tree basal area (*A*), species richness, and *B* (Girardin et al. 2013) with elevation with a more abrupt transition once the forests have reached the clouded elevations (Stevens 1992). The decrease of *B* with increasing elevation has mainly been explained by a decrease of the stature of the vegetation: studies have demonstrated that tree *H* decreases with increasing elevation at a faster rate than *DBH* (Grubb 1977), and maximum *H* can be reached independently of maximum *DBH* (Feldpausch et al. 2010). This decreasing tendency of *H* with increasing elevation has been attributed to an influence of external environmental variables (light availability, past disturbances) (Lieberman et al. 1996) and to the capacity of the tree to gain and allocate C using the environment (Moser et al. 2008).

Wood density is a structural plant trait that is related to the capacity of a tree to survive or adapt to changing water availability (Malhi et al. 2006, Poorter et al. 2010). Global studies aiming to provide better understanding of the trends of ϱ have suggested that ϱ traits are maintained at the phylogenetic level, and that variation of ϱ at the genus level can be up to 74% (Chave et al. 2006). However, the relationship between ϱ and its relation with wood traits, as well as its plasticity as an ecological biome adaptation, are still not entirely understood (Chave et al. 2009). For example, detailed studies were conducted on co-existing rainforest tree species in Bolivia in a semi-wet forest (where in one month (Dry Season Length, DSL), evapotranspiration exceeded the precipitation). In relation to plant performance and wood traits, it was found that tree growth was positively related to potential specific hydraulic conductance (K_p) and negatively related to ϱ (Poorter et al. 2010). Moreover, a study conducted on a lower montane tropical forest in Indonesia with a DSL of 1-2 months suggested that taller sun-exposed trees invest more in high hydraulic conductivity (K) of the stems due to water demand in comparison with shaded trees, as temperature at the canopy is higher than in lower strata (Zach et al. 2010).

Neotropical studies on spatial patterns of ϱ have highlighted the importance of tree hydraulic architecture as a major determinant of tree distribution, being directly related to the capacity of the tree to adapt to environmental transpiration and daily water usage demands (Chave et al. 2006, Malhi et al. 2006, Swenson and Enquist 2007). In addition, Choat et al. (2007) demonstrated that the hydraulic capacity of a tree to avoid xylem cavitation decreases as mean annual precipitation (MAP) increases. Moreover, a study of the relationship between K and xylem anatomy in a seasonally dry forest in Australia suggested that species that were more adapted to seasonally dry conditions had better hydraulic architectures, as demonstrated by wider xylem vessels, lower ϱ, and higher maximum rates of sapwood-specific K. However, as a result, these trees were more vulnerable to embolism (Choat et al. 2005). In addition, Choat et al. (2007) examined intra- and inter-specific variation of tree vulnerability to xylem embolism on a precipitation gradient from wet to seasonal forest for the same tree species. They concluded that trees adapted to wetter conditions had a lower possibility of surviving in comparison with species growing in drier forest (Choat et al. 2007).

Likewise, differences in light availability beneath the canopy are likely to define tree growth rates and ϱ. Henry et al. (2010) attributed 62% of the observed variability in ϱ to tree species, guild status (non-pioneer light-demanding species, pioneer species, and shade tolerant species), pith-to-bark distance, and tree size in Ghanian forest. Moreover, ϱ in two different lowland tropical forest areas in central regions and Mato Grosso of Brazil with DSLs of 3 and 6 months were strongly related to the ω of the bole (Nogueira et al. 2008). In dense forests, ϱ

decreased towards the bark for 82% of the trees. In contrast, for open forest dominated by low ϱ colonizing tree species, ϱ increased toward the bark in 63% of species.

The aim of this study was to quantify the effects of climate and soil characteristics on the above ground biomass along an altitudinal gradient. Also, in order to improve estimations of above ground biomass with respect to elevation, wood core samples were obtained from common species along the gradient. Species were classified according to canopy strata location (sun-exposed and shaded) to observe how ϱ varied with increasing tree diameter. A study of intra-specific and inter-specific variations of ϱ was considered in order to incorporate this variability in future C stock estimations in tropical forests. The questions addressed were:

- How elevation and soil nutrients affect the total above ground biomass?
- How do elevation and soil nutrients affect the intra-and inter-specific variation of wood density for sun-exposed and shaded tree species?
- How does wood density vary with increasing tree diameter for sun-exposed and shaded tree species?
- How do tree growth rates vary with elevation for sun-exposed and shaded tree species?

4.2 Material and methods

4.2.1 Study sites

The study sites were located in the lowland to montane tropical forests of north-eastern Australia (Fig. 4.1) at elevations ranging from 50 m to 1500 m above sea level (asl) (Table 4.1). The sites were established between 2007 and 2010 by the Commonwealth Scientific and Industrial Research Organisation (CSIRO), except for site ROB-01 established as part of 'The Terrestrial Ecosystem Research Network' (TERN http://www.tern.org.au/), and the sites KBL-01, KBL-03, and KCR-01 established by the 'Tropical Biomes in Transition' (TROBIT) project (www.geog.leeds.ac.uk/TROBIT) (Torello-Raventos et al. 2013). Each site was classified as wet, moist, or dry according to MAP and DSL (Chave et al. (2005).

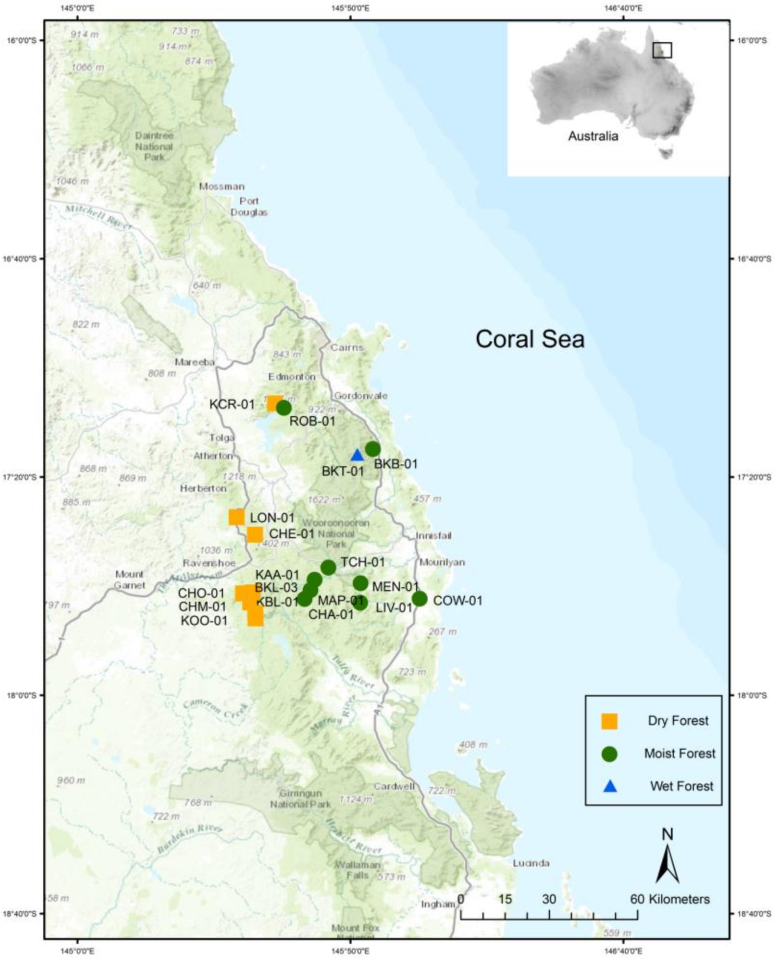


Fig. 4.1. Map displaying the location of the study sites. Different symbols explain the forest type as wet, moist, or dry according to (Chave et al. 2005).

The selected size of the study area for all the sites was 50 m x 20 m. All the tree species with a diameter at breast height (DBH) > 0.1 m were identified and tagged at the time that the sites were established.

Table 4.1. Site name, label, location, elevation, mean annual temperature (MAT), mean annual precipitation (MAP), dry season length (DSL), forest type classification, and establishment year for each of the study sites.

Site name	Label	Lat.	Long.	Elev. (m)	MAT (° C)	MAP (mm)	DSL	Forest type+	Year establ.
Bellenden Ker	BKT-01	-17.263	145.853	1500	16.7	7855	0	Wet	2010
Charappa	CHA-01	-17.705	145.693	720	20.6	2367	4	Moist	2007
Charmillan	CHM-01	-17.716	145.525	890	20	1589	7	Dry	2007
Cheelonga	CHE-01	-17.509	145.544	1100	19.1	1524	7	Dry	2007
Cochoombirum	CHO-01	-17.688	145.505	1010	19.5	1384	7	Dry	2007
Cowley	COW-01	-17.705	146.044	25	23.5	3406	3	Moist	2007
Harvey	BKB-01	-17.248	145.901	50	23.7	3925	2	Moist	2010
Kaaru	KAA-01	-17.647	145.724	510	21.7	2707	4	Moist	2007
KBL-01	KBL-01	-17.765	145.544	758	20.5	1744	6	Dry	2009
KBL-03	KBL-03	-17.685	145.534	1060	19.1	1398	7	Dry	2009
KCR-01	KCR-01	-17.108	145.603	813	20.5	1958	5	Dry	2009
Koolmoon	KOO-01	-17.748	145.542	800	20.4	1748	7	Dry	2007
Liverpool	LIV-01	-17.717	145.862	95	23.3	3195	4	Moist	2007
Longlands	LON-01	-17.456	145.486	1210	18.7	1334	7	Dry	2007
Maple	MAP-01	-17.679	145.711	590	20.9	2528	4	Moist	2007
Mena	MEN-01	-17.657	145.864	210	22.7	3260	4	Moist	2007
Robson	ROB-01	-17.122	145.630	700	21.2	2095	5	Moist	2010
Tchupala	TCH-01	-17.609	145.766	440	21.9	2898	4	Moist	2007

+According to (Chave et al. 2005).

4.2.2 Climatic and site descriptors

MAP and MAT were obtained from the ~30 arc-second WorldClim dataset (Hijmans et al. 2004) (http://worldclim.org). In order to determine the potential water available to vegetation based only on meteorological data, we considered an index of plant water supply in relation to evaporative demand W (Table 4.2) following the work by Berry and Roderick (2005). This was estimated at every study site as follows:

$$W = MAP - Qs/(\varrho\lambda) \quad (1)$$

where MAP is mean annual precipitation, Qs is mean annual global solar radiation, ϱ is the density of liquid water, and λ is the latent heat of evaporation for H_2O. Qs was obtained from the free access website https://eosweb.larc.nasa.gov.

MAP and seasonality were selected as explanatory variables to estimate the DSL and to classify the forest vegetation into three main forest types following work by Chave et al. (2005). Species diversity, as described by the Shanon Diversity Index, was also included in our analysis, as we aimed to study its relationship with site elevation. Climate variables MAT and MAP were only inversely related with a coefficient of determination of 0.93 if the site BKT-01 was excluded, which has an extremely high annual mean precipitation of 7855 mm as the wettest meteorological weather station in Australia (Bureau of meteorology, Australia). BKT-01 is an extremely wet site in comparison to the rest of the sites, but it was the only wet site around the study area.

Table 4.2. Climate variables, diversity index, and structural descriptors of the vegetation at each study site.

Site	Shanon diversity index	W	Number trees (ha^{-1})	A (m^2 ha^{-1})	Max. DBH (cm)	Avg. ϱ (kg m^{-3}) literature$^+$	B* (Mg ha^{-1})
BKT-01	2.7	6498	640	15.9	37.4	634	75.04
CHA-01	3.68	1010	1280	58.66	62.9	600	407.1
CHM-01	3.24	1589	870	34.64	34.9	636	251.16
CHE-01	3.56	167	720	50.09	80.2	580	309.49
CHO-01	3.28	1384	710	58.78	98.5	596	438.99
COW-01	3.39	1941	620	49.06	116.5	596	395.97
BKB-01	2.97	2568	450	42.92	102	630	526.02
KAA-01	3.5	2707	930	47.15	79.3	604	381.53
KBL-01	3.4	1110	590	36.83	77	633	290.75
KBL-03	2.6	1456	740	49.89	73.8	627	450.46
KCR-01	3.19	896	540	36.48	73.1	548	314.70
KOO-01	3.39	391	1250	49.52	52.9	599	330.07
LIV-01	3.38	3195	910	35.71	62.8	622	389.90
LON-01	3.04	1334	800	60.79	79.1	624	433.44
MAP-01	3.48	2528	920	53.46	79.7	583	465.86
MEN-01	3.22	3260	750	39.01	92.5	600	345.85
ROB-01	2.52	738	800	38.68	58.6	540	376.28
TCH-01	3.35	2898	830	46.57	79.3	616	382.44

$^+$Wood density values from Illic et al. (2010). **B* is calculated using the equation from (Chave et al. 2005) including tree height. *W* is an index of plant water supply in relation to evaporative demand, *A* is the basal area and *B* is the above ground biomass.

Data collection

In total, 407 individuals were monitored across the 11 study sites. 243 dendrometer bands were deployed, and 198 wood samples were collected (Appendix Ch.4, Table 1). We selected a range of tree species that occurred through the entire altitudinal gradient to determine the environmental drivers of intra- and inter-specific variation of ϱ. We also selected spacially restricted tree species along the transect which occurred at one of the study sites to obtain accurate measurements of *B* at each site to fill in the allometric equations.

The selection criteria of the individual trees excluded the trees with *DBH* < 0.1 m, or multi-stemmed, leaning more than 10 °, fluted, hollow, rotten, or snapped. Individual trees were classified according to their forest canopy strata or niche location at the time as sun-exposed or shaded trees. Wood coring was performed using a Suunto 400 mm increment borer (Vantaa, Finland). After collection, the length of the sampled core was measured using an electronic digital calliper (0.01 mm resolution) of 50 cm length (ISO 9001). Wood cores were stored in drinking straws before being dried at 105 °C to constant weight. Wood specific density (ϱ) was calculated according to $\varrho = m/v$, where m is the dry weight of the sample core, and v is its associated green or fresh volume.

Dendrometer bands were made from 6.53 mm wide stainless steel (BAND-IT, Denver, U.S.) and placed on the trees at the end of 2010 and in mid-2011, when the access at the sites was restored after the passage of cyclone Yasi in February, 2011. Tree growth was measured at the onset and end of the wet season in December and April, respectively, and annually up to the start of December, 2013. Measurements were done using a standard digital calliper with an accuracy of 0.01 mm (Appendix Ch.4, Table 2). *H* was measured using a LaserAce® hypsometer (Measurement Devices Ltd., Aberdeen, Scotland, U. K.), while *DBH* was determined using a Richter 5m Enamelled Steel Diameter Tape 349D (349D; RICHTER Deformationsmesstechnik GmbH, Burkersdorf, Germany).

Basal area (*A*) and biomass (*B*) were estimated at each study site, which had an area of 1000 m^2. The results were extrapolated to a site size of one hectare. Tree species at each site were identified when the sites were established. Calculations of *B* using the allometric equation from Chave et al. (2005) were conducted using the measured *DBH* and tree height (*H*) in the field. The wood density values used were obtained with tree coring as a first option, but for species not sampled, ϱ was obtained from the dataset created by Ilic (2000).

Radial variation of wood density was calculated by measuring different individuals within a range of diameters where the minimum diameter was 0.1 m. After, radial variation was calculated within tree species and between tree species from tree wood samples obtained by the use of an increment borer.

4.2.3 Soil sampling

Five soil samples were collected from the first 0 m to 0.3 m depth at the study sites summarized in Table 4.3 during 2012 based on the sampling protocol by Quesada et al. (2010). C and N abundances were determined using an Elemental Analyzer (Costech Analytical Technologies, CA, USA). One pooled sample from the 0 m to 0.3 m depth for each study site was sent to by Research Laboratories Limited Laboratories (Awatoto, New Zealand) for determination of exchangeable cations and total phosphorus.

Table 4.3. Soil description of the study sites included in the data analysis.

Study site	**Elev. (m)**	**Electr. cond.**	**Effective CEC**	**Nitrate-N (H_2O)**	**P. (Colwell)**	**Exch. K**	**Exch. Mg**	**Exch. Ca**	**Exch. Na**	**Al (KCl)**	**pH [CaCl]**	**pH [H_2O]**	**Roots**	**Gravel**
		(Ds m^{-1})	**(me $100g^{-1}$)**	**(mg kg-1)**		**(me $100g^{-1}$)**							**(prop)**	**(prop)**
BKB-01	50	0.12	3.0	42.0	26	0.23	0.5	1.1	0.05	1.1	4.3	5.0	0.39	51.73
TCH-01	440	0.16	4.4	64.7	10	0.38	1.59	0.4	0.11	1.92	4.3	5.0	2.38	38.08
CHA-01	720	0.14	2.5	43.8	7	0.28	0.27	0.1	0.05	1.84	4.2	4.7	1.16	33.76
KOO-01	800	0.12	3.8	9.0	6	0.34	0.65	0.0	0.13	2.73	4.2	4.9	1.60	52.39
CHM-01	890	0.11	2.7	21.5	10	0.19	0.24	0.3	0.03	1.96	4.3	5.1	2.29	34.04
CHE-01	1100	0.16	3.6	65.8	11	0.20	0.33	0.1	0.06	2.92	4.3	4.9	0.91	36.79
BKT-01	1500	0.11	2.8	0.50	17	0.15	0.19	0.0	0.03	2.48	3.8	4.3	2.03	3.47

4.2.4 Statistical analysis

The effects of elevation on the descriptors of the vegetation

To determine if elevation has an effect on the structure of the vegetation, we developed a linear regression where *DBH*, *H*, *B,* and *A* are plotted against elevation. We also plotted the Shanon Diversity Index versus site elevation.

Radial tree growth rates with elevation

Growth increments derived from dendrometer band measurements were used to determine basal area (*A*) at every starting *DBH* (cm^2 month^{-1}) at all the study sites. We plotted asymptotic curves and nonlinear regressions to model the species radial growth trends. Previous studies have indicated that radial tree growth for different tropical forest species can decrease from the pith towards the bark, or vice versa (Nogueira et al. 2005). Linear regressions would be unable to completely represent this phenomenon. We only plotted the curves for the species sampled at least 5 times at each site and across different study sites.

Better predictor of wood density

Wood density versus tree height and DBH, which is a better predictor

We performed non-linear regression analyses to determine which physiognomic variable, *DBH* or *H,* was a better predictor of ϱ within tree species. The analyses included asymptotic curves to examine increasing or decreasing trends of ϱ along with *DBH.*

Wood density versus elevation: Kendall tau

We performed two different analyses to study the relationship between ϱ and site elevation. First, we plotted the geometric average of ϱ for each tree species against site elevation to explore the inter-specific variation of ϱ. Then, we performed Kendall tau test on the selected tree species to determine the coefficient of correlation between ϱ and site elevation.

Multilevel analysis: what are the significant variables that define wood density?

Our multi-level analyses of the determinants of ϱ variation with respect to site elevation included the variables *site*, tree *species*, *height, diameter,* and *niche* occurrence. We followed the approach by Snijders and Bosker (1999), which defines the better model by first creating an empty or null model and then adding the significant explanatory variables. For this study, we first developed a null model to examine the variance component of the model including tree species as a random effect. Wood density is the sum of a general mean. The equation is defined as:

$$\rho_{isp} = \gamma_{000} + U_s + R_{isp} \qquad (1)$$

where ϱ_{isp} is ϱ for the individual trees measurements i from the different tree species s and at different temperature p, γ is an average term for all the samples trees, U_s is a random variable that controls the variation between tree species at species level, and R_{is} is the residual at the individual level. We then developed a multi-level analysis to study ϱ variations by adding a site-dependent deviation or fixed effects:

$$\rho_{isp} = \gamma_{000} + \beta_{001} P + U_s + R_{isp} \tag{2}$$

where $\beta_{001}P$ is an intercept term that varies along with MAT for the study sites. Subsequently, we added the significant variables following the systematic analysis by dropping the non-significant terms according to (Zuur et al. 2009) and keeping the significant terms:

$$\rho_{isp} = \gamma_{000} + \beta_{001} P + \gamma_{010} + \beta_2 PN_{0s} + U_s + R_{isp} \tag{3}$$

where $\beta_2 PN_{0s}$ is the intercept for the canopy niche location of the tree species (sun-exposed and shaded):

$$\rho_{isp} = \gamma_{000} + \beta_{001} P + \gamma_{010} + \beta_2 PN_{0s} + \gamma_{001} + \beta_3 PC1_{0p} + \gamma_{001} + \beta_4 PC2_{0p} + U_s + R_{isp} \tag{4}$$

where $\beta_3 PC_{0p}$ and $\beta_4 PC2_{0p}$ are the fixed intercept for the canopy niche location of the tree species of sun-exposed and shaded trees and are represented on the first two axes of the Principal component analysis (PCA) for soil fertility. PCA was used instead of the soil fertility index to define the relationships between the soil data descriptors (Legendre and Legendre 2012) in a simplified scaled axes-spatial projection. The soil variables included were the exchangeable cations, pH, Al, and C:N ratio.

All explanatory variables were tested for statistical significance and for high variance inflation factors. The model included a random factor term for the tree species. Variance of the residuals and the covariance were defined as:

$$\mathrm{var}(R_{isp}) = \sigma^2 \quad , \quad \mathrm{var}(U_s) = \tau_0^2 \quad , \quad \mathrm{cov}(U_{isp}) = \tau_{01}$$

Model selection was determined by the analysis of the residuals and the Akaike information criterion (AIC) value, with lower values indicating a better model. The next step was to calculate the deviation of the predicted values from the measured values in the field as $(\varrho_{tp} - \bar{\varrho}_{tp}) / \varrho_{tp}$, where $\bar{\varrho}_{tp}$ is the fitted value. Explanatory variables were centered to have an harmonic mean of 0 in order to better explain the fixed effects of MAT (Snijders and Bosker 1999). All the analyses were carried out using the R statistical platform (R Development Core Team, 2008).

The packages *vegan* and *stats* were used to calculate the Shanon Diversity Index and to do the Principal Component Analysis, respectively. Multilevel models were constructed using the package *nlme*.

4.3 Results

Using the collected dataset, we first examined how the structure of the vegetation varied along with elevation. We next examine the effects of elevation on the tree growth rates measured from the different tree species with respect to the study sites. Then, we identified whether *DBH* or *H* was better for explaining the intra-specific variation of ϱ. Last, we inspected what parameters significantly describe the variation of ϱ along with elevation by creating a multi-level model. The potential explanatory parameters included climate, soil characteristics, and tree physiognomy (*DBH* and *H*).

4.3.1 Effects of elevation in the structure of the vegetation

Our study suggests that only three statistically significant parameters changed with respect to site elevation: *B* and maximum DBH_{max}, both of which decreased with site elevation ($R^2 = 0.25$ and $R^2 = 0.28$, respectively, $p < 0.05$), as shown in Fig. 4.2 and Table 4.2. In contrast, *A* increased with site elevation ($R^2 = 0.39$, $p < 0.05$). However, the figure of *B* versus elevation had an outlying site of BKT-01. When excluded, the relationship between elevation and *B* was not significant and no longer representative ($R^2 = 0.06$). The variation of *B* and *A* according to forest type (Chave et al. 2005) was significant ($p < 0.05$, $p < 0.1$, respectively). The parameters *W*, number of stems, *DBH,* and average of ϱ were not significant.

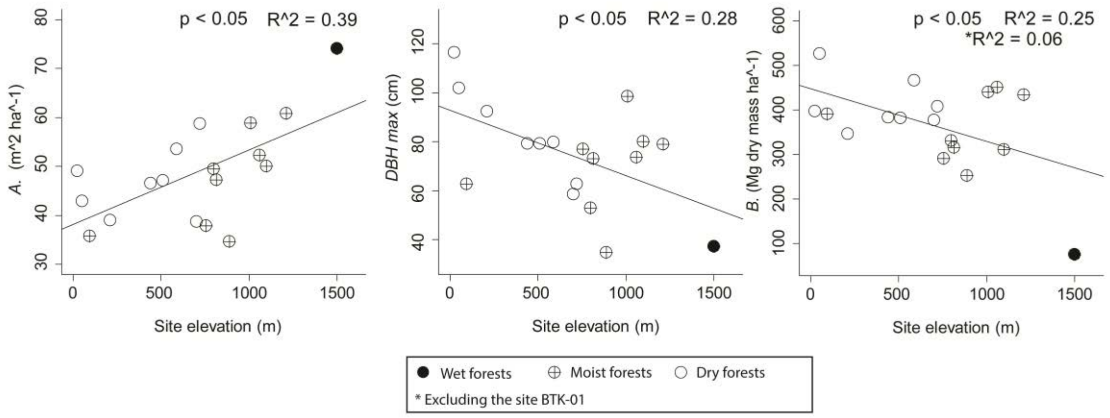


Fig. 4.2. Description of the site of characteristic basal area (*A)* (m^2 ha^{-1}), DBH_{max} (cm), and above ground biomass (*B)* (Mg dry mass ha^{-1}) versus site elevation (m) for all the study sites. Different symbols explain forest classification according to Chave et al. (2005). * Coefficient of determination excluding the site BKT-01.

4.3.2 Tree growth rates: basal area increment

Tree growth rate trends for shaded tree species were opposite those of sun-exposed tree species for the two species investigated (Fig. 4.3).

