

**Allometry, biomass and litter decomposition of the New Zealand
mangrove *Avicennia marina* var. *australasica***

Phan Tran

A thesis submitted to Auckland University of Technology
in partial fulfilment of the requirements for the degree
of
Masters of Science (MSc)

2014

School of Applied Sciences

Table of contents

Table of contents	i
List of Figures	iii
List of tables	vi
Attestation of authorship	vii
Co-Authored Works	viii
Acknowledgements	ix
Abstract	x
Chapter 1. Introduction	1
1.1 Mangrove ecosystems.....	2
1.2 Global patterns of mangrove forests.....	3
1.3 Mangrove ecosystem services	4
1.4 Mangrove carbon studies	6
1.5 New Zealand mangroves	7
1.6 Research questions:.....	9
1.7 Outline of chapters:.....	9
Chapter 2. Allometry and biomass allocation.....	10
2.1 Introduction.....	11
2.2 Methods and Materials.....	14
<i>Study areas</i>	14
<i>Allometry and Leaf Area Index (LAI)</i>	15
<i>Above-ground biomass:</i>	16
<i>Below-ground biomass</i>	19
2.3 Results.....	20
<i>Allometry and LAI of mangrove stands</i>	20
<i>Biomass partitioning</i>	21
<i>Vertical distribution of biomass</i>	23
2.4 Discussion.....	24

<i>Above-ground biomass</i>	24
<i>Belowground biomass</i>	26
<i>Allometric equation:</i>	27
<i>Limitations</i>	28
Chapter 3: Litter production and decomposition	30
3.1 Introduction	31
<i>Litterfall</i>	31
<i>Litterfall in mangrove forests</i>	32
<i>Litter decomposition</i>	33
<i>Mangrove litter decomposition</i>	33
3.2 Methodology	35
<i>Site selection</i>	35
<i>Litterfall</i>	35
<i>Decomposition</i>	37
3.3 Results	37
3.3.1 <i>Litterfall</i>	37
3.3.2 <i>Litter decomposition</i>	42
3.4 Discussion	45
<i>Litterfall</i>	45
<i>Litter decomposition</i>	48
3.5 Conclusions	49
Chapter 4. General discussion and implications for conservation and management	51
4.1 Summary of main results	52
<i>Allometry and LAI</i>	52
<i>Biomass distribution</i>	52
<i>Litterfall production</i>	52
<i>Litter decomposition</i>	53
4.2 Conclusions and implication for conservation and management	53
References	56

List of Figures

- Figure 1. Major components of (mangrove) forest carbon pool and its cycle among ecosystems. Figure modified from Bouillon et al.(2008). 6
- Figure 2. Mangawhai Heads with five study sub-sites of Jack Boyd (JB), Molesworth (MO), Island (IS), Insley (IN) and Black Swamp (BS). 15
- Figure 3. Basal area against dry wood and leaf mass at Black Swamp, Mangawhai Harbour Estuary. The linear model $Y = x * ba$ was used, with Y the wood / leaf dry weight and *ba* the basal area. R-squared is 0.94 for both plots. 18
- Figure 4. Biomass allocation (%) estimated from the mean values of JB and MO sites in Mangawhai Harbour. 23
- Figure 5. Vertical distribution of biomass estimated for compartments per players on Mangawhai Harbour, with mean values and standard errors estimated among the sub-sites of JB, MO, IS and IN for wood and leaf biomass, JB,MO, and IS for pneumatophores and seedling, fine roots biomass and coarse roots under 40cm deep, and JB, MO and BS for coarse roots from 0-40cm deep. 24
- Figure 6. Quadratic model $Y = x * ba^2$ used for the regression of dry wood on basal area, with Y the dry wood mass, *ba* the basal area. Data from the Black Swamp site at Mangawhai Harbour Estuary. 27
- Figure 7. Basal area against total leaf mass (a) and leaf mass by height (b) at Black Swamp, Mangawhai Harbour Estuary. The linear model $Y = x * ba$ was used, with Y the leaf dry weight and *ba* the basal area. R-squared is 0.94 for the relationship between *ba* and total leaf dry weight, and are 0.34, 0.54, 0.52, and 0.79 for the relationship between *ba* and leaf dry weight at 150-200cm, 200-250cm, 250-300cm, and 300-350cm respectively. 28
- Figure 8. Locations of litter traps and litter bags at JB (a), MO (b), and IS (c) at the Mangawhai Harbour study area. 36

- Figure 9. Seasonal litter production at Mangawhai Harbour ($\text{gm}^{-2}\text{day}^{-1}$), with the mean values for each litter component calculated from thirty traps across all sites. Error bars represent one standard error ($n=30$). 39
- Figure 10. Site-specific seasonal litter production and monthly mean temperature ($^{\circ}\text{C}$) measured at Mangawhai Harbour. Error bars represent the standard errors for the mean values of litter from ten traps ($n=10$) for each site Jack Boyd (JB), Molesworth (MO) and Island (IS). 40
- Figure 11. Site-specific seasonal litter production and monthly max wind speed (kmh^{-1}) measured at Mangawhai Harbour. Error bars represent the standard errors for the mean values of litter from ten traps ($n=10$) for each site Jack Boyd (JB), Molesworth (MO) and Island (IS). 41
- Figure 12. Site-specific seasonal litter production and monthly total rainfall (mm) measured at Mangawhai Harbour. Error bars represent the standard errors for the mean values of litter from ten traps ($n=10$) for each site Jack Boyd (JB), Molesworth (MO) and Island (IS). 42
- Figure 13. Mangrove leaf litter decomposition measured at Mangawhai Harbour, expressed as the percentage of initial dry weight remaining over time. Error bars represent the standard errors for the mean values twelve litter bags ($n=10$) collected each site Jack Boyd (JB), Molesworth (MO) and Island (IS). 43
- Figure 14. Asymptotic model fit $y = \text{Asym} + (R_0 - \text{Asym}) * \exp(-\exp(\text{lrc}) * x)$ with y the remaining weight over time), R_0 the estimated intercept on the y-axis, Asym the asymptote parallel to the x-axis, and lrc is the estimated logarithm of the rate constant, applied generally for litter decomposition process at Mangawhai Harbour. 44
- Figure 15. Asymptotic fit model $y_{\text{site}} = \text{Asym} + (R_0 - \text{Asym}) * \exp(-\exp(\text{lrc}_{\text{site}}) * x)$, with y the the percentage of remaining weight over time, R_0 the estimated intercept on the y-axis, Asym the asymptote parallel to the x-axis, and lrc the estimated logarithm of the rate constant applied site-specifically for IS (a), MO (b), and JB (c) at Mangawhai Harbour. 45

Figure 16. Carbon pools (kg C m^{-2}) and fluxes ($\text{kg C m}^{-2}\text{y}^{-1}$) of *A.marina* with study results at Mangawhai Harbour (black text) and assumed figures (red text) based on data from Suwa et al. (2006), Ray et al. (2011), and Alongi (2014). 54

List of tables

Table 1. Traditional uses of mangroves	5
Table 2. Allometric characteristics of the eleven sample trees at BS	17
Table 3. R-squared values for linear regressions between basal area and biomass of the individual layers.....	19
Table 4. Measurement methods (cores/blocks) for below-ground biomass conducted at each sites of Jack Boyd (JB), Molesworth (MO), Island (IS) and Black Swamp (BS) .	20
Table 5. Allometry of <i>Avicennia marina</i> in the study transects at Insley (IN), Island (IS), Jack Boyd (JB) and Molesworth (MO).....	21
Table 6. Leaf area index (LAI) and Specific Leaf Area (SLA) for the sites Black Swamp (BS), Island (IS), Jack Boyd (JB) and Molesworth (MO)	21
Table 7. Biomass allocation in wood, leaf, roots and pneumatophores and seedlings for the sites Insley (IN), Island (IS), Jack Boyd (JB) and Molesworth (MO).....	22
Table 8. Biomass estimation for <i>A. marina</i> in Australia and New Zealand sites	25
Table 9. Total litter fall (gm^{-2}) at IS, JB, and MO from April 2013 to March 2014.....	38
Table 10. Litterfall production of <i>A. marina</i> presented in order of latitudes	46

Attestation of authorship

“I hereby declare that this submission is my own work and that, to best of my knowledge and belief, contains no material previously published or written by another person (except where explicitly defined in the acknowledgements), nor material which to a substantial extent has been submitted to the award of any other degree or diploma of university or other institution of higher learning.”

Signed

A handwritten signature in blue ink, appearing to be 'R. Hal', written over a horizontal line.

Date: Aug 22, 2014

Co-Authored Works

The two main chapters of this thesis are in preparation to be submitted to the New Zealand Journal of Marine and Freshwater Research. To this work, although I am the principal author, I have received intellectual contribution from my supervisors through their valuable advice, which can hardly weigh. I identify authorship contribution as 85 % from myself, 10 % from Sebastian Leuzinger (primary supervisor), and 5 % from Andrea Alfaro (secondary supervisor).

Signatures:

Principal author:



Phan Tran

Co-Author



Sebastian Leuzinger

Co-Author



Andrea C. Alfaro

Acknowledgements

I would like to express my deepest gratitude to my primary supervisor, Dr. Sebastian Leuzinger, for giving me the opportunity to complete this thesis. I could hardly have done without his devoted guidance and valuable advice. My sincere thanks are also to my secondary supervisor, Prof. Andrea C. Alfaro and my senior Jarrod Cusens for their helpful comments to make this study much better.

I owe the Mangrove research team, especially Iana Gritcan, and other student peers for their dedicated help during my field work, which were highly labour-intensive. I also found myself indebted to the New Zealand Ministry of Foreign Affairs and Trade for their sponsorship for my study with AUT under New Zealand ASEAN Scholars Awards program.

It would be difficult for me to finish this study without supports and encouragement from my family and especially my husband, Jobi George, for his sharing of family responsibilities during my academic years.

Last but not least, I would like to reserve my thankfulness to AUT Applied Sciences LAB staff for their supports, which is also much important for me to complete my study.

Abstract

Accurate estimates for biomass pools and fluxes are the key for assessing the potential of vegetation to counteract anthropogenic carbon emissions. However, such data are laborious to retrieve and still missing for many ecosystems. In this study, I used the harvest method to estimate above- and below-ground biomass, and litter traps and litterbags to measure litterfall and decomposition of the New Zealand mangrove *Avicennia marina* var. *australasica* at Mangawhai Harbour, northern New Zealand from April 2013 to March 2014.

Total above-ground biomass of *A. marina* was estimated at 2.69 - 8.88 kg m⁻² and below-ground biomass at 11.62 - 14.7 kg m⁻². The root-shoot ratio at this site was 1.73. Fine roots contributed most to the biomass stock with almost 50 % of the below-ground and 37 % of the total biomass. Woody biomass made up 32 %, coarse roots 27 %, leaf biomass 3 %, and pneumatophores and seedlings 1 % of the total biomass. More than 70 % of the root mass was located within 40 cm below the surface.

Annual litterfall production of *A. marina* was estimated as 331.94±69.8 - 476.63±66.1 g m⁻² y⁻¹, with leaf litter accounting for 66.6 % - 82.3 %. Litterfall production positively correlated with temperature but it did not show any relationship with monthly maximum wind speed nor total rainfall. Leaf litter of *A. marina* at Mangawhai harbour decomposed rapidly during the first 37-39 days with 50-60 % of the initial dry weight lost. A further ~15-25 % was lost during the following 40 days, after which biomass loss became even slower. Litter decomposition was 96.5 % complete after 332 days with the average (linear) rate of decomposition of -3.99 % per day.

From my findings, New Zealand mangroves store a total of 0.2 - 1.1 Mt carbon (C) above-ground and 1.06 - 1.72 Mt C below-ground. This, together with the high carbon density (6 - 9.9kg C m⁻²), implies that New Zealand mangroves are carbon-rich ecosystems.

Chapter 1. Introduction

1.1 Mangrove ecosystems

Mangroves are salt-tolerant plants that are well adapted to intertidal areas within estuaries and protected coastlines. According to Alongi (2002), there are about 70 species of mangroves belonging to 27 genera, 20 families and 9 orders; while Spalding et al. (2010) considered 73 species and hybrids as ‘true mangroves’ – the species that ‘have adapted to this environment and are rarely, if ever, found elsewhere’. Among these, Spalding et al. (2010) also highlighted 38 ‘core’ species, which dominate in most locations. The uncertain classification of mangrove species is due to hybridization commonly observed in mangroves (Clough, 2013).

Mangrove plants are tolerant to high salinity, long periods of inundation and soil anoxia (Saenger, 2002). Paliyavuth et al. (2004) showed that many species of mangrove can grow well in salinity of up to 40 ‰ and exclude from 85 % up to 99 % of the external salt (sodium and chloride) during water uptake, although the mechanisms involved in salt exclusion are still not fully understood.

To cope with the inundated and anaerobic condition of the ground, most mangrove species have specialised aerial roots that extend above the ground for oxygen. In addition, since mangroves occur at places which are often exposed to high winds and strong waves or near-shore ocean currents, their root systems are adapted to keep them upright and stable in soft, unstable soils (Saenger, 2002).

Mangroves have a range of leaf adaptations that can help to reduce water loss, including sunken stomata, leaf hairs that cover the surface of the leaf, thick cuticles and waxy coatings. Their propagules are often dispersed by water currents, and may survive in the water column while dispersed as far as fifty kilometres away from their parent trees (Clarke, 1993).

Mangroves act as a natural boundary between terrestrial and marine environments, providing habitats and resources, including spawning grounds, nurseries and nutrients (FAO, 2007), for a variety of faunal communities from mammals, reptiles, birds, crustaceans, molluscs, fish, insects, worms, to microscopic organisms such as nematodes, fungi and bacteria (Clough, 2013).

1.2 Global patterns of mangrove forests

The total area of mangrove forests was estimated to be 157,050 km² (FAO, 2007), which made up less than 1 per cent of tropical forests worldwide, and less than 0.4 per cent of the global total forest estate area (Spalding et al., 2010). Mangroves are mainly distributed in the warm climate of the tropics and subtropics with a few species extending to temperate regions. In the northern hemisphere, they extend to 35°68 N (Japan) and their southernmost limit is 38°03'S (Australia and New Zealand) (FAO, 2007).

The global occurrence of mangroves were categorised differently, either in six distinct zones from east to west separated by land or oceanic barriers that prevent migration from one zone to another (Clough, 2013), or the ten regions with major breaks by latitudinal limitation, distance and temperature condition (Spalding et al., 2010). FAO (2007), however, divided mangrove ecosystems into five regions corresponding to continental division with Asia showing the largest extent of mangroves (almost 40 %) followed by Africa and North and Central America.

The region comprising Southeast Asia and the western Pacific Islands (the Indo-Pacific) is the global epicentre of mangroves and tropical forests (FAO 2007). Approximately 40 % of the world's mangroves, or 6 million ha, occur in this region alone. There, standing biomass per unit surface area reaches higher values than in any other place (Komiya et al. 2008). Another study on mangroves in this region also showed that the total carbon pool (total living biomass) in these tropical mangrove ecosystems, which ranged from 8.6 to 10.7 kg C m⁻², was exceptionally high compared with most forest types (Murdiyarso et al., 2010). This resulted from a combination of large-stature forest (with trees up to 2 m in diameter) and organic-rich sediment to the depth of 5 metres or more (Murdiyarso et al., 2010) in these forests.

Temperate mangroves comprise up to six species to their northern global limits and up to three species at the southern limits (Morrissey et al., 2010). The genus *Avicennia* has most common species that persist within temperate regions (*marina* and *germinans*). Small xylem vessel diameters found in these species help prevent the formation of air bubbles (cavitation) in the xylem at freezing temperatures but, at the same time, affects the rate of water transport within stems, which in turn limits photosynthesis and carbon gain, potentially reducing growth rates (Stuart et al., 2007).

Temperate mangroves provide different ecosystem services than their tropical counterparts. Saenger & Snedaker (1993) suggested temperate mangroves had lower productivity and biomass, although this was not true for shorter temperate mangrove communities, which produced larger litter-fall relative to their biomass than tropical ones. Ellison (2002), by considering the relationships between species richness and latitude, illustrated that mangroves at higher latitudes had lower species richness. This pattern is actually common for other terrestrial forests (Gaston, 2007) and a universal pattern among almost all plants and animals (Hillebrand, 2004). Temperate mangroves were also found to have lower faunal densities than their tropical counterparts (Ellis et al., 2004) and also support a lower density and diversity of benthic fauna compared to adjacent estuarine habitats (Alfaro, 2006).

1.3 Mangrove ecosystem services

Mangrove products are traditionally used by many indigenous populations, especially in developing countries where livelihoods still heavily depend on primary resources. Spalding et al. (2010) reviewed the economic values of mangrove ecosystems, which were believed to make up to a total of 2,060-9,270 USD/ha/year.

The uses of mangrove products are summarised in Table 1.

Table 1. Traditional uses of mangroves

Fuel	Fuel-wood, charcoal
Construction	Timber, construction, scaffolding, mining props, railway sleepers, boat-building, dock pilings, thatch or matting, beams and poles, flooring, fence posts, paneling, chipboard
Fishing	Fishing stakes, wood for smoking fish, fishing boats, tannin for nets/lines, fish-attracting shelters
Textile, leather	Synthetic fibres (rayon), tannin for leather preservation, dye for cloth
Other natural products	Fish, crustaceans, honey, wax, mammals, birds, reptiles, other fauna
Food, drugs and beverages	Sugar, cooking oil, alcohol, vinegar, fermented drinks, tea substitute, dessert topping, condiments (bark), vegetables (fruit/leaves), sweetmeats (propagules)
Agriculture	Fodder
Household items	Glue, hairdressing oil, tool handles, rice mortar, toys, match sticks, incense
Other forest products	Packing boxes, wood for smoking sheet rubber, medicines, paper, hard soap, and ecotourism resources

Source: modified from FAO (2007), Lacerda & Santos (2004) and Ong & Gong (2013)

Mangroves play a special role in bio-filtration with their ability to constrain water movements and to trap sediments, which is particularly important in retaining contaminants from nearby catchments and urban areas. Their high productivity (Spalding et al., 2010) enables them to remove excess nutrients and other pollutants from sewage and aquaculture discharge.

Similar to coral reefs, mangroves are believed to absorb and attenuate wave energy (Alongi, 2009) and serve as natural barriers against storm surges that can cause damage to coastlines and communities. Their complex root systems help bind and consolidate sediment, reducing erosion. Apart from playing a protective role shoreward to coastal environments, mangrove forests, in connectivity with other marine ecosystems, also help increase the resilience of offshore coral reefs by supporting habitats for coral grazing species (parrot fish, Mumby & Hastings 2008).