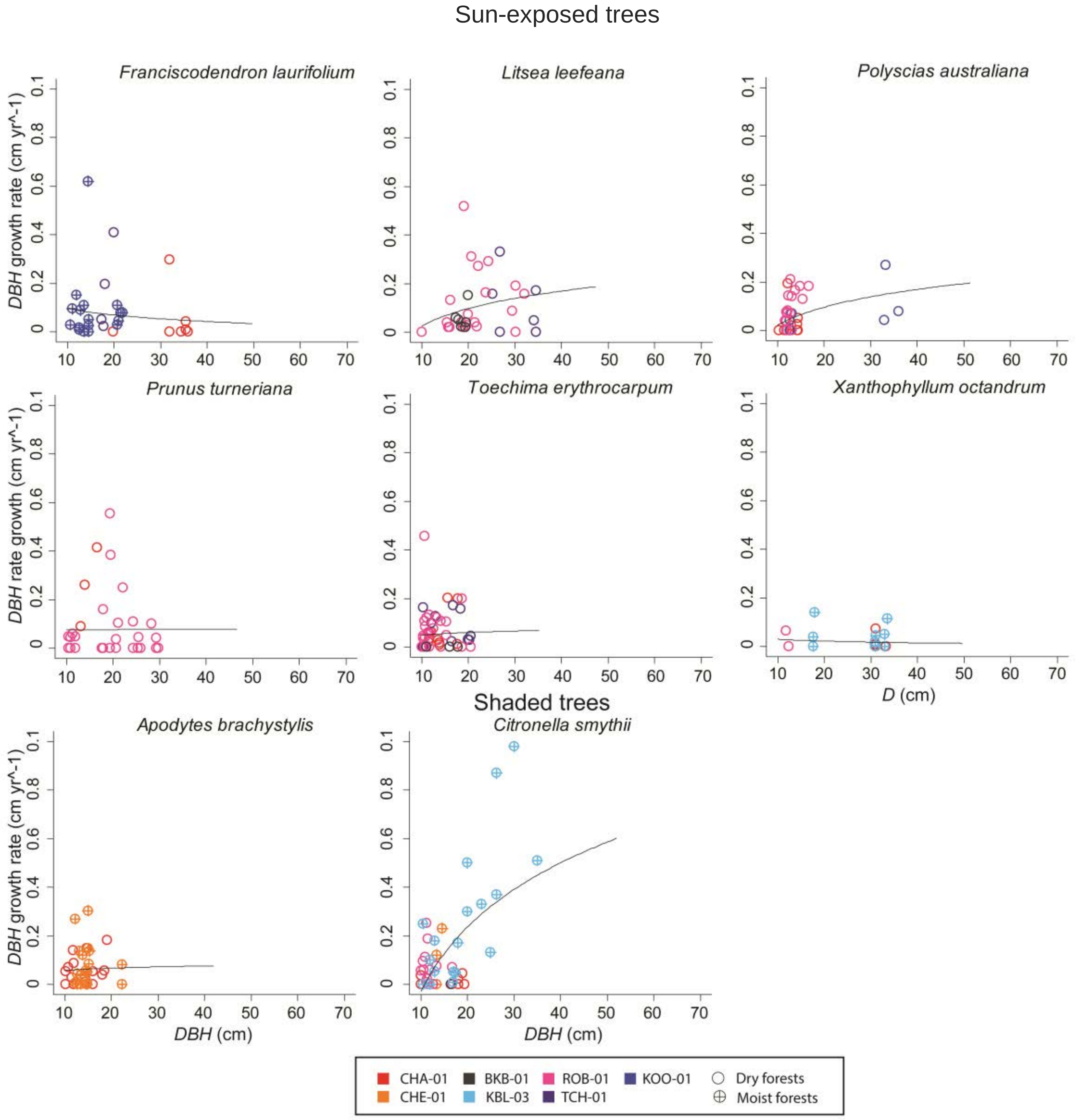
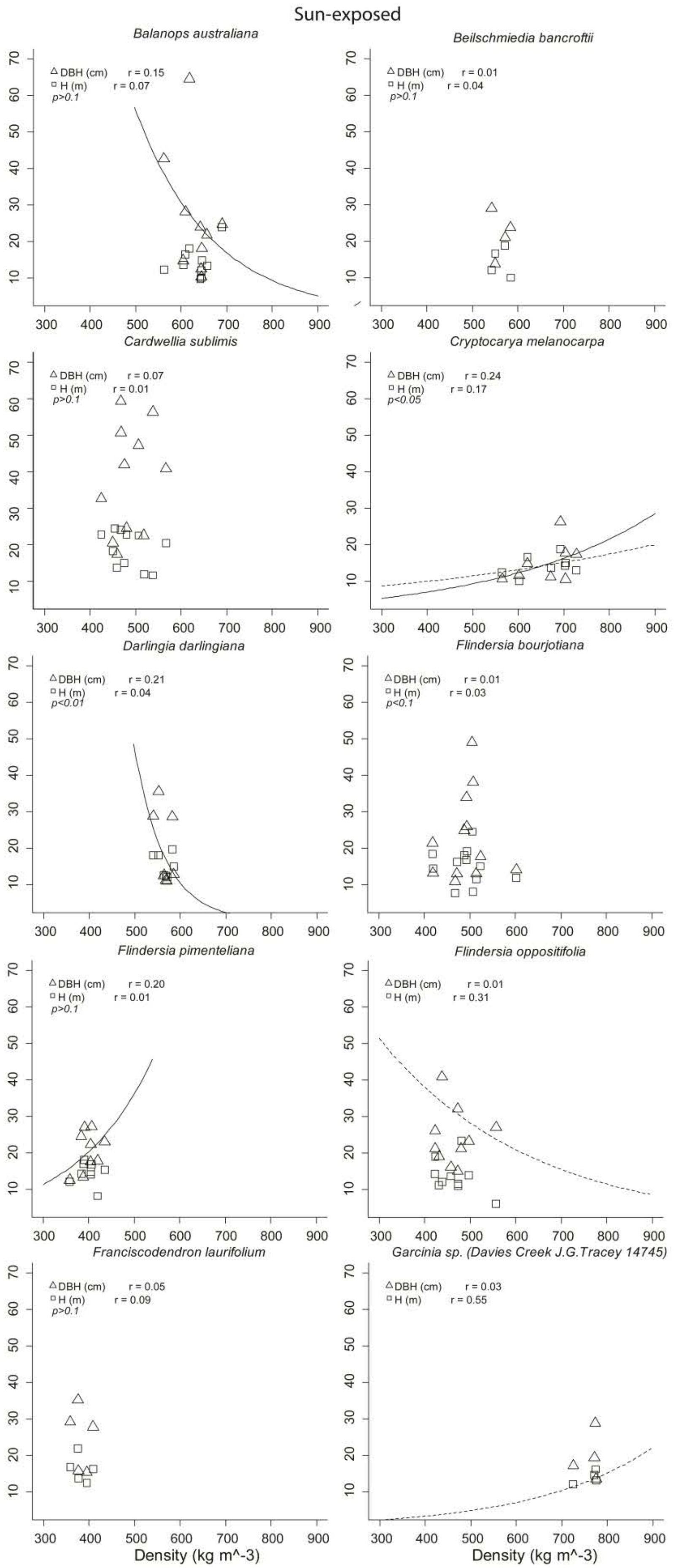
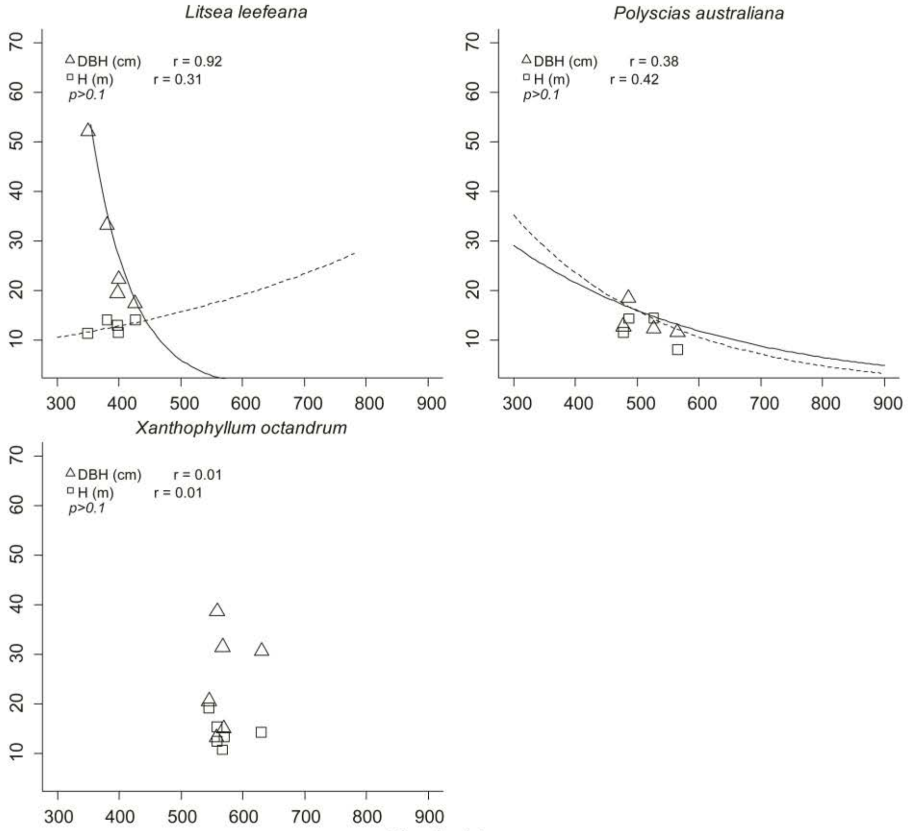


Fig. 4.3 Basal area increment (cm yr^{-1}) versus *DBH* (cm) for sun-exposed and shaded tree species from the study sites.

4.3.3 Better predictor of wood density: tree height versus diameter

The results shown in Fig. 4.4 suggest that *DBH* is a better predictor of ϱ than *H* for 12 of the 17 total tree species studied. Significant relationships between ϱ and *DBH* are indicated in the figure. However, an absence of relationship was found between *DBH* and *H* for the species *Beilschmedia bancroftii*, *Cardwellia sublimis*, *Flindersia bourjotiana*, *Franciscodendron laurifolium*, and *Xanthophyllum octandrum*. *H* was instead a better predictor of ϱ for the species *Flindersia oppositifolia*, *Garcinia sp.*, and *Polyscias australiana*. The asymptotic relationships between ϱ and *DBH* were mainly negative for sun-exposed tree species, except for *Beilschmedia bancroftii*, *Cardwellia sublimis*, *Cryptocarya melanocarpa*, *Flindersia bourjotiana*, *Flindersia pimenteliana*, *Flindersia oppositifolia*, *Garcinia sp.*, and *Xanthophyllum octandrum*; and the shaded species *Cryptocarya putida*. For most of the tree species, *H* and *DBH* were positively related, except for the sun-exposed species *B. bancroftii*, *F. oppositifolia*, *Litsea leefeana,* and *X. octandrum,* and the shaded *Citronella smythii*.


Sun-exposed
Balanops australiana
△ DBH (cm) r = 0.15
□ H (m) r = 0.07
p>0.1
Beilschmiedia bancroftii
△ DBH (cm) r = 0.01
□ H (m) r = 0.04
p>0.1
Cardwellia sublimis
△ DBH (cm) r = 0.07
□ H (m) r = 0.01
p>0.1
Cryptocarya melanocarpa
△ DBH (cm) r = 0.24
□ H (m) r = 0.17
p<0.05
Darlingia darlingiana
△ DBH (cm) r = 0.21
□ H (m) r = 0.04
p<0.01
Flindersia bourjotiana
△ DBH (cm) r = 0.01
□ H (m) r = 0.03
p<0.1
Flindersia pimenteliana
△ DBH (cm) r = 0.20
□ H (m) r = 0.01
p>0.1
Flindersia oppositifolia
△ DBH (cm) r = 0.01
□ H (m) r = 0.31
Franciscodendron laurifolium
△ DBH (cm) r = 0.05
□ H (m) r = 0.09
p>0.1
Garcinia sp. (Davies Creek J.G.Tracey 14745)
△ DBH (cm) r = 0.03
□ H (m) r = 0.55
10
20
30
40
50
60
70
300
400
500
600
700
800
900
Density (kg m^-3)
Density (kg m^-3)



Shaded trees

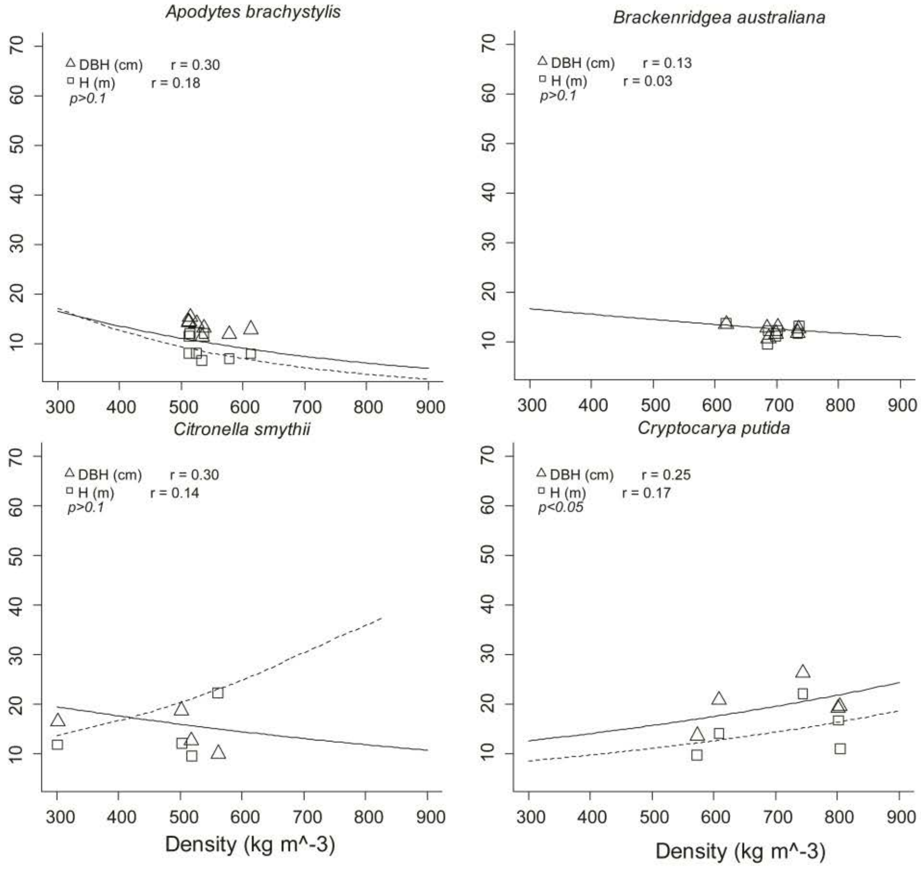


Fig. 4.4 Asymptotic regressions of *DBH* (cm), and *H* (m) versus ϱ (for sun-exposed and unexposed trees: In addition, linear regressions of *H* (m) versus *DBH* (cm). Statistical significance analysis (p) is for relationships between ϱ and *DBH* (cm). r is the coefficient of determination.

4.3.4 Radial variation of wood density within tree species

According to the results collected in this study (Table 4.4), ϱ decreased from the pith toward the bark between 8% and 25% for six species for the thirteen sun-exposed tree species sampled, while for seven species, ϱ increased from the pith towards the bark between 7% and 24%. Variation of ϱ for the shaded tree species increased by 29% from the pith toward the bark for one of the four species sampled, and it decreased for the three remaining species between 16% and 46%.

Table 4.4. Kendall tau results (variation of wood density between site elevation, being elevation an independent variable) from the sun exposed and shaded tree species. No is the number of individual trees and sites sampled. C.V. is the coefficient of variation.

Family	Tree species	No.	No. sites	Forest type^{+}	Literature ϱ (kg m^{-3}) *	Sampled ϱ range (kg m^{-3})	C.V. ϱ	Fraction of variation ϱ	*DBH* (cm) range	*H* (m)	Kendall tau
Sun-exposed											
Araliaceae	*Polyscias australiana*	4	2	D,M	470	478-565	-0.08	0.15	11.5-18.4	8-14	
Balanopaceae	*Balanops australiana*	10	5	M,D,W	735	562-690	-0.05	0.18	10.2-64.5	10-24	-0.07
Clusiaceae	*Garcinia sp. (Davies Creek J.G.Tracey 14745)*	4	1	D	735	725-776	+0.04	0.07	13.5-28.8	12-16	
Fabaceae	*Castanospermum australe*	3	2	M	583	492-740			18.0.81.0	15-18	-0.82
Lauraceae	*Beilschmiedia bancroftii*	4	3	D,M	520	542-584	+0.04	0.07	13.8-28.9	10-19	-0.18
	Beilschmiedia collina	3	2	D,M	590	583-588			11.2-31.3	8-21	-0.82
	Cryptocarya angulata	3	2	D,M	667	550-590			12.8-34.5	7-16	0.82
	Cryptocarya mackinnoniana	3	2	M	751	614-670			10.0-14.3	12-15	0.45
	Cryptocarya melanocarpa	8	3	D,M	578	564-727	+0.09	0.22	10.5-26.3	10-19	0.45
	Litsea leefeana	5	2	M	421	350-426	-0.05	0.18	17.4-52.1	11-14	-0.52
Malvaceae	*Franciscodendron laurifolium*	5	3	D,M	388	359-409	-0.17	0.12	15.4-35.2	12-22	0.12
Polygalaceae	*Xanthophyllum octandrum*	6	2	D,M	689	545-630	+0.05	0.14	13.1-38.6	10-19	-0.43
Proteaceae	*Cardwellia sublimis*	11	4	D,M	436	425-567	-0.10	0.25	17.3-61.3	12-24	0.17
	Darlingia darlingiana	7	3	D.M	656	541-586	-0.03	0.08	11.0-35.5	12-20	0.22
	Gevuina bleasdalei	3	2	D,M	538	481-505			14.6-42.5	12-19	
	Musgravea stenostachya	3	1	W	581	479-499			13.5-23.2	9-20	
Rutaceae	*Flindersia bourjotiana*	12	4	D,M	412	418-602	+0.11	0.31	10.9-48.9	8-25	-0.29
	Flindersia oppositifolia	10	1	W	621	423-557	+0.10	0.24	15.0-40.8	6-23	
	Flindersia pimenteliana	9	3	D,M	531	358-435	+0.06	0.18	12.5-27.2	8-18	0.07
Sapindaceae	*Toechima erythrocarpum*	3	3	D,M	676	470-551			10-11.13	10-19	0.33
Shaded											
Icacinaceae	*Apodytes brachystylis*	8	2	D,M	530	513-613	-0.06	0.16	11.4-15.3	7-12	0.07
	Citronella smythii	4	3	D,M	590	302-561	-0.27	0.46	10-18.7	10-22	0.55
Lauraceae	*Cryptocarya putida*	5	3	D,M	578	573-804	+0.16	0.29	13.6-26.3	10-22	0.45
Myrtaceae	*Gossia grayi*	3	2	D	768	749-858			11.3-19.4	11-13	
Ochnaceae	*Brackenridgea australiana*	7	3	D,M	600	618-736	-0.06	0.16	10.7-13.5	10-14	-0.46

Wood density values are from Illic et al. (2010). $^{+}$Classification of forest type according to Chave et al. (2005). W is for wet, D is for dry, and M is for moist forests.

4.3.5 Analysis of the determinants of wood density according to elevation

Geometric mean and Kendall tau: wood density and site elevation

The geometric mean of ϱ for each tree species for sun-exposed and shaded trees was plotted against site elevation to study the trend of ϱ (Fig. 4.5). This analysis was done previously to calculate Kendall tau to study the correlation between ϱ and site elevation, with site elevation being an independent variable. Kendall tau results are summarized in Table 4.4. The results for Kendall tau values for the sun-exposed and shaded species were positive and significant for 8 of the 15 sun-exposed tree species and 3 of the 4 total shaded tree species.

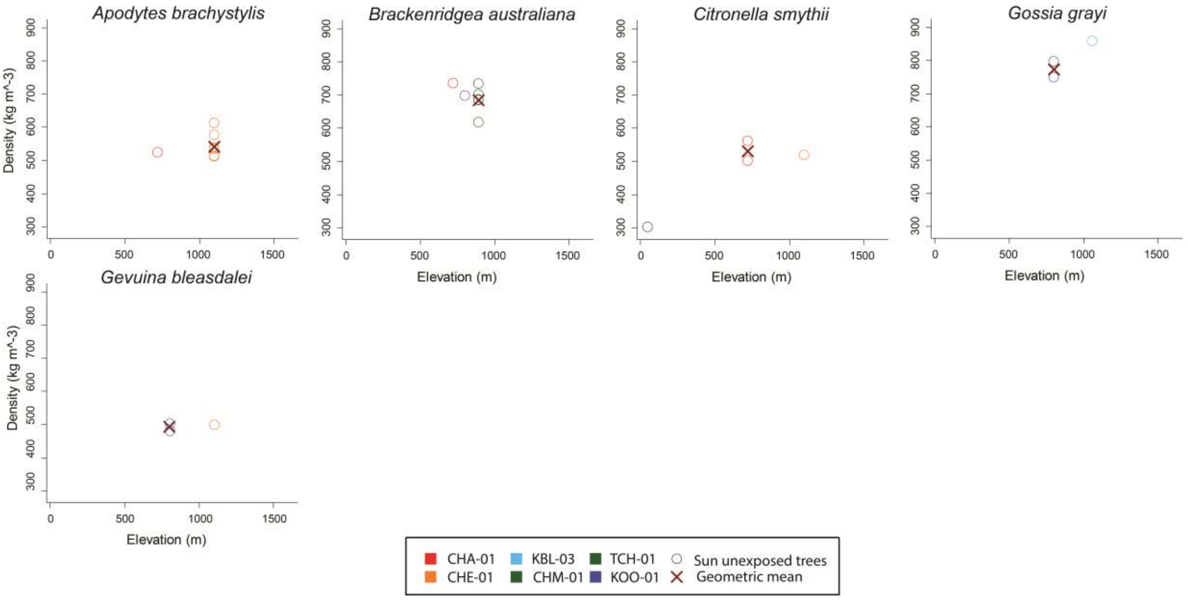


Fig. 4.5. Geometric mean of ϱ for sun-exposed *Gevuina bleasdalei* and unexposed tree species *Apodytes brachystylis*, *Brackenridgea australiana*, *Citronella smythii* and *Gossia grayi* from the study sites.

4.3.6 Additive mixed modelling

Table 4.5 compares the simple *Null* model with that including site effect only. This gave a *Null* model intercept ϱ of 557 kg m^{-3}, a variance component associated with species identity of 11286, and an unexplained variance of 3007 (reflecting within-species variability as well as any experimental error). Thus, before accounting for any site effects, about 0.79 of the dataset variation was attributable to trees species. Adding site-to-site variation through MAT leads to improvement of the model with about 0.82 of the dataset variation being explained. Note that species identity has been implicitly included in the model as part of the random effects term and with our fixed effect estimates, giving an indication of any site effects on ϱ not mediated through differences in species composition. Thus, only minor effects are discernible when all species are considered as potentially responding in the same way to any differences in growing location.

Table 4.5. Estimates for the *Null model* and the *Site Effects* models. *PC2 axis is converted to the main axis by changing the symbol (from negative to positive) of the second PCA axis.

Fixed Effect	***Null model***				***Niche / Temp***				***Niche/(Temp + fertility)***			
Parametric terms	**Coefficient**	**S.E.**	t	p	**Coefficient**	**S.E.**	t	p	**Coefficient**	**S.E.**	t	p
Intercept	556.89	13.98	39.83	0.0001	561.16	16.08	34.90	0.0001	561.19	15.83	35.45	0.00001
Shaded					-8.00	25.66	-0.31	0.7558	-6.83	26.30	-0.26	0.7955
PC2									-26.59*	11.36	2.34	0.0210
PC1									-15.12	8.53	-1.77	0.0791
MAT					0.65	6.16	-0.11	0.9158	18.22	10.65	1.71	0.0899
PC2*Shaded									-91.69*	36.53	-2.51	0.0135
PC1* Shaded									-62.82	30.86	2.04	0.0441
MAT* Shaded					-25.06	13.46	-1.86	0.0652	-86.30	28.23	-3.06	0.0028
Random effect	**Variance component**				**Variance component**				**Variance component**			
Level 2 variance (species)												
$\tau_0^2 = var\ (U_s)$	11286				12522				12009			
Level 2 variance												
$\tau_0^2 = var\ (U_s)$	3007				2838				2774			
AIC	2183				2163				2135			

It is evident from Table 4.4 and previous analyses that *ρs* of the sun-exposed and shaded species may have been responding to elevation in different directions. This possibility was enabled through a light-niche/site interaction term, which significantly improved model fit, showing a clear and significant tendency for *ρ* to decline for sun-exposed tree species with increasing elevation. However, the opposite effect was observed for shaded species. Soil fertility described by the two main axes from the PCA analysis *PC1* had a negative relationship with *ρ* for sun-exposed with increasing MAT and *ρ,* and *PC2* a positive relationship. The opposite trend was observed for shaded species.

The centered variable in the model (Table 4.5) for the sun-exposed tree species when MAT = 1 °C, *PC1* = 1, and *PC2* = 1 is 561 kg m^{-3}, and that for shaded tree species is 554 kg m^{-3}. Note that for the centered mean population, MAT = 0 °C, *PC1* = 0, and *PC2* = 0. This means that respective increases from 0 to 20 °C (centered MAT value 0.27), to -1.86 for *PC1,* and to 1.49 for *PC2* increases the fitted scaling coefficient to 498 kg m^{-3} for sun-exposed tree species and decreases it to 324 kg m^{-3} for shaded tree species. The model results suggest *DBH* is not a significant term. Interestingly, as the model fit was improved, both the absolute and proportional amount of the random effect variance attributable to tree species identity increased at the expense of the residual variance term. It was also found that the model *Niche /(Temp+fertility)* explained the *ρ* variation much better than when *DBH* or related precipitation variables were substituted for T, *PC1,* and *PC2.* The simple *Null* model presented a random variance of 11286 attributable to tree species and a residual variance of 3007. The *Niche/(Temp+fertility)* presented a random variance of 12009 and a residual variance of 2774.

Model validation for the models *Niche/(Temp+fertility)* indicates a good fit to the data. The model (Fig. 4.6) presented heterogeneous residuals when the standards of residuals were plotted against the fitted values. Fig. 4.6 also represents the modelled *ρ* versus the field-measured *ρ* for the model *Niche/(Temp+fertility).* PCA results summarized in Table 4.6 indicate that *PC1* is strongly associated with K and Na. K decreases with decreasing site MAT. Na had no relationship with temperature, but there was a positive relationship with K. *PC2* was strongly related to Ca and Al, with Ca decreasing and Al increasing with decreasing site MAT (i.e. increasing elevation) along the elevation transect.

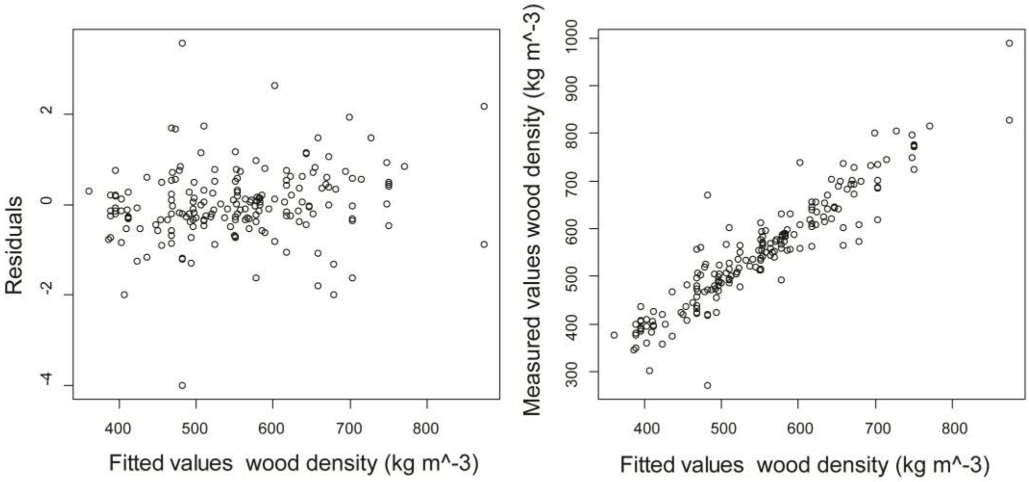


Fig. 4.6 Residuals of the model versus fitted values of wood density (kg m^{-3}) and fitted versus field-measured wood density values (kg m^{-3}).

Table 4.6. Results of principal component analysis (PCA) performed on the soil fertility values for the study sites included in the model.

Axis definition	*PC1*	*PC2*
Cumulative proportion	0.43	0.73
Prop. Total variance	0.43	0.302
pH [H_20]	0.304	-0.392
P.(Colwell) (mg kg^{-1})	-0.281	-0.318
Exch. K (me $100g^{-1}$)	0.510	-0.046
Exch. Mg (me $100g^{-1}$)	0.495	-0.112
Exch. Ca (me $100g^{-1}$)	0.066	-0.567
Exch. Na (me $100g^{-1}$)	0.500	0.104
Al (KCl) (me $100g^{-1}$)	0.032	0.560
C:N-ratio	-0.263	-0.290

4.4 Discussion

4.4.1 Structural and biomass descriptors with respect to elevation

The results of this study indicate that the structure of the vegetation varied significantly ($p<0.05$) as DBH_{max} decreased significantly with increasing elevation (Table 4.4, Fig. 4.2b). Related findings have been presented in other studies across continents (Grubb (1977) and in Venezuela (Hernández et al. 2012). The outcomes of this study also indicate a significant increase in A with increasing site elevation (Fig. 4.2a), while B did not decrease significantly with increasing elevation, so the site BKT-01 was excluded (Fig. 4.2c). The wet site BKT-01 is tropical montane forests located at 1500 m asl and with an MAP above 8000 mm. The climatic characteristics of the study site probably affect the structural composition of the vegetation significantly. It was only possible to find one wet forest in our area of study due to the rest of the forests being seasonal. Thus, this study might have been more robust if at least two more wet sites were included. B estimations would be comparable to altitudinal gradients that range from lowlands to tropical montane forests. Previous studies investigating lowland to montane forests in the Peruvian Andes found that *B* decreased from 124 MgC ha^{-1} at 194-m elevation to 47 MgC ha^{-1} at 3020 m (Girardin et al. 2010). However, exceptions to this general trend reinforce the importance of accounting for spatial variability in *B* in tropical forests. Alves et al. (2010) found an increase in *B* with increasing elevation with values of 209 Mg dry mass ha^{-1} for lowland forest and up to 283 Mg dry mass ha^{-1} in a montane forest in Brazil. Therefore, the variability in the structural composition of the vegetation along elevational gradients does not always follow the same trends.

4.4.2 Basal area increment

Previous studies also found an inverse relationship between shade-tolerant and intolerant tree species between H_{max} and ϱ (Gelder et al. 2006). Shaded trees are characterized by slower growth rates, higher ϱ, and adaptation to enhance survival in shaded environments (Poorter et al. 2010) compared to sun-exposed trees, because usually, morphological characteristics are more important to survival than for trees that are exposed to light.

4.4.3 Better predictor: tree height or diameter at breast height in defining wood density and tree growth rates

Allometric equations for forest trees have been widely used to describe the relationship between *H* and *DBH* (Feldpausch et al. 2010, Feldpausch et al. 2012). The results from this study suggest that *DBH* is a better predictor of ϱ than *H* when both are plotted against sun-exposed and shaded tree species (Fig. 4.4). For example, Henry et al. (2010) also reported that the size of the trees influenced ϱ in a seasonal forest in Ghana, increasing with *DBH* for all pioneer, light-demanding, and shade-tolerant species. These outcomes might support the idea that ϱ is more related to tree growth, and therefore, *DBH* would be a better predictor than *H*.

4.4.4 Intra-specific variation of wood density radially

In addition, ϱ decreased or increased from the pith towards the bark for sun-exposed tree species (Fig. 4.4). Henry et al. (2010) found that ϱ did not vary significantly between guild status (pioneer, pioneer light demanders, and shade), but it did vary significantly between tree species. In addition, ϱ can vary with *DBH* in seasonal forests. For example, after sampling 310 trees (122 cm > *DBH* > 5 cm), Nogueira et al. (2005) found that ϱ increased for 18% of trees, while ϱ decreased with increasing *DBH* for 80%, suggesting a more common trend for ϱ to decrease with increasing *D*. However, the study did not include the species classification by guild status.

Previous studies have also suggested a general trend of decreasing ϱ with increasing *DBH* that has been related to adaptive traits of the emergent or light-demanding trees species in moist-wet forests. These traits fulfil the high evapotranspirative demand of full-sun, canopy-exposed leaves and reduce the risk of xylem embolism (Poorter 1999, Poorter et al. 2010). However, more research is needed to understand the causes of this ϱ variation. Poorter et al. (2010) and Zach et al. (2010) suggested that the hydraulic traits of light-demanding trees have a stronger relationship with adult tree stature rather than non-light demand. In contrast, for trees occupying lower forest strata, shaded Kendall tau increased with increasing site elevation. This might be explained by the increase of *A* (Fig. 4.2). The results suggest that the mechanisms of adaptation to the medium for sun-exposed trees differ from those of shaded trees.

4.4.5 Analysis of the determinants of wood density with respect to elevation

Geometric mean and Kendall tau

The decrease in ϱ with increasing elevation for the sun-exposed trees may be attributed to a survival adaptation to transport water under very low VPD, as well as low UV availability. Such a conclusion is supported by Zach et al. (2010), who suggested that tree stomatal responses are very sensitive to atmospheric evaporative demand in wet lower montane forests in Indonesia. Moreover, in a study along an altitudinal gradient in a location near that of the present study, tree transpiration for Australian tropical forests was dependent on VPD and solar radiation (McJannet et al. 2007a). However, in our study, neither VPD or UV light availability were measured.

The model

Annual mean temperature itself is not significant

The effects of *Niche/Temp* without accounting for soil fertility in the multi-level model were not significant (Table 4.6), although MAT was significant in the interaction of *Niche/(Temp+fertility)*. This means that the fertility changes in the soils along the elevation gradient had a significant effect on ϱ. Similar results were found in the Neotropics by Malhi et al. (2004). The model that best predicted ϱ within tree species and across the sites included temperature and soil fertility as significant variables. The model *Niche/(Temp+fertility)* suggest that sun-exposed and unexposed trees have divergent ecophysiological responses, as trends in ϱ as a function of temperature (site elevation) were of opposite sign for sun-exposed and shaded tree species. This might be explained by differences related to niche occupancy in terms of sunlight exposure and associate evapotranspirative demands as well as hydraulic traits such as hydraulic conductance (Poorter et al. 2010).

The results also suggest that soils with higher K and Na increased the ϱ of the sun-exposed trees (Table 4.6). These outcomes are supported by Paoli et al. (2008), who found that fertile soils with elevated K and phosphorus limited the ϱ of emergent trees in Borneo. Soil fertility has also been identified as a significant variable in the variation of ϱ at the regional level (Baker et al. 2004, Patiño et al. 2008), although no significant relationship with climate or soils has also been found to date (Nogueira et al. 2008). A general trend of increasing ϱ with decreasing elevation has also been described recently for a lower mountain evergreen forest in Venezuela (Hernández et al. 2012) and across the Neotropics (Chave et al. 2006). In addition, Wiemann and Williamson (2002) demonstrated that phosphorus was a better predictor of ϱ variation than MAT. All these studies have demonstrated that there is an inter-specific relationship between ϱ and environmental variables, but intra-specific variation was not examined in these previous studies.

In addition, previous studies of regional intra-specific ϱ variation have detected a tendency for ϱ to increase as phosphorus in tropical forest soils decreases (Wiemann and Williamson 2002, Chave et al. 2006, Swenson and Enquist 2007, Baker et al. 2009, Henry et al. 2010). The model results from this study suggest that intra-specific variation of ϱ is best explained by axes 1 (*PC1*) and 2 (*PC2*) of the results of the PCA soil fertility analysis (Table 4.5). The multi-level analyses also indicate that *DBH* was not a significant variable. This might be explained by the fact that a combination of seasonal and non-seasonal study sites was used in this study. Sun-exposed species in this analysis were composed of tree species, where ϱ both increased and decreased from the pith towards the bark. Similar results were also found in seasonal forest by Henry et al. (2010) in Ghana.

4.5 Conclusion

Studies along elevation gradients can assist in predicting how climate change will affect tropical forests (Malhi et al. 2010). Model studies have suggested that climate change could produce a range of responses in tropical forests, from a dieback of the rainforest due to drought (Cox et al. 2004) to a CO_2 fertilization effect (Huntingford et al. 2013). However, the consequences of climate change are still uncertain, and this study has aimed to contribute to a better understanding of C forest dynamics in the tropics.

Previous studies have documented a decrease in tree stature with increasing elevation, probably as a result of decreases in solar radiation, temperature, and water vapour deficit (Alves et al. 2010), as well as an increase in wind exposure and differences in soil properties (soil compaction, fertility) with elevation (Feldpausch et al. 2010). In this study, linear regressions indicated that the basal area varied significantly with elevation. Above ground biomass decreased with increasing elevation when the wet site was included (Fig. 4.2).

Canopy strata occupancy has been shown in this study to be a significant determinant of ϱ variation. Previous studies have also suggested that ϱ is strongly related to the plant hydraulic conductance of trees and thus to the forest canopy strata occupancy (Poorter et al. 2010). The results suggest that the variation of wood density is divergent for the forest strata occupancy, decreasing with elevation for sun-exposed trees and behaving oppositely for shaded exposed trees.

The diameter at breast height was not significant in the model, but asymptotic regressions suggested that it was a better predictor of wood density than tree height for sun-exposed tree species. Diameter at breast height has also been suggested as a better predictor than tree height in previous studies (Henry et al. 2010). Kendall tau results for sun-exposed tree species (Table 4.4) suggested a decrease of wood density with increasing elevation. In contrast, Kendall tau test for shaded tree species explained an increase of wood density with increasing elevation. This suggests different tree morphology between sun and shade-exposed trees (Poorter 1999, Poorter et al. 2003).

The results of the multi-level modelling suggest that temperature and soil fertility explained a decrease in wood density for sun exposed species and an increase in wood density with elevation for sun-exposed tree species. Similar results were obtained by (Wiemann and Williamson 2002, Baker et al. 2004, Patiño et al. 2009, Alves et al. 2010).

Chapter 5

A model for predicting coarse woody debris residence times in tropical forests along an altitudinal gradient in Australia

5.1 Introduction

Estimates of the total carbon (C) in forests on earth have indicated that tropical forests have a larger reserve of C on average (157 MgC ha^{-1}) than both boreal and temperate forests (53 MgC ha^{-1} and 96 MgC ha^{-1}, respectively) (Watson and Albritton 2001). In pristine forests, living and dead trees are estimated to store approximately 60 % of the total C, while soils and litter pools comprise the remaining approximately 40 % (Russell et al. 2013). Further, coarse woody debris (CWD) represents between 10 % and 20 % of the total plant biomass that is stored by tropical forests (Cornwell et al. 2009). CWD includes standing and fallen dead trees and their remaining branches. It is currently uncertain how climate change might affect CWD C stocks (Russell et al. 2013), particularly in tropical forests.

Previous studies have demonstrated that the atmospheric C pool is gradually increasing due to C release caused by fossil fuel consumption, deforestation, land use change and cement production (Houghton et al. 2009, IPCC 2013). However, the future consequences of this atmospheric increase in C for global C dynamics remain unknown (Phillips et al. 1998, Clark 2004, Fearnside 2004, Lewis et al. 2004, Malhi and Wright 2004, Lewis 2006, Gloor et al. 2009, Lewis et al. 2009a, Chapin III et al. 2011, Grace et al. 2014). To anticipate the effects of climate change on tropical ecosystems, Malhi et al. (2010) suggested using altitudinal gradients as alternatives to laboratory experiments. Temperature varies with elevation, and precipitation might also correlate with elevation, depending on the geography of the terrain.

Carbon in the CWD pool is either returned to the atmosphere through decaying organisms or stored in the soil organic matter pool (SOM). Quantification of CWD production in tropical forests, primarily in Neotropical regions, has generated of estimates between approximately 2.12 and 4.16 MgC ha^{-1} $year^{-1}$ (Malhi and Wright 2004, Chave et al. 2008). CWD decay is caused by different processes. Recent Neotropical studies demonstrated that C loss that occurs through the heterotrophic respiration of CWD via microbial decomposition can be estimated by measuring the diameter of the tree at breast height (*DBH*) and the wood specific density (ϱ) of the CWD (Chao et al. 2009, Hérault et al. 2010).

CWD provides ecological benefits for forest ecosystems. The CWD pool is a significant reservoir of C but contains few nutrients (Laiho and Prescott 1999, Cornwell et al. 2009). The ratio of C:nutrients in wood is high, and gymnosperms exhibit lower concentrations of N, potassium and calcium than angiosperms (Cornwell et al. 2009). In addition, lignin composition differs between angiosperms and gymnosperms: gymnosperms contain only guaiacyl lignin, and angiosperms also contain syringyl lignin; guaiacyl lignin is more resistant to microbial decomposition than syringyl lignin (Cornwell et al. 2009). As the CWD pool decomposes, nutrients and C gradually return to the soil to be reused by plants and other organisms. The residence time of C in the CWD pool depends on various factors: interrelationships between the environmental conditions, the structural and chemical characteristics of the wood, the structural composition of the forests (i.e., the number of trees per hectare and tree height and diameter) and the size of the pool of biotic wood consumers (Cornwell et al. 2009).

The main source of decomposition is believed to be microbial decomposition, which is primarily performed by fungi and may also be performed by bacteria, although sufficient studies have not been performed to confirm the role of bacteria in this process (Cornwell et al. 2009). Fungi that are capable of decaying wood by degrading lignin must produce oxidative enzymes (i.e., either oxygen or peroxide) (Cornwell et al. 2009). The dominant fungal clades involved in this process are Ascomycetes, Basidiomycetes and Zygomycetes, and each clade has different groups with different specializations and different rates of lignin degradation (Cornwell et al. 2009). Thus, plant characteristics, such as wood density, lignin characteristics, structure and chemicals, together with fungal groups will influence the rate at which CWD can decay. Invertebrate organisms, primarily beetles and termites, comprise the second group (i.e., the group after fungi and bacteria) that plays an important role in CWD decomposition (Cornwell et al. 2009). However, beetles do not play a significant role in CWD decomposition in tropical forests. Moreover, a recent study of global CWD trends reported that unlike forests in the Neotropics or Paleotropics, Australian rainforests have a low abundance of invertebrates that consume wood (Cornwell et al. 2009) and that biotic decomposition may be accomplished primarily by microbial decomposition. After consumption by living organisms, physical degradation is the next important determinant of the CWD decay process. Dead wood is decayed via photodegradation, leaching and physical damage (Cornwell et al. 2009).

The physical and chemical properties of soils in combination with the characteristics of the pool of decaying organisms are an important determinant of the CWD decay dynamics. The amount of SOM stored by soils is primarily defined by the CWD residence time (CWDτ) (via chemical and physical decay) and the C stored through the decay process of the roots of dead vegetation. Moreover, nutrients and C turnover will depend on the properties of the soil that stores them and on the environmental variables that favor the activity of the decaying organisms.

Net primary productivity (NPP) is inter-related with the amount of nitrogen (N) that is in the soil and available to the plants. N is an essential element that enables photosynthesis, which is the process that fixes C in plants. The N that is available in soils for plants to consume depends to a certain degree on the proportion of bacteria or fungi present in the soil that are responsible for converting the organic N from the CWD into the nitrate ion form. Studies of the C:N ratio in decaying CWD over time observed an increase in N with increasing sample degradation (Iwashita et al. 2013) in Hawaii and in a sub-tropical forest in China (Yang et al. 2010). The latter study also found that the main drivers of the CWDτ process were soil fertility and decomposer organisms. Thus, studies of C:N ratio differences as a function of time concluded that this parameter is a good indicator of CWDτ, as N increases with sample degradation (Laiho and Prescott 1999, Guo et al. 2006, Olajuyigbe et al. 2011). This increase in N over time is attributed to the N-fixing organisms that colonize dead wood. In addition, decomposing fungi and/or bacteria preferentially colonize more rapidly decayed woods due to their more degraded structure (Cornwell et al. 2009). Therefore, when investigating CWDτ, it is important to study how the C:N ratio changes over time and also to determine the soil nutrient content.

The importance of wood density (ϱ) and environmental parameters for defining the CWDτ has been previously discussed in a small number of publications. CWDτ is directly affected by environmental variables, but the same environmental variables also define the ϱ of the growing tree species to a certain degree. Therefore, CWDτ can be affected directly and indirectly by ϱ. Indirectly, CWDτ is explained by variations in ϱ that occur with changing environmental parameters and therefore, with changing tree species, soil properties, and climate. Researchers confirmed that wood structure is inter-related with the surrounding environment; studies of tropical tree physiology indicated that the wood traits that define ϱ are strongly related to tree growth and the survival rate in the environment (Malhi et al., 2006; Chave et al. 2009; Poorter et al., 2010). For example, spatially, ϱ has been found to decrease with increasing altitude and to decrease in wet forests in comparison to dry forests (Chave et al. 2006). These indirect changes in ϱ and therefore in CWDτ might be modified in the long term and be impacted by the effects of climate change. For instance, Keeling and Phillips (2007) suggested that faster turnover rates of tropical trees, which may occur as a consequence of climate change, would enhance the representation of low ϱ species. In contrast, an additional consequence of climate change may be increasing tree mortality rates that affect forest structure, composition and dynamics (Phillips et al. 2010); according to some recent studies, the tree mortality for low ϱ tropical trees may be increasing due the effects of climate change (Lewis et al. 2009a; Lewis et al., 2009), resulting in an annual biomass C reduction of 1.60 PgC in tropical forests. Thus, recent studies suggested that increases in global temperatures and in tree mortality might result in a gradual modification of the actual forest dynamics, thereby potentially affecting the CWDτ. In addition, evolutionary studies of ϱ across species confirm that angiosperm tree species exhibit larger variations in ϱ than gymnosperms (Swenson and Enquist 2007); therefore; these species might be more susceptible to climate change.

Recent studies estimated that the ϱ of tree species accounts for 74 % of the total variance at the genus level (Chave et al. 2003), but intra- and inter-specific variation in wood traits might also affect the site-level ϱ of the tree species (Eviner, 2004). Consequently, the structural composition of wood varies among species and their associated adaptations to the environment. For example, species that belong to seasonal tropical forests and ecotones are believed to invest in higher ϱ structures to be more efficient in water transport from the roots to the canopy leaves and avoid cell cavitation (Zach et al. 2010).

The direct effects of ϱ on CWDτ are felt in the amount of time required to decay different wood structures that originate from dissimilar tree species. Tropical forests are highly diverse in terms of tree species and exhibit a wide range of ϱ in comparison to temperate forests, thereby creating a large uncertainty in C sink/source estimations. Denser woods will require more time to decay than less dense woods. However, the actual mechanisms are not completely understood. The physical and chemical composition of the wood is also directly related to the CWDτ. For instance, studies have found a strong relationship between vessel diameter/density and ϱ in forest species. Wood is primarily composed of cellulose and lignin, along with other non-structural secondary chemical components that are responsible for defining other properties of the wood, such as color, odor and luster (Hoadley, 1990). These secondary components that are present in the heartwood of some tree species, such as xanthones or tannins, can be toxic to decaying organisms, causing an increase in the CWDτ in comparison to toxin-free species with similar ϱ values. Therefore, species with similar ϱ values might exhibit different CWDτ due to the presence of minor secondary compounds. This effect might be more notable in fresh woods or woods that have not been exposed to decaying organisms for a long period of time. In addition, within individual trees, toxic components typically increase from the bark toward the heartwood, while the sapwood is richer in sugars and therefore more easily degradable (Harmon 1986, Cornwell et al. 2009).

Malhi et al. (2010) described elevation gradients in tropical forests as field laboratories for studying the potential effects of climate change on these ecosystems. This study aimed to improve our understanding of the dynamics of the CWD pool in tropical Australian forests to predict the long-term effects of climate change on C cycle dynamics. Altitudinal gradients can be used as natural laboratories because climate variables, such as temperature, vary naturally with increasing site elevation, providing an opportunity to observe the effects of climate on τ. To describe the mechanisms that influence the CWDτ, several authors attempted to explain the interactions between annual net primary productivity and CWD pool dynamics. The results demonstrated that the τ is more strongly affected by soil fertility than by climate, with CWDτ increasing in progressively more weathered soils across datasets from the Neotropics and Paleotropics (Galbraith et al. 2013).

An additional study that was located in non-tropical Australian forests and focused on CWDτ as a function of different tree species and tree diameters, concluded that τ was primarily related to temperature, which accounted for up to 34 % of the total variation (Mackensen et al., 2003). Temperature was followed in importance by initial ϱ and the diameter of the logs (Mackensen et al. 2003); however, soil fertility was not included as a variable in that study. Similarly, in the Neotropics, Hérault et al. (2010) also concluded that ϱ and tree diameter were the main predictors of the CWD decay rate. In addition, one study of a tropical Hawaiian forest concluded that CWD C storage was negatively related to mean annual temperature (MAT), as CWD C storage values varied from 12.2 MgC ha^{-1} at 13 °C to 104.6 MgC ha^{-1} at 18.2 °C and represented approximately 17 % of the total above ground C storage (Iwashita et al. 2013). Temperature in combination with humidity has also been related to the CWDτ; colder and drier climates were found to inhibit microbial activity, while warmer, more humid climates enhanced microbial activity (Cornwell et al. 2009). In addition, studies conducted in dry climates observed that the CWDτ was primarily controlled by the physical breakdown of the wood. Therefore, climate is an important driving variable that defines the CWDτ in tropical forests. Thus, the small number of studies conducted in Australia in comparison to other well-studied areas, such as the Neotropics, reinforces the current need for additional studies in Australia.

In this study, we aimed to quantify the processes that control CWDτ in relation to environmental variables and plant wood traits along an altitudinal gradient. This approach allows us explore the possible effects of climate change on the CWD pool in tropical forests in the near future. Specifically, we addressed the following questions:

a) How does CWDτ vary with increasing site altitude (i.e., temperature)?
b) How does CWDτ vary among different species with a wide range of wood densities?
c) How will the C:N ratio change over time? How is this parameter related to wood density?
d) What are the effects of seasonality on CWDτ?

The results were obtained from a study that was performed in tropical forests in Australia, where soils originate from the same parent material. In addition, the CWDτ of seven species with a wide range of ϱ was estimated after one wet season (i.e., after six months of exposure) and after 15 months of exposure to the field conditions to study the gradual decay of the samples over time.

5.2 Materials and methods

5.2.1 Study sites

The study was conducted along an elevation gradient ranging from 102 m to 1500 m above sea level (asl) in North East Queensland, Australia (Table 5.1; Fig. 5.1). The study sites were located at the top (BK-T; 1,500 m elevation) and bottom (BK-B; 102 m elevation) of Mt. Bellenden Ker in Wooroonooran National Park and near Charappa Creek in Wooroonooran National Park (CHA; 720 m elevation). The BK-T site receives an average annual precipitation (MAP) of 8,150 mm, has a MAT of 16.7 °C and has no dry months, which are defined as months in which the potential evapotranspiration exceeds precipitation and are also indicated using dry season length (DSL). The CHA site has a MAP of 3337 mm, has a MAT of 20.6 °C and has a dry season length (DSL) of 4 months. The BK-B site has a MAP of 4682 mm, has a MAT of 23.7 °C and has a DSL of 2 months. The parent soil material for all of the study sites is granite, according to the base map from the Department of Mines and Energy in Queensland, Australia's National Mapping Agency, 1984, Innisfail, sheet SE 55-6). The size of the study plots was 1,000 m^2, and the sites were established as long-term monitoring sites by Commonwealth Scientific and Industrial Research Organisation in 2007 (CHA) and 2010 (BK-T and BK-B).