Although carbon uptake and sequestration are fundamental characteristics of plant ecosystems, the small total area of mangroves (less than 0.4 per cent of the global total forest estate, Spalding et al. 2010) may easily lead to an underestimation of their role in

mitigating carbon emission. In fact, their larger proportion of below-ground biomass (compared to above-ground, Briggs, 1977) makes their total biomass carbon per unit surface area the higher ($\sim 21.8 \text{ kg C m}^{-2}$) than that of taller terrestrial forests ($\sim 14.5 \text{ kg C m}^{-2}$ in tropical rainforest and 12.4 kg C m^{-2} in tropical mountain systems) as reviewed by Pan et al. (2013). Komiyama et al. (2008) also highlighted that mangrove forests are highly efficient carbon sinks in the tropics. This motivates the investigation of the role mangroves may play in global carbon budgets in the topical context of global warming.

1.4 Mangrove carbon studies

A carbon budget is the balance between carbon accumulation and release of a given ecosystem. Forests are complex ecosystems, and good estimates for carbon uptake and release are can be extremely difficult to achieve. The same is true for estimating carbon pools, as particularly underground carbon pools are difficult to quantify.

Plants accumulate carbon through carbon dioxide capture from the atmosphere and growth and release it in the process of respiration. Dead plant material (wood, leaves, roots) enters the pool of necromass (dead biomass) before it is eventually respired and thus released back to the atmosphere (Figure 1). This flux can be measured relatively easily above ground using litter fall traps. The final quantity of interest in a forest carbon budget is the net change of the total carbon pool over time. A carbon pool can either be a carbon sink (net accumulation of carbon over time) or a carbon source (net loss of carbon over time).

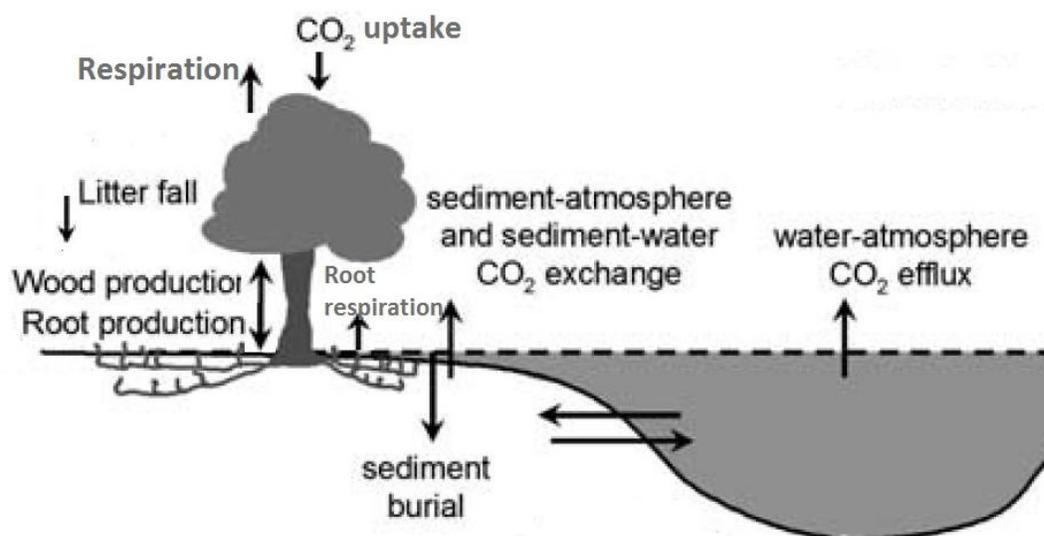


Figure 1. Major components of (mangrove) forest carbon pools and fluxes among ecosystems. Figure modified from Bouillon et al. (2008).

Global studies/reviews of plant carbon stocks (Litton et al. 2007, Gorte 2009, Pan et al. 2013, Le Quere et al. 2013) have presented tropical forests as the biggest carbon pools, followed by boreal forests, then temperate forests. Pan et al. (2013) have showed the extremely high carbon density of mangrove forests compared to rest of the ecosystems.

Mangrove forests also appeared to be highly productive ecosystems with canopy net carbon uptake estimated about $2.9 \text{ kg C m}^{-2}\text{y}^{-1}$ (Clough, 1998) and gross primary productivity (GPP) of $7.5 - 15 \text{ kg C m}^{-2}\text{y}^{-1}$ (Eong, 1993). C fluxes from mangrove forests were, however, also comparatively high with 80 % - 90 % of the GPP returned to the atmosphere as respired carbon dioxide, leaving an estimated $0.7-1.8 \text{ kg C m}^{-2}\text{y}^{-1}$ as net primary productivity (NPP) (Eong, 1993). In another study, Bouillon et al.(2008) presented an estimate of $218 \pm 72 \text{ Tg C y}^{-1}$ of global mangrove primary production, of which only about 45 % was reported as carbon burial, organic carbon export and CO_2 emission from sediments and the water column, leaving $112 \pm 85 \text{ Tg C y}^{-1}$ unaccounted for in current budgets. In comparison to the total C flux of the world's forests (900 Tg C y^{-1}) (Dixon, 1994), mangrove C fluxes are considerable especially considering that mangroves make up less than 0.4 per cent of the global forest (Spalding, 2010). Donato et al. (2011) suggested that high productivity and C flux rates in mangroves were indeed accompanied by high C storage, especially below ground, implying mangroves are a globally important surface C reserve.

The change in standing biomass as a result of imbalances between carbon in- and output is a key variable for understanding forest carbon budgets. Direct measurement of changes in biomass density helps indicate the magnitude and distribution of at least the largest carbon sources (from land use change) and sinks (from woody growth). While litterfall, which made up ~ 31 % of NPP (Bouillon et al 2008) is important for the study of mangrove primary production, litter decomposition estimates how fast the accumulated biomass dissolves back to other pools. This information is needed for our understanding of the carbon cycle, including better information on the magnitude and mechanisms that make forests sources or sinks of carbon.

1.5 New Zealand mangroves

New Zealand has only one mangrove species, *Avicennia marina* var. *australasica* and it grows only in northern estuaries of the north island, ranging from Ohiwa Harbour ($38^{\circ}03'S$;

southern limit) to Northland (34°27'S; Harty, 2009). This species is able to grow and reproduce in variable conditions of tide, climate and edaphon. It occupies, therefore a diverse range of coastal habitats and displays great variability of growth forms (Morrisey et al., 2010). In contrast to tropical mangroves, there is evidence for the expansion of *A. marina* var. *australasica* over the past decades in New Zealand (Morrisey et al, 2007). The public view of mangroves also remains polarised, with some advocating for the conservation of mangroves while others see mangroves as a nuisance and relate their expansion to a loss of economic and aesthetic values of the harbours. Despite New Zealand's principal environmental legislation (the Resource Management Act 1991), which allows governing bodies to uphold protection of mangroves against indiscriminate destruction or reclamation, management initiatives have conflicted due to limited available scientific information and diverging views of how mangrove expansion may affect the various stakeholders' interests.

A number of studies have been conducted on the benthic assemblages and species of mangrove forests in New Zealand. Alfaro (2006) found mangrove forests have the lowest faunal assemblages among six distinct habitats of mangrove stands, the pneumatophore zones, seagrass, channels, banks and sand-flats. Ellis et al. (2004) studied the effects of high sedimentation rates on mangrove communities and associated benthic community composition and found sediment mudflats without mangroves had similar benthic composition to mangrove sites, suggesting that increased silt/clay fraction from sedimentation is more meaningful to the benthic composition than the presence or absence of the mangroves themselves. These results contradict those in tropical mangroves (Thailand), where impacts of mangrove forest development and maturity on benthic faunal richness and diversity showed a tendency toward more diverse assemblages in undisturbed and mature forests (Suzuki et al., 1997, 2002). Ongoing monitoring and research conducted in New Zealand for both intact mangrove systems and those where mangroves have been removed are contributing to answer the scientific and management question.

Although annual net primary production of temperate mangroves is known to be lower than their tropical counterparts, knowledge of how they differ in other components of the carbon budget is not well documented. A better understanding of mangrove carbon budgets and their nutrient cycling will contribute to better management and conservation of mangrove ecosystem in New Zealand.

In Mangawai Harbour Estuary, located 100 km northern of Auckland city, mangrove removal is currently debated and partly approved by council permits (0.26-ha fringe of mangrove trees for water access). This provides an opportunity to conduct studies on the ecological importance of mangrove *A. marina* var. *australasica* in New Zealand.

1.6 Research questions:

- How much above- and belowground standing biomass is present *A. marina* var. *australasica* stands in the Mangawhai Harbour estuary ?
- How much litterfall is produced by these stands and what are the rates of litter decomposition ?

The specific aims include:

- To identify the basic allometric parameters (height, stem diameter distribution) and leaf area index (LAI) of *A. marina* var. *australasica* in Mangawhai.
- To determine total biomass of mangrove forests in Mangawhai, layered horizontally and as contribution from tree components.
- To determine litter production and decomposition rates, in relation to sediment/substrate and hydrological conditions using litter traps and litter bags.

1.7 Outline of chapters:

Chapter 1 provides a general introduction about mangrove ecosystems and their position in the global carbon budget.

Chapter 2 describes allometry and biomass of both above and below ground, layered horizontally and partially (wood and leaf).

Chapter 3 describes the litter fall and litter decomposition process, relating to the function of tidal immersion and substrate types, seasonal temperature and velocity.

Chapter 4 concludes the study results and implies conservation and management of mangrove in New Zealand.

Chapter 2. Allometry and biomass allocation

2.1 Introduction

The largest pool of terrestrial carbon is found in the woody biomass of forests (ca. 80 % of terrestrial carbon; Saugier, Roy, & Mooney, 2001). In the context of global warming, the study of tree biomass is helpful in the identification of important carbon pools for better land use management. Biomass studies also provide the baseline for studies of the carbon cycle (carbon fluxes). Biomass inventories therefore provide a comprehensive basis for estimates on carbon pools and fluxes for climate change reports.

Biomass in plant science is defined as "the total weight of the living components (producers, consumers, and decomposers) in an ecosystem at any given moment" (Albany, 2013) and usually expressed as dry weight per unit area. Biomass can be divided between above-ground (all the living parts of the plants above the soil surface) and below-ground biomass (the entire biomass of all live roots). Necromass, dead plants and the dead parts of living plants, is not included in this definition.

The total biomass of the world was recently estimated at 363 Pg C, with a mean density of 9.4 kg C m⁻² (Pan et al., 2013). Biomass is not evenly spread across biomes and values range from less than 0.5 kg C m⁻² in grasslands, croplands, and deserts to more than 30kg C m⁻² in some tropical forests (Houghton et al., 2009). The average biomass carbon density of mangrove trees has been reported to be 21.8 ±17.3kg C m⁻² (Pan et al., 2013), which puts mangrove forests among the largest carbon pools per unit surface area on Earth.

With increasing latitudes, mangroves are ultimately limited by temperature and have a trend of declining biomass (Morrisey et al., 2010). Mangrove biomass estimates have been reported to range from 5.7–43.6 kgm⁻² in the tropics between 23°N to 23°S, to 0.8–16.4 kgm⁻² between 23 and 30° (Saenger & Snedaker, 1993). At smaller scales, waves, tides, rivers and rainfall are major factors affecting the abundance and biomass of mangroves because these factors affect water circulation, influencing the rate of erosion and deposition of sediments on which mangroves grow (Alongi, 2002).

While aboveground terrestrial forest biomass accounts for 70–90 % of total forest biomass (Cairns et al., 1997), mangroves maintain a bottom-heavy tree form, allocating the majority of biomass to their roots (Ong et al., 2004). In fact, Pan et al. (2011) reported that tropical evergreen forests have the highest root biomass densities of about 2.5 kg C m⁻², while mangrove (*Avicennia marina* [Forsk.] Vierh) forests near Sydney (Australia) have been

estimated to have 14.73 (± 0.19) - 16.03 (± 0.41) kg m⁻² of belowground biomass (Briggs, 1977), which is equivalent to an approximate of 7-8 kg C m⁻². This suggests that mangrove forests may have much higher belowground biomass density than tropical terrestrial forests and underlines the importance of mangrove forests as carbon stores.

However, there is limited research on belowground biomass as it is not always possible to destructively harvest or measure belowground biomass or develop allometric equations, especially in the estuarine environment. Very few allometric equations are available for belowground biomass of forests, and mangroves in particular.

Small-flower mangrove species, *Avicennia marina*, has three varieties based on morphology, electrophoretic patterns and carbohydrate composition; such as *Avicennia marina* var. *australasica*, *Avicennia marina* var. *marina*, and *Avicennia marina* var. *eucalyptifolia* (Duke, 1995). *Avicennia marina* var. *australasica* is the only mangrove species of New Zealand. It also occurs in south-eastern Australia and in the tropics (Duke, 1990).

Saenger & Snedaker (1993) reviewed the trends in biomass of mangroves (incorporating 91 studies of litter-fall across species and locations, including New Zealand), which revealed decreasing biomass with increasing latitude. This pattern suggests that mangroves in New Zealand would be relatively small carbon pools compared to their tropical equivalents. To my knowledge there has been only one study on New Zealand mangrove biomass (Woodroffe 1985). Woodroffe (1985) reported above-ground biomass density of *A. marina* of 7.6 t ha⁻¹ (~0.7 kg m⁻²) in Tuff Crater, Auckland. However, 94 % of the Tuff Crater basin was covered sparsely by short trees (<1 m) and making it difficult to generalise other New Zealand mangrove sites where trees reach up to five to six metres in height (Morrissey et al., 2007).

Other studies of *A. marina* estimated aboveground biomass density to be 10.2 - 12.95 kg m⁻² (Briggs, 1977) and 11.0 - 34.1 kg m⁻² (Mackey, 1993). Belowground biomass was also estimated at 15.4 kg m⁻² (Briggs, 1977) and 10-12 kg m⁻² (Mackey, 1993). Comley & McGuinness (2005) also suggested an equation for root biomass estimation for *A. marina* as $W_r = 1.28DBH^{1.17}$ with root weight (W_r) and diameter at breast height (DBH). However, these referred to either tropical *A. marina* or ones at lower latitudes with bigger mean tree

height (7-10 metres). This thesis contributes with a direct and detailed estimate of both below and above ground biomass of a typical *A. marina* stand in northern New Zealand.

Common methods for estimating the biomass of forests include harvest method, satellite or remote sensing, and modeling based on available equations (FAO 2009, Ravindranath & Ostwald 2008). Harvest methods involve measuring directly the weight of the trees in the sample plots, which gives the accurate estimate of biomass at the time of harvest. However, this method is destructive, labour- intensive and may not be feasible due to local land use regulations. Satellite or remote sensing methods involve the use of different techniques such as aerial photography, optical parameters and radar to interpret the biomass stocks based on relationship between the parameters of a forest stand and their spectral representation. Although this method provides spatially explicit information and enables repeated monitoring even in remote locations, it is usually not suitable as the only method. Rather remote sensing methods are used to supplement other methods due to the high cost and requirement of technical and institutional capacity. Modelling methods use the available equations developed based on the relationship between biomass and allometric parameters of specific species. This method is rapid and sometimes the only approach to estimate the biomass stock of some forest stands. However, allometric equations are not always available and even if they are, difference in the maturity and geographical locations of the stands may lead to inaccuracy of the biomass estimation.

The total weight of an individual tree in tropical mangrove forests often reaches several tons (Komiyama et al., 2005) making it almost impossible to use the harvest method. In New Zealand, however, *A. marina* towards the southern limit of its occurrence rarely grow to heights of greater than 6 m (Kuchler, 1972) making these trees more manageable for harvest methods; the most accurate estimate of the biomass stocks. Therefore, a destructive method was developed based partly on the technical paper by FAO (2002) for their UN-REDD program, with modification to be more suitable for mangrove forests, to quantify biomass stocks of mangrove stands in Mangawhai Harbour. This study aims to identify the basic allometric parameters (height, stem diameter distribution), leaf area index (LAI), and total biomass of *A. marina* var. *australasica* stands in Mangawhai, layered horizontally and separated into different tree components.

2.2 Methods and Materials

Study areas

Mangawhai Harbour Estuary (36° 07' 00" S, 174° 36' 00" E) is located about 100 km north-east of Auckland, New Zealand (Figure 2). It is characterised as a typically deltaic estuary with two main channels, Tara Creek that drains into the Tara volcanic area north of the study area and Bob Creek that drains into the Waitemata sediments to the west. There is a variety of wetlands including salt marshes, sand/mud flats, and about 87 ha of mangroves. This site is the main field site for a larger estuarine ecosystem programme under the Mangrove Research Group (Auckland University of Technology and the University of Auckland).

Jack Boyd (JB) is situated at the upper tidal zone of Tara Creek, furthest from the shore with more sandy substrate and shortest inundation. The Molesworth (MO) stand is located in the middle of the waterway of Tara Creek, on the east side of Molesworth Drive, with more muddy substrate and longer inundation. The Mangrove Island (IS) is located even closer to shore but not too far away from MO, at the stream junction where Tara Creek and Bob Creek meets. IS has a quite similar sediment although inundation was observed to be shorter than MO.

For the allometry and biomass study, three sites JB, MO, IS were identified, plus Insley (IN) located on Bob Creek stream on the side of Insley street. A transect (2 x 100 m) was set up for each site, starting from the edge to the middle of each stand to be able to include trees of different sizes; trees were usually taller at the edge and shorter towards the middle of the stand. As felling trees were not legally possible at the public sites, sample trees were harvested at a private site in Black Swamp (BS), located along Bob Creek and closer to IN. Weight of sample tree at BS was combined with allometric measurements at JB, MO, IS and IN for biomass estimation (see details of the method in the Above-ground biomass section). Leaves were harvested from four sites JB, MO, IS, and IN for LAI calculation. Figure 2 shows the locations of the sites on study area of Mangawhai Harbour.