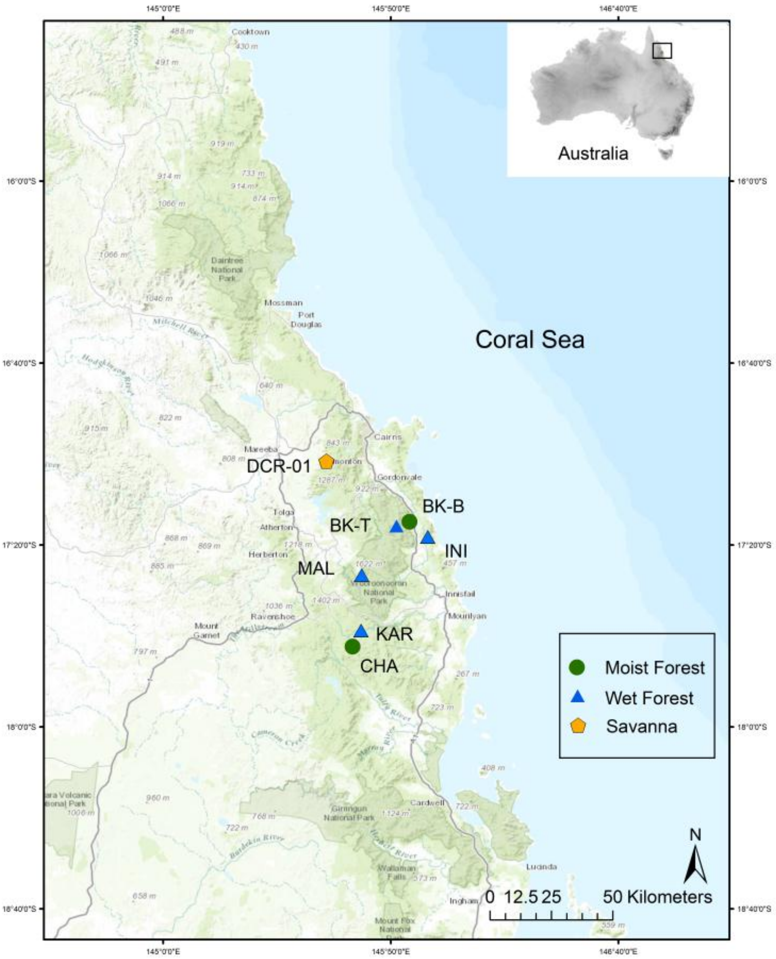


Fig. 5.1. Map of the main study sites and the collection study sites. Forest classifications are presented according to (Chave et al. 2005)Chave et al. (2005).

Table 5.1. Location and climatic descriptors in the study sites. Latitude (Lat.), longitude (Long.), elevation (m), dry season length (DSL), mean annual temperature (MAT), mean annual precipitation (MAP), mean temperature of the wettest quarter (TWQ), mean temperature of the driest quarter (TDQ) and sum of the precipitation *Pm* from November 2011 to May 2012 and P_f from May 2012 to February 2013. Climatic data is from the Australian Bureau of Meteorology for the study sites and from wordclim.org for the extra collection sites.

Site	Lat.	Long.	Elev. (m)	DSL	MAP (mm)	MAT (°C)	TWQ (°C)	TDQ (°C)	Sum PPT (mm) Nov. to May 2012 (*Pm*)	Sum PPT (mm) May to Febr. 2013 (*Pf*)
Study sites										
BK-T	-17.264	145.853	1500	0	8150	16.7	19.4	15.3	5847	3516
CHA	-17.705	145.693	720	4	3337	20.6	23.4	19.2	3158	1668
BK-B	-17.254	145.905	102	2	4682	23.7	26.3	22.2	4658	1950
Extra collection sites										
KAR	-17.647	145.724	510	4	2707	21.7	n/a	n/a	n/a	n/a
MAL	-17.443	145.726	620	4	2684	20.8	n/a	n/a	n/a	n/a
INI	-17.303	145.968	83	2	4682	23.7	n/a	n/a	n/a	n/a
DCR-01	-17.026	145.597	683	5	2050	21.2	n/a	n/a	n/a	n/a

During the field collection of the wood samples, it proved impossible to find species that ranged from light to dense woods to complete the dataset in the designated study sites. To fill this gap, it was necessary to utilize complementary collecting sites that had similar elevations and climatic settings as the three main study sites. The site near Kaaru Creek in Wooroonooran National Park (KAR) was 510 m asl and was located within 5 km of CHA, with granite as a parent soil material. The MAL site was located off of Towalla Rd., next to Topaz, in Wooroonooran National Park; this site was at 620 m asl, with parent soil materials composed of metasediments and quartzite. The INI site was located next to Innisfail at 83 m asl, with a metamorphic parent soil material.

An additional savanna collection site was also selected to obtain wood samples from *Eucalyptus* sp. The site was located in the Davies Creek National Park (DCR-01), with an elevation of 683 m asl (Torello-Raventos et al. 2013). Data for the species *Eucalyptus* sp. are not included in later model analyses due to the large difference in wood structural characteristics (Choat et al., 2007) between savanna and forest species, but the results are included in the tables.

Climate data for the study sites (Table 5.1) were obtained from the website www.worldclim.org (Hijmans et al. 2004)(Hijmans et al., 2004), except for monthly precipitation values, which were obtained from the Australian Bureau of Meteorology from weather stations located 50 m from the BK-T site, 6 km from CHA and 2.5 km from BK-B; all stations were at a similar altitude. The structural and floristic composition of the study sites varied along the elevation gradient (Table 5.2). As explained in Table 5.2 tree density increased and individual tree diameter decreased with increasing elevation. This structural forest variation results from the adaptation of forest ecosystems to changing environmental variables along the transect.

Table 5.2. Characteristics of the study sites. Number of trees (ha^{-1}), above ground biomass (*B*) according to Chave et al. (2005) ($Mg\ ha^{-1}$), basal area (*A*) ($m^2\ ha^{-1}$), average of tree diameter for stems bigger than 10 cm diameter and Shanon Diversity Index.

Study site	Num. trees (ha^{-1})	*B* (Mg dry mass ha^{-1})	*A* ($m^2\ ha^{-1}$)	Avg. of *DBH* (cm)	Shanon Div. Index
BK-T	640	73.04	15.9	17.44	2.7
CHA	1280	407.1	58.66	21.19	3.68
BK-B	450	526.02	42.92	31.22	2.97

5.2.2 Species selection, wood density, CWDτ and decay classes

Decay status classification

Decay status (*DS)* was assessed using three of the five classes defined by Harmon (1986 and 1995). The number of classes was limited to the first, last and intermediate categories of that classification to simplify the sampling procedure. The first class was defined as fresh wood samples (W_F) and was composed of samples from living trees or recently fallen timber that still had leaves or twigs attached. The second class was characterized by mid-decayed wood samples (W_M) from dead trees in which the wood structure was still firm and tree bark was still present but no attached leaves or twigs were present. The final class included decayed wood samples (W_D) from trees whose structure was no longer firm and whose bark was already decayed or absent. The samples collected at the pre-established sites represent tagged trees that had fallen since plot establishment (i.e., within 4 years (CHA, KAR) or within 1.5 years (BK-T and BK-B)).

Wood density and DS

Different species were collected across a broad range of ϱ (400 kg m^{-3} < ϱ < 1100 kg m^{-3}) throughout the study sites and the complementary sites. The criteria for the selection of these species were defined according to site occurrence, except for the species *Balanops australiana*, which was present from lowland to montane forests. At some sites, W_M and W_D were not physically present; thus, the datasets for these parameters were less complete than the dataset for W_F.

The most common tree species along the elevation gradient (i.e., *B. australiana*) was selected to study the intra-specific variation of CWDτ in relation to site-specific plant traits (Table 5.3). In addition, the tree species *Franciscodendron laurifolium*, which was common at two sites, was selected for the same purpose.

Table 5.3. Summary of all species collected at different elevations and the status of those species at the time of collection. W_F indicates fresh samples, W_M indicates mid-decayed samples and W_D indicates decayed samples.

			Elev. (m)	
Family	**Species**	**1500**	**510-683**	**100-102**
Myrtaceae	*Backhousia bancroftii*			$W_{F,M,D}$
Balanopaceae	*Balanops australiana*	$W_{F,M,D}$	$W_{F,M,D}$	$W_{F,M,D}$
Lauraceae	*Cryptocarya oblata*		$W_{F,M}$	
Elaeocarpaceae	*Elaeocarpus ferruginiflorus*	$W_{F,M}$		
Malvaceae	*Franciscodendron laurifolium*		$W_{F,M}$	$W_{M,D}$
Myrtaceae	*Leptospermum wooroonooran*	$W_{F,M,D}$		
Myrtaceae	*Eucalyptus* sp.		W_F	

The list of the tree species collected for each *DS* class and the range of ϱ that was observed for each species are summarized in Table 5.4.

Table 5.4. Ranges of the wood density values obtained for all of the trees species collected in each decay status class.

Decay status	*Tree species*	*Range of* ϱ
W_F		
	Backhousia bancroftii	$710\ \mathrm{kg\ m^{-3}} < \varrho < 960\ \mathrm{kg\ m^{-3}}$
	Balanops australiana	$780\ \mathrm{kg\ m^{-3}} < \varrho < 960\ \mathrm{kg\ m^{-3}}$
	Cryptocarya oblata	$850\ \mathrm{kg\ m^{-3}} < \varrho < 960\ \mathrm{kg\ m^{-3}}$
	Elaeocarpus ferruginiflorus	$290\ \mathrm{kg\ m^{-3}} < \varrho < 570\ \mathrm{kg\ m^{-3}}$
	Franciscodendron laurifolium	$490\ \mathrm{kg\ m^{-3}} < \varrho < 640\ \mathrm{kg\ m^{-3}}$
	Leptospermum wooroonooran	$820\ \mathrm{kg\ m^{-3}} < \varrho < 1090\ \mathrm{kg\ m^{-3}}$
	Eucalyptus sp.	$870\ \mathrm{kg\ m^{-3}} < \varrho < 1040\ \mathrm{kg\ m^{-3}}$
W_M		
	Backhousia bancroftii	$410\ \mathrm{kg\ m^{-3}} < \varrho < 460\ \mathrm{kg\ m^{-3}}$
	Balanops australiana	$440\ \mathrm{kg\ m^{-3}} < \varrho < 900\ \mathrm{kg\ m^{-3}}$
	Elaeocarpus ferruginiflorus	$210\ \mathrm{kg\ m^{-3}} < \varrho < 430\ \mathrm{kg\ m^{-3}}$
	Franciscodendron laurifolium	$390\ \mathrm{kg\ m^{-3}} < \varrho < 540\ \mathrm{kg\ m^{-3}}$
	Leptospermum wooroonooran	$350\ \mathrm{kg\ m^{-3}} < \varrho < 730\ \mathrm{kg\ m^{-3}}$
W_D		
	Backhousia bancroftii	$150\ \mathrm{kg\ m^{-3}} < \varrho < 380\ \mathrm{kg\ m^{-3}}$
	Balanops australiana	$340\ \mathrm{kg\ m^{-3}} < \varrho < 730\ \mathrm{kg\ m^{-3}}$
	Franciscodendron laurifolium	$430\ \mathrm{kg\ m^{-3}} < \varrho < 490\ \mathrm{kg\ m^{-3}}$
	Leptospermum wooroonooran	$520\ \mathrm{kg\ m^{-3}} < \varrho < 670\ \mathrm{kg\ m^{-3}}$

Sample preparation and processing

Wood density was calculated according to $\varrho = m/v$, where m is the dry weight of the sample and v its associated fresh or green volume. After the physical collection of the logs, the wood samples were systematically cut to a size of $2.5\ \mathrm{cm}^3$ per side using an industrial saw to obtain smooth cubes; this process allowed standardization of the decay process and to obtain results after a relatively short time. After preparation, the cubes were sterilized at 121 °C for 20 minutes using an autoclave to avoid biological cross-contamination and to provide the samples with the same "substrate" conditions for microbial re-population of the material at each field site. Previous research concerning the application of autoclaving to soils demonstrated that this technique reduces or eliminates the presence of N by evaporation (Serrasolsas and Khanna, 1995). After the autoclaving process, the wood samples were dried at 60 °C to obtain a constant weight. The volume was measured by using an electronic digital calliper (0.01-mm resolution) of 50 cm length (ISO 9001).

For field deployment, matrices were constructed from PVC pipes with a 5 cm diameter, such that each cube was separated from the other cubes but in direct contact with the soil surface. The top and bottom of the pipes were covered with a polyester net (diameter 1 mm) to limit the possibility of sample loss and disturbance by large organisms. To allow the ingress of invertebrates into the pipes, two holes were made in the nets using a 5 mm metal stick. Three replicates of every sample (Table 5.3) were randomly placed into the matrices. In total, three matrices, which each contained three replicates of all starting materials from each reference elevation site, were placed randomly at the three main study sites in November 2011. Figure 5.2 illustrates the design of the matrices and their placement in the field.

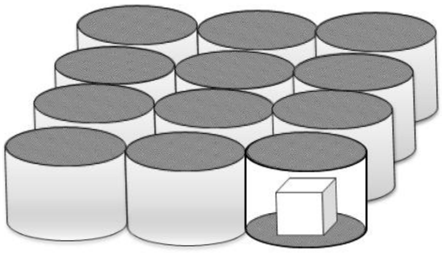


Fig. 5.2. Design of the sample matrices and positioning of the samples in the field.

The first sets of samples were collected in June 2012 at the BK-B and CHA sites after the end of the wet season (i.e., after six months of exposure, from November 2011 to May 2012) and the second sets of samples were collected on March 2013 at the BK-T, BK-B and CHA sites (i.e., after 15 months of exposure, from November 2011 to February 2013). As listed in Table 5.1, the year 2013 had a relatively dry wet season (*Pf*) in comparison to previous years (*Pm*).

5.2.3 CWD residence time (τ) index calculation and C and N concentrations

The sample cubes were dried to a constant weight at 60 °C and then weighed to calculate mass loss by drying the samples before and after placement in the field at the study sites (Baker et al. 2007). The annual CWD decay rate (k) was calculated (Galbraith et al. 2013) by applying a decay exponential function that relates the amount of mass lost over time, assuming a constant weight loss over time:

$$k_t = \frac{\ln W_f - ln\, W_i}{t_f - t_i} \qquad \text{Eqn. 1}$$

where W_i and W_f are the weight of the dried sample at the start of the experiment and after the collection of the samples from the field, respectively. t_i and t_f are the times in years between the deployment and collection of the samples. CWD τ was calculated as the inverse function of the k, where CWDτ is the CWD residence time in years after half of a year CWDτ_m and after one year CWDτ_f.

The dried cubes were subsequently milled to a powder. The C and N concentrations for the control cube (C_i and N_i), samples that were exposed to field conditions for six months (C_m and N_m) and for fifteen months (C_f and N_f) were determined by dry combustion using an elemental analyser (Costech 4010 CHNS-0, Valencia, CA, U.S.A). The amounts of N and C in the control samples at the start of the experiment were N_i and C_i, respectively; for the samples collected after six months, these values were N_m and C_m, respectively, and for the samples collected after fifteen months, these values were C_f and N_f, respectively.

5.2.4 Soil sampling and preparation

At each study site, five soil cores were extracted from the first 30 cm of depth. The soil samples were weighed in the field and after oven drying at 60 °C. The dried soils were sieved to separate the roots and gravel > 2 mm diameter. A subsample of the sieved soil was ground using a ring mill (Rocklabs, Onehunga, New Zealand). A weighed aliquot was used to determine C and N concentrations by dry combustion in an elemental analyser (Costech Analytical Technologies, Valencia, CA, U.S.A.). The samples were analyzed by Research Laboratories Limited Laboratories (Awatoto, New Zealand) for pH, cation exchange capacity (CEC), electrical conductivity, and levels of N, phosphorus, sulfate, potassium, magnesium, calcium, sodium and aluminum.

5.2.5 Statistical analysis

Nonlinear regression

All analyses were performed using the R statistical platform with the package *stats*. Exponential regression was used to estimate the relationships between CWDτ_f, C:N and ϱ across different *DS* classes and along the altitudinal gradient. Regression and analysis of variance were performed using the same packages.

Multilevel model

The dataset in this study presented nested sources of variability along the altitudinal gradient. Multi-level analyses were chosen in this study because this analysis allows the data to be tested without assuming homogeneity of regression, in contrast to analysis of covariate. In addition, this analysis allows for the analysis of nested data with many levels. We used the packages *lme4* and *nlme* to develop the multilevel models.

The model was developed separately for every *DS*. First, a linear regression model was tested for its ability to explain CWDτ_f versus ϱ and *DS* as a function of altitude. Then, a multilevel analysis was performed. Initially, a null model was created using tree species as a random factor to study the amount of the total variance that was explained by species; this model is described as:

$$\tau_{ms} = \gamma + U_s + R_{ms} \tag{1}$$

where CWDτ_{ms} is the residence time index for the individual measurements m for cubes from different tree species s, γ is an average term for each of the separate models W_F, W_M and W_D, U_s is the random intercept variable that indicates the variation between tree species and R_{ms} is the residual at the individual level. Thereafter, a multi-level analysis was developed to study CWDτ_f variations by adding a plot-dependent deviation or fixed effects. We did not use temperature, as continuous variable measurements were only collected at three study sites. These calculation are described as:

$$\tau_{ms} = \gamma + \beta_1 S_{ms} + U_s + R_{ms} \tag{2}$$

where $\beta_1 S_{ms}$ is a slope term that can vary between plots. Thereafter, only the significant covariate terms that were not dropped from the model during the process of finding the optimal variance structure were used; thus, only ϱ and C:N were added, as follows:

$$\tau_{ms} = \gamma + \beta_1 S_{ms} + \beta_2 \varrho_{ms} + \beta_3 C{:}N_{ms} + U_s + R_{ms} \tag{3}$$

where $\beta_2 \varrho_{ms}$ is the slope term for ϱ and $\beta_3 C{:}N_{ms}$ is the slope term for the C:N ratio.

Centering of the C:N and wood density

The full dataset for W_F varied between $-234.34 < \text{C:N} < 322.24$ and -490 kg m^{-3} $< \varrho <$ 310 kg m^{-3}. For W_M, the data varied between $-136.26 < \text{C:N} < 316.67$ and -320 kg m^{-3} $< \varrho <$ 360 kg m^{-3}, and for W_D, the data varied between $-124.60 < \text{C:N} < 331.95$ and -320 kg m^{-3} $< \varrho <$ 260 kg m^{-3}. Both explanatory variables were centered on their respective means to make the computations more efficient and to make the interpretation of the model coefficients easier (Snijders and Bosker 1999). The model intercept (γ) then gives the average CWDτ for the average of the C:N and ϱ terms for a given reference site (i.e., in this study, BK-B).

Model validation

The heteroscedasticity of the model residuals was tested at level two for the two random effects the intercept and the slope; these effects are usually correlated (Snijders and Bosker

1999)(Snijders and Bosker, 1999). The residuals were plotted against the fitted values of τ for the three models (i.e., W_F, W_M and W_D).

5.3 Results

The CWD residence time (CWDτ) was calculated as the inverse of the total mass loss of the dry weight over time. CWDτ was measured to determine the physical degradation of the wood samples. CWDτ was studied over time with respect to the following parameters for each decay class (*DS*): elevation, seasonality, ϱ and C:N. First, regressions were plotted to study how CWDτ varied over time separately for each parameter, with the purpose of studying inter-relationships between variables. A multilevel analysis was subsequently performed to select the significant variables that explained the CWDτ variations for each *DS* over time. We then studied the effects of elevation versus intra-specific variation of ϱ across the study sites. The aim was to determine whether environmental variables were more important than wood characteristics (ϱ) when explaining CWDτ.

5.3.1 CWD residence time in relation to site elevation, wood density and carbon:nitrogen ratio.

The effects of elevation

CWDτ values were compared according to site elevation separately for the samples collected after 6 months in the field (CWDτ_m) and after 15 months in the field (CWDτ_f) to study how site elevation (temperature) affects CWD decomposition. The CWDτ_f results for the same tree species and *DS* class along the altitudinal gradient (Table 5.5) exhibited a positive relationship with site elevation. For example, *F. laurifolium* samples with a *DS* of W_F that were collected at the KAR site had an average ϱ of 610 kg m^{-3} at BK-T, 530 kg m^{-3} at CHA and 590 at BK-B kg m^{-3}, and the calculated CWDτ_f values were 7.5 years, 3.2 years and 2.8 years, respectively. These results reveal a significant difference in CWDτ_f among the study sites on the elevation transect ($p < 0.005$).

Table 5.5. Range of wood density values and CWD residence times. Samples collected after 6 months (τ_m) and after 15 months in the field (τ_f) at all study sites.

		BK-T	CHA		BK-B	
Species	Range of wood density (kg m^{-3})	τ_f	τ_m	τ_f	τ_m	τ_f
Backhousia bancroftii						
W_F	710 kg m^{-3}< ϱ < 960 kg m^{-3}	26.5	5.3	9.7	4.8	12.5
W_M	410 kg m^{-3}< ϱ < 460 kg m^{-3}	5.0	1.9	1.6	1.4	1.4
W_D	150 kg m^{-3}< ϱ < 380 kg m^{-3}	1.1	0.8	1.2	0.6	1.2
Balanops australiana						
W_F	780 kg m^{-3}< ϱ < 960 kg m^{-3}	6.7	2.4	4.1	2.1	3.6
W_M	440 kg m^{-3}< ϱ < 900 kg m^{-3}	7.2	2.8	3.8	2.1	3.2
W_D	340 kg m^{-3}< ϱ < 730 kg m^{-3}	4.0	2.2	2.9	1.6	2.5
Cryptocarya oblata						
W_F	850 kg m^{-3}< ϱ < 960 kg m^{-3}	45	5.1	14.6	4.4	8.6
Elaeocarpus ferruginiflorus						
W_F	290 kg m^{-3}< ϱ < 570 kg m^{-3}	3.5	1.6	3.3	1.3	2.0
W_M	210 kg m^{-3}< ϱ < 430 kg m^{-3}	3.1	1.7	2.0	1.8	2.0
Franciscodendron laurifolium						
W_F	490 kg m^{-3}< ϱ < 640 kg m^{-3}	7.5	2.5	3.2	2.5	2.8
W_M	390 kg m^{-3}< ϱ < 540 kg m^{-3}	5.3	2.2	3.8	2.2	2.6
W_D	430 kg m^{-3}< ϱ < 490 kg m^{-3}	5.6	2.1	2.8	1.8	2.4
Leptospermum wooroonooran						
W_F	820 kg m^{-3}< ϱ < 1090 kg m^{-3}	22.0	5.0	13.8	4.4	12.4
W_M	350 kg m^{-3}< ϱ < 730 kg m^{-3}	8.2	3.7	7.2	3.7	5.5
W_D	520 kg m^{-3}< ϱ < 670 kg m^{-3}	8.0	3.4	5.5	2.5	3.0
Eucalyptus sp.						
W_F	870 kg m^{-3}< ϱ < 1040 kg m^{-3}	29.7	4.8	23.2	4.5	13.5

The effects of wood density

The CWDτ_m and CWDτ_f results were studied for all of the tree species between the decay classes (defined as W_F, W_M and W_D) at each study site to determine how differences in ϱ affected the CWDτ. The CWDτ_m and CWDτ_f results exhibited a positive relationship with ϱ within a given *DS* class for all six forest tree species (Fig. 5.3 a, c and e for CWDτ_m and b, d and f for CWDτ_f). For example, in Table 5.5, *Backhousia bancroftii* had average ϱ values at the BK-T site of 820 kg m^{-3} for W_F, 430 kg m^{-3} for W_M and 270 kg m^{-3} for W_D and τ_f values of 26.46 years, 5.02 years and 1.08 years, respectively.

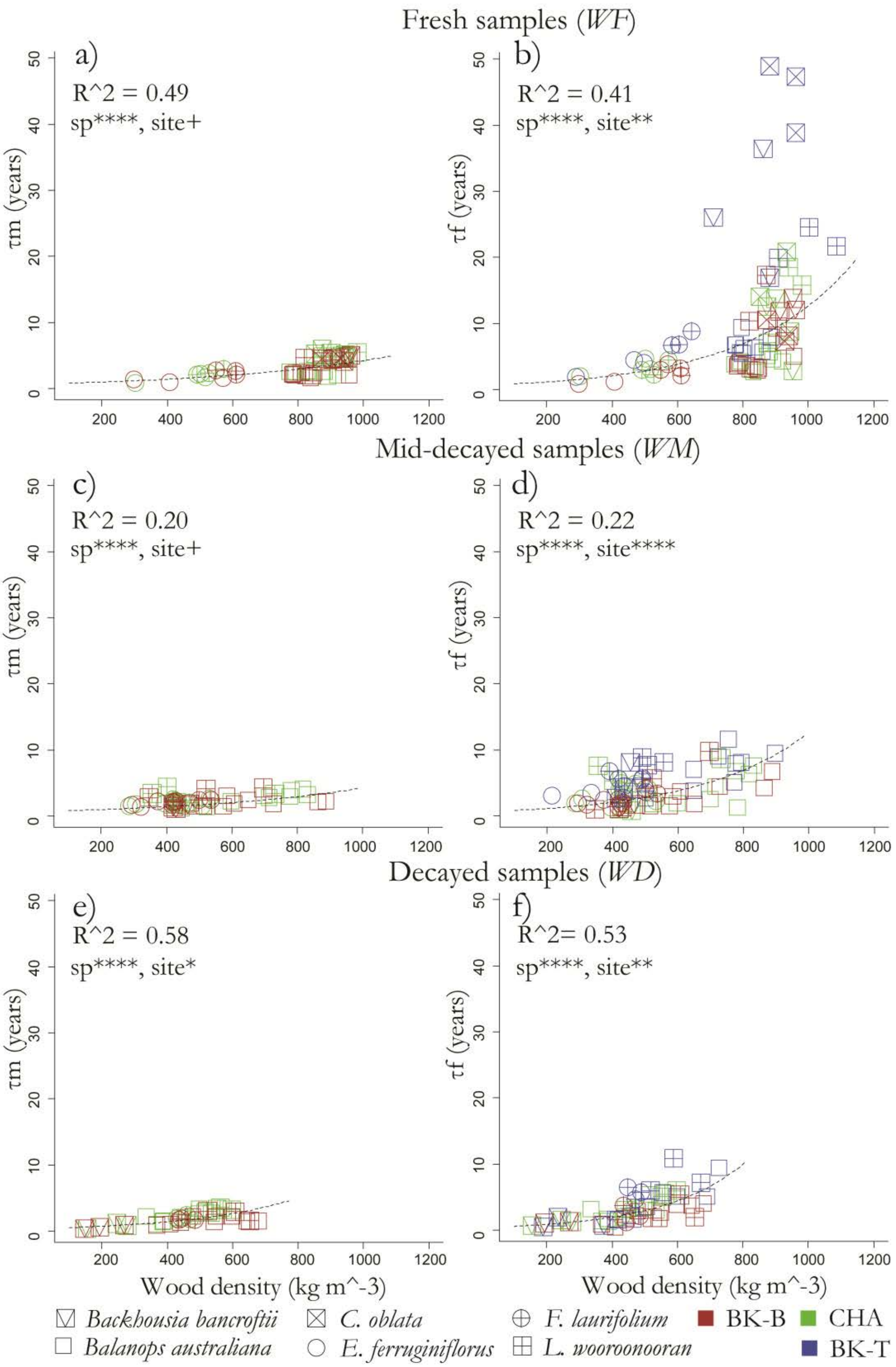


Fig. 5.3. CWDτ for the samples collected after 6 months and 15 months in the field ($\tau_{m,f}$) versus wood density for the different decay classes (i.e., W_F, W_M and W_D). *** significant at 0.05, ++significant at 0.1.

Figure 5.3 b also indicated that for tree species within the decay class W_F that presented similar ϱ values (for example, between 600 kg m^{-3} and 800 kg m^{-3}), CWDτ_f ranged between 2 years and nearly 50 years. This variation might explained the structural and chemical differences of the wood that exist between tree species. This range of CWDτ_f is more pronounced in fresh wood (W_F) than in mid-decayed (W_M) and decayed wood (W_D), as both the structure and chemicals of fresh wood remain unprocessed by decomposing organisms (Fig. 5.3 d, f).

The effects of seasonality

The CWDτ_m (i.e., after 6 months in the field during the wet season) and CWDτ_f (i.e., after 15 months in the field, including the previous wet season and one dry season) results were compared to observe differences in the CWDτ in relation to seasonal changes in the environmental conditions (i.e., total moisture content of the wood and temperature). A comparison of CWDτ_m and CWDτ_f between the CHA and BK-B study sites suggested that decomposition during the wet season was much faster than decomposition during the dry season (Table 5.5). For example, for the tree species *B. bancroftii* at the CHA site, W_F had a τ_m of 5.31 and a τ_f of 9.7 years; at the BK-T site, W_F had a τ_m of 4.83 and a τ_f of 12.5 years.

The effects of the carbon:nitrogen ratio

With respect to N dynamics, previous studies demonstrated an increase in N content over time during the decaying process of CWD (Iwashita et al., 2013; (Yang et al. 2010). This study aimed to determine the relationship between mass loss over time and the evolution of the C:N over time, elevation and ϱ.

Wood samples collected at the end of the experimental period (i.e., 6 months and 15 months) were analyzed for C and N content (C:N_m and C:N_f, respectively). The results were compared to the C and N content values of the samples that were previously placed in the field (i.e., control samples C_i and N_i) and that were previously autoclaved to destroy all living organisms.

C_i [%] exhibited a gradual decrease within ϱ and *DS* classes ($p < 0.01$) (Table 5.6). For example, the species *B. bancroftii* had C_i values of 49.29 [%] for W_F, 45.26 [%] for W_M and 44.37 [%] for W_D. The concentrations of N_i [%] were very low for the control cubes and had no initial relationship with ϱ (Table 5.6). The observed differences in N_i concentrations between samples with different ϱ and *DS* were not statistically significant ($p > 0.1$). In contrast, the variations in C:N_i that occurred across *DS* classes were statistically significant ($p < 0.01$).

Table 5.6. Carbon and Nitrogen concentrations over time in the study sites. Initial C concentrations (C_i) and C:N for the initial samples ($C{:}N_i$) and the samples collected after 6 months ($C{:}N_m$) and 15 months ($C{:}N_f$).

	Control		**BK-T**		**CHA**		**BK-B**	
Species	**C_i [%]**	**$C{:}N_i$**	**$C{:}N_m$**	**$C{:}N_f$**	**$C{:}N_m$**	**$C{:}N_f$**	**$C{:}N_m$**	**$C{:}N_f$**
Backhousia bancroftii								
W_F	49.29	325	n/a	234	327	285	311	278
W_M	45.26	534	n/a	243	366	106	233	170
W_D	44.37	477	n/a	79	128	94	118	89
Balanops australiana								
W_F	46.41	877	n/a	381	487	303	363	261
W_M	46.27	526	n/a	314	452	233	292	213
W_D	45.71	411	n/a	192	447	192	207	136
Cryptocarya oblata								
W_F	48.13	345	n/a	366	376	391	470	251
Elaeocarpus ferruginiflorus								
W_F	46.39	313	n/a	141	165	149	207	109
W_M	46.19	311	n/a	140	178	108	223	118
Franciscodendron laurifolium								
W_F	47.56	339	n/a	199	240	188	297	192
W_M	46.63	258	n/a	156	194	126	197	111
W_D	46.13	322	n/a	179	211	120	211	222
Leptospermum wooroonooran								
W_F	47.85	514	n/a	400	547	503	413	415
W_M	47.49	649	n/a	291	463	333	348	289
W_D	48.67	445	n/a	288	467	290	302	177
Savanna sp.								
W_F	46.71	917	n/a	786	1138	1569	1105	655

C_f concentrations were unrelated to ϱ (Appendix Chapter 5, Tables 1 and 2) (Fig. 5.4 a, d and g). N_f concentrations increased within species with decreasing *DS* (Appendix Chapter 5, Tables 1 and 2) (Fig. 5.4 c, f and i). For example, samples of the species *B. australiana* that were collected at BK-T had values of 0.13 %, 0.14 % and 0.22 % for W_F, W_M and W_D, respectively. In addition, the results indicate that N_f was higher for W_D than for W_M and W_F- for samples with similar ϱ (Fig. 5.4 c, f and i). The results also indicate positive relationships between N_m and N_f and site elevation (Fig. 5.4 c, f and i). For example, *B. australiana* had N_f concentrations of 0.13 %, 0.14 % and 0.18 % at the study sites BK-T, CHA and BK-B, respectively (Appendix Chapter

5, Tables 1 and 2). Statistical analysis of variance revealed significant differences in N_f concentrations between sites ($p < 0.005$).

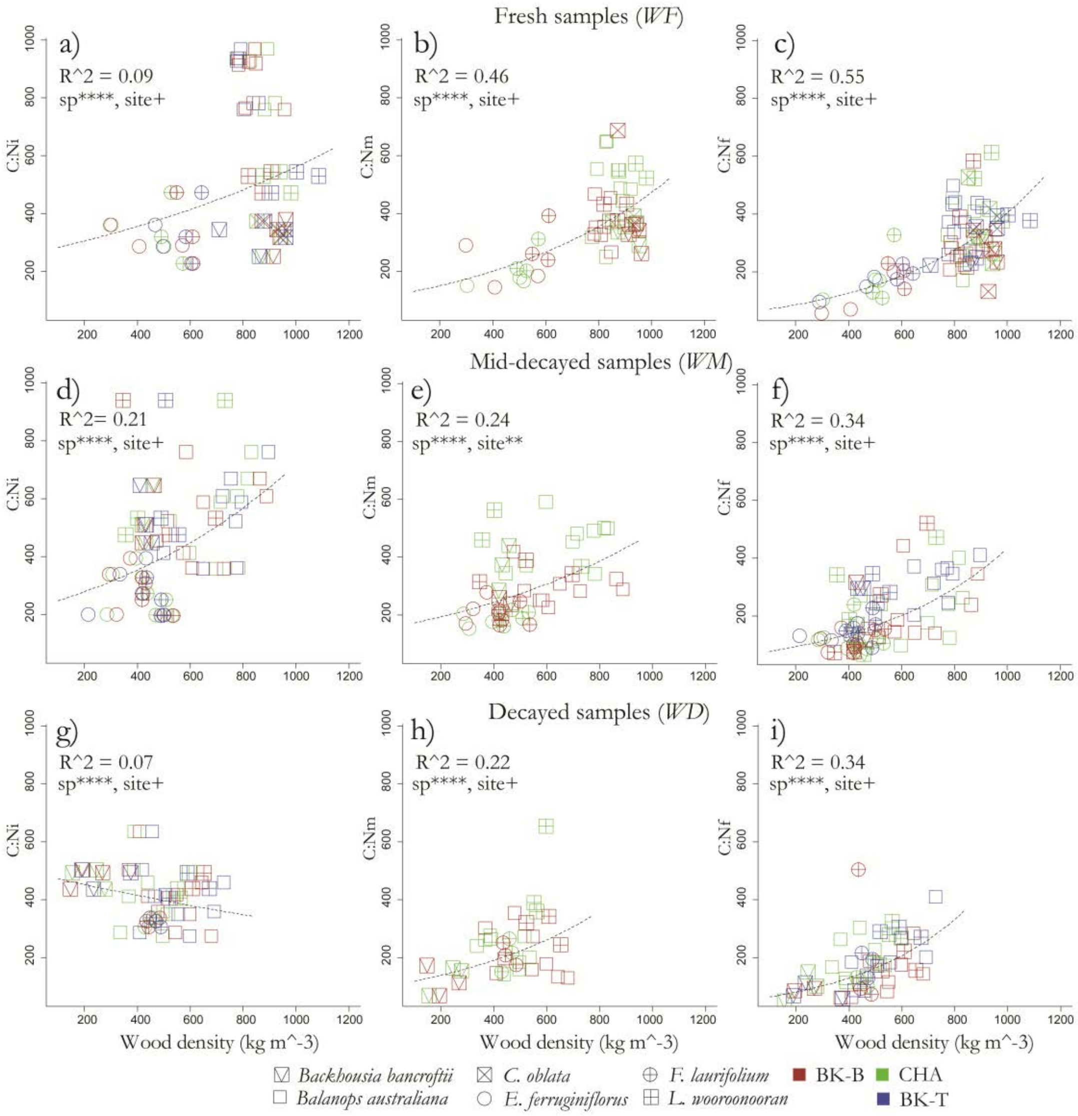


Fig. 5.4. C:N for the initial samples and the samples that were in the field for 6 months and 15 months ($C:N_{i,m,f}$) plotted versus wood density for all decay classes (i.e., W_F, W_M and W_D). *** significant at 0.05, ++significant at 0.1.

The $C:N_{m,f}$ ratio was defined by the amount of $N_{m,f}$ that accumulated in the CWDτ over time, as $C_{m,f}$ had a small range of variation over time (Appendix Chapter 5, Table 2). The results indicate that the $C:N_f$ ratios decreased with an increasing degree of decay of the cubes (i.e., from W_D towards W_F) (e.g., *B. bancroftii* at CHA had $C:N_f$ values of 285 for W_F, 106 for W_M and 94 for W_D). In addition, within species, the $C:N_{m,f}$ ratio tended to decrease with decreasing site elevation (Table 5.6). For example, *B. australiana* had $C:N_f$ values of 381 at BK-T, 303 at CHA and 261 at BK-B.

In addition, the data indicate that the C:N$_f$ values are lower than the C:N$_m$ values. For example, at the CHA site, *B. bancroftii* W_F has a C:N$_m$ of 327 and a C:N$_f$ of 285; at the BK-B site, these values are 311 and 278, respectively (Table 5.6).

The results also revealed a strong relationship between CWDτ_f and C:N$_f$ (Fig. 5.5 d, h and l). Figure 5.5 demonstrates that N$_f$ also has a strong relationship with CWDτ_f. When the wood samples stay in the field longer, the N$_f$ concentrations decrease. The relationships between CWDτ_f and C:N$_f$ and N$_f$ are stronger with increasing *DS*. For example, for W_D, the relationship between CWDτ_f and C:N$_f$ was 0.65, for W_M, this relationship was 0.52 and for W_F, this relationship was 0.39. This decrease in N$_f$ content with increasing freshness of the sample (i.e., $W_F < W_M < W_D$) might be explained by the resistance of less decayed samples to decay.

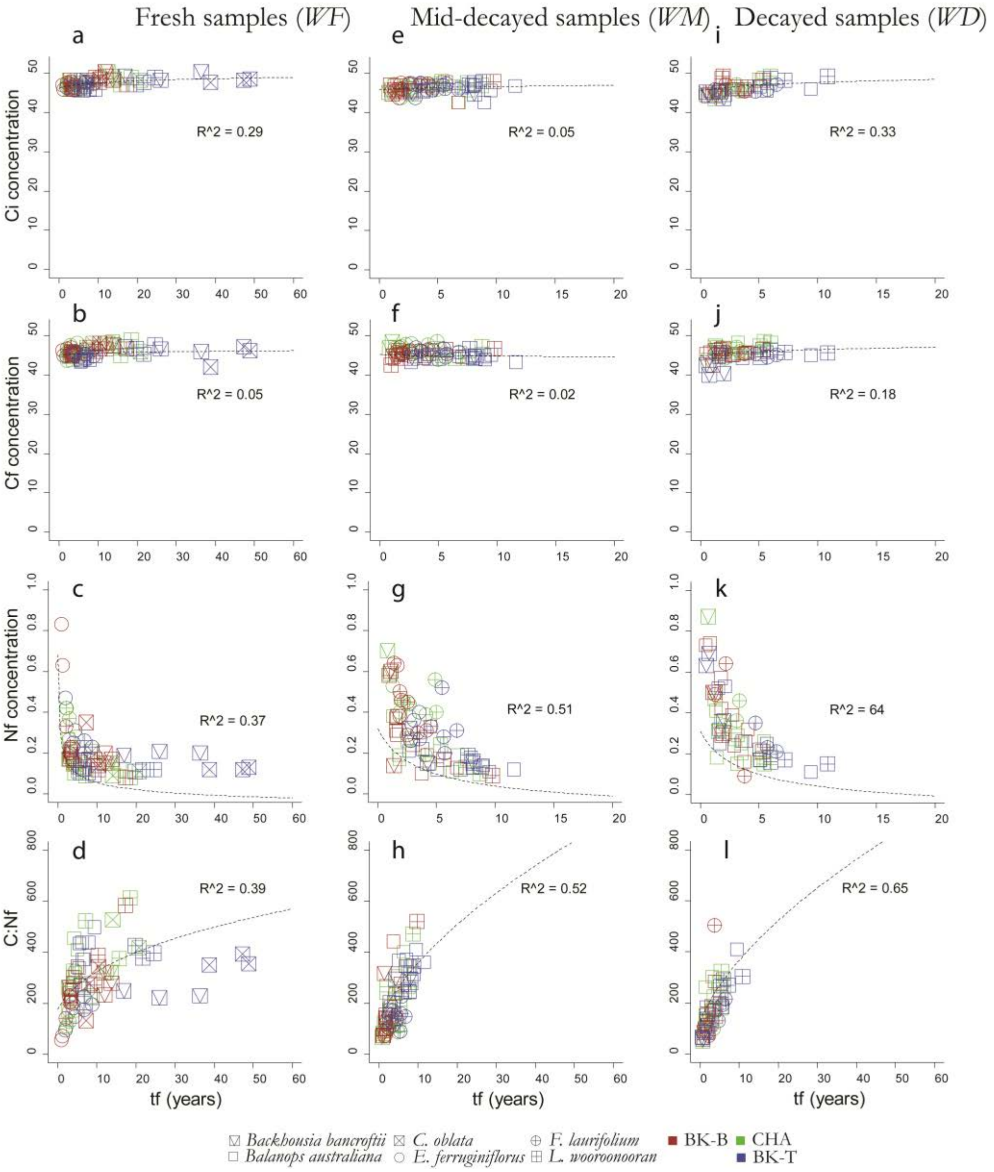


Fig. 5.5. CWDτ_f versus C$_i$, C$_f$, N$_f$ and C:N$_f$.

Savanna tree species

The savanna tree species *Eucalyptus* sp., which has different wood traits and secondary chemicals than forest trees species, exhibited slightly dissimilar CWDτ, but these values were still larger than the values observed for forest species with similar ϱ. For example, *Eucalyptus* sp. Of the decay class W_F had a ϱ = 1010 kg m^{-3} at the BKT-01 site and a CWDτ_f = 29.7 years, but the tree forest species *Leptospermum wooroonooran* had a ϱ = 1000 kg m^{-3} and a CWDτ_f = 22.0 years. The savanna tree species *Eucalyptus* sp also exhibited higher values for C:N$_f$ than the forest species with similar ϱ. For instance, *Eucalyptus* sp. of the decay class W_F had a ϱ = 1010 kg m^{-3} at the BKT-01 site and a C:N$_f$ = 916.67, while the tree forest species *L. wooroonooran* had a ϱ = 1000 kg m^{-3} and a C:N$_f$ = 514.28.

5.3.2 Additive mixed modelling

The calculated CWDτ was obtained from an exponential equation that assumed a constant mass loss over time. This model demonstrated that the CWDτ can be also estimated as a function of ϱ and the C:N ratio over time. Thus, this model classifies the *DS* of the wood into three classes, accounting for the variation of ϱ and also taking into account the C:N ratio over time, which will vary according to the wood properties and the environment. This model represents an approach for calculating CWDτ using a non-decay exponential function that assumes that mass loss over time is constant.

The results presented in the previous section demonstrated that the concentrations C$_i$ and C$_f$ do not vary considerably over time (Fig. 5.5 a and b for W_F, e and f for W_M and i and j for W_D). However, N$_f$ concentrations increase significantly over time with decreasing ϱ (Table 5.4). For example, *L. wooroonooran,* which has 820 kg m^{-3} < ϱ < 1090 kg m^{-3}, gained less in total N$_f$ over time than *Elaeocarpus ferruginiflorus*, which has 290 kg m^{-3} < ϱ < 570 kg m^{-3}. N$_f$ concentrations also increase with *DS* (i.e., W_F has lower N$_f$ concentrations than W_M, and W_M has lower N$_f$ concentrations than W_D). This relationship between ϱ, C:Nf and CWDτ_f was analyzed using multi-level models.

Models were created for each *DS*, which were classified according to section 5.2.2. Tables 5.7, 5.8 and 5.9 compare the simple *Null* model with models that include site effects and the covariate variables ϱ and C:N$_f$. Every table presents data related to a different *DS*: Table 5.7 addresses W_D, Table 5.8 addresses W_M and Table 5.9 addresses W_D. The intercepts of CWDτ_f for the *Null* model were 8.8 years for W_F, 3.1 years for W_M and 2.5 years for W_D, with variance components associated with the species identity of 41.35 %, 2.06 % and 1.69 % and unexplained variance values, which reflect within-species variability and experimental error, of 72.21 %, 2.95

% and 2.04 % for W_F, W_M and W_D, respectively. Thus, before accounting for any covariate effects, approximately 0.37 %, 0.41 % and 0.45 % of the response of the models was attributable to trees species variation for the *DS* classes W_F, W_M and W_D, respectively. Although all lower elevation sites apparently gave rise to a higher τ_f than the highest altitude site, site CHA was not significantly different from the next highest site (i.e., BK-T) for the models W_F, W_M or W_D (p > 0.1). Note here that species identity has been implicitly included in the model as part of the random effects term and the fixed effect estimates, thus giving an indication of any plot effects on τ_f that are not mediated by differences in species composition. This strategy ensures that when all species are considered as potentially responding in the same way to any differences in decay location, only minor effects are discernable.

Table 5.7. W_F fixed intercepts, fixed slope for CWD τ_f and C:N$_f$, variance of tree species and residuals.

Fixed Effect	***Null model***				***Sites + ϱ + C:N***			
Parametric terms	**Coefficient**	**S.E.**	***t***	***p***	**Coefficient**	**S.E.**	***t***	***p***
Intercept (BK-B)	8.82	2.856	3.087	0.0030	9.15	2.262	4.046	0.0001
BK-T	3.36	0.391	8.589	0.0000	2.63	0.363	7.246	0.00001
CHA	0.51	0.391	1.313	0.1938	0.26	0.323	0.808	0.4224
C:N [%]					0.007	0.002	3.501	0.0008
Wood density (kg m^{-3})					0.0085	0.002	3.730	0.0004
Random effect	**Variance component**				**Variance component**			
Level 2 variance (species)								
$\tau_0^2 = \text{var}(U_{0S})$	41.55				25.82			
Level 2 variance								
$\sigma_0^2 = \text{var}(R_{i,S})$	72.21				85.52			
AIC	374				358			

Table 5.8. WM fixed intercepts, fixed slope for CWDτf and C:Nf variance of tree species and residuals.

Fixed Effect	***Null model***				***Sites + ϱ + C:N***			
Parametric terms	**Coefficient**	**S.E.**	***t***	***p***	**Coefficient**	**S.E.**	***t***	***p***
Intercept (BK-B)	3.12	0.725	4.300	0.0001	3.48	0.509	6.838	0.00001
BK-T	2.13	0.364	5.856	0.00001	2.11	0.340	6.191	0.00001
CHA	0.51	0.364	1.411	0.1629	0.72	0.334	2.154	0.0351
C:N [%]					0.013	0.002	6.627	0.00001
Wood density (kg m^{-3})					0.004	0.002	2.421	0.0184
Random effect	**Variance component**				**Variance component**			
Level 2 variance (species)								
$\tau_0^2 = \text{var}(U_{0S})$	2.06				0.98			

Level 2 variance $\sigma_0^2 = \mathrm{var}(R_{i,S})$	2.95	1.86
AIC	305	274

Table 5.9. W_D fixed intercepts, fixed slope for CWDτ_f and C:N$_f$ variance of tree species and residuals.

Fixed Effect	***Null model***				***Sites + ϱ + C:N***			
Parametric terms	**Coefficient**	**S.E.**	***t***	***p***	**Coefficient**	**S.E.**	***t***	***p***
Intercept (BK-B)	2.53	0.775	3.263	0.0020	2.75	0.423	6.497	0.00001
BK-T	1.99	0.527	3.772	0.0004	1.35	0.387	3.483	0.0011
CHA	0.41	0.527	0.777	0.4410	0.75	0.401	1.841	0.0721
C:N [%]					0.008	0.002	4.078	0.0002
Wood density (kg m^{3})					0.009	0.002	5.136	0.00001
Random effect	**Variance component**				**Variance component**			
Level 2 variance (species) $\tau_0^2 = \mathrm{var}(U_{0S})$	1.69				0.33			
Level 2 variance $\sigma_0^2 = \mathrm{var}(R_{i,S})$	2.04				2.74			
AIC	231				202			

Interestingly, as the model fit was improved for the W_F model, (*viz.* W_F AIC (Akaike information criterion)) (Snijders and Bosker 1999) (i.e., the fit increased from 374 for the *Null* model to 358 for the *Sites* + ϱ + *C:N* model), both the absolute and proportional variance attributable to species identity increased relative to the residual variance term. The model *Site* + ϱ + *C:N* explained the CWDτ_f variation much better than when C or N were substituted for the C:N ratio term. The same finding was observed for W_M and W_D.

Models W_F, W_M and W_D

The results from W_F, W_M and W_D indicate that longer CWDτ_f occurs with increasing study site elevation (Tables 5.7, 5.8 and 5.9).

With respect to W_F, as shown in Table 5.7, the inclusion of ϱ and C:N$_f$ as covariates further improved the model (*p = 0.0001*). The centered variable for τ_f when C:N$_f$ = 0 and ϱ = 0 was 9.2 years. As the mean population C:N$_f$ = 290 and ϱ = 780 kg m^{-3}, an increase of C:N$_f$ from 0 to 290 increased the fitted scaling coefficient from 0 to 2.0 years and an increase of ϱ from 0 to 780 kg m^{-3} increased the fitted scaling coefficient from 0 to 6.6 years. Thus, CWDτ_f at site BK-B when C:N$_f$ and ϱ are centered is 17.8 years, which is explained by the sum of the intercept and both parameters multiplied by their respective coefficients. Thus, at site BK-T, CWDτ_f = 20.4 years and at CHA, CWDτ_f= 18.3 years.

With respect to W_M, Table 5.8 demonstrates that the inclusion of ϱ and C:N$_f$ as covariates further improved the model ($p = 0.0001$). The centered variable for CWDτ_f when C:N$_f$ = 0 and ϱ = 0 kg m^{-3} was 3.5 years. As the mean population C:N$_f$ = 203.32 and ϱ = 531.70 kg m^{-3}, an increase in C:N$_f$ from 0 to 203 augmented the fitted scaling coefficient from 0 to 2.6 years and an increase in ϱ from 0 to 532 kg m^{-3} augmented the fitted scaling coefficient from 0 to 2.1 years. Thus, CWDτ_f at site BK-B is 8.25 years when C:N$_f$ and ϱ are centered. Consequently, at site BK-T, CWDτ_f = 10.4 years and at CHA, CWDτ_f = 9.0 years.

With respect to W_D, as explained in Table 5.9, the addition of ϱ and C:N$_f$ as covariates further improved the model ($p = 0.0001$). The centered variable for CWDτ_f was 2.8 years when C:N$_f$ = 0 and ϱ = 0 kg m^{-3}. As the mean population C:N$_f$ =172 and ϱ = 463 kg m^{-3}, an increase in C:N$_f$ from 0 m to 172 augmented the fitted scaling coefficient from 0 to 1.4 years and an increase in ϱ from 0 to 463 kg m^{-3} increased the fitted scaling coefficient from 0 to 4.2 years. Therefore, CWDτ_f at site BK-B is 8.3 years when C:N$_f$ and ϱ are centered. Hence, at site BK-T, CWDτ_f = 9.6 years and at CHA, CWDτ_f= 9 years.

The results from the models of CWDτ were plotted against the original data in Fig. 5.6 for the decay classes W_F, W_M and W_D to test the fit of the data.