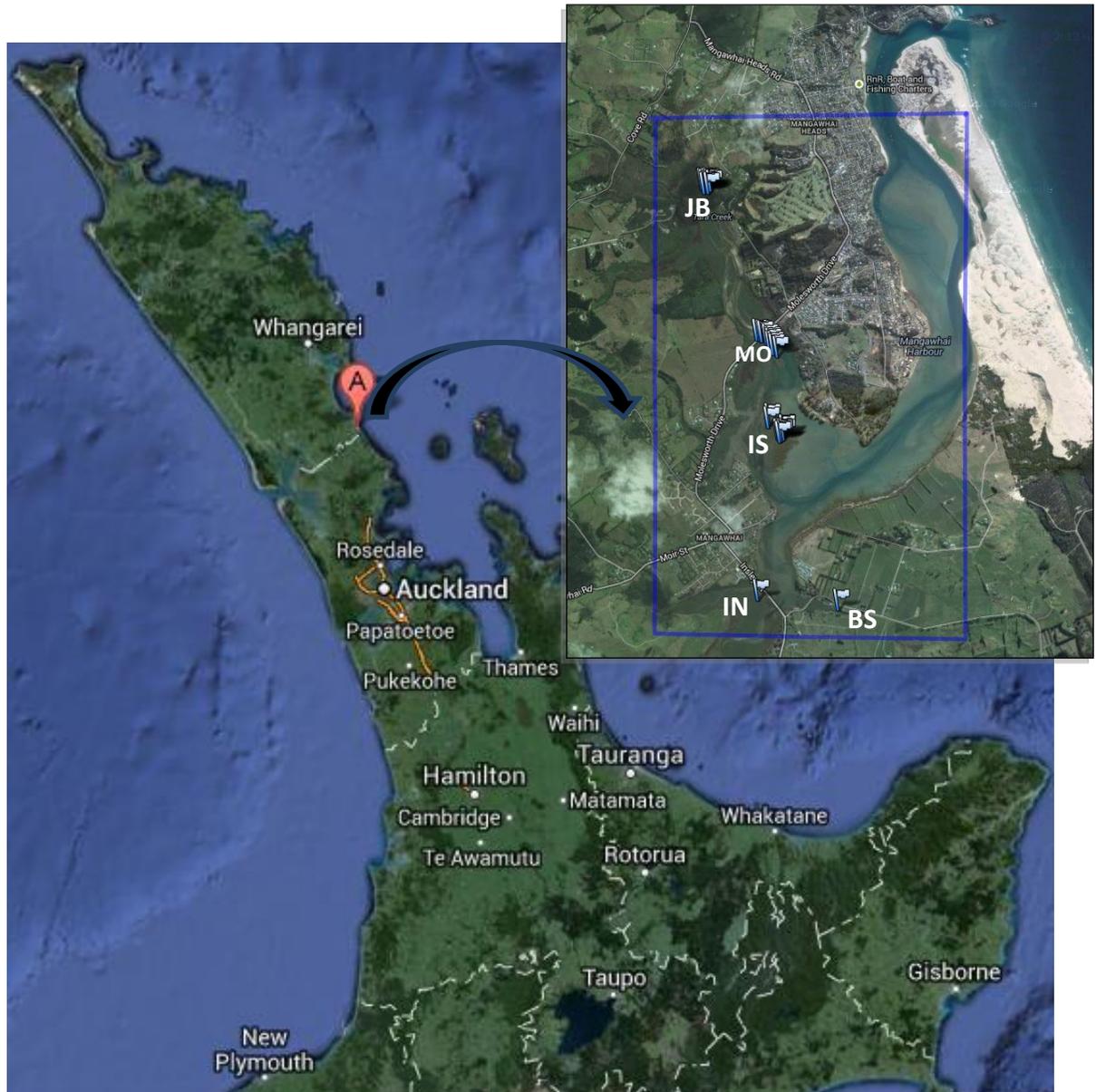


Figure 2. Mangawhai Heads with five study sub-sites of Jack Boyd (JB), Molesworth (MO), Island (IS), Insley (IN) and Black Swamp (BS).

Allometry and Leaf Area Index (LAI)

Stem diameters at ground (20cm from ground) were measured at the four transects (as described above) at JB, MO, IS and IN. Trees which branched at 20cm or lower were considered multi-stem trees, in which case stems were measured separately. Trees with diameter smaller than 2cm were excluded because there were not many plants in this cohort and they were therefore not representative for the stands. Average tree height was estimated for each 20-meter segment of each transect and tree density was calculated.

Leaf area index (LAI) was measured directly by relating total leaf area of eleven harvested trees at BS to stem diameter distributions at all three sites of JB, MO, and IS. Fifty-five leaves from four sites of JB, MO, IS, and BS were randomly harvested, including leaves of different ages from different tree layers. Leaf samples from each collection were divided into groups of 1 to 10 leaves, weighed, scanned and total leaf area was estimated using the software package ImageJ. Subsamples were then dried at 65°C to constant weight and the relationship between leaf area and dry mass was used to calculate specific leaf area (SLA). Mean leaf area was inferred by multiplying total dry mass of leaves for all eleven harvested trees for which diameters were known. Finally, mean LAI for each of the sites was estimated by relating tree diameters from the transects (200 m² each) to leaf area and scaling to one square meter.

Regression analyses of the subsamples of 55 leaves for each of the four sites (JB, MO, IS and BS) showed a significant linear relationship between leaf dry weight and leaf area, with R-squared values >0.99 for all four sites. Leaf area is related to leaf dry weight by the equation:

$$Y = X\beta$$

with leaf area Y , leaf dry weight X , and the coefficient β found to be 48.47 ± 1.05 , 53.81 ± 0.39 , 46.9 ± 0.81 and 49.23 ± 0.63 for JB, MO, IS, and BS, respectively.

To calculate the leaf area for each site, the basal area for each transect was estimated using stem diameter information. The linear relationship between basal area and leaf dry weight was also developed (R-squared = 0.93).

While leaf area sub samples are available for the site of BS, allometry data were not collected for this site. LAI values were therefore estimated for the remaining three sites.

Above-ground biomass:

Biomass was estimated by the harvest method. For above-ground biomass, eleven trees were felled at the BS site, layered in 50 cm height bands. Stem, branches and twigs were then separated from leaves, weighed fresh at the site and sub-samples taken to the lab and oven dried at 70°C to constant weight to get the ratio of fresh/dry weight. Total wood and leaf biomass was then calculated for the eleven sample trees. One of the sample trees differed from the other trees sampled having a crown that was lower and larger in

diameter than others (see tree number 6 in Table 2). This tree was identified as an outlier and excluded from the analysis.

Table 2. Allometric characteristics of the eleven sample trees at BS

Tree	Height (cm)	Diameter (cm)	Total wood dry weight (kg)	Total leaf dry weight (kg)
1	300	9.24	8.7	1.1
2	300	12.74	35.2	3.3
3	350	7.48	8.2	0.4
4	300	6.05	5.5	0.2
5	350	13.85	55.2	2.7
6	250	8.92 + 8.12 ^(*)	16.5	1.8
7	250	3.98	1.0	0.1
8	250	4.14	3.1	0.3
9	300	11.15	23.3	2.7
10	200	3.03	0.7	0.07
11	350	10.19	19.5	1.2

(*) tree branched from ground with two separate stems

Basal area of the sample trees was calculated from stem circumference measured at 20 cm above ground. Regressions between basal area and dry wood and leaf dry weight were established to estimate biomass for the sites (JB, MO, IS, and IN) based on the allometry data measured from the four transects. The linear model $Y = x * ba$, with biomass Y and basal area ba was used. For wood and leaf biomass, the linear model fitted well, with R-squared values of >0.94 for both (Figure 3).

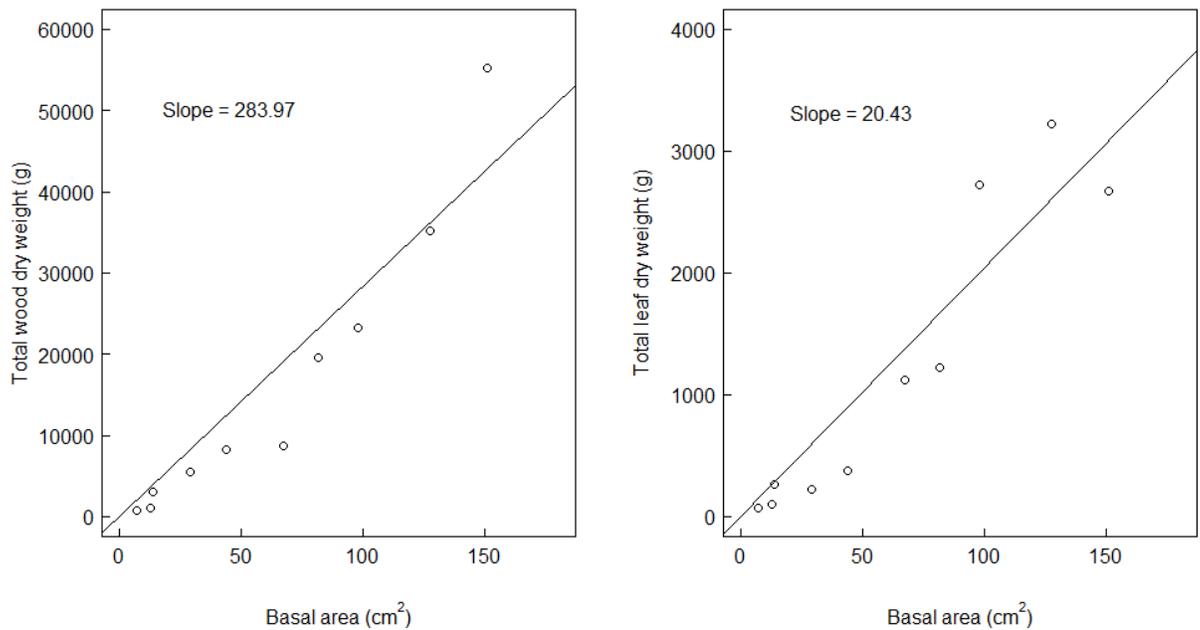


Figure 3. Basal area against dry wood and leaf mass at Black Swamp, Mangawhai Harbour Estuary. The linear model $Y = x * ba$ was used, with Y the wood / leaf dry weight and ba the basal area. R-squared is 0.94 for both plots.

Fruit biomass could not be estimated with this method, as only two trees bore fruit.

Instead, fruit biomass was estimated using litter traps (see Chapter 2).

The relationship between basal area and biomass was also calculated for each layer separately. The R-squared values for these relationships are given in Table 3.

Table 3. R-squared values for linear regressions between basal area and biomass of the individual layers

Height (cm)	R squared for linear regression between basal area and wood biomass of the layers	R squared for linear regression between basal area and leaf biomass of the layers
0-50	0.88	NA
50-100	0.65	NA
100-150	0.95	NA
150-200	0.93	0.34
200-250	0.84	0.54
250-300	0.58	0.52
300-350	0.76	0.79

To estimate the biomass of pneumatophores and seedlings, pneumatophores and seedlings were harvested to ground level from five 1 m² plots at each of the three sites (JB, MO and IS). Samples were rinsed to remove mud and algae, oven-dried at 65°C to constant weight. The mean values of dried pneumatophores and seedlings from the five harvested plots of each sites were added to the total above-ground biomass.

Below-ground biomass

Ten sediment cores (length from 40 to 100 cm, and 5.5 cm diameter) were taken manually haphazardly at the sites (JB, MO and IS). Each core was divided into segments of 10cm from the surface to depth. The root samples per segment were rinsed to remove mud and sand and oven-dried at 65°C to constant weight.

Below-ground biomass (including fine roots and coarse roots) per unit surface area were intended to be calculated from these cores. However, coring seemed to miss a considerable amount of coarse roots due to the hardness of roots and the substrates.

Therefore, another 9 blocks of 30 x 30 cm x 40 cm deep were dug out at JB, MO, and BS to provide a coarse root estimate. The soil blocks were rinsed to remove mud, sand and fine roots. Only coarse roots (diameter >3 mm) and pneumatophores (underground) from the blocks were accounted for.

Hence, only the fine roots from the cores were considered for the first 40cm below ground.

As the soil block samples were not available for the Island, coarse root biomass was estimated by the mean of the three sites JB, MO and BS for the first layer belowground (0-40 cm) while the deeper layers (coarse roots) were estimated from the core samples taken three sites of JB, MO and IS. Therefore, only at JB and MO coarse root profile was complete for all layers when considering the total biomass allocation by site.

Mean values of fine roots and coarse roots were estimated by segments of 0-40cm, 41-70cm, and 71-100cm below ground, then scaled up to one square meter. A summary of the measurement methods for below-ground biomass is presented in Table 4.

Table 4. Measurement methods (cores/blocks) for below-ground biomass conducted at each sites of Jack Boyd (JB), Molesworth (MO), Island (IS) and Black Swamp (BS)

Depth (cm)	0 - 40		41 -70		71 - 100	
	Fine-root	Coarse-root	Fine-root	Coarse-root	Fine-root	Coarse-root
JB	cores	blocks	cores	cores	cores	cores
MO	cores	blocks	cores	cores	cores	cores
IS	cores	N/A	cores	cores	cores	cores
BS	N/A	blocks	N/A	N/A	N/A	N/A

2.3 Results

Allometry and LAI of mangrove stands

The stand at JB had the highest density of 1.03 trees per square meter, and it also had the tallest trees of up to five meters high. The largest stems (up to 16.9cm in diameter) were found in MO. Trees at the IN site were the smallest with the lowest mean values in both height and diameter (Table 5). The shortest trees (about one meter high) were found at IS. However, big trees up to three meters high with larger canopy were also found at IS, which, together with the lowest density (0.37 tree per square meter), made the mangrove stand at IS irregular among the rest of the sites.

Table 5. Allometry of *Avicennia marina* in the study transects at Insley (IN), Island (IS), Jack Boyd (JB) and Molesworth (MO)

Transect	Coordinate		No. trees per 200m ²	No. stems per 200m ²	Mean tree height (\pm s.e)	Mean stem diameter (\pm s.e)
IN	NA	NA	145	152	1.89 \pm 0.04	5.15 \pm 0.22
IS	-36.11675S 174.58212E	-36.11763S 174.58177E	73	121	2.30 \pm 0.07	5.28 \pm 0.23
JB	-36.09665S 174.57354E	-36.10974S 174.57965E	206	300	3.10 \pm 0.06	5.86 \pm 0.13
MO	-36.09710S 174.57283	-36.11058S 174.57918E	108	146	1.94 \pm 0.03	6.48 \pm 0.23

Leaf area indices ranged widely from 1.6 (at IS) to 4.6 (at JB), which are consistent with tree densities at each site. However, Specific Leaf Area (SLA) was similar among the sites (see Table 6) and not related to tree density.

Table 6. Leaf area index (LAI) and Specific Leaf Area (SLA) for the sites Black Swamp (BS), Island (IS), Jack Boyd (JB) and Molesworth (MO)

Sites	Leaf Area Index (LAI) (m ² m ⁻²)	Specific Leaf Area (SLA) (m ² kg ⁻¹)
BS	NA	49.23 \pm 0.63
IS	1.6	46.9 \pm 0.81
JB	4.6	48.47 \pm 1.05
MO	3.2	53.81 \pm 0.39

Biomass partitioning

Biomass varied among sites and was consistent with tree density. At JB, where tree density was at least twice as high than at the other sites, there was a significantly greater biomass in all tree components. However, the relative biomass distribution among wood, leaf, root and pneumatophores were similar among sites, with the highest biomass found in fine roots, followed by coarse roots (in case of MO) or wood (in case of JB) (see Table 7).

More aboveground pneumatophores and seedlings were found at JB where the sediment was more stable, and fewer pneumatophores at sites with muddier sediment (IS and MO).

Table 7. Biomass allocation in wood, leaf, roots and pneumatophores and seedlings for the sites Insley (IN), Island (IS), Jack Boyd (JB) and Molesworth (MO)

Site	Wood biomass (kg/m ²)	Leaf biomass (kg/m ²)	Pneumatophores and seedlings (kg/m ²)	Coarse root (kg/m ²)	Fine roots (kg/m ²)
IN	5.3	0.4	NA	NA	NA
IS	2.3	0.2	0.19	NA	3.73
JB	8.0	0.6	0.28	5.46	9.24
MO	5.0	0.4	0.07	5.63	5.99

Due to the unavailability of full coarse root values at IS, it was impossible to involve this site when considering biomass distribution as a whole for each site. The proportion distribution of biomass per square meter was therefore estimated from the mean values from the two sites of JB and MO.

Biomass was highest in fine roots, with an average of 37 %, followed by wood biomass (32 %), then coarse roots (27 %). Leaf biomass made up a small component of total biomass of 3 % and, pneumatophores and seedlings contributed least with only 1 % of the total biomass (Figure 4).

The root-shoot ratio was calculated by the mean aboveground biomass of JB and MO divided by the mean belowground of these two sites.

$$\frac{\text{Root}}{\text{Shoot}} = 1.73$$

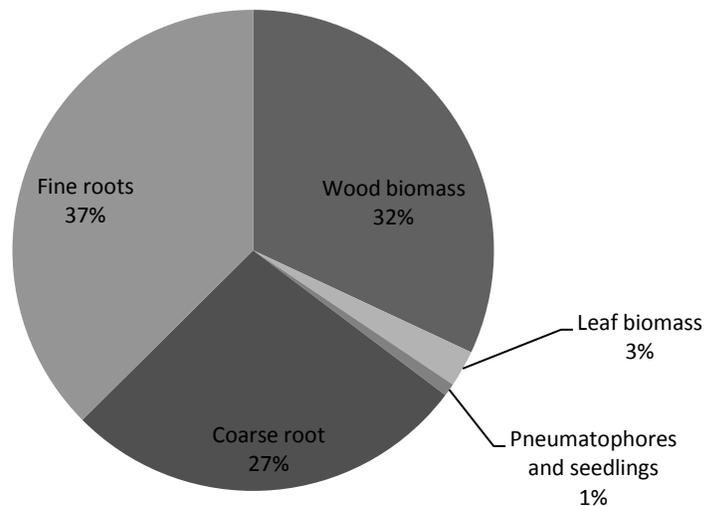


Figure 4. Biomass allocation (%) estimated from the mean values of JB and MO sites in Mangawhai Harbour, standard errors for coarse-roots, fine-roots, wood, leaf, and pneumatophores and seedlings were 4.9, 2.1, 2.3, 0.1, and 0.4, respectively.

Vertical distribution of biomass

Below-ground biomass accounted for the largest part of total *A. marina* biomass, with the bulk of the roots ($> 8 \text{ kgm}^{-2}$) in the first 40 cm. More than 70 percent of the total below-ground biomass was located in this layer and almost 50 percent of the total was from fine roots alone. Root biomass was reduced significantly with increasing depth, with the deepest measurable roots at 100 cm (Figure 5).