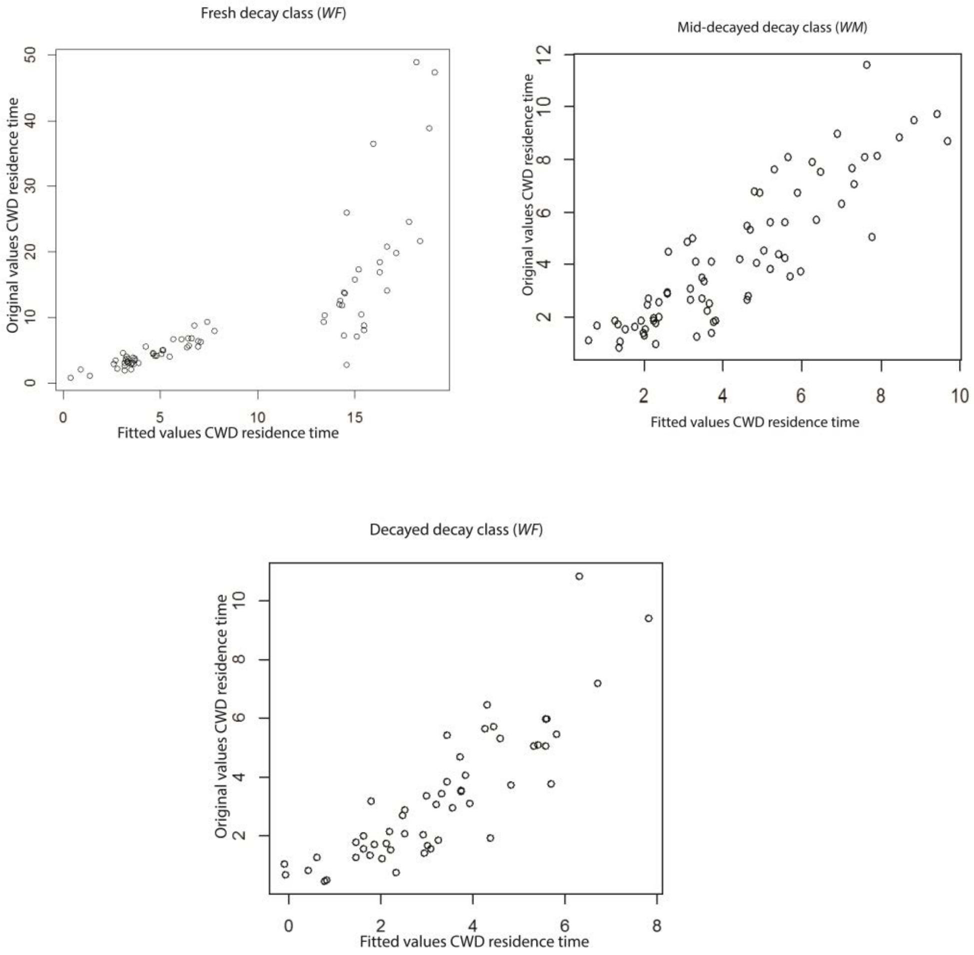


Fig. 5.6. Modelled values of CWDτ versus original values of CWDτ for each decay status: W_F, W_M and W_D.

Validation of the models

The validation of the CWDτ obtained using the *Site* + ϱ + *C:N* models (Tables 5.7, 5.8 and 5.9) indicates a good fit to the data. All models (Fig. 5.7) presented heterogeneous residuals when the standards of the residuals of the model were plotted against the fitted values for the CWDτ for the model described in Tables 5.7, 5.8 and 5.9 (i.e., for W_F, model *Site* + ϱ + *C:N*; for W_M, model *Site* + ϱ + *C:N* and for W_D, model *Site* + ϱ + *C:N*.)

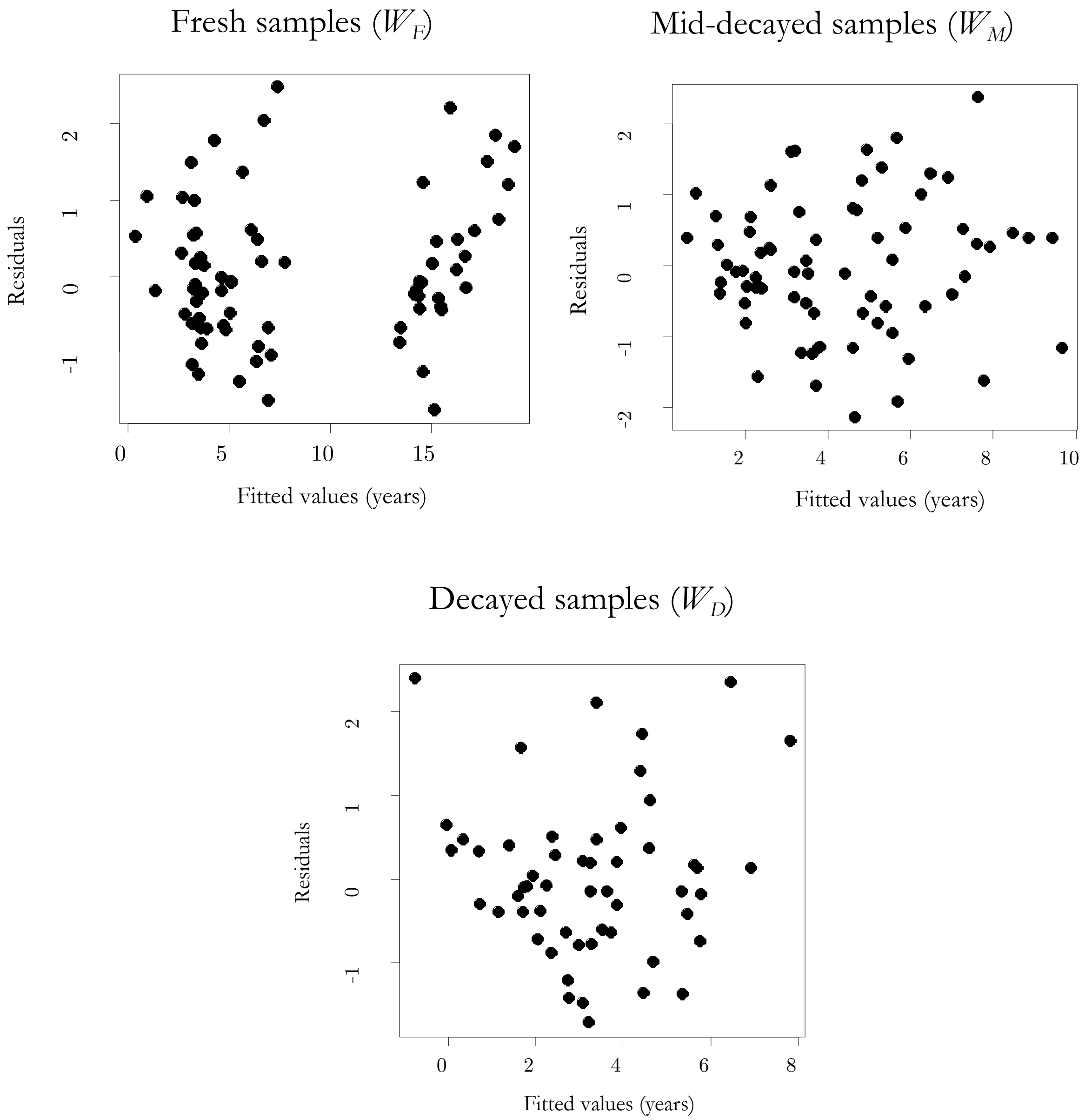


Fig. 5.7. Modelled CWDτ fitted values (years) versus residual values for the models described in Tables 5.7, 5.8 and 5.9 for the W_F, W_M and W_D models, respectively.

According to the results described in the previous section (Tables 5.7, 5.8 and 5.9) for the three models for the different decay status (*DS*) classes, across all *DS* classes, a negative relationship was observed between CWDτ_f and *DS*; for example, a sample with a C:N$_f$ of 200 and ϱ = 500 kg m^{-3} will have τ_f values of 17.1 years, 11 years and 8.9 years for W_F, W_M and W_D, respectively. Figure 5.7, which validates the model, indicates that fresher samples (W_F) require up to 20 years to decay (fitted values), mid-decayed (W_M) samples require up to 10 years to decay and decayed (W_D) samples require up to 8 years to decay.

5.3.3 Intra-specific variation of wood density versus site elevation: Which parameter is a stronger determinant of CWD residence times?

Intra-specific variation of ϱ within the two studied tree species *B. australiana* and *F. laurifolium* generally had no effect on the $C{:}N_f$ over time (Table 5.10). Such an effect was only observed for a small number of cases, where the *DS* class was W_M and W_D and the CWDτ_f varied within the study sites for samples from the same species that were collected at different elevations. For example, the tree species *B. australiana* from the study sites BK-T, CHA and BK-K exhibited a significant difference in CWDτ_f for samples with a *DS* W_M and W_D that were collected at different collection sites ($p < 0.01$, 0.01 and 0.1 (*p*-intra), respectively). However, for two of the study sites (i.e., CHA and BK-B) ϱ values were significantly different at the start of the experiment ($p < 0.01$ and 0.1, respectively).

Table 5.10. Intra- and inter-specific variation of CWD residence times and C:N. Samples collected after 15 months in the field (C:N_f ; τ_f) and decay status (*DS*) classes.

Main study sites

		BK-T					**CHA**					**BK-B**				
	p^a-*inter*	**Collection sites**					**Collection sites**					**Collection sites**				
		p^b-*intra*	INI	MAL	BK-T	Avg.	p^b-*intra*	INI	MAL	BK-T	Avg.	p^b-*intra*	INI	MAL	BK-T	Avg.
Balanops australiana																
W_F																
ϱ ($kg\ m^{-3}$)		0.1677	820	840	780	810	0.0636*	880	860	800	850	0.143	840	870	790	830
C:N_f	0.007***	0.1248	349	417	377	381	0.6572	285	280	345	303	0.854	248	270	265	261
CWDτ_f	0.0001***	0.6452	5.60	6.85	7.63	6.69	0.7677	3.97	4.45	3.85	4.09	0.2706	3.15	3.98	3.80	3.64
W_M																
ϱ ($kg\ m^{-3}$)		0.2801	640	790	740	720	0.0015***	520	810	730	690	0.0687*	520	780	660	650
C:N_f	0.08*	0.2858	259	362	321	314	0.339	202	301	194	233	0.4408	142	256	242	213
CWDτ_f	0.004***	0.0014***	3.84	10.02	7.70	7.19	0.0017***	1.87	6.91	2.74	3.84	0.0858*	1.56	4.64	3.34	3.18
W_D																
ϱ ($kg\ m^{-3}$)		0.0968*	450	640	520	540	0.1869	380	490	450	440	0.0224**	410	560	610	520
C:N_f	0.24	0.1342	104	260	211	192	0.398	167	234	175	192	0.1173	77	196	133	136
CWDτ_f	0.23	0.1276	1.73	6.01	4.13	3.95	0.0146**	1.49	3.19	4.02	2.90	0.0402**	1.02	3.11	3.21	2.45
Franciscodendron laurifolium																
W_M			BK-B	KAR		Avg.		BK-B	KAR		Avg.		BK-B	KAR		Avg.
ϱ ($kg\ m^{-3}$)		0.0151**	410	490	n/a	450	0.0046***	430	500	n/a	470	0.1628	420	480	n/a	450
C:N_f	0.264	0.342	149	163	n/a	156	0.7529	151	101	n/a	126	0.0575**	87	136	n/a	111
CWDτ_f	0.002***	0.8656	5.63	4.93	n/a	5.28	0.49	3.92	3.73	n/a	3.82	0.0311**	1.75	3.36	n/a	2.56

[a] is the *p* value for the inter-specific variation of wood density, C:N_f and CWDτ_f. [b] is the intra-specific variation of wood density, C:N_f and CWDτ_f at one specific study site for different woods with the same *DS* that were collected at the collection sites. The significance of *p* values is indicated as follows: ***<0.01, **<0.05 and *<0.1.

Consequently, the effects of intra-specific variation in ϱ on CWDτ are less significant than the effects of wood decay along site elevation. Therefore, environmental variables seem to dominate wood decay more than differences in the intra-specific variation of wood densities. For instance, *p* values for comparisons between the study sites (p-inter) were significant for both C:N$_f$ and CWDτ_f for W_F and W_M for the tree species *B. australiana* and for CWDτ_f for the tree species *F. laurifolium* (Table 5.10). It is possible that the differences observed for W_D between sites were not significant due to the advanced status of the decomposition of the wood samples, as less favorable environmental variables for the performance of decaying organisms exist at the higher elevation. (Cornwell et al. 2009) suggested that decaying organisms preferred to colonized more degraded samples because the wood structures of these samples were easier to digest.

5.3.4 Soil characteristics

The soil characteristics (Table 5.11) revealed a slightly acidic pH, which is typical of tropical forests; the pH increased with decreasing site elevation. Nitrate-nitrogen concentrations were very low at the highest site (i.e., BK-T) due to very low temperatures. Site CHA exhibited the highest values for nitrate-nitrogen, ammoniacal nitrogen, P buffer index, sulfate-sulfur, exchangeable K and electrical conductivity. Site BK-T exhibited the highest values for pH, P, exchangeable Mg, Ca, effective CEC and organic C. Site BK-T only exhibited higher values than sites CHA and BK-B for aluminum content.

Table 5.11. Soil properties of the main study sites.

Soil nutrients	BK-T	CHA	BK-B
pH(H_2O)	4.3	4.7	5
pH(CaCl)	3.8	4.2	4.3
Nitrate-Nitrogen (mg/kg)	0.5	43.8	42
Ammoniacal Nitrogen (mg/kg)	33.6	59.3	26.6
P (mg/kg)	17	7	26
P Buffer Index	145	481	120
Sulfate-Sulfur (me/kg)	23	29	9
Exch. K (me/100 g)	0.15	0.28	0.23
Exch. Mg (me/kg)	0.19	0.27	0.5
Exch. Ca (me/kg)	0.0	0.1	1.1
Exch. Na (me/kg)	0.03	0.05	0.05
Effective CEC (me/kg)	0.28	0.25	0.3
Electrical conductivity (dS/m)	0.11	0.14	0.12
Aluminum (me/kg)	0.25	0.18	0.11
Organic carbon (%)	5.11	4.48	5.27

5.4 Discussion

CWDτ is a parameter that is used to estimate the amount of time required for organic C and nutrients to return to the atmosphere via respiration by organisms or to be stored in the soil for later use by living beings. Thus, CWD is a pool of both nutrients and C.

The first attempts to define the CWDτ applied the inverse of a decay exponential function that included the total mass lost over time as a variable (Baker et al. 2007, Galbraith et al. 2013). The aim of this study was to develop a model for optimizing the determination of CWDτ by analyzing the significant interactions between the structural characteristics of the wood and the surrounding environmental parameters. For this purpose, three models were developed (i.e., one model for each decay class (i.e., W_F, W_M and W_D)) to describe the interaction between ϱ, C:N variation over time and the effects of site elevation on the CWDτ.

5.4.1 CWD residence time is explained by wood density, C:N and site elevation

The model that best predicted differences in CWDτ_f for all *DS* classes within tree species and across the sites included ϱ and C:N_f as explanatory variables. *DS* models indicated that CWD$\tau_{f,}$ increased in the order $W_F > W_M > W_D$ (Fig. 5.4). Other studies of decay across different *DS* classes also suggested that decayed woods decay faster than comparable fresh woods (Harmon, 1986; Cornwell et al., 2009) as a consequence of both physically more fragile structures and a lower concentration of secondary defense compounds. Other studies have also demonstrated that the negative relationship between ϱ and *DS* for distinct tree species (Zell et al., 2009; Iwashita et al., 2013) can be explained by the capacity of the wood to hold moisture at higher ϱ and by the physical anoxia that is created by the absence of empty pore space (Chambers et al., 2001; Nogueira et al., 2008; Hérault et al., 2010). Additional studies also concluded that ϱ is strongly related to wood structural traits, such as cell diameter and number (Poorter et al. 2010) in tropical forest species and is also related to plant physiological characteristics, such as tree respiration and growth (Patiño et al. 2012). These species-based differences related to wood traits might explain the difficulty encountered by detritivores when decomposing dead wood (Eviner, 2004); these differences might be related to the C:N ratio, as N increases with wood decomposition.

Figure 5.8 reveals a increase in CWD$\tau_{m,f}$ between sites at successively higher elevation, which might be driven by a decrease in mean annual temperature. The lower site (i.e., BK-B) exhibited similar relationships between ϱ and CWDτ_f for all decay classes. In addition, C:$N_{m,f}$ and CWD$\tau_{m,f}$ increased gradually with site elevation (Fig. 5.8). Previous studies also demonstrated that temperature affects the τ of the CWD across different study sites (Mackensen et al., 2003; Zell et al., 2009; Iwashita et al., 2013). Meier et al. (2010) showed that biomass fungal accumulation nearly quadrupled for an increase of 10 °C in temperature. Lower temperatures inhibit the activity of microbial communities and therefore promote CWD accumulation (Muller and Lul, 1991; Woldendorp and Keenan, 2005). A study by Baker et al. (2009) also suggested that temperature was a more important variable for CWDτ than the ϱ-site relationship at a regional level.

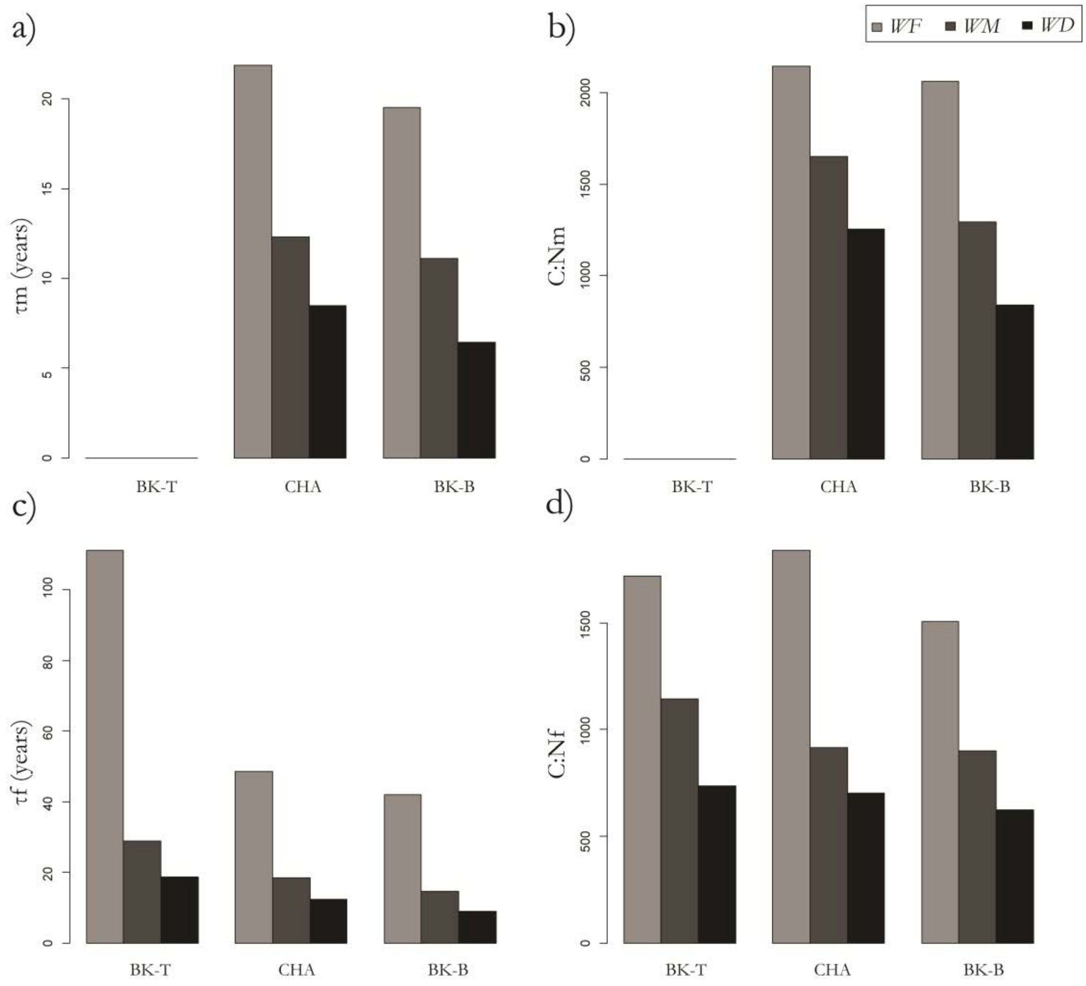


Fig. 5.8. CWD decay classes for the collected samples after 6 months a) and 15 months c) ($\tau_{m,f}$) and C:N$_{m,f}$ averages c) and d) at every study site for all decay classes.

The study sites are all located on moderately acidic soils. Acidic soils are common in tropical forests due to heavy weathering and fast turnover rates of organic matter. These soils may represent a comparatively hostile environment for microorganisms. Wal et al. (2007) concluded that soil conditions influence wood decay and that fungi tolerate a wider range of soil pH than bacteria, but the latter organisms are more efficient at decomposition. The results obtained in the present study did not sample the decomposer organisms in the wood samples, but a positive relationship was found between elevation, *DS* and τ, suggesting that climate has a strong influence on the CWDτ.

Baker et al. (2007) summarized the decomposition rate (k) for different tropical forest types (Eqn. 1). Lowland forests ranged between k =0.1 and k =0.5, and montane forests had a value of k =0.2. The average k for the forest species in our study ranged from k = 0.02 to k = 0.3 at BK-T, k = 0.2 to k = 0.6 at CHA and k = 0.2 to k = 0.8 at BK-B. Comparisons suggested that site elevation explains the observed decrease in k with increasing site elevation. Differences in k between experiments might be explained by different environmental and soil fertility conditions.

5.4.2 Seasonality affects physical and chemical decay rates in short-term experiments

This study specifically examines the effect of seasonality on CWD$\tau_{m,f}$ for the study sites CHA and BK-B. A difference in CWD$\tau_{m,f}$ was observed between samples collected after a single wet season and after two wet seasons and a dry season (Fig. 5.9), with faster CWDτ_m during the single wet season (CWDτ_m). Figure 5.9 also shows that the C:N ratios for all of the *DS* classes were much smaller for C:N_m than for C:N_f. This finding is also true for the CWD$\tau_{m,f}$, where $W_D < W_M < W_F$.

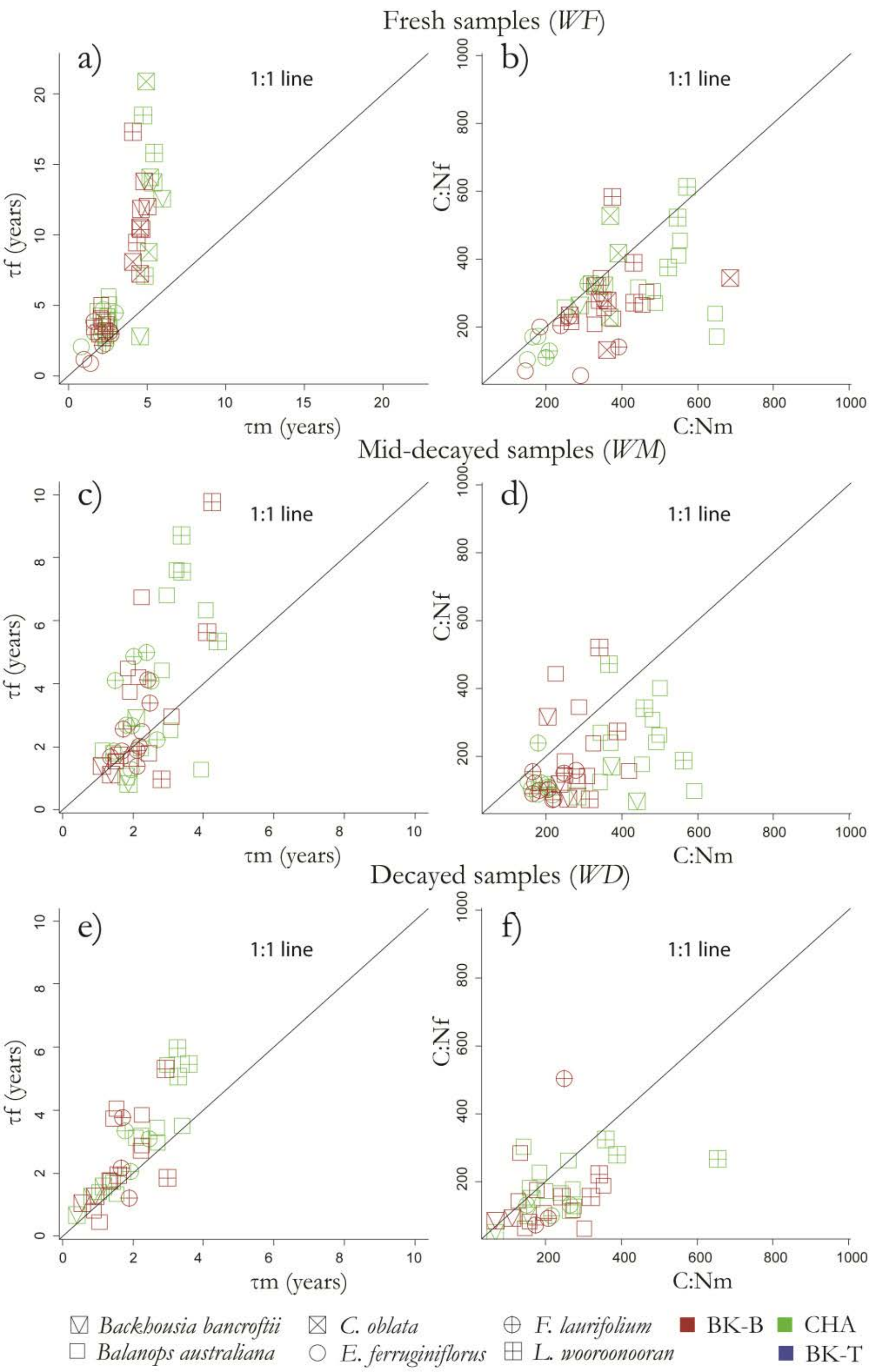


Fig. 5.9. CWDτ for the samples collected after 6 months in the field (CWDτ_{m}) versus the samples collected after 15 months in the field (CWDτ_{f}) and C:N values: C:N_m versus C:N_f at the study sites BK-B and CHA for all decay classes (i.e., W_F, W_M and W_D).

Differences in CWD$_\tau$ between seasons could be explained either by seasonality or as a colonizing effect of decaying organisms on samples that were autoclaved prior to placement in the field. Figure 5.9 indicates that N_m concentrations were higher than N_f concentrations, demonstrating that CWD decomposition rates were faster during the first 6 months of the experiment. This finding might be explained by either the higher precipitation and temperatures values that occur during the wet season (Table 5.1, $Pm > Pf$ and TWQ > TDQ) and enhance microbial activity and the physical degradation of the samples or the use of the autoclaving technique as a standardization method. The effects of autoclaving might cause an initial rapid colonization of the wood samples. In addition, Fig. 5.5 revealed higher N_f concentrations with increasing wood freshness (i.e., $W_D > W_M > W_F$).

The results suggest that higher moisture content enhances decomposition, with an optimal range between 1,200 mm and 1,300 mm of precipitation, according to Mackensen et al. (2003). Mackensen et al. (2003) also suggest that slower decomposition might result from lower moisture contents, such as those that occur in the dry season. Our results are consistent with Laiho and Prescott (1999), who suggest that models that use constant CWDτ cannot offer accurate estimates of the seasonal decay of CWD. However, such models can be a useful tool for comparing values between different study sites and forest types. Therefore, a long-term study of the effects of climate on the CWDτ might be of interest. Seasonality patterns might be affected by climate change and might alter the long- and short-term dynamics of CWDτ.

5.4.3 Applicability of the model

The precipitation levels at our study sites were not directly linked to elevation; CHA-01, which is at an elevation of 720 m asl, had the lowest rainfall. The results of this study suggest that temperature may be the most appropriate single variable for explaining differences in τ along an elevation gradient where moisture is not limiting.

The model was used to examine the variation of ϱ across a broad ϱ range to predict CWDτ for most of the wood densities that occur for tree species in tropical forests. The results emphasize the importance of including the density and C:N abundances of wood in further studies on CWDτ, as both of these parameters might explain the inter-relation of the CWD substrate and the environment.

5.4.4 Intra-specific variations in wood traits are reflected in chemical/physical decay rates

The results demonstrate that site-specific variation of ϱ within the tree species *B. australiana* and *F. laurifolium* failed to significantly impact the CWDτ_f for W_F. This finding might be explained by the highly complex structure of fresh samples, which makes the decay process very laborious for detritivores, and by the chemical and physical homogeneity of the starting substrate. However, the significant differences in τ_f and C:N_f that were observed for *B. australiana* and *F. laurifolium* for W_M and W_D and for *F. laurifolium* for W_M may be explained by the fact that the wood structures were degraded prior to sample collection for this experiment. Thus, colonization by decaying organisms was faster and significant differences were observable over the study period. However, inter-specific variation has a stronger effect on CWDτ than site-specific variation.

5.4.5 Autoclaving as a method of standardizing the initial sample state

The N_i abundance after autoclaving the wood samples indicated very low values, suggesting an N-volatilization effect during the sterilization procedure of the wood samples (Ferrasolsas and Khana, 1995). Thus, the samples from different *DS* classes had values of N_i close to zero (st. dev. = 0.036, variance = 0.001) prior to placement in the field. In contrast, when the samples were collected, N_f values increased gradually with increasing the *DS* for all of the samples. Therefore, higher N content indicated that the samples were decayed over the length of the experiment, not that the samples had a higher N abundance at the start of the experiment. Therefore, the autoclaving technique allowed the experiment to directly examine those environmental factors that would enhance the ability of a microbial community to colonize a sample by removing variations in N_i abundance between the samples. The autoclaving process may have also removed secondary defense chemicals, again facilitating a direct comparison of ρ and environmental drivers of decomposition.

5.5 Conclusion

This study modelled the major components of CWD dynamics in combination with elevation to explain how one environmental gradient (elevation as a proxy of temperature) define ecological dynamics in the terrestrial C pool. Site effects along an elevation gradient are a stronger determinant of CWDτ than intra-specific site variation in ρ. This study also demonstrated the importance of including the *DS* of the tree species when estimating CWDτ because partly decayed samples decomposed faster at all sites.

The results of the model defined τ_f as a function of C:N_f and ρ. N_f concentrations increased with decreasing wood decay and with increasing ρ, but C_f concentrations exhibited no relationship with ρ over time, suggesting a lower abundance of decaying organisms on fresher wood samples. N abundance was more variable and is dependent on both the wood and the environmental characteristics; this parameter increased with increasing *DS* (Yang et al. 2010, Iwashita et al. 2013). The outcomes also demonstrated the significance of climatic contrast between the tropical seasons and the influence of these changes on CWDτ in comparatively short-term studies. During the wet season, precipitation and temperature were not limiting factors for decomposition; however, the results suggest that during the dry season, low ω could be a limiting factor, as the conditions are far from optimal for decay.

Autoclaving the wood samples prior to placement in the field standardized the colonizing substrate for colonization by eliminating the entire living population of organisms at time zero. The levels of N in the control samples were very low to zero, allowing control of the process of sample colonization by decaying organisms. Therefore, this technique represents an excellent strategy for future experiments that study CWDτ in tropical forests. However, this study did not account for the volatilization of secondary components from the freshly collected samples; this process may have resulted in an underestimation of CWDτ if the volatilized secondary compounds conferred additional resistance to degradation.

Chapter 6

Synthesis

This chapter includes a summary, discussion of the main results, implications for future research and recommendations to help to mitigate the effects of climate change in tropical forests.

6.1 Summary

The effects of climate change on Australian and Papua New Guinea tropical forests

Little is known about the effects of climate change on tropical forests in Australia and Papua New Guinea. Australian tropical forests are highly diverse and have a significant proportion located in World Heritage Areas, while Papua New Guinean tropical forests represent some of the largest intact tracts in the world. Studies performed in Australian tropical forests are suggesting that annual precipitation plays an important role in tree survival, especially for inland ecosystems (Wallace and McJannet 2012). Moreover, the available literature on the ecology of tropical montane forests in Australia expresses a general concern as to the future of these ecosystems as cloudiness may decrease as consequences of climate change (Wallace and McJannet 2012). One possible consequence of decreased cloudiness might be a decrease in water availability leading in turns to an increase in tree mortality. Interestingly, studies of the evolution of tropical flora suggest that Australian floras might have developed under different conditions to Neotropical and Paleotropical vegetation. This could diminish the applicability of the results of overseas studies in the context of Australian tropical forests. Another characteristic of Australian tropical forests are the exposure to comparatively frequent cyclones introducing a new disturbance to forest dynamics and ecosystem functioning in comparison with tropical forests that are less exposed around the world.

This thesis augments existing studies on the effects of climate change on tropical forests by examining the importance of the wood density as a key component of above ground tropical forest biomass and therefore of carbon dynamics from a range of perspectives. The carbon stocks of trees are closely related to the wood density and wood density influences above ground carbon stocks and dynamics in a number of ways that have been addressed in this thesis.

The importance of altitudinal gradients

Altitudinal gradients are important natural laboratories in which to study the effects of climate change on tropical forests through field data collection. Mean annual temperature decreases gradually, precipitation regime varies and soil properties can also change with increasing elevation. Using altitudinal gradients rather than laboratory studies or other different field experimental designs for the study of above ground biomass and carbon dynamics of the vegetation offer substantial advantages: a) the ability to measure the responses of the vegetation to climate change under natural conditions using elevation to control different environmental parameters (i.e. temperature, precipitation, soil nutrients), b) the gradual superposition of species niches with elevation offers the opportunity to study both the changing stature of the vegetation and also the wood properties of the different tree species. Both parameters are key components fo the determination of vegetation carbon stocks, c) the possibility to use the elevation gradients as a surrogate for increases in temperature associated with climate change in order to better predict the responses of vegetation in a future warmer world d) the understanding of ecosystem function (i.e. dynamics and productivity) in response to environmental drivers and elevation.

6.2 Discussion

Design and data collection

First, a non-destructive method to study wood density in living trees in tropical forests was developed and tested in Australia, Papua New Guinea and Vanuatu. Measurements were performed across dry (Australia), moist (Australia, Vanuatu) and wet forests (Australia and Papua New Guinea) within an elevation range from 50 m in Australia asl to 2939 m asl in Papua New Guinea. I addition, a canopy crane was used at one study site to perform measurements along individual tree boles in both the dry and wet season and wood density along the stem was also measured destructively in Vanuatu by cutting down the trees. The study assessed the effects of seasonality on the ultrasonic testing equipment; as well the accuracy of the method to estimated variation of wood density within tree species and between tree species and across different ecosystems.

Measurements were performed by using a TICO Ultrasonic Testing Instrument. Stand error of the mean of the two cross cardinal measurements suggested good reproducibility of the measurements. Intra-specific variation of wood density the tree species *E. medullosum* in Vanuatu indicate a coefficient of determination of 0.66 between conventional and ultrasonic measurements performed below 30 °C, but measurements above that temperature were inconsistent; also measurements along the bole suggest a decrease of wood density with increasing tree height.

Intra-specific variation of wood density for all tree species studied suggests a coefficient of correlation between ultrasonic pulse velocity and measured wood density of 0.81, excluding one tree species (*Cardwellia sublimis*) that presented higher velocities for its average wood density possibly explained by the known higher abundance of aluminum in the wood than other species (Webb 1954). Previous ultrasonic studies have been conducted on wood in the laboratory have suggested a positive relationship between wood density and pulse velocity (Bucur and Feeney 1992, Bucur 2006, de Oliveira and Sales 2006), but this is the first application of the technique to living trees across different tropical forests types.

Second, 221 tree cores from 18 tree sun exposed and shaded tree species were collected at four study sites at the Yopno-Uruwa-Som (YUS) conservation area in Papua New Guinea ranging between 1753 m asl and 2939 m asl. These cores were used to study the intra-specific variation of wood density as a function of site elevation, tree stature and niche occupation. Individual tree measurements included height, diameter and canopy light index. Analysis of the variation of wood density included multi-level analyses. The results showed that elevation, tree diameter and niche explained variation of wood density within trees species along the altitudinal gradient. The results further suggest that tree diameter was a better predictor for wood density than tree height for both sun-exposed and shaded tree species. Also, the wood density for the sun-exposed tree species decreased with increasing site elevation with the opposite relationship found for shaded specie.

Third, 18 study sites in tropical forests in Australia along an elevation gradients between 50 m asl ad 1500 m asl were used to assess the relationships between above ground biomass, basal area, species diversity, soil fertility and plant water supply index as a function of elevation and from dry to wet forests. In total, 407 trees from the most common tree species across all study sites and a few species common at few study sites were monitored for a period of two years. Measurements included the use of dendrometer bands, wood cores, tree height and diameter. Studied species were classified by niche as sun-exposed or shaded. Data analysis included multi-level analyses to study the significant variables that explained wood density variation with elevation and Kendall's tau rank correlation coefficient to study how wood density varied with elevation for the common tree species. Elevation, soil fertility and niche occupancy best predicted the variation of wood density along the elevation gradient. Total site basal area was negatively related to elevation. In this study diameter was not significant in results of the multi-level analysis. This might be explained by the seasonal differences of the study sites, as previous studies on seasonal forests suggested both increases and decreases in wood density from the pith towards the bark for different trees species (Nogueira et al. 2005, Henry et al. 2010). The multi-level results indicated that elevation (temperature) and soil fertility explained the variation of wood density with site elevation. Other studies have also found regional variations of wood density related to soil fertility in the Neotropics (Baker et al. 2004, Patiño et al. 2008). A relationship of wood density with topographical characteristics has also been found in the Neotropics (Chave et al. 2006, Hernández et al. 2012).

Fourth, the thesis examined the coarse woody debris residence time for six forest tree species ranging in wood density from a 200 kg m^{-3} to 940 kg m^{-3}. The environmental controls on wood density physical and chemical decay were assessed using an elevation gradient. Samples were emplaced at three study sites at altitudes of of 102 m asl, 720 m asl and 1500 m asl on soils derivd from common granite parent material. In total 482 wood cubes were analyzed for weight loss and carbon and nitrogen abundance at the start of the experiment and after a period of six and fifteen months being in the field. Samples were autoclaved to standardize the colonizing substrate at the start of the experiment. The study found that seasonality was a significant parameter determining wood residence times as the moisture content of the woods increased along with mean annual temperature in the wet season – occurring from November to May. Multi-level analysis suggests that CWD residence times were bestr explained by wood density and the Carbon:Nitrogen ratio. Previous studies have also shown that wood density is positively related to wood residence times (Cornwell et al. 2009) as more complex structures are less easily degradable by physical fractionation and also by detritivorous organisms. Carbon:Nitrogen ratio has also previously been found to be inversely related to wood residence times, as wood is consumed by nitrogen fixing bacteria (Garrett et al. 2012). The results suggest an increase in wood residence times with increasing elevation (decreasing temperature). Similar results have been also recently suggested by Iwashita et al. (2013) for a tropical wet montane forest in Hawaii.

6.3 Implications and recommendations for further research

The importance of altitudinal gradients

There is general concern regarding the lack of accuracy of global biomass estimations across tropical forests - especially in remote areas where land access is logistically difficult and expensive (Asner et al. 2012, IPCC 2013). Global predictive models rely heavily on measured net biomass responses to environmental conditions and changes in environmental conditions. Policy makers working toward the mitigation of climate change effects on tropical forests are also dependent on the accessibility and accuracy of biomass carbon stocks, the responses of these ecosystems to climate change and to other anthropogenic activities – land use change – or natural disturbances (*viz.* fire, drought, cyclones) across the globe (IPCC 2013). Estimates of how climate change will affect C dynamics in tropical forests can help to refine predictions of the impact of future climate change scenarios on the net primary productivity of tropical forests. These estimates are critically dependent on accurate forest carbon inventories.

The importance of ground measurements

Remote sensing techniques are increasingly used to generate estimate regional estimates of carbon storage in tropical forest, but these techniques remain dependent on complementary ground-based measurements (Goetz et al. 2009, Asner et al. 2012, Hudak et al. 2012, Mitchard et al. 2014). The non-destructive technique to determine wood density in the field developed in this thesis has the potential to both simplify and accelerate the acquisition of above ground biomass measurements in tropical forests. The technique offers many advantages over the traditional methods; the method is faster and requires less physical effort in the field than coring, resulting in an increase of the potential number of trees that can be sampled and eliminating the costs of labor required for laboratory preparation and species identification. Besides, this ultrasound testing technique combines both fast and reliable results that facilitate the determination of wood density on living trees. Therefore this method can help to improve the accuracy and reduce the costs of the estimation of the above ground biomass estimations for living trees in tropical forests.

The importance of biomass of tropical forests as C sinks

The importance of wood density in defining the above ground biomass in tropical forests have been stated by Chave et al. (2005) and Baker et al. (2004). Both authors conclude that wood density is, after diameter the most important variable that converts the volumes of the trees to tons of biomass. Wood density might be an indicator of the potential productivity of an ecosystem as it is negatively related to the tree growth rates and to the energy required to decompose CWD. Tropical forest responses to climate change might be include an increase in tree mortality as a result of an increase of tree growth rates accompanying a CO_2 fertilization effect (Huntingford et al. 2013). The possible consequences of a global increase in temperatures together with an increase of tree mortality rates on CWD dynamics are still unclear. Global warming may modify CWD dynamics and residence time. Studies using elevation transects provide an opportunity for the researchers to investigate ecosystems responses to temperature change and thus anticipate alterations in ecosystem function as a result of climate change.

Tropical montane forests are vulnerable ecosystems in the face of increasing drought events accompanying global warming (Chu et al. 2014). The wood structures of trees of these ecosystems are not resistant to severe droughts (Bruijnzeel and Veneklaas 1998). Previous studies on the Neotropics have demonstrated that sun-exposed trees invest in high conductance structures to compensate for both the decrease of water vapor deficit and solar radiation with elevation; whereas shaded tree species are more resistant to xylem embolism as they have a lower hydraulic conductance (Poorter et al. 2010). Thus, predictions of an increase in dry season length as a consequence of climate change might place for fog-dependent ecosystems under considerable stress. In addition, the loss of water interception from clouds during extreme long periods of drought can also enhance fire, an example is the year 1996 when El Niño caused several burns of montane forests in Papua New Guinea (Fox et al. 2010).

The importance of wood density

This research contributed to a better understanding of ecosystem functioning in terms pf above ground net productivity of tropical forests in Australia and Papua New Guinea. The results showed that there is an effect of elevation on the carbon dynamics of the vegetation. It has been demonstrated through the study of species niches, functionality and physiognomy together with soil fertility and climatic variation along elevation that it is possible to identify the mechanism that defines the *B* and productivity dynamics of an ecosystem.

The results of this study have emphasized the importance of wood density as a significant variable controlling biomass carbon stocks. For example, this study has suggested that carbon stocks in tropical montane forests in Papua New Guinea are likely under-estimated due to the use of calculations that generally based on logged trees, belonging generally to a large size classes where wood density decreases from the pith towards the bark. Moreover, results for above ground biomass along an altitudinal gradient in Australia suggested a decrease in wood density with increasing elevation, explained by a decrease in tree stature with elevation. Both studies in Papua New Guinea and Australia suggest a decrease in wood density for sun-exposed tree species, with increasing elevation, in contrast to shade tree species where wood density increase with increasing elevation. Thus, future model calculations for forests biomass in these regions could be refined by accounting for the systematic differences in wood density with elevation and niche occupancy documented in this thesis.

The CWD component of this study suggested that wood density, seasonality and temperature all affect the CWD decay rates. Thus, if climate change is increasing temperature and / or modifying the length of the dry season and / or changing wood density through changing growth rates, then these changes will necessarily influence the residence times of CWD in the future. The results from this study provide a basis from which to estimate the impact of future climate change ion CWD decay rates.

6.4 Limitations and applicability of this study

The limitations of this study are several. First, the development of an ultrasonic technique to study non-destructively wood density on tropical forests identified significant effects of temperature on ultrasonic pulse velocity for measurements above 30 °C. Also, the transducers that were used in this study were 5 cm wide, causing an extra challenge to the researcher to ensure the total surface of the transducers were in solid contact with the tree. In some cases, the bark of the trees needed to be sanded to ensure that noise from this thick natural barrier did not affect the quality of the pulse velocity. Furthermore, it was observed that operator skill and familiarity was required to ensure consistency between readings. Future research on transducer design may be able to overcome the short-comings of the system used in this study. As trees with diameters at breast height larger than 70 cm – which can account up to 33 % of the total biomass in a plot (Chave et al. 2003) – it may be advisable to also obtain a core for direct wood density determination. For smaller trees the method holds the promise of rapid wood density assessment without the need for coring and without the need for species identification – the latter a significant constraint in species-rich tropical forests.

Research conducted in Papua New Guinea was designed before departure and in the field, together with the help of the villagers. Lack of prior knowledge of the tree species that were present in the field area was a limiting factor in determining which tree species were best to sample. However, we were able to sample most of the common shaded tree species. The poor availability of descriptions of the vegetation in the tropical montane forests in Papua New Guinea was also restrictive. Information on ecosystem function in terms of above ground biomass in tropical montane forests in Papua New Guinea is scarce. This study is a contribution to a better understanding what the potential responses of these ecosystems to drought induced by the effects global warming. Consequences of climate change (i.e. deficiency of available water) for these drought intolerant ecosystems could include major episodes of tree mortality both thought stress and fire, and therefore ecosystem loss.

Australian responses of tropical forests – ranging from lowlands to montane forests – are poorly understood. The target of this study was focused on the effects of climate change of the ecosystem productivity with special attention to biomass and basal area increment. The results highlight the importance of preserving these ecosystems as carbon reservoirs. Limitations faced at the development stage of this study were the lack of availability of information on wood traits of common and rare tree species (*viz.* cell diameter, density, hydraulic conductance) at the study sites. Also, during the research experimental period most of the established sites experienced a major disturbance during cyclone Yasi on February 2011. Thus, tree branches, canopy tops and leaves were snapped changing the original structure (i.e. tree height and canopy width) of the study sites. Also, some canopy trees were uprooted or broken. Ecosystems dynamics in terms of living biomass loss and regrowth caused by cyclones represent a pressing opportunity for further research that needs to be conducted in Australian tropical forests.

The experiment determining the CWD residences times was developed at only three study sites with common soil parent material (granite) along an elevational gradient. So, it is speculated that temperature is the main driver of decay rates together with seasonality in the climatic drivers that produced differences in CWD residence times. This results is supported by previous studies (Mackensen et al. 2003, Zell et al. 2009, Meier et al. 2010, Iwashita et al. 2013). But there is also previous literature suggesting that soils also play a major role in controlling CWD residence times (Galbraith et al. 2013), a conclusion that could not be tested in this study due to the common soil parent material. CWD turnover processes are complex and involves many interrelated processes (*viz.* wood density, climatic variables, soil fertility and pool of decomposers organisms). This study is a small additional input to the literature on CWD dynamics as previous studies in Australian forests were available.

This thesis aimed to contribute to a better understanding of the effects of global warming on tropical forests in Australia and Papua New Guinea. To sum up, this thesis has evaluated: 1) a non-destructive method to determine the intra-specific and inter-specific variation of wood density in living trees; 2) the effects of elevation and seasonality on coarse woody debris residence times in tropical forests in Australia; 3) the effects of elevation, tree niche and stature on the intra-specific variation of wood density in a wet forests in Papua New Guinea; and 4) the effects of elevation and soil fertility in above ground biomass, basal area, tree growth and wood density, as well as the variation of wood density with elevation, tree statures and niche.

Short biography

Mireia Torello Raventos was born in Barcelona, Spain on 1979. In 2003 she obtained a B.S. Degree in Environmental Science from Fairleigh Dickinson University, New Jersey, United States of America. Afterwards, she worked in the Catalan Autonomous Government, Barcelona, issuing environmental licenses to existing activities (industrial, mining, farming and waste management. In August 2009 Mireia obtained a MS. in Forest and Nature Management at Wageningen University, The Netherlands. For her thesis she joined the multidisciplinary leading project TROpical Biomes In Transition (TROBIT) (University of Leeds) to study the delimitation of transitional forest-savanna ecosystems. In February 2010 she started her PhD candidature at James Cook University, Cairns, Australia.

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Conflict of interests

None declared.

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Appendix

Appendix Ch3

Fig. 1. Geometric mean of wood density (kg cm^{-3}) at each study site for all the sun-exposed species.

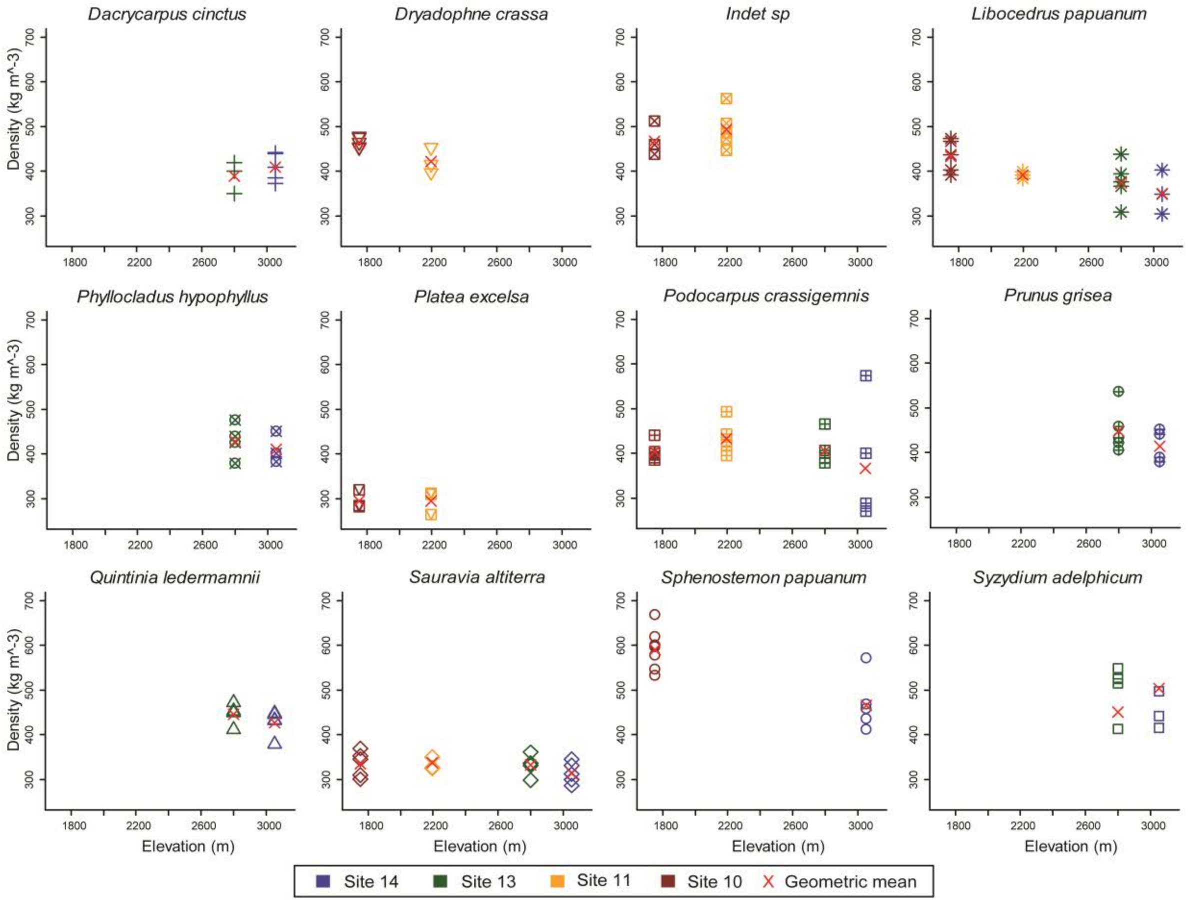


Fig. 2. Geometric mean of wood density (kg cm^{-3}) for all the study sites for the shaded species.