Wood biomass increased slightly with height and reached a peak of $>1 \text{ kgm}^{-2}$ at 200 cm from the ground, and then significantly diminished at higher layers where small branches and twigs replaced big stems. Leaf biomass was found from 200cm above the ground upwards, but its contribution was small and the distribution was unpredictable with height. Pneumatophores and seedlings also contributed for a small part to the total above-ground biomass (see Figure 5).

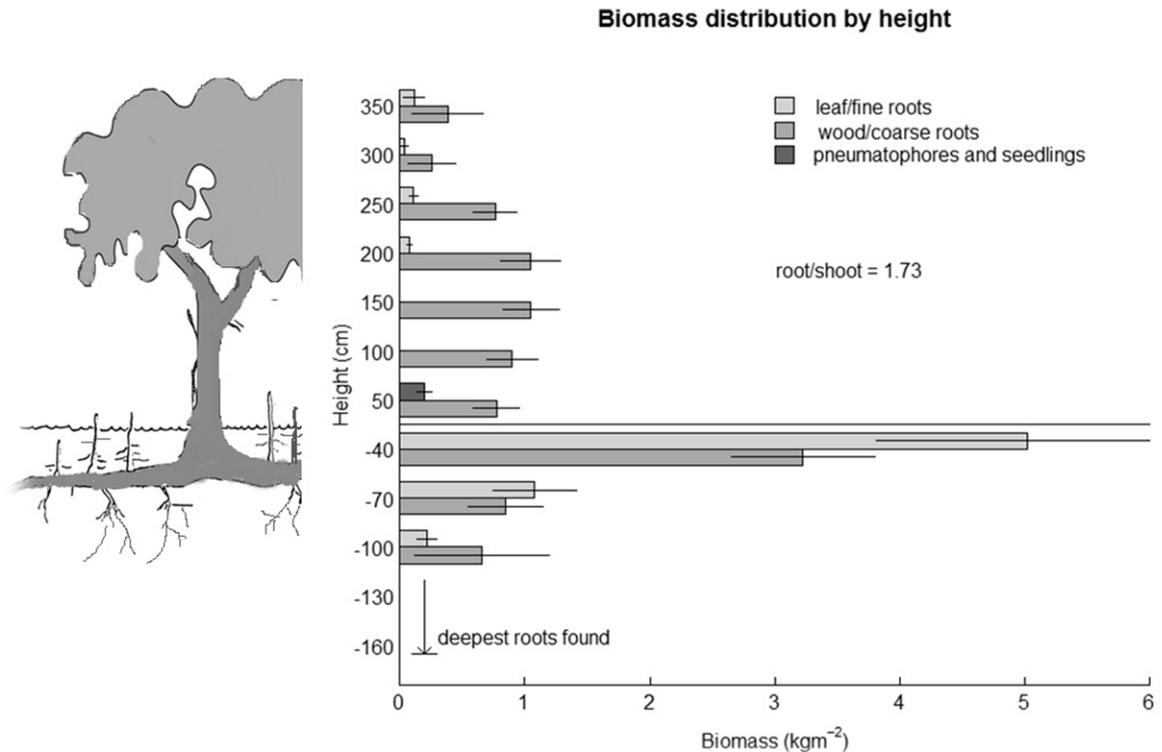


Figure 5. Vertical distribution of biomass estimated for compartments per players on Mangawhai Harbour, with mean values and standard errors estimated among the sub-sites of JB, MO, IS and IN for wood and leaf biomass, JB,MO, and IS for pneumatophores and seedling, fine roots biomass and coarse roots under 40cm deep, and JB, MO and BS for coarse roots from 0-40cm deep.

2.4 Discussion

Above-ground biomass

The biomass results found in Mangawhai were comparable to those of previous studies at the same mangrove species (see Table 7). At the present study site there was a lower aboveground biomass than other sites, which could be due to the generally smaller trees. Above-ground biomass of *A. marina* were found to be up to 16.2 kgm⁻² in Brisbane, Australia (MacKey, 1993) and 14.45 kgm⁻² in Sydney, Australia (Briggs, 1977) while the biggest above-ground biomass in Mangawhai found at JB was 8.88 kgm⁻². The comparison presented in Table 8 shows a relationship between above-ground biomass with tree size (height and/or diameter) among the sites in this study and other published studies on biomass of *A. marina*. One exception is the taller stand in Tuff Crater where trees were shorter and less dense than those at JB yet biomass density was higher. The lack of stem diameter information in the study by Woodroffe (1985) at Tuff Crater made

a closer look at this inconsistency difficult although it is important, especially when studies on New Zealand mangrove biomass are rare.

Table 8. Biomass estimation for *A. marina* in Australia and New Zealand sites

Site	Mean tree height (m)	Mean tree diameter (cm)	Tree density (tree/ m ²)	Aboveground biomass (kgm ⁻²)	Belowground biomass (kgm ⁻²)	References
Boggy Creek, Brisbane, Australia	9.7	7.42	0.49	16.2	10.9	Mackey (1993)
Boggy Creek, Brisbane, Australia	16.4	32.5	0.05	34.1	12.1	Mackey (1993)
Boggy Creek, Brisbane, Australia	5.3	3.89	0.97	11.0	12.6	Mackey (1993)
Strangers Creek, NSW, Australia	8.15	23.1	0.1	14.45	14.73	Briggs (1977)
Strangers Creek, NSW, Australia	6.53	13.9	0.28	11.23	16.03	Briggs (1977)
Dampier, Western Australia (WA), Australia	NA	4.9	0.9	5.5	23	Alongi et al. (2003)
Port Hedland, WA, Australia	NA	8.9	0.6	12.5	10.5	Alongi et al. (2003)
Mangrove Bay, WA, Australia	NA	7.2	1.1	13.2	38	Alongi et al. (2003)
Tuff Crater, Auckland, New Zealand	2.75	NA	0.33	10.4	NA	Woodroffe (1985)
Tuff Crater, Auckland, New Zealand	0.44	NA	1.6	0.7	NA	Woodroffe (1985)
Mangawhai, Northland, New Zealand (IS)	2.30	5.28	0.37	2.69	NA	present study
Mangawhai, Northland, New Zealand (JB)	3.10	5.86	1.03	8.88	14.7	present study
Mangawhai, Northland, New Zealand (MO)	1.94	6.48	0.54	5.47	11.62	present study

Biomass of pneumatophores and seedlings was very low at MO compared to other two sites, although tree density was higher than that of IS. The muddy sediment and the tidal current at MO may prevent the exposure of pneumatophores causing the low above-ground pneumatophore and seedling biomass found at this site. Indeed, pneumatophores exposed up to 20 - 30cm above ground at JB and IS, while at MO most of them were found shorter than 5cm.

Belowground biomass

Below-ground biomass at Mangawhai, was similar to that of sites with bigger trees (Table 8), with exceptions from the sites studied by Alongi et al. (2003) where biomass contributed from live and dead roots reached 38 kgm^{-2} . Small sampling size (three cores per site) by Alongi et al. (2003) might have caused bias in estimating below-ground biomass. Below-ground biomass at other sites in Australia ranged from 10.9 to 16.03 kgm^{-2} , while biomass at Mangawhai was 11.62 kgm^{-2} (at MO) and 14.7 kgm^{-2} (at JB). This, together with the lower above-ground biomass, resulted in the root-shoot ratio in Mangawhai to be among the highest recorded to date (1.73 compared to 1.20 at Strangers Creek and in 0.58 at Boggy Creek; the ratio of 4.2 at Napier and 2.9 at Mangrove Bay, Australia (Alongi et al, 2003) can be considered odd values). High accuracy is expected in this measurement since belowground biomass was assessed by direct harvesting of root samples at all sites with ten cores and three blocks per site. Further consideration of the age and density of the stand in relation with root biomass is needed.

Although *A. marina* has a flat root system and no single tap root was expected for the trees, the short "core" that supports cable roots was found to account for a considerable share of total root weight. Only two of these "cores" (from trees with basal areas of 67 cm^2 and 113.67 cm^2) were collected from the sample trees, with dry weights of 0.85 kg and 0.89 kg respectively. These samples were not adequate for extrapolating the biomass of these tap roots. The absence of these plant parts (which were roughly estimated to be 0.07 - 0.27 kgm^{-2} , based on average dry weight of the taps per average basal area) from the total biomass estimation may have led to a slight under-estimation of total belowground biomass of *A. marina* in Mangawhai. Furthermore, taking root samples by manual coring limited the measuring depth to one meter belowground, while the deepest fine roots were found at 1.6 meter belowground (Figure 4) from viber-core sampling by another study at the same study site (Hulbert, 2014).

Allometric equation:

The linear model $Y = x * ba$, with ba is the basal area, gave satisfactory results for the biomass of *A. marina* in Mangawhai, although this equation was not applied in any of the previous studies. *A. marina* biomass was estimated using the relationship between stem girth and tree volume (*via* wood density) (Briggs 1977, Mackay 1993), dry weight and tree height (Woodroffe, 1985), and, closer to parameters used in our study, dry weight and breast-height diameter (Comley & McGuinness, 2005) where dry weight is related to diameter by a quadratic model (aboveground biomass = $0.0942 * DBH^{2.54}$). This quadratic equation was also found in another study by Ong et al. (2004).

Fitting quadratic model ($Y = x * ba^2$) was tried first in this study to relate basal area to dry wood. This curve best described the variance with an R-squared value of 0.98 (see model fit in Figure 6). However, this model underestimated biomass of small diameter trees. Because almost 80 % of the trees at our site had a basal area of $<50 \text{ cm}^2$, this model gave values that were too low compared to previous studies on similar stands.

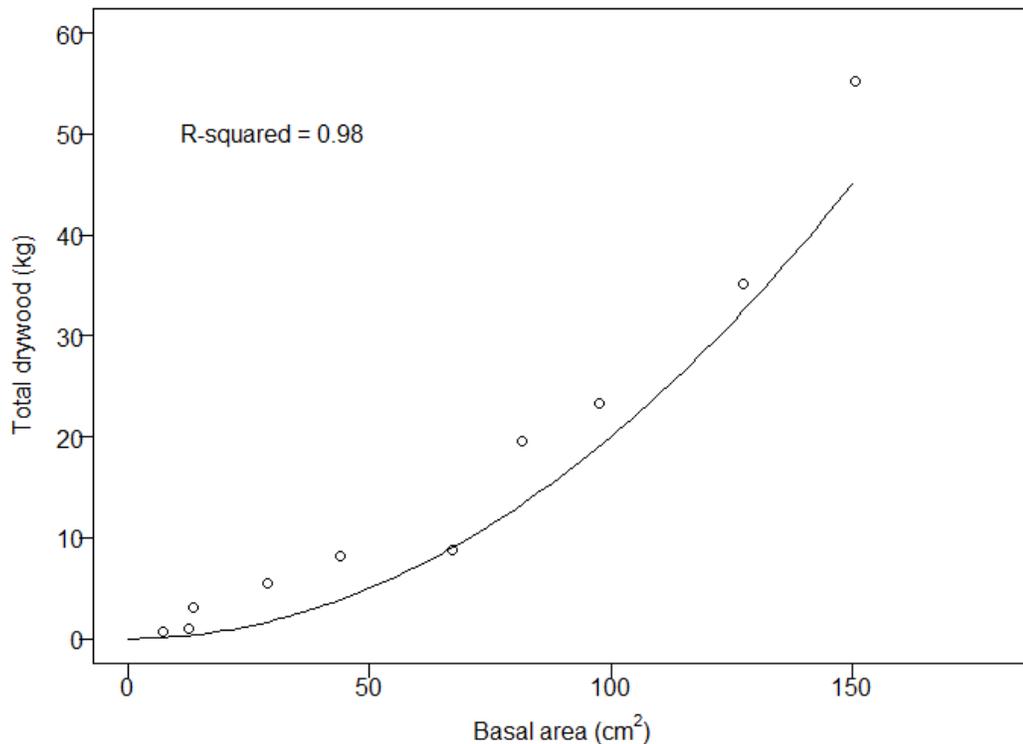


Figure 6. Quadratic model $Y = x * ba^2$ used for the regression of dry wood on basal area, with Y the dry wood mass, ba the basal area. Data from the Black Swamp site at Mangawhai Harbour Estuary.

Limitations

The limitations in the samples of harvested trees for biomass quantification from a small stand in a private farm (11 trees between 2 and 4 m high) may have introduced some bias, because half of the trees found in the transects at IN, IS and MO were shorter than two meters, and some trees at the JB site were taller than 4 meters. However, the mean basal area was not significantly different between sites so this should help reduce the bias in estimation of total biomass based on the basal area.

The estimation of leaf biomass by horizontal layers was complicated due to the unpredictable canopy shape. Plotting leaf dry weight of each layer against basal area did not show a clear relationship (and the linear model applied gave very low R-squared values) (see Figure 7), suggesting that predicting vertical distribution of leaf biomass based on basal area was not ideal as it was for total leaf biomass estimate.

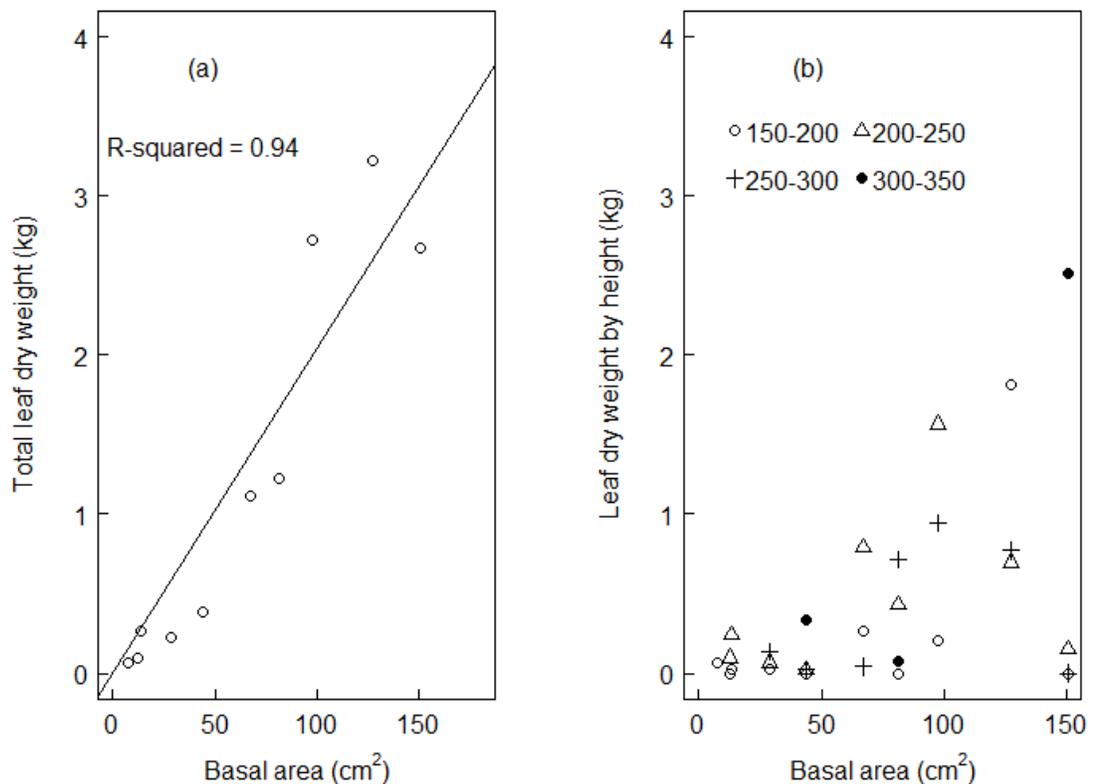


Figure 7. Basal area against total leaf mass (a) and leaf mass by height (b) at Black Swamp, Mangawhai Harbour Estuary. The linear model $Y = x * ba$ was used, with Y the leaf dry weight and ba the basal area. R-squared is 0.94 for the relationship between ba and total leaf dry weight, and are 0.34, 0.54, 0.52, and 0.79 for the relationship between ba and leaf dry weight at 150-200cm, 200-250cm, 250-300cm, and 300-350cm respectively.

The stand canopy at IS was dissimilar from the rest of the sites with significantly bigger crowns and highly variable tree height. Therefore, the estimation of biomass of trees at IS based on the sample trees from BS may not give a satisfactory result, despite the fact that the basal areas at the two sites were similar.

Chapter 3: Litter production and decomposition

3.1 Introduction

Comprehensive characterisations carbon cycles require measurement of two key components, namely the carbon pool and fluxes between the pools. A carbon pool is the total amount of carbon stored in an ecosystem, where as carbon fluxes are the transfer of carbon from one pool to another, usually expressed as a rate per time unit. In forest ecosystems, carbon is transferred from the atmosphere to living plants through photosynthesis and from plants to the soil/water mainly through litter production. Litter production is the process in which dead plant materials are lost to the ground, where they enter the process of decomposition.

Litterfall

Litterfall is a key parameter in the carbon cycle linking plant carbon to carbon in the soil and, in the estuarine environment as in the case of mangroves, the ocean. Litter biomass and its chemical contents are important in quantifying the annual return of elements and organic matter to the soil (Chapin et al., 2002).

Litter production represents an important component of net primary production and is usually measured as productivity. However, it is important to recognize that litterfall alone does not completely represent net primary production (Bellot et al. 1992, Morrissey et al. 2010). Litterfall measurements are often an important component of general ecological monitoring programs (Harrison et al., 2012) since changes in litterfall can be in response to disturbance caused by biotic (e.g. insect pests) and/or environmental factors like frost, drought, wind, or pollution. Monitoring litterfall provides temporal information about the phenological development of a tree stand. Litterfall is commonly measured by litter traps, which is time-consuming and laborious. The longest record of litterfall worldwide to date is on-going in the Orangutan Tropical Peatland Project which started in 2005 (Harrison, 2012).

A comprehensive review of more than four hundred measurements of litterfall globally by Zhang et al. (2014) showed that seasonal patterns of litterfall are diverse and are determined by both physiological mechanisms and environmental variables (mostly temperature, solar radiation and wind). Litterfall peaks differed in their temporal occurrence among forest types: spring or winter for tropical forests, autumn for temperate deciduous broadleaved and boreal evergreen needle-leaved forests, and various seasons for

temperate broadleaved and needle-leaved evergreen forests. The total annual litterfall varied significantly by forest types, ranging from 0.3 - 1.1 kg dry mass m⁻² y⁻¹ (Zhang et al., 2014).

Litterfall in mangrove forests

Mangrove forests, whose role in the carbon budget of the coastal zone has long been debated, are highly productive with a global average primary production estimated to be 1.36 kg C m⁻² y⁻¹ (Bouillon et al., 2008). A review by Alongi (2002) stated that most inter-annual variability in above-ground production and litterfall can be attributed to soil salinity, minimum air temperature, and minimum rainfall.

Mangrove litterfall accounts for 31 % of overall mangrove production (Bouillon, 2008) and decreases with increasing latitude (Saenger & Snedaker 1993, Bouillon et al. 2008). High litterfall was found at latitudes between 0 and 10° with an average of 1.04 ± 0.46 kg m⁻² y⁻¹, which decreases with increasing latitudes and rather low production found at latitudes >30° with 0.47 ± 0.21 kg m⁻² y⁻¹ (Bouillon et al., 2008).

The pattern of decreasing litterfall with increasing latitude suggests that mangroves in New Zealand have relatively low litterfall rates compared to their tropical counterparts. Published papers about New Zealand mangrove litterfall included studies at Tuff Crater by Woodroffe (1982), Rangaunu Harbour by May (1999), and recently in Whangamata Harbour by Gladstone-Gallagher et al. (2013). Litterfall production of *A. marina* in New Zealand was found to be higher in stands closer to shore (0.39 - 0.81 kg m⁻² y⁻¹) than further inland (0.18 - 0.36 kg m⁻² y⁻¹, May 1999, Woodroffe 1982). Gladstone-Gallagher et al. (2013) found that litterfall production 40 m within the mature stand (0.54±0.07 kg m⁻² y⁻¹) was significantly higher than under younger trees at the edge of the stand (0.32±0.04 kg m⁻² y⁻¹). Leaf material contributed between 56 % and 86 % of the mangrove litter all year round (Woodroffe 1982, May 1999, Gladstone-Gallagher et al. 2013). However, litterfall was minimal during the colder months from March to October and as much as 77 % of the total annual litterfall appeared during the warmer months of November to February (Gladstone-Gallagher et al., 2013).

These data from New Zealand mangroves reveal that rates of litter production may vary considerably among locations and were not related to latitude. Highest litterfall rates (0.7 - 0.8 kg m⁻² y⁻¹) were recorded at the Tuff Crater site near Auckland (36°48'S) followed by

Whangamata Harbour (37°10'S) with 0.3 - 0.5 kg m⁻² y⁻¹, while the lowest rate found at the most northerly site (Rangaunu Harbour, 34°57'S) with 0.2 - 0.6 kg m⁻² y⁻¹.

According to Morrisey (2010), recorded litterfall rates for *A. marina* in New Zealand are below the maximum values reported from other parts of its distribution (found in tropical *A. marina* stands). However, they are comparable with values from subtropical and temperate Australia where the average litterfall rate was reported to be 0.62 kg m⁻² y⁻¹ (Morrisey, 2010).

Litter decomposition

Litter decomposition is a critical process in global carbon cycling. It is the main pathway for nutrient and carbon fluxes and determines the organic matter input to forest soils, which strongly influences the forest productivity (Chapin et al., 2002). Litter decomposition rates are commonly known to be controlled by three main factors: temperature, moisture, litter quality (i.e. rates of litter decomposition increase with both increasing temperature and precipitation) (Karberg, Scott, & Giardina 2008, Jacob et al. 2010). The possible fourth important factor influencing litter decomposition is faunal community structure within the forests since a suite of decomposer organisms directly or indirectly consumes a variable proportion of forest litter (Alongi 2002, Dechaine et al. 2005). Illustrative of the global variability in litter mass rates, Tuomi et al. (2009) showed that typical conifer litter had ~ 68 % of its initial mass still remaining after 2 years decomposing in the cold tundra with little available liquid water, while deciduous litter had only 15 % remaining after two years in the tropics which are warm and wet.

Mangrove litter decomposition

Transport and cycling of organic and inorganic matter in mangrove forests is driven by physical (daily tides, runoff, and rainfall) and biological factors (litterfall, decomposition, mineral uptake, faunal activities, Lugo & Snedaker, 1974). Among mangrove forests, leaves of *Avicennia* spp. and *Kandelia* spp. are more rapidly decomposed than other mangrove species because of their relatively high nitrogen content, low carbon-to-nitrogen (C/N) ratio, low content of structural lignocellulose and tannin (Robertson 1988, Alongi 2009). Given the predominance of these genera (*Avicennia* and *Kandelia*) in temperate mangrove forests, Morrisey et al. (2010) suggested that decomposition processes may be faster in temperate compared with tropical mangroves. On the other hand, Alfaro (2006)

suggested that lower temperatures and lower tidal inundations might result in slower organic matter decomposition rates in temperate (New Zealand) coastal areas compared with tropical and subtropical mangrove ecosystems.

Morrissey et al. (2010) also made a comparison of the decomposition rates between tropical and temperate mangroves reported for Australia, New Zealand and South Africa and suggested that rates are not necessarily slower at higher latitudes (Morrissey et al., 2010).

Previous studies on leaf litter decomposition of *A. marina* in New Zealand report that litter lost 50 % of its dry weight after 42 - 84 days of decomposition, varying with seasons (Woodroffe 1982, Morrissey 2010, Gladstone-Gallagher et al. 2013). There were, however, seasonal differences and it appeared that decomposition happened much faster in the warmer months of summer and autumn (Woodroffe 1982, Gladstone-Gallagher et al. 2013). Buried leaf litter (10 -15 cm below the sediment surface, where decomposition processes would have been anaerobic) decomposed 1.3 - 1.4 times slower than litter laid on the sediment surface (Gladstone-Gallagher et al. 2013). The review by Morrissey (2010) also revealed that decomposition rates of New Zealand *A. marina* leaves were 8–12 % slower when macrofauna were removed from the sediment on which the leaves were placed. This implied the mesh bags used in decomposition experiments may underestimate rates of decomposition by preventing larger macrofauna from breaking up the litter.

Methods for measurement of decomposition were synthesized in studies by Karberg (2008) and Benhard-Reversat (1982) including mass balance, litterbags, tethered leaves, and the cohort layered screen. Mass balance techniques are based on annual input of fresh litter and used to estimate litter decomposition for whole ecosystems, and are often employed when direct measurement is too cumbersome or expensive. The cohort layered window screen method, with layers of mesh screen, are used to separate successive layers of litter on the forest floor; leaf litter then decomposes in *situ*. The cohort layered screen method is applied to long-term decomposition studies of three years or more. The litterbag approach, with fresh leaf litter enclosed in mesh bags, placed on the ground, and collected at periodic intervals for measurement of the mass remaining, is widely used to study decomposition at the sediment surface due to its simplicity and accurate direct measurement. The tethered leaf approach is quite similar to the litterbag, with leaves tied together in bundles rather than placed in litterbags which may cause difficulty at the later stage of experiment when size of detritus left is important to infer the remaining mass.

In this study, the litterbag method was used to measure the decomposition rate of *A. marina* in Mangawhai Harbour. This, together with litterfall measurements, was conducted as part of the project on New Zealand mangrove carbon and water relations. These data are fundamental for a better understanding of temperate mangrove productivity and carbon storage in mangrove-dominated estuaries and will provide basic information for future research on nutrient, water, and carbon cycling conducted at the same site.

3.2 Methodology

Site selection

For the litter fall and decomposition study, three sites were selected: Jack Boyd (JB) with more sandy substrate and shortest inundation, Molesworth (MO) with more muddy substrate and longer inundation, and the Mangrove Island (IS) with quite similar sediment although inundation was observed to be shorter than MO.

Litterfall

Litterfall was measured using litter traps placed under the mangrove canopy. Ten litter traps made of heavy-duty woven polyethylene fabric were placed haphazardly at each of the sites of JB, MO, and IS (see Figure 8). Traps were 55 cm in diameter, their height varied with the available space between canopy and the high tide mark (10-20 cm above the high tide water level). Each trap was tied to 4 plastic coated stakes which were driven into the substrate. Holes were made in the traps to ensure water drainage, preventing possible decomposition of litter in the trap. Litter was collected at intervals of about 40 days.



Figure 8. Locations of litter traps and litter bags at JB (a), MO (b), and IS (c) at the Mangawhai Harbour study area.

The collected litter was rinsed if necessary (i.e. even though the traps were set above the highest tide level, dry mud/dust was occasionally found with the litter), then oven-dried at 65 degree Celsius to constant weight. Leaves, twigs, reproductive parts (fruits and inflorescences) and unidentified fragments of less than 2mm were weighed separately. Litter was collected for one year from May 2013 to April 2014.

Weather data (temperature, rainfall and wind speed) were collected for the full year and considered for possible drivers of litterfall patterns.

Decomposition

The litterbag method was used to measure the leaf litter decomposition rate. Twelve heavy duty 3mm-diameter- mesh bags were placed at each of the 3 selected sites (JB, MO, and IS) along with the litter traps, each containing leaves of ~50g fresh weight.

Four bags from each site were collected randomly at the interval of about 40 days. The litter bags were then rinsed to clean off the mud, detritus bigger than the mesh size (6 mm²) stayed in the bags, rinsed again in a 500 μ sieve, oven dried at 65°C to constant weight and weighed to infer mass loss. This study was completed within 12 months, from April 2013 to March 2014.

An asymptotic model $y = Asym + (R_0 - Asym) * \exp(-\exp(lrc) * x)$, with y the percentage of remaining weight over time, R_0 the estimated intercept on the y-axis, $Asym$ the asymptote parallel to the x-axis, and lrc the estimated logarithm of the rate constant, was selected from a series of exponential models and most satisfactorily used to describe the decomposition process of leaf litter. The model was fitted for each site separately, as well as for all sites in common, and ANOVA was used to compare significant model improvements using site-specific parameters. Model assumptions were tested using various diagnostic plots (qq-plots, residual vs. fitted plots). No violations of model assumptions (normality, homoscedasticity) were observed. Environmental factors (inundation and sediment organic matter) were then qualitatively considered as possible covariates.

3.3 Results

3.3.1 Litterfall

Litterfall production

Highest total annual litterfall was found at MO with $476.63 \pm 66.1 \text{ g m}^{-2} \text{ y}^{-1}$, followed by IS with $371.35 \pm 43.7 \text{ g m}^{-2} \text{ y}^{-1}$ then JB with $331.94 \pm 69.8 \text{ g m}^{-2} \text{ y}^{-1}$ (see Table 9). Leaves were the major part of the litter, accounting for 82.3 % at IS, 76.7 % at MO and 66.6 % at JB. Twigs made up the second largest part, except for the case of IS, with 20 % at JB and 15.8 % at MO. At IS, twigs made up only 7.6 %, less than the 9.8 % of reproductive parts in collected litter. Reproductive parts in the litter at JB and MO accounted for 13 % and 6.7 %, respectively.

Table 9. Total litter fall (gm^{-2}) at IS, JB, and MO from April 2013 to March 2014.

Site	Litterfall dry weight (gm^{-2}) \pm se				Total
	Leaves	Twigs	Reproductive parts	Unidentified fragments	
IS	305.63 \pm 33.4	28.08 \pm 9.0	36.49 \pm 14.6	1.13 \pm 0.6	371.35 \pm 43.7
JB	220.97 \pm 31.0	66.27 \pm 43.3	43.35 \pm 18.9	1.34 \pm 0.6	331.94 \pm 69.8
MO	365.74 \pm 38.1	75.38 \pm 38.4	32.01 \pm 12.0	3.48 \pm 1.6	476.63 \pm 66.1

Leaf litter dominated all year round except for the winter period from June to July when it made up about the same amount as twigs (see Figure 9). Twig litter appeared to be relatively consistent throughout the year, but minimal in August. Reproductive parts made up a tiny proportion of litter almost all year round, except for the month of February where it peaked and exceeded twig litter. Unidentified fragments smaller than 2mm were also added to the total litterfall production.

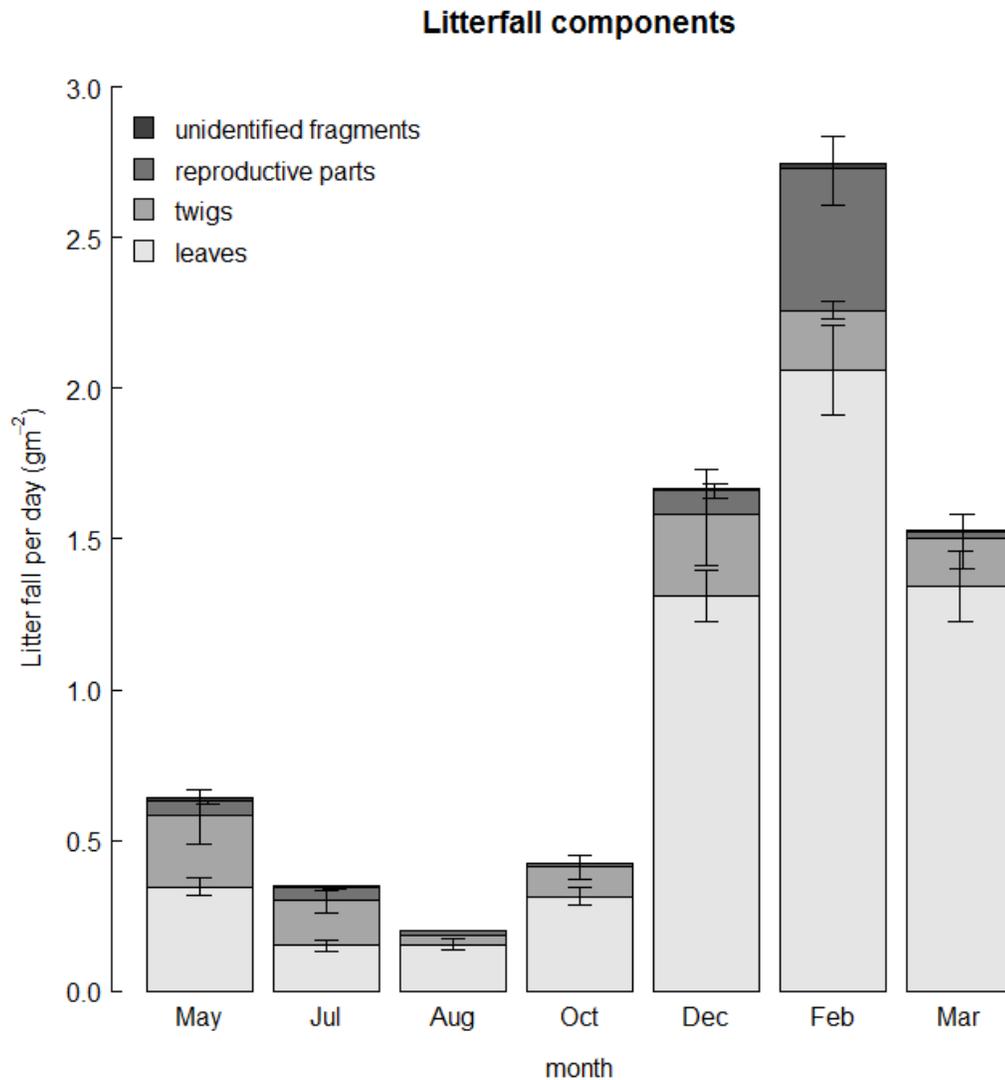


Figure 9. Seasonal litter production at Mangawhai Harbour ($\text{gm}^{-2}\text{day}^{-1}$), with the mean values for each litter component calculated from thirty traps across all three sites (JB, MO, IS). Error bars represent standard error ($n=30$).

Litterfall and environmental conditions

Seasonal litterfall production was compared to monthly mean temperature (Figure 10), maximum wind speed (Figure 11), and total rainfall (Figure 12). The correlation tests showed a positive relationship between litterfall production and monthly temperature (Linear model, $p\text{-value} = 0.006$, $R\text{-squared} = 0.80$). Litterfall production was lowest during the coldest months of winter and increased with increasing temperature (Figure 10). In contrast, although there was no significant correlation between litterfall and maximum wind speed ($p\text{-value} = 0.17$), litterfall production was found to peak in the month with lowest

wind speed and lowest during the months with highest wind speed (Figure 11). There was no clear relationship between rainfall and litterfall production (Figure 12).

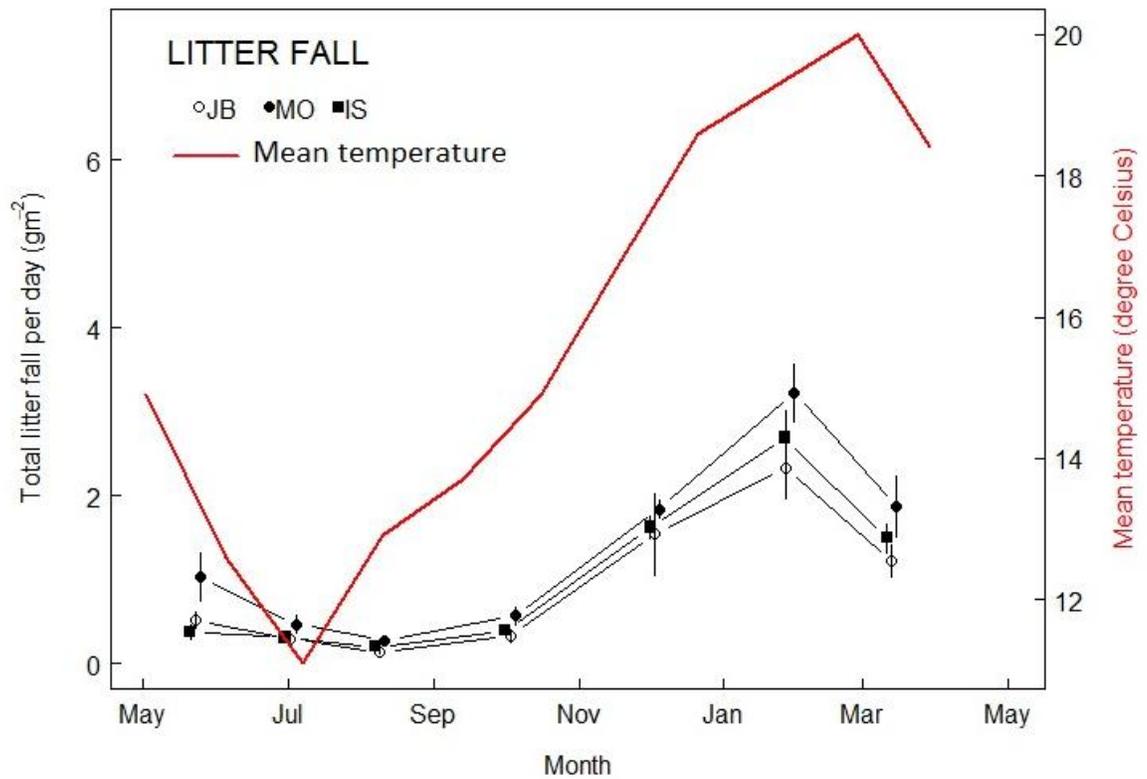


Figure 10. Site-specific seasonal litter production and monthly mean temperature ($^{\circ}\text{C}$) measured at Mangawhai Harbour. Error bars represent the standard errors for the mean values of litter from ten traps ($n=10$) for each site Jack Boyd (JB), Molesworth (MO) and Island (IS).