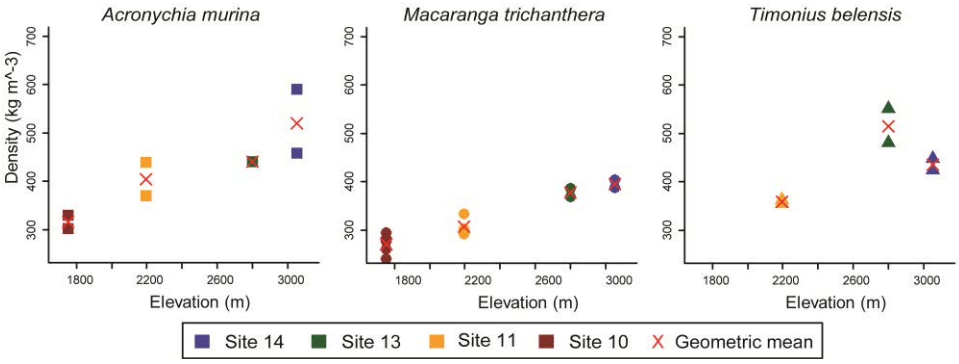
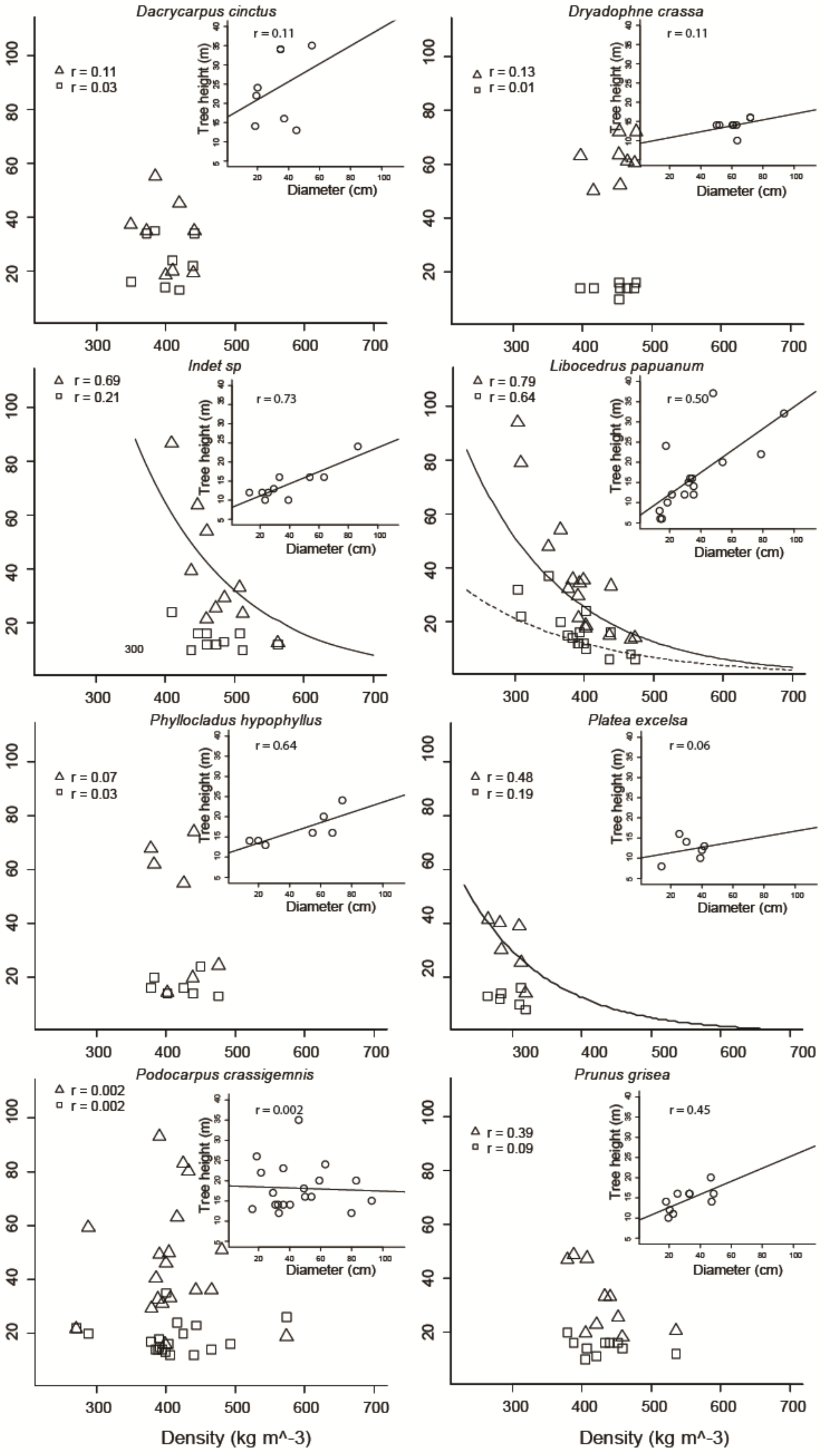


Fig. 3. Density (kg m^{-3}) versus *H* (m) and *DBH* (cm) for all the species. Linear determination coefficients (r) are for the graphs of *DBH* (cm) versus *H* (m).



Appendix Ch4

Table 1. Tree species measured at every study site.

Tree species	**Study site**	**# individuals**
Acmena hemilampra var orophilla		**5**
	BKT-01	5
Antirhea tenuiflora		**6**
	CHA-01	3
	CHE-01	1
	COW-01	1
	ROB-01	1
Apodytes brachystylis		**14**
	CHA-01	7
	CHE-01	7
Argyrodendron peralatum		**6**
	MEN-01	3
	TCH-01	3
Arytera pauciflora		**1**
	CHA-01	1
Balanops australiana		**11**
	CHA-01	1
	CHM-01	3
	CHE-01	2
	KBL-03	1
	KOO-01	2
	BKT-01	2
Beilschmiedia bancroftii		**4**
	KBL-03	1
	CHE-01	1
	TCH-01	2
Beilschmiedia collina		**3**
	CHA-01	1
	CHE-01	2
Beilschmiedia tooram		**6**
	CHA-01	5
	MEN-01	1
Bobea myrtoides		**1**
	KOO-01	1
Brackenridgea australiana		**7**
	CHA-01	1
	CHM-01	5
	KOO-01	1
Brombya platynema		**6**
	COW-01	4
	MEN-01	1
	TCH-01	1
Bubbia semecarpoides		**1**
	CHA-01	1
Canarium australasicum		**1**
	KOO-01	1
Canarium muelleri		**1**
	CHA-01	1
Cardwellia sublimis		**16**
	CHA-01	4
	CHE-01	3
	KBL-03	1
	KOO-01	2

	ROB-01	6
Castanospermum australe		**4**
	BKB-01	2
	MEN-01	1
	TCH-01	1
Cinnamomum laubatii		**1**
	CHE-01	1
Citronella smythii		**19**
	BKB-01	1
	KBL-03	5
	CHA-01	3
	CHE-01	1
	COW-01	2
	BKB-01	1
	MEN-01	1
	ROB-01	5
Cnesmocarpon dasyantha		**1**
	KOO-01	1
Crypoticarya putida		**1**
	CHA-01	1
Cryptocarya angulata		**9**
	CHM-01	2
	CHE-01	3
	KOO-01	2
	ROB-01	2
Cryptocarya bellendenkerana		**3**
	BKT-01	3
Cryptocarya corrugata		**2**
	CHA-01	1
	CHE-01	1
Cryptocarya leucophylla		**2**
	CHE-01	2
Cryptocarya lividula		**2**
	CHM-01	2
Cryptocarya mackinnoniana		**8**
	CHA-01	5
	BKB-01	1
	TCH-01	2
Cryptocarya melanocarpa		**14**
	CHA-01	2
	CHM-01	3
	KOO-01	3
	ROB-01	6
Cryptocarya oblata		**1**
	CHE-01	1
Cryptocarya putida		**5**
	CHA-01	1
	CHM-01	2
	KOO-01	2
Darlingia darlingiana		**17**
	CHA-01	4
	CHM-01	3
	KOO-01	2
	ROB-01	8
Diploglottis smithii		**1**
	COW-01	1
Doryphora aromatica		**2**
	BKB-01	1
	MEN-01	1
drypetes acuminata		**1**
	KBL-03	1

Dysoxylum klanderi		**1**
	CHA-01	1
Elaeocarpus largiflorens ssp. largiflorens		**3**
	CHA-01	1
	CHM-01	1
	CHE-01	1
Elaeocarpus sericopetalus		**1**
	CHM-01	1
Elaeocarpus sp. (Mt Bellenden Ker L.J.Brass 18336)		**3**
	CHE-01	1
	KOO-01	2
Endiandra compressa		**1**
	BKB-01	1
Endiandra dichrophylla		**1**
	CHA-01	1
Endiandra leptodendron		**1**
	COW-01	1
Endiandra montana		**2**
	KOO-01	2
Endiandra palmerstonii		**1**
	CHA-01	1
Flindersia bourjotiana		**31**
	CHA-01	5
	CHM-01	3
	KOO-01	10
	ROB-01	10
	TCH-01	3
Flindersia brayleyana		**4**
	KBL-03	2
	KOO-01	1
	ROB-01	1
Flindersia oppositifolia		**3**
	BKT-01	3
Flindersia pimenteliana		**10**
	CHA-01	2
	CHM-01	6
	KOO-01	2
Franciscodendron laurifolium		**17**
	CHA-01	4
	KOO-01	11
	ROB-01	1
	TCH-01	1
Garcinia sp. (Davies Creek J.G.Tracey 14745)		**4**
	CHM-01	4
Gevuina bleasdalei		**3**
	CHE-01	1
	KOO-01	2
Gossia grayi		**2**
	KOO-01	2
Halfordia kendack		**1**
	KOO-01	1
Hedycarya loxocarya		**1**
	CHE-01	1
Irvingbaileya australis		**1**
	CHM-01	1
Leptospermum wooroonooron		**6**
	BKT-01	6
Litsea leefeana		**11**
	BKB-01	2

	ROB-01	6
	TCH-01	3
Lomatia fraxinifolia		**4**
	CHE-01	1
	KOO-01	2
	ROB-01	1
Melicope vitiflora		**1**
	COW-01	1
Mischocarpus lachnocarpus		**1**
	TCH-01	1
Musgravea stenostachya		**5**
	BKT-01	5
Myristica globosa ssp. muelleri		**4**
	COW-01	4
Myristica globulosa		**2**
	BKB-01	2
Myrsine achradifolia		**1**
	CHM-01	1
Myrsine porosa		**1**
	KOO-01	1
Neolitsea dealbata		**1**
	CHE-01	1
Polyscias australiana		**15**
	CHA-01	6
	KOO-01	3
	ROB-01	6
Pouteria euphlebia		**1**
	CHM-01	1
Pouteria myrsinodendron		**1**
	COW-01	1
Prunus turneriana		**10**
	CHA-01	1
	ROB-01	9
Pullea stutzeri		**2**
	KOO-01	2
Rhodamnia blairiana		**1**
	KOO-01	1
Sarcotoechia cuneata		**1**
	CHE-01	1
Sarcotoechia lanceolata		**3**
	CHA-01	2
	KOO-01	1
Sloanea langii		**1**
	TCH-01	1
Sloanea macbrydei		**1**
	TCH-01	1
Steganthera laxiflora ssp. laxiflora		**1**
	CHE-01	1
Sundacarpus amarus		**1**
	CHA-01	1
Symplocos cochinchinensis var. glaberrima		**1**
	KOO-01	1
Synima cordierorum		**1**
	COW-01	1
Syzygium apodophyllum		**3**
	CHA-01	3
Syzygium canicortex		**1**
	CHE-01	1
Syzygium cormiflorum		**2**
	COW-01	1

	TCH-01	1
Syzygium kuranda		**1**
	KOO-01	1
Syzygium wesa		**1**
	CHM-01	1
Toechima erythrocarpum		**23**
	BKB-01	2
	CHA-01	5
	COW-01	2
	BKB-01	1
	ROB-01	8
	TCH-01	3
Toechima monticola		**2**
	CHE-01	2
Uromyrtus metrosideros		**5**
	BKT-01	5
Xanthophyllum octandrum		**14**
	CHA-01	5
	CHM-01	3
	KBL-03	3
	MEN-01	2
	ROB-01	1

Table 2. Diameter growth rate at the study sites for the different tree species measured for a year (2010-2011), at the dry season of 2011, at the wet season of 2012 and at the wet season of 2013.

		Diameter growth rate (cm time^{-1})							
Species		**2010-2011**		**2011-d**		**2012-w**		**2013-w**	
	Study site	**min**	**max**	**min**	**max**	**min**	**max**	**min**	**max**
Acmena hemilampra var orophilla									
	BKT-01	0.05	0.07						
Antirhea tenuiflora									
	CHA-01	0.05	0.05			0.02	0.05		
Apodytes brachystylis									
	CHA-01			0.04	0.10	0.05	0.18		
	CHE-01	0.01	0.01	0.04	0.27	0.05	0.30	0.14	0.15
Argyrodendron peralatum									
	TCH-01			0.05	0.16	0.17	0.54	0.26	0.33
Balanops australiana									
	CHA-01					0.02	0.02		
	CHE-01	0.05	0.05	0.23	0.49	0.29	0.66	0.12	0.12
	KBL-03			0.01	0.01				
	KOO-01			0.08	0.08	0.19	0.27	0.17	0.18
Beilschmiedia bancroftii									
	CHE-01	0.04	0.04						
	TCH-01			0.05	0.38	0.25	0.46	0.19	0.22
Beilschmiedia tooram									
	CHA-01			0.06	0.25	0.04	0.21		
Brombya platynema									
	COW-01	0.11	0.37						
Canarium muelleri									
	CHA-01			0.03	0.03				
Cardwellia sublimis									
	CHA-01	0.13	0.13	0.02	0.25	0.28	0.33		
	CHE-01	0.31	0.31	0.36	0.36				
	KBL-03			0.26	0.26				
	KOO-01	0.04	0.04	0.20	0.20	0.05	0.23	0.21	0.21
	ROB-01	0.12	0.24	0.25	0.38	0.06	0.68	0.03	0.69
Citronella smythii									

	CHA-01	0.04	0.04			0.02	0.04		
	CHE-01			0.12	0.12	0.23	0.23		
	KBL-03			0.06	0.63				
	ROB-01	0.06	0.11	0.03	0.06	0.06	0.25	0.08	0.08
Crypoticarya putida									
	CHA-01			0.20	0.20	0.30	0.30		
Cryptocarya angulata									
	CHE-01	0.17	0.17	0.12	0.12	0.07	0.12	0.06	0.06
	ROB-01	0.03	0.03	0.05	0.44	0.08	0.11	0.11	0.16
Cryptocarya leucophylla									
	CHE-01			0.38	0.38	0.18	0.18		
Cryptocarya mackinnoniana									
	CHA-01			0.10	0.10	0.04	0.24		
	TCH-01			0.08	0.08				
Cryptocarya melanocarpa									
	CHA-01					0.21	0.21		
	KOO-01								
	ROB-01	0.05	0.05	0.02	0.18	0.02	0.09	0.04	0.25
Cryptocarya putida									
	CHA-01			0.08	0.08				
Darlingia darlingiana									
	CHA-01			0.10	0.15	0.06	0.15		
	ROB-01	0.04	0.14	0.02	0.08	0.03	0.38	0.13	0.36
Diploglottis smithii									
	COW-01	0.11	0.11						
Elaeocarpus largiflorens ssp. largiflorens									
	CHA-01					0.25	0.25		
Endiandra dichrophylla									
	CHA-01			0.15	0.15	0.16	0.16		
Endiandra palmerstonii									
	CHA-01	0.59	0.59	0.45	0.45	0.19	0.19		
Flindersia bourjotiana									
	CHA-01	0.44	0.44	0.05	0.68	0.24	0.47		
	KOO-01	0.38	0.93	0.06	0.66	0.01	0.32	0.10	0.19
	ROB-01	0.01	0.10	0.02	0.23	0.09	2.23	0.16	0.54
	TCH-01			0.06	0.14	0.22	0.26	0.13	0.13
Flindersia brayleyana									
	KBL-03			0.22	0.50				
	KOO-01							0.06	0.06
	ROB-01					0.14	0.14	0.26	0.26
Franciscodendron laurifolium									
	CHA-01			0.05	0.05	0.30	0.30		
	KOO-01	0.62	0.62	0.03	0.12	0.08	0.15	0.03	0.05
	TCH-01			0.07	0.07				
Leptospermum wooroonooron									
	BKT-01	0.07	0.07						
Litsea leefeana									
	BKB-01					0.13	0.21		
	ROB-01	0.09	0.09	0.06	0.10	0.08	0.52	0.13	0.29
	TCH-01	0.05	0.16			0.17	0.33		
Lomatia fraxinifolia									
	CHE-01					0.44	0.44		
	ROB-01			0.19	0.19	0.18	0.18	0.23	0.23
Musgravea stenostachya									
	BKT-01	0.02	0.13						
Myristica globosa ssp. muelleri									
	COW-01	0.25	0.25						
Myristica globulosa									
	BKB-01					0.12	0.16		
Neolitsea dealbata									

	CHE-01					0.11	0.11		
Polyscias australiana									
	CHA-01	0.19	0.19			0.02	0.05		
	KOO-01	0.04	0.04	0.27	0.27	0.04	0.08	0.07	0.07
	ROB-01	0.08	0.14	0.12	0.17	0.07	0.21	0.04	0.18
Prunus turneriana									
	CHA-01			0.35	0.35	0.41	0.41		
	ROB-01	0.05	0.10	0.04	0.16	0.04	0.55	0.05	0.25
Syzygium apodophyllum									
	CHA-01			0.32	0.41	0.06	0.32		
Syzygium cormiflorum									
	TCH-01	0.09	0.09						
Toechima erythrocarpum									
	CHA-01	0.20	0.20	0.01	0.05	0.06	0.20		
	COW-01	0.06	0.06						
	BKB-01								
	ROB-01	0.04	0.11	0.05	0.20	0.04	0.46	0.05	0.12
	TCH-01	0.02	0.02	0.07	0.17				
Toechima monticola									
	CHE-01	0.09	0.09					0.05	0.05
Uromyrtus metrosideros									
	BKT-01	0.04	0.04						
Xanthophyllum octandrum									
	CHA-01					0.02	0.07		
	KBL-03								
	ROB-01	0.07	0.07						

Appendix Ch5

Table 1. ϱ and CWDτ_f for the forest and savannah tree species at the study sites for all the *DS*.

	ϱ (g cm^{-3})						CWD τ_f (years)					
Tree species	**Study site**											
	BK-T		**CHA**		**BK-B**		**BK-T**		**CHA**		**BK-B**	
Collection site	**Av.**	**Cv**	**Av.**	**Cv**	**Av.**	**Cv**	**Av.**	**Cv**	**Av.**	**Cv**	**Av.**	**Cv**
Backhousia bancroftii												
BK-B												
W_F	820	0.20	910	0.08	940	0.05	26.46	0.47	9.70	0.20	12.54	0.86
W_M	430	0.10	440	0.09	440	0.10	5.02	0.34	1.59	0.28	1.40	0.64
W_D	270	0.49	230	0.44	200	0.45	1.08	0.25	1.17	0.42	1.84	0.33
Balanops australiana												
BK-T												
W_F	780	0.02	800	0.06	790	0.01	5.60	0.96	3.97	0.66	3.15	0.85
W_M	740	0.18	730	0.11	660	0.17	3.84	0.52	1.87	0.92	1.56	0.94
W_D	520	0.32	450	0.35	610	0.20	1.73	0.73	1.49	0.78	1.02	0.25
MAL												
W_F	840	0.09	860	0.06	870	0.15	10.02	0.77	6.91	0.83	4.64	0.44
W_M	790	0.19	810	0.06	780	0.34	6.85	0.79	4.45	0.47	3.98	0.64
W_D	640	0.30	490	0.18	560	0.26	6.01	0.38	3.19	0.85	3.11	0.73
INI												
W_F	820	0.08	0.88	0.10	840	0.03	7.63	0.72	3.85	0.83	3.80	0.87
W_M	640	0.35	0.52	0.26	520	0.17	7.70	0.87	2.74	0.29	3.34	0.40
W_D	0.45	0.10	0.38	0.05	410	0.17	4.13	0.29	4.02	0.59	3.21	0.43
Cryptocarya oblata												
KAR												
W_F	940	0.08	910	0.10	910	0.07	45.00	0.79	14.57	0.42	8.61	0.69
Elaeocarpus ferruginiflorus												
BK-T												
W_F	420	0.42	440	0.41	430	0.48	3.47	0.42	3.25	0.44	1.96	0.23
W_M	330	0.51	330	0.28	330	0.21	3.14	0.79	1.95	0.48	2.01	0.67
Franciscodendron laurifolium												
BK-B												
W_M	410	0.11	430	0.04	420	0.03	5.63	0.67	3.92	0.53	1.75	0.68
W_D	470	0.08	450	0.08	450	0.10	5.62	0.72	2.83	0.61	2.38	0.32
KAR												

W_F	610	0.09	530	0.14	590	0.10	7.45	0.76	3.21	0.51	2.75	0.68
W_M	590	0.02	500	0.11	480	0.22	4.93	0.62	3.73	0.46	3.36	0.62
Leptospermum wooroonooran												
BK-T												
W_F	1000	0.16	930	0.11	870	0.10	22.04	0.81	13.78	0.38	12.37	0.54
W_M	520	0.12	500	0.51	520	0.50	8.22	0.87	7.20	0.61	5.45	0.10
W_D	590	0.23	570	0.07	590	0.20	8.00	0.55	5.49	0.85	3.03	0.35
Eucalyptus sp.												
DAV												
W_F	1001	0.05	1001	0.05	960	0.17	29.72	0.82	23.15	0.99	13.53	0.84

Table 2. C_f and N_f for the forest and savannah tree species at the study sites for all the *DS*.

Tree species	**C_f abundance**						**N_f abundance**					
	Study sites											
	BK-T		**CHA**		**BK-B**		**BK-T**		**CHA**		**BK-B**	
Collection site	**Av. C**	**Cv**	**Av.C**	**Cv**	**Av. C**	**Cv**	**Av. N**	**Cv**	**Av. N**	**Cv**	**Av. N**	**Cv**
Backhousia bancroftii												
BK-B												
W_F	46.62	0.97	44.45	0.93	47.43	0.97	0.20	0.90	0.16	0.88	0.17	0.75
W_M	44.27	1.00	47.14	0.95	44.70	0.98	0.21	0.47	0.52	0.39	0.37	0.23
W_D	40.95	0.94	43.19	0.92	44.34	0.92	0.56	0.52	0.55	0.36	0.64	0.54
Balanops australiana												
BK-T												
W_F	44.59	0.99	44.92	0.95	45.47	0.99	0.13	0.53	0.14	0.59	0.18	0.68
W_M	44.57	0.98	44.23	0.97	44.92	0.95	0.14	0.67	0.26	0.39	0.25	0.30
W_D	45.65	0.99	46.61	0.94	46.02	0.98	0.22	0.68	0.27	0.86	0.38	0.46
MAL												
W_F	44.13	0.98	45.75	0.98	45.02	0.99	0.11	0.83	0.18	0.41	0.17	0.62
W_M	44.13	0.96	44.80	0.96	44.93	0.99	0.12	0.79	0.16	0.58	0.19	0.54
W_D	44.50	0.98	45.80	0.97	45.23	0.99	0.20	0.42	0.21	0.56	0.26	0.41
INI												
W_F	43.71	0.99	45.24	0.97	45.22	0.98	0.13	0.63	0.16	0.74	0.18	0.85
W_M	44.04	0.96	45.76	0.99	45.51	0.97	0.18	0.55	0.28	0.36	0.32	0.78

W_D	44.84	0.98	46.39	0.97	45.46	0.99	0.46	0.60	0.32	0.44	0.63	0.57
Cryptocarya oblata												
KAR												
W_F	45.13	0.89	47.12	0.96	47.17	0.96	0.12	0.92	0.14	0.43	0.22	0.40
Elaeocarpus ferruginiflorus												
BK-T												
W_F	45.48	0.97	45.87	0.91	45.75	0.97	0.34	0.53	0.32	0.64	0.56	0.28
W_M	46.19	0.97	46.35	0.98	46.28	0.97	0.34	0.65	0.44	0.72	0.43	0.46
Franciscodendron laurifolium												
KAR												
W_F	45.14	0.99	46.45	0.96	46.56	0.98	0.23	0.77	0.31	0.33	0.25	0.61
W_M	46.08	0.97	45.83	0.98	46.36	0.99	0.33	0.38	0.47	0.70	0.35	0.67
BK-B												
W_M	45.00	0.98	45.80	0.94	45.52	0.99	0.26	0.60	0.39	0.74	0.41	0.14
W_D	45.53	0.96	44.90	0.97	45.54	0.99	0.31	0.85	0.34	0.43	0.53	0.72
Leptospermum wooroonooran												
BK-T												
W_F	46.55	0.95	47.02	0.92	46.48	0.99	0.12	0.92	0.10	0.67	0.12	0.47
W_M	45.53	0.96	45.51	0.94	45.28	0.91	0.16	0.68	0.16	0.42	0.28	0.16
W_D	45.91	0.99	47.98	0.98	46.02	0.96	0.16	0.88	0.17	0.83	0.27	0.70
Eucalyptus sp.												
DAV												
W_F	46.27	1.00	47.07	0.97	46.91	0.98	0.06	0.71	0.03	1.00	0.10	0.26