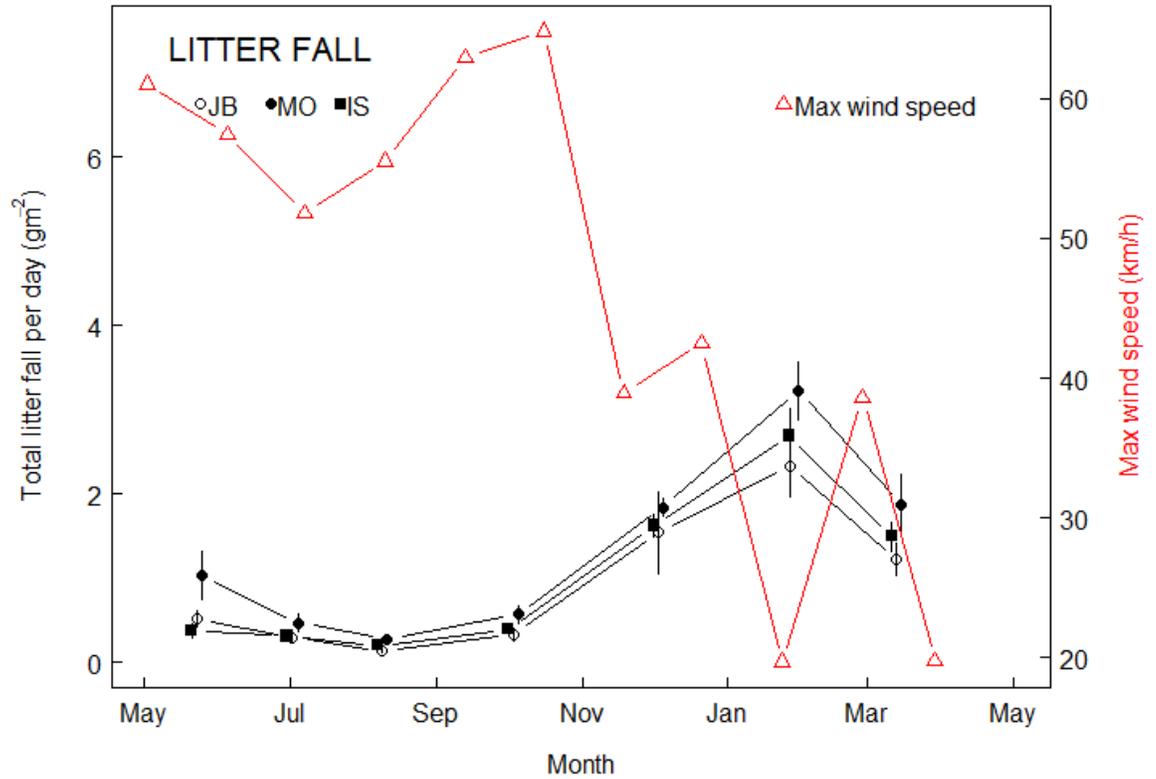


Figure 11. Site-specific seasonal litter production and monthly max wind speed (kmh^{-1}) measured at Mangawhai Harbour. Error bars represent the standard errors for the mean values of litter from ten traps ($n=10$) for each site Jack Boyd (JB), Molesworth (MO) and Island (IS).

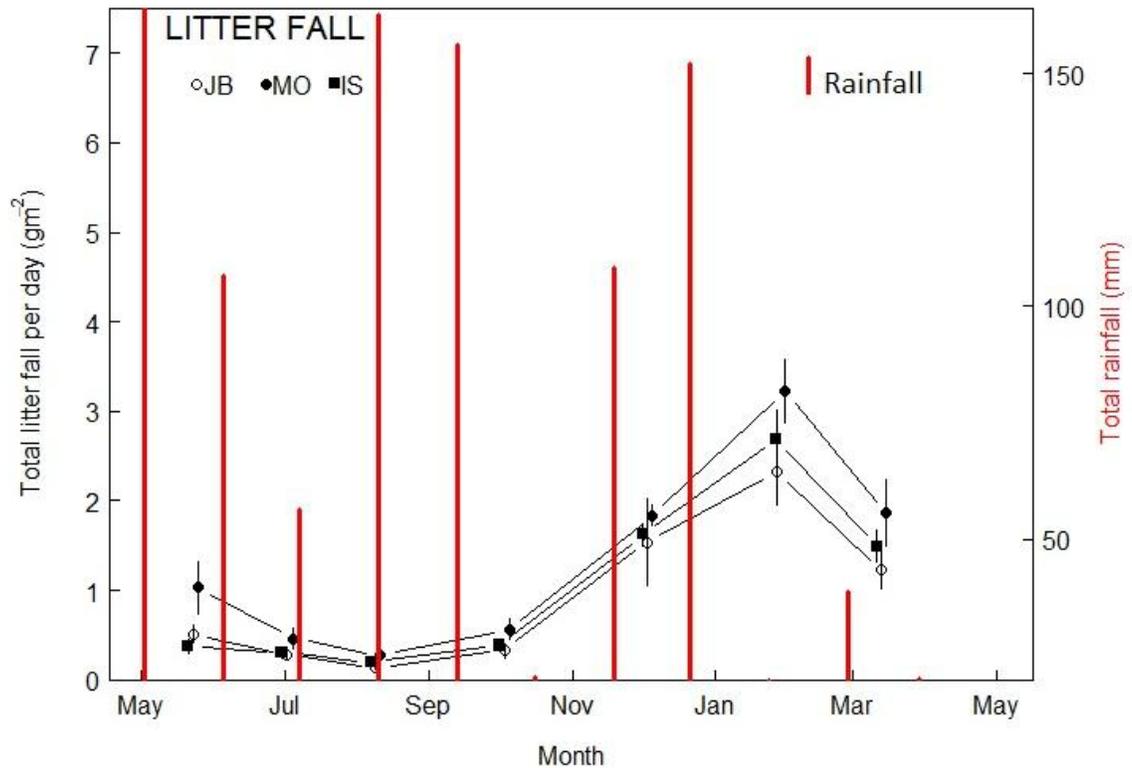


Figure 12. Site-specific seasonal litter production and monthly total rainfall (mm) measured at Mangawhai Harbour. Error bars represent the standard errors for the mean values of litter from ten traps ($n=10$) for each site Jack Boyd (JB), Molesworth (MO) and Island (IS).

3.3.2 Litter decomposition

Remaining dry weight

Rapid decomposition occurred during the first 37-39 days, when 60 % of the litter at MO and ~50 % of the litter at other sites had decomposed (Figure 13). Decomposition slowed down for the next 40 days with the loss of further ~15-25 %. The decomposition process then became even slower, especially at the upper tidal site of JB, but at all sites the remaining litter dry weights were relatively close to zero after 332 days.

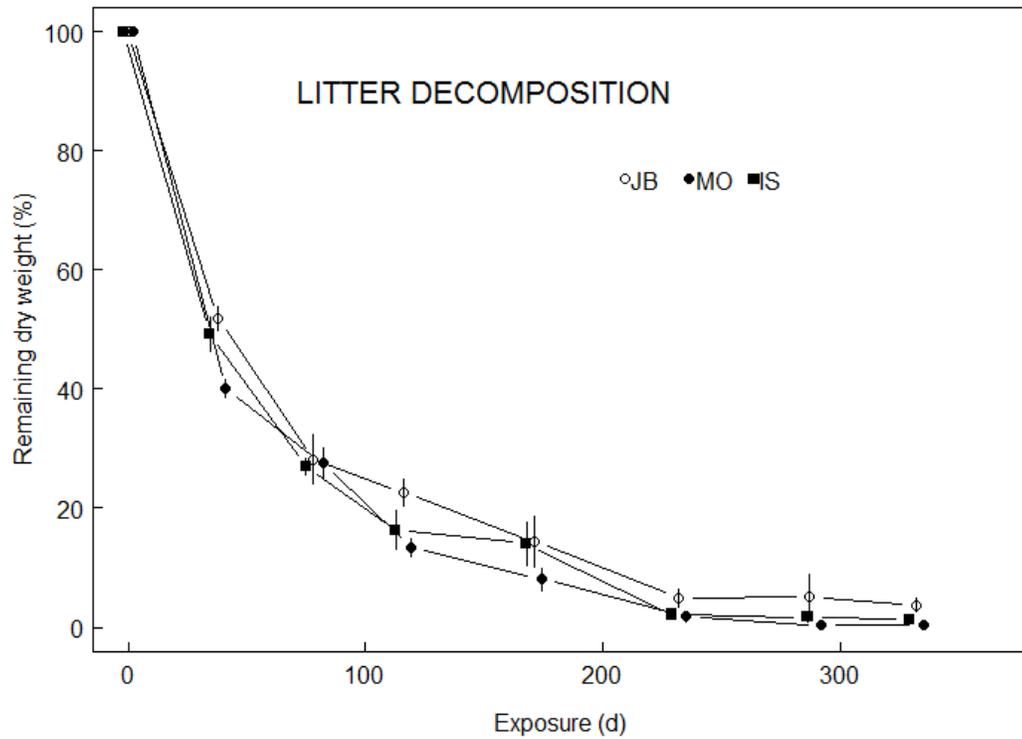


Figure 13. Mangrove leaf litter decomposition measured at Mangawhai Harbour, expressed as the percentage of initial dry weight remaining over time. Error bars represent the standard errors for the mean values of four litter bags ($n=4$) collected at each site Jack Boyd (JB), Molesworth (MO) and Island (IS).

Decomposition rate

The Asymptotic model $y = Asym + (R_0 - Asym) * \exp(-\exp(lrc) * x)$ was applied generally for the decomposition process across sites at Mangawhai Harbour (Figure 14).

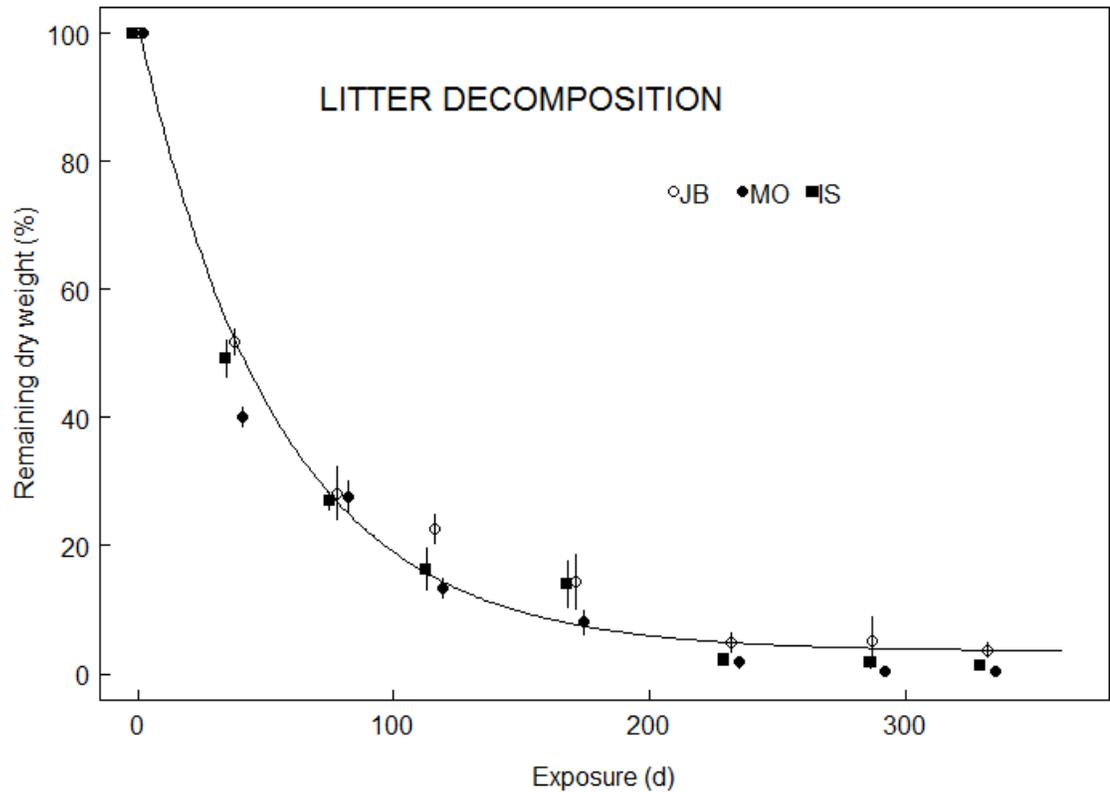


Figure 14. Asymptotic model fit $y = Asym + (R_0 - Asym) * \exp(-\exp(lrc) * x)$ with y the remaining weight over time), R_0 the estimated intercept on the y-axis, $Asym$ the asymptote parallel to the x-axis, and lrc is the estimated logarithm of the rate constant, applied generally for litter decomposition process at Mangawhai Harbour.

Across all sites, on average 3.5 % of the litter ($Asym = 3.5$) remained after 332 days and the constant rate of decomposition -3.99 ($lrc = - 3.99$).

However, an ANOVA showed a significant difference between the above general model and the site-specific model, but only for the parameter lrc (p-value = 0.09). This was expected since the intercepts were actually the initial dry weight (indicated in the graph as one hundred percent) which were set equally for all sites. The composition rates lrc were, however, significantly different among sites. It was - 4.0 (i.e. 4 % of the litter decomposed per day) for both IS and MO, but was - 3.9 for JB.

The final model was thus $y_{site} = Asym + (R_0 - Asym) * \exp(-\exp(lrc_{site}) * x)$. Figure 15 presents the model fit on decomposition data at IS, JB and MO.

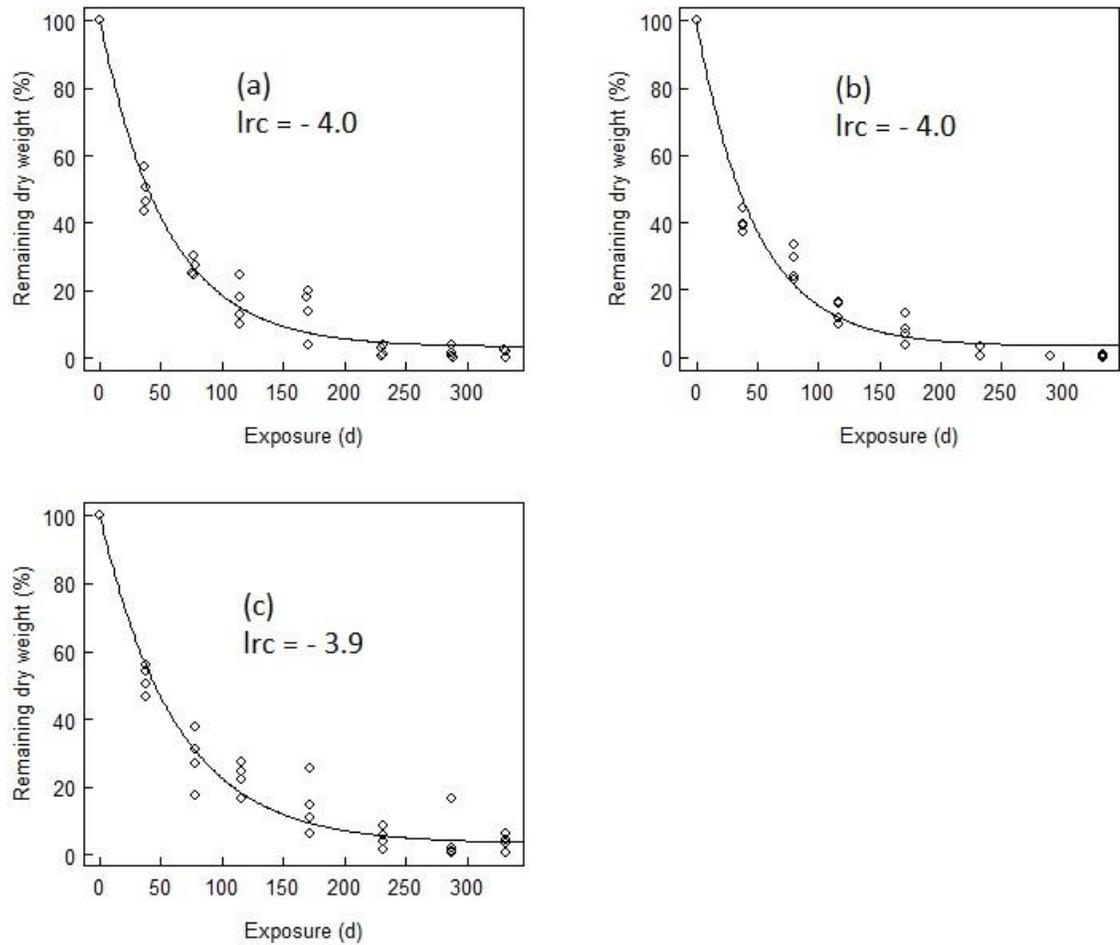


Figure 15. Asymptotic fit model $y_{site} = Asym + (R_0 - Asym) * \exp(-\exp(lrc_{site}) * x)$, with y the the percentage of remaining weight over time, R_0 the estimated intercept on the y -axis, $Asym$ the asymptote parallel to the x -axis, and lrc the estimated logarithm of the rate constant applied site-specifically for IS (a), MO (b), and JB (c) at Mangawhai Harbour.

3.4 Discussion

Litterfall

Among the study sites, litterfall production was found to be least at the site with the tallest canopy (>3m) and highest density (1.03 trees/m²) (at JB) while the highest values were found at the lowest canopy (<2m) of MO.

Litterfall production of *A. marina* at Mangawhai Harbour (0.33 - 0.48 kg m⁻² y⁻¹) is within the range reported for *A. marina* (0.18 - 0.81 kg m⁻² y⁻¹, May 1999, Woodroffe 1982, Ochieng 2002, Gladstone-Gallagher et al. 2013). This is also true when considering

litterfall at IS ($0.37 \text{ kg m}^{-2} \text{ y}^{-1}$) and MO ($0.48 \text{ kg m}^{-2} \text{ y}^{-1}$) in the range of stands closer to shore, which were reported to be higher ($0.39 - 0.81 \text{ kg m}^{-2} \text{ y}^{-1}$, May 1999, Woodroffe 1982) and JB ($0.33 \text{ kg m}^{-2} \text{ y}^{-1}$) in the range of stands further inland ($0.18 - 0.36 \text{ kg m}^{-2} \text{ y}^{-1}$, May 1999, Woodroffe 1982).

Table 10. Litterfall production of *A. marina* presented in order of latitudes

Site	Latitude	Tree height (m)	Tree density (tree/m ²)	Leaf litter proportion (%)	Total litter (kg m ⁻² y ⁻¹)	Peak time (month)	Sources
Gazi Bay, Kenya	4°25'S	2.0 - 5.0	0.09	81.8	0.62	Jul/Aug	Ochieng (2002)
Rangaunu Harbour, NZ	34°57'S	6.23±0.78	0.12	75.8	0.62	Dec/Jan	May (1999)
Rangaunu Harbour, NZ	34°57'S	5.12±0.60	0.14	55.7	0.48	Dec/Jan	May (1999)
Rangaunu Harbour, NZ	34°57'S	3.06±0.7	0.17	75.0	0.39	Dec/Jan	May (1999)
Rangaunu Harbour, NZ	34°57'S	1.68±0.30	0.36	86.4	0.18	Dec/Jan	May (1999)
Mangawhai Harbour, NZ	36°10'S	2.30±0.07	0.37	82.3	0.37	Jan	Present study
Mangawhai Harbour, NZ	36°10'S	3.10±0.06	1.03	66.6	0.33	Jan	Present study
Mangawhai Harbour, NZ	36°10'S	1.94±0.03	0.54	76.7	0.48	Jan	Present study
Tuff Crater, NZ	36°48'S	3.5 - 4	0.33	69.4	0.81	Jan	Woodroffe (1982)
Tuff Crater, NZ	36°48'S	< 1.0	1.6	74.5	0.37	Jan	Woodroffe (1982)
Whangamata Harbour, NZ	37°10'S	1.5 - 3.0	0.14	60 - 65	0.54	Dec	Gladstone-Gallagher et al. (2013)
Whangamata Harbour, NZ	37°10'S	1.2 - 1.9	0.07	60 - 65	0.32	Dec	Gladstone-Gallagher et al. (2013)

Table 10 shows a comparison of *A. marina* litterfall production among New Zealand sites and one tropical site. It is difficult to predict a specific pattern for litterfall of *A. marina* since there was no relationship found between litterfall values with latitude, tree height, nor tree density. Although it is reasonable to predict litterfall to be higher in taller and denser stands, the tallest stand (>6m, Rangaunu Harbour) had a lower litterfall than that of Tuff Crater where tree height was only 3.5 - 4m. Litterfall under lowest canopy (<1m, Tuff Crater) was in the lower part of the reported ranges, but not the lowest. The densest stands (1.3 tree/m², Mangawhai Harbour and 1.6 tree/m², Tuff Crater) were in the lower part of the litterfall range. Litterfall rates among locations were not proportional to latitude (Table 9). Along the New Zealand coast, the highest litterfall rates (0.7 - 0.8 kg m⁻² y⁻¹) were recorded at the Tuff Crater site near Auckland (36°48'S) followed by Whangamata Harbour (37°10'S) with 0.3 - 0.5 kg m⁻² y⁻¹, while the lowest rate found at the most northerly site (Rangaunu Harbour, 34°57'S) with 0.2 - 0.6 kg m⁻² y⁻¹. However, this latitudinal range may be insufficient to result in significant differences in environmental conditions, temperature in particular, that affect litter production.

These results are not consistent with suggestion by Saenger and Snedaker (1993) that there are positive relationships between temperate mangrove litterfall, tree height and latitude. Morrissey (2010) also suggested that litterfall rates for *A. marina* in New Zealand are below the maximum values reported for tropical *A. marina* while among the range of temperate ones. The one tropical site reviewed (Kenya, 4°25'S) in this study had litterfall rates similar to those reported here. However, this is only one tropical site and it had considerable lower tree density compared to New Zealand sites. More tropical sites are needed to draw robust conclusions about latitudinal patterns of *A. marina* litterfall at a larger scale.

The environmental factor that seemed to be correlated with litterfall was temperature. Litterfall of *A. marina* at Mangawhai Harbour increased with increasing temperature, which is highly consistent with May (1999), who suggested that leaf litter, the major part of litterfall, was closely related to temperature. However, this is unlikely to be a causal relationship, since litterfall of tropical *A. marina* in Gazi Bay (Kenya) peaked in Jul/Aug and temperature for this site was stable between 25-30°C year-round.

There was no clear relationship between litterfall and rainfall, although May (1999) found that litterfall was negatively correlated with water availability (which was calculated by the difference between total rainfall and total evaporation). Litterfall at Mangawhai Harbour

decreased, surprisingly, with increasing wind speed. Maximum litterfall was recorded during the least rainfall and *vice versa*. There was no storm recorded for Mangawhai during the study period, although strong wind (exceeding 60 kmh^{-1}) was recorded between September and November 2013 but this did not have any effect on the litterfall pattern.

Litter decomposition

Although decomposition rates were similar for MO and IS (-4.0 \% day^{-1}), decomposition happened fastest at MO especially during the first 37-39 days when litter at MO lost as much as 60 % of its weight while only 50 % at the IS site. Locations of the three sites were different clearly in terms of inundation and distance from the shore. No inundation time measurement was available, but MO was observed to have longer and higher inundation than the other sites. In addition, although it is slightly further away from the shore compared to IS, the site of MO is on the waterway during inundation, which may cause the litter bags at MO being buried naturally by the mud. This may help speed up decomposition rates at MO. Although the macrofauna was reported to have an impact on the decomposition rates of mangrove leaves (Morrisey, 2010), this may not be an important factor for the fast decomposition process at MO because the animals found in the litter bags during sample collecting were not different between MO and IS (small mud crabs and amphipod *Orchestia*) with similar frequency (1-2 crabs and 4-5 amphipods/bag).

Litter decomposition happened most slowly at JB, the site farthest inshore where inundation time is shortest with sandier substrate. Litter bags collected from JB were always in comparatively dry and clean conditions, compared to the bags heavily covered with mud found at IS and especially MO. Together with the amphipod *Orchestia*, abundance of scavenger snail *Z. lutulentus* was found at JB instead of mud crabs. In addition, the slightly lower water content in the leaves at JB (fresh/dry weight ratio of 2.7 compared to 2.9 at MO and IS) may contribute to the slower decomposition process.

Sediment organic matter (OM) content was also collected (for another research project, Hulbert 2014) and considered as a driving factor for the decomposition process. However, the variation in OM among sites (4.9 - 8.8 % of sediment contents at MO, 2.6 - 3.4 % at IS, and 20.47 % at JB) did not show any relationship with the decomposition patterns.

The decomposition rate of *A. marina* at Mangwhai Harbour is the fastest recorded in New Zealand so far with >50 % of litter lost after 37-39 days. Other studies on leaf litter

decomposition of *A. marina* in New Zealand was reported to lose 50 % of its dry weight after 42 - 84 days of decomposition (Woodroffe 1982, Morrisey 2010, Gladstone-Gallagher et al. 2013), Although it was reported that decomposition happened much faster in the warmer months of summer and autumn (Woodroffe 1982, Morrisey 2010), this does not help explain the faster decomposition of mangrove litter at the initial stage in Mangawhai Harbour compared to other New Zealand sites because the experiment at Mangawhai was set up in April, when it was more likely to be colder than the study at Tuff Crater (in March) and at Whangamata (in February).

Mesh size of the litter bags possibly influenced litter decomposition patterns in the present study. The litter bag mesh size used here was bigger (6 mm² compared to 4 mm² mesh size used at Tuff Crater and Whangamata Harbour, Woodroffe 1982, Gladstone-Gallagher et al. 2013), which may have enhanced access from macrofauna to the litter and at the same time this may have allowed bigger chunks of detritus to escape the bags while washed by tidal inundation or when rinsed in the lab. The common benthic species found in New Zealand mangroves are the mud crab *Helice crassa*, the amphipod *Orchestia* and the scavenger snail *Z. lutulentus* (Woodroffe 1982, Alfaro 2006, Morrisey et al. 2010). Although their abundance appeared to vary among locations (Woodroffe 1982, Alfaro 2006) and it was not clear if they feed on mangrove leaves, their appearance was proven to be important to the decomposition process (Morrisey, 2010).

The asymptotic model fit best described the decomposition process at Mangawhai Harbour, although this model has not been used before for decomposition of leaf litter on the surface. Woodroffe (1982) used a linear fit with R-squared of 56-83 %, which was acknowledged not to be ideal to describe the decomposition process that happened rapidly at the beginning but slower later on. A single exponential decay model was used by Gladstone-Gallagher et al. (2013) to describe the decomposition of leaf litter on the sediment as an alternative to the one used here.

3.5 Conclusions

Litterfall production of *A. marina* at Mangawhai Harbour is among the range reported for New Zealand mangroves. However, when considering litterfall results among the sites at Mangawhai Harbour and with other sites in New Zealand, there is no relationship between litterfall production and stand size (tree height and density). Neither is there any specific

latitudinal pattern of litterfall production. There is a positive correlation between litterfall and temperature. However, more studies of litterfall of *A. marina* at lower latitude and tropical sites is needed to be able to draw any conclusion about the causal relationship between temperature and litterfall. Rainfall and wind speed do not affect the litterfall production.

Among the sites at Mangwhai Harbour, litter decomposition of *A. marina* happens faster at sites with clearly longer inundation time and muddy substrate than sandy site with shorter inundation. However, quantitative data of inundation time at the three sites should be collected to confirm this possible relationship. OM of the sediment does not affect the decomposition rate. Compared to other New Zealand sites, leaf litter at Mangawhai decomposes faster, especially during the first 40 days, which is possibly because of the bigger mesh size bags used in this study.

Chapter 4. General discussion and implications for conservation and management

4.1 Summary of main results

Allometry and LAI

A. marina stands at Mangawhai Harbour showed a density from 0.37-1.03 trees per square metre, with tree height varying from 1-5 m. The tallest and densest stand was at Jack Boyd (JB) but larger stems of up to 16.9 cm in diameter were found at Molesworth (MO). Mean stem diameter varied from 5.15 ± 0.22 to 6.40 ± 0.23 cm. LAI ranged widely from 1.6 (at IS) to $4.6 \text{ m}^2\text{m}^{-2}$ (at JB) and SLA was 46.9 ± 0.81 to $53.81 \pm 0.39 \text{ m}^2\text{kg}^{-1}$.

Biomass distribution

Total above-ground biomass of *A. marina* at Mangawhai Harbour was $2.69 - 8.88 \text{ kgm}^{-2}$, which is lower than in other temperate *A. marina* stands in New Zealand and Australia. Below-ground biomass ranged from 11.62 kgm^{-2} to 14.7 kgm^{-2} , which is similar to that of sites with larger trees. The root-shoot ratio in Mangawhai was estimated at 1.73, which is among the highest reported for *A. marina*.

More than 70 % of the total below-ground biomass was located within 40 cm below the surface and almost 50 % of the total was from fine roots alone. The deepest fine roots were found at 1.6 m. Fine roots contributed most to the total biomass with an average of 37 %, followed by woody biomass (32 %), and then coarse roots (27 %). Leaf biomass contributed a only 3 % and pneumatophores and seedlings contributed least, with only 1 % of the total biomass.

The linear model $Y = x * ba$, with Y the biomass and ba the basal area, was used to satisfactorily estimate the biomass of *A. marina*.

Litterfall production

Annual litterfall production of *A. marina* at Mangawhai Harbour was estimated to be from 331.94 ± 69.8 to $476.63 \pm 66.1 \text{ gm}^{-2}$, with leaves as the major part of the litter accounting for 66.6 % - 82.3 %. Litterfall production positively correlated with temperature, suggesting a seasonal trend with more litterfall during late summer. There was no relationship between litterfall and maximum wind speed although litterfall was found to peak in the month with lowest wind speed and was minimal during the months with the highest maximum wind speed. Monthly total rainfall did not affect the seasonal litterfall pattern.

Litter decomposition

Leaf litter of *A. marina* at Mangawhai harbour decomposed rapidly during the first 37-39 days with 50-60 % of the initial dry weight lost. This was slowed down during the following 40 days with the loss of further ~15-25 % of litter mass and then even slower. After 332 days an average of 3.5 % of the initial litter mass remained. The average (linear) rate of decomposition was -3.99 % per day.

Litter decomposition happened more rapidly at muddy sites with longer inundation, although no quantitative data about inundation time was available. Sediment organic matter (OM) did not affect the decomposition process. Because I only had three sites, my data are not adequate for statistical tests of the correlation between litter decomposition and the site characteristics.

The asymptotic model $y_{site} = Asym + (R_0 - Asym) * \exp(-\exp(lrc_{site}) * x)$, with y percentage of remained litter, R_0 the estimated intercept on the y-axis, $Asym$ the asymptote parallel to the x-axis, and lrc is the (site-specific) estimated logarithm of the rate constant, best described the decomposition process of leaf litter at Mangawhai Harbour.

4.2 Conclusions and implication for conservation and management

Despite the shorter stands of *A. marina* at Mangawhai Harbour compared to other sites in New Zealand and Australia, the total estimated biomass is within their range. Particularly the very high below-ground biomass density makes *A.marina* stands important carbon stores. With a carbon content of 44 % in wood, 41 % in roots, and 31 % in the leaf of *A. marina* (Gritcan, unpublished data), mangrove stands at Mangawhai Harbour store 4.8 - 6 kg C m⁻² below-ground, 1.2 - 3.9 kg C m⁻² above-ground, and produce 0.1 - 0.2 kg C m⁻²y⁻¹ of litter, which takes around one year to completely decompose and transfer to other pools.

Assuming that *A.marina* at our site shows similar rates of growth, carbon fixation, canopy respiration, and sediment burial as those reported for other mangrove forests (Suwa et al. 2006, Ray et al. 2011, Alongi 2014), the carbon cycle for New Zealand mangroves can be roughly described as in Figure 16. Root respiration was not quantified in this study and are generally difficult to measure. No study was found which would have allowed to assign a value to this carbon flux. However, given that root biomass was significantly higher than aboveground biomass it is reasonable to assume that root (or total soil) respiration is a significant carbon flux from mangrove ecosystems.

The assumptions made in Figure 16 are merely to fill in the current gaps in the picture of a carbon cycle and may not match the actual values for fluxes in *A. marina* stands. On-going studies about photosynthesis and respiration at the same study site will give a more complete picture of carbon pools and fluxes in *A. marina*, allowing better inference on a potential role of these stands as future carbon sinks.

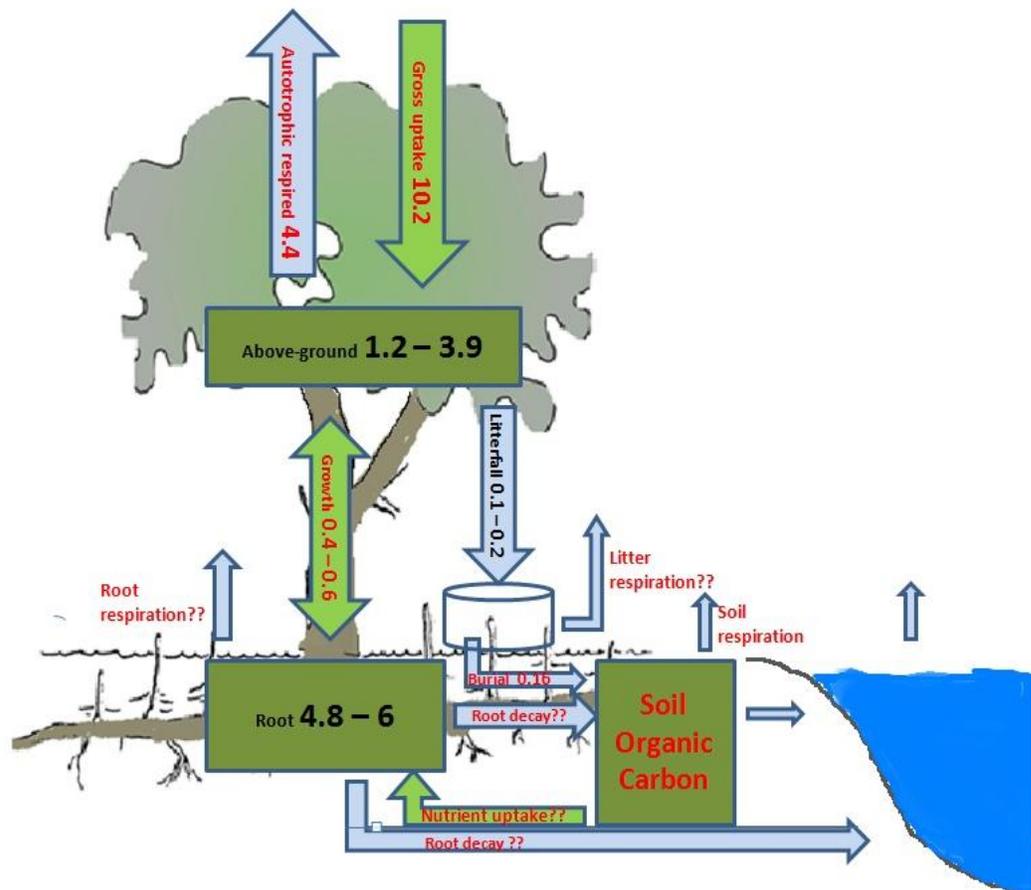


Figure 16. Carbon pools (\square , kg C m^{-2}) and fluxes (\Rightarrow , $\text{kg C m}^{-2}\text{y}^{-1}$) of *A. marina* with study results at Mangawhai Harbour (black text) and assumed figures (red text) based on data from Suwa et al. (2006), Ray et al. (2011), and Alongi (2014).

New Zealand mangroves occupy a total areas of 22,200 - 28,700 ha (Morrisey, 2010).

According to my findings, (assuming all other stands have similar allometric characteristics as those at Mangawhai Harbour) they store a total of 0.2 - 1.1 Mt C above-ground and 1.06 - 1.72 Mt C below-ground. Although this is a very small value compared to the total estimated 363 Pg C in the world's forests (Pan et al., 2013), the high carbon density ($6 - 9.9\text{kg C m}^{-2}$) of this mangrove stand compared to the mean density of 9.4kg C m^{-2} in the world's forests (Pan et al., 2013) implies that New Zealand mangroves are important

carbon stores regarding land use management. This is an important point in the context of the ongoing expansion of mangroves in New Zealand and the fact that the absence of any industrial or commercial use of this vegetation have led to management initiatives that are more likely to support their removal than their restoration.

The removal of all stands of *A.marina* in New Zealand when considering their above- and below-ground biomass stocks, would remove at least 1-2 Mt of carbon from the current pools. In contrast, if they remain undisturbed, their expansion with an average of 4.1 % y^{-1} in New Zealand (Morrisey et al., 2010) could even add up to 0.05 - 0.1 Mt C y^{-1} . This amount of carbon of course only is sequestered once the stands are mature, which could take decades. Given the fact that New Zealand's total greenhouse gas emissions reached 76 Mt CO₂ equivalent (CO₂-e) in 2012 (an increase by 25.4 % since 1990), while CO₂ sinks totalled 26.6 Mt CO₂-e during the same time span (New Zealand Ministry of Environment, 2014), my results combined with their rate of mangrove expansion clearly supports their protection in the current context of global warming.

However, data are incomplete to draw any final conclusions on the C fluxes of *A.marina*. More studies on carbon uptake, canopy and root respiration, wood and root production are needed to contribute to the full picture of the carbon cycle in New Zealand mangrove ecosystems. The ongoing debate about the ecological role of New Zealand mangroves in coastal ecosystems has highlighted the need for more comprehensive information than what is available to date. This will be helpful not only for communities seeking guidance or action on mangrove management, but also for the related governing agencies.

References

- Albany, M. (Ed.). (2013). *A dictionary of plant sciences*: Oxford University Press.
- Alfaro, A. C. (2006). Benthic macro-invertebrate community composition within a mangrove/seagrass estuary in northern New Zealand. *Estuarine, Coastal and Shelf Science*, 66(1–2), 97-110. doi:http://dx.doi.org/10.1016/j.ecss.2005.07.024
- Alongi, D. M. (2002). Present state and future of the world's mangrove forests. *Environmental Conservation*, 29(03), 331-349. doi:doi:10.1017/S0376892902000231
- Alongi, D., Clough, B., Dixon, P., & Tirendi, F. (2003). Nutrient partitioning and storage in arid-zone forests of the mangroves *Rhizophora stylosa* and *Avicennia marina*. *Trees*, 17(1), 51-60. doi:10.1007/s00468-002-0206-2
- Alongi, D.M. (2009) Paradigm shifts in mangrove biology. Coastal wetlands: an integrated ecosystem approach (ed. by G.M.E. Perillo, E. Wolanski, D.R. Cahoon and M.M. Brinson), pp. 615–640. Elsevier, Amsterdam.
- Alongi, D. M. (2009). *The energetics of mangrove forests*: Springer Dordrecht.
- Alongi, D. M. (2014). Carbon sequestration in mangrove forests. *Carbon Management*, 3(3), 313-322. doi:10.4155/cmt.12.20
- Bandaranayake, W. M. (1998). Traditional and medicinal uses of mangroves. *Mangroves and Salt Marshes*, 2(3), 133-148. doi:10.1023/a:1009988607044
- Bellot, J., Sánchez, J. R., Lledó, M. J., Martínez, P., & Escarré, A. (1992). Litterfall as a measure of primary production in Mediterranean holm-oak forest. *Vegetatio*, 99-100(1), 69-76. doi:10.1007/bf00118211
- Bouillon, S., Borges, A. V., Castañeda-Moya, E., Diele, K., Dittmar, T., Duke, N. C., ... Twilley, R. R. (2008). Mangrove production and carbon sinks: A revision of global budget estimates. *Global Biogeochemical Cycles*, 22(2), GB2013. doi:10.1029/2007gb003052
- Briggs, S. V. (1977). Estimates of biomass in a temperate mangrove community. *Australian Journal of Ecology*, 2(3), 369-373. doi:10.1111/j.1442-9993.1977.tb01151.x

- Burchett, M. D., Field, C. D., & Pulkownik, A. (1984). Salinity, growth and root respiration in the grey mangrove, *Avicennia marina*. *Physiologia Plantarum*, *60*(2), 113-118. doi:10.1111/j.1399-3054.1984.tb04549.x
- Cairns, M. A., Brown, S., Helmer, E. H., & Baumgardner, G. A. (1997). Root biomass allocation in the world's upland forests. *Oecologia*, *111*(1), 1-11. doi:10.1007/s004420050201
- Chapin, F. S. F. S., Matson, P. A. P. A., & Mooney, H. A. (2002). *Principles of terrestrial ecosystem ecology*. New York: Springer.
- Clarke, P. J. (1993). Dispersal of grey mangrove (*Avicennia marina*) propagules in southeastern Australia. *Aquatic Botany*, *45*(2-3), 195-204. doi:http://dx.doi.org/10.1016/0304-3770(93)90021-N
- Clough, B. (1998). Mangrove forest productivity and biomass accumulation in Hinchinbrook Channel, Australia. *Mangroves and Salt Marshes*, *2*(4), 191-198. doi:10.1023/a:1009979610871
- Clough, B. F. (2013). *Continuing the Journey Amongst Mangroves*: International Society for Mangrove Ecosystems. Retrieved from <http://books.google.co.nz/books?id=9rchnwEACAAJ>
- Clough, B. F., & Sim, R. G. (1989). Changes in gas exchange characteristics and water use efficiency of mangroves in response to salinity and vapour pressure deficit. *Oecologia*, *79*(1), 38-44. doi:10.1007/bf00378237
- Comley, B. W. T., & McGuinness, K. A. (2005). Above- and below-ground biomass, and allometry, of four common northern Australian mangroves. *Australian Journal of Botany*, *53*(5), 431-436. doi:http://dx.doi.org/10.1071/BT04162
- Curran, Cole, & Allaway. (1986). Root Aeration and Respiration in Young Mangrove Plants (*Avicennia marina* (Forsk.) Vierh.). *Journal of Experimental Botany*, *37*(8), 1225-1233. doi:10.1093/jxb/37.8.1225
- Dechaine, J., Ruan, H., Sanchez-de Leon, Y., & Zou, X. (2005). Correlation between earthworms and plant litter decomposition in a tropical wet forest of Puerto Rico. *Pedobiologia*, *49*(6), 601-607. doi:http://dx.doi.org/10.1016/j.pedobi.2005.07.006

- Donato, D. C., Kauffman, B. J., Murdiyarso, D., Kurnianto, S., Stidham, M., & Kanninen, M. (2011). Mangroves among the most carbon-rich forests in the tropics. *Nature Geoscience*, 4(5). doi:<http://dx.doi.org/10.1038/ngeo1123>
- Duke, N. (1990). Phenological trends with latitude in the mangrove tree *Avicennia marina*. *The Journal of Ecology*, 113-133.
- Duke, N. C. (1995). Genetic diversity, distributional barriers and rafting continents—more thoughts on the evolution of mangroves. *Hydrobiologia*, 295(1-3), 167-181.
- Ellis, J., Nicholls, P., Craggs, R., Hofstra, D., & Hewitt, J. (2004). Effects of terrigenous sedimentation on mangrove physiology and associated macrobenthic communities. *Marine Ecology Progress Series*, 270, 71-82. doi:10.3354/meps270071
- Ellison, A. (2002). Macroecology of mangroves: large-scale patterns and processes in tropical coastal forests. *Trees*, 16(2-3), 181-194. doi:10.1007/s00468-001-0133-7
- FAO. (2007). *The world's mangrove 1980 – 2005*
- Gaston, K. J. (2007). Latitudinal gradient in species richness. *Current Biology*, 17(15), R574. doi:10.1016/j.cub.2007.05.013
- Gladstone-Gallagher, R. V., Lundquist, C. J., & Pilditch, C. A. (2013). Mangrove (*Avicennia marina* subsp. *australasica*) litter production and decomposition in a temperate estuary. *New Zealand Journal of Marine and Freshwater Research*, 48(1), 24-37. doi:10.1080/00288330.2013.827124
- Gorte, R. W. (2009, August). Carbon sequestration in forests. US of Library of Congress, Congressional Research Service.
- Harrison, M. E., Marchant, N. C., and Husson, S. J. (2012) *Ecological Monitoring to Support Conservation in Kalimantan's Forests: Concepts and Design*. Orangutan Tropical Peatland Project Report, Palangka Raya, Indonesia
- Harty, C. (2009). Mangrove planning and management in New Zealand and South East Australia – A reflection on approaches. *Ocean & Coastal Management*, 52(5), 278-286. doi:<http://dx.doi.org/10.1016/j.ocecoaman.2009.03.001>
- Hillebrand, H. (2004). On the Generality of the Latitudinal Diversity Gradient. *The American Naturalist*, 163(2), 192-211

- Hulbert, C. (2014). *Modern estuarine habitats and organism-sediment interactions at Mangawhai Estuary, North Island, New Zealand*. The University of Auckland, Auckland.
- Jacob, M., Viedenz, K., Polle, A., & Thomas, F. (2010). Leaf litter decomposition in temperate deciduous forest stands with a decreasing fraction of beech (*Fagus sylvatica*). *Oecologia*, *164*(4), 1083-1094. doi:10.1007/s00442-010-1699-9
- Karberg, N., Scott, N., & Giardina, C. (2008). Methods for Estimating Litter Decomposition. In C. Hoover (Ed.), *Field Measurements for Forest Carbon Monitoring* (pp. 103-111): Springer Netherlands. Retrieved from http://dx.doi.org/10.1007/978-1-4020-8506-2_8. doi:10.1007/978-1-4020-8506-2_8
- Kauffman, J. B., & Donato, D. C. (2012). *Protocols for the measurement, monitoring and reporting of structure, biomass and carbon stocks in mangrove forests*. Bogor, Indonesia: CIFOR Working paper 86.
- Knowledge. Auckland Regional Council Technical Publication Number 325
- Komiyama, A., Ong, J. E., & Pongpan, S. (2008). Allometry, biomass, and productivity of mangrove forests: A review. *Aquatic Botany*, *89*(2), 128-137. doi:<http://dx.doi.org/10.1016/j.aquabot.2007.12.006>
- Kuchler, A. W. (1972). The mangrove in New Zealand. *New Zealand Geographer*, *28*, 113 - 129.
- Lacerda, L. D. d., & Santos, N. P. d. (May 2004). Mangroves and the Development of the Chemical Industry in Brazil. *4*.
- Le Quéré, C., Peters, G. P., Andres, R. J., Andrew, R. M., Boden, T., Ciais, P., ... Yue, C. (2013). Global carbon budget 2013. *Earth Syst. Sci. Data Discuss.*, *6*(2), 689-760. doi:10.5194/essdd-6-689-2013
- Leuzinger, S., & Hättenschwiler, S. (2013). Beyond global change: Lessons from 25 years of CO₂ research. *Oecologia*, *171*(3), 639-51. doi:<http://dx.doi.org/10.1007/s00442-012-2584-5>
- Litton, C. M., Raich, J. W., & Ryan, M. G. (2007). Carbon allocation in forest ecosystems. *Global Change Biology*, *13*(10), 2089-2109. doi:10.1111/j.1365-2486.2007.01420.x

- Lugo, A. E., & Snedaker, S. C. (1974). The Ecology of Mangroves. *Annual Review of Ecology and Systematics*, 5(ArticleType: research-article / Full publication date: 1974 / Copyright © 1974 Annual Reviews), 39-64.
- Mackey, A. (1993). Biomass of the mangrove *Avicennia marina* (Forsk.) Vierh. Near Brisbane, South-eastern Queensland. *Marine and Freshwater Research*, 44(5), 721-725. doi:<http://dx.doi.org/10.1071/MF9930721>
- May, J. D. (1999). Spatial variation in litter production by the mangrove *Avicennia marina* var. *australasica* in Rangaunu harbour, Northland, New Zealand. *New Zealand Journal of Marine and Freshwater Research*, 33(2), 163-172. doi:10.1080/00288330.1999.9516866
- Medeiros, T. C. C., & Sampaio, E. V. S. B. (2008). Allometry of aboveground biomasses in mangrove species in Itamaracá, Pernambuco, Brazil. *Wetlands Ecology and Management*, 16(4), 323-330. doi:10.1007/s11273-007-9069-z
- Methods for Below-Ground Biomass. (2008). In *Carbon Inventory Methods Handbook for Greenhouse Gas Inventory, Carbon Mitigation and Roundwood Production Projects* (Vol. 29, pp. 149-156): Springer Netherlands. Retrieved from http://dx.doi.org/10.1007/978-1-4020-6547-7_11. doi:10.1007/978-1-4020-6547-7_11
- Morrisey, D. et al. (2007). The New Zealand Mangrove: Review of the Current State Of
- Morrisey, D., Swales, A., Dittmann, S., Morrison, M., Lovelock, C., & Beard, C. (2010). The Ecology and Management of Temperate Mangroves. *Oceanography and Marine Biology*, 48, 43-160. doi:doi:10.1201/EBK1439821169-c2
- Mumby, P. J., & Hastings, A. (2008). The impact of ecosystem connectivity on coral reef resilience. *Journal of Applied Ecology*, 45, 854–862. doi:10.1111/j.1365-2664.2008.01459.x
- Murdiyarso, D., Donato, D., Kauffman, J. B., Kurnianto, S., Stidham, M., & Kanninen, M., &. (2010). *Carbon storage in mangrove and peatland ecosystems: a preliminary account from plots in Indonesia* Bogor, Indonesia: Center for International Forestry Research (CIFOR).

- New Zealand's Greenhouse Gas Inventory 1990–2012*. (2014): New Zealand Ministry of the Environment. Retrieved from <http://www.mfe.govt.nz/publications/climate/greenhouse-gas-inventory-2014-snapshot/index.html>
- Ong, J.E. & Gong, W.K. (2013) *Structure, Function and Management of Mangrove Ecosystems*. ISME Mangrove Educational Book Series No. 2. International Society for Mangrove Ecosystems (ISME), Okinawa, Japan, and International Tropical Timber Organization (ITTO), Yokohama, Japan
- Paliyavuth, C., Clough, B., & Patanaponpaiboon, P. (2004). Salt uptake and shoot water relations in mangroves. *Aquatic Botany*, 78(4).
doi:<http://dx.doi.org/10.1016/j.aquabot.2004.01.002>
- Pan, Y., Birdsey, R. A., Fang, J., Houghton, R., Kauppi, P. E., Kurz, W. A., ... Hayes, D. (2011). A Large and Persistent Carbon Sink in the World's Forests. *Science*, 333(6045), 988-993. doi:10.1126/science.1201609
- Pan, Y., Birdsey, R. A., Phillips, O. L., & Jackson, R. B. (2013). The Structure, Distribution, and Biomass of the World's Forests. *Annual Review of Ecology, Evolution, and Systematics*, 44(1), 593-622. doi:doi:10.1146/annurev-ecolsys-110512-135914
- Ravindranath N.H., & Ostwald, M. (2008). *Carbon Inventory Methods* (Vol. 29): Springer.
- Ray, R., Ganguly, D., Chowdhury, C., Dey, M., Das, S., Dutta, M. K., ... Jana, T. K. (2011). Carbon sequestration and annual increase of carbon stock in a mangrove forest. *Atmospheric Environment*, 45(28), 5016-5024.
doi:<http://dx.doi.org/10.1016/j.atmosenv.2011.04.074>
- Saenger, P. (2002). *Mangrove Ecology, Silviculture and Conservation*: Springer. Retrieved from <http://books.google.co.nz/books?id=FDXCLuG9ZCcC>
- Saenger, P., & Snedaker, S. (1993). Pantropical trends in mangrove above-ground biomass and annual litterfall. *Oecologia*, 96(3), 293-299. doi:10.1007/bf00317496
- Spalding, M., Kainuma, M., & Collins, L. (2010). *World atlas of mangroves* (M. Kainuma & L. Collins, Trans)

- Stuart, S. A., Choat, B., Martin, K. C., Holbrook, N. M., & Ball, M. C. (2007). The role of freezing in setting the latitudinal limits of mangrove forests. *New Phytologist*, *173*(3), 576-583. doi:10.1111/j.1469-8137.2006.01938.x
- Suwa, R., Khan, M. N. I., & Hagihara, A. (2006). Canopy photosynthesis, canopy respiration and surplus production in a subtropical mangrove *Kandelia candel* forest, Okinawa Island, Japan. *Marine Ecology Progress Series*, *320*, 131-139. doi:10.3354/meps320131
- Suzuki, T., Nishihira, M., & Paphavasit, N. (2002). Size structure and distribution of *Ovassiminea brevicula* (Gastropoda) in a Thai mangrove swamp. *Wetlands Ecology and Management*, *10*(3), 265-271. doi:10.1023/a:1020115411316
- Tackenberg, O. (2007). A New Method for Non-destructive Measurement of Biomass, Growth Rates, Vertical Biomass Distribution and Dry Matter Content Based on Digital Image Analysis. *Annals of Botany*, *99*(4), 777-783. doi:10.1093/aob/mcm009
- Tuomi, M., Thum, T., Järvinen, H., Fronzek, S., Berg, B., Harmon, M., Trofymow, J.A., Sevanto, S. & Liski, J. 2009. Leaf litter decomposition - Estimates of global variability based on Yasso07 model. *Ecological Modelling* *220* (23), 3362-3371. doi:10.1016/j.ecolmodel.2009.05.016
- Woodroffe, C. D. (1982). Litter production and decomposition in the New Zealand mangrove, *Avicennia marina* var. *resinifera*. *New Zealand Journal of Marine and Freshwater Research*, *16*(2), 179-188. doi:10.1080/00288330.1982.9515961
- Woodroffe, C. D. (1985). Studies of a mangrove basin, Tuff Crater, New Zealand: I. Mangrove biomass and production of detritus. *Estuarine, Coastal and Shelf Science*, *20*(3), 265-280. doi:http://dx.doi.org/10.1016/0272-7714(85)90042-3
- Zhang, H., et al. (2014) Seasonal patterns of litterfall in forest ecosystem worldwide. *Ecol. Complex.* , http://dx.doi.org/10.1016/j.ecocom.2014.01.